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Alison Rowe, Isabelle Kruta, Loïc Villier, Isabelle Rouget. A new vampyromorph species from the Middle Jurassic La Voulte-sur-Rhône Lagerstätte. *Papers in Palaeontology*, 2023, pp.e1511. 10.1002/spp2.1511 . hal-04147373

HAL Id: hal-04147373

<https://hal.science/hal-04147373v1>

Submitted on 22 Feb 2024

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A new vampyromorph species from the Middle Jurassic La Voulte-sur-Rhône Lagerstätte

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Typescript received 1 December 2022; accepted in revised form 17 April 2023

Abstract: Eight coleoid genera have so far been described from the Callovian-aged La Voulte-sur-Rhône Lagerstätte (c. 165 Ma; Ardèche, France), a locality noted for its unique three-dimensional preservation of soft tissues. Here, we used high resolution x-ray-based imaging methods, in conjunction with reflectance transformation imaging, to study the soft tissues of a previously undescribed coleoid from the La Voulte-sur-Rhône locality. This analysis identified both an ink sac and internal light organs, a combination of defence mechanisms present in the Recent, although not previously described from the coleoid fossil record, as well as the presence of Octobranchia-type arm musculature and *Vampyroteuthis*-like sucker attachments. The morphology of

the gladius could not be attributed to any known coleoids and therefore justified the assignment of this single specimen to a new taxon: *Vampyrofugiens atramentum*. The addition of this new vampyromorph species not only increases the coleoid diversity known from the site, but also broadens the morphological variation observed in the co-occurring coleoid taxa. These findings suggest that there was a high diversity of cephalopods occupying differentiated communities during the Middle Jurassic.

Key words: soft-tissue preservation, Vampyromorpha, synchrotron microtomography, reflectance transformation imaging, coleoid, La Voulte-sur-Rhône Lagerstätte.

JURASSIC coleoid diversity is mostly recorded from the Lower Jurassic Lagerstätten such as the Posidonia Shales (Lower Toarcian, Holzmaden) as well as the Upper Jurassic (Kimmeridgian–Tithonian) lithographic limestones of Nusplingen, and Solnhofen (southern Germany) (Klug *et al.* 2005, 2015, 2021; Fuchs 2007; Fuchs *et al.* 2007, 2010, 2013). The Middle Jurassic coleoid record (e.g. Christian Malford, UK (Wilby *et al.* 2004; Fuchs 2014) and La Voulte-sur-Rhône, France) (Fischer 2003) is less well known. More than one-third of the genera of non-belemnoid coleoids (Fuchs 2020) known from the Middle Jurassic are represented at La Voulte-sur-Rhône, making this an important site for understanding coleoid evolutionary history. Cephalopods constitute c. 11% of the diversity from the locality, with eight currently described coleoid genera (Fischer & Riou 2002; Fischer 2003; Charbonnier 2009; Fuchs 2014). Other groups include arthropods (Charbonnier 2009; Audo *et al.* 2014, 2019; Jauvion *et al.* 2016, 2017; Vannier *et al.* 2016), which comprise the majority (c. 50%) of the taxa, as well as echinoderms (Charbonnier *et al.* 2007; Charbonnier 2009; Villier *et al.* 2009), annelids, bivalves, brachiopods and a few vertebrate taxa (Crocodylia, Sarcopterygii and Actinopterygii) (Charbonnier 2009; Charbonnier *et al.* 2014).

Attempts to reconstruct the palaeoenvironment and ecology of the site have proven challenging. This is due both to its complex submarine topography, a result of the Callovian reactivation of a number of Hercynian faults (Charbonnier 2009; Charbonnier *et al.* 2014), and to the seemingly contradictory habitats of the faunal assemblage (Charbonnier *et al.* 2007, 2014; Charbonnier 2009; Vannier *et al.* 2016; Audo *et al.* 2019). Although based on a synthesis of the geology and fossil fauna of La Voulte-sur-Rhône, the fossil-bearing locality has been interpreted to represent a somewhat deep (200+ m) offshore environment (bathyal zone) around the slope–basin transition (Charbonnier 2009; Charbonnier *et al.* 2014).

The increased use of powerful imaging techniques over the last decade has enabled the reappraisal of many fossil specimens, including coleoids from La Voulte-sur-Rhône (Kruta *et al.* 2016; Rowe *et al.* 2022). The three-dimensional (3D) preservation seen in these coleoids is particularly well suited to x-ray-based approaches, which provide unparalleled opportunities for the observation of internal and external morphology (Jauvion *et al.* 2016, 2020; Kruta *et al.* 2016; Rowe *et al.* 2022). The exceptional preservation is a result of rapid replacement of the soft tissues with authigenic iron-rich minerals (see

Allison 1988, Wilby *et al.* 1996, Clements *et al.* 2017 and Jauvion 2020 for a description of the mineral replacement phases producing this level of preservation). Results from these studies have contributed to the discovery of previously unknown anatomical characters and also to palaeoecological and palaeoenvironmental interpretations of La Voulte-sur-Rhône.

Indeed, recent tomographic analysis of an arthropod specimen (Thylacocephalan, *Dollocaris*) (Vannier *et al.* 2016) contradicts the deep-water environment hypothesis for La Voulte-sur-Rhône. Analysis of its eyes and stomach contents indicates that *Dollocaris* was a visual ambush predator, which suggests that its palaeoenvironment was illuminated. Additionally, work on the vampyromorph coleoid *Vampyronassa rhodanica* (Rowe *et al.* 2022) from the locality has identified previously unknown morphologies in Jurassic taxa, which are indicative of a pelagic and predatory mode of life. This is in contrast to the deep-sea lifestyle of the extant coleoid *Vampyroteuthis infernalis*, which is positioned as its only extant relative.

Here, we describe a previously unpublished vampyromorph specimen (MNHN.F.A32491) from La Voulte-sur-Rhône, which was preliminarily assigned to *Vampyronassa rhodanica*. We used a variety of imaging techniques that enabled observation of the internal morphology, including many characters belonging to the arm crown. This appraisal demonstrates the benefits of these imaging methods to facilitate a clearer understanding of the morphology and lifestyle behaviours of Jurassic vampyromorph coleoids.

Although there is not, as yet, a definitive understanding of the palaeoecology at La Voulte-sur-Rhône, the increasing amount of gathered data is beginning to suggest that this locality represented a complex Jurassic ecosystem, with a larger coleoid diversity than previously understood.

MATERIAL AND METHOD

The specimen studied here (MNHN.F.A32491) is catalogued in the collections of the Muséum national d'Histoire naturelle (MNHN), Paris, France.

The specimen was imaged using propagation phase contrast synchrotron x-ray microcomputed tomography (PPC-SR- μ CT) at the European Synchrotron Radiation Facility (ESRF, ID 19 beamline, Grenoble, France), at both a 12.64 μ m (entire specimen) and 3.5 μ m (arm crown) voxel size (see Rowe *et al.* 2022 for acquisition methods and <http://paleo.esrf.fr/> for data and metadata). The resulting PPC-SR- μ CT files were manipulated in ImageJ to reduce the size (binning and cropping) before segmentation, which was done using Mimics software

(v.21.0; Materialise NV). Internal and external features for segmentation were identified using the density of the mineralized soft tissues, which appear as contrasting gray-scale in the reconstructed files.

These data were then compared with three segmented and reconstructed *Vampyronassa rhodanica* specimens (MNHN.F.B74247; MNHN.F.B74244; MNHN.F.B74243) described in Rowe *et al.* (2022). The existing tomographic data of *V. rhodanica* enabled a direct comparison of features, specifically characters in the arm crown (arm length, sucker and cirri configuration). Additional comparisons were carried out on previously described fossil specimens (Fuchs 2020), including some from La Voulte-sur-Rhône, as well as extant taxa. Special attention was paid to the ink sac and luminous organs given that these were preserved in MNHN.F.A32491.

The specimen was also photographed using reflectance transformation imaging (RTI) at the MNHN to analyse the external morphology in relief from the matrix (Rouget *et al.* 2022).

Measurements of the specimen were taken following the delineations for Octobranchia shown in Nixon (2011, fig. 3), with the central lateral eye line marking the boundary between anterior and posterior sections. All measurements were composite and followed the natural line of the specimen where possible.

Using the RTI images and measurement parameters from Fuchs (2016, 2020), we attempted to reconstruct the gladius ratios and size for MNHN.F.A32491. A reconstruction of this was used to determine systematic placement (Fuchs 2020). Given that the specimen shows compaction and loss in certain areas, these results should be interpreted with appropriate caution.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; MNHN, Muséum national d'Histoire naturelle, Paris, France; ZMB, Museum für Naturkunde, Berlin, Germany.

SYSTEMATIC PALAEOLOGY

Superorder OCTOBRACHIA Haeckel, 1866
 Order VAMPYROMORPHA Robson, 1929
 Suborder LOLIGOSEPIINA Jeletzky, 1965
 Family GEOPELTIDAE Regteren Altena, 1949
 Genus VAMPYROFUGIENS nov.

LSID. <https://zoobank.org/nomenclaturalacts/FA6A1790-3915-4F77-9452-E3CBDE01F48A>

Type species. *Vampyrofugiens atramentum*.

Derivation of name. The name *Vampyrofugiens* is composed of the original Serbian word *Vampir* and the Latin *fugiens* (fleeing) to reflect the escape behaviours of this new vampyromorph taxon.

Diagnosis. As for type and only species.

Vampyrofugiens atramentum sp. nov.

LSID. <https://zoobank.org/nomenclaturalacts/CF14CBF1-D8BF-4898-972A-A8E4AB71FA06>

Holotype. MNHN.F.A32491.

Derivation of the name. The species name *atramentum* (Latin word for ink) is assigned and reflects the occurrence of an ink sac.

Diagnosis. Mantle bullet-shaped; arm length moderate (arm length : mantle length ratio of 0.6 although the distal tips are not preserved), no elongated arm pair; suckers radially symmetrical, uniserial, sucker rings absent; cirri biserial; head dorsally fused with mantle; ink sac present; luminous organs present internally; fins subterminal.

Type locality. La Voulte-sur-Rhône, France.

Type horizon. Middle Jurassic (Lower Callovian), *gracilis* Biozone.

Description

Body. MNHN.F.A32491 is positioned in dorsal view (Fig. 1A). The body and head region have undergone slight rotation and non-uniform compaction prior to fossilization. The distalmost part of the arms has been lost. The total preserved, measurable length (posterior part of the mantle to the preserved anterior tips of the arms) is c. 81 mm. The head and dorsal mantle are fused although the head is clearly outlined, suggesting that the anterior part of the mantle margin is positioned posterior to the eyes (Fig. 2). The mantle is posteriorly tapered and measures c. 55 mm in length from the central eye to the posteriormost margin. There is no evidence of mantle-locking cartilage. A funnel is visible in the PPC-SR- μ CT slices (Fig. 1D) with the most anterior part terminating slightly posteroventrally to the eyes.

The combination of μ CT and RTI reveals previously unseen internal and external morphological details, as well as showing topographic contouring on parts of the mantle. It is possible that these contours correspond, in part, to sections of the original gladius morphology (Fig. 2).

Fins. The specimen has one pair of posterior fins located in a subterminal position (Figs 1A–C, 3A, B, D, E), the tissue of which is draped across the posteriormost section of the mantle (Figs 1C, 3D). Not all of the tissue is preserved (Fig. 1A). What

remains is narrowest in the posteriormost section and flares slightly anteriorly. The margins appear rounded. Here, we interpret the fins to be paddle-like in shape, similar to those of *Vampyroteuthis infernalis* (Pickford 1949). The internal fin cartilage is well preserved and appears clearly in the PPC-SR- μ CT slices as defined linear structures in a paired lateral position (Fig. 3E).

Head. The head is fused to the mantle and measures c. 22 mm at its widest section. Both eyes are retained. The eyes are sub-spherical, c. 5 mm in diameter, and are located on different planes, which is consistent with the slight rotation of the specimen prior to fossilization. In cross-section, parts of the cephalic cartilage appear to be preserved (Fig. 3F).

Dorsally, a thin elongate structure (<1 mm in diameter) is draped perpendicular to the arm crown, just slightly anterior to the eyes (Figs 1A, 4). It is not continuous across the width of the head and does not appear to be fused with the tissue. Additionally, the internal composition of this element, visible in the PPC-SR- μ CT slices, does not resemble a filamentous retractile appendage, or the internal musculature of the preserved arms. There is no evidence to suggest that this structure is part of the specimen, rather that it is a preserved piece of associated fauna, possibly a section of a brittle star arm (Fig. 4E), given that these are common taxa in the La Voulte-sur-Rhône locality (Charbonnier *et al.* 2014).

Arm crown. Eight arms are present in the arm crown, each with uniserial, radially symmetrical suckers and biserial cirri that are evident from the most proximal sections of the arms to the distal, truncated boundary (Figs 1A, 5). Without the distalmost parts it is not possible to define a precise length for each of the arms or determine with absolute certainty that there is no elongate pair. However, the extent of the preserved arms ranges from c. 24 mm to 29 mm. Although each shows evidence of compaction, they are all similar in dimension, morphology and tapering, which suggests that they all share a comparable length. The diameter of the arms measures c. 5–7 mm towards the base and c. 2–4 mm at the truncated distal section. Neither the PPC-SR- μ CT nor the RTI data show evidence of an elongate pair of filamentous structures, or of hectocotylization. The internal musculature of the arms is clearly visible in the PPC-SR- μ CT slices and has an Octobranchia-like configuration (Fig. 6). The muscle layers in the fossil form replicate the distinct gross musculature regions. An axial nerve chord is encircled by the transverse muscle, which in turn is surrounded by a band of longitudinal muscle. These appear striated in cross-section (Fig. 6A) and on coronal view (Fig. 6B).

Suckers. The uniserial suckers are radially symmetrical and present along the entire length of the arm (Fig. 5B, C). They show only slight variation in diameter (c. 1.2–1.9 mm), with those in the centre of the arm being marginally larger than those at the proximal and distal sections. Approximately 10 suckers are preserved on each arm and are flanked by interspersing cirri (Fig. 5C). Given that the arm tips are missing, it is likely that there were more on the living animal.

Each sucker is connected to the arm with a *Vampyroteuthis*-like attachment (Figs 7A–D, 8B–C). These attachments extend

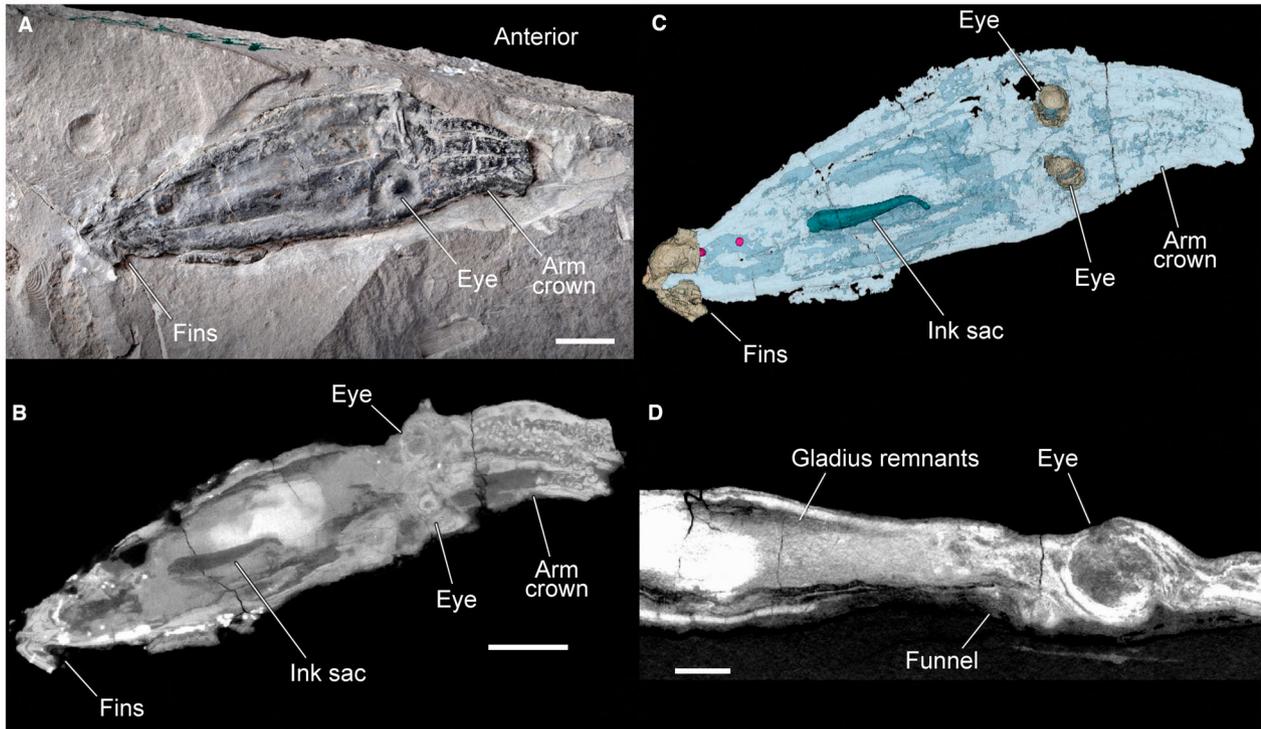


FIG. 1. Photograph, 3D rendering, and PPC-SR- μ CT slices (binned dataset, voxel size: 25.28 μ m) of the undescribed specimen (MNHN.F.A32491) acquired at the ESRF (Grenoble, France). A, photograph (P. Loubry, CR2P) of the specimen showing the 3D preservation of the mineralized soft tissue. B, composite of PPC-SR- μ CT slices showing the greyscale contrast used to segment the specimen. C, 3D rendering showing the location of the fins (beige), ink sac (teal) and internal luminous organs (pink). D, longitudinal slice showing the location of the funnel, and an area interpreted to be remnants of the gladius in longitudinal view. Rendered in Mimics software (v.21.0). Scale bars represent: 10 mm (A–B); 2 mm (D).

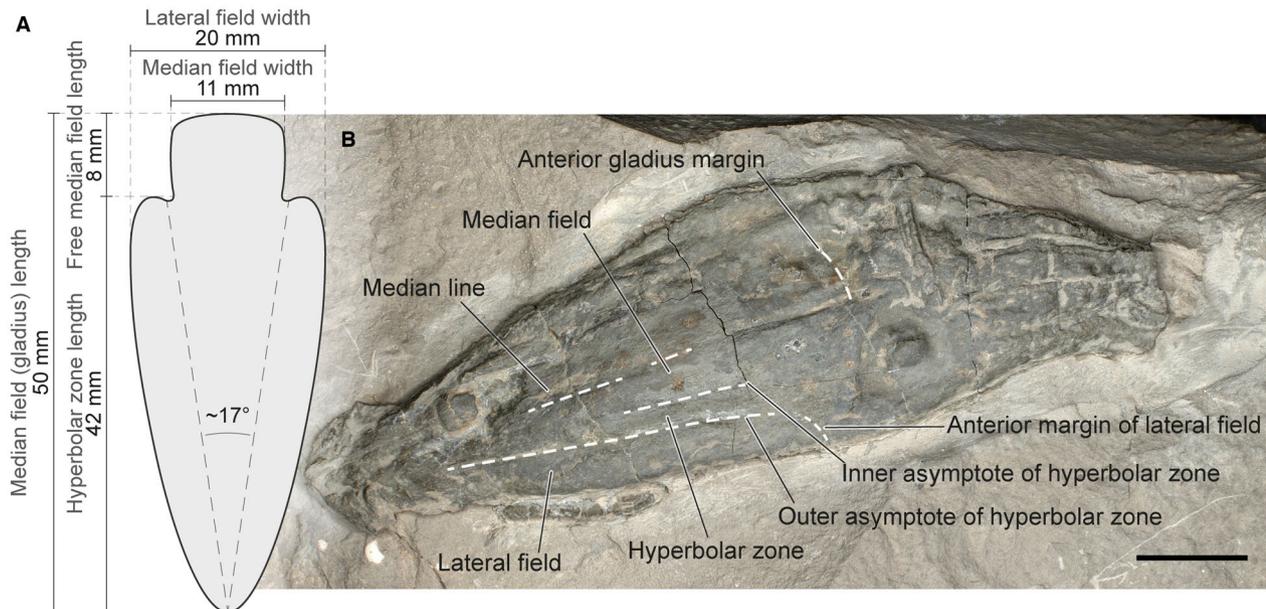


FIG. 2. A, hypothesized illustration of the gladius of *Vampyrofugiens atramentum* based on interpreted measurements and diagnostic indices. B, MNHN.F.A32491, highlighting some of the inferred elements and contours preserved on the gladius (photograph courtesy of P. Loubry, CR2P). Scale bar represents 10 mm.

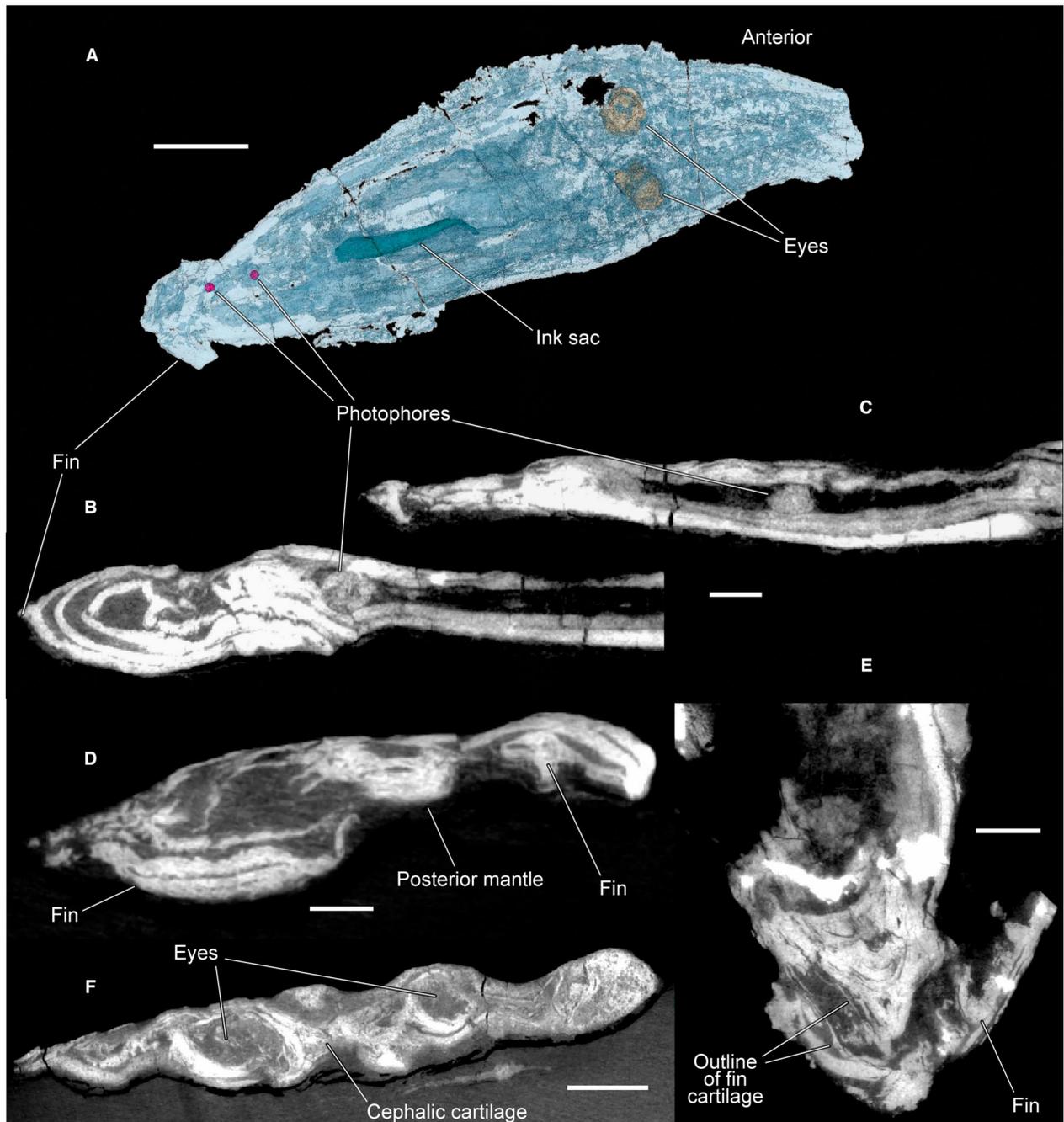


FIG. 3. 3D rendering and PPC-SR- μ CT slices (binned dataset, voxel size: 25.28 μ m) showing the internal luminous organs and preserved cartilaginous structures. A, overall rendering of the specimen indicating the anterior–posterior positioning of the photophores (pink). B–C, two longitudinal PPC-SR- μ CT slices showing the photophores *in situ*. D, cross-section of the posteriormost section (looking anteriorly) showing the folded tissue of the laterally situated fins. E, coronal view of the posterior section showing the fin cartilage; here, it is visible on the left side of the image and appears as a faint white line encircling a dark, elongate area. F, cross-section of the head region showing the subcircular eyes and cephalic cartilage in an X shape between them. Rendered in Mimics software (v.21.0). Scale bars represent: 10 mm (A); 1 mm (B–C); 2 mm (D–E); 3 mm (F).

distally into the base of the acetabulum. Proximally, they are not clearly attached to the arm muscle. The infundibular muscle lines are also preserved on some of the suckers (Fig. 7A).

Pronounced ovoid cavities encircle the outer margins of most suckers. They are not uniform in size (they range up to c. 230 μ m in diameter) and do not appear to be connected to each

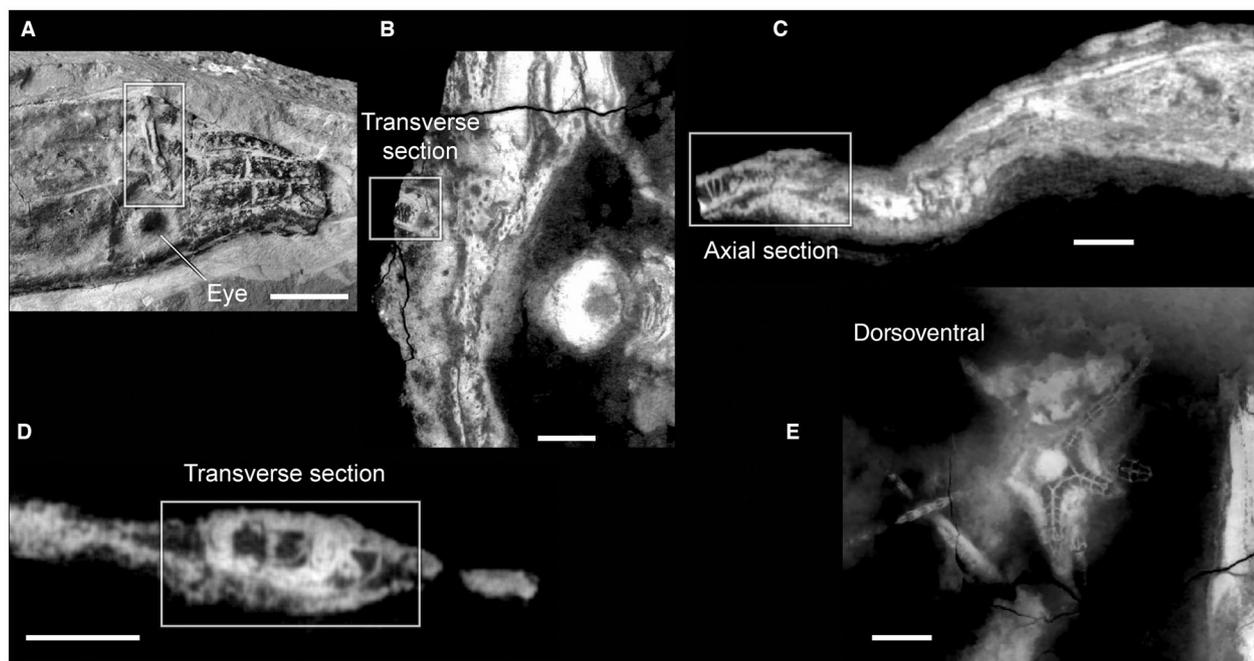


FIG. 4. A–D, images of MNHN.F.A32491 indicating the placement of the section of the supposed brittle star: A, photograph by P. Loubry (CR2P); B–D, PPC-SR- μ CT slices (ESRF, binned dataset, voxel size: 25.28 μ m); the assigned views represent the orientation of the brittle star, not the coleoid. E, example of a brittle star from the locality showing the preserved internal structure (PPC-SR- μ CT slice; ESRF, binned dataset, voxel size: 25.28 μ m). Scale bars represent: 10 mm (A); 2 mm (B, E); 1 mm (C–D).

other within the muscle layers of the sucker's soft tissue (Fig. 8A–C, E, F).

Ink sac. A clearly defined ink sac is positioned medioventrally in the mantle and appears as a cylindrically tapered, opaque black structure, *c.* 16 mm in length (Figs 1B, C, 3A). The smaller, anteriormost section of the ink sac is oriented toward the ventral margin of the body.

Luminous organs. Two uniformly spherical structures (*c.* 1 mm in diameter) are nestled inside the specimen, in a posterior cavity positioned just anterior to the fins (Fig. 3A–C). One sphere is anterior to the other and they both lie along the axial plane. The density of the structures is consistent with the variation seen in the rest of the preserved anatomy, and no other structures are located in the same cavity. We interpret these spheres as luminous organs rather than as other internal organs such as oocytes, which form clusters, or oviductal organs, which are laterally symmetrical. By their size and density they do not appear to be pyritic framboids, which have been described from La Voulte-sur-Rhône as being often >1 cm (Briggs & Crowther 2008).

Gladius. The PPC-SR- μ CT data did not allow for concise visualization or full reconstruction of the gladius. However, the RTI data showed an external topographic relief that is consistent with the placement and shape of a gladius and is herein interpreted as such (Fig. 2). This external topography is supported by the preservation of internal mineralized sections visible anteriorly in

the PPC-SR- μ CT slices. Due to the lamellar composition and location (Fig. 1D), we conclude that these areas are preserved sections of the gladius.

The interpreted outline and parameters of the gladius remains formed the basis for a number of diagnostic measurements outlined in Fuchs (2020), and enabled a hypothesized reconstruction (Fig. 2). The length of the gladius (*c.* 50 mm) corresponds with that of the mantle and its width ratio (gladius width_{max} : gladius length) is moderate (0.4). The median field ratio (median field width_{hypz} : hyperbolar zone length) is slender (0.26) with an opening angle (between the inner asymptotes) of *c.* 17°. It features two very long hyperbolar zones (hyperbolar zone length : median field length ratio, 0.84) that extend into moderate lateral fields (lateral fields width_{max} : median field width_{max} ratio, 1.8).

Given that it was not possible to make observations and measurements directly on the gladius, these interpretations should be viewed with caution.

DISCUSSION

Konservat-Lagerstätten, such as La Voulte-sur-Rhône, play a key role in the preservation of soft tissue, identification of behaviours and tracking of the timing of evolutionary innovations (Fuchs *et al.* 2010; Kruta *et al.* 2016; Klug *et al.* 2021). Despite the considerable amounts of morphological information retained, interpreting the

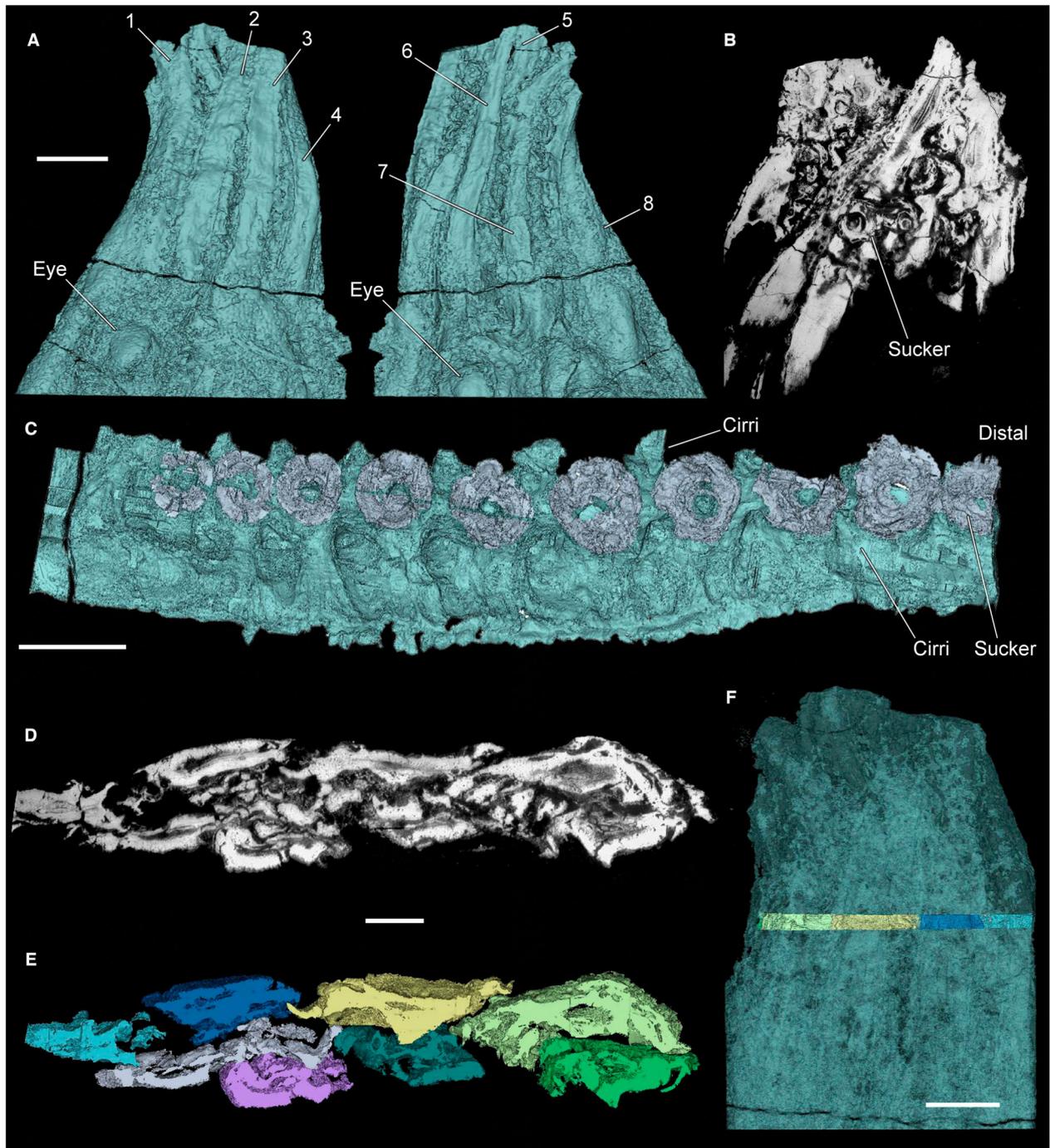


FIG. 5. 3D renderings and PPC-SR- μ CT slices showing arm crown elements of MNHN.F.A32491 (binned dataset, voxel size: 7 μ m). A, rendering of the arm crown in dorsal and ventral view showing eight arms in the undifferentiated arm crown. B, PPC-SR- μ CT slice of the arm crown showing the radially symmetrical suckers, internal musculature and ovoid cavities in the soft tissues. C, 3D rendering of an arm showing the uniserial sucker row and biserial cirri configuration. D, PPC-SR- μ CT slice in cross-section showing the eight arms. E, rendering of the cross-section in D; each arm is rendered in a different colour. F, semi-transparent rendering of the arm crown showing the location of the cross-section. Rendered in Mimics software (v. 21.0). Scale bars represent: 5 mm (A); 2 mm (C); 1 mm (D–E); 3 mm (F).

taxonomic and ecological implications of these characters can still be challenging. This is reflected in the new species described here.

Gladius. The gladius is the key diagnostic element used in fossil coleoid systematics; indeed, it forms the basis for the current taxonomy of Mesozoic coleoids (Young &

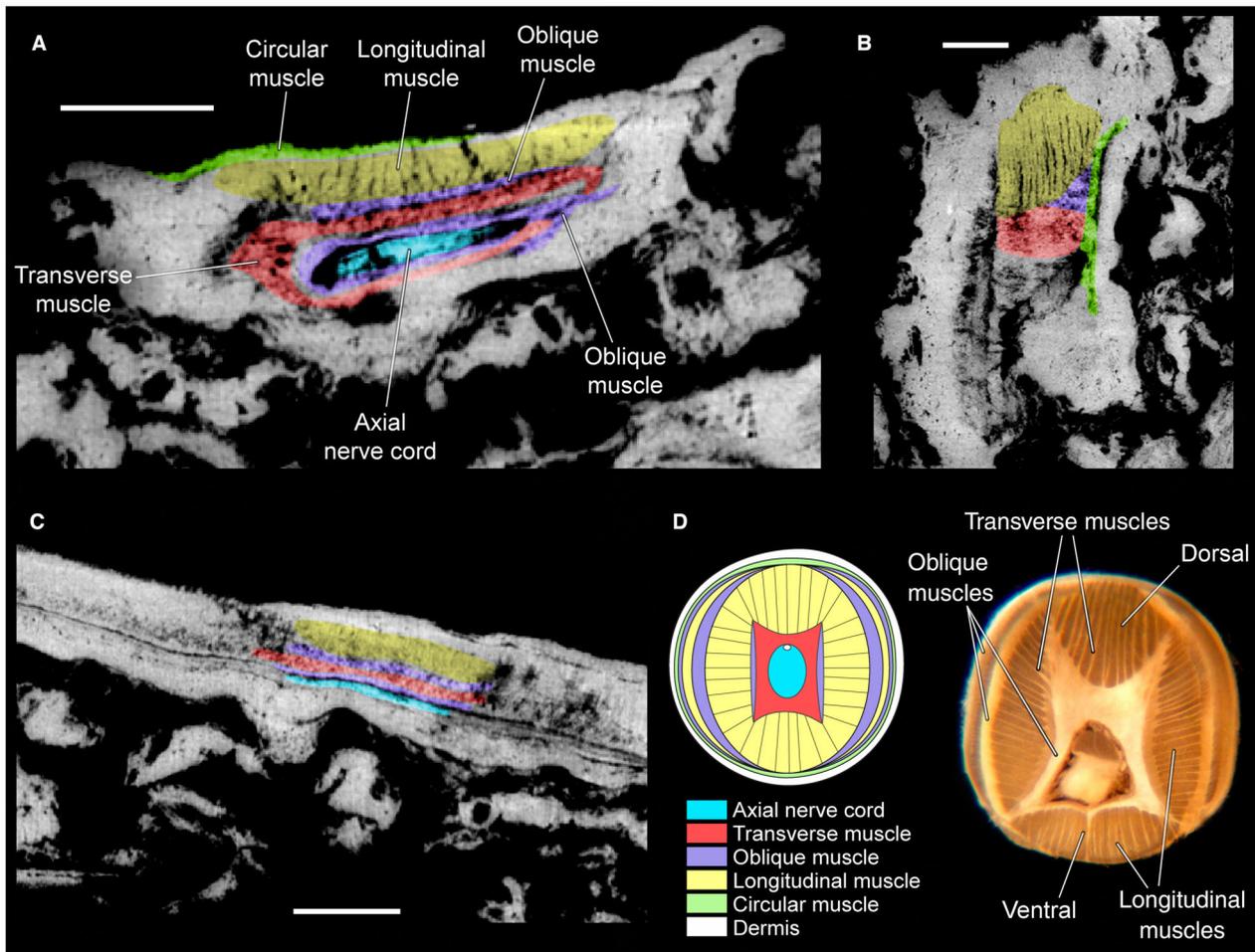


FIG. 6. A–C, slices (PPC-SR- μ CT, binned dataset, voxel size: 7 μ m) of an arm of MNHN.F.A32491 in: A, cross-section; B, coronal; C, longitudinal view. D, on the left, an illustration by Nödl (2015) outlines musculature regions and indicates the colours used in A–C; these bundled muscle groups reflect the different orientations and gross musculature seen in the cross-section of the extant octopus arm shown on the right (from Feinstein *et al.* 2011). In MNHN.F.A32491 the bundles of longitudinal muscle seem to be the best preserved. All scale bars represent 500 μ m.

Vecchione 1996; Lindgren *et al.* 2004; Kruta *et al.* 2016; Sutton *et al.* 2016; Fuchs 2020). However, there are many inherent, widely recognized uncertainties in the present framework. These unknowns are a consequence of the limited sample size, which is constrained by the specific taphonomic conditions required for exceptional preservation (Marroquín *et al.* 2018). Additionally, the samples are preserved only in varying degrees and often show compaction or loss of taxonomic characters (Marroquín *et al.* 2018). These conservation parameters contribute to the limited understanding of the diagnostic characteristics and intraspecies-level variation and, as yet, it has not yet been possible to reconstruct a supported phylogeny (Lindgren *et al.* 2004; Kröger *et al.* 2011; Kruta *et al.* 2016; Sutton *et al.* 2016; Košťák *et al.* 2021).

One established diagnostic feature is the configuration of growth lines present on the gladius (Fuchs 2006; Fuchs

& Weis 2008; Marroquín *et al.* 2018). Those located in the hyperbolic zone vary in levels of concavity and have been shown to be sufficient markers for the positive classification of fossil coleoids (Fuchs & Weis 2008). However, the mantle tissue preserved in MNHN.F.A32491 conceals the gladius and, therefore, any growth lines that could be used for diagnostic purposes.

The use of RTI uncovered details that were not seen on either μ CT or visual observation. These enabled us to interpret the overall outline of the gladius (Fig. 2). Based on the interpreted morphology (apical angle, distinct hyperbolic zone, lack of lateral keels, and the width of median field) it is possible to rule this specimen out as a member of the Prototeuthid suborder (Fuchs 2016, 2020). In the Teudopseina suborder, the genera described in the corresponding biostratigraphic age range are the Teudopseidae, *Teudopsis* and *Teudopseina*, and the

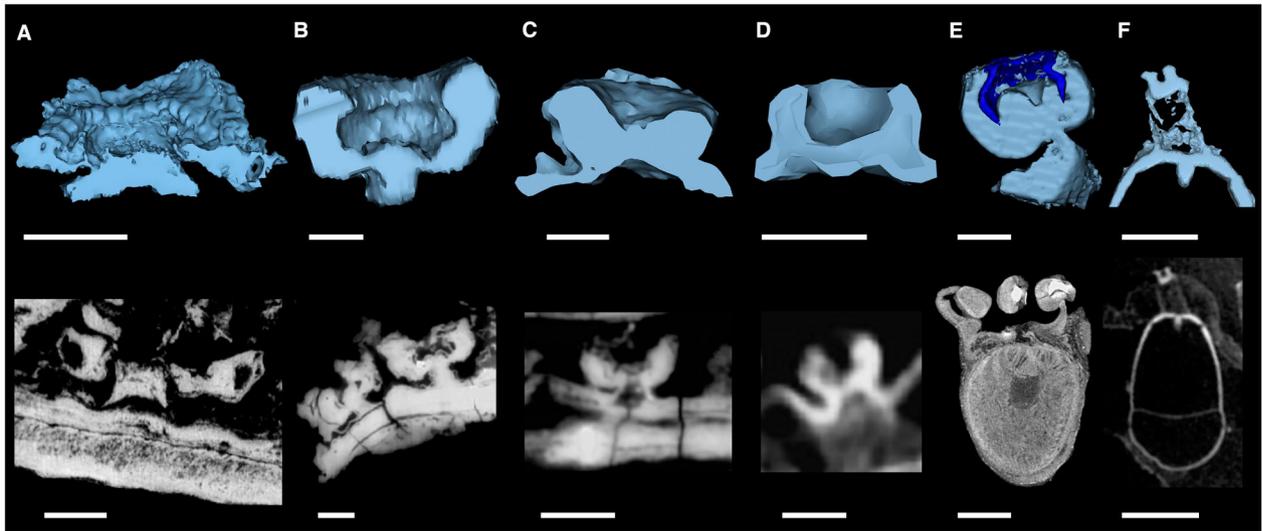


FIG. 7. 3D renderings (top) and PPC-SR- μ CT, and μ CT slices (bottom) of sucker profiles: A, *Vampyrofugiens atramentum*. PPC-SR- μ CT slice (binned dataset, voxel size: 7 μ m); B–C, dorsal (B) and non-dorsal (C) arms of *Vampyronassa rhodanica* (MNHN.F.B74244) (PPC-SR- μ CT, binned dataset, voxel size: 25 μ m); D, *Vampyroteuthis infernalis* (AMNH IZC 361496; μ CT, voxel size 38.40 μ m) (Vampyromorpha); E, commercial *Loligo* (Decabrachia) sample (μ CT, AST-RX platform, MNHN); F, *Grimpotoothis* (ZMB 240160) (Octobrachia) CT data reconstructed from (Ziegler *et al.* 2018); E–F, extant material was stained prior to scanning. Rendered in Mimics software (v.21.0). Scale bars represent (top row renderings): 500 μ m (A–D); 2 mm (E); 5 mm (F); (bottom row PPC-SR- μ CT and μ CT slices) 400 μ m (A); 1 mm (B–C); 500 μ m (D); 5 mm (E); 10 mm (F).

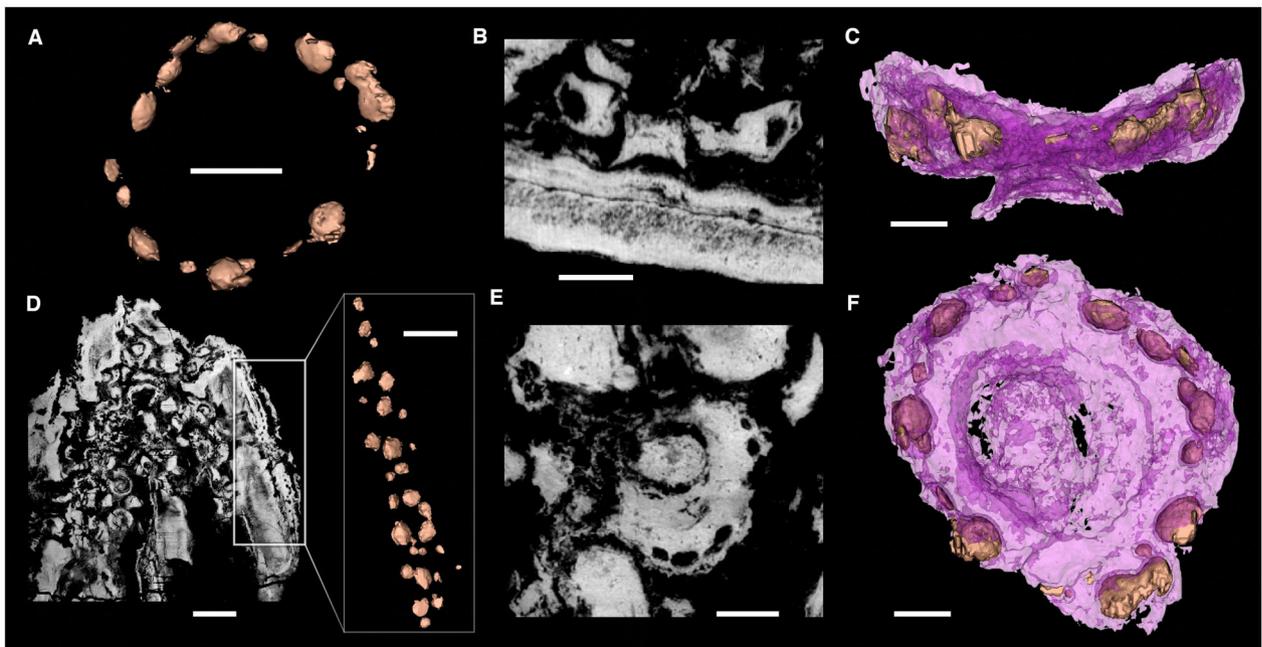


FIG. 8. PPC-SR- μ CT slices (ESRF, binned dataset, voxel size: 7 μ m) and 3D renderings of the ovoid cavities in the sucker (A–C, E, F) and arm tissue (D) of MNHN.F.A32491. A, coronal view showing a rendering of the cavities encircling the outer perimeter of the sucker. B, E, longitudinal and coronal view, respectively, of the sucker in the PPC-SR- μ CT slice. C, F, rendering in longitudinal and coronal view, respectively, of the same sucker. D, PPC-SR- μ CT slice of the ovoid cavities in the arm tissue, with an inset rendering of the cavities. Rendered in Mimics software (v.21.0). Scale bars represent: 400 μ m (A–B, E); 200 μ m (C, F); 2 mm (D); 500 μ m (inset in D).

Trachyteuthidae, *Trachyteuthis* (Fuchs 2020). The gladius morphology of MNHN.F.A32491 is not consistent with any of these genera, nor indeed with members of the more derived cirrata or incirrata suborders. The gladius is also very different from the two specimens known from the Vampyromorphina suborder, extant *Vampyroteuthis* and the Oligocene-aged *Necroteuthis*. By process of elimination, the gladius belongs to a vampyromorph coleoid, probably in the Loligosepiina suborder.

The measurements of MNHN.F.A32491 do not fit exactly within the parameters listed for any of the genera in the four families of this suborder (Fuchs 2020), although they are most dissimilar to the families of Leptotheuthidae (*Leptotheuthis*, *Donovaniteuthis*) and Mastigophoridae (*Mastigophora*, *Doryanthes*). The genera of the Loligosepiidae family (*Loligosepia* and *Jeletzkyteuthis*) have longer hyperbolar zones than MNHN.F.A32491 and have anteriorly pointed lateral fields, which have not been seen in the new specimen (Fig. 9).

Of all of the members of Loligosepiina, the gladius reconstruction is closest to the geopeltid *Parabelopeltis*. It conforms to the diagnostic widths of both the gladius and median field, and is constrained by the upper limit of the hyperbolar zone length (Fig. 2). However, even here the measurements are not an exact match, given that the width of the lateral fields exceeds that of *Parabelopeltis*.

Additionally, the 'small' size of MNHN.F.A32491, as designated by the parameters outlined in Fuchs (2020), is not consistent with its placement in the 'medium-sized' Geopeltidae family. It is possible, however, that this specimen could be a sub-adult member.

Excluding the lateral field width and overall body size, all other known measurements are consistent with those of the genus *Parabelopeltis*. This genus is represented by only one Jurassic species, *P. flexuosa* (Fuchs 2020), from localities in Germany, Luxembourg, UK, Switzerland, Russia and Canada (Alberta) (Marroquín *et al.* 2018; Fuchs 2020).

Without direct observation of the gladius, the reconstructed shape (Fig. 2) was not sufficient to assign MNHN.F.A32491 to an already described species. Our hypothesized reconstruction indicates that although it could be close to *Parabelopeltis* (Fig. 9) there are some differences in its size and proportions, which justify a new species. As such, we suggest that MNHN.F.A32491 represents a new genera in the geopeltid family. Further discoveries will ideally provide additional information on the soft tissues of *Parabelopeltis*, or a better understanding of the gladius morphology in the newly assigned genus.

Ink sac. Like the gladius, the ink sac is included in the character matrix of fossil systematics (Young & Vecchione 1996; Lindgren *et al.* 2004; Kruta *et al.* 2016;

Whalen & Landman 2022). However, the exceptional taphonomic conditions required for coleoid fossilization constrain our understanding of the extent of this feature in fossil taxa (Nishiguchi & Mapes 2008). Therefore, the presence of this character remains uncertain in many of the genera included in the morphology-based phylogenies (Young & Vecchione 1996; Lindgren *et al.* 2004; Kruta *et al.* 2016; Whalen & Landman 2022). However, Strugnell *et al.* (2014) have argued the volatility of this character and its suitability for determining high-level phylogenetic relationships, given that it has been lost in numerous lineages. As such, we refrain from attempting to contextualize the ink sac of the new species in a taxonomic framework, and instead we use it as an indicator of behaviour and of the implications for ecologic niche occupation.

Luminous organs. Although common and varied in families of extant Decabrachia, (Herring 1994; Herring *et al.* 1994) there are very few luminous genera in the extant Octobrachia (Herring 1988). Those known include two incirrate octopoda (*Japetella* and *Eledone*), as well as *Vampyroteuthis infernalis*, the only extant vampyromorph. This latter taxon has three sources of bioluminescence (Pickford 1949; Herring *et al.* 1994; Robison *et al.* 2003) including two photophores on the surface margin of the mantle, which are positioned dorsolaterally at the base of the pair of posterior fins (Herring 1988).

Photophores vary in structure and complexity, and there may be several types in one species. Their placement and variety differs between and within species, and can also be linked with sexual dimorphism (Herring 1988; Herring *et al.* 1992, 1994; Cavallaro *et al.* 2017). They can be distributed across the body (Cavallaro *et al.* 2017), where they potentially emit light from the arm crown, the eye and head region and mantle, or internally, where they are observed in brachial, anal and abdominal positions (Butcher *et al.* 1982; Nixon & Young 2003).

Unlike *Vampyroteuthis infernalis*, the luminous organs observed in MNHN.F.A32491 are internal and positioned with anterior–posterior symmetry. We interpret this to be the original orientation. Although the specimen does show evidence of some rotation prior to fossilization, the amount needed to reorient the symmetry of these structures seems inconsistent with what is observed.

Instead, the internal luminous organs of MNHN.F.A32491 are similar to the intestinal photophores specific only to a few species in extant Decabrachia (Nixon & Young 2003; Nixon 2011; Lindgren *et al.* 2019), although the medial anterior–posterior symmetry and visceral placement is not common (Jereb & Roper 2010). This alignment is found in some oegopsiids, specifically certain members of the enoploteuthid families, Lycoteuthidae and Pyroteuthidae (Jereb & Roper 2010).

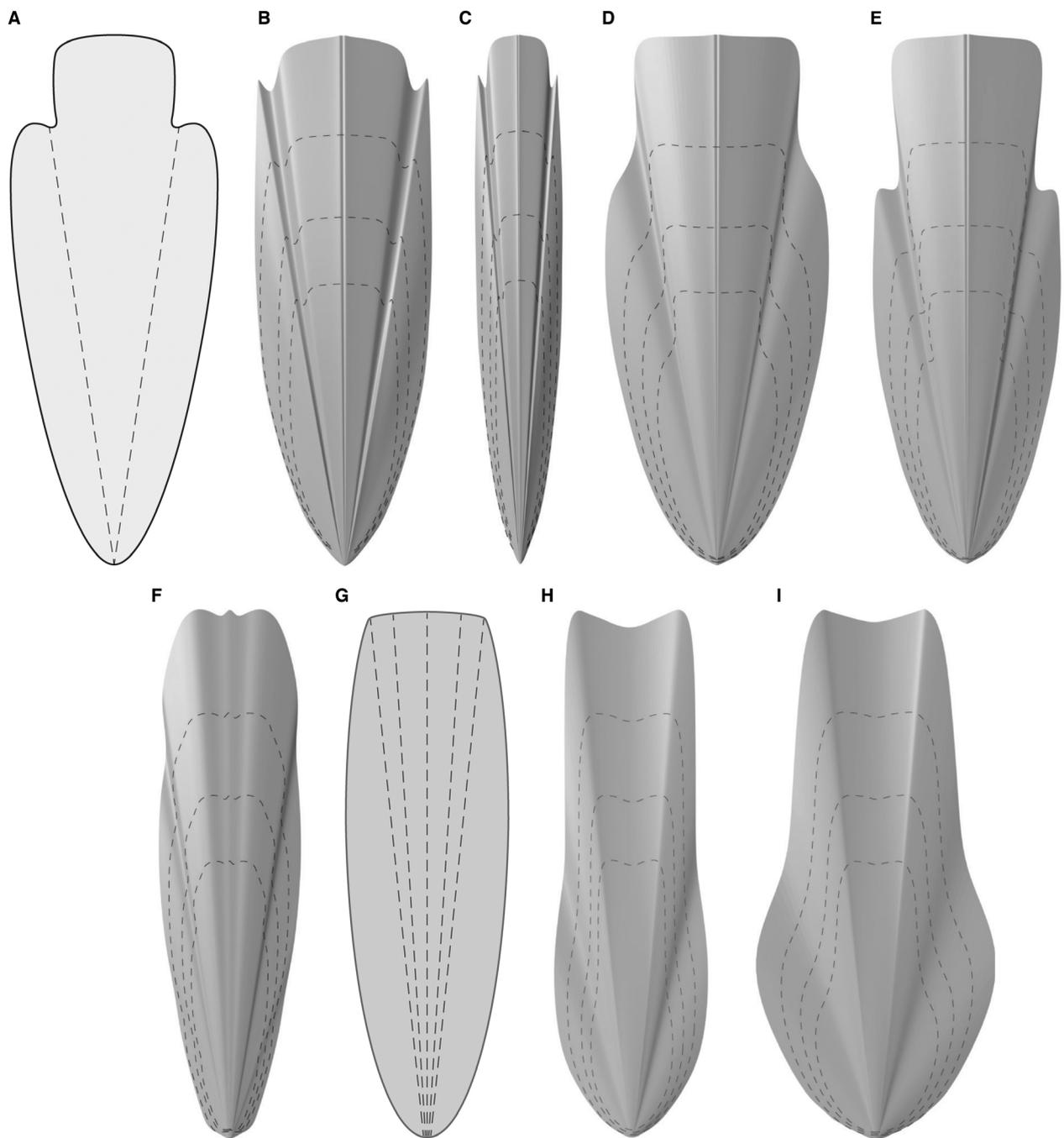


FIG. 9. Genus-level gladius illustrations from the Suborder Lologosepiina Jeletzky, 1965, adapted from Fuchs (2020), with the addition of the new species. A, *Vampyrofugiens atramentum* gen. et sp. nov. B–C, Family Lologosepiidae Regteren Altena, 1949: B, *Lologosepia* Quenstedt, 1839; C, *Jeletzkyteuthis* Doyle, 1990. D–E, Family Geopeltidae Regteren Altena, 1949: D, *Geopeltis* Regteren Altena, 1949; E, *Parabelpeltis* Naef, 1921. F–G, Family Leptotheuthidae Naef, 1921: F, *Leptotheuthis* Meyer, 1834; G, *Donovaniteuthis* Engeser & Keupp, 1997. H–I, Family Mastigoporidae Engeser & Reitner, 1985: H, *Mastigophora* Owen, 1856; I, *Doryanthes* Münster, 1846. Gladius illustrations are for morphological comparison and not to scale.

Species in these genera typically have multiple photophores on the body, although the position and axial symmetry of the two photophores seen in MNHN.F.A32491 (Fig. 3A–C) most closely resemble those of the abdominal

light organs in the oegopsiid *P. microlampas* (Pyroteuthidae) (Lindgren *et al.* 2019). These are of a similar size and are positioned along the median line with one posterior to the other.

This symmetry is also seen in the onychoteuthid *Onychoteuthis banksii*, a species that is used in the phylogenies combining extant and fossil morphological characters (Lindgren *et al.* 2004; Kruta *et al.* 2016; Sutton *et al.* 2016; Rowe *et al.* 2022; Whalen & Landman 2022). However, in *O. banksii* the two photophores show a variation in size, with the anterior photophore being smaller than the posterior one by *c.* 75%, and they are more widely spaced along the intestine (Bolstad 2008; Jereb & Roper 2010; Bolstad *et al.* 2019).

Although luminous organs have been proposed in taxa from La Voulte-sur-Rhône (Fischer & Riou 2002), none has so far been positively identified using μ CT (Kruta *et al.* 2016; Rowe *et al.* 2022). Furthermore, to our knowledge, this configuration of photophores is the only example of this arrangement observed in fossil coleoids. In extant forms, when the two internal anterior–posterior photophores are present they are accompanied by additional photophores elsewhere on the body (Jereb & Roper 2010).

Despite this uncommon symmetry, it is not possible to use this character for phylogenetic assertions because the high diversity of bioluminescence observed in extant cephalopods indicates that this feature has multiple independent evolutionary origins (Haddock *et al.* 2010). Within Octobranchia, bioluminescence has been identified as evolving independently in three lineages: in one incirrate family Bolitaenidae, the cirrates, and also in the *Vampyroteuthis* clade (Lindgren *et al.* 2012).

Lifestyle implications

Ink sac. The oldest confirmed record of the ink sac is linked with fossils from Upper Carboniferous Lagerstätte sediments (Nishiguchi & Mapes 2008; Doguzhaeva & Mapes 2017), indicating that inking behaviours have long been used in coleoid lineages. The use of ink is a distinctive part of extant coleoid behaviour, with taxa using concealment and confusion as a means to avoid predators (Bush & Robison 2007; Nixon 2011; Derby 2014). The use of ink has also been proposed as a chemical deterrent or disruptor (Bush & Robison 2007) or as a conspecific alarm cue (Derby 2014). The various forms of the ejected ink (including clouds, pseudomorphs and ropes), are associated with different defence strategies that include either direct escape or crypsis (Bush & Robison 2007).

Many taxa in extant lineages have lost their ink sac (Strugnell *et al.* 2014), including deep-water species, and a potential correlation between loss of ink sac and habitat depth has been explored (Allcock & Piertney 2002; Bush & Robison 2007). However, ink has been observed to be used by many coleoid species that inhabit dark, deep-sea conditions in addition to bright-light and low-light

environments (10.6–1842.1 m) (Bush & Robison 2007; Derby 2014; Strugnell *et al.* 2014). Most occurrences are in the mesopelagic zone (200–1000 m), where *c.* 99% of the surface light is attenuated (Bush & Robison 2007). The use of ink in these aphotic conditions indicates that ink is not only a visual cue, but supports the hypothesis that its chemical composition also plays a role in predator evasion (Bush & Robison 2007; Miller *et al.* 2014; Strugnell *et al.* 2014). The loss of ink sac is also observed in some shallow-water forms. Rather than rely on this character for crypsis, these photic species use alternate methods of obfuscation such as aposomatic colours, or other decoy behaviours (Strugnell *et al.* 2014).

Luminous organs. Extant coleoids also use bioluminescence as a form of crypsis, and as an effective visual cue and method of communication. It is common in groups that inhabit meso- and bathypelagic depths (Bush & Robison 2007), and shapes ecologic and social interactions (Young & Roper 1977; Young 1983; Herring 1988, 1994; McFall-Ngai 1990; Haddock *et al.* 2010). Unlike acoustic forms of signalling, bioluminescence can be directed (e.g. it is commonly ventrally located for countershading), and can be detected across great distances (Young & Roper 1977; Young 1983; Herring 1994).

The combination of ink and luminescence in the same animal is observed in some extant taxa. For example, some cranchids fill their transparent mantle cavities with ink and then use their photophores to counter-illuminate shadows from their eyes, digestive gland and ink sac to avoid predators below (Bush & Robison 2007). The presence of luminous organs and an ink sac in MNHN.F.A32491 indicates that these types of anti-predation behaviours were also used in the Jurassic (Fig. 10).

Sucker cavities. The peripheral location of the ovoid-shaped sucker cavities suggests that they are not likely to be remnants of sucker rings, which are known from the internal perimeter of some decabrachians (Young & Vecchione 1996; Young *et al.* 1998; Fuchs *et al.* 2021). Indeed, no residual evidence of sucker rings is observed. Furthermore, the size and configuration seem inconsistent with the cavities being the remainder of infundibular pegs such as those seen on the oral sucker surface in some extant forms (Nixon & Young 2003). They have also been observed in the suckers of other fossil specimens from the La Voulte-sur-Rhône locality (Rowe *et al.* 2022). The cavities are not restricted only to the suckers in MNHN.F.A32491, but are also present in soft tissues of the arm crown (Figs 5B, 8).

These somewhat resemble Kölliker's organs seen in some extant octopod juveniles, however, in the extant forms the Kölliker's organs are present in both the arm



FIG. 10. Hypothesized reconstruction of *Vampyrofugiens atramentum* gen. et sp. nov. based on the data from this study (A. Lethiers, CR2P).

and mantle tissues, and disappear by the sub-adult stage (Brocco *et al.* 1974; Nixon & Young 2003; Villanueva *et al.* 2021). In MNHN.F.A32491 these are preserved only on the arm crown. Without further diagnostic information, we interpret the cavities on the suckers and the arms as a manifestation of degraded epithelial tissue.

Lifestyle implications for Vampyrofugiens atramentum. The mosaic of characters in MNHN.F.A32491 provide insight into the palaeoenvironment and complex ecological networks at La Voulte-sur-Rhône during the Middle Jurassic.

A synthesis of the geology and fossil fauna from the locality (Charbonnier 2009) indicated that it probably represented a deep, bathyal environment, probably situated around the slope–basin transition of the Ardèche margin to the Rhône basins. However, the diverse ecology of selected taxa from the site has raised questions regarding the palaeoenvironmental interpretation. These include work on *Dollocaris*, a thylacocephalan arthropod (Vannier *et al.* 2016), and *Voulteryon parvulus* (Audo *et al.* 2019), a polychelid lobster, both common to the locality. Specifically, *Dollocaris* has a combination of characters that indicate that it was a nektobenthic visual hunter, and therefore inhabited an illuminated setting. Similarly, a shallow-water palaeoenvironment is assumed for *Voulteryon parvulus*. However, the presence of episymbiotic thecideoid brachiopods, which are associated with dimly lit environments, on the carapace of the species suggests that La Voulte-sur-Rhône records a combination of settings

that is consistent with its complex geology (Audo *et al.* 2019). Fossil assemblages from the site may reflect the various environments inhabited by the local fauna, while also recording temporal shifts in ecological affinities for some of the associated taxa. As an example, today stalked crinoids are restricted to deep marine environments, although during the Mesozoic they were living also in shallow marine settings (Charbonnier *et al.* 2014; Whittle *et al.* 2018).

A reappraisal of the soft tissues of three coleoid specimens (*Vampyronassa rhodanica*) identified a combination of morphological characters that indicate that the species had a pelagic lifestyle in the La Voulte-sur-Rhône setting, and occupied a predatory niche (Rowe *et al.* 2022). The mosaic of characters in *V. atramentum* highlight that it used both predatory and defensive strategies, with a combination of defence mechanisms so far unknown from the fossil record.

The presence of an ink sac (Figs 1B, C, 3A, 10) indicates that *V. atramentum* was likely to be prey to contemporaneous taxa and used concealment as a tool for evasion. Its photophores (Figs 3, 10) suggest that it used bioluminescence as a form of obfuscation and communication (Young & Roper 1977; Young 1983; Herring 1988, 1994; McFall-Ngai 1990; Bush & Robison 2007; Haddock *et al.* 2010). The anterior–posterior symmetry of these internal light organs has not previously been described from the fossil record and is limited today to only a few extant oegopsiid Decabrachia. These extant forms include *Onychoteuthis banksii* and

Pterygioteuthis microlampas, which are both known to inhabit epi-mesopelagic waters (Jereb & Roper 2010). Given the multiple evolutionary origins of bioluminescence and the convergent link with a pelagic lifestyle (Lindgren *et al.* 2012), it is possible that the photophores in these three species arose due to similar selective pressures.

The configuration of the arms and suckers in *V. atramentum* in conjunction with the sensory functionality of the cirri (Fig. 5A, C), suggests that it used both to detect and capture prey. The absence of a differentiated arm crown, like those seen in other genera (*Gramadella piveteaui*, *Proteroctopus ribeti* and *Vampyronassa rhodanica*) from the locality, however, indicates a less specialized usage (Fischer & Riou 1982, 2002; Kruta *et al.* 2016; Rowe *et al.* 2022). It is likely that the manipulation strategies used by *V. atramentum* were similar to those seen in extant Octobranchia given that the internal arm musculature mirrors that present in the extant eight-armed group (Fig. 6). This is the first evidence of this type of arm musculature preserved in Jurassic forms.

Not only does the description of this new taxon increase the known coleoid diversity at La Voulte-sur-Rhône, but the different co-occurring lifestyles seen in the coleoid fauna from the locality suggest a high diversity of ecological niches occupied by cephalopods. Of the octobranchiate coleoids from La Voulte-sur-Rhône, three of the seven genera have previously been described with an ink sac. As discussed by Kruta *et al.* (2016), taphonomy could play a role in whether or not this feature is preserved, but given the exceptional preservation at the site, it is likely that this reflects the original anatomy. The La Voulte-sur-Rhône genera described with an ink sac include two prototeuthids, *Romaniteuthis* and *Rhomboteuthis* (Family: Plesiototeuthidae) (Fischer & Riou 1982; Fischer 2003) and the loligosepiid *Mastigophora* (Family: Mastigophoridae) (Fuchs 2014). The addition of this new loligosepiid, *V. atramentum*, indicates this character was more prevalent in this locality than previously understood. Furthermore, of the two diagnostic sucker attachments, those that are clearly attached to the arm musculature and those that are not (Young & Vecchione 1996; Lindgren *et al.* 2004; Whalen & Landman 2022), *V. atramentum* possessed the latter (Fig. 7A–D). Today, this is known in only one species, *Vampyroteuthis infernalis*, but the latter attachment type was also present in *Vampyronassa rhodanica* (Rowe *et al.* 2022). The presence of this character in two species from La Voulte-sur-Rhône shows that it was more widespread in Jurassic vampyromorphs than it is today.

If all of the coleoids described from La Voulte-sur-Rhône inhabited the same area, then the ecological network was highly structured, with well demarcated niches. Some species were more specialized to predatory behaviours, and others to defensive behaviours; those with high

swimming abilities probably occupied pelagic settings, while others were more nektonic. The co-occurrence of forms with traits reflecting adaptation to varied light conditions emphasizes the complexity of the palaeoenvironments.

CONCLUSION

The use of high-resolution imaging techniques, PPC-SR- μ CT and RTI, provides new observational data on the soft tissues, internal organs and gladius of an unpublished vampyromorph specimen (MNHN.F.A32491) from La Voulte-sur-Rhône.

The imaging shows that the individual had an Octobranchia-type arm configuration and musculature, *Vampyroteuthis*-like sucker attachments, an ink sac, and two internal light organs with anterior–posterior symmetry. The combination of the ink sac and internal luminous organs is known from the Recent, although not from fossil coleoids. Additionally, the observed gladius morphology in MNHN.F.A32491 differs from previously described coleoids and therefore justifies the assignment of this individual to a new taxon, *Vampyrofugiens atramentum* gen. et sp. nov.

Acknowledgements. We are grateful to Fernando Ángel Fernández-Álvarez for thoughtful discussion regarding extant Ommastrephidae, to Alexandre Lethiers (CR2P) for the figures, illustrations and hypothesized reconstruction, and to Evariste Monvoisin who contributed to the preliminary analysis of the scans, and to P. Loubry for the photograph of the specimen. Thanks also go to the team on the AST-RX platform (plateau d'Accès Scientifique à la Tomographie à Rayons X du MNHN, UAR 2700 2 AD CNRS) Paris, for providing the initial scans of MNHN.F.A32491. In addition to preliminary analyses, these were used to support the synchrotron proposal for further tomographic imaging. We acknowledge the European Synchrotron Radiation Facility for provision of synchrotron radiation facilities (Proposal ES36), and Vincent Fernandez for his help as a local contact during the acquisition and storing of the data. Additionally, we thank Olivier Bethoux and Valentin Buffa for assistance with the reflectance transformation imaging data collection. We also thank Christian Klug and Dirk Fuchs for their reviews of the manuscript.

Author contributions. **Conceptualization** I. Kruta (IK), I. Rouget (IR), A. J. Rowe (AJR); **Investigation** AJR; **Visualization** AJR, A. Lethiers, P. Loubry; **Writing – Original Draft Preparation** AJR; **Writing – Review & Editing** AJR, IK, IR, L. Villier.

DATA ARCHIVING STATEMENT

This published work and the nomenclatural acts it contains, have been registered in ZooBank: <https://zoobank.org/References/49A109A7-4ED7-4106-AEFD-70750E1D4DB1>.

PPC-SR- μ CT scan data and μ CT scan data for MNHN.F.A32491 are archived at the European Synchrotron Radiation Facility (ESRF), Grenoble (<http://paleo.esrf.fr/>), and the Muséum national d'Histoire naturelle (MNHN), Paris (<http://coldb.mnhn.fr/catalogue/mnhn/f/a32491>), respectively. RTI data are available here: <https://doi.org/10.48579/PRO/QIYKGW>.

Editor. Dieter Korn

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