Abnormal trilobites from the Silurian and Devonian of Europe

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Malformed trilobites have been documented in deposits ranging from the Cambrian to the Permian. Continued examination of novel malformed specimens provides insight into how trilobites recovered from injuries, experienced genetic abnormalities, and adapted to pathological conditions. This study focuses on trilobites from the Silurian and Devonian of Europe, presenting new records of: (i) a moulting-related injury in *Lioharpes venulosus*; (ii) genetic malformations in *Calymene blumenbachii* and *Treveropyge* sp.; and (iii) a moulting injury or genetic anomaly in *Scutellum* (*Scutellum*) *pardalios*. Additionally, we record evidence of bryozoan growth on a *C. blumenbachii* specimen. Our findings provide important data for contextualizing the paleobiology of early and middle Paleozoic trilobites, especially related to responses to ecological pressures.

Key words: Trilobita, *Calymene*, *Treveropyge*, *Lioharpes, Scutellum,* evolution, injuries, malformations, teratologies.

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Introduction

Trilobites are a morphologically disparate group of marine Paleozoic arthropods that spanned the Cambrian to the end-Permian extinction (Fortey and Owens 1999; Webster 2007; Hughes 2007; Bault et al. 2022). The biomineralised dorsal exoskeleton trilobites exhibited resulted in an exceptional taxonomic record (Lee et al. 2012; Pérez-Huerta et al. 2018; Murdock 2020). These exoskeletons also preserve malformations, providing insight into ecological interactions, developmental anomalies, and evolutionary pressures experienced by the group (Owen 1985; Babcock 1993, 2003, 2007; Pates et al. 2017; De Baets et al. 2022; Bicknell and Kimmig 2023), illustrating how trilobites recovered from injuries, molting issues, genetic malfunctions, or parasites (Šnajdr 1979, 1981; Babcock 1993; Pates et al. 2017; Pates and Bicknell 2019; Bicknell and Smith 2021; Bicknell et al. 2022b; De Baets et al. 2022). Documentation of malformed trilobites therefore enhances our understanding of trilobite paleobiology. To expand the record of malformed specimens and build on synthetic works (see Owen 1985; Babcock 1993, 2003; Bicknell and Smith 2022; Zong et al. 2023), we examined five abnormal trilobites from the Silurian and Devonian of Europe. In doing so, we illustrate evidence for injuries, developmental malformations, and interactions with bryozoans.

Institutional abbreviations.—NHMUK PI, Natural History Museum, Invertebrate Palaeontology Collection, London, UK; NYSM, New York State Museum, Albany, USA.

Material and methods

Trilobite specimens from the NHMUK PI and NYSM were examined for potential malformations.

Photographs of the malformed specimens were taken under LED lighting using an Olympus E-M1 Mark III (NYSM) and a Canon EOS 600D DSLR camera (NHMUK PI). Specimens from the NHMUK PI were photographed without any coating, while NYSM specimens were treated with ammonium chloride to improve the image contrast. Measurements of the specimens were obtained from the photographs using ImageJ software (Schneider et al. 2012).

Terminology.—Malformation: Examples of injuries, pathologies, or teratologies observed in trilobite exoskeletons.

Injury: Exoskeletal breakages that occurred while the organism was alive. Injuries can indicate failed predation attempts, interactions with environmental hazards, or complications during molting (Rudkin 1985; Owen 1985; Babcock 1993; Fatka et al. 2015; Bicknell et al. 2018; Bicknell and Pates 2020). Notably, injuries are usually localized, while extensive breakages typically reflect post-mortem compaction processes (Leighton 2011). Larger injuries have L-, U-, V-, or W-shapes (Babcock 1993; Bicknell et al. 2022a, 2023b), whereas smaller indentations are typically single spine injuries (SSI) (Pates and Bicknell 2019; Bicknell and Pates 2020). Additionally, evidence of cicatrization and repair is frequently present, although this varies based on the extent of exoskeletal recovery (Rudkin 1979; Owen 1985; Babcock 2007; Bicknell and Paterson 2018).

Teratology: Observable external manifestations of developmental, embryological, or genetic disturbances in the exoskeleton (Šnajdr 1981; Owen 1985). Although rare, teratological features may coincide with injuries (Owen 1985; Bicknell et al. 2024a, b). These malformations can include the addition or loss of nodes, segments, or spines, as well as irregular rib and furrow shapes (Owen 1985; Bicknell and Smith 2021, 2022).

Pathology: Malformed exoskeletal regions that reflect parasitic activity or infections. Such structures typically present as circular or oval swellings (Šnajdr 1978; Owen 1985; De Baets et al. 2022).

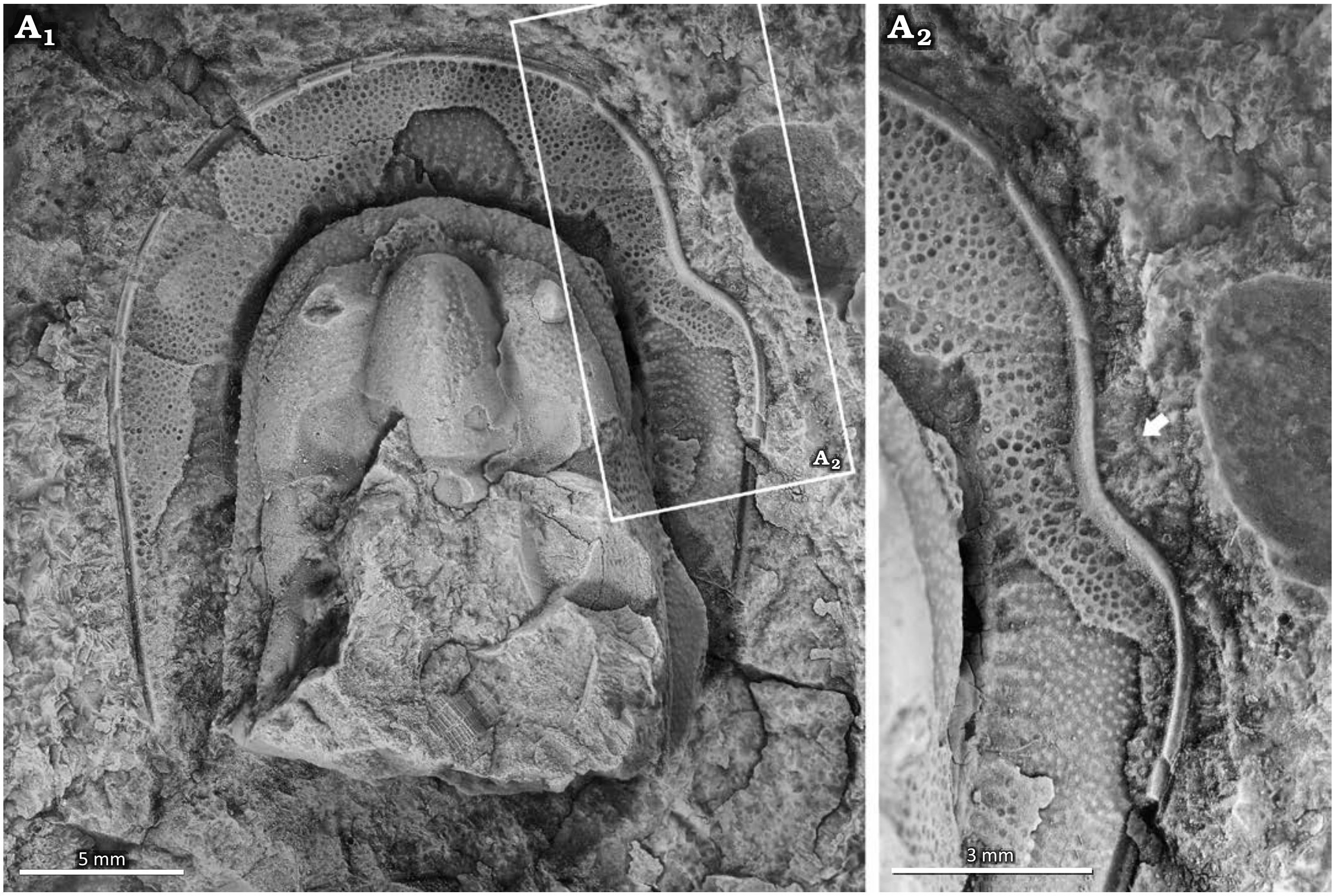

Fig. 1. Malformed harpetid trilobite *Lioharpes venulosus* (Hawle & Corda, 1847), NYSM 19739 from the Koněprusy Limestone, Pragian, Lower Devonian, Koněprusy, Czech Republic. A_1, complete cephalon; A_2, close up showing U-shaped indentation (arrow). Specimen coated in ammonium chloride sublimate.

Results

Lioharpes venulosus (Hawle & Corda, 1847); NYSM 19739. Koněprusy Limestone, Pragian, Lower Devonian, Koněprusy, Czech Republic (Fig. 1).

NYSM 19739 is an isolated cephalon that is 26.2 mm long and 22.3 mm wide with a malformation consisting of disrupted and irregular pygidial ribs on the right side (Fig. $1A_2$). The malformation is a U-shaped indentation in the marginal rim. The indentation is 5.6 mm long and extends 1.9 mm towards the midline. Fringe pits proximal to indentation are irregular, ovate, and occasionally fused into larger pits.

Calymene blumenbachii Brongniart in Desmarest, 1817; NHMUK PI In 19857; NHMUK PI In 65061. Much Wenlock Limestone Formation, Wenlock, Homerian Silurian, England, UK (Fig. 2).

NHMUK PI In 65061 is an articulated *Calymene blumenbachii* specimen showing a partial cephalon, thorax, and pygidium. The specimen is 92.9 mm long and 48.6 mm wide across the cephalon (Fig. $2A_1$). The specimen has a structure on the second thoracic axial ring that is an elevated, hollow, rounded crater, 1.7 mm in diameter and is covered with closely spaced pits or openings (Fig. $2A_2$). The exoskeleton around the crater is not deformed and the pattern of closely-spaced openings continues across the axial ring.

NHMUK PI In 19857 is an isolated, partial pygidium that is 13.2 mm long and 18.2 mm wide with a malformation on the right side (Fig. 2B). Disrupted and irregular pygidial ribs are observed in this area. Two ribs terminate 1.6 mm from the pygidial margin (Fig. 2B) and two other ribs are fused 1.2 mm from the pygidial axis (Fig. 2B).

Treveropyge sp., NYSM 19740. Saint Céneré Formation, Lochkovian, Lower Devonian, Mayenne, France (Fig. 3).

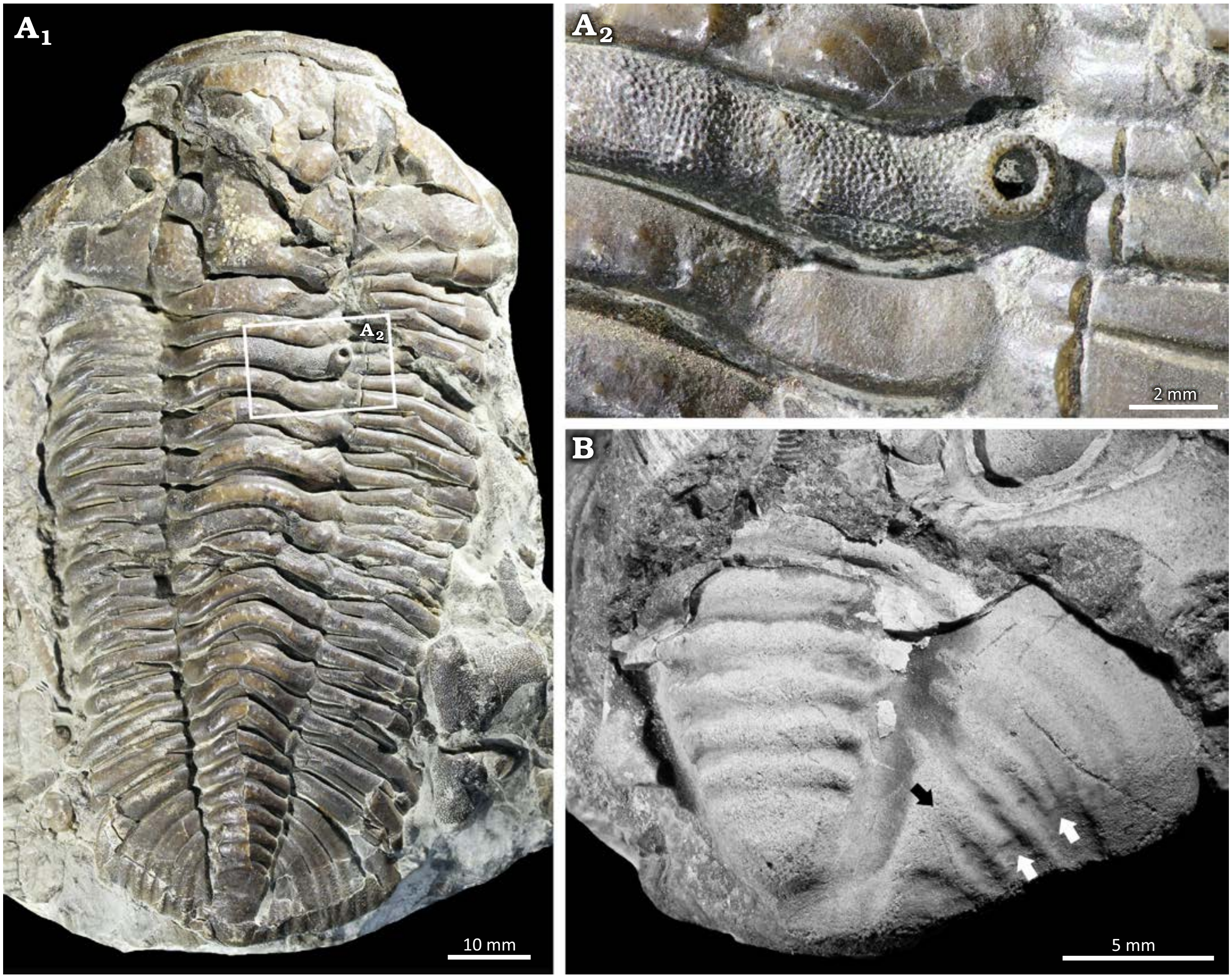

Fig. 2. Abnormal calymenid trilobites *Calymene blumenbachii* Brongniart in Desmarest, 1817 from the Much Wenlock Limestone Formation, Homerian, Wenlock, Silurian, England, UK. **A**. NHMUK PI In 65061. A_1, complete specimen; A_2, close up showing the large bryozoan growth. **B**. NHMUK PI In 19857 showing pygidial ribs that terminate early (white arrows) and are fused proximal to the medial lobe (black arrow).

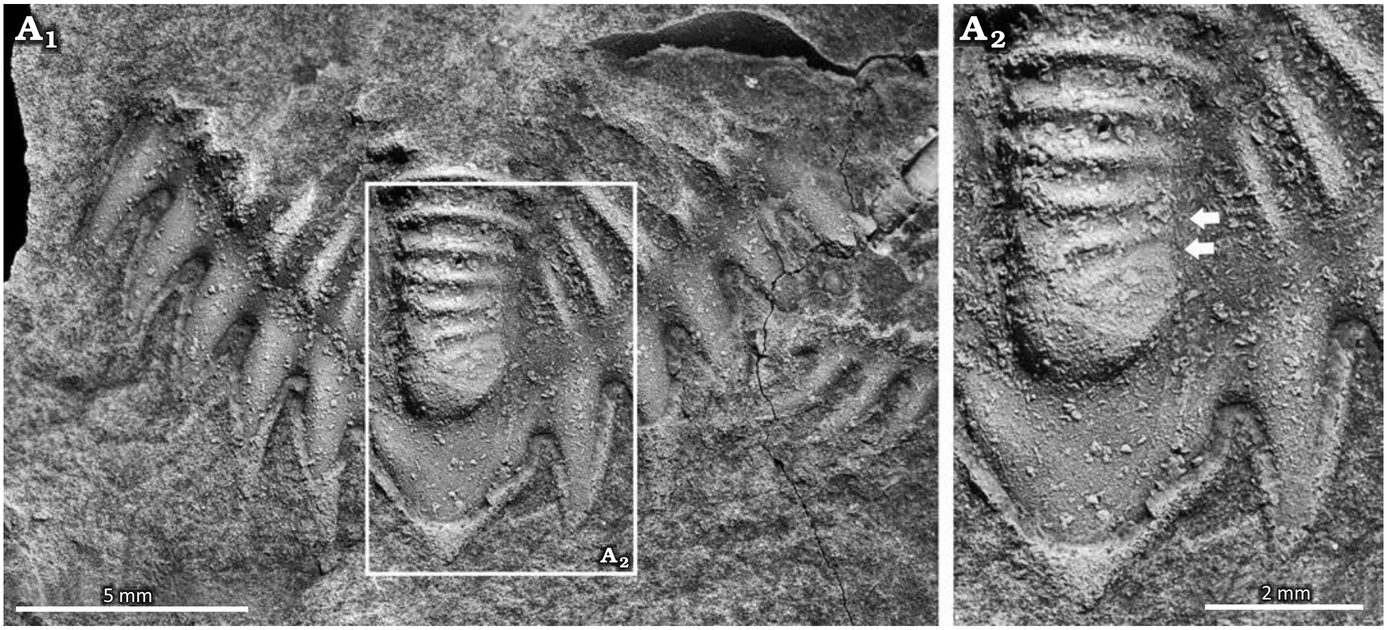

Fig. 3. Malformed acastid trilobite *Treveropyge* sp.*,* NYSM 19740 from the Saint Céneré Formation, Lockkovian, Lower Devonian, Mayenne, France. A_1, complete pygidium; A_2, close up showing asymmetrical axial lobe and incomplete axial ring (arrows). Specimen coated in ammonium chloride sublimate.

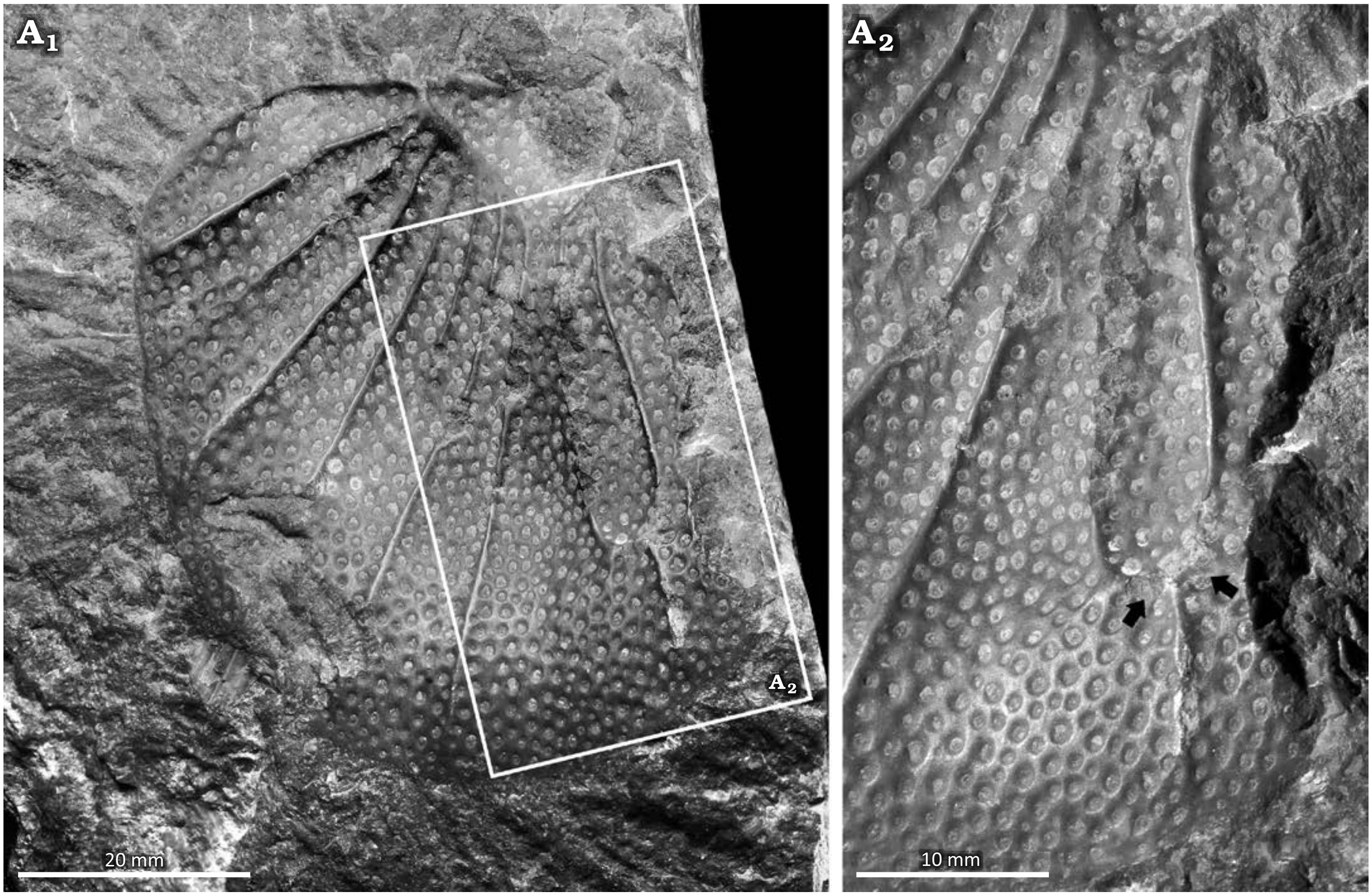

Fig. 4. Malformed styginid trilobite *Scutellum* (*Scutellum*) *pardalios* (Whidborne, 1889), NHMUK PI I 1108 from the Barton Limestone Member, Torquay Limestone Formation, Givetian, Middle Devonian, England, UK. A_1, pygidium preserved as external impression; A_2, close up showing fused pygidial pleurae (arrows).

NYSM 19740 is an isolated pygidium that is 11.6 mm long and 17.9 mm wide (Fig. $3A_1$). The specimen has an asymmetrical axial lobe (Fig. $3A_2$). Two axial rings are malformed, slightly curved to the right and extend across ~60% the axial lobe.

Scutellum (*Scutellum*) *pardalios* (Whidborne, 1889), NHMUK PI I 1108. Barton Limestone Member, Torquay Limestone Formation, Givetian, Middle Devonian, England, UK (Fig. 4).

NHMUK PI I 1108 is an isolated, partial pygidium preserved as an external impression that is 59.5 mm long and 44.0 mm wide (Fig. 4). The specimen has a malformation on the right side (left side in life) (Fig. $4A_2$). The specimen shows fusion of two pygidial ribs into a singular rib. Fusion occurs 29.1 mm from the pygidial axis (Fig. $4A_2$). The fused rib terminates 4.8 mm from the pygidial margin.

Discussion

Examining the specimens presented herein revealed evidence of exoskeletal injuries and morphologies indicative of genetic anomalies. Furthermore, one specimen shows signs of epibiont interactions. We explore each group of abnormalities separately and propose possible explanations for the observed morphologies.

Injuries.—The examined *Lioharpes venulosus* has a U-shaped indentation along the cephalic fringe. This morphology is comparable to malformations in other harpetid trilobites assigned to injuries (see Warburg 1925; Sinclair 1947; Prantl and Přibyl 1954; Šnajdr 1979; Owen 1983, 1985; Přibyl and Vaněk 1986). We, therefore, propose that this malformation is an injury, expanding the record of injured *L. venulosus* (Prantl and Přibyl 1954; Přibyl and Vaněk 1986). Determining the injury origin is complicated as injured harpetid cephala have been attributed to moulting complications (Owen 1983), failed predation (Šnajdr 1979; Owen 1983), and unknown origins (Fatka et al. 2022). The large cephalic region is commonly considered to have been damaged during moulting, as the soft-shelled exoskeleton was prone to tearing (Owen 1983, 1985). We align with this proposal, suggesting that the injury records a complicated moulting event.

The fringe pits along the injury margin are deformed and show possible fusion. This recovery system broadly reflects the pattern proposed for trinucleid trilobites (Šnajdr 1979; Owen 1985), indicating similar exoskeletal growth pathways. However, the Owen (1985) trinucleid model did not illustrate larger pits or pit fusion, highlighting subtle differences between trinucleid and harpetid recovery, despite their parallel evolutionary adaptations (Beech et al. 2024).

Injuries that remove sections of the cephalic fringe could significantly affect the functionality of the individual (Owen 1985; Babcock 1993; Bicknell et al. 2018). Harpetid fringes likely served multiple functions (Pates and Drage 2024; Beech et al. 2024) including filtering for food (Fortey and Owens 1999), sensory roles (Schoenemann 2021), sediment ploughing (Staff and Reek 1911; Ebach and McNamara 2002), hydrostatic support (Richter 1920), cephalic reinforcement (Miller 1972; Ebach and McNamara 2002), burrowing (Pates and Drage 2024), and enhancing hydrodynamic efficiency (Pates and Drage 2024). Regardless of the primary function, a cephalic injury would have been detrimental. We, therefore, propose that the cephalon would recover relatively quickly over subsequent moulting events (Owen 1985), as more critical exoskeletal regions receive priority in regeneration (Zong and Bicknell 2022; Bicknell and Cuomo 2024).

Teratologies.—Teratological malformations in trilobites often reflect the addition, reduction, or deformation of spines, furrows, ribs, tergites, and nodes (Owen 1985; Babcock 1993, 2007; Bicknell et al. 2023a). In the examined specimens, teratologies in *Calymene blumenbachii*, *Scutellum* (*Scutellum*) *pardalios*, and *Treveropyge* sp. pygidia were documented. These reflect asymmetry, abnormal axial rings, and fusion of pygidial ribs, common examples of teratologies in the trilobite fossil record (see Šnajdr 1958, 1981; Přibyl and Vaněk 1973; Strusz 1980; Owen 1985; Budil et al. 2010; Nielsen and Nielsen 2017; Zong 2021).

The isolated *Calymene blumenbachii* pygidium shows irregular and fused ribs. This is comparable to malformed specimens of *Dalmanities pleuroptyx* (Green, 1832) (Bicknell et al. 2024a: fig. 12), *Dechenella macrocephalus* (Hall, 1859) (Rudkin 1985: fig. 2), *Niobina* sp. (Tjernvik 1956: pl. 5: 17), and *Prionopeltis archiaci* (Barrande, 1846) (Šnajdr 1981: pl. 5: 4), all of which exhibit significant rib disruption. Larger teratologies with comparable morphologies are attributed to major developmental malfunctions (Rudkin 1985). As the teratology is limited to the pleural region, this was likely a genetic or developmental issue that was not detrimental to the individual (Owen 1985).

The *Treveropyge* sp. pygidium has an asymmetrical axial lobe with two malformed axial rings. These morphologies are similar to malformed *Calliops marginatus* Tripp, 1962 (Tripp 1962: pl. 28: 16), *Dolicholeptus licticallis* Öpik, 1982 (Bicknell et al. 2023b: fig. 2E), and *Sceptaspis lincolnensis* (Branson, 1909) (Rudkin 1985: fig. 1E–G). These minor malformations have been attributed to genetic malfunctions (Owen 1985; Bicknell et al. 2024a), particularly incomplete development (Rudkin 1985), or non-functional somites (Nielsen and Nielsen 2017). We propose that a genetic malfunction occurred for NYSM 19740. As the malformed region is not proximal to vital organs, this teratology would not have impacted the individual (Nielsen and Nielsen 2017).

Scutellum (*Scutellum*) *pardalios* (Fig. 4) shows evidence of two pygidial ribs fusing into one rib distally. As there are no exoskeletal regions devoid of ornamentation, a condition expected of failed predation in styginids (Šnajdr 1990a, b; Holloway 1996), we exclude this option here. Most other malformed styginids reflect molting complications resulting in abnormal recovery (Šnajdr 1960, 1990b; Erben 1967), genetic malfunctions (Holloway 1996), or parasitic infestation during earlier developmental stages (Šnajdr 1990a, b). A review of the literature highlighted only one other malformed styginid with distal fusion of two ribs, *Bojoscutellum obsoletum* (Šnajdr, 1960) (Šnajdr 1990b: fig. 2), and this is attributed to parasitism (Šnajdr 1990b). As there is no evidence for parasitism, we propose that NHMUK PI I 1108 may have experienced a complicated moult due to its macropygous pygidium (see Šnajdr 1960, 1990b; Erben 1967), or had a genetic malfunction during early development, either of which may have resulted in fused ribs. Determining the impact of the malformation on the individual is complex. However, as the disruption is minor, it likely would not have led to significant functional impairment of the pygidial region.

Epibionts.—Trilobite exoskeletons with encrusting animals are important examples of organismal interactions (see Prokop 1965; Morris and Rollins 1971; Sprinkle 1973; Kesling and Chilman 1975; Brandt 1996; Taylor and Brett 1996; Kacha and Šarič 2009; Key et al. 2010; Vinn et al. 2017). Within the trilobites examined here, we report one *Calymene blumenbachii* specimen (NHMUK PI In 65061, Fig. 2) with epibionts resembling those on *Flexicalymene* Shirley, 1936 (Brandt 1996: figs. 1.4, 1.6). This is an encrusting trepostome bryozoan forming a low mat with an ovate zoarium preserved on the 3rd thoracic tergite. The restricted encrustation region within the area bounded by articulating sclerite margins suggests that the encrustation occurred while the animal was alive (see Brandt 1996; Key et al. 2010).

Conclusions

Novel records of trilobite abnormalities are explored herein using Silurian and Devonian species. In doing so, we demonstrate additional examples of injuries, teratologies and possible bryozoan interactions. This presents further insight into trilobite paleoecology and sheds more light on how trilobites recovered from such conditions.

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