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Research Paper

Shelly coprolites record durophagous predation in the Late Ordovician Bohdalec Formation (Katian; Prague Basin, Czech Republic) ☆

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ABSTRACT

Trace fossils can illustrate important palaeobiological interactions within a fossil assemblage that body fossils do not record. A group of trace fossils that showcase feeding ecology, and evidence of predation, are coprolites. Shelly coprolites are useful for documenting records of durophagous predators or scavengers within a substrate. To expand the record of these traces from the lower Paleozoic, here we present 12 shelly coprolites from the Late Ordovician (Katian) Bohdalec Formation of the Czech Republic. These coprolites contain abundant *Onnia superba* (Bancroft, 1929) fragments with marked breakages across exoskeletal sections. Rarer evidence for gastropods, bivalves, crinoid debris, and another indeterminate shelly material are also observed within the coprolites. While the producer cannot be irrevocably determined, possible options are explored. We propose that larger, co-occurring trilobites and predatory cephalopods likely made the majority of coprolites. Furthermore, large unbiomineralised arthropods, such as phyllocarids and eurypterids are highlighted as possible producers. Continued examination of these trace fossils will highlight when and where similar interactions between trophic levels had occurred.

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1. Introduction

Shelly aggregates containing the remains of disarticulated trilobite exoskeletons present important insight into Paleozoic predator-prey systems. The majority of Paleozoic shelly aggregates, often considered coprolites, are known from Cambrian deposits (Mikuláš, 1995; Nedin, 1999; Vannier and Chen, 2005; English and Babcock, 2010; Daley et al., 2013; Kulkarni and Panchang, 2015; Kimmig and Strotz, 2017; Bicknell and Paterson, 2018; Kimmig and Pratt, 2018; Bicknell et al., 2022a). Cambrian coprolites are considered the result of durophagous predation by trilobites (Daley et al., 2013; Bicknell et al., 2021, 2022a), polychaetae worms (Shen et al., 2014; Kulkarni and Panchang, 2015), priapulid worms (Vannier, 2012; Kimmig and Strotz, 2017; Kimmig and Pratt, 2018; Pratt and Kimmig, 2019), and large, unbiomineralised arthropods (Mikuláš, 1995; Nedin, 1999; Zhu et al., 2004). Trilobite-rich, shelly coprolites from younger Paleozoic deposits

have been attributed to predation by large, pterygotid eurypterids (Bicknell et al., 2022c, 2023) and polychaetae worms (Toom et al., 2020). The restricted record of shelly coprolites from non-Cambrian Paleozoic deposits has limited detailed consideration of trace makers from these formations. To expand the record of Ordovician coprolites and considered possible durophagous predators from this time period, here we consider 12 shelly aggregates from the Late Ordovician (Katian) aged Bohdalec Formation, Czech Republic. These shelly aggregates contain fragmented sections of the trilobite *Onnia superba* (Bancroft, 1929), as well as rare bivalves, gastropod, crinoid debris, and indeterminate shelly material. These aggregates present important insight into the trophic interactions and food web preserved within the formation.

2. Geological context

Examined specimens were collected from siltstone beds in the Bohdalec Formation (middle Katian, Upper Ordovician; Fig. 1(B)). The formation is located in the Bohemian Massif, centre of the Czech Republic (Kraft et al., 2023), in the Prague Basin (Fig. 1(A)). This basin consists of Ordovician to Middle Devonian

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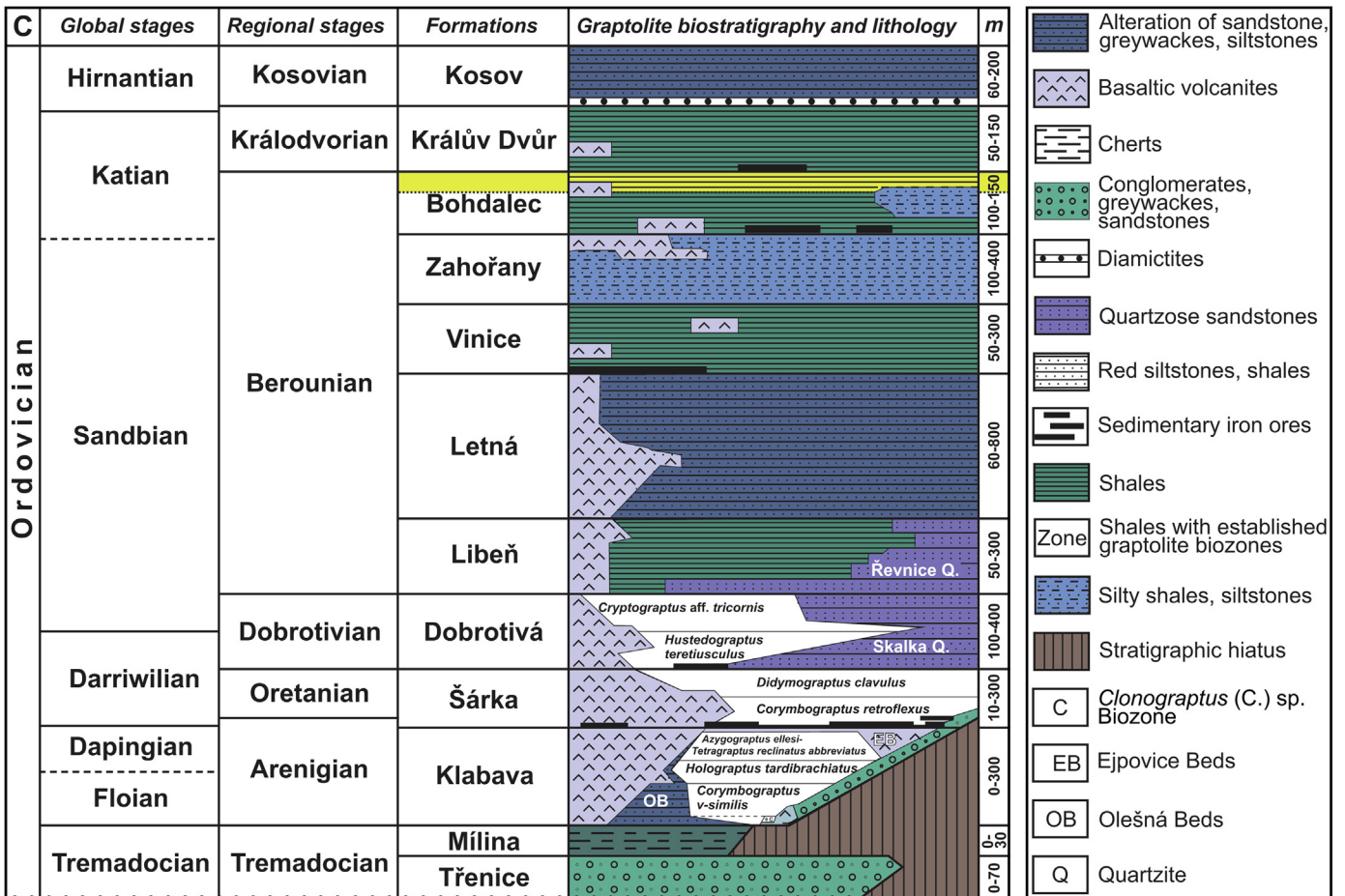
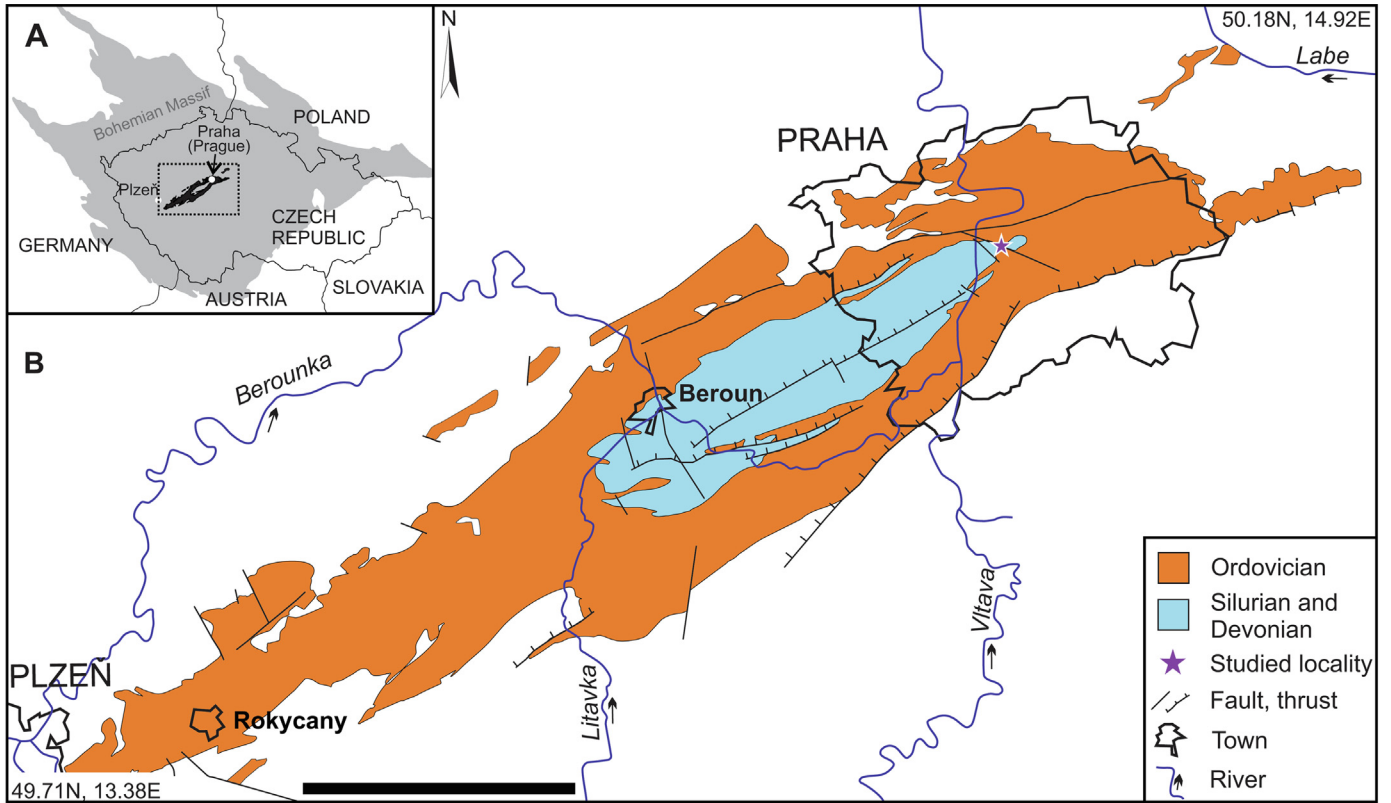


Table 1
Summary of dimensions for the examined shelly aggregates.

Specimen	Length (mm)	Maximum width (mm)	Material contained within	Fig.
NM L 64614	37.8	28	<i>Onnia superba</i>	Fig. 2(A, B)
NM L 64615	69.9	36.2	<i>Onnia superba</i>	Fig. 2(F, G)
NM L 64616	37.6	29.9	<i>Onnia superba</i>	Fig. 2(C–E)
NM L 64617	19.2*	15.2*	Indet. shelly material	Fig. 3(A)
NM L 64618	37.8	14.8	<i>Onnia superba</i>	Fig. 3(B)
NM L 64619	20.4	10.7*	<i>Onnia superba</i> , gastropod indet.	Fig. 3(C)
NM L 64620	28.7	16.5*	<i>Onnia superba</i>	Fig. 3(D)
NM L 64622	27.4	16.1*	<i>Onnia superba</i>	Fig. 4(C)
NM L 64623	42.2	20.8	<i>Onnia superba</i> , bivalve indet., crinoid indet.	Fig. 4(A, B)
NM L 64626	30.1	26.2	<i>Onnia superba</i>	Fig. 5(A)
NM L 64654	78.9	32.6	Unprocessed bivalve indet., indet. shelly material	Fig. 5(C)
NM L 64655	44.1	40.2	<i>Onnia superba</i>	Fig. 5(B)

* Minimal measurement value as the specimen is broken at the rock edge.

volcano-sedimentary deposits preserved as a long, narrow, denudation relict.

The Bohdalec Formation consists of black-grey silty shales. The silty shales often contain disseminated pyrite, indicative of a poorly oxygenated environment (Havlíček, 1998). The formation base is defined by the so-called Karlík Iron Ore Horizon that locally replaced shales with oolitic and carbonate admixture (Havlíček, 1998). The lower section of the Bohdalec Formation consists of grey and grey-black shales that commonly preserve the trilobite *Declivolithus alfredi* (Želízko, 1906). The grey and grey-black shales are overlain by shales and siltstones commonly preserving *Onnia superba*. Additional fossils include other trilobites, minute gastropods, bivalves, cephalopods, hyoliths, disarticulated machaeridians, conulariids, rare orthid and linguliform brachiopods, and graptolites (Röhlich, 2006; Bruthansová et al., 2023). The dark shales are occasionally overlain by the so-called Michle Facies that consists of centimeter to decimeter thick calcareous siltstone to sandstone layers, with thin shale interbeds (Bouček, 1928; Mikuláš, 1988, 1989, 1990; Röhlich, 2006). These beds preserve a fauna composed of trilobites, bryozoans, crinoids, and large brachiopods (Bouček, 1928; Röhlich, 2006). In general, fossils within the Bohdalec Formation are preserved as external and internal molds that are completely pyritized in a limited number of beds. Fossil abundance fluctuates between almost barren beds with limited disarticulated fossils through to fossiliferous accumulations of many (>100), mostly disarticulated specimens. In addition to body fossils, beds often preserve evidence of bioturbation. In particular, *Chondrites* isp., *Jamesonichites* isp., accumulations of *Tomaculum* isp. and minute pyritized tunnels have been observed (Mikuláš, 1989). Occasionally, fossils and traces are preserved within nodules of variable roundness and size classes.

One of the most common trilobites within the Bohdalec Formation is the trinucleid *Onnia superba* (Bancroft, 1929). This species is frequently preserved within silty shale beds and is observed in large quantities on some bedding planes. Specimens are found as disarticulated individuals in these mass occurrences and as complete specimens from both holaspid and meraspid stages (Bruthansová, 2019; Bruthansová et al., 2023). *Onnia superba* likely lived within deeper water conditions as the species is almost com-

pletely absent in the more shallow-water Michle Facies (Bruthansová et al., 2023). This contrasts trilobites such as *Phacopidina quadrata* (Hawle and Corda, 1847) and *Eudolites angelini* (Barrande, 1852) that are found throughout the Bohdalec Formation. Additional, rarer trilobite species observed in the silty shales are *Selenopeltis vultuosa* Příbyl and Vaněk, 1966, *Chlustinia keyserlingi* (Barrande, 1846), *Flexicalymene pragensis* Vaněk and Vokáč, 1997, and *Calymenella media* (Barrande, 1852). These forms are commonly observed as disarticulated specimens. Furthermore, there are rare records of cephalata and pygidia from *Nobiliasaphus kumatox* Šnajdr, 1982, *Sokhretia solitaria* (Barrande, 1846), *Chattiaspis oioponia* Vaněk and Vokáč, 1997, and *Dalmanitina asta* Šnajdr, 1982.

The faunal assemblage of the beds that preserved the shelly aggregates documented here is a low diversity biota that lived within an offshore environment, below the storm wave base. This palaeoenvironment is considered a muddy seafloor with temporary local influxes of sand. Most fossils are thought to be allochthonous or parautochthonous and likely experienced limited transport. Additionally, enrolled or complete outstretched trilobites and brachiopods preserved in butterfly position indicate an autochthonous origin for these forms.

3. Methods

Specimens were collected by J.B. while examining a recently constructed metro line in the Praha-Pankrác region. The excavation of these tunnels presented a unique opportunity to acquire palaeontological and sedimentological datasets from multiple, hundred-meter-long sections of the Bohdalec Formation. (Bruthansová et al., 2023). The shelly aggregates were coated with ammonium chloride and photographed under low angle light using a Nikon EOS 6D housed at the National Museum (NM), Prague, Czech Republic. The specimens are housed within the National Museum and assigned NM L numbers. Measurements of the specimens were made from images using ImageJ (Schneider et al., 2012).

Fig. 1. Geographical and stratigraphic information for the Prague Basin and the Bohdalec Formation. **A, B.** Geological map of the Prague Basin (Bohemia, Czech Republic), showing position of locality Praha-Pankrác (modified with permissions from Zicha et al., 2020: fig. 1.1). **A:** Position of the Prague Basin within the Czech Republic; **B:** Prague Basin geology. **C.** Stratigraphy of the Ordovician deposits within the Prague Basin showing the formation ranges proportional to the average, recorded thickness (modified with permissions from Kraft et al., 2001, and Lajblová and Kraft, 2014). Studied section of the Bohdalec Formation highlighted in yellow. Abbreviations: m, thickness in metres; Sr, Series; St, System. Scale bar: 20 km (B).

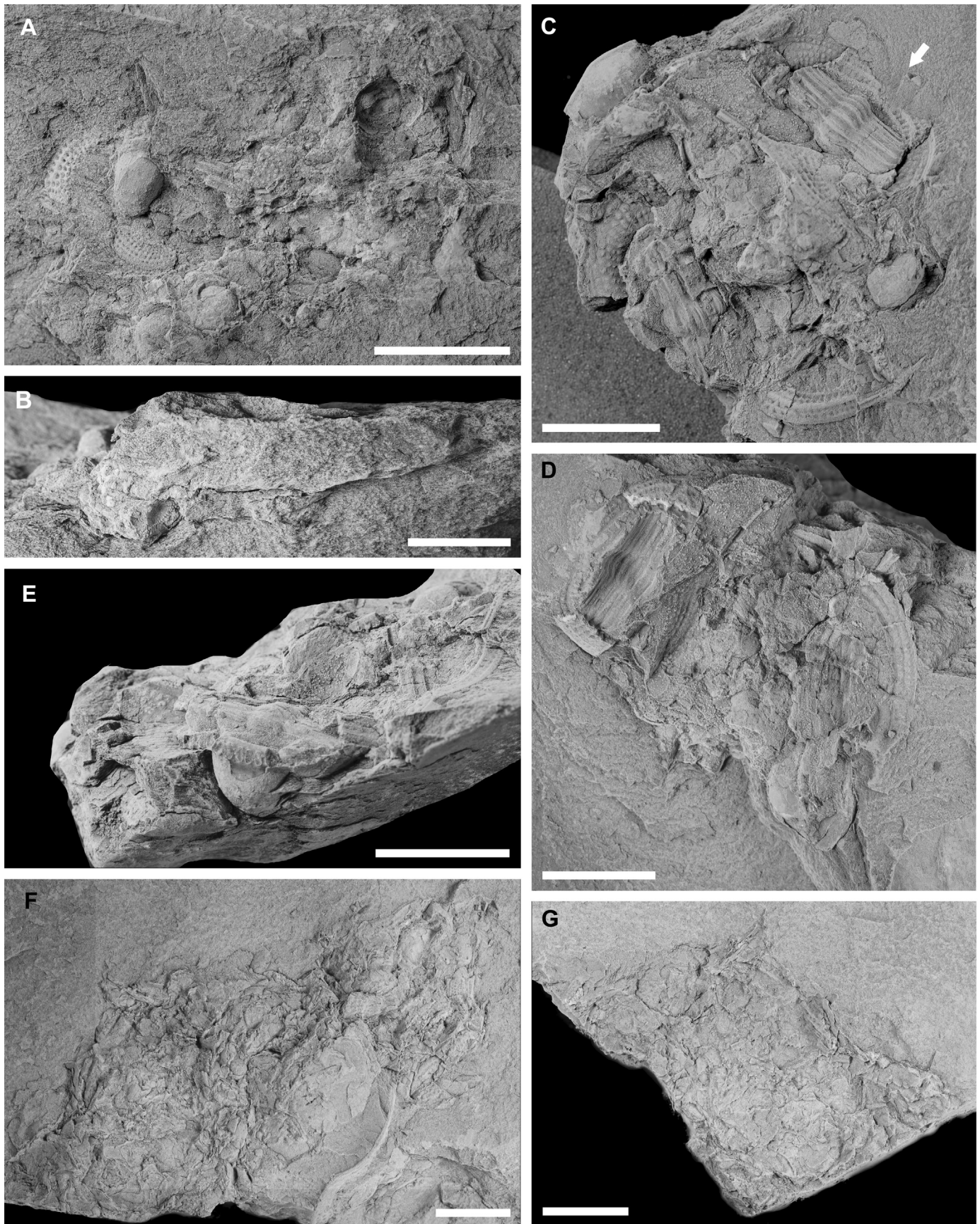


Fig. 2. Shelly coprolites containing extensive, fragmented *Onnia superba*. **A, B.** NM L 64614 in top-down (A) and side-on (B) views. **C–E.** NM L 64616, coprolite showing trilobite in an enrolled orientation (white arrow in C). **C, E:** Part, in top-down (C) and side-on (E) views; **D:** Counter-part. **F, G.** NM L 64615. **F:** Part; **G:** Counter-part. Specimens were coated with ammonium chloride. Images were converted to greyscale. Scale bars: 10 mm.

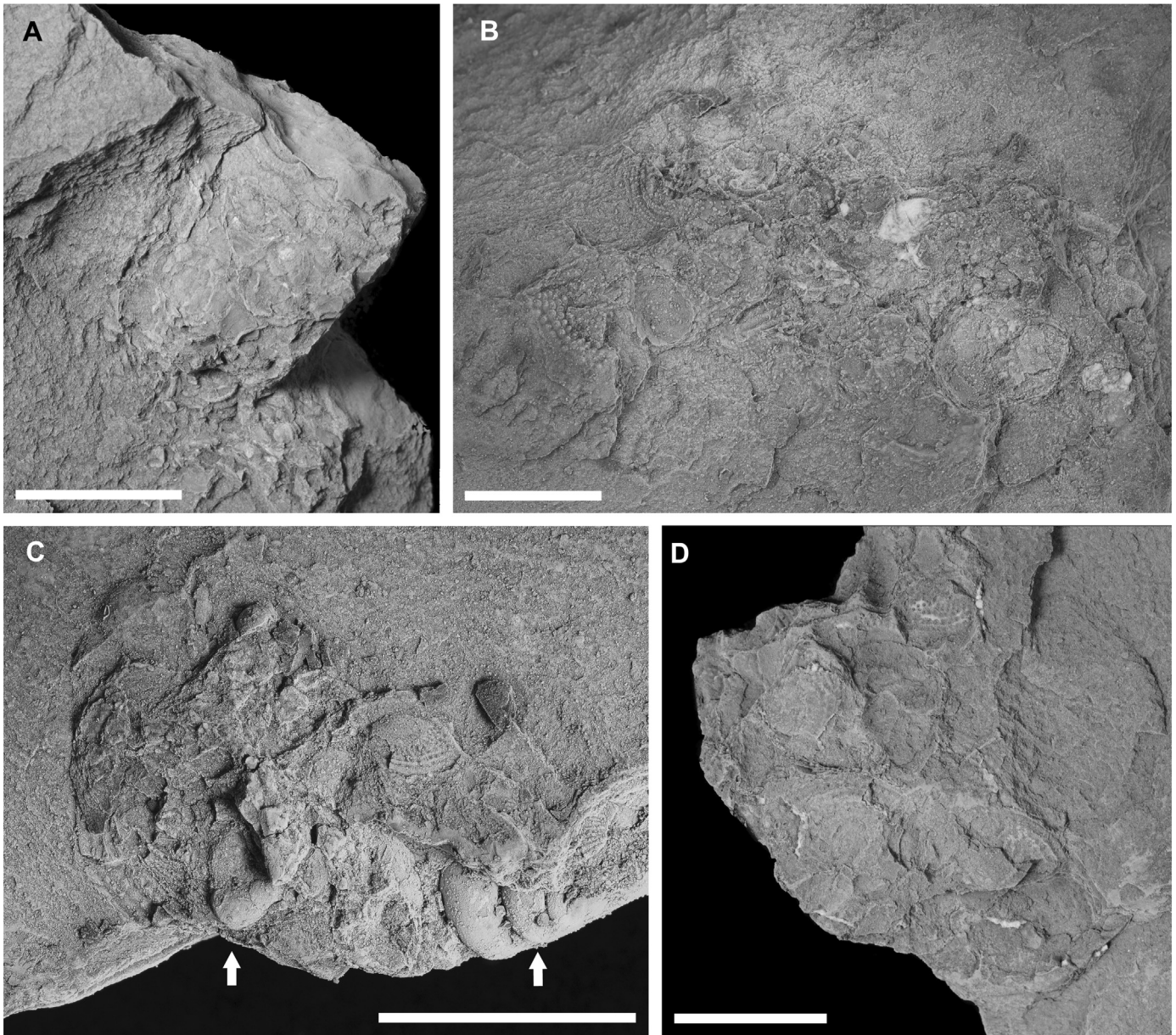


Fig. 3. Shelly coprolites containing indeterminate shelly material, gastropods, and fragmented *Onnia superba*. **A.** NM L 64617, specimen lacking trilobites, consisting possibly of unbiomineralised arthropod cuticle. **B, D.** Specimens containing fragmented trilobite sections. **B:** NM L 64618; **D:** NM L 64620. **C.** NM L 64619, specimen containing an unprocessed gastropod (white arrows) and trilobite fragments. Specimens were coated with ammonium chloride. Images were converted to greyscale. Scale bars: 10 mm.

4. Results

A total of 12 shelly aggregates are documented as both isolated traces and as part and counterpart that show no soft-tissue preservation (Table 1; Figs. 2–5). Specimens range in size from 19.2–78.9 mm long and 10.7–36.2 mm wide (Table 1). The aggregates range from being elongate and ovate to almost quadrate in morphology. Ten specimens have randomly arranged fragmentary cephalic, thoracic, and pygidial segments of *Onnia superba*. Additionally, an *O. superba* individual within one specimen appears partly enrolled (Fig. 2(C)). One shelly aggregate (Fig. 3(C)) has a gastropod shell within the aggregation. Two aggregates show sections of unprocessed bivalves (Fig. 4(A), Fig. 5(C)) and one shows possible crinoid debris (Fig. 4(A, B)). Additionally, one aggregate contains indeterminate shelly material, lacking any trilobite fragments (Fig. 3(A)). Viewing the aggregates from the side shows no evidence for burrowing, demonstrating that these are surface

traces (Fig. 2(B, E)). Finally, four specimens (NM L 64614, 64616, 64618, and 64655) have pyrite-rich borders.

5. Discussion

The aggregates documented here are comparable to the ichnogenus *Dactylostercus* Buchholz and Grimmerger, 2012, from the late Cambrian, as they both preserve trilobite remains. However, the aggregates are not string-shaped and do not conform with the morphology of the ichnogenus (Knaust, 2020). As such, we have left these specimens in open nomenclature, as is common for macroscopic Cambrian (Daley et al., 2013; Kimmig and Strotz, 2017; Kimmig and Pratt, 2018; Bicknell et al., 2022a), Ordovician (Aldridge et al., 2006; Hawkins et al., 2018), and Silurian (Bicknell et al., 2023) aggregates. Given this decision, we compare the Bohdalec Formation aggregates to other trilobite-rich aggregates considered coprolites (Babcock, 2003; Vannier and

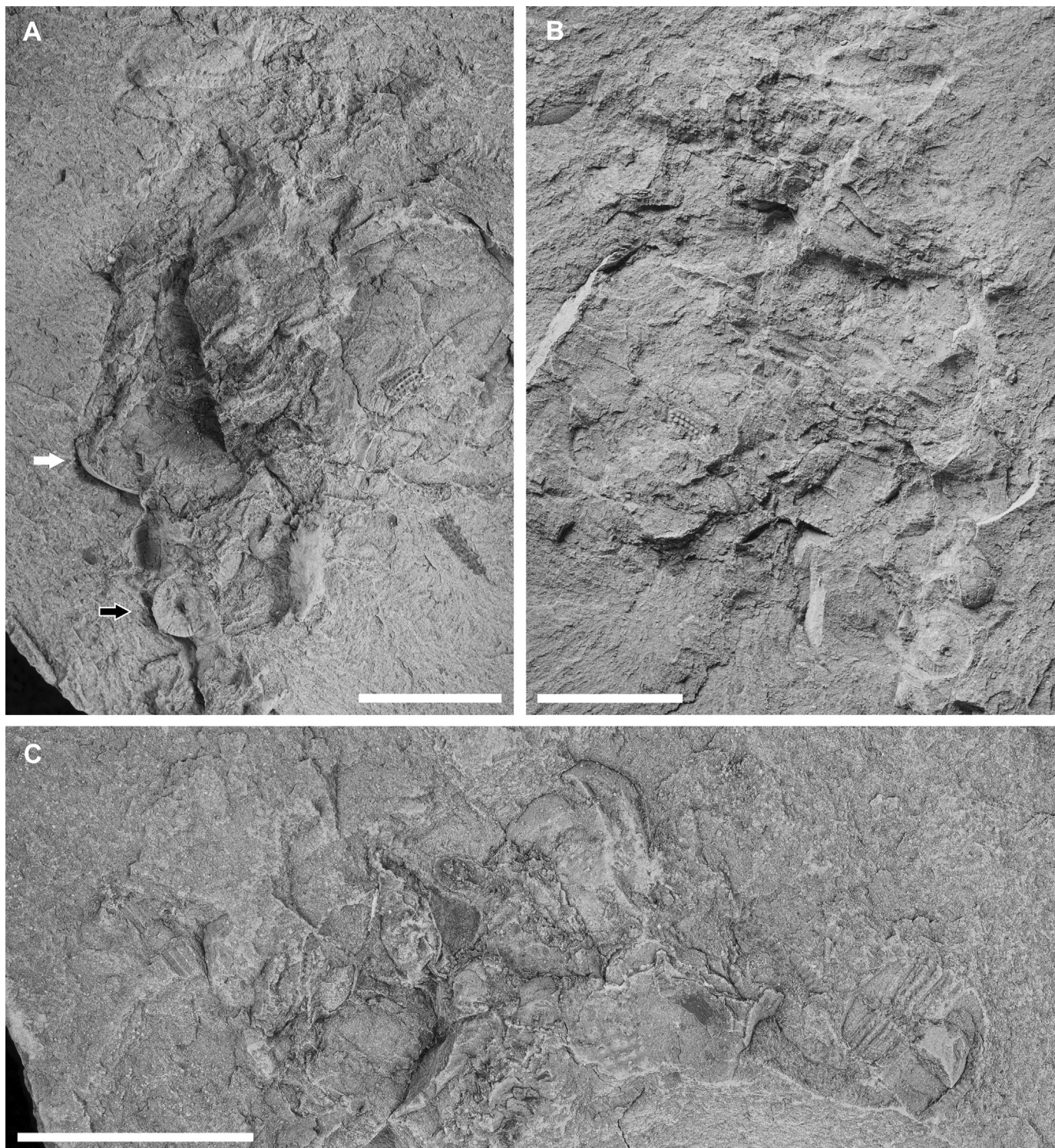


Fig. 4. Shelly coprolites containing bivalves, crinoid, and *Onnia superba*. **A, B.** NM L 64623, specimen showing trilobites, an unprocessed bivalve (white arrow), and a crinoid fragment (black arrow). **A:** Part; **B:** Counterpart. **C.** NM L 64622, specimen containing fragmented trilobite sections. Specimens were coated with ammonium chloride. Images were converted to greyscale. Scale bars: 10 mm.

Chen, 2005; Daley et al., 2013; Kimmig and Pratt, 2018; Ding et al., 2020; Bicknell et al., 2022a). This comparison highlights a similarity in terms of the fragmented nature of trilobite sections and preservation on the bedding plane. We suggest that the fragmented shelly sections likely reflect “incompletely digested skeletal elements of prey items” (Hawkins et al., 2018: p. 9) and the

pyritised rings record microbial biofilm haloes or the decomposition of faecal matter, followed by a diffusion of organic compounds/fluidized components that resulted in a redox gradient around the specimens (Nedin, 1999; Vannier and Chen, 2005; English and Babcock, 2010; Kimmig and Pratt, 2018). Finally, there is no evidence of a gut from a possible predator around the

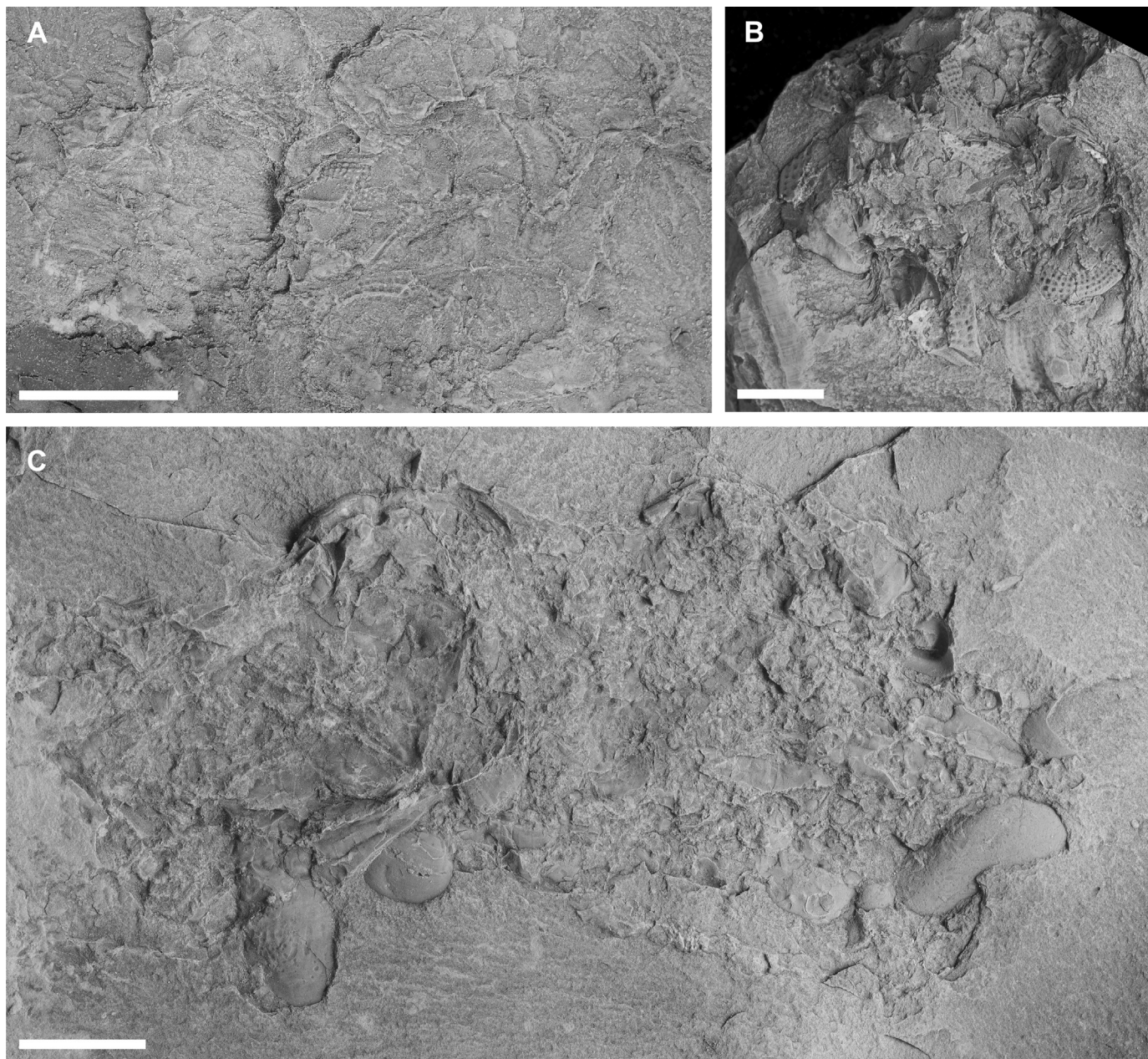


Fig. 5. Further shelly coprolites unprocessed containing bivalves, indeterminate shelly material, or fragmented *Onnia superba*. **A, B.** Specimens with highly fragmented *Onnia superba*. A: NM L 64626; B: NM L 64655. **C.** NM L 64654, specimen with unprocessed bivalves and indeterminate shelly material. Notably, there is a lack of *Onnia superba* within the coprolite. Specimens were coated with ammonium chloride. Images were converted to greyscale. Scale bars: 10 mm.

aggregates. As such, we consider the aggregates to be shelly coprolites illustrating the presence of durophagous predators or scavengers within the Bohdalec biota, rather than cololites (Hunt, 1992).

Unless coprolites are found associated with the possible makers, there is limited scope for unambiguous assignments of coprolite producers (Hunt, 1992; Hawkins et al., 2018). As we lack this fortuitous association, possible producers are presented based on the co-occurring fauna (Bruthansová et al., 2023) and other proposed lower Paleozoic predators (Klug et al., 2018). In doing so, we highlight three possible groups that could have produced these coprolites: large cephalopods, arthropods, and carnivorous worms.

Cephalopod molluscs were likely apex predators within Ordovician paleoecosystems (Brett and Walker, 2002). They have

been presented as the cause for injured Ordovician trilobites (Rudkin, 1985; Brett, 2003; Klug et al., 2018; Bicknell et al., 2022d), and bromalites from the Soom Shale Lagerstätte (Late Ordovician, Rawtheyan–Hirnantian) of South Africa have been attributed to cephalopods (Aldridge et al., 2006). Furthermore, trilobites located within the crop of Ordovician cephalopods strongly support predation on biomineralised prey (Brett and Walker, 2002). Indeed, gathering trilobites with tentacles for subsequent processing with a re-enforced beak is a plausible means of predation on benthic species. It is therefore very plausible that the large cephalopods from the Bohdalec Formation (Fig. 6(B)) could have produced the coprolites considered here.

There are three main arthropod groups that could have made these coprolites: eurypterids (sea scorpions), phyllocarids, and

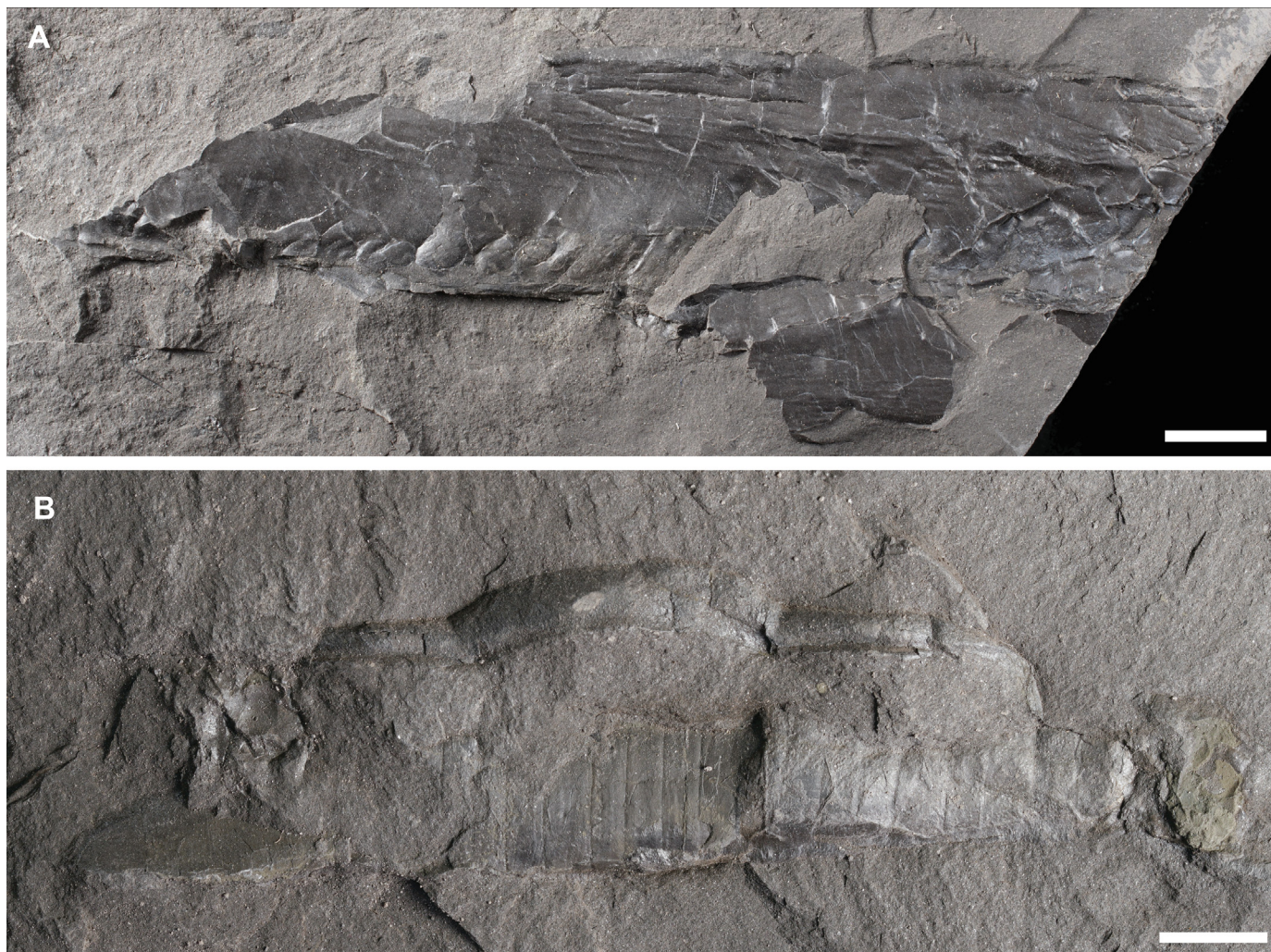


Fig. 6. Selection of possible predators from the Bohdalec Formation. **A.** NM L 64624, possible exoskeletal section of a large arthropod. **B.** NM L 64869, a large cephalopod, either Orthoceratoidea or Pseudorhocerida indet. Scale bars: 10 mm.

trilobites. Eurypterids are known from Ordovician-aged marine deposits across the globe (Caster and Kjellesvig-Waering, 1964; Tollerton, 2003; Lamsdell et al., 2013, 2015; Van Roy et al., 2015; Hawkins et al., 2018; Bicknell et al., 2022b; Braddy and Gass, 2023; Wang et al., 2023). These marine chelicerates had appendages effective for capturing prey (Bicknell et al., 2022b; Schmidt et al., 2022) and re-enforced gnathobasic spines – robust, spiny basal endites – on walking and swimming leg coxae (Selden, 1981; Poschmann et al., 2017; Bicknell et al., 2018c) for processing prey. This means of consuming prey is analogous to predation by extant horseshoe crabs (Shuster Jr., 1982; Botton, 1984; Bicknell et al., 2018a, 2018b, 2019). Ordovician sea scorpions likely targeted trilobites in the post-moult, soft-shelled stage (Bicknell et al., 2018c; Schmidt et al., 2022) and any trilobite-rich coprolites attributed to eurypterid predation show limited breakage across trilobite exoskeletal regions (Caster and Kjellesvig-Waering, 1964; Rolfe, 1973; Bicknell et al., 2023). As such, eurypterids unlikely produced the coprolites containing biomineralised remains but may have produced coprolites containing indeterminate shelly material (NM L 64617 and 64654).

Paleozoic phyllocarids fall into the highly diverse, well-distributed Archaeostraca (Collette and Hagadorn, 2010; Bicknell et al., 2020; Liu et al., 2022, 2023). These crustaceans played key roles as predators or scavengers, feeding on molluscs, arthropods,

and carrion (Bergström et al., 1987; Vannier et al., 1997; Bergmann and Rust, 2014; Liu et al., 2022) using large, re-enforced mandibles (Brett and Walker, 2002; Brett, 2003). However, Ordovician phyllocarids did not exceed 50 mm in length (Racheboeuf and Crasquin, 2010; Fatka et al., 2022; Liu et al., 2023) and, as such, would not have produced the larger coprolites here. They may have produced some of the smaller specimens.

Trilobites are highlighted as likely producers of lower Paleozoic surface coprolites (Bicknell and Paterson, 2018). Although rarely preserved, trilobite walking legs (Whittington, 1975, 1980; Ramsköld and Edgecombe, 1996; Fortey and Owens, 1999; Hou et al., 2009; Holmes et al., 2020; Losso and Ortega-Hernández, 2022) had gnathobasic spines ideal for a predatory, occasionally durophagous life mode, similar to sea scorpions and horseshoe crabs (Whittington, 1975; Selly et al., 2016; Bicknell et al., 2021). Large (>10 cm long) trilobites are known from the Bohdalec Formation (e.g., *Calymenella*, *Eudolatites*, and *Nobiliasaphus*) and could have targeted *Onnia superba* as prey and have produced these coprolites. Furthermore, coprolites produced by trilobites often have highly fractured shelly content (Bicknell et al., 2022a, 2023), similar to the specimens observed here. Conversely, the bivalve and gastropod shells, as well as crinoid pieces in select coprolites (Fig. 3(C), Fig. 4(A, B)) may be explained by opportunistic benthic detritivores – a life mode likely exhibited by many trilobite species

(Fortey and Owens, 1999; Kimmig and Pratt, 2018). For these specimens, the trilobites would have been much less selective regarding what was consumed, likely processing anything on the ocean floor.

Another group that has been highlighted as possible producers of Cambrian-aged coprolites are carnivorous priapulid worms (Vannier and Chen, 2005; Schwimmer and Montante, 2007; Kimmig and Strotz, 2017; Bicknell and Paterson, 2018; Kimmig and Pratt, 2018). These suggestions are supported by records of biomineralised prey – hyolithid conchs, brachiopods, and small trilobite fragments – found within the guts of Cambrian priapulid worms (Babcock and Robison, 1988; Schwimmer and Montante, 2007; Vannier, 2012). The reversible pharynx housing rows of teeth would have been capable of capturing slow-moving benthic animals for processing and consumption (Huang et al., 2004; Vannier and Chen, 2005). However, coprolites attributed to predation by carnivorous worms show much less processing of biomineralised material than observed here (Vannier and Chen, 2005). Further, these coprolites are often, but not exclusively, found in burrows (Kimmig and Strotz, 2017; Kimmig and Pratt, 2018; Pratt and Kimmig, 2019). As such, we can exclude carnivorous worms as possible producers of the primarily *Onnia superba* composed trilobites. However, they might have been the producers of the coprolites containing gastropod, bivalve, and crinoid pieces, as they might have picked them up while consuming detritus on the seafloor.

The apparently enrolled *Onnia superba* in NM L 64614 (Fig. 2(C)) individual presents additional insight into the predator size. This enrolled individual is similarly fragmented as the rest of the trilobite sections, suggesting it was consumed in a comparable manner to the other trilobites. This individual was likely alive and enrolled for protection, ingested completely, partly processed, and excreted in a slightly enrolled orientation. The producer of this coprolite therefore must have processed and swallowed an enrolled trilobite. This also suggests, that the trilobite was an arthropod rather than a priapulid worm, as enrolled agnostoids found in worm coprolites from the Cambrian Rockslide Formation do not show signs of processing (Kimmig and Pratt, 2018).

The predator(s) creating the *Onnia superba*-rich coprolites must have been much larger than the trilobites to consume them close to whole. The coprolites solely composed of *Onnia superba* suggest that: (i) *Onnia superba* was the most abundant and readily available prey, (ii) the predator had the sensory capacity to detect moving prey and was likely efficient in its prey selectivity, targeting solely *Onnia superba*, and (iii) the coprolites were produced by a larger arthropod or cephalopod.

Additionally, the presence of sessile benthic faunal elements in a subset of the coprolites (Fig. 3(C), Fig. 4(A)) supports the possibility of a second detrital producer of coprolites. This second producer would have been a detritivore, being less selective and capturing all bioclasts present on the sea floor. In this case that producer could represent a benthic arthropod or a worm, as the bioclasts could have already been processed before the detritivore consumed them.

6. Conclusions

We present the first evidence of shelly coprolites from the Late Ordovician (Katian) Bohdalec Formation. We illustrate that most of these coprolites contain fragmented *Onnia superba*, with rarer evidence of coprolites containing gastropods, bivalves, crinoid debris, and other indeterminate material. We propose that trilobites or cephalopods likely produced the larger, shelly coprolites, while phyllocarids, eurypterids, or worms could have produced the other coprolites. We conclude that these specimens illustrate important

and unique insight into a complex Ordovician palaeoecosystem and the ever evolving evolutionary arms race.

Data availability

No data was used for the research described in the article.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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