



Insights into stylophoran anatomy and taphonomy based on an exceptionally preserved mitrate from the Lorraine Group (Upper Ordovician) of New York, USA

Thomas BOISSET¹, Bertrand LEFEBVRE¹, Rich MOOI², Andreas KROH³, Viola WINKLER⁴, Jérôme ADRIEN⁵
and Markus J. MARTIN⁶

⁽¹⁾ Université Claude Bernard Lyon 1, UMR CNRS 5276 LGLTPE, Villeurbanne, France

⁽²⁾ Department of Invertebrate Zoology and Geology, California Academy of Sciences, San Francisco, California, USA

⁽³⁾ Department of Geology & Palaeontology, Naturhistorisches Museum Wien, Vienna, Austria

⁽⁴⁾ Central Research Laboratories, Naturhistorisches Museum Wien, Vienna, Austria

⁽⁵⁾ UMR CNRS 5510 Laboratoire MATEIS, INSA de Lyon, Villeurbanne, France

⁽⁶⁾ Watertown, New York, USA

Corresponding author: bertrand.lefebvre@univ-lyon1.fr

Abstract: Several levels of the Lorraine Group (Upper Ordovician) in upstate New York (USA) have yielded low-diversity, exceptionally preserved, pyritized invertebrate assemblages dominated by the trilobite *Triarthrus eatoni*. Sedimentological and taphonomic features suggest dysoxic bottom-water conditions, with limited transport and rapid burial by distal turbidites. Echinoderms are extremely rare in these strata. Here we report, for the first time, the occurrence of the anomalocystiid mitrate *Enoploura popei* in the Konservat-Lagerstätte of Beecher's Trilobite Bed. A pyritized specimen of this stylophoran was CT-scanned and three-dimensionally reconstructed. The mitrate is laterally compressed, but its 3D-rendering provided several insights into its internal anatomy and taphonomy. The recurved position of the single feeding appendage (aulacophore) is consistent with ligament-induced, post mortem contraction. This posture and the collapse of one lateral series of cover plates indicate that the individual was probably not buried alive. Nevertheless, a portion of the distal aulacophore shows clear evidence of exceptionally preserved soft parts (ambulacral system) in between two sets of slightly open cover plates and the underlying ossicles. One of the most intriguing features of this specimen is its close association with a sinuous, elongated, pyritized trace fossil, which enters the stylophoran through the mouth and disappears into the proximal aulacophore. In marked contrast with other skeletal parts of the specimen (theca and distal part of the aulacophore), the proximal rings of the aulacophore are heavily disrupted and disarticulated. Proximal rings are usually decay-resistant skeletal regions in stylophorans. Therefore, close association of this disrupted region with a trace fossil penetrating it suggests the action of an unknown infaunal scavenger. Location of this trace suggests targeting during early decay of the large muscular proximal aulacophore.

Résumé : *Aperçu de l'anatomie des stylophores et taphonomie fondée sur un mitrate exceptionnellement bien préservé du Groupe de Lorraine (Ordovicien supérieur) de l'état de New York (USA).* Dans le nord de l'État de New York (États-Unis), plusieurs niveaux du Groupe de Lorraine (Ordovicien supérieur) ont livré des assemblages peu diversifiés d'invertébrés marins exceptionnellement préservés (pyritisés), dominés par le trilobite *Triarthrus eatoni*. Les caractéristiques sédimentologiques et taphonomiques de ce site suggèrent des conditions dysoxiques au niveau du fond, avec un transport limité et un enfouissement rapide par des turbidites distales. Les échinodermes sont extrêmement rares dans ces niveaux. La présence du mitrate anomalocystitide *Enoploura popei* est reportée ici pour la première fois dans le Lagerstätte de Beecher's Trilobite Bed. Un échantillon pyritisé de celui-ci a été scanné et reconstruit en trois dimensions. Le mitrate est comprimé latéralement, mais sa reconstitution 3D apporte des informations importantes sur son anatomie interne et sa taphonomie. La position recourbée de son appendice nourricier (aulacophore) résulte probablement d'une contraction *post mortem* induite par le ligament inter-ossiculaire. Cette posture et l'effondrement de l'une des deux séries de plaques de couverture indiquent que l'individu n'a probablement pas été enfoui vivant. Néanmoins, une partie de l'aulacophore distal montre clairement des parties molles exceptionnellement préservées (système ambulacraire) entre deux séries de plaques de couverture entrouvertes et les ossicules sous-jacents. L'une des caractéristiques les plus intrigantes de ce spécimen est son association étroite avec une trace fossile sinueuse, allongée et pyritisée, qui pénètre à l'intérieur du mitrate par la bouche et disparaît dans l'aulacophore proximal. Contrairement au reste du spécimen (thèque et partie distale de l'aulacophore), les anneaux proximaux sont fortement désarticulés. Or, ces anneaux constituent normalement un module particulièrement résistant à la décomposition. Par conséquent, l'association étroite de cette région désarticulée avec une trace fossile qui la pénètre suggère l'action d'un organisme nécrophage au cours des stades précoces de décomposition des muscles abrités par les anneaux proximaux de l'aulacophore.

Keywords: Biotic interactions • Lagerstätten • Ordovician • Stylophora • Taphonomy

Introduction

Stylophorans are an extinct class of echinoderms, which is traditionally subdivided into the two orders Cornuta (middle Cambrian-Late Ordovician) and Mitrata (middle Cambrian-Late Carboniferous). These organisms are characterized by a flat, asymmetric body (theca), and a single appendage (aulacophore). The aulacophore comprises a short and flexible proximal region (attached to the theca) made of numerous telescopic rings, and a longer, narrower distal region, consisting of one lower series of elements (stylocone and ossicles) and two upper sets of opposite (left and right) movable cover plates. The main difference between cornutes and mitrates is that, in the latter, the distal aulacophore could be flexed vertically, whereas it formed a rigid structure in cornutes (Lefebvre, 2003).

Because of their unusual morphology, stylophorans have long remained difficult to compare to extant echinoderms, all of which characterized by pentaradial symmetry. Stylophorans possess a typical echinoderm-like calcite skeleton, but the presence of the ambulacral system (another apomorphy of the phylum Echinodermata) was disputed (Lefebvre et al., 2024). Stylophorans were considered either as primitive, pre-radial members of the phylum (Smith,

2005; Zamora & Rahman, 2014) or as highly derived echinoderms, having secondarily lost the five-fold symmetry, because of their vagile, epibenthic mode of life (David et al., 2000; Lefebvre, 2003). The debate was partially resolved with the discovery of a specimen of cornute in the Fezouata Lagerstätte (Lower Ordovician, Morocco), in which soft part traces are preserved in its distal aulacophore (ambulacral canal and podia), proximal appendage (foregut) and theca (hindgut). This specimen provided evidence that the aulacophore was not a stem or tail, but an echinoderm-like feeding appendage, bearing a single ambulacral ray (Lefebvre et al., 2019 & 2022; Guensburg et al., 2023). However, this discovery leaves open the question of the phylogenetic position of stylophorans, and of their internal (thecal) anatomy, including whether they possessed gill slits (a character lost in all extant echinoderms, but likely present in their last common ancestor with hemichordates; Rahman & Zamora, 2024) or not (Mooi et al., 2024).

In this context, the recent discovery of a single specimen of mitrate (Fig. 1A) in the Beecher's Trilobite Bed Lagerstätte (Late Ordovician) is particularly important, because it has the potential to bring new information on the still poorly known internal anatomy of stylophorans. The Beecher locality has yielded

a remarkable low diversity pyritized fauna, with appendages and internal soft parts (digestive system, eggs) preserved in trilobites and ostracods (Farrel et al., 2011; Siveter et al., 2014). Consequently, the main objective of this study is to probe, through three-dimensional imagery (CT-scan), the potential for soft part organic remains in the appendage and theca of this mitrate from the Beecher's Trilobite Bed Lagerstätte.

Material and Methods

Material

The fossil was collected from Beecher's Trilobite Bed (Lorraine Group, Katian, Upper Ordovician) in upstate New York (USA). The extensive black shales indicate a deep, quiet marine environment, below storm-wave base. Sedimentological and taphonomic features suggest dysoxic bottom-water conditions, with limited transport and rapid burial by distal turbidites (Farrell et al., 2011). These particular conditions made pyritization possible. The Lagerstätte yielded a low-diversity assemblage dominated by the trilobite

Methods

The studied specimen (Fig. 1A) was first scanned using a Phoenix v|tome|x CT-scan at the MATEIS laboratory, INSA (Villeurbanne). The scans were performed with a voltage of 140 kV, a resolution of 20 μm , an intensity of 80 μA and a 667 ms exposition time. Although the 1200 produced scans showed good contrast, resolution was insufficient for detailed analyses. Consequently, a second, higher resolution-though less well contrasted-scanning was made using a MicroCT YXLON FF35 CT-scan at the Natural History Museum of Vienna (Austria). The 3D modeling was made with the software Avizo 9.5.0.

Results

CASG 103358 represents a fully articulated, almost complete pyritized specimen of mitrate (Fig. 1A & B). Its morphology was color-coded on the 3D model, with posterior spines in purple, theca in blue, proximal rings in green and distal aulacophore in brown (Fig. 1B).

The presence of two posterior spines implies that the mitrate belongs to the family Anomalocystitidae (see e.g., Ruta, 1999; Lefebvre & Ausich, 2021).

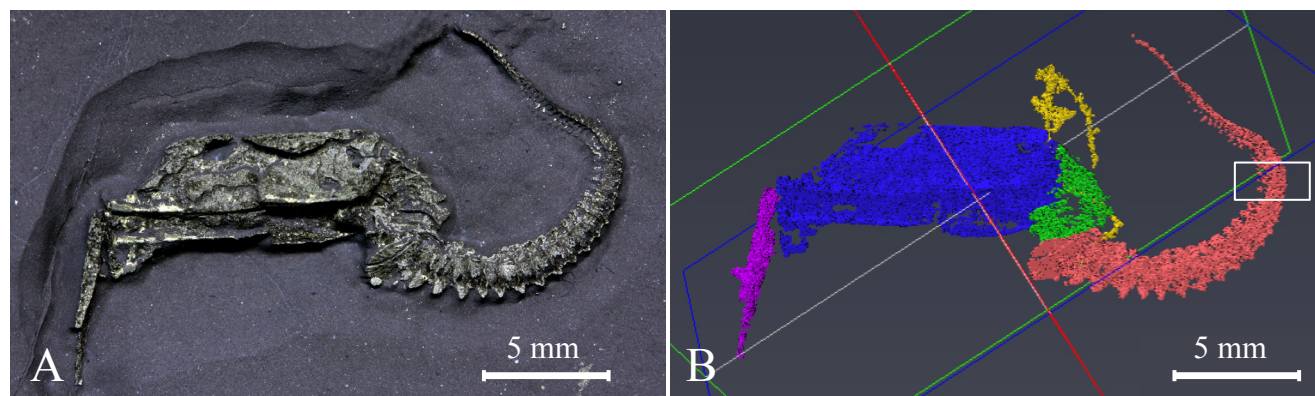


Figure 1. *Enoploura popei*, Beechers's Trilobite Bed, Lorraine Group (Katian), New York (USA), CASG 103358. **A.** Original specimen in right lateral view. **B.** Three-dimensional reconstruction of the CT-scanned specimen, in right lateral view, with posterior spines (purple), theca (blue), proximal (green) and distal (salmon) aulacophore, and associated trace fossil (yellow); white box indicates position of view in figure 2B.

Triarthrus eatoni (Hall, 1838) (Farrel et al., 2009), along with less common ostracods (Siveter et al., 2014), brachiopods and graptolites (Farrel et al., 2011). Echinoderms are extremely rare, with only a handful of specimens belonging to the classes Crinoidea and Ophiuroidea, and, so far, only a single mitrate. The studied specimen (Fig. 1A) is repositied in the palaeontological collections of the California Academy of Sciences (San Francisco) under catalogue number CASG 103358.

Moreover, its thecal plate pattern and the presence of a wide transverse "collerette" on the stylocone both support its assignment to the genus *Enoploura* Wetherby, 1879. The widely expanded, rounded morphology of the "collerette" flanges (Figs 1B, 2A) suggests affinities with *E. popei* Caster, 1952, rather than with *E. balanoides* (Meek, 1872) or *E. punctata* Bassler, 1932, as both of the latter are characterized by narrower lateral flanges that form a sharper ploughshare-shaped transverse blade (Parsley, 1991).

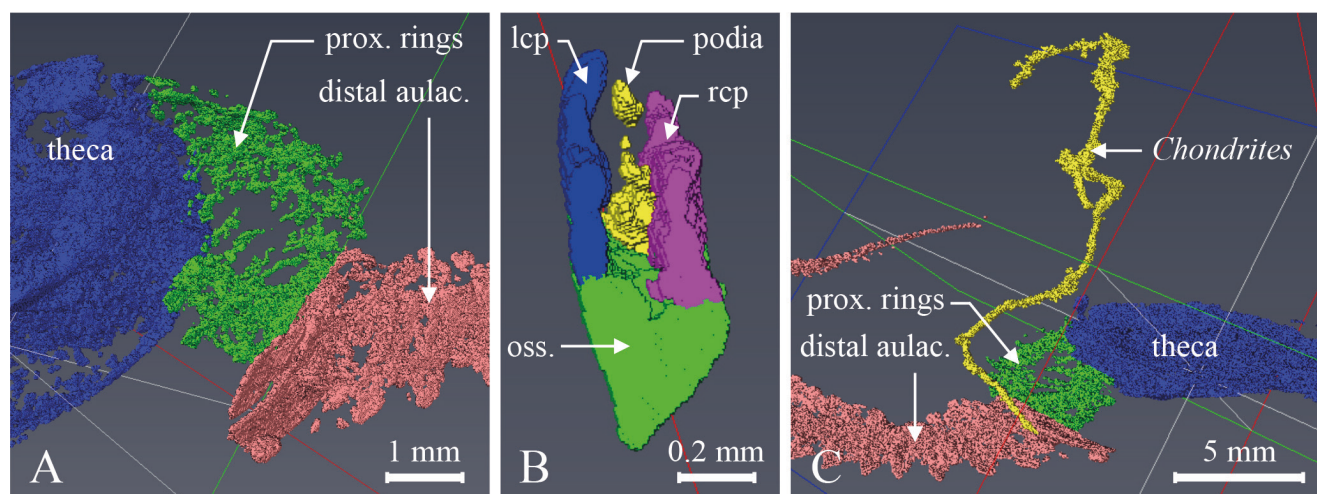


Figure 2. *Enoploura popei*, Beechers's Trilobite Bed, Lorraine Group (Katian), New York (USA), CASG 103358. **A.** Heavily disrupted and disarticulated proximal rings, between theca and distal aulacophore; two large transverse, "ploughshare-like" blades of stylocone visible. **B.** Three-dimensional reconstruction of part of distal aulacophore, with ossicle (in cross section), cover plates, and exceptionally preserved soft parts (ambulacral system). **C.** Left lateral view of 3D reconstruction of specimen, with elongate, sinuous trace fossil (*Chondrites*) penetrating proximal rings through mouth on stylocone. Abbreviations: distal aulac.: distal aulacophore; lcp: left cover plates; oss: ossicle; prox. rings: proximal rings; rcp: right cover plates.

Preparation revealed the mitrate in lateral aspect (Fig. 1A & B). During compaction (early diagenesis), the theca was crushed almost perpendicularly to the (life) orientation of the organism, with its upper surface bulging outwards, and its lower surface forming a re-entrant inside the theca. This compaction produced an anomalous V-shape in cross-section of the theca. No soft parts were detected inside the theca.

In marked contrast with other parts of the organism, the proximal rings are heavily disrupted and disarticulated (Fig. 2A & C). In cornute stylophorans, the proximal aulacophore generally represents the most decay-resistant skeletal region (Saleh et al., 2023).

The distal aulacophore, preserved in flexed position (Fig. 1A & B), was prepared to reveal a lateral view. This structure comprises the stylocone and over 35 articulated, additional ossicles. Only the left series of cover plates is present along the entire distal aulacophore. Most cover plates of the right series are missing, except in the most strongly bent (flexed) part of the appendage. In that region, three-dimensional internal structures are preserved (Fig. 2B), more or less enclosed by the ossicles (below) and the two opposite sets of cover plates (above and laterally).

Discussion

In mitrates, the preservation of the aulacophore in recurved position is generally interpreted as resulting from a ligament-induced, post mortem contraction

(Ruta & Bartels, 1998; Lefebvre, 2003; Lefebvre & Ausich, 2021; Saleh et al., 2023). This posture and the collapse of one series of cover plates suggest that the Beecher mitrate was probably not buried alive, but soon after its death.

Internal (soft) structures are only preserved in the bent part of the distal aulacophore (Fig. 2B), probably because this is the only region, that remained "closed" (ossicles and cover plates are still present), thus providing a favorable micro-environment for soft-tissue preservation (Saleh et al., 2023). The location and morphology of the relict soft parts are compatible with their interpretation as probable ambulacral tube feet. Their taphonomy and appearance are very similar to those described in cornutes (Lefebvre et al., 2019) and fossil ophiuroids (Glass & Blake, 2004).

Ichnological study of the Beecher's Trilobite Bed remains nascent, with research centered on the site's exceptional preservation. Recent work (M. Martin, unpublished observations) has revealed significant bioturbation, offering new insights into specific behaviors of trace makers. The upper 25 mm of the 40 mm thick Beecher's Trilobite Bed include pyritized burrows of *Palaeophycus* horizontal to the bedding plane. The lower 15 mm of the Bed (Trilobite Zone) contain the exceptionally preserved arthropods and other fauna for which the site is known. Preparation of the Trilobite Zone has begun to reveal previously undetected large numbers of pyritized *Chondrites* feeding traces. The *Chondrites* exhibit probing and targeting behaviors, likely driven by the abundance of

carcasses in the Trilobite Zone. The burrows suggest specific interaction with the soft tissues of trilobites, navigating between appendages or entering carcasses near large soft tissue structures. Trilobites subjected to burrowing activities exhibit significant degradation similar to that seen in the specimen of *Enoploura*.

Chondrites-like burrows are relatively common in the matrix surrounding the mitrate. The course of the longest one, plus its connection to the fossil are not random (Fig. 2C). Similarly to the situation in trilobites, this burrow penetrates the mouth (located on the stylocone) into the proximal aulacophore cavity, which in life, housed both powerful muscles and the foregut. Therefore, it is likely that the unusual total disarticulation of the proximal aulacophore, supposedly one of the most decay-resistant modules of stylophorans (Saleh et al., 2023), resulted from the scavenging action of an unknown organism. This part of the body provided a potentially large food source for scavengers.

Similar trace fossils left by scavenging organisms exploiting freshly buried organisms have been described in other Lagerstätten (see e.g. Mangano et al., 2019). Traces of other types of biotic interactions are known in other stylophorans. For example, in the Upper Ordovician of Kentucky, a well-defined, circular hole piercing the upper thecal surface of a specimen of *Enoploura popei* was interpreted as evidence of predatory or parasitic drilling (Deline, 2008). The Darriwilian of the Czech Republic yielded clusters of small pellets left by unknown organisms in internal moulds of mitrate thecae (Bruthansová and Kraft, 2003), as well as abundant disarticulated stylophoran remains in the guts of trilobites (Kraft et al., 2023).

Conclusions

This study shows the importance of 3D modeling in the case of extinct, enigmatic organisms, such as stylophorans. The only known specimen of mitrate recovered from Beecher's Trilobite Bed Lagerstätte is identified as *Enoploura popei*. It preserves some evidence of exceptionally preserved soft parts, including potential water vascular elements, in its distal aulacophore. This is the first time such structures are identified in mitrates, and support previous evidence for a radial vessel plus tube feet in stylophorans. Arguably, among the most intriguing features of this specimen is the ichnological evidence left by an unknown scavenging organism penetrating the mitrate carcass through its mouth. This organism likely fed on soft parts (muscles, foregut) originally housed inside the rings that usually shield the proximal aulacophore.

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Data availability:

Boisset Thomas, Lefebvre Bertrand, Mooi Rich, Kroh Andreas, Winkler Viola Christina, Adrien Jérôme, Martin Markus. (2025). CT-Scans of *Enoploura popei* (Echinodermata: Stylophora: Anomalocystitidae) - Supplementary material to Boisset T. et al. (2024): «Insights into stylophoran anatomy and taphonomy based on an exceptionally preserved mitrate from the Lorraine Group (Upper Ordovician) of New York, USA». [Dataset]. Naturhistorisches Museum Wien (NHMW). <https://doi.org/10.57756/ammjqp>

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