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Simoniteuthis, a new vampyromorph coleoid with prey in its arms from the Early Jurassic of Luxembourg

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Abstract

The evolutionary history of the cephalopod order Vampyromorpha with its only recent representative, *Vampyroteuthis infernalis*, the deep-sea vampire squid, is still obscure and a new specimen from the Early Jurassic of Luxembourg, provides new information on the vampyromorph morphology at this period. The new taxon *Simoniteuthis michaelyi*. gen. n. sp., which is based on a nearly complete gladius with associated head–arm complex, is morphologically intermediate between the families Loligosepiidae and Geopeltidae. Interestingly, the arm crown displays only four arm pairs, although an arm configuration consisting of five arm pairs should be expected in vampyromorph stem lineage representatives. This observation encouraged us to critically review the presumed homology of the filaments of *Vampyroteuthis* and the lost arm pair in cirrate and incirrate octopods. Moreover, two bony fishes in the mouth region implicated that *Simoniteuthis michaelyi* n. gen. n. sp. preyed upon them in hostile water depths, a taphonomic phenomenon called distraction sinking. By contrast to modern *Vampyroteuthis infernalis*, *Simoniteuthis michaelyi* n. gen. n. sp. roamed and hunted in shallower waters as typical for Mesozoic stem lineage vampyromorphs. According to the current fossil record, a vertical migration into deeper waters (probably associated with a shift in feeding behaviour) occurred at least since the Oligocene.

Keywords Octobrachia, Vampyromorpha, *Leptolepis*, Toarcian, Bascharage, Evolution, Predation

Introduction

Because of its mosaic of characters of both Octobrachia and Decabrachia, the iconic deep-sea cephalopod *Vampyroteuthis infernalis* is commonly seen as a relic species. A fully developed gladius or a rudimental fifth arm pair initially misled many researchers to place *Vampyroteuthis* within the Decabrachia (thus the common name "vampire squid"). Meanwhile, its position

within the Octobrachia has been asserted by the help of twenty-first century molecular techniques (e.g., Lindgren et al., 2022; López-Córdova et al., 2022; Strugnell et al., 2017; Tanner et al., 2017; Uribe & Zardoya, 2017). Thanks to the efforts of Bandel and Leich (1986) and Engeser (1988), it became also clear that *Vampyroteuthis* is a survivor of a lineage that was particularly successful during the Jurassic (see Fuchs, 2020 and literature therein). The vampyromorph suborder Loligosepiina (Sinemurian—Aptian) unifies forms with a gladius morphology very similar to modern *Vampyroteuthis.* Thirteen to fourteen loligosepiid genera are therefore considered as extinct members of the order Vampyromorpha (Fuchs, 2020). Oligocene *Necroteuthis hungarica* is so far the only fossil representative of the suborder Vampyromorphina (Košťák et al., 2021). While the evolutionary transformations from Jurassic stem octopods to Cretaceous crown

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octopods are comparatively well known (Fuchs et al., 2019), the pathways of the vampyromorph lineage is still obscure.

The "Schistes Carton" is a renowned Konservat-Lagerstaette exposed in Luxembourg that yielded typical lower Jurassic vampyromorphs (Fuchs & Weis, 2008; Weis et al. submitted). A digging campaign recently revealed a vampyromorph specimen with to-date unknown gladius characteristics and, to our surprise, the remains of two bony fish in its arm crown. It is accordingly the goal of the present contribution to describe and introduce the new vampyromorph *Simoniteuthis michaelyi* n. gen. n. sp., to reconstruct the death scenario of this rare taphocoenosis, and to discuss relevant paleobiological implications.

Geological setting

The vampyromorph described in the present paper was found in bituminous black shales in Bascharage, southeast Luxembourg, dated to the Early Toarcian and considered as a lithostratigraphic equivalent of the famous Posidonia Shale of southwest Germany. The fossil richness of these deposits in the Luxembourg area has been known for a long time (e.g., Woodward, 1938; Godefroit 1994; Henrotay et al., 1998; Delsate, 1999). Deposition of the black shales took place in a relatively shallow part of the northwestern peri-Tethys area close to the southeastern shores of the emerged landmass of London-Brabant (Röhl et al., 2001). The evidence at hand, i.e. the fine lamination lacking any trace of bioturbation, the absence of benthic faunal elements, the high content in organic carbon, and the preservation of articulated skeletons and soft tissue, suggests that deposition of the black shale succession in Bascharage took place under quiet conditions with an oxygen-depleted sea floor.

So far, stratigraphic correlation of the Toarcian bituminous black shale succession in Luxembourg with other European equivalents has been hampered by a poor sampling precision and a lack of continuous sections (Cooper & Maxwell, 2022). During a scientific excavation by the National Museum of Natural History in May 2022, however, the lower part of the bituminous shale succession was exposed and systematically studied. For the first time, it was possible to collect a continuous record of litho-, bio- and chemostratigraphic evidence, allowing for a precise assessment of the stratigraphy of these highly fossiliferous strata. Pending publication of the results, the evidence at hand allows to provide a precise age for the bed that yielded the vampyromorph described herein.

Material and methods

The remains of the new vampyromorph are preserved in a concretion as slab and counter-slab. The concretion was found in situ during paleontological excavations in the Edward Steichen Industrial Zone, northeast of the town of Bascharage (Fig. 1). It is part of a near-continuous layer of hard, finely laminated, micritic carbonate nodules, which are up to 10 cm in thickness. The nodules are rich in terrestrial insect remains (Szwedo et al. 2017 *cum lit.*), bony fish (*Leptolepis* and Pachycormidae indet.) and shells of presumed planktic gastropods (*Coelodiscus*; Teichert & Nützel, 2015). Coleoid cephalopods are rare in this bed, with the exception of *Chondroteuthis wunnenbergi* Bode, 1933 (Fuchs, 2006: pl. 10, fig. C) and the vampyromorph described in the present paper. The coleoid cephalopod is preserved with parts of the soft tissues and the fossilized ink. Teleost fish remains are preserved in the head–arm complex and are identified as *Leptolepis* sp. indet., a widely distributed genus in the Luxembourg Toarcian (Delsate, 1999).

The concretion level is dated from the Serpentinum Chronozone, Exaratum Subchronozone (Page, 2003) by the accompanying ammonite fauna consisting of *Lobolytoceras* cf. *ceratophagum*, *Hildaites murleyi* and *Cleviceras exaratum* (Thuy & Weis, unpublished data).

The unusual gladius morphology, which intuitively appeared to be intermediate between loligosepiid and geopeltid vampyromorphs, encouraged us to perform a cluster analysis that should localize the most similar gladius outlines. The analysis includes gladius outlines of 11 taxa (10 Jurassic; 1 Recent) and 10 characters containing gladius length/width proportions. The hierarchical cluster analysis was performed with Mesquite 3.80. The clustering method used distances from Character Matrix; Uncorrected Distance; Single Linkage criterion; max. number of equally good trees: 100.

Structural morphologies are not considered and a phylogenetic analysis was omitted. Morphology, systematics, measurements, categories, and terminologies follow Fuchs (2020).

Abbreviations

MNHNL: Musée national d'histoire naturelle, Luxembourg

Systematic palaeontology

Class Coleoidea Bather, 1888
Subclass Octobrachia Haeckel, 1866
Order Vampyromorpha Robson, 1929
Suborder Loligosepiina Jeletzky, 1965
Family undetermined (?Loligosepiidae Regteren Altena, 1949 Or Geopeltidae Regteren Altena, 1949)

Remarks: The main difference between the Loligosepiidae and the Geopeltidae concerns the length of the hyperbolar zone, which is shorter in Geopeltidae than in Loligosepiidae. An additional character that delimits these two closely related families represents the shape of the hyperbolar zone (V-shaped in Loligosepiidae and arcuated in Geopeltidae).
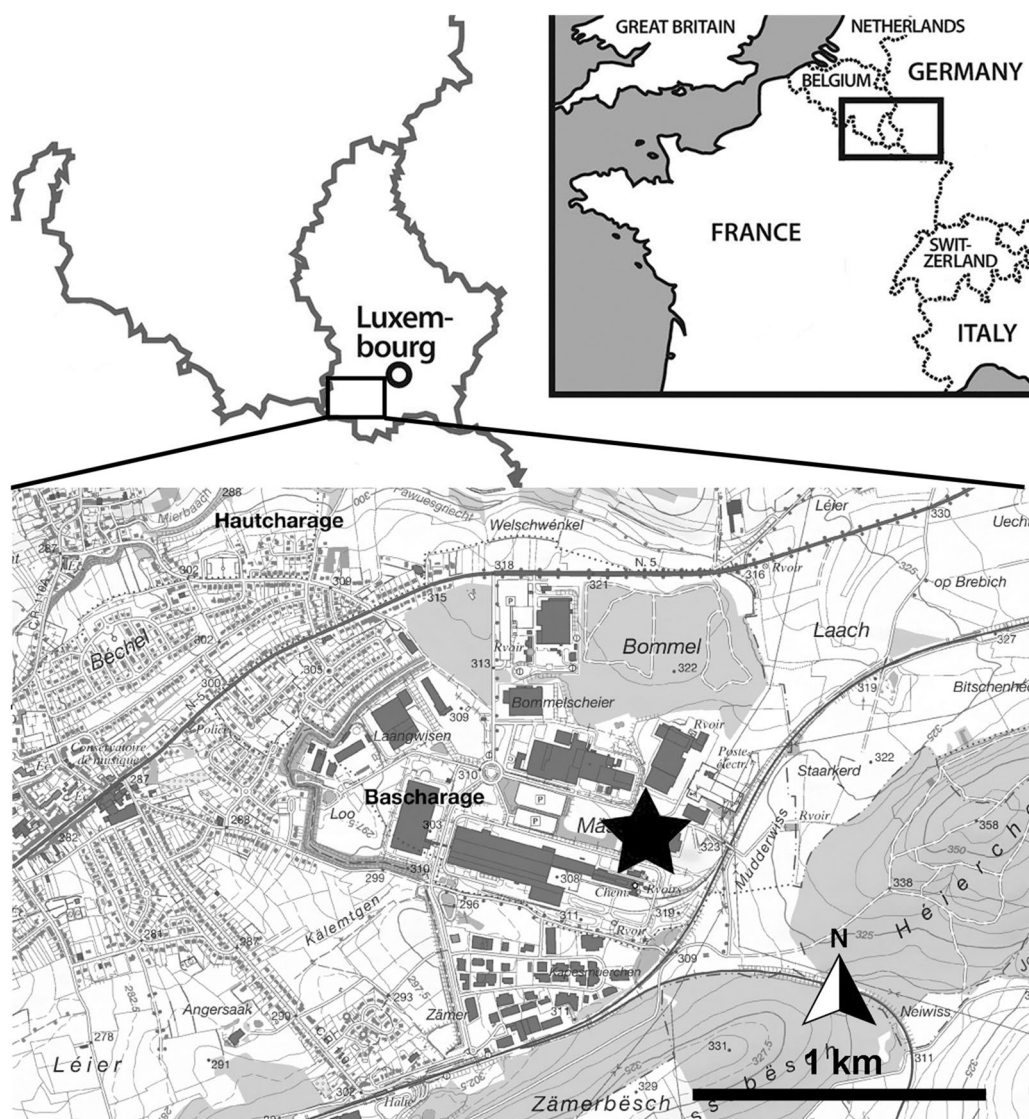
Fig. 1 Detailed map of the Edward Steichen Industrial Zone, northeast of the town of Bascharage in southwest Luxembourg. The area marked by a black asterisk corresponds to the place of finding (© Carte topographique: Adm. Du Cadastre et de la Topographie, Luxembourg)

Genus Simoniteuthis n. gen.

Type species: *Simoniteuthis michaelyi* n. sp.

Other species: Only the type species.

Occurrence: Known only from the type locality.

Derivation of name: Dedicated to Jo Simon, scientific volunteer collaborator of the National Museum of Natural History Luxembourg, who skilfully and patiently cleaned the fossil in the nodule and unveiled the soft part preservation.

Diagnosis: Medium-sized loligosepiids, gladius moderately wide (gladius width$_{max}$-to-gladius length 0.30–0.40); median field very slender to slender (median field width$_{hypz}$-to-hyperbolar zone length 0.15–0.25; = opening angle 9–14°), laterally reinforced, anterior median field margin convex; hyperbolar zone very long (hyperbolar zone length-to-median field length 0.80–0.89), deeply V-shaped incised; anterior limit of lateral field thus distinctly projected, spine-like pointed, lateral fields moderately wide (lateral field width$_{max}$-to-median field width$_{max}$ 1.85–1.95).

Simoniteuthis michaelyi n. sp.

Figures 2–3

Holotype: MNHNL TI024, consisting of slab and counter-slab.

Type locality: Bascharage, Industrial Zone Edward Steichen (Fig. 1; formerly "Bommelscheier") (Henrotay et al., 1998; Szwedo et al., 2017).

Type horizon: Near-continuous level of bituminous finely laminated carbonate nodules rich in insect and teleost remains, approximately 90 cm above the base of the bituminous black shale succession; Lower Toarcian, Serpentinum Chronozone, Exaratum Subchronozone.

Derivation of name: Dedicated to Patrick Michaely, Director of the Natural History Museum Luxembourg with a passion for palaeotological research.

Description: The holotype exhibits structures of the gladius as well as the head–arm complex. The latter is only visible on the slab (Figs. 2A–D, 2G, 3A, B);

the counter-slab is unfortunately missing the head–arm complex (Figs. 2E, F, 3D, E). The head–arm complex of the slab is represented by proximal and middle parts of the arms, eyeballs, and the above-mentioned bony fish (Fig. 2C, D). UV-light reveals scarce remains of the arm musculature (Fig. 2D). The arm tips are obviously not conserved in the concretion. One can count eight arms; evidence of a rudimentary (filamentous) fifth arm pair does not exist. Further details such as suckers or arm length are not determinable. The two fishes are situated between two greyish eyeballs and obviously take the former position of the buccal mass.

Leaked ink unfortunately hampers the reconstruction of the gladius. The preserved length of the gladius
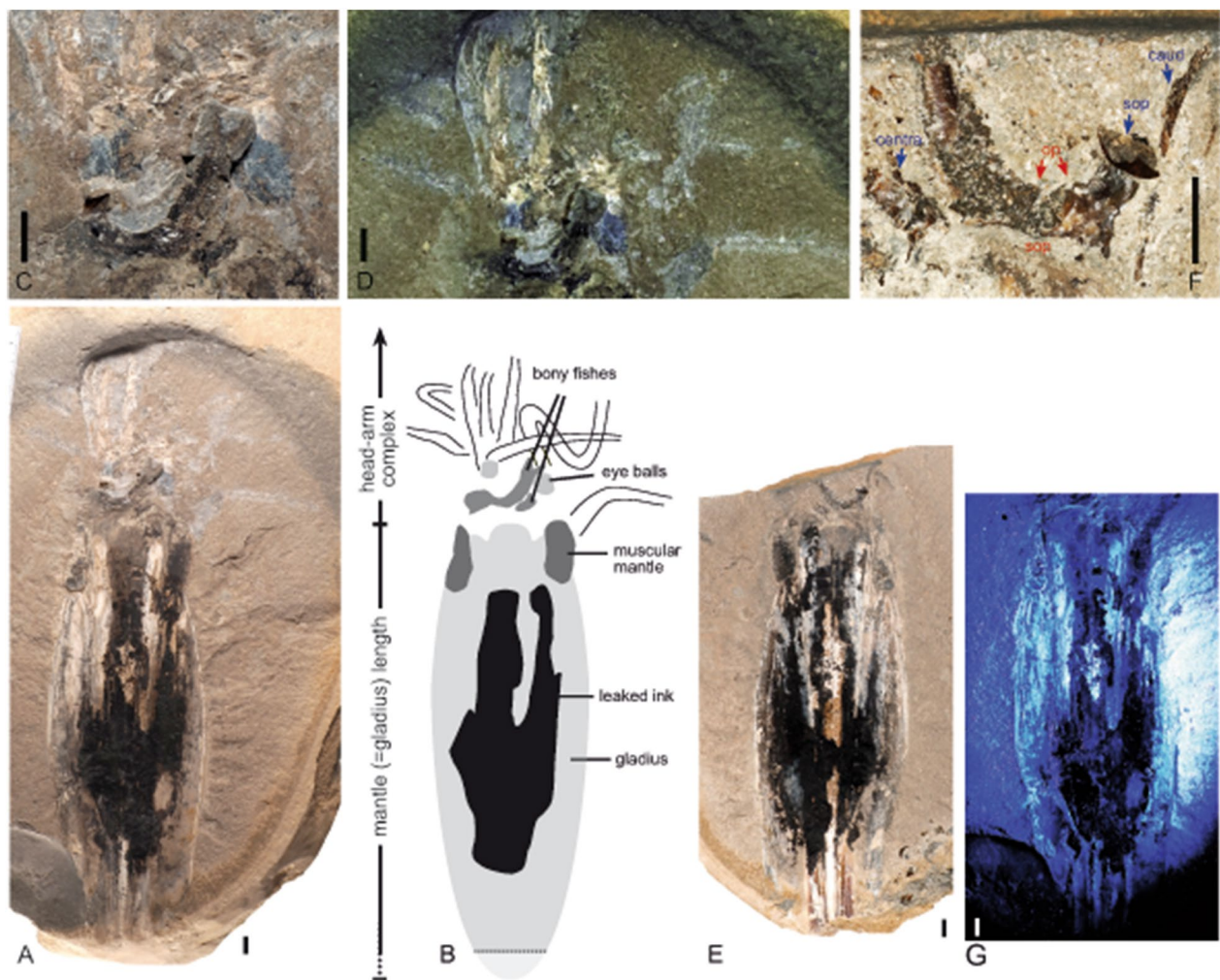

Fig. 2 *Simoniteuthis michaelyi* n. gen. n. sp., holotype (MNHNL Tl024), Lower Toarcian, *Serpentinum* Chronozone, *Exaratum* Subchronozone, Bascharage. **A–D** slab; **E–G** counter-slab. **A** overview; **B** camera lucida drawing of **A**; **C** close-up of the head–arm complex; **D** same under UV-light showing the weakly illuminating arm musculature; **E** overview; **F** close-up of the preyed fishes, red colour Specimen 1 (op = opercle; sop = subopercle), blue colour Specimen 2 (caud = caudal fin; sop = subopercle; centra = central vertebra); **G** same under UV-light. Scale bars = 10 mm
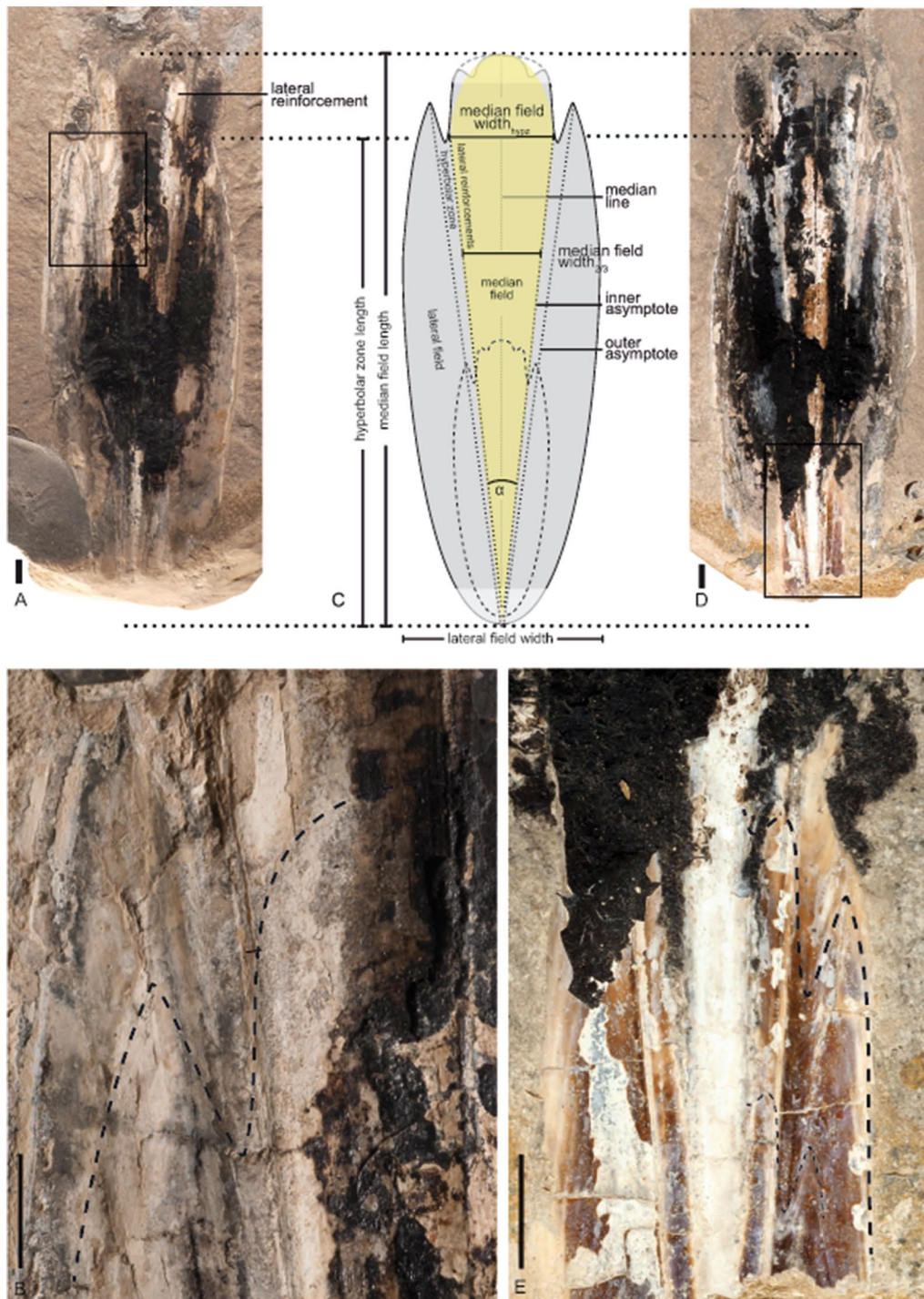
Fig. 3 Gladius morphology of *Simoniteuthis michaelyi* n. gen. n. sp., holotype (MNHNL TI024), Lower Toarcian, *Serpentinum* Chronozone, *Exaratum* Subchronozone, Bascharage. **A** overview of the slab; **B** close-up of the anterior hyperbolar zone showing the course of growth increments; **C** schematic morphology and measurements; **D** overview of the counter-slab; **E** close-up of the posterior gladius showing the course of growth increments. Scale bars = 10 mm

measures 23 cm (Fig. 3A–E). Only 1–2 cm of the conus part is missing as can be assessed by well-developed diverging inner asymptotes. The maximum width of the lateral fields reaches 8.2 cm suggesting a moderately wide gladius (gladius width$_{max}$-to-gladius length = 0.33). Taking into account a certain degree of dorsoventral compaction the overall width was slightly less. Apart from this issue, parts of the lateral field are poorly visible. In particular, their anterior extensions are hidden behind mantle musculature and thus complicate interpretations. Outer asymptotes (opening angle c.15°) as well as growth increments suggest that the transition from the parabolar lateral field to the hyperbolar zone is sharp (pointed) and distinctly projected. The hyperbolar zone is accordingly V-shaped and deeply incised. The hyperbolar zone takes 21 cm of the total median field length (ratio of the hyperbolar zone length to total gladius length = 0.86), which is categorized as very long. Where the hyperbolar zone joins the median field, the latter is 4.3 cm wide. This is simultaneously the widest part of the median field; anteriorly, its width is decreasing. The ratio median field width at anterior end of the hyperbolar zone to hyperbolar zone length of 0.21 suggests a slender to very slender opening angle of the median field of 11–12°. The lateral margins of the median field (adjacent to the hyperbolar zones) are plate-like reinforced. Anteriorly, these diverging reinforcements reach a maximum width of 0.9 cm and are slightly shorter than the anterior gladius margin. The shape of the latter, particularly the transition from lateral reinforcements to central median field is problematic due to the lack of informative growth increments (Fig. 3C). Anteriorly, the lateral reinforcements appear parabolar (?and projected; Fig. 3A–C) suggesting a second zone of hyperbolar growth lines intercalated between the parabolar reinforcements and parabolar central median field. Such a "secondary hyperbolar zone" is very unusual and a series of anteriorly parabolar structures imprinted in the leaked ink (?remains of growth structures) alternatively imply an evenly convex anterior gladius margin (Fig. 3B). The median field bears a median line, but is insufficiently preserved for a detailed description. A median keel is certainly absent.

Comparisons: The cluster analysis (Fig. 4A) of the gladius outline exposes *Vampyrofugiens atramentum* Rowe et al., 2023 from the Callovian of La Voulte-sur-Rhône to be most similar to *Simoniteuthis michaelyi* n. gen. n. sp. However, the gladius of this deep-sea vampyromorph is based solely on a tomographic outline reconstruction and thus still poorly understood.

Besides, the gladius shape of *Simoniteuthis michaelyi* n. gen. n. sp. is most similar to contemporary geopeltid (*Geopeltis simplex, Parabelopeltis flexuosa*) and loligosepiid vampyromorphs (*Loligosepia aalensis,*

Jeletzkyteuthis coriaceus). The distinctly forward-projected lateral fields combined with the deeply incised V-shaped hyperbolar zones are typical for loligosepiids, although the relative length of the hyperbolar zones is slightly shorter in *Simoniteuthis michaelyi* n. gen. n. sp. than in loligosepiids. In geopeltids, the hyperbolar zone is shorter than in *Simoniteuthis michaelyi* n. gen. n. sp. and evenly arcuated (rather than sharply recurved).

The plate-like lateral reinforcements as described for *Simoniteuthis michaelyi* n. gen. n. sp. are unusual for loligosepiids, but known from *Geopeltis simplex, Leptotheuthis gigas* and *Paraplesioteuthis sagittata* (Fig. 4B). The latter is a contemporary taxon and belongs to the prototeuthid clade owing to the absence of a hyperbolar zone. Tithonian *Leptotheuthis gigas* differs from *Simoniteuthis michaelyi* n. gen. n. sp. through a wider median field and a constriction of the lateral fields in the posterior third of the gladius.

Discussion
Systematic implications
The overall gladius morphology unambiguously places *Simoniteuthis michaelyi* n. gen. n. sp. in the Loligosepiina (Sinemurian-Aptian), the extinct suborder of the recent order Vampyromorpha (Fuchs, 2020). Gladius proportions include typical characters of the families Loligosepiidae Regteren Altena, 1949 and Geopeltidae Regteren Altena, 1949 (Fig. 4A). In addition, the gladius of *Simoniteuthis michaelyi* n. gen. n. sp. exhibits structural similarities characteristic of both families (Fig. 4B). The V-shaped hyperbolar zone is loligosepiid-like whereas the plate-like lateral reinforcement is typical for *Geopeltis simplex*. Because of this morphologic heterogeneity we refrain here from providing a definite classification on the family level. The deeply incised hyperbolar zone is unique and makes the erection of a new genus and species necessary.

Implications on the vampyromorph arm crown
It is widely accepted that five arm pairs is a plesiomorphic feature within the Coleoidea (e.g., Klug et al., 2019). *Simoniteuthis michaelyi* n. gen. n. sp. exhibits four arm pairs; evidence of a fifth arm pair is missing. This observation is important, because the origin and evolution of the unusual filaments of the extant deep-water cephalopod *Vampyroteuthis infernalis* is still puzzling (Figs. 4B, 5). *Vampyroteuthis* uses this fifth arm pair to collect floating detritus ("marine snow") and small planktic organisms (Hoving and Robinson 2012; Golikov et al., 2019). It has been suggested that this pair of retractile filaments is homologous to the second dorsolateral arm pair of decabrachian coleoids, which is lost in non-vampyromorph octobrachians (e.g., Boletzky, 1999; Pickford, 1940; Vecchione et al., 1999; Young & Vecchione, 1999; Young, 2019).
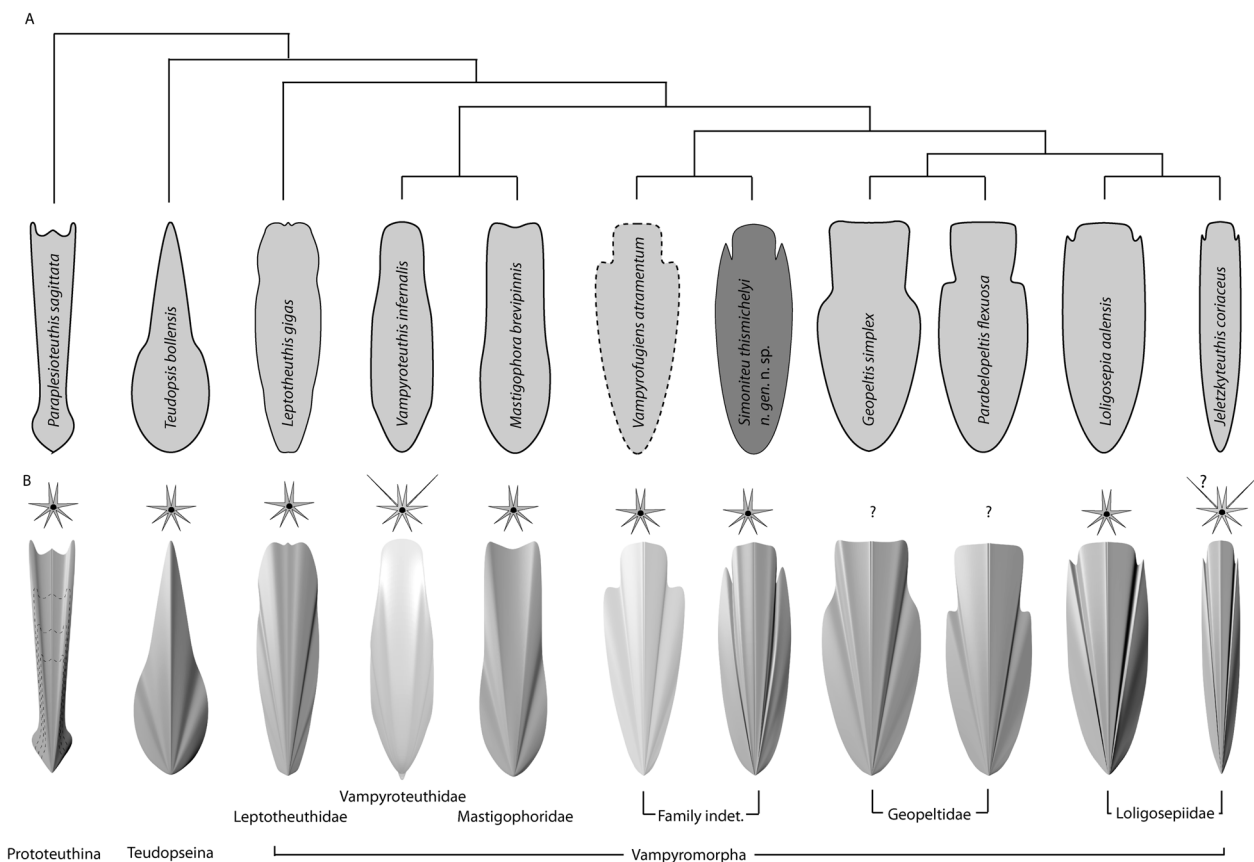
Fig. 4 Comparative gladius morphology of selected octobrachiate coleoids. **A** Topology of the cluster analysis based on gladius outlines; **B** 3-reconstructions of the same gladiuses systematically sorted (after Fuchs, 2020). Where known arm configurations are indicated. Note the gladius outline of *Vampyrofugies* (based on Rowe et al., 2023) is approximated

With few exceptions (see below), Mesozoic gladius-bearing octobrachians have commonly been demonstrated to lack such filamentous appendages (e.g., Donovan & Fuchs, 2016). While this view is unproblematic in the stem lineage of the Octopoda (cirrate and incirrate octopuses), it contains question marks in the lineage leading to *Vampyroteuthis* (Fig. 5). If the paired filaments of *Vampyroteuthis* are indeed rudiments of a fifth arm pair, the initial transformation step from a fully developed dorsolateral arm pair to retractile filaments should have begun before the divergence of the "pseudo-octobrachiate" Vampyromorpha and the Octopoda. In this context, it is important to note that a multiple independent reduction of the dorsolateral arm pair (one on the vampyromorph and one on the octopod clade) is considered as unlikely. The suborder Prototeuthina (e.g., *Plesioteuthis*, *Senefelderiteuthis*, *Dorateuthis*), variously regarded as stem octobrachians (Fuchs, 2020), stem vampyromorphs (Kruta et al., 2016), or even stem octopods (Sutton et al., 2015), provide evidence solely for arm configurations without a fifth arm pair (Fig. 5).

Anyway, taxa belonging to the vampyromorph clade (e.g., Engeser, 1988; Fuchs, 2020; Haas, 2002) should definitely display an arm crown consisting of either ten well-developed arms or eight arms plus a rudimental pair (Fig. 5). However, palaeontological information for such an arm crown configuration is weak. Out of 13 genera assigned to the Vampyromorpha, nine genera with fossilized arm crowns are known (*Vampyronassa, Vampyrofugiens, Proteroctopus, Gramadella, Loligosepia, Jeletzkyteuthis, Mastigophora, Doryanthes, Leptotheuthis*). Recently, tomographic observations on exceptionally well-preserved three-dimensional vampyromorphs (*Proteroctopus, Vampyronassa, Vampyrofugiens*) from the famous La Voulte-sur-Rhône Lagerstätte in France by Kruta et al. (2016) and Rowe et al., (2022, 2023) confirmed the absence of a fifth arm pair.

So far, vague hints of filamentous appendages have been reported only from two specimens. Vecchione et al. (1999) assumed filament-like structures in a single specimen of *Mastigophora brevipinnis*
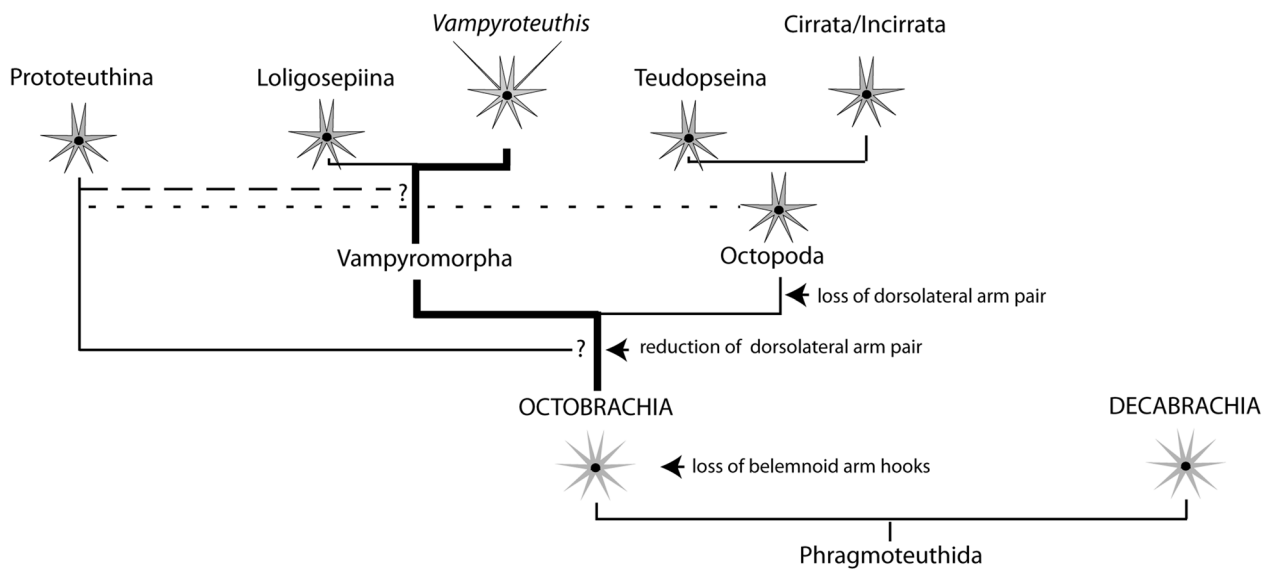
Fig. 5 General phylogenetic tree of the Neocoleoidea (proostracum-bearing coleoids) indicating arm crown modifications within the Octobrachia. If the filamentous arm pair of Recent *Vampyroteuthis* is a homologue of the lost arm pair of the Octopoda, the vampyromorph stem lineage (thicker) should theoretically exhibit evidence of a rudimental dorsolateral (5th) arm pair

(Mastigophoridae: Loligosepiina) from the Callovian of Christian Malford (UK). Coeval *Mastigophora brevipinnis* from the La Voulte Lagerstätte, however, show no evidence for such filaments (Fuchs, 2014). Klug et al. (2021) tentatively interpreted "two worm-like structures" associated with a specimen of *Jeletzkyteuthis coriaceus* from the Toarcian Posidonia Shale as the filamentous arm pair of a vampyromorph.

This brief review about the ancient number of vampyromorph arms shows that—despite an extraordinary fossilization potential of arm musculature—palaeontologists are currently unable to date and reconstruct the reduction of the fifth arm pair within the Vampyromorpha.

Taphonomic implications

The taphonomic situation of bony fish remains in the mouth region of a coleoid cephalopod can be explained either by chance or predation. The fish fossils consist of (a) remains of a juvenile leptolepid, with the head destroyed proximally to the operculum; (b) eight vertebral centra, half a caudal fin, and an operculum of an adult leptolepid (D. Delsate, personal communication). We strongly assume that the presence of these two fish specimens is due to predation, because it is very unlikely that two different specimens of *Leptolepis* would have been buried accidentally amidst the arm crown, both bent in the same way. Moreover, small teleost fish such as *Leptolepis* are well documented as prey of coleoid cephalopods during the Early Toarcian (Jenny et al., 2019).

Mapes et al., (2019: 148) described a taphonomic phenomenon called "distraction sinking". This is a death scenario, ".... in which copulation or a fight for survival or mating partners may have distracted the ammonoids, so that they sank into the poorly oxygenated waters near the bottom and became asphyxiated." In our case, we postulate that the individual of *Simoniteuthis michaelyi* n. gen. n. sp. was distracted by hunting small fish and did not realize that it entered hostile water depths. This is apparently a common venture, because Klug et al. (2021) found evidence for a similar cause of death. In this case, two aligned octobrachian vampyromorphs, a larger individual of *Jeletzkyteuthis coriaceus* with a smaller individual of *Parabelopeltis flexuosa* in its arm crown, accordingly sank and died while fighting (see also Mironenko et al., 2021).

Implications on in situ predator prey interactions

The role of coleoids as marine predators is unquestioned and the position of two specimens of *Leptolepis* in the former buccal mass region strongly suggests that the *Simoniteuthis michaelyi* n. gen. n. sp. specimen holds its prey in its mouth. Although discoveries were sporadically published, conclusions on predator prey interactions were based on indirect evidence such as stomach contents, coprolites, or other trace fossils such as bore holes (e.g., Fuchs & Larson, 2011; Klompmaker et al., 2014; Quenstedt, 1858; Schweigert, 2018). Direct records based on in situ associations of both predators and prey are obviously rare (e.g., Fuchs & Larson, 2011; Přikryl et al., 2012; Wilby et al., 2004). Since 2019, however, such hunting associations got into a

particular focus of cephalopod paleobiology. Jenny et al. (2019) documented belemnoid coleoids from the Holzmaden shales that likewise caught *Leptolepis*. Hoffmann et al. (2020) reported on a plesioteuthid octobrachian that was probably attacked by a pterosaur in the Tithonian Solnhofen lagoon. Klug et al. (2021) found a very rare hunting behaviour. In this case, *Jeletzkyteuthis* preyed upon *Parabelopeltis*, both of which close relatives of *Simoniteuthis michaelyi* n. gen. n. sp. (see above). Weis et al. (submitted) portray further predator prey interactions involving pachycormid fish and octobrachian coleoids from the Lower Jurassic of Luxembourg.

Implications on the vampyromorph life habitat and feeding behaviour

Vampyroteuthis infernalis is well known to be a widely distributed deep-sea dweller particularly feeding on organic matter (Golikov et al., 2019). Although there is fossil evidence of Jurassic vampyromorphs inhabiting deeper waters, at least their earliest representatives more likely roamed and hunted in shallower waters (see below). *Simoniteuthis michaelyi* n. gen. n. sp. here confirms that Early Jurassic precursors of the Vampyromorpha were either limited to or had a range including continental shelves. It is still unclear whether some vampyromorphs from the Callovian La Voulte deep-sea Lagerstätte lived pelagic, mesopelagic, or even bathypelagic (Charbonnier et al., 2007; Fischer, 2003; Rowe et al., 2022). However, the migration of vampyromorphs into deeper waters occurred at least since the Oligocene as the palaeoenvironment of *Necroteuthis hungarica* suggests (Košťák et al., 2021). The shift from a carnivorous to a more detritivorous feeding behaviour probably went along with the invasion of the aphotic zone.

Author contributions
DF described, compared, and discussed morphologic-systematic aspects. RW and BT introduced the geological setting and formulated the taphonomic implications.

Availability of data and materials
The material described and illustrated here comes from the following public collection: paleontological collection of the Musée national d'histoire naturelle de Luxembourg (MNHNL). No supplementary material is available.

Declarations

Competing interests
We declare no competing interests involved in this study.

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