Vampyromorph coleoid predation by an ichthyosaurian from the Early Jurassic Lagerstätte of Luxembourg (#116115)

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Vampyromorph coleoid predation by an ichthyosaurian from the Early Jurassic Lagerstätte of Luxembourg

Robert Weis [Corresp., Equal first author, 1], **Valentin Fischer** [Corresp., Equal first author, 2], **Dominique Delsate** [1], **Francesco Della Giustina** [2], **Pierre Wintgens** [2], **Dirk Fuchs** [3], **Ben Thuy** [1]

[1] Section Paléontologie, Musée National d'histoire Naturelle, Luxembourg, Luxembourg

[2] Evolution & Diversity Dynamics Lab, Université de Liège, Liège, Belgium

[3] Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany

Corresponding Authors: Robert Weis, Valentin Fischer
Email address: robert.weis@mnhn.lu, v.fischer@ulg.ac.be

Many Early Jurassic marine predators were seemingly adapted to hunt soft and fast prey items such as cephalopods. However, deciphering what these animals ate and, therefore, the intensity of their competition is challenging, as fossilised gut content is biased by multiple factors. In this paper, we report a loligosepiid vampyromorph coleoid in the gut of a specimen of the ichthyosaurian *Stenopterygius triscissus* from the early Toarcian Bascharage Lagerstätte of Southern Luxembourg. This is the first report of octobrachian predation in ichthyosaurians. The coeval pachycormid teleosts *Pachycormus macropterus* and *Saurostomus esocinus*have recently been reported to feed on loligosepiid octobrachians as well, indicating partial reliance on the same food resources. We use this opportunity to compare the functional anatomy of these taxa and re-evaluate the affinities of coleoids preserved as ichthyosaurian gut content.

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Valentin Fischer[1], Robert Weis[2], Dominique Delsate[2], Francesco Della Giustina[1], Pierre Wintgens[1], Dirk Fuchs[3] & Ben Thuy[2]

[1] Evolution & Diversity Dynamics Lab, UR Geology, Université de Liège, Belgium

[2] Section Paléontologie, Musée National d'histoire Naturelle, 25 rue Münster L-2160 Luxembourg, Grand Duchy of Luxembourg

[3] Bayerische Staatssammlung für Paläontologie und Geologie, Richard Wagner Straße 10, D-80333 München, Germany

Corresponding Authors:

Valentin Fischer[1] , Robert Weis[2]

[1] Evolution & Diversity Dynamics Lab, UR Geology, Université de Liège, Belgium

[2] Section Paléontologie, Musée National d'histoire Naturelle, 25 rue Münster L-2160 Luxembourg, Grand Duchy of Luxembourg

Email addresses: v.fischer@uliege.be ; robert.weis@mnhn.lu

Abstract

Many Early Jurassic marine predators were seemingly adapted to hunt soft and fast prey items such as cephalopods. However, deciphering what these animals ate and, therefore, the intensity of their competition is challenging, as fossilised gut content is biased by multiple factors. In this paper, we report a loligosepiid vampyromorph coleoid in the gut of a specimen of the ichthyosaurian *Stenopterygius triscissus* from the early Toarcian Bascharage Lagerstätte of Southern Luxembourg. This is the first report of octobrachian predation in ichthyosaurians. The coeval pachycormid teleosts *Pachycormus macropterus* and *Saurostomus esocinus* have recently been reported to feed on loligosepiid octobrachians as well, indicating partial reliance on the same food resources. We use this opportunity to compare the functional anatomy of these taxa and re-evaluate the affinities of coleoids preserved as ichthyosaurian gut content.

Introduction

A series of Lagerstätten deposits have revealed, over the last 170 years, a formidable diversity of marine reptiles that populated the European epicontinental seas during the Toarcian (late Early Jurassic) (e.g. Hauff, 1953; Godefroit, 1994; Röhl et al., 2001; Großmann, 2007; Maisch, 2008; Benson et al., 2010, 2011; Johnson et al., 2018; Stöhr & Werneburg, 2022). These localities indicate the presence of several coeval predators: neoichthyosaurians, thalattosuchian crocodyliforms, and plesiosaurians. Many of them have long snout and small, acute teeth, suggesting that they relied on soft prey items such as cephalopods and small teleosts (Massare, 1987; Bardet, 1994; Godefroit, 1994; Fischer et al., 2022a). Competition among marine reptiles, as well as with other

vertebrates such as teleosts or chondrichthyans, is likely, as evidenced in some Mesozoic formations (Martin et al., 2017; Foffa et al., 2018; Cortés & Larsson, 2024). However, precise data on the prey items found in marine reptile gut content is generally lacking. The Bascharage Lagerstätte of Southern Luxembourg has recently revealed that multiple pachycormid teleosts fed on octobranchian cephalopods (Weis et al., 2024), while coleoids as a whole are often regarded as a resource consumed by other marine reptiles, notably ichthyosaurians and thalattosuchians based on gut content and dental anatomy (Massare, 1987; Böttcher, 1989; Lomax, 2010). Consumption of cephalopods by ichthyosaurians has indeed been known since the 19th century (Buckland, 1829; Quenstedt, 1858). Based on masses of arm hooks in their fossilised gut contents, ichthyosaurians have indeed been regarded as 'teuthophages', probably preferring belemnoid coleoids (Dick, Schweigert & Maxwell, 2016). Here, we add to this body of evidence by (i) describing the ecomorphology and the gut content of a specimen of the baracromian ichthyosaurian *Stenopterygius triscissus* from the Bascharage Lagerstätte, (ii) comparing it with those of coeval pachycormid teleosts, and (iii) reviewing the systematic attribution of prey items in fossilised ichthyosaurian gut contents.

Materials & Methods

Geological setting

The 'Schistes bitumineux', also known as 'Couches à Harpoceras falciferum' (Lo1) or the Bascharage Lagerstätte, is a geological formation in Luxembourg that crops out over an area approximately 30 km wide between Rodange and Bascharage in the west and

Bettembourg and Dudelange to the east (Dittrich, 1993); its thickness reaches 40-45 m (Lucius, 1945). This formation is the local expression of a widespread phenomenon of anoxia that affected the European epicontinental seas during the early Toarcian, known as the Toarcian Oceanic Anoxic Event (T-OAE) or the Jenkyns Event. As such, the Schistes bitumineux Formation is coeval with other bituminous formations in western Europe, such as the Posidonienschiefer Formation in southwestern Germany, the Jet Rock Formation in the UK, the Schistes Carton in France, and the Grandcourt Formation in Belgium (Muscente et al., 2023).

The bituminous shales outcropping in the south of Luxembourg and the neighbouring Gaume and Lorraine regions in France and Belgium are known for their rich fossil record since the 19th century: Chapuis & Dewalque (1853) mentioned fossils of 'fish' and 'squids' in Aubange, on the Belgian-Luxembourgish border. Since the 1930s, when two ichthyosaurian skeletons were unearthed (Faber & De Muyser, 1947), marine reptiles are surely amongst the most iconic and mostly sought-after fossils from the 'Schistes bitumineux' Formation. Several specimens have been discovered since; see Godefroit (1994) for a detailed analysis of this material, as well as Vincent et al. (2017), Johnson et al. (2018), Laboury et al. (2022), and Wallstedt et al. (2024) for recent contributions on plesiosaurians, thalattosuchians, and ichthyosaurians, respectively.

The ichthyosaurian specimen studied herein originates from the Schistes bitumineux Formation, more precisely the Serpentinum ammonite zone. It was found during construction works for the 'Luxguard' factory in the industrial zone next to Dudelange

(coordinates: 49°30’06’’N; 6°04’55’’E) by D. Watrinelle, a private fossil collector, in the late ’80s or early ’90s and subsequently donated to the MNHNL. The specimen had been described and illustrated as *Stenopterygius quadriscissus* by Godefroit (1994: pl. 3, fig. c) and is exhibited in the permanent gallery at the MNHNL. A recent restoration by O. Kunze (Stuttgart, Germany) revealed further anatomical details. A 3D model of the full specimen can be accessed freely online: https://sketchfab.com/3d-models/stenopterygius-quadriscissus-tv211-v2024-930e539b4f6e4ef7816d2ad4f4a65227.

Functional traits

We gathered a series of craniodental and postcranial traits that summarise the feeding and swimming capabilities of three coeval species, known to have ingested loligosepiid coleoids: the ichthyosaurian *Stenopterygius triscissus* and the pachycormiforms *Pachycormus macropterus* and *Saurostomus esocinus*. We selected the following traits to be compared for each taxon: the absolute total body size (a proxy for energy consumption, among other factors), the mandibular aspect ratio (mandible area divided by the square of mandible length (Friedman, 2012); a proxy for lower jaw stiffness), the closing mechanical advantage of the jaw, computed at the middle part of the dentigerous section (distance from the quadrate/articular articulation to the coronoid process divided by the distance from the quadrate/articular articulation to the mid-dentigerous point in the mandible; a proxy for relative bite strength), the crown shape (crown height divided by crown basal diameter, for tooth in the middle part of the dentigerous section, a proxy for the piercing capability of the crown), the absolute diameter of the opening of the sclerotic

ring (a proxy for the size of the dilatated pupil and therefore of low-light vision), and the aspect ratio of the pectoral and caudal fins (fin area divided by the square of the fin proximo-distal length; a proxy for swimming speed). We obtained these data from the literature for pachycormids (Friedman, 2012; Williams, Benton & Ross, 2015; Cawley et al., 2019; Cooper & Maxwell, 2022) and from measurements of MNHNL TV211, complemented by the literature (Lingham-Soliar, 2001; Maisch, 2008) for the ichthyosaurian. The caudal aspect ratio for the ichthyosaurian is taken for the species *Stenopterygius quadriscissus* instead of *Stenopterygius triscissus*, as no specimen of the latter have been reported with an intact caudal fin outline preserved. Articulated apical and postflexural skeletal regions suggest that both species possessed a similarly shaped caudal fin (Maisch, 2008; Maxwell, 2012).

Institutional abbreviations: BRLSI: Bath Royal Literary and Scientific Institution, Bath, UK. GPIT: Paläontologische Sammlung der Universität Tübingen, Germany. MNHNL: Palaeontological collections of Musée National d'Histoire Naturelle, Luxembourg. NHMUK: Natural History Museum, London, UK. SMF: Natur-Museum Senckenberg, Frankfurt, Germany. SMNS: Staatliches Museum für Naturkunde Stuttgart, Germany.

Results

Identity and age of the ichthyosaurian

The specimen MNHNL TV211 is a partial ichthyosaurian preserving the skull, neck, torso, scapular girdle, and right anterior forefin, in articulation (total anteroposterior length = 1047 mm; mandible length = 424 mm). The preserved portion suggests that the animal

was ≈2000 mm long in vivo. The prefrontal is small and does not participate in the bony narial aperture; the maxilla is anteroposteriorly short; the teeth are small, straight, and lack conspicuous enamel ornamentation but have apicobasal ridges texturing the root; the coracoid is rounded, with an anterior notch and lacks a posterolateral emargination; the scapula forms a large acromion; the humerus is constricted at mid-shaft and solely connects distally to two large epipodial hexagonal elements (radius and ulna); the radius and the radiale are notched and the intermedium solely contacts the distal carpal 3. This combination of features is unique to the genus *Stenopterygius* (Godefroit, 1994; Maisch, 2008; Caine & Benton, 2011; Maxwell, 2012; Maxwell & Cortés, 2020; Fischer et al., 2022b).

The rostrum is ≥0.63 the length of the mandible (its anteriormost margin is broken off); the dorsoventral height of the maximal at the level of mid-naris is 0.38 times the dorsoventral height of the rostrum in the same zone; the maxilla forms the ventral border of the bony narial aperture; the trunk appears slender. This suite of features suggests that the specimen belongs to the species *Stenopterygius triscissus* (Godefroit, 1994; Maisch, 2008; Maxwell, 2012), the most abundant ichthyosaurian species from the Toarcian of Luxembourg (Godefroit, 1994). Godefroit (1994) reported that the maxilla forms the ventral border of the naris in *Stenopterygius longifrons* (=*Stenopterygius triscissus* (Maisch, 2008)), yet a specimen from Strawberry Bank, UK, has the maxilla excluded from the bony narial aperture by a combination of the subnarial process of the premaxilla and the anteroventral process of the lacrimal (Caine & Benton, 2011). This feature therefore appears interspecifically variable and should not be used in isolation to identify

the species of *Stenopterygius*. Additionally, it is worth mentioning that the specimen is likely not a fully mature adult (the species is supposed to grow to a size of 3500 mm) and might not have developed all the diagnostic features of the species, notably the long rostrum (70% of total mandible length in adults only, only ≥63% in the present specimen) (Godefroit, 1994; Maisch, 2008). Its probable subadult growth stage also explains the presence of a fully functional dentition. Indeed, *Stenopterygius* is known to lose teeth upon reaching the adult stage; the timing and degree of tooth reduction appears however interspecifically variable (Godefroit, 1994; Maisch, 2008; Dick & Maxwell, 2015).

Functional anatomy of the ichthyosaurian

With an estimated body length of 2 m, the ichthyosaurian analysed here is about the same size as the common dolphin, *Delphinus delphis* (Ridgway & Harrison, 1999). Being an early thunnosaurian ichthyosaurian (Motani, 1999), *Stenopterygius* has a thunniform body outline (Lingham-Soliar & Plodowski, 2007) and was likely adapted for fast, sustained swimming (Motani, 2002; Gutarra et al., 2019). This is also evidenced by the high aspect ratio of the forefin and the caudal fin (Figure 3).

The rostrum is long and slender, as in most ichthyosaurians. The coronoid process of the surangular is small, as is the postorbital region of the skull. These factors result in a weak bite force; the mechanical advantage computed at the mesialmost tooth of the snout = 0.08 (Figure 3). Such a value is, for example, one-third to one-half of the value found in most mosasaurids and short-necked plesiosaurians (MacLaren et al., 2022; Fischer et al. in prep). The long, slender, and tubular snout of *Stenopterygius triscissus* (mandibular

aspect ratio = 0.038; Figure 3) could be ideal for fast lateral snapping of small prey items, even in the context of reduced head mobility in ichthyosaurians (VanBuren & Evans, 2016). The tooth crown in the middle part of the rostrum in MNHNL TV211 has an apicobasal height/basal ratio of 6.1 mm / 2.4 mm = 2.5 (Figure 3) and is therefore slender compared to many other marine amniotes. In *Stenopterygius quadriscissus*, the teeth (when retained) are usually blunter at mandible lengths of ≥400 mm (Dick, Schweigert & Maxwell, 2016). The small, narrow crowns of *Stenopterygius triscissus* are straight and lack enamel ornamentation. This suggests a diet of small, soft prey items (Massare, 1987; Fischer et al., 2022a). The eyes of *Stenopterygius triscissus* are large: the mean diameter of the right orbit of MNHNL TV211 is 91.5 mm, and that of the inner opening of the right sclerotic ring (a direct proxy for the size of the dilatated pupil) is 36.1 mm (Figure 3), slightly larger than the pupil of the fast swimming swordfish (Nilsson, Warrant & Johnsen, 2014). Such a pupil allows a ≈32 m vision range of a 10 cm black target at a depth of 350m in clear oceanic waters (Nilsson, Warrant & Johnsen 2014).

Identity of the gut content in MNHNL TV221

The preserved gut content corresponds to the fragmentary remains of a gladius-bearing coleoid, more precisely a loligosepiid octobranchian. This assignation is based on the presence of an extended hyperbolar zone on the gladius, which also lacks the keel that is otherwise typical of contemporary teudopseid octobrachians. However, a more precise determination is hampered by the fragmentary preservation and the diagnostic course of the growth lines within the hyperbolar zone is not observable on this specimen. Fossils of loligosepiids are widespread in the Lower Toarcian sediments across Central and

Western Europe and have been described for instance from Southern Germany, France, Luxembourg and the UK (e.g. Riegraf, Werner & Lörcher, 1984; Doyle, 1990; Guérin-Franiatte & Gouspy, 1993; Fuchs & Weis, 2008, 2010; Jattiot et al., 2024). In the Schistes bitumineux Formation, they usually have phosphatized soft tissue and ink sacs, in addition to the unmineralized gladius. The vampyromorph faunal list in this formation comprises three teudopsid species (*Teudopsis bunelii, Teudopsis subcostata* and *Teudopsis bollensis*) and three loligosepiid species (*Loligosepia aalensis, Parabelopeltis flexuosa, Jeletzkyteuthis coriaceus)* as well as one recently discovered species, *Simoniteuthis michaelyi* (Fuchs & Weis, 2008, 2010; Fuchs, Weis & Thuy, 2024).

Functional anatomy of coeval octobranchian-eating pachycormids

Several species of pachycormids are found in the same deposits as MNHNL TV221: *Pachycormus macropterus*, *Saurostomus esocinus*, *Sauropsis latus*, *Euthynotus incognitus*, and *Haasichthys michelsi* (Delsate, 1999a,b) but only the former two have coleoid remains in their gut content (Weis et al. 2024). Both are smaller than *Stenopterygius triscissus*, with skull lengths of around 150mm for *Saurostomus* (of which mandible length accounts for 45-50 %; total body length up to 1374 mm (Friedman, 2012; Cawley et al., 2019) and 170 mm for *Pachycormus* (of which mandible length accounts for 40-55 %; total body length up to 600 mm (Friedman, 2012; Cawley et al., 2019; Cooper & Maxwell, 2022)). *Pachycormus macropterus* and *Saurostomus esocinus* have a highly hydrodynamic, fusiform profile, suggesting rapid swimming. This is also supported by the aspect ratios of the pectoral and caudal fins, which are fairly similar for *Stenopterygius* and the three pachycormids considered (Figure 3).

228

229 Besides these similarities in global body shape and fin aspect ratios, the ichthyosaurian
230 and the pachycormids fundamentally differ in the shape and mechanism of their feeding
231 apparatus. Firstly, *Pachycormus* and *Saurostomus* lack a rostrum; the anteorbital portion
232 of their skull is short. This results in marked differences in the closing mechanical
233 advantage, which is ≈ 0.22 for *Saurostomus esocinus,* and 0.25 for *Pachycormus*
234 *macropterus*, therefore nearly or more than three times that of *Stenopterygius triscissus*
235 (Figure 3). Similarly, the mandible aspect ratio is about five times higher in *Saurostomus*
236 *esocinus* and *Pachycormus macropterus* than in *Stenopterygius triscissus* (Figure 3).
237 This suggests that *Pachycormus macropterus* and *Saurostomus esocinus* did not employ
238 lateral snapping, but rather suction to aid capturing prey items. The tooth crowns of
239 *Pachycormus macropterus* are small and elongated (crown shape ratio = 2.7; (Friedman,
240 2012)), with a slight labio-lingual compression (Cooper & Maxwell, 2022), and lack any
241 evident external texture (although 3 µm-wide apicobasal ridges are present; D.D. pers.
242 obs.). Tooth crowns of *Saurostomus esocinus* are larger, and less elongated (crown
243 shape ratio = 1.84 (Friedman, 2012), and curved lingually (Cooper & Maxwell, 2022), with
244 conspicuous folds in the enamel. *Pachycormus macropterus* and *Saurostomus esocinus*
245 possess pupils that are absolutely smaller than those of *Stenopterygius triscissus* (18 mm
246 and 21 mm VS 36 mm; Figure 3), resulting in a vision range of a 10 cm black target at a
247 depth of 350m in clear oceanic waters (≈ 23 m (Nilsson, Warrant & Johnsen, 2014), while
248 it was ≈ 32 m for *Stenopterygius triscissus*).

249

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Discussion

Gut content in Early Jurassic ichthyosaurians

Gut contents have been reported in ichthyosaurians, mostly in the Early Jurassic medium-sized thunnosaurians *Ichthyosaurus* and *Stenopterygius* (Pollard, 1968; Massare, 1987; Dick, Schweigert & Maxwell, 2016). Buckland (1829, p. 226) inferred that Early Jurassic ichthyosaurians preyed upon cuttlefish (suborder Sepiida; crown Decabrachia), as he regarded ring-like structures in putative ichthyosaurian coproliths as the horny sucker rings of sepiids. The occurrence of sepiids in the Jurassic has however been repeatedly rejected (Fuchs, 2023 and references therein), because fossils with a minimum set of sepiid characters are recorded from the latest Cretaceous onward, thus well after the extinction of ichthyosaurians (Bardet, 1992; Fischer et al., 2016). Subsequently, the idea grew that hooklets associated with ichthyosaurian remains belonged to squids (suborder Oegopsida; crown Decabrachia) such as the present day *Onychoteuthis* (Moore, 1856). The idea of 'fossil teuthids' was popular at that time popular, but has become obsolete since the works of Bandel & Leich (Bandel & Leich, 1986; Fuchs, 2020). More recently, the fossilised diet of *Ichthyosaurus* appears to be restricted to belemnoid hooklets (Pollard, 1968; Massare, 1987) and without much variation (nor more details) among species. Two specimens are also known to preserve teleost scales (Buckland, 1836; Lomax, 2010), along with multiple belemnoid hooklets. Keller (1976) and Massare (1987) reported belemnoid hooklets and rare fish fragments in *Stenopterygius quadriscissus*, *Stenopterygius crassicostatus* (=*Stenopterygius quadriscissus* or *Stenopterygius uniter*), and *Stenopterygius megalorhinus* (=*Stenopterygius triscissus* or *Stenopterygius uniter*) (Maisch, 2008). The diet of the species *Stenopterygius quadriscissus* seems to follow an

ontogenetic trend increasing the proportion of cephalopods while decreasing that of teleosts (Dick, Schweigert & Maxwell 2016). Individuals with mandible length > 420 mm seemingly solely relied on cephalopods; which corresponds to the moment when teeth reduce in relative size, eventually becoming non-functional (Dick & Maxwell, 2015). In *Stenopterygius triscissus*, teeth remain large enough to protrude from the dental groove at larger skull sizes (Maisch, 2008; this work). Larger species of Early Jurassic ichthyosaurians seem to add amniotes to their diet (Fischer et al., 2022a): fragments of a smaller ichthyosaurian have been reported in the gastric content of '*Leptopterygius acutirostris*' (Massare, 1987) (some specimens of that entity are now referrable to the large parvipelvian *Temnodontosaurus zetlandicus*, while some smaller specimens possibly belong to early baracromians (Maisch 2010; Laboury et al. 2022)). Böttcher (1989) reported 200 ichthyosaur centra (as well as a series of coleoid hooklets) in the gastric mass of '*Leptopterygius burgundiae*' (=*Temnodontosaurus trigonodon*) (Maisch 1998; McGowan & Motani 2003; Bennion et al. 2024).

However, there has been confusion, or perhaps a lack a precision, in the literature regarding the possible owners of hooklets found in ichthyosaurian guts. These claw-like structures were interpreted as the arm hooklets of 'belemnites' (Pollard, 1968) and this somehow became the interpretation by default. In fact, the coleoid order Belemnitida is essentially typified by ten hooklet-bearing arms (Fuchs & Hoffmann, 2017), and a massive calcitic rostrum covering the primary shell, as well as the presence of mega-onychites (Hoffmann & Stevens, 2020). The absence of such rostra in the stomach of ichthyosaurians was longtime enigmatic until Valente et al. (2010) suggested that most

297 of the arm hooklets in the stomachs of Early Jurassic parvipelvians do not belong to
298 'belemnites' *sensu stricto*, but rather to rostrum-less clades, essentially referrable to
299 Phragmoteuthida, Belemnoteuthina, and Diplobelida (Fuchs, Donovan & Keupp, 2013;
300 Fuchs, 2019). So far, unambiguous evidence of ichthyosaurians feeding on belemnitids
301 is rare; sporadic records of mega-onychites (Dick, Schweigert & Maxwell, 2016) suggest
302 that Early Jurassic thunnosaurians occasionally preyed upon rostrum-bearing
303 belemnites, potentially snapping off the hard part (Valente, Edwards & Pollard, 2010), but
304 preferentially hunted rostrum-less coleoids.
305
306 **Competition or chance?**
307 The fossil record of octobrachian coleoids as ichthyosaurian gut content is exceedingly
308 rare; the specimen we described above represents the first evidence of this behaviour,
309 even though Dick et al. (2016) noted that these species may have been part of
310 ichthyosaurian diets. The fossil record of octobrachians as gut content has been regarded
311 as certainly biased, because octobrachians usually lack strongly mineralised tissues and
312 hooklets (Dick, Schweigert & Maxwell, 2016). The fact that none are preserved in German
313 specimens of *Stenopterygius quadriscissus* prompted Dick et al. (2016) to suggest that
314 this species avoided octobrachians. With hundreds of specimens known (Hauff, 1953),
315 *Stenopterygius quadriscissus* dominates the marine reptile fossil record in early Toarcian
316 German localities and is usually regarded as the ideal representative of the ecology of
317 *Stenopterygius*. Yet, *Stenopterygius triscissus* is more common in Luxembourg
318 (Godefroit, 1994, 1996) and only 15 German specimens of *Stenopterygius triscissus* are
319 preserved with gut content (Dick, Schweigert & Maxwell, 2016). Moreover, there are

subtle differences in the gross anatomy (Maisch, 2008; Maxwell, 2012) and in the retention of functional teeth at adult size (Dick & Maxwell, 2015; Dick, Schweigert & Maxwell, 2016) between the two species, which could lead to slightly distinct diets.

Fossilised gut contents represent a biased record of the diet of marine predators, whose fossil record is also strongly biased (e.g. Benson et al., 2010). It is therefore difficult to assess the biological significance of our find, as a frequent or infrequent ingestion of easily dissolved prey would result in fossil records that are difficult to dissociate. If this occurrence is chance fossilisation of a rare behaviour, it slightly improves our understanding of the ecological capabilities of *Stenopterygius triscissus*. However, if octobrachian consumption was not uncommon in *Stenopterygius triscissus*, it would document a case of competition among dissimilar predators. Indeed, our comparisons of *Stenopterygius triscissus* with coeval, loligosepiid-eating pachycormid teleosts (Figure 3) indicate that these taxa differ in most aspects of their craniodental shapes. This is reinforced by the complexity of the jaw opening and closing in teleosts, as the maxilla and the ceratohyals can rotate, markedly widening the bucco-pharyngeal cavity. This adds suction as an essential mechanism in prey capture (e.g. Day et al., 2015). Closing the mouth forces water to exit behind the operculas, causing a stronger water flux (pushing the prey) at the entry of the oesophagus than in reptiles. This enabled pachycormids to capture and consume relatively larger prey items than ichthyosaurians did. Indeed, *Pachycormus* is known to feed on juveniles of its own kin (Cooper, 2023) as well as ammonites (Cooper & Maxwell, 2023). Such profound functional differences between marine amniotes and ‘fish’ result in the absence of a ‘convergence requirement’ to feed

on similar prey items in the marine realm, which likely explains why attempts to unify the feeding guilds of marine amniotes and sharks have been challenging (Ciampaglio, Wray & Corliss, 2005), despite palaeontological and neontological evidence that both groups competed for similar resources (e.g. Martin et al., 2017). Exceptional preservation in the early Toarcian Bascharage Lagerstätte of Southern Luxembourg indicates that this might also have applied between *Stenopterygius triscissus*, *Pachycormus macropterus*, and *Saurostomus esocinus*, although the true intensity of this competition remains far from clear.

Conclusions

We report on the gut content of a specimen of the ichthyosaurian *Stenopterygius triscissus* from the early Toarcian Bascharage Lagerstätte of Southern Luxembourg. The gut contains an identifiable gladius of a loligosepiid vampyromorph; this marks the first record of gladius-bearing octobrachians in the diet of ichthyosaurians. The coeval pachycormid teleosts *Pachycormus macropterus* and *Saurostomus esocinus* have also been reported to feed on the same food resource, although through a fully distinct mechanism given the functional differences between these taxa. The intensity of the competition between ichthyosaurians and pachycormids during the Early Jurassic remains, however, elusive.

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601

602 ## Figure captions

603

604 **Figure 1. Localisation of the Bascharage locality.**

605

606 **Figure 2**. **Photographs and interpretation of specimen MNHNL TV211**. A, overview
607 of the specimen. B, anatomical interpretation of the right lateral portion of the skull. C,
608 zoom on the fossilised gut content, showing a vampyromorph gladius.

609

610 **Figure 3. Comparison of functional traits of the vampyromorphan predators from**
611 **the Bascharage Laggerstätte.** See Table 1 and supplementary information 1 for
612 details.

613

614

615 ## Tables

616

617 **Table 1**. Functional traits used to compare vampyromorphan predators from the
618 Bascharage Laggerstätte. See supplementary information 1 for the individual
619 measurements and data sources. Uncited references used: (Lingham-Soliar, 2001;
620 Williams, Benton & Ross, 2015; Wretman, Blom & Kear, 2016).

621

Species	Total length	Mandibula aspect	Closing mech advantag	Crown shape	Sclerotic ring openin	Pectoral fin aspect	Caudal fin aspect

			e		**g**		
Stenopterygius triscissus	2000	0.03764	0.082369397	2.44	36.1	3.652830189	3.011764706
Pachycormus macropterus	600.2926	0.17632	0.249741	2.7	18	4.281670205	4.343163539
Saurostomus esocinus	1374.667	0.15351	0.218336	1.84	21	2.356267672	3.006531714

622

Figure 1

Localisation of the Bascharage locality

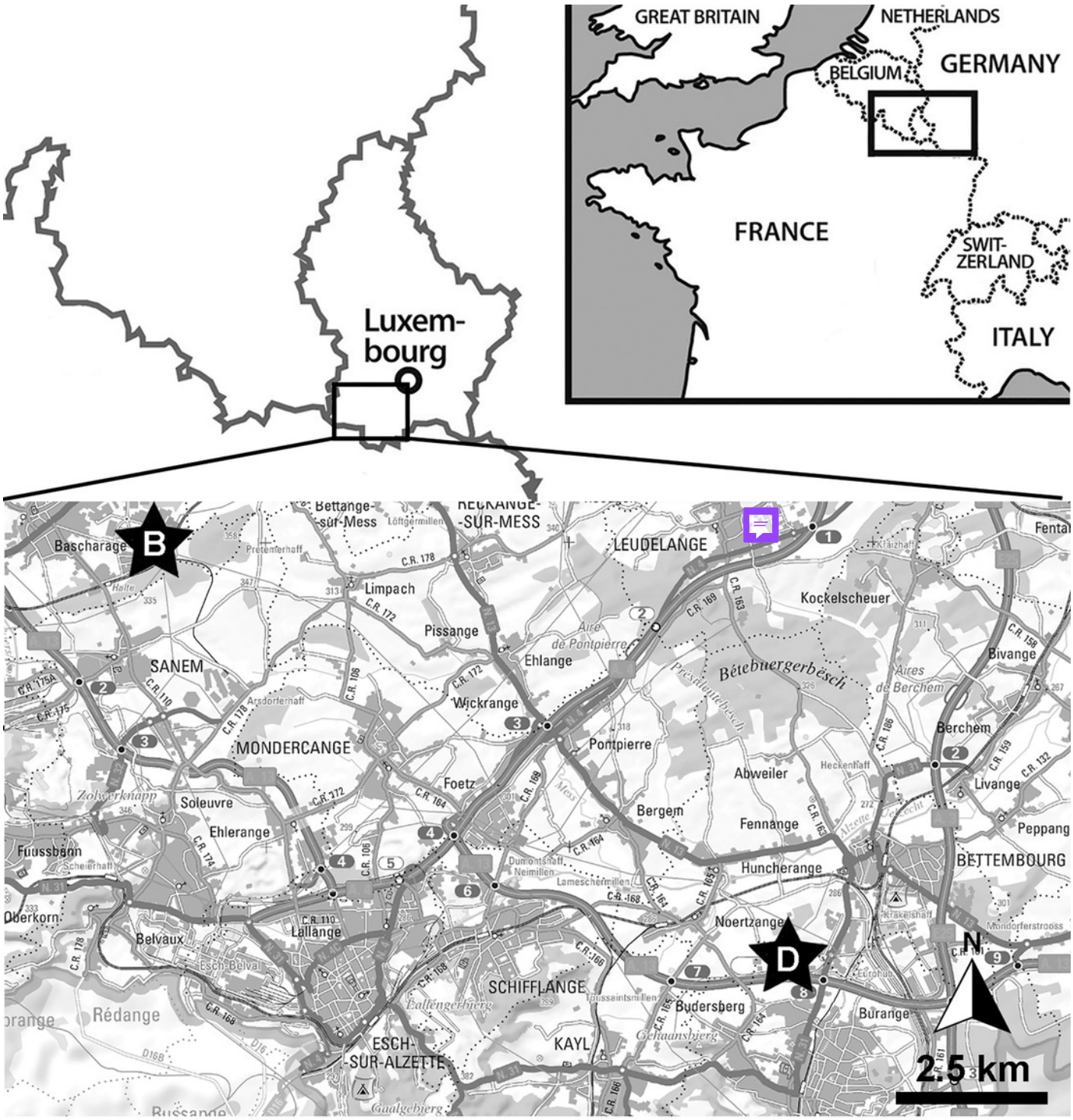
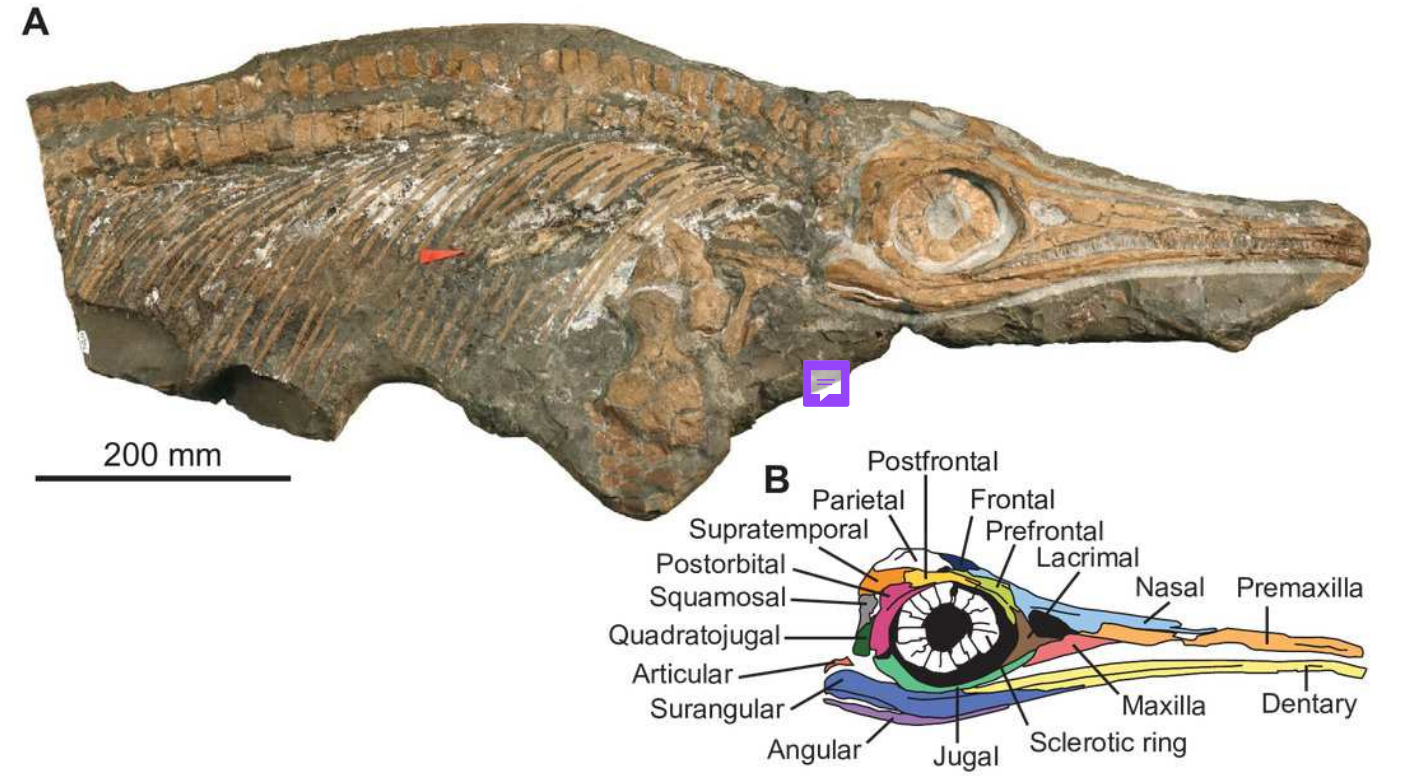


Figure 2

Photographs and interpretation of specimen MNHNL TV211

A, overview of the specimen. B, anatomical interpretation of the right lateral portion of the skull. C, zoom on the fossilised gut content, showing a vampyromorph gladius.


A
200 mm
B
Postfrontal
Parietal
Frontal
Supratemporal
Prefrontal
Lacrimal
Postorbital
Nasal
Premaxilla
Squamosal
Quadratojugal
Articular
Surangular
Maxilla
Dentary
Angular
Jugal
Sclerotic ring


C
50 mm

Figure 3

Comparison of functional traits of the vampyromorphan predators from the Bascharage Laggerstätte

See Table 1 and supplementary information 1 for details.