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Parasitic infestation in a Middle Ordovician *Illaenus* (Trilobita)

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Abstract

Evidence for parasites in the fossil record is rare. As such, any examples present insight into parasitism in deep time. Trilobites have often been used for documenting parasites in the Paleozoic. Here we examine an *Illaenus* sp. pygidium from the Middle Ordovician of Estonia that displays thirteen small structures with domical to crater-like shapes. These morphologies are consistent with circular depressions on the pygidium inner surface. We propose that these structures formed while the trilobite was alive and record an infestation located within soft tissue. The trace maker seems to have influenced pygidial mineralization and caused a pathological reaction. The symbiont may have been capable of bioerosion, excavating these depressions by dissolving the trilobite's mineral tissues; however, this scenario is less likely considering comparisons with syndromes and pathologies known in modern arthropods. The parasitic organism may have fed on the trilobite's tissues or utilized nutrients within the trilobite's body for growth. These observations are consistent with a parasitic organism.

Non-technical Summary

Parasites are rarely found in the fossil record, making any discovery of such organisms incredibly valuable for understanding ancient ecosystems. Trilobites, an ancient group of arthropods, are particularly useful in studying parasitism in deep time. In this study, we look at a fossil of *Illaenus*, a genus of trilobite, which shows thirteen small, round depressions on its rear section (called the pygidium). These depressions likely formed while the trilobite was still alive and suggest the presence of a parasite that may have lived within the soft tissue of the trilobite. The parasite could have caused changes in the mineralization of the trilobite's skeleton or, possibly even eaten or absorbed nutrients from the trilobite's body. This discovery provides new evidence that parasitic relationships existed hundreds of millions of years ago.

Introduction

Trilobites are a highly diverse group of Paleozoic arthropods, first appearing in the early Cambrian (Fortey and Owens, 1997; Jell, 2003; Geyer, 2019). In northern Estonia, the trilobite fauna was diverse throughout the Middle and Upper Ordovician, with approximately 100 genera or subgenera (Rõõmusoks, 1997). Biogeographically, the Estonian Ordovician benthic fauna is part of the Baltoscandian Province (see Jaanusson, 1979). Fossils of illaenids are very common in the Middle Ordovician carbonate facies of northern Estonia; usually represented as pygidia and cranidia (Rõõmusoks, 1997). They inhabited a shallow temperate sea with normal salinity.

Malformations in trilobites have been extensively documented. Most records reflect injuries and developmental issues (Owen, 1985; Babcock, 2003, 2007; Zong, 2021a, b; Bicknell and Smith, 2022, 2023; Bicknell et al., 2021, 2023a,b). There has been less examination of structures linked to disease or parasitism, which are considered (paleo)pathologies (Babcock, 2007; De Baets et al., 2021b). Parasitism in trilobites is thought to be recorded in swellings, pits and lesions, and certain types of borings (Conway-Morris, 1981; Owen, 1985; Geyer, 1990; Babcock, 2007; De Baets et al., 2021a; Montagna and Ruggiero, 2023; Bicknell et al., 2023a, 2024). As trilobites have been extinct since the Paleozoic, the best way to understand their pathologies is to compare specimens to similar phenomena in modern marine arthropods, such as decapods and horseshoe crabs (De Baets et al., 2021b).

Shell boring within the exoskeleton may reflect parasites (Babcock and Peng, 2001) and are known from live individuals and carcasses (Babcock, 2007). Borings produced while the trilobite was alive coincided with a cellular response and present insight into responses to drilling

(Babcock, 2007). The most compelling evidence of drilling parasitism in the Paleozoic comes from agnostoids, which show signs of tissue growth and deformation of the exoskeleton around small pits (Babcock, 2007). Babcock (1993) and Babcock and Peng (2001) illustrated a boring that was internally sealed by a pearl-like protrusion and morphologically similar to borings made by nematodes in foraminiferans (Sliter, 1971; Lipps, 1983, p. 357; Babcock, 2007).

In this study, symbiosis is considered any long-term, close biological interaction between two or more different organisms, whether parasitic, commensalistic, or mutualistic. Modern ecology and biology textbooks typically use the "de Bary" definition, which applies symbiosis to all long-term interspecific interactions, moving away from the narrower definition that restricted symbiosis to mutualism (de Bary, 1878; Martin and Schwab, 2013). Parasitism is defined here as a relationship in which one organism benefits at the expense of another, negatively impacting the host (i.e., Conway-Morris, 1990; Tapanila, 2008; Robin, 2021). Here we expand the fossil record of parasitism by describing domical to crater-like structures in a mold of *Illaenus* sp. pygidium, discuss the origin of these morphologies, and explore the paleoecology of the association.

Geological background

During the Ordovician, Baltica drifted from the temperate into a subtropical climatic zone (Cocks and Torsvik, 2005; Torsvik et al., 2013). In the Darriwilian, the region of modern Estonia was submerged under a shallow epicontinental sea that had minimal bathymetric variation and an extremely low sedimentation rate (Nestor and Einasto, 1997). A sequence of grey argillaceous and calcareous sediments accumulated along the shelf, with bioclasts (mostly echinoderms and brachiopods) decreasing and clay content increasing away from shore (Nestor and Einasto, 1997).

In northern Estonia, limestones are predominantly exposed, having formed in the shallow part of a normal marine basin (Nestor and Einasto, 1997; Meidla et al., 2024). The Middle Ordovician limestones are temperate water carbonates (Meidla et al., 2024). They are usually light grey in color due to clay minerals and pyrite content when fresh, and often reddish when weathered. The shelly fossils are usually well preserved. In northeast Estonia, the Middle Ordovician limestones are often dolomitized (Meidla et al., 2024).

Material and methods

Collections with Ordovician trilobites from Estonia were examined. These are in the Natural History Museum, University of Tartu (n=2,000) and the Department of Geology at Tallinn University of Technology (GIT) (n≥650). A total of 54 pygidia of *Illaenus* were checked. An isolated *Illaenus* sp. pygidium GIT 437-107 from the Darriwilian of northern Estonia was identified with abnormal structures. Due to a lack of meta-data, the exact locality of the specimen is unknown. This specimen was photographed using a Leica Z16 APO system, and measurements of the specimen were obtained from photographs using computer software. Additional photographs were taken after covering the fossil with sublimate ammonium chloride.

Repository and institutional abbreviation. Studied specimen is deposited at the Department of Geology, Tallinn University of Technology (GIT).

Results

The examined specimen is an internal mold of an *Illaenus* sp. pygidium that is 33 mm long and 47 mm wide. The surface of the mold shows thirteen smooth bumps on its surface with height of 0.4 to0.7 mm (Figs. 1–3); otherwise the surface is smooth with only a weak impression of the axial lobe. Five bumps have a small depression in the center and are located about the pygidial median axis. Two bumps are located on the right pleural field and one on the left pleural field. The bumps never touch each other. The structures range between 0.9–1.8 mm ($\bar{x}$=1.3 mm, σ=0.25 mm) and central depression range between 0.3–0.6 mm (n=7, $\bar{x}$=0.5 mm, σ=0.12 mm). The outer slopes of the simple bumps are steep and their external contours are rather sharp. The inner slopes in crater-shaped bumps are similarly steep and the contours of the central depression are sharp.

Discussion

The asymmetrical distribution of structures, the irregular spacing, and overall smoothness of this *Illaenus* pygidium illustrate that these structures are not a standard pygidial morphology. Despite being damaged, exoskeletal remains are visible along the specimen edge. The circular structures must therefore have been depressions in the pygidial inner surface. They may have coincided with exoskeletal thinning and the preserved exoskeleton indicates that the depressions would have almost punctured the pygidium in these

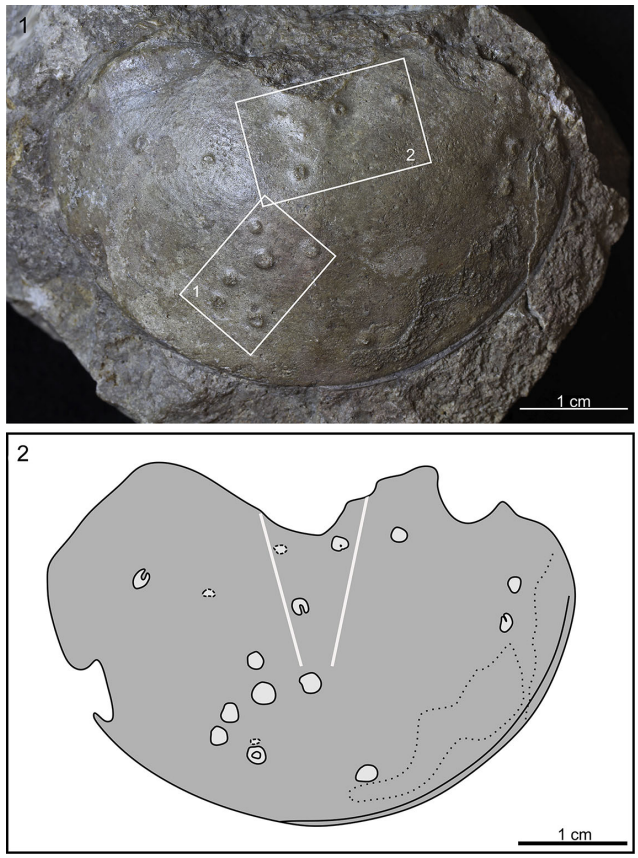

Figure 1. Internal mold of *Illaenus* sp. pygidium with traces of parasitic infestation from Darriwilian of northern Estonia (GIT 437-107); (**1**) Complete specimens. Rectangle 1 shows location of detailed Fig. 2.1, and rectangle 2 shows location of detailed Fig. 2.2. (**2**) Drawing of the pygidium.

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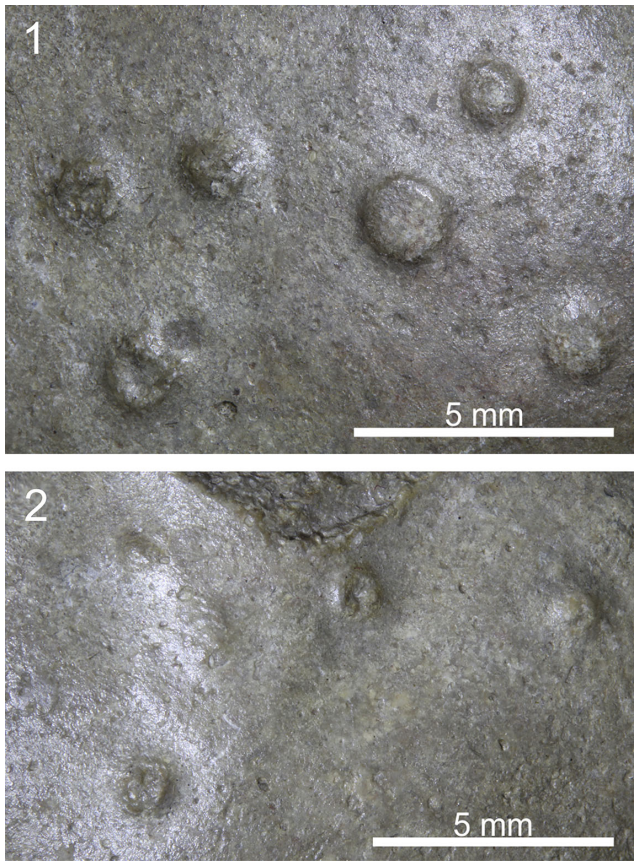

Figure 2. Internal mold of *Illaenus* sp. pygidium with traces of parasitic infestation from the Darriwilian of northern Estonia (GIT 437-107); (**1**) Detail view of traces; showing two simple bumps and four crater-like structures, (**2**) Detail views of traces; showing two simple bumps and two crater-like structures.

areas. Due to the variety of possible explanations for these structures, we present all possibilities below, and attempt to systematically exclude options that are unlikely.

Drilling. The morphology of the depressions is not indicative of predatory drillings or shell disease (De Baets et al., 2021). While the shape of depressions somewhat resembles *Oichnus* drillings, the depression orientations are 180° opposite the expected orientation for drill holes originating at the external exoskeletal surface. The pits have variable diameters, suggesting multiple mistaken attacks by predators of different sizes. This seems very unlikely, as it requires an array of distinct drilling predators. Even if these pits were mistakenly created by the trace maker (i.e., a drilling predator) of *Oichnus paraboloides*, at least some holes should have penetrated the entire skeleton (Wisshak et al., 2015). We can therefore exclude drilling predators as an option here.

Epizoans. Some pits in trilobite exoskeletons are superficially reminiscent of attachment sites of epizoans (Babcock, 2007). However, these would have been encrusted on the external surface and would result in different morphologies, excluding this option.

Microbially induced disease. Bacteria may cause shell diseases that result in external cuticular damage or perforations that can impact soft tissues in the final stages (Sindermann and Rosenfield, 1967; Noga et al., 2000; Shields et al., 2015; Klompmaker et al., 2016; Newton and Smolowitz, 2018; De Baets et al., 2021). Microbes typically cannot penetrate the exoskeleton and usually rely on external injuries, which are not present in our specimen. More importantly, shell disease typically starts on the external exoskeleton and results in pits with different morphologies. Also, unicellular algae or fungi have been implicated in shell disease of marine arthropods, but the resulting morphologies are inconsistent with morphologies observed here (De Baets et al., 2021).

Post-mortem bioerosion. The depressions are too shallow to be domiciles of boring organisms but could record attachment scars of a bioeroding encruster. However, no bioerosional attachment structures with these semi-circular morphologies are known. These structures are therefore not post-mortem bioerosional traces.

Tremichnus. This is a trace fossil that records the embedment of an animal within a crinoid. The structures do resemble *Tremichnus* in crinoids (Brett 1978, 1985). However, the depressions are located on the internal surface of the pygidium, not externally as in crinoids. Moreover, *Tremichnus* occurs in accretionary skeletons as a modification of a living mesoderm, as opposed to a mineralized cuticular skeleton of trilobites.

Tumors. The structures are morphologically comparable to tumors within modern arthropods. However, the confident identification of tumor-like growth, particularly those related to cancer, is very rare and isolated in modern marine arthropods like decapods or horseshoe crabs (Sparks, 1985; Vogt, 2008; Miroliubov et al., 2023). True neoplasia are seldom produced by cancer in arthropods (Chong, 2022) and usually other organisms are implicated in their formation (De Baets et al., 2012). As such, we conservatively exclude this option here.

Symbiotic interactions. Conway Morris (1981), Babcock (2007), and De Baets et al. (2021) provide summaries of parasitism in trilobites. Parasitic infestations commonly consist of gall-like or tumor-like growths known as neoplasms of the exoskeleton (e.g., Snajdr, 1978a, b, 1981; Conway Morris, 1981; Owen, 1985; Babcock, 1993, 2003, 2007).If the structures in *Illaenus* were formed *syn vivo*, the trace maker would have been located within the trilobite's soft tissues. The trace maker may therefore have lodged or attached itself within the soft-tissue and inhibited pygidial biomineralization around the foreign organism. The 'infestation' may have occurred during a moulting event, resulting in scars underneath the exoskeleton. It is also possible that parasites maintained their position in the following molt. Alternatively, the symbiont excavated these depressions by dissolving the trilobite exoskeleton. In either case, the symbiotic organism could have affected the exoskeleton and mechanically weakened the pygidium and likely used the trilobite tissues and other nutrients to grow. We found an endobiotic parasite to be the most likely explanation for the structures in *Illaenus* because the other explanations explored above can either easily be rejected or they seem considerably less likely.

Šnajdr (1978a) traced the ontogenetic development of galls in the various molt stages of the trilobite, and this approach makes it possible to distinguish two main types of neoplasms: those formed by parasites that lived beneath the exoskeleton and survived one or more molting events, and those formed by organisms located at or near the exoskeletal surface and thus were lost during molting (De Baets et al., 2021). The downwards broadening morphology of depression in the inner surface of the *Illaenus*

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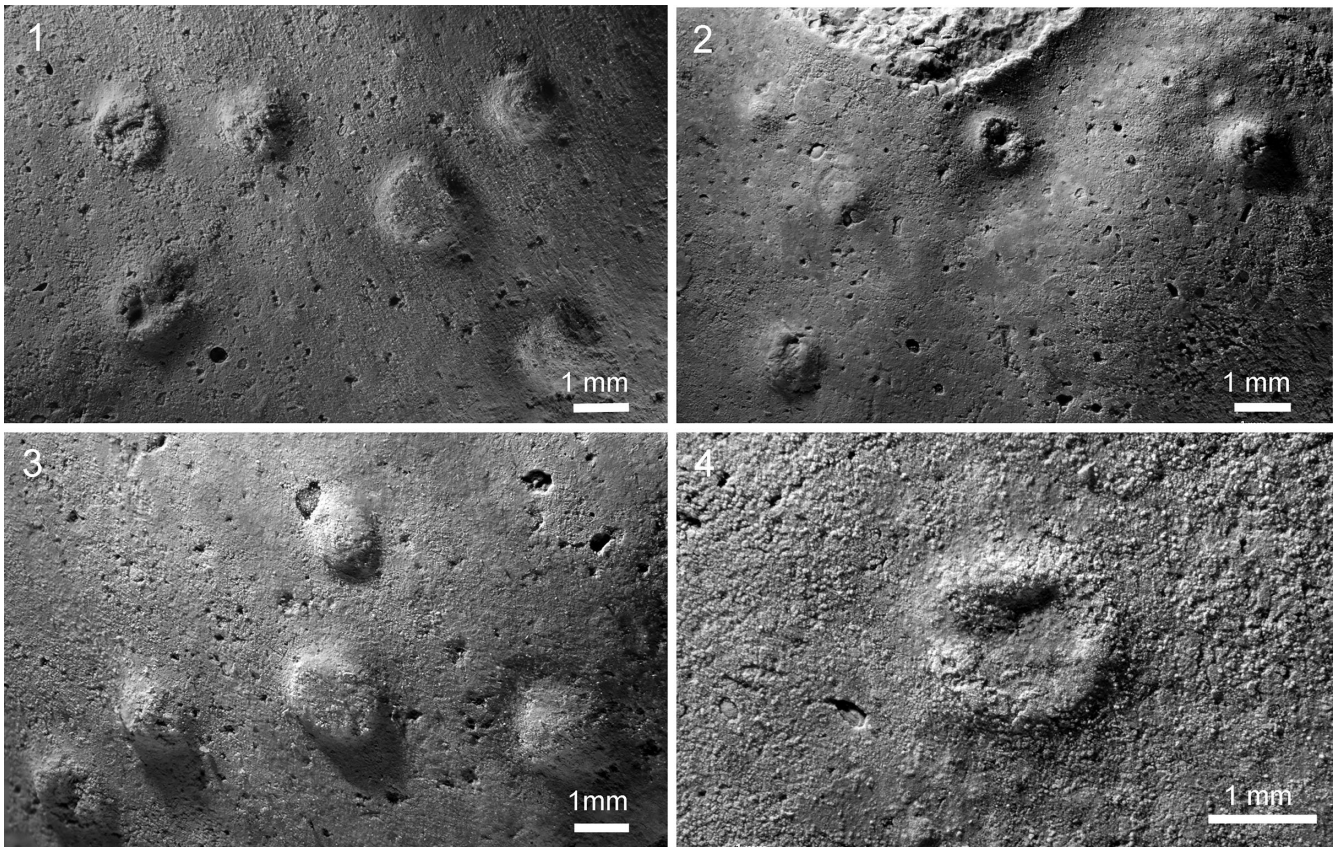

Figure 3. Internal mold of *Illaenus* sp. pygidium with traces of parasitic infestation from the Darriwilian of northern Estonia (GIT 437-107); (**1**–**4**) Detail view of traces; showing simple bumps and crater-like structures.

pygidium is more consistent with a parasite that lived beneath the exoskeleton. Neither teratology, however, shows strong site selectivity—an indicator of ectoparasites—consistent with parasites common occurrence in the protective hollows of pleural furrows (Jell, 1989). The depressions in the inner surface of the *Illaenus* pygidium do not correspond to protective hollows of pleural furrows, thus supporting the endoparasite nature of the infesting organism. However, Jell (1989) figured five bulges in *Moatunia distincta* and four bulges in a specimen of *Eymekops hermias* associated with the caecal system, suggesting that endoparasites might have been lodged in the digestion and absorption system and had bulged the exoskeleton around them. While this is interesting, we lack evidence to suggest this also occurred here.

Circular pits with slightly irregular edges that partially penetrate the exoskeletons are called "borings" (Whiteley et al., 2002, fig. 2.15D-F), and usually the pit-makers did not significantly harm the hosts (Brandt, 1996). The same would be expected for the pits in the *Illaenus* sp. pygidium if those pits were made on the external surface of the pygidium. However, the trace maker was likely within the trilobite's soft tissues, suggesting markedly more significant harm to the individual and more ability to respond by changing growth patterns. Furthermore, processes in arthropods would markedly differ from those in other biomineralized groups, as molting would effectively remove symbionts (Duneau and Ebert, 2012; De Baets et al., 2021). The most similar cases from modern marine arthropods are internal cyst-like or small tumor-like masses from spore-forming Microsporidia (Sokolova et al., 2015).

A rare exception that could lead to superficially similar indented pathologies was observed in modern decapods (mud crabs) inflicted by "rust spot" shell disease (Andersen et al., 2000). These authors found no evidence for an infectious or parasitic culprit involved in this modern mud crab disease during histopathological investigations, and the main histological features in the decapod *Scylla* included endocuticular indentation below cavities in the upper endocuticle, among various other phenomena in soft-tissues which would be difficult to preserve in fossil arthropods. The development of indentations of rust spot shell disease is less regular in morphology, size and spacing than the structures observed in the trilobite. Given these differences, the observed morphologies are unrelated to bacteria or unicellular organisms. Various eukaryotic organisms, including helminths, could also produce cyst-like or tumor-like structures in invertebrates, although no structures with these characteristics have yet been reported from marine arthropods (Vogt, 2008; De Baets et al., 2021b). Regardless of the precise identification of the culprits, infestation during life by parasitic organisms or a pathological response by the trilobite is the mostly likely explanation for the structures observed here.

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