RESEARCH ARTICLE

Pachycormid fish fed on octobrachian cephalopods: new evidence from the 'Schistes bitumineux' (early Toarcian) of southern Luxembourg

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Abstract

A re-examination of the early Toarcian fish fossils preserved in public paleontological collections in Luxembourg revealed 70 specimens of large Toarcian pachycormid fish with an excellent three-dimensional preservation within calcareous nodules. Six of them are associated with octobrachian coleoid gladii in their oesophagus or stomach, an association not previously described from Luxembourg. The pachycormids are ascribed to *Pachycormus macropterus* (Blainville, 1818) and *Saurostomus esocinus* Agassiz, 1843 while the octobrachian gladii are ascribed to *Teudopsis bollensis* Voltz, 1836, *Teudopsis* sp. indet. and Loligosepiidae indet. The position and orientation of the gladii provide direct evidence of these fishes feeding on coleoids and thus a teuthophagous diet, rather than an accidental joint burial. Together with evidence from coeval deposits in Germany, these findings suggest that teuthophagy was a widespread feeding strategy at the base of the clade that contains the suspension-feeding pachycormid giants of the Jurassic–Cretaceous.

Keywords Toarcian food web, Predator–prey relationship, Pachycormidae, Loligosepiidae, Teudopsiidae, Toarcian Oceanic Anoxic Event, Jenkyns Event, Serpentinum Chronozone

Introduction

The early Toarcian 'black shales' ('Schistes bitumineux') of southern Luxembourg and neighbouring areas of Belgium (Province de Luxembourg) and France (Lorraine)

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have been known since more than a century as a Lagerstätten similar to coeval deposits in South Germany or the UK (Faber, 1916; Lucius, 1948; Moris, 1854; Woodward, 1938). Pachycormid fish (referred to by the genera *Pachycormus* and *Saurostomus*) and octobrachian cephalopods (teudopsids and loligosepiids, squid-like coleoids) are well-known elements of the fossil record of the 'Schistes bitumineux' (Delsate, 1999a; Fuchs & Weis, 2008, 2010; Henrotay et al., 1998; Streitz, 1983). The aforementioned strata share with the coeval deposits in Germany, the UK and France some of the earliest fossil occurrences of pachycormids, which appear to have rapidly evolved specialized pelagic predatory ecomorphologies, broadly reminiscent of those of modern tunas (Cooper & Maxwell, 2022; Friedman, 2012). Among the Toarcian ichthyofauna of Luxembourg (Delsate, 1999a),

only pachycormids are occasionally associated with octo-brachian gladii (Delsate et al., 2008).

Although markedly scarce in the fossil record, identifiable gut contents open invaluable windows into the trophic dynamics of ecosystems from deep-time, as well as the autoecologies of long-extinct taxa. Fossilized co-occurrences of different species where one individual is preserved within the other are usually directly linked with predation, and constitute reliable markers of fossilized behaviour (Boucot, 1990). Prey contents within the abdominal cavities of Jurassic pachycormids have received attention in the scientific literature, especially due to their potential informativeness on the ancestral ecologies that underpinned the rise of gigantism and suspension feeding in the clade (Cooper & Maxwell, 2022, 2023; Cooper et al., 2022; Friedman, 2012; Gouiric-Cavalli & Arratia, 2022). We herein describe six specimens of pachycormid fishes of the genera *Pachycormus* and *Saurostomus* from Luxembourg with teudopseid (4 specimens) and loligosepiid (2 specimens) gladii contained in their guts. We illustrate the specimens and discuss the nature of these co-occurrences.

Geological setting

The top of the Lower Jurassic (Toarcian) in Luxembourg is represented by the 'Schistes bitumineux' formation (Faber, 1947; Guérin-Franiatte et al., 2010; Maquil, 2010; Song et al., 2014), also called erroneously 'Schistes carton' formation (Hermoso et al., 2014). The lateral equivalent in Belgium corresponds to the Grandcourt Formation (Boulvain et al., 2001a, 2001b; Schintgen, 2015). This black shale facies is well constrained stratigraphically by numerous ammonite findings which show that its age extends from the Tenuicostatum Chronozone to the upper part of the Serpentinum Zone (Guérin-Franiatte et al., 2010; Hermoso et al., 2014; Vincent et al., 2019) and can therefore be directly correlated with the better known bituminous Fossil-Lagerstätten in the areas of Whitby (UK) and Holzmaden (Southwest Germany). The series consists of up to 160 m thick bituminous clay and marl, with a thin silty-calcareous lamination ('Schistes Cartons', paper shales, black shales), passing towards the top into a sandier laminated marl rich in septaria. The series has been deposited during and in the aftermath of the Toarcian Oceanic Anoxic Event (TOAE, also termed Jenkyns Event: Müller et al., 2017) (Song et al., 2014). It is notable that the 'black shales' of the basal Lower Toarcian (lower part of Serpentinum Chronozone: Guérin-Franiatte et al., 2010; Henrotay et al., 1998; Vincent et al., 2019) yielded numerous articulated fish and reptile specimens (Delsate, 1999a, 1999b, 1999c; Faber & de Muyser, 1947; Godefroit, 1994; Johnson et al., 2019; Laboury et al., 2022; Lucius, 1948; Streitz, 1983; Taverne & Steurbaut

2017; Vincent et al., 2019; Woodward, 1938;). The study of these specimens and enclosing strata give insight about the depositional conditions and taphonomy of the specimen described here. Various levels of nodules or flat concretions at the base of the 'Schistes bitumineux' are fossiliferous, as well as the marls themselves. Vertebrates are either found three-dimensionally in carbonate nodules or crushed in laminated marl beds; they can occur as complete, articulated skeletons (early burial) or as disarticulated remains (delayed burial), with or without necrotic bend or deformation (Reisdorf & Wuttke, 2012). The vertebrate-bearing, finely laminated calcareous argillites and their nodules (strongly biconvex concretions) and 'lenses' (flat benches or very flattened nodules) were formed under anoxic to strongly dysoxic conditions (Hermoso et al., 2014). Hanzo (1979), in her study of the calcareous nodules from the Toarcian, recognizes a very early diagenetic phase (presumably fast because of the good conservation of small ammonites and ostracods, compared to the preservation in the argillites) that likely affected a poorly consolidated, muddy sediment. It has been estimated that, after the first compaction phase affecting both the shales and still soft spheroids nodules, the second (post-nodular) compaction phase reduced their original thickness as much as to one-quarter of their original thickness (Hanzo, 1978, 1979). Carbonate precipitation can be explained by a local bacterial activity (see Thies, 1992; Plet et al., 2016) during the decomposition of bodies accumulated at the bottom of the sea in 'soupy' sediments (Martill, 1993), allowing for the preservation of articulated specimens in both two and three dimensions.

The fish fauna reported from the Serpentinum Chronozone of Luxembourg has been the object of a preliminary inventory (Delsate, 1999a, 1999b, 1999c; Streitz, 1983). More recently, Taverne & Steurbaut (2017) established the new genus *Luxembourgichthys* based on material from Luxembourg (Delsate, 1999a, 1999c) and neighbouring Belgian localities. The taxa currently recognized from the Serpentinum Chronozone of Luxembourg are summarized in Table 1.

The octobrachian fauna of the Luxembourg lower Toarcian black shale deposits (Serpentinum Chronozone) has been studied by Fuchs and Weis (2008, 2010); additionally, the presence of the genus *Jeletzkyteuthis* (Fuchs, 2020) has been recognized. Octobrachians from the Serpentinum Chronozone of Luxembourg are summarized in Table 2.

Materials

We examined the extensive collections of Toarcian fish preserved in public and private collections in Luxembourg. 8.5% (6 of 70) of the large specimens of

Table 1 Ichthyofauna from the Serpentinum Chronozone, lower Toarcian, of Luxembourg

Family	Species	Reference
Saurichthyidae	*Saurorhynchus* cf. *hauffi* (Maxwell & Stumpf, 2017)	Delsate, 1999a emend. by Maxwell & Stumpf, 2017
Semionotidae	*Lepidotes elvensis* Blainville, 1818	Streitz, 1983; Delsate, 1999a; Henrotay et al., 1998
Dapediidae	*Dapedium pholidotum* Agassiz, 1832	Delsate, 1999a; Mudroch et al., 1999
	Dapedium stollorum Thies & Hauff, 2011	Delsate, 1999a [as *D. punctatum*]
	Tetragonolepis semicincta Bronn, 1830	Streitz, 1983; Delsate, 1999a
Pachycormidae	*Pachycormus macropterus* Blainville, 1818	Woodward, 1938; Streitz, 1983; Delsate, 1999a; Delsate et al., 2008; this work
	Saurostomus esocinus Agassiz, 1843	Delsate, 1999a; Delsate et al., 2008; Cooper & Maxwell, 2022; this work
	Sauropsis latus Agassiz, 1832	Delsate, 1999a; Delsate unpublished data
	Euthynotus incognitus Blainville, 1818	Delsate, 1999a
	Haasichthys michelsi Delsate, 1999a, 1999b, 1999c	Delsate, 1999a, 1999c; Liston et al., 2019; Cooper & Maxwell, 2022
Pholidophoridae	*Luxembourgichthys friedeni* (Delsate, 1999c)	Delsate, 1999c; Taverne & Steurbaut 2017
	Pholidophorus cf. *germanicus* Quenstedt, 1858	Delsate, 1999a
Leptolepidae	*Leptolepis normandica* Nybelin, 1962	Streitz, 1983; Delsate, 1997, 1999a

Table 2 Octobrachian fauna of the Serpentinum Chronozone, lower Toarcian, of Luxembourg

Genus	Species	Reference
Loligosepia Quenstedt, 1839	*Loligosepia aalensis* (Schübler in Zieten, 1832)	Fuchs & Weis, 2008
Parabelopeltis	*Parabelopeltis flexuosa* (Münster, 1843)	Fuchs & Weis, 2008
Teudopsis Eudes-Deslongchamps, 1835	*Teudopsis bunelii* Eudes-Deslongchamps, 1835	Fuchs & Weis, 2010
	Teudopsis bollensis Voltz, 1836	Fuchs & Weis, 2010
	Teudopsis subcostata (Münster, 1843)	Fuchs & Weis, 2010
Jeletzkyteuthis	*Jeletzkyteuthis coriaceus* (Quenstedt, 1849)	Fuchs & Weis, 2008
Gen. nov	Sp. nov	Fuchs et al. in prep

Luxembourg Toarcian pachycormids (55 *Pachycormus* and 15 *Saurostomus*) preserve ingested coleoids. We did not find ingested coleoids in smaller Toarcian pachycormiforms (*Haasichthys*, *Sauropsis*, *Euthynotus*).

This topic is tightly related with bromalites preserved inside the fossilized body, which were classified by Hunt et al. (2012). Independent of whether the items are recognizable or not, these bromalites were subdivided into esophagolites (in the oesophagus), gastrolite (in the stomach, not to be confused with gastroliths), and colo-lites (in the intestines; see also Argyriou et al., 2016). It is not possible to apply these terms to the coleoid remains portrayed here. We have to take into account that guts are amongst the first tissues to decay and fish carcasses tend to explode from the build-up of gasses. Thus, the anterior gastrointestinal tract itself is certainly not preserved and guts contents might have moved after decay/gas release.

All six specimens described herein belong to publicly accessible collections. Five of them are housed in the paleontological collections of National Museum of Natural History Luxembourg (Musée national d'histoire naturelle, Luxembourg; acronym MNHNL), a sixth is preserved in the collections of the private museum Streitz in Itzig, Luxembourg, available to researchers on demand (Collection Jean-Claude Streitz; acronym JCS). All specimens have been examined morphologically and photographed at the MNHNL.

Systematic palaeontology

The six fish fossils we describe here are pachycormiforms and belong to the genera *Pachycormus* and *Saurostomus*. Most of the general characters of the group are visible: amioid type scales, an elongated body, strong jaws articulating far behind the posterior border of the orbit, absence of a coronoid process of the mandible. The two recognized genera are easily distinguished, although there has been confusion, for example between large *Pachycormus* and *Saurostomus*, because of the similarity in body size. The anterior pectoral fin ray, the squamation, the presence and structure of chordacentra are considered arguments for

distinguishing *Saurostomus* from *Pachycormus* (Cooper & Maxwell, 2022; Cooper et al., 2022; Hauff & Hauff, 1981; Woodward, 1895, 1896, 1908, 1916). Yet, these are poor criteria because of allometry and old-fashioned preparation tools and methods that might have altered often incompletely preserved specimens. *Saurostomus* and *Pachycormus*, possess falciform or sickle morphed scythe shaped pectoral fins (revised pachycormid pectoral fin classification scheme proposed by Liston et al. (2019), with distally segmented rays, asymmetrically bifurcating in Y-fashion. Accordingly, the best criteria in the present study are found in the skull anatomy:

•*Saurostomus* has a more massive skull with larger and stronger bones, a preopercle forming a splint-like dorsal limb and a fan-like anteroventral limb, a large trapezoidal, shield-shaped opercle, a rectangular subopercle, a robust hyomandibula with a waisted medial region and a well-defined opercular process, robust rectangular ceratohyals, but no suborbitals. *Saurostomus* is monospecific. Cooper and Maxwell (2022) provide the highly awaited revision of *Saurostomus esocinus*, with precise anatomical descriptions. Among the Luxembourg *Saurostomus esocinus* specimens examined by Cooper and Maxwell (2022) only specimen TU987 is part of the present study. Cooper and Maxwell (2022) report the original anatomical absence of the postorbitals, infraorbitals and suborbital plates in any of the studied material of *Saurostomus esocinus.* Several features seen in our material of *Saurostomus* can differentiate it from its newly erected Toarcian relative *Germanostomus* Cooper et al., 2022, including: stronger ornamentation of dermal bones; stronger dentition, hyomandibula being clearly waisted and bearing a well-defined opercular process and convex articulation surfaces (Cooper et al., 2022).

•*Pachycormus* presents: a higher number of dermatocranial ossifications, which include two posteriorly extended suborbitals that laterally cover the hyomandibula; a more massive triangular and crescent-shaped preopercle; has more delicate bones, a triangular opercle, a trapezoidal (posteriorly deeper) subopercle, slender ceratohyals.

The genus *Pachycormus* is monospecific with the species *P. macropterus*. A recent morphometric study of the genus (Wretman et al., 2016) ascribed skull biometric differences to an ontogeny-depended morphocline, possible sexual dimorphism and morphospace overlap, as seen in other actinopterygians. Wretman et al. (2016) thus considered *P. curtus*, which encompasses smaller specimens, as a junior synonym of *P. macropterus*. Similarly, larger specimens ascribed to *P. bollensis* are indistinguishable from *P. macropterus*, or re-identified as *Saurostomus esocinus* (Cawley et al., 2019).

Estimate of the total length of the fish: summary

Body size is an important parameter in determining diet in fishes, so we provide here rough scaling ratios to estimate the total length of the concerned predatory fishes, based on the data of Cooper and Maxwell (2022, 2023) and our measurements from Wenz (1967), Wretman et al. (2016), Cooper and Maxwell (2022, 2023).

- *Saurostomus esocinus*: The factor from the standard length to total length of *Saurostomus esocinus* is $\times 1.17$ (data from Cooper & Maxwell, 2022). The factor from the {opercle maximal length} to the total length varies from $\times 9.5$ to $\times 19$, which is too imprecise or doubtful because of preservation, measurements or figure quality, and possible ontogenetic variability in *Saurostomus esocinus*. The factor from the {head length (generally evident), estimated at the posterior junction between opercle and subopercle} to the total length is $\times 4.3 \pm 0.2$. The mean factor from the mandible length to the head length is $\times 2.1$. The mean measured factor from mandible length to the total length is $\times 8.84$.
- *Pachycormus macropterus*: The factor from the standard length to the total length of *Pachycormus macropterus* is $\times 1.13$ (from data in tables of Wretman et al., 2016 and Cooper & Maxwell, 2023). The factor from the {dorsal length of the opercle} to {the total Length} of *Pachycormus* approximates $\times 10$, but reaches $\times 20$ in very large specimens, thus is not very informative. The mean factor from the head length to the standard length is $\times 3.58$ (variation 2.96–5.87) (data from Cooper & Maxwell, 2023). The factor from the head length to the total length of *Pachycormus macropterus* is $\times 4$ (variation 3.3–5.4). The factor from the mandible length to the head length is $\times 1.66$ (variation 1.42–1.73) (data from Cooper & Maxwell, 2023). The mean factor from the mandible length to the standard length is $\times 5.6$ (variation 5–6) (data from Cooper & Maxwell, 2023).The factor from the mandible length to the total length is $\times 6.3$.

The gladius represents the demineralized shell remain in the dorsal mantle of octobrachian and teuthid coleoids (Fuchs & Iba, 2015). The morphology and systematics of the associated octobrachian gladii follow Fuchs (2016, 2020). The observed gladii belong to the families Teudopsidae and Loligosepiidae. Teudopsids represent the stem group of the Octopoda, while loligosepiids were identified as precursors of the Vampyromorpha with its only extant representative *Vampyroteuthis infernalis* (e.g., Fuchs et al., 2019; Klug et al., 2021a; Rowe et al., 2022).

Neopterygii Regan, 1923

Pachycormiformes Berg, 1937

Pachycormidae Woodward, 1895

Asthenocorminae *sensu* Cooper et al., 2022

***Pachycormus* Agassiz,** 1833

Specimen MNHNL TU899: *Pachycormus macropterus* (**Blainville**,1818) *Teudopsis* **sp. indet and** (Fig. 1).
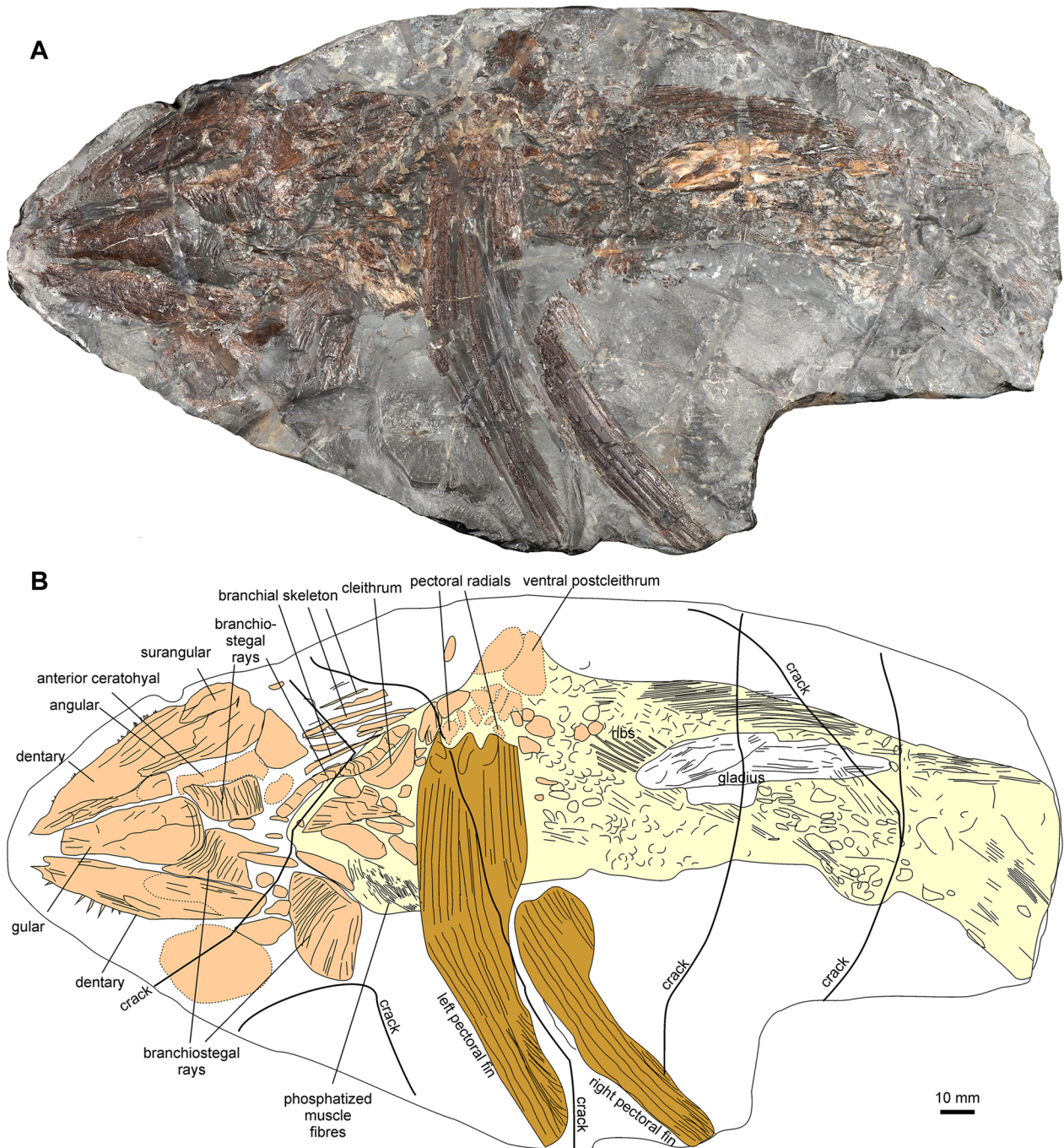

Fig. 1 Specimen MNHNL n° TU899: *Pachycormus macropterus* (Blainville, 1818) and *Teudopsis* sp. indet.; Serpentinum Chronozone, Foetz

Locality Foetz, industrial zone, collected by Jo Simon; 'Schistes bitumineux' formation, Serpentinum Chronozone.

Dimensions Preserved length of the fish 320 mm. Mandible length 70–75 mm. Total length estimation: mandible length × 6.3 = 441–472 mm. Preserved length of the gladius: 79 mm.

Exposed anatomic features The skull is dorsoventrally crushed and seen in ventral view with the jaws split away but keeping symphyseal connection.

Identification of the fish The fins, the smaller scales and teeth, the plates (smaller gular) and bones have the aspect of *Pachycormus* (more slender dentaries, cerato-hyals), not the robustness of *Saurostomus*. Unfortunately, the absence of the orbit, the suborbital and the opercular apparatus do not allow a cranial biometric assessment of the species.

Identification and position of the gladius The gladius is identified as *Teudopsis* sp. (Teudopsidae, Teudop-seina, Octobrachia, Coleoidea) due to its well-developed median keel (Fuchs & Weis, 2010). It lies 180 mm away from the mandibular symphysis, for a dentary length about 70 mm axial, the gladius has a proximodistal (= craniocaudal) direction. It is situated far behind the buccopharynx and gills, far behind the pectoral fin implantation, certainly in the stomach (gastrolite sensu Hunt & Lucas, 2012, consumulite in a broader sense).

Specimen MNHNL n° TU932: ***Pachycormus macropterus* (**Blainville, 1818**) and** *Teudopsis* **sp. indet** (Fig. 2).

Locality Dudelange-Bettembourg, Galvalange factory construction site, collected by J. Valentiny; 'Schistes bitumineux' formation, Serpentinum Chronozone.

Dimensions Preserved length of the fish 355 mm. Mandible length 61 mm. Total length estimation: mandible length × 6.3 = 384 mm. Preserved length of the gladius: 78 mm.

Identification of the fish The triangular opercular and the trapezoidal subopercular are typical of the genus *Pachycormus.* The right side of fish is exposed, the skull is missing the orbit and the suborbitals, exposing the hyomandibular. The dorsal fin and the right pectoral fin are preserved.

Identification and position of the gladius The gladius is partially preserved and the presence of a well-developed

keel indicates the genus *Teudopsis* (Fuchs & Weis, 2010). The gladius is preserved between the pectoral fin laminae and internal to the ribs of the right side, ventral to the basiventral or ventral arcocentra; its posterior end lies 2 cm in front of the anteriormost point of the dorsal fin. The gladius is axially oriented, in anatomical position corresponding to the oesophago-stomachal or stomachal position (oesophagolite or gastrolite sensu Hunt & Lucas, 2012, consumulite in a broader sense).

Specimen MNHNL n° TU989: ***Pachycormus macropterus*** (Blainville, 1818) **and** ***Teudopsis bollensis*** Voltz, 1836 (Fig. 3)

Locality Foetz, collected by J. Valentiny; 'Schistes bitumineux' formation, Serpentinum Chronozone.

Dimensions Preserved length of the fish 270 mm. Maximum length of the opercle: 70 mm. Length estimation: in absence of further data, we use the opercle length × 10 = 700 mm. Preserved length of the gladius: 75 mm.

Identification of the fish The very large suborbital area and opercular system area, the pectoral fin structure, are all typical of *Pachycormus*.

Identification and position of the gladius The partially preserved gladius can be safely attributed to *Teudopsis bollensis* owing to the presence of a well-developed median keel and a triangular anterior part (Fuchs & Weis, 2010). The gladius is situated internal to the ribs and squamation; it is 5 mm thick at the posteriormost preserved part on the slab. The position of the gladius tip is 35 mm behind the cleithral remains, with an axial orientation, 55 mm under the mid-length of the notochord, 25 mm dorsally to the level of the pectoral implantation base, 25 mm posteriorly to the pectoral fin posterior implantation point. Its position is probably stomachal with its posterior part in cephalic direction of the fish (gastrolite *sensu* Hunt & Lucas, 2012, consumulite in a broader sense). The gladius has thus been caught head and arms first.

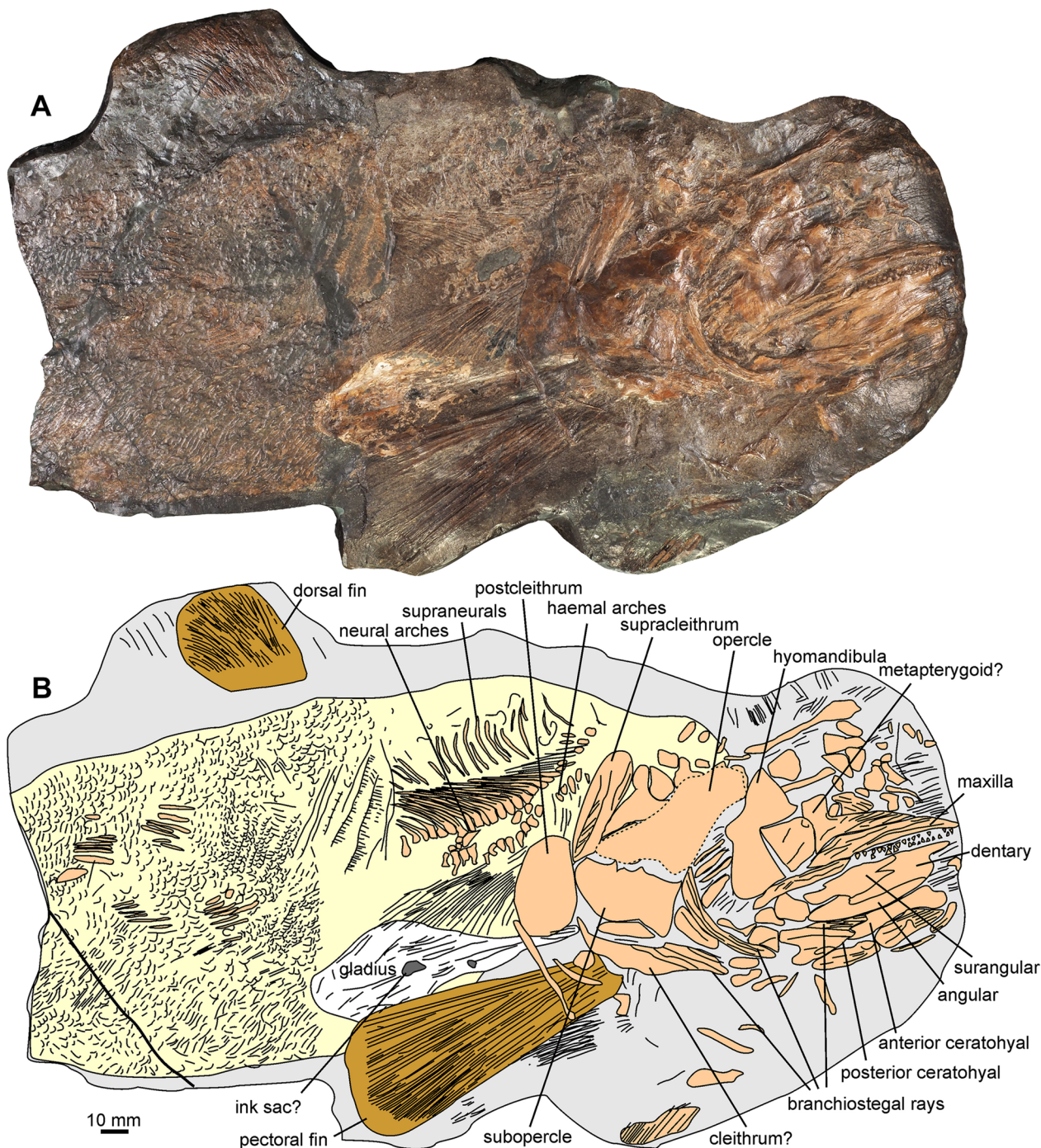**Specimen JCS n° P39:** ***Pachycormus macropterus*** (Blainville, 1818) **and Octobrachia indet** (Fig. 4).

1983 *Pachycormus* sp. – Streitz: p. 97.

Locality Dudelange, 'op Mëchelacker'; 'Schistes bitumineux' formation, Serpentinum Chronozone.

Dimensions Preserved length of the fish 350 mm. Skull length 165 mm to the posterior most point of the opercle. Maximum length of the opercle: 62 mm. Mandible length: 97 mm. Length estimation from the skull length: 165 mm × 4 = 660 mm; from the opercle length: 62 mm × 10 = 620 mm; from the mandible length: 97 mm × 6.3 = 611 mm. Preserved length of the gladius: 150 mm.

Identification of the fish The left side of the fish is exposed: the skull, the anterior part of the trunk, with the left long pectoral fin: the 2 large suborbitals, the

Fig. 2 Specimen MNHNL n° TU932: *Pachycormus macropterus* (Blainville, 1818) and *Teudopsis* sp. indet.; Serpentinum Chronozone, Dudelange-Bettembourg
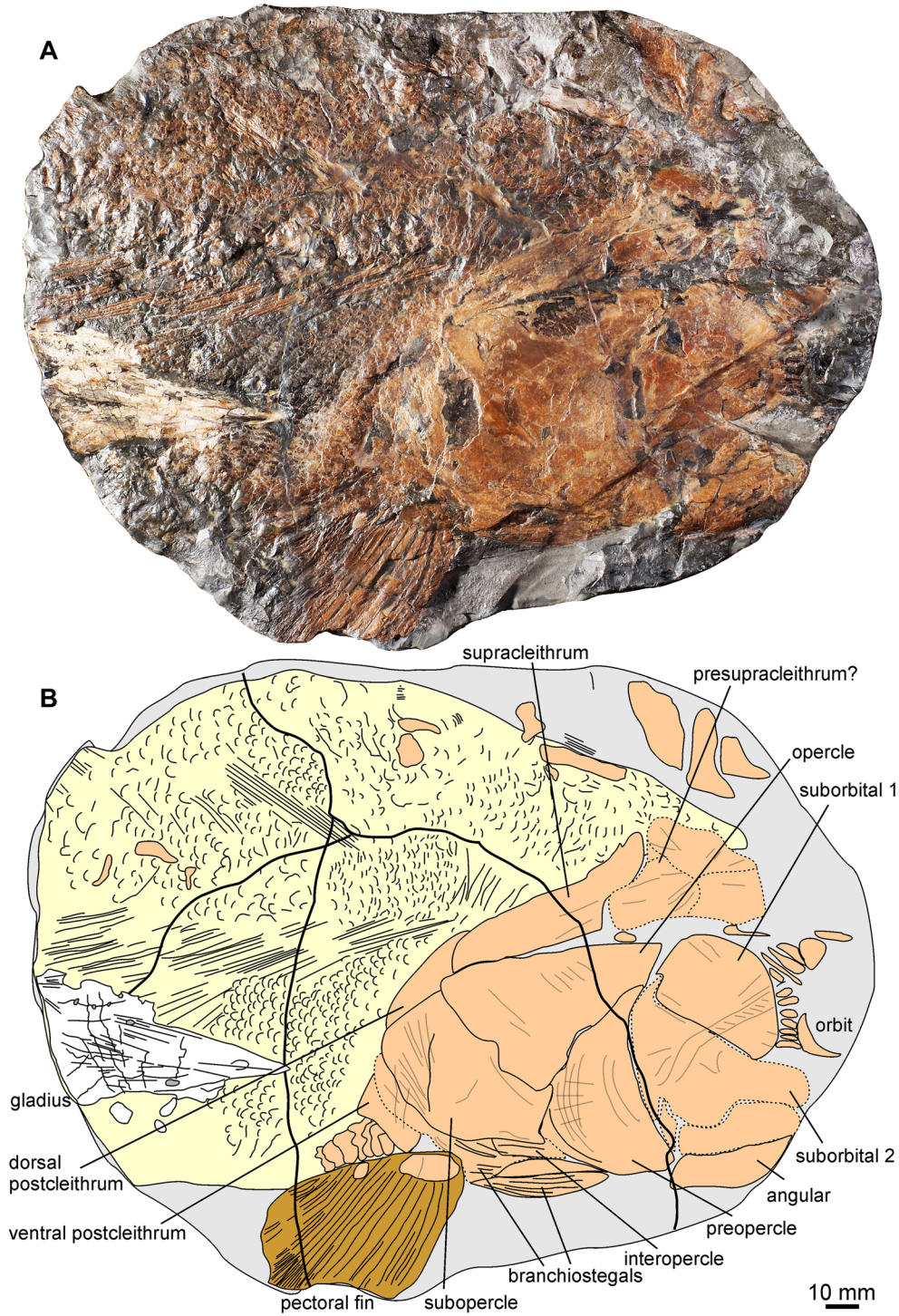
Fig. 3 Specimen MNHNL n° TU989: *Pachycormus macropterus* (Blainville, 1818) and *Teudopsis bollensis* Voltz, 1836; Serpentinum Chronozone, Foetz

triangular shaped opercle, the pectoral girdle elements are typical of *Pachycormus macropterus.*

Identification and position of the gladius The large sized gladius is laterally embedded and partially covered by fossilized mantle tissue; the hyperbolar zone is not visible, therefore we assign it to Octobrachia indet. The
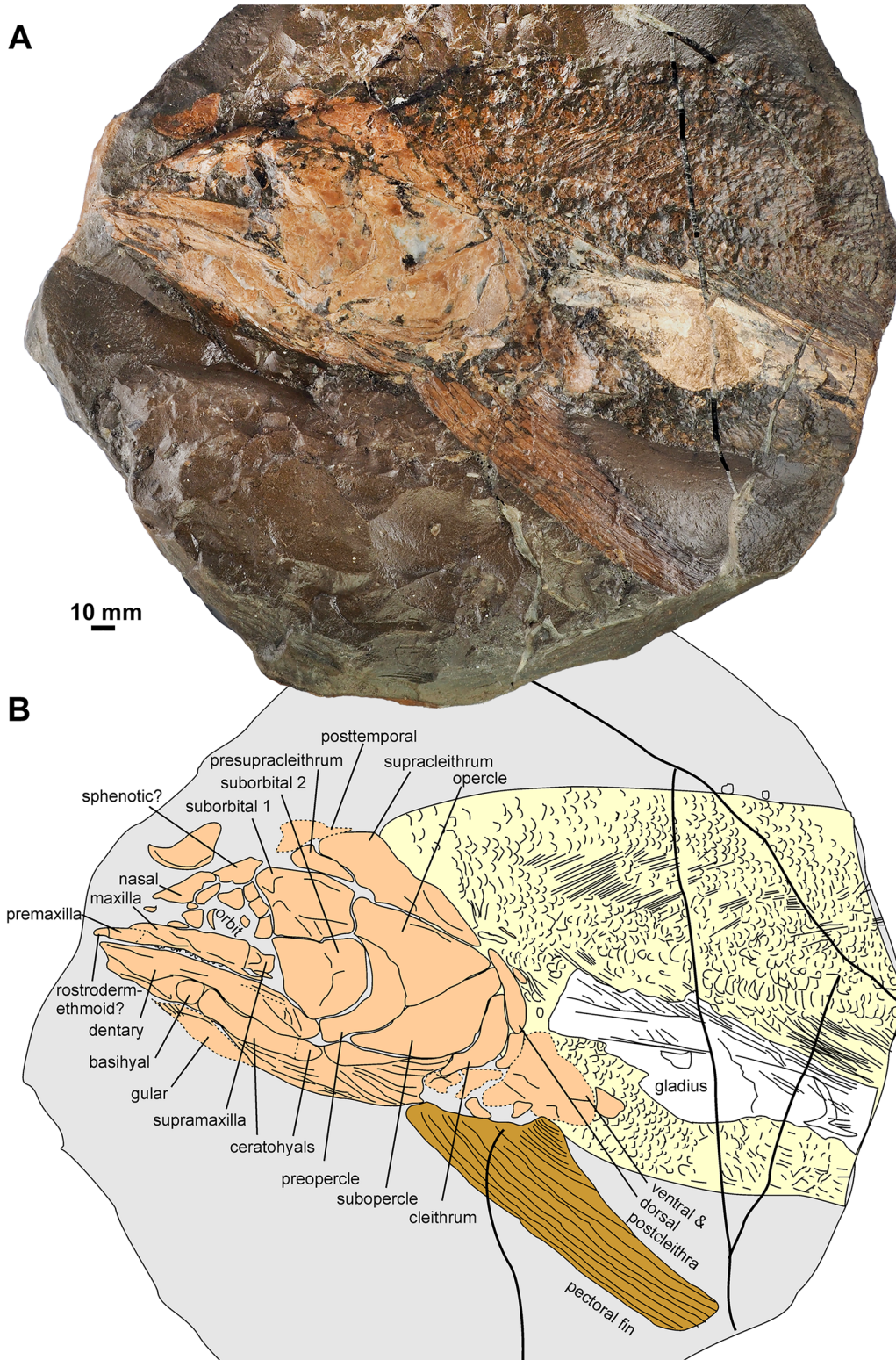
Fig. 4 Specimen JCS n° P39: *Pachycormus macropterus* (Blainville, 1818) and Octobrachia indet.; Serpentinum Chronozone, Dudelange

ribs cover the mantle, i.e. the coleoid body lies inside the abdominal cavity of the fish. The gladius appears to be clearly ventral to the notochord. The body is axially directed, immediately behind the cleithrals, far in front of the dorsal fin, which is not present on the sample: thus, the body did not arrive in the stomach ante mortem, resting just at the exit of the bucco-pharyngeal region, in the possibly distended oesophagus (oesophagolite *sensu* Hunt & Lucas, 2012, consumulite in a broader sense). The orientation of the gladius in specimen P39 remains to be determined.

Genus *Saurostomus* Agassiz, 1843

Specimen MNHNL n° TU987a-b: *Saurostomus esocinus* Agassiz, 1843 **and Loligosepiinae indet** (Fig. 5).

1999a Pachycormiforme aff. *Saurostomus*; Delsate: fig. 16.

Locality Bascharage, collected by D. Watrinelle; 'Schistes bitumineux' formation, Serpentinum Chronozone.

Dimensions Preserved length of the fish 250 mm. Length of the opercle ca. 86 mm. In absence of further data, we use the opercle length; 86 mm × 9.5 = 817 mm, 86 mm × 19 = 1634 mm. Preserved length of the gladius: 50 mm.

Identification of the fish Left side of the fish preserving the articulated skull (cranial length 25 cm but the anterior region of the skull is damaged), the partial abdominal flank, and the partially preserved left pectoral fin. The large opercular (dimensions: around 70 mm long axis) has a shield shape typical for *Saurostomus* (see Wenz, 1967: fig. 65), different from the triangular opercular of *Pachycormus.* Specimen TU987 is fully conformed to Cooper and Maxwell (2022) describing *Saurostomus esocinus*, and this specimen is part of the specimens they examined.

Identification and position of the gladius The small, partially preserved gladius can be attributed to the Loligosepiinae owing to its extended hyperbolar zone (Fuchs & Weis, 2008). Its position is axial, in the antero-posterior axis of the fish, contacting the posterior border of the dorsal postcleithrum, and supposedly in esophageal position (esophagolite *sensu* Hunt & Lucas, 2012, consumulite in a broader sense).

Specimen MNHNL n° TV228: *Saurostomus esocinus* Agassiz, 1843 **and *Teudopsis bollensis* Voltz,** 1836 (Fig. 6)

2010 *Teudopsis bollensis*: Fuchs & Weis: fig. 4D.

Locality Bascharage, collected by D. Delsate; 'Schistes bitumineux' formation, Serpentinum Chronozone.

Dimensions Preserved length of the fish 300 mm. Head length: 177 mm; maximal length of the opercle: 92.5 mm. Length estimation from the head length: 177 mm × 4.3 = 761 mm; from the opercle length: 92.5 × 9.5 = 878 mm (probably realistic), to 92.5 × 19 = 1757 mm. Preserved length of the gladius: 135 mm.

Identification of the fish The large scute or shield-shaped opercular, the large rectangular subopercular, the robust hyomandibula, which forms a waisted thickened core and forms an opercular process, and robust ceratohyals indicate *Saurostomus esocinus.*

Identification and position of the gladius The completely preserved gladius is safely attributed to the genus *Teudopsis* characterized by a median keel and the species *T. bollensis* thanks to the triangular shape of the anterior part of the gladius (Fuchs & Weis, 2010). Its position is nearly vertical and lies behind the clewithrum. The posterior tip of the gladius reaches the level of the junction between the preserved portions of the cleithrum/subopercular, with the whole posterior part arranged in cephalic direction of the fish. The coleoid was thus caught head and arms first. Itis evidently not in anatomical position: it might have been displaced *post mortem*, or it might have caused a perforation of the oesophagus. This appears to be also an oesophagolite sensu Hunt and Lucas (2012; consumulite in a broader sense).

Discussion

In Europe, the claystone and clayey carbonates of the Toarcian often show characters of stagnate conservation deposits (Riegraf et al., 1984; Röhl et al., 2001, 2002; Seilacher, 1970; Seilacher et al., 1985). Accordingly, biotic interactions between predator and prey animals are occasionally fossilized. In recent years, several examples have been published, some including fish and cephalopods (Hart et al., 2020; Jenny et al., 2019; Klug et al., 2021a, 2021b). Additionally, regurgitalites were reported from the Toarcian (Hoffmann et al., 2020; Thies & Hauff, 2012). Accordingly, it is well established that actinopterygians and chondrichthyans often preyed upon cephalopods
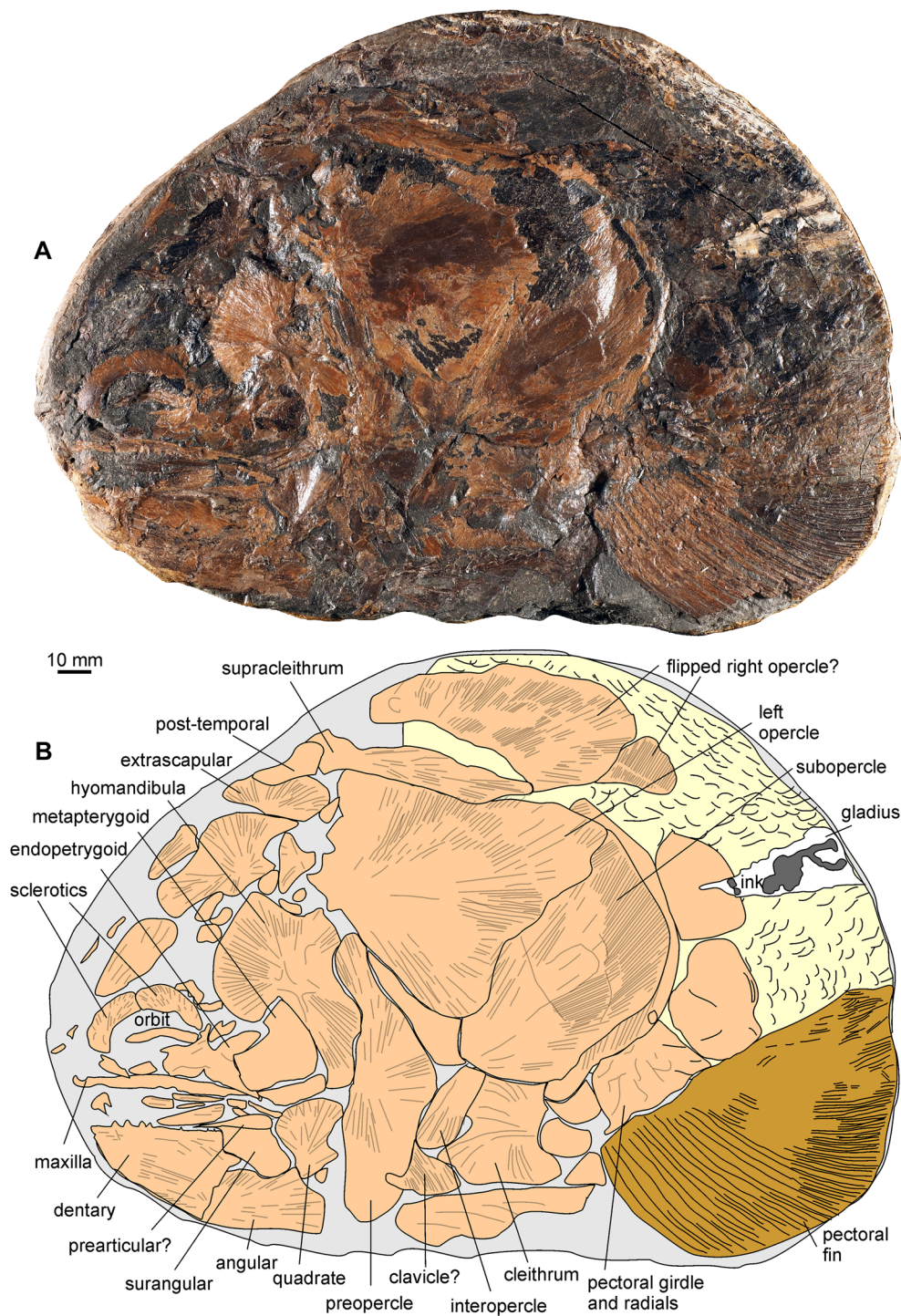
Fig. 5 Specimen MNHNL n° TU987a-b: *Saurostomus esocinus* Agassiz, 1843 and Loligosepiinae indet.; Serpentinum Chronozone, Bascharage

(Boucot, 1990; Doyle & Macdonald, 1993; Hoffmann & Stevens, 2020; Klug et al., 2021b), that cephalopods fed on other cephalopods (Klug et al., 2021a), but that cephalopods also fed on actinopterygians (Hart et al., 2020; Jenny et al., 2019). Recently, Cooper and Maxwell (2022) reported gastrointestinal contents of the pachycormid fish *Saurostomus esocinus* that comprise octobrachian (loligosepiid) and belemnoid remains, indicating a rather diversified but mostly coleoid-based diet.
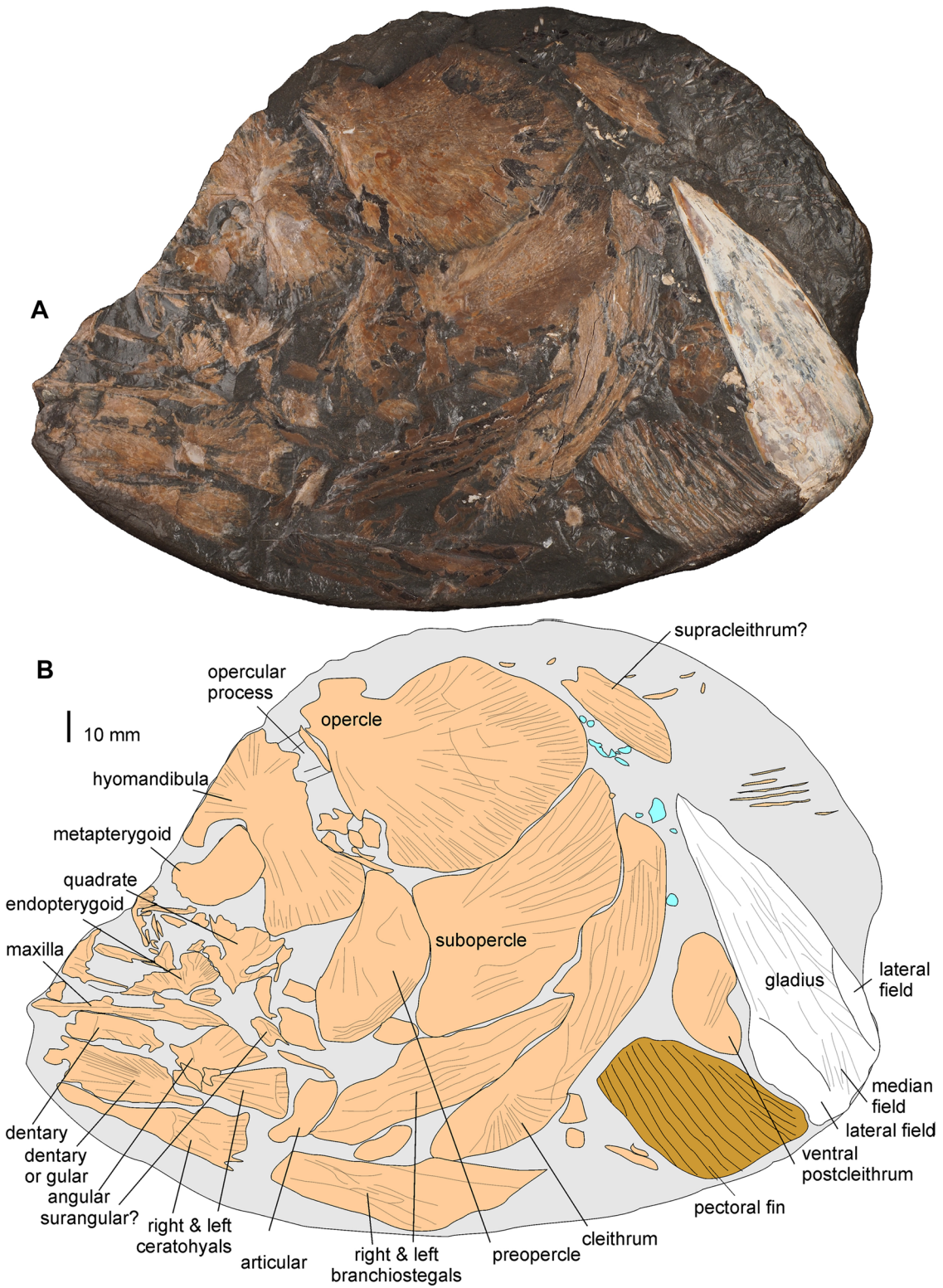
Fig. 6 Specimen MNHNL n° TV228: *Saurostomus esocinus* Agassiz, 1843 and *Teudopsis bollensis* Voltz, 1836; Serpentinum Chronozone, Bascharage

Pachycormid fishes are understood as forming two rather distinct phylogenetic lineages (e.g., Cooper et al., 2022; Friedman, 2012; Gouiric-Cavalli & Arratia, 2022; Schumacher et al., 2016; Wretman et al., 2016). One contains mostly small to mid-sized tusked ichthyophagous forms, as exemplified by the Late Cretaceous *Protosphyraena*, and the other containing gigantic edentulous suspension feeders, such as the emblematic Late Jurassic *Leedsichthys* (e.g., Cooper et al., 2022; Friedman, 2012; Gouiric-Cavalli & Arratia, 2022; Schumacher et al., 2016; Wretman et al., 2016). Most phylogenies recover *Saurostomus* as a basal member of the lineage containing the suspension feeders (Cooper et al., 2022; Friedman, 2012; Schumacher et al., 2016; Wretman et al., 2016), but this is not unanimously accepted (Gouiric-Cavalli & Arratia, 2022). On the other hand, *Pachycormus* was recovered in a basal polytomy with the two clades (e.g., Wretman et al., 2016), as nested within the 'ichthyophagous' clade (Gouiric-Cavalli & Arratia, 2022), or as a stem member of the 'suspension feeders' clade (Cooper et al., 2022; Friedman, 2012; Schumacher et al., 2016). The clade containing suspension feeders, to the inclusion of *Pachycormus*, was termed Asthenocorminae by Cooper et al., 2022.

Previously reported evidence for the utilization of coleoid prey by Jurassic pachycormids, suggests that teuthophagy was common amongst asthenocormin pachycormids (Cooper et al., 2022; Friedman, 2012; Přikryl et al., 2012). Amongst members of the ichthyophagous clade (e.g., Cooper et al., 2022; Gouiric-Cavalli & Arratia, 2022), the possible utilization of coleoid prey has only been putatively inferred for the Middle–Late Jurassic hypsocormines (Martill et al., 1994). Most Toarcian asthenocormin pachycormids that are associated with coleoid prey, in the form of gut contents, preserve only hooklets or gladial fragments in their gastrointestinal tracts (Cooper & Maxwell, 2022; Cooper et al., 2022; Přikryl et al., 2012). This could be indicative of a feeding strategy that involved the shearing and ingestion of only parts of the coleoid animal; mainly its arms. Evidence for a different feeding strategy which entails the ingestion of complete belemnite coleoids is scant, and is restricted to a single individual of *Saurostomus esocinus* (Cooper & Maxwell, 2022), or is subject to interpretation in the case of the holotype of *Ohmdenia multidentata* (Friedman, 2012). Here, we provide new direct evidence that the actinopterygian genera *Pachycormus* and *Saurostomus* fed on gladius-bearing cephalopods. 8.5% (6 out of 70 specimens) of the large specimens of Luxembourg Toarcian pachycormids (55 *Pachycormus* and 15 *Saurostomus*) preserve ingested coleoids. In these specimens, we did not find evidence of other prey (e.g., fish), but we cannot exclude a preservation or observation bias. We did not find ingested coleoids in smaller Toarcian pachycormiforms (*Haasichthys*, *Sauropsis*, *Euthynotus*). The latter is indicative of possible resource and niche partitioning amongst Toarcian pachycormids. Surprisingly, we also failed to find any belemnoid hooks by contrast to Cooper and Maxwell (2022), who documented them in nine out of ten specimens with preserved gastric contents of *Saurostomus esocinus*. This might show some dietary partitioning, with *Pachycormus* preferring non-arm hook-bearing coleoids, so this difference may be the result of denser sampling of *Pachycormus* compared to *Saurostomus* in the present study (2/3 vs. 1/3). However, Přikryl et al. (2012) also report arm hooks in *Pachycormus* from South Western Great Britain, so it could also be a regional dietary difference between the samples.

Cephalopod remains such as coleoid arm hooks can be visibly preserved undigested in coprolites (Hunt et al., 2012: p. 16), probably produced by fishes. Those in the stomach can eventually show signs of digestion caused by dissolution by acid or disruptions of anatomical structures due to enzymatic breakdown. However, we have not identified structures suggesting either of these processes in our study. Remains of the digested cephalopods enter easily into the intestine as a solution of dissolved soft proteolysed chitin and saccharides. The oblique position in specimen MNHNL TV228 ascribed to *Saurostomus esocinus* could indicate a possible perforation of the digestive tract before digestion. If such an incident is confirmed by additional better-preserved fossil findings, it will be the second mode of death of pachycormid fishes caused by the voracious ingestion of cephalopods. Recently described findings from the Toarcian of Germany indicated that the ingestion of a complete ammonite was the most likely cause of death of a *Pachycormus macropterus* individual (Cooper & Maxwell, 2023). According to their positions in the fish bodies, we conclude that the octobrachian remains represent mostly gastrolites and some oesophagolites *sensu* Hunt and Lucas (2012; i.e. *consumulites sensu lato*).

The orientation of the gladii remains indicate that the prey had been captured and ingested head first (Table 3). This observation corroborates the findings of Cooper and Maxwell (2022), who describe a similar orientation of loligosepiid gladii in *Saurostomus esocinus*. It is remarkable that the fish swallowed the whole animal, hardly reducing prey size prior to ingesting the prey. This could hint at a feeding strategy that entails the active chase of the coleoid prey and its complete capture.

Table 3 Overview of the described specimens and position of the octobrachian gladii

Collection n°	Fish	Octobrachian	Prey orientation	Prey position
TU899	*Pachycormus macropterus*	*Teudopsis* sp.	Head and arms first	Axial
TU932	*Pachycormus macropterus*	*Teudopsis* sp.	Head and arms first	Axial
TU989	*Pachycormus macropterus*	*Teudopsis bollensis*	Head and arms first	Axial
P39	*Pachycormus macropterus*	Loligosepiidae	?	Indeterminate
TU987	*Saurostomus esocinus*	Loligosepiidae	Head and arms first	Axial
TV228	*Saurostomus esocinus*	*Teudopsis bollensis*	Probably head and arms first	Vertical

Conclusions

The predatory pachycormiform genera *Pachycormus* (four specimens) as well as *Saurostomus* (two specimens) fed without preference on octobrachian coleoids such as either *Teudopsis* (four specimens), Loligosepiinae (one specimen) and Octobrachia indet. (one specimen). Usually, as far as demonstrated in our material, these actinopterygians grasped the head and tentacles first prior to ingesting the coleoids. Thus, the coleoid remains are preserved in axial direction, with the posterior end of the gladius pointing in anterior (cephalic) direction of the fish. New evidence from the Toarcian of Luxembourg supports previous observations suggesting a coleoid-based diet of *Saurostomus esocinus* advanced based on material from South Germany (Cooper & Maxwell, 2022). Furthermore, the material under study hints at a similar diet for *Pachycormus macropterus.* Collectively, evidence from asthenocormin pachycormids (following Cooper et al., 2022) from the Toarcian of Germany and Luxembourg reinforce previous notions (Cooper & Maxwell, 2022; Friedman, 2012) that teuthophagy was a feeding strategy widespread amongst forms at the stem of the Jurassic–Cretaceous gigantic edentulous suspension feeders. It, thus, represents a possible intermediate stage towards the evolution of the latter ecomorph in ray-finned fishes.

Author contributions
RW gathered the study material, designed the study, contributed to the determination of the octobrachians, made photographs of specimens and contributed to writing the article. DD determined the pachycormiforms and contributed to writing the article. CK made drawings and contributed to the discussion. TA contributed to the anatomical interpretation of pachycormids and the writing of the manuscript. DF contributed to the determination of the octobrachians and the discussion.

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