Research Article
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COPROLITES IN THE RAVENS THROAT RIVER LAGERSTÄTTE OF NORTHWESTERN CANADA: IMPLICATIONS FOR THE MIDDLE CAMBRIAN FOOD WEB

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ABSTRACT: The Rockslide Formation (middle Cambrian, Drumian, *Bolaspidella* Zone) of the Mackenzie Mountains, northwestern Canada, hosts the Ravens Throat River Lagerstätte, which consists of two, 1-m thick intervals of greenish, thinly laminated, locally burrowed, slightly calcareous mudstone yielding a low-diversity and low-abundance fauna of bivalved arthropods, 'worms', hyoliths, and trilobites. Also present are flattened, circular, black carbonaceous objects averaging 15 mm in diameter, interpreted as coprolites preserved in either dorsal or ventral view. Many consist of aggregates of ovate carbonaceous flakes 0.5–2 mm long, which are probably compacted fecal pellets. Two-thirds contain a variably disarticulated pair of arthropod valves, and many also contain coiled to fragmented, corrugated 'worm' cuticle, either alone or together with valves. A few contain an enrolled agnostoid. In rare cases a ptychoparioid cranidium, agnostoid shield, bradoriid valve, or hyolith conch or operculum is present; these are taken to be due to capture and ingestion of bioclasts from the adjacent seafloor. Many of the coprolites are associated with semi-circular spreiten produced by movement of the worm-like predator while it occupied a vertical burrow. Its identity is unknown but it clearly exhibited prey selectivity. Many coprolites contain one or more articulated hyoliths, ptychoparioid trilobites, or outstretched agnostoid arthropods oriented dorsal side up. These are interpreted as opportunistic coprovores drawn to the organic-rich fecal mass while it was lodged near the entrance to the burrow. This argues that hyoliths were mobile detritivores, and agnostoids were mainly nektobenthic or benthic, like the ptychoparioid trilobites. Fecal matter was probably an important source of nutrition in the Cambrian food web.

INTRODUCTION

Fossil coprolites have long been recognized as a biodeposition structure and occur in many forms, such as fecal pellets, fecal strings, and extruded objects left by ancient animals. For example, the ichnogenus *Alcyonidiopsis* (senior synonym of *Tomaculum*–Uchman 1999; Buatois et al. 2017) consists of strings or elongated aggregates of millimeter-sized, ellipsoidal to cylindrical objects regarded as fecal pellets (Eiserhardt et al. 2001; Bruthansová and Kraft 2003; Buatois et al. 2017). Coprolites belong to a family of features termed bromalites, which are the fossilized remains sourced from an animal's digestive system (Hunt 1992). Other kinds of bromalites include cololites, which are intestinal contents, gastrolites, which are stomach contents, and regurgitites (or regurgitalites), which consist of vomited material. Preservation of fecal matter is rare overall, however, as it may be only weakly cohesive, and scavenging, current action, compaction, diagenesis, and other factors may destroy or obscure it. Thus it is only under exceptional circumstances that coprolites can be recovered (e.g., Vannier and Chen 2005; Zhang and Pratt 2008;

English and Babcock 2010; Shen et al. 2014; Peel 2015). The paltry fossil record of bromalites overall obviously belies their paleoecological importance, given the realization that a great deal if not most of the fine-grained sediments in modern and ancient seas consists of mud aggregates much of which are fecal or pseudo-fecal pellets (e.g., Potter et al. 2005, p. 32).

While some invertebrate coprolites exhibit specific morphological shapes, most lack identifiable characteristics linking them to their producer (e.g., Kraeuter and Haven 1970). For this reason, despite exquisite preservation phosphatized fecal pellets reported from the middle Cambrian Gaotai Formation of South China (Shen et al. 2014) and the lower and middle Cambrian of North Greenland (Peel 2015), as well as those in the upper middle Cambrian of Sweden (Eriksson and Terfelt 2007), cannot be assigned to their producer, although a deposit-feeding strategy seems indicated by the fine particle size in many specimens.

In some cases remains of organisms have been reported from coprolites (Conway Morris and Robison 1986; Chin et al. 1998; Kiel 2008; Kimmig and Strotz 2017), which can lead to identification of their producer (Vannier and Chen 2005; Edwards et al. 2012; Izumi 2013). Some Cambrian coprolites consist of undigested aggregates of invertebrate sclerites or more refractory elements such as bradoriid valves and 'worm' cuticle (Vannier and Chen 2005; Zhang and Pratt 2008; Shen et al. 2014; Peel 2015). The uniform composition of each of these kinds of pellets is suggestive of individually sophisticated feeding strategies involving prey selectivity. Possible coprolites from the lower Cambrian Maotianshan Shale in South China (Vannier and Chen 2005) are dense accumulations of hyoliths and bradoriids. Likewise, skeletons and shell fragments of Cambrian arthropods and hyoliths in gut contents have been regarded as prey remains (Vannier et al. 2014). All these comprise tangible evidence of the complexity of the Cambrian food web (Zhu et al. 2004; Vannier and Chen 2005; Aldridge et al. 2006; Vannier 2012; Shen et al. 2014; Peel 2015).

In this paper we describe an unusual suite of coprolites from the middle Cambrian (Drumian) Ravens Throat River Lagerstätte of the Mackenzie Mountains of northwestern Canada. They occur together with a low-diversity fauna of soft-bodied fossils exhibiting Burgess Shale-type preservation (Kimmig and Pratt 2015, 2016). These coprolites offer an opportunity to explore the workings of the Cambrian food web, animal behavior, and the benthic community dynamics on this 500 million year old sea floor.

GEOLOGICAL SETTING

The middle Cambrian (Series 3, Drumian) Rockslide Formation in the Mackenzie Mountains is up to 500 m thick and consists of unmetamorphosed, relatively deep-water facies deposited on a west-facing slope flanking the Selwyn Basin (Gabrielse et al. 1973; Fritz 1979; Pratt 1989). Burgess Shale-type (BST) preservation of soft-bodied fossils as carbonaceous films (Butterfield 2003; Butterfield et al. 2007; Gaines 2014) is only known from the location referred to as the Ravens Throat River Lagerstätte where about 175 m of the lower Rockslide Formation are exposed (Fig. 1A, 1B; Kimmig and Pratt 2015, 2016). It consists of an overall regressive succession, from silty shale at the base that grades upwards into interbedded shale and lime mudstone with scattered debris-flow conglomerates, and thence into thin-bedded lime mudstone with calcareous mudstone exhibiting BST preservation. Above this is silty dolomitic lime mudstone passing upward into shallow-water carbonates. The Rockslide Formation overlies a thin dolomite and limestone unit belonging to the lower Cambrian Sekwi Formation, which itself rests

on shallow-marine sandstones of the Ediacaran to Terreneuvian Backbone Ranges Formation. At the Lagerstätte, the Sekwi Formation and lowermost part of the Rockslide Formation are displaced against the upper Backbone Ranges Formation by a westward-dipping synsedimentary listric fault.

Two approximately 1-m thick units exhibiting BST preservation within distinctive greenish-colored mudstones are present 134 m and 162 m above the base of the Rockslide Formation where they are intercalated with thin-bedded lime mudstone (Fig. 1C). The lower one yields virtually all of the fossil diversity, including the coprolites described herein, whereas the upper one contains only sporadic branch fragments of *Margaretia dorus*, which is considered a macrophytic alga (or possibly tubes built by hemichordates–Nanglu et al. 2016). The host lithology is dense, thinly laminated claystone that is variably silty and slightly calcareous, with common carbonaceous flecks. It is not fissile, and split surfaces are often slightly oblique to the lamination. Fresh surfaces are nearly black in color. Sedimentary structures like ripples and scoured surfaces are absent. The lithology, geochemistry, and ichnology indicate deposition on a deeper water ramp under an oxic to disoxic water column (Kimmig and Pratt 2016). Along with relatively rare soft-bodied organisms, articulated and disarticulated ptychoparioid trilobites (including *Elrathia*), agnostoid arthropods (*Hypagnostus*), and hyoliths (*Haplophrentis*) are sporadically present. These indicate that the fossil-bearing intervals belong to the *Bolaspidella* Biozone and this part of the Rockslide Formation is therefore of similar age to the Wheeler and Marjum formations of western Utah.

MATERIAL AND METHODS

About 150 coprolite specimens were collected during four field campaigns (1983, 1998, 2004, and 2012) mostly from the scree slope, with a few via excavation of the cliff exposure. They are the most common non-mineralized fossil objects in the lower interval, compared to several taxa of carapace-bearing arthropods and probable priapulid worms. Nevertheless, they are not abundant, given that many thousands of rock surfaces were inspected and found to be barren.

Like the soft-bodied fossils, coprolites are compacted parallel to bedding. This means some are views of the upper surface and some are views of the underside, while others are views of the interior because of splitting through the coprolite.

Using a Nikon D80 camera with a 60 mm Nikkor macro lens the coprolites were photographed both dry and submerged under ethanol to bring out surface detail, as well as dusted with ammonium chloride sublimate to show surface relief. Because the coprolite specimens are black and rather similar to the dark greenish-gray color of the host mudstone, photographic images were manipulated using Adobe Photoshop for optimal tone and contrast.

Elemental composition of about 20 rock samples was determined using a JEOL JXA-8600 Superprobe with backscattered scanning electron microscope (Kimmig and Pratt 2016). However, elemental mapping was not performed on the carbonaceous specimens because they have relief, which would give distorted quantitative results.

All specimens are housed in the Royal Tyrrell Museum of Palaeontology (TMP prefix) in Drumheller, Alberta.

BACKGROUND BIOTA

The two greenish mudstone intervals are only sparsely fossiliferous (Kimmig and Pratt 2015, 2016). The most common elements in the lower interval are poorly preserved ‘worms’ up to about 0.5 mm in diameter and 10 cm in length, some of which may be priapulids. Fossils not associated with coprolites are mostly isolated

individuals, and include sparse arthropod valves mostly belonging to *Perspicaris*?, and rare disarticulated, decalcified and compressed hyoliths, agnostoids, and ptychoparioids. A large dolichometopid is represented by sclerites in half a dozen samples. In addition, possible meiofaunal elements are represented by small carbonaceous fossils that are too poorly preserved to be identified (N. J. Butterfield personal communication).

In contrast to the majority of specimens collected, six slabs contain accumulations of a number of fossils. The largest one is an irregular but slightly elongate cluster 6 cm long and 4 cm wide consisting of at least 13, non-oriented, flattened arthropod carapace valves about 5–10 mm in length (Fig. 2A, 2B). The second is 2 cm long and 2 cm at its widest point and consists of a cluster of four or five, non-oriented, flattened arthropod carapaces (Fig. 2C, 2D). In addition to these two specimens there are two clusters of hyoliths, most of which are disarticulated (Fig. 3A, 3B). There are also two bedding surfaces showing 2–3 cm wide, dense accumulations of disarticulated, partially pyritized ptychoparioid trilobite sclerites (Fig. 3C).

The isolated specimens of the various arthropods probably include both molts and carcasses that were dispersed by gentle bottom currents. The hyoliths are likely individuals that died on the sea bottom. The overall rarity of fossils indicates that the epibenthic biota was not abundant. The clustered specimens, however, suggest a process that concentrated living specimens of the same taxon, such as a certain food resource, followed by mass mortality, or mass molting for the arthropods. Another possibility is that these clusters represent individuals that were preyed upon, with the hard parts expelled as a form of regurgitite, although none shows evidence of damage, there are no carbonaceous flakes associated with the valves, and there are no other soft tissues preserved. Accumulations of similar form and size composed of ostracode valves in the Mississippian Bear Gulch Lagerstätte have been interpreted as having been produced by a vertebrate, although no predator is preserved (Hunt et al. 2012).

BIOTURBATION

A single specimen of a diffuse, centimeter-sized *Rhizocorallium*-like trace visible on one bedding plane and some simple burrows appearing as furrows under one arthropod carapace (fig. 8A–8D in Kimmig and Pratt 2016) give the impression that bioturbation is uncommon in the Lagerstätte interval. This would be consistent with the rarity of ichnofossils in other BST deposits (e.g., Gaines and Droser 2010; Mángano 2011), which has been taken as evidence for anoxic to dysoxic bottom waters. On the other hand, some BST deposits do show that bioturbation was not as rare as often assumed (Caron et al. 2014). Thin sections and sawn surfaces oriented perpendicular to bedding reveal local, millimeter-sized domains of disturbed lamination due to small horizontal and vertical burrows that have been compacted during burial by about 80–85% (Kimmig and Pratt 2016), an estimate that accords with other evidence in BST Lagerstätten (Whittington 1985).

About one-third of the coprolites are associated with vertical burrows, about 11–15 mm wide, exhibiting spreiten, in this case recording lateral migration of the burrows. Coprolite diameter is usually about the same as the burrow diameter but in some cases it is up to one-third smaller. Spreiten are expressed indistinctly on bedding plane-parallel surfaces by slightly differing mud sizes and carbonaceous flecks (Figs. 4A–4C, 5A, 5B, 6C). They are mostly smooth, evenly arcuate, and overlapping each other by variable amounts, but typically are offset by less than one to several millimeters. In vertical cross-section, these burrows appear as roughly rectangular areas up to 8 mm deep with ragged lateral margins due to compaction, filled with

gently concave-up laminae (Fig. 5C, 5D). In most cases the trajectory of burrow migration as shown by spreiten overlap is crudely unidirectional with small deviations in some instances. The amount of lateral shift ranges from 18 mm to 36 mm, involving up to some half a dozen bundles of spreiten. However, cross-cutting relationships of the spreiten visible in a surface cut below one specimen (Fig. 5A, 5B) suggest that the burrower migrated from the upper left to the lower right, then the burrow deepened temporarily before migrating back towards the upper left again at a shallower depth. In all cases the coprolites are located adjacent to the final spreite.

These are compressed vertical burrows, and using an 80–85% degree of compaction, they were originally up to about 7 cm deep. Their circular plan view indicates that the occupant possessed a cylindrical shape. The lateral migration of the spreiten indicates that during the occupation of the burrow the producer moved sideways, presumably via muscle contractions and expansions, although why it engaged in this behavior is unclear. It is possible that some coprolites are localized on or in burrows but no spreiten were produced because the animal did not shift laterally. The laminae in the burrows appear to represent mostly later passive filling rather than meniscate backfilling such as that seen in other burrows (e.g., *Taenidium*–Keighley and Pickerill 1994). The location of the coprolites with respect to the spreiten indicates that defecation was the last activity of the burrower, seemingly near the entrance as it abandoned the burrow. Spreiten-burrows were only observed in association with a coprolite whereas just a single specimen, without spreiten, was observed not terminating in a coprolite. It is noteworthy that Huang et al. (2004) have inferred that predatory priapulid taxa from the Maotianshan Shale occupied vertical burrows, although the burrows are not preserved.

COPROLITES

The coprolite specimens are carbonaceous objects flattened parallel to bedding. In cross-section they are mostly tabular, i.e., disk-shaped, but some are gently lenticular. They have sharp margins and undisturbed specimens range in size from 8 mm to 37 mm, averaging 15 mm, forming a normal distribution (Fig. 6). Their surfaces are somewhat irregular owing to the rock having split around or through the structure and its constituents. They are separated into two types for the sake of description.

Coprolite Types

About one-third of the coprolites belong to type 1, which consist of variably dense aggregates of up to hundreds of carbonaceous flakes (Fig. 4A; also Figs. 10A, 10B, 13E, 16A–16D). The flakes can be discriminated in the less dense aggregates, where they are oval to elliptical in outline and approximately 0.5–2 mm across. The length-to-width ratio is consistently about 2:1. They are uniform in size in each aggregate.

One specimen belonging to type 1 consists of a lens-shaped aggregate of flakes surrounded by loosely distributed flakes (Fig. 7A, 7B) that were likely sloughed off the top of the fecal mass. Three specimens, 2–5 cm in diameter, display a ring shape with an empty central area, and in one the central area shows concentric spreiten (Fig. 7C). In some 20 mudstone samples, fairly well-sorted flakes 1–5 mm long are scattered over the surface up to 1 cm apart (Fig. 7D). The flakes are identical to those in the intact coprolites and represent fecal masses that have been physically disaggregated, presumably by gentle bottom currents. Lamination-parallel carbonaceous wisps of similar length are common, as seen in thin sections and surfaces cut vertical to bedding, and these are probably flakes and fragments of flakes.

The other two-thirds belong to type 2, consisting of very dense flake aggregates containing articulated to partly disarticulated arthropod valves (Figs. 4B, 4C, 5A, 8A–8F; also Figs. 11A, 11B, 13B, 14A, 14C), or a coiled segment of corrugated 'worm' cuticle and cuticle fragments (Fig. 9A–9F), or in some cases both cuticle and valves. The arthropod valves are either spread out in an apparent 'butterflied' position or flattened sideways and superimposed or slightly 'scissored'. Two specimens exhibit up to about a dozen short cylindrical pellets about 1 mm in length packed more or less side-by-side (Fig. 9E). In a few specimens there is a diffuse, discontinuous carbonaceous halo up to 4 mm wide that is located 2–4 mm away from the outer edge; the inner margin of the halo is better defined than the outer margin which fades away irregularly and gradationally (Fig. 8A). The haloes do not coincide with spreiten.

Some specimens of both types contain a bioclast, such as a hyolith conch or operculum (Figs. 10A–10C, 11C, 13B, 13E), an enrolled agnostoid (Figs. 11A–11C, 13C), a ptychoparioid cranidium (Fig. 15C), a bradoriid valve (Fig. 16A, 16B), or an agnostoid shield (Fig. 16B).

Associated Fauna

About one-third of both types 1 and type 2 coprolites have articulated hyoliths, ptychoparioid trilobites, and/or agnostoid exoskeletons on or embedded in them (Figs. 12A, 12B, 13A–13F, 14A–14C, 15A–15C, 16A–16D). The hyoliths are mostly, but not always (Fig. 14B), oriented dorsal side up and the conchs are typically fairly uniform in size, 6–11 mm in length; helens are lacking in all but a single specimen where one is situated nearby. Some coprolites exhibit two or three hyoliths and the conchs are oriented side-by-side in the same direction, in an apex-to-aperture position, or on top of each other but positioned such that the opercula do not overlap. One specimen exhibits four hyoliths lying on top of probably another two or three (Fig. 12A, 12B). The hyoliths do not extend beyond the perimeter of the coprolite except in two cases in which the apex extends a short distance (Fig. 15B).

The ptychoparioids and agnostoids are also articulated and stretched out, oriented dorsal side up in all cases but one (Fig. 15C). Specimens of each group are fairly uniform in size, the ptychoparioids being about 13 mm long and the agnostoids are approximately 5–7 mm in length, apart from one case in which contains a number of them that are about 1.5 mm long and exhibit a dominant subparallel and subordinate orthogonal orientation (Fig. 16B–16D). One specimen contains an articulated meraspid ptychoparioid (Fig. 15B).

INTERPRETATION

Coprolite Origin

These carbonaceous aggregates are interpreted as coprolites from the compaction of fecal masses instead of isolated or remnant microbial mats, gut contents, or other objects because: (1) they are well formed with sharp, circular margins; (2) their carbonaceous composition attests to a high original C_{org} content, too high to be formed by a microbial biofilm; (3) constituent flakes have an elongated shape with rounded terminations, which were most likely produced as pellets inside the gut of animals; and (4) they often contain arthropod valves and pieces of 'worm' cuticle, which point to mechanical and chemical digestion. The presence of arthropod valves is somewhat similar to coprolites described from the lower Cambrian Maotianshan Shale (Vannier and Chen 2005). By contrast, the well-defined shape of the carbonaceous disks argues against them being pseudofeces, that is, regurgitites, which are typically poorly formed and the components diffuse or dispersed (Vannier and Chen 2005). An origin as *in situ* gut contents from the death and decay of a soft-

bodied organism like a sea anemone is unlikely because the coelenteron does not break up more refractory material like 'worm' cuticle, nor does it pelletize digested material (e.g., Kruger and Griffiths 1997). The apparent absence of spreiten-burrows without carbonaceous aggregates argues against occasional preservation of *in situ* gut contents of another worm-like organism. None of the outstretched 'worm' fossils contains bioclasts, unlike gut contents in priapulids from the Burgess Shale (Vannier 2012) and "vermiform" fossils from the Pioche and Spence shales (Broce and Schiffbauer 2017). It is also unlikely that the structures represent poorly preserved jellyfish, eldonids, or Ediacaran-like discoidal fossils, as no typical features of such fossils, such as rays, ridges, or circular structures, are preserved (Liu et al. 2015; Lieberman et al. 2017; Sappenfield et al. 2017).

Carbonaceous haloes, which are locally present, have been interpreted in other examples as microbial biofilm haloes (e.g., English and Babcock 2010) or as diffusion of fluidized components (Nedin 1999; Vannier and Chen 2005). In this case, they probably formed under shallow burial by the decomposition of the organic matter in the fecal mass, followed by outward diffusion of organic compounds, which set up a redox gradient in the adjacent sediment. Experiments have shown that organic carbon remineralization close to its source is possible over centimeter scales (Reimers et al. 2013) and it is possible that this was the case here. Similar processes have been described from decomposition of animals in experimental scenarios (Sagemann et al. 1999; Butler et al. 2015). Because it has the same outline as the coprolite, this suggests that the fecal mass had no more than a gently lenticular shape and the diffusion of organic matter took place along a sediment lamina after the fecal mass had mostly collapsed. The outline of the coprolites, which usually follows one edge of incorporated arthropod valves, argues that these fecal masses did not expand laterally with compaction, in contrast to what was suggested by Vannier and Chen (2005) for specimens in the Maotianshan Shale.

The rare ring-shaped specimens likely represent fecal material that was disturbed by burrowing, probably by the producer itself. In aggregates from the Maotianshan Shale, the hyolith conchs surrounding an eldoniid disk were interpreted as deposited around the carcass by "whirling currents" (Vannier and Chen 2005). This explanation is unlikely here because of the absence of evidence for anything more than the weakest bottom currents in the Lagerstätte intervals.

Arthropods, worm-like animals without refractory components, and those with transversely corrugated cuticle were the primary prey, despite the apparent absence of representatives of the last form in the non-coprolite biota (Kimmig and Pratt 2015). The flakes, as pellets, likely represent digested soft tissues from these animals and were expelled along with the carapace and cuticle, which were not digestible. The elongate pellets in rare specimens may represent dense fecal pellets that were in the gut of a prey animal and fortuitously escaped disintegration during digestion. The disarticulated exoskeletons and shells found in some specimens are interpreted to have been bioclasts that were accidentally consumed by the predator. On the other hand, it is likely that the enrolled agnostoids were taken live and they enrolled as a defense mechanism, although they did not survive the digestion process. By contrast, in the guts of the priapulid *Ottoia prolifica* from the Burgess Shale agnostoids are disarticulated, although two complete specimens are preserved outstretched, but none is enrolled (Vannier 2012). Almost all the other elements are similarly disarticulated. Trilobites in coprolites in the lower Cambrian Emu Bay Shale of South Australia are only preserved as isolated sclerites (Nedin 1999; Daley et al. 2013), as they are in the Maotianshan Shale (Vannier and Chen 2005). By contrast, fecal strings and elongate

to round coprolites in the lower Cambrian Indian Springs Lagerstätte in Nevada consist of helicoplacoid ossicles and/or trilobite sclerites which may be "macerated" (English and Babcock 2010), and those in the middle Cambrian Kaili biota of South China are filled with trilobite "fragments" (Lin et al. 2010). In these examples trilobites were the targeted prey.

Coprolite Producer

The common association between the large vertical spreiten-burrows and coprolites indicates that the predator was likely worm-like and at least partially infaunal, dwelling in a vertical burrow. It was round in cross-section and the smooth, arcuate spreiten suggest that the animal lacked large setae, spines or protuberances on its body. It moved up and down as it hunted and digested its prey, indicating it possessing circular muscles. The spreiten show that it typically moved sideways as well, but how it accomplished this is not clear. Possibly the vertical movements led to sediment falling into the burrow and in a sense forcing the animal to shift laterally. Whatever sort of grasping jaw-like apparatus or proboscis the producer possessed at the feeding end is unknown, but ingestion of bioclasts favors the latter. The large size of the coprolite suggests a correspondingly large and likely flexible anus. Digested material was formed into pellets along with undigested chitinous valves and collagenous cuticle, although much of the latter seems to have been fragmented in the process. No examples with more than a single pair of valves were observed, suggesting that the predator occupied the burrow for a single, but probably somewhat protracted, feeding episode. Extrusion of the fecal mass near the entrance to the burrow appears to represent the final activity while the burrow was being abandoned. It is possible that the fecal mass rendered the burrow uninhabitable.

The predator had the sensory capacity to detect moving prey and appears to have been efficient in its prey selectivity, only occasionally capturing bioclasts (and living agnostoids) more or less by accident from the surrounding sea floor. Assuming the bivalved arthropods were nektobenthic, it is likely that the 'worms' it preyed upon were also epifaunal, at least at times. The size range of the coprolites (and spreiten), with none less than 8 mm, suggests that either small individuals did not live in this location or there were size-related feeding and behavioral differences. If the latter, it is possible that small forms selected different kinds of prey composed of labile organic tissues, and consequently did not produce preservable, C_{org}-rich fecal masses (see also Vannier and Chen 2005).

Associated Fauna

The articulated nature of hyoliths, ptychoparioid trilobites, and agnostoids located on and sometimes in the coprolites suggests that they are not digested bioclasts. Rather, they are interpreted to be preserved in feeding position, scavenging residual organic matter in the fecal mass itself or possibly on microbial biofilms that may have grown on it (see also Vannier and Chen 2005). This is supported by the positioning of these elements, especially the hyoliths, which almost without exception lie within the perimeter of the coprolite. This would be expected if detritivores were drawn into the entrance of a burrow. It is also supported by the examples where they sit adjacent to each other such that feeding activities under the opened operculum are not interfered with. Cases where articulated hyoliths are preserved in and upside-down under the coprolite can be explained as animals that pushed into or under the loose fecal mass. Apparent overlapping in some coprolites appears to be a function of later compaction. Similarly, the outstretched agnostoids in the large coprolite are oriented side by side and do not overlap.

The guts of some specimens of the priapulid worm *Ottoia prolifica* from the Burgess Shale contain a few of the hyoliths that are still articulated (Vannier 2012), but presumably by the time defecation occurred the conch and operculum would have separated in most cases. By contrast, the articulated aspect and dominant dorsal side up orientation of the hyoliths, ptychoparioids, and agnostoids in the coprolite-associated specimens means they could not have been digested prey. On the other hand, the hyoliths here lack attached helens and they do not appear to have been retracted into the conch (cf. Babcock and Robison 1988). They were probably weakly attached in life as suggested by the rarity of complete individuals in the associated biota as well as in the Burgess Shale (Caron and Jackson 2006), and it is possible they could have been deliberately shed. The mortality of these articulated detritivores *in situ* was probably the result of a brief episode of lethal bottom anoxia, followed by burial.

DISCUSSION

Paleoecological and Paleobiological Implications

During deposition of the lower Lagerstätte interval of the middle Cambrian Rockslide Formation the water column had sufficient productivity to sustain a benthos and lead to sedimentation and shallow burial of organic matter (Kimmig and Pratt 2016). The sea floor was populated sporadically by infaunal 'worms' of several types, including both deposit-feeders that made horizontal burrows as well as filter- or deposit-feeders that lived in U-shaped burrows. It is not known whether the possible priapulids preserved on bedding planes were normally epifaunal or part of the infauna and they died after vacating their burrows (Kimmig and Pratt 2015). The worm-like animal with corrugated cuticle was at least partly epifaunal and it was either a deposit-feeder or a carnivore that consumed the meiofauna. Scattered nektobenthic bivalved arthropods belonging to several taxa were probably carnivores feeding off tiny invertebrates that lived close to or on the sea bottom. Only larger individuals are preserved on bedding planes and in the coprolites. This might be representative of the populations that occupied this setting or a possible taphonomic bias against the preservation of small specimens because their thinner cuticle biodegraded. Ptychoparioid trilobites were also sparse elements of the nektobenthos and, in possessing a natant hypostome, were particle-feeders, i.e., detritivores (Fortey and Owens 1999). The agnostoids were most likely nektobenthic particle-feeders as well, rather than pelagic. Hyoliths were part of the epibenthos too, and similarly were sparsely distributed. None of the hard parts of these animals exhibits evidence that would suggest predation involving breakage of exoskeletons or shells (cf. Pratt 1998).

The isolated occurrence of the coprolites suggests that the predatory 'worms' were not predisposed to clustering, as seen in many occurrences of *Skolithos* burrows in lower Cambrian sandstone (Desjardins et al. 2010). They show prey selectivity: relatively large bivalved arthropods—seemingly only *Perspicaris*? and not co-occurring taxa like *Isoxyx*—and at times the 'worms' with corrugated cuticle as well as probably other worm-like animals. The predator clearly had the sensory capacity to detect its prey, in water depths probably near the limit of the photic zone. Trilobite cranidia, agnostoid shields, bradoriid valves, and hyolith conchs and opercula were occasionally consumed unintentionally, and so were living agnostoids, which promptly enrolled for protection. This contrasts with previous described examples of coprolites and gut contents packed with shells and sclerites. The occurrence in the coprolites of articulated hyoliths—albeit without helens—as well as complete ptychoparioid trilobites and outstretched agnostoids, all mostly oriented dorsal side up, provides strong evidence that these animals were drawn to the fecal masses as an

opportune food source. These animals were not obligate coprovores but normally detritivores that fed on low-grade organic particles in the sediment. Figure 17 presents a simplified depiction of these interactions.

The outstretched agnostoids are taken to demonstrate that this is the normal feeding attitude, as implied by Fortey and Owens (1999) and suggested by individuals entombed in hyolith conchs, in priapulid tubes, and under paradoxidid trilobites (Chatterton et al. 2003; Fatka et al. 2009; Fatka and Szabad 2011; Fatka and Kozák 2014). This is in contrast to the notion based on phosphatized specimens pf *Agnostus pisiformis* in the Alum Shale of Sweden which have been taken to indicate they were planktic filter-feeders that kept their shields slightly agape (Eriksson and Horn 2017). Presence of enrolled specimens in the coprolites suggests that enrolment was likely a defense mechanism.

Moysiuk et al. (2017) documented soft tissues in hyoliths in the Burgess Shale and proposed that they were sessile lophophorates rather than mollusks, sipunculan-like, or belonging to an extinct phylum (Runnegar et al. 1975; Babcock and Robison 1988; Malinky and Yochelson 2007; Devaere et al. 2014). The occurrence here of articulated specimens on and in coprolites is evidence rather that they were mobile, drawn to feed on the fecal mass. It has been suggested that hyoliths used their helens for locomotion (Martí Mus and Bergström 2005), but these are absent in almost all specimens in the coprolites. Perhaps underneath the operculum was a foot-like feature that enabled movement. The fringe structure may have been part of that but acted as tentacles for collecting food particles from the sea floor instead of filter-feeding. A mollusk affinity is suggested.

CONCLUSIONS

Relatively few examples of invertebrate coprolites are known from the fossil record and therefore a key dimension of paleobiology and paleoecology is poorly understood. The deeper water, low-energy Ravens Throat River Lagerstätte of middle Cambrian age in northwestern Canada yields intact coprolites around 15 mm in diameter, along with a sparse biota consisting of several taxa of bivalved arthropods, ptychoparioid trilobites, agnostoids, hyoliths, possible priapulids, and infaunal worms. These coprolites have a circular outline and consist of variably dense aggregates of oval carbonaceous flakes that probably represent flattened pellets, as well as, in many cases, arthropod valves and fragments of worm cuticle. Bioclasts, including enrolled agnostoids, are rare in the coprolites and probably were not the intended prey. The producer was a large worm-like predator that occupied a vertical burrow, which it abandoned after it defecated.

The articulated hyoliths, ptychoparioid trilobites, and agnostoids present on many coprolites can be explained as benthic detritivores that were attracted opportunistically to the food resource presented by the still organic-rich feces. In addition, these specimens provide evidence that agnostoids fed in an outstretched attitude and hyoliths were mobile and mollusk-like rather than sessile lophophorates.

Soft-bodied preservation in the Ravens Throat Lagerstätte favors only the more resistant elements of the biota. Thus, these coprolites most likely represent only a small proportion of the total fecal matter that was deposited on the sea floor. In other settings fecal matter also probably played an important nutritional role but currents, biological disturbance, and biodegradation typically erased their record and the evidence of the animals that consumed them.

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FIGURE CAPTIONS
FIG. 1.—**A**) Map showing the location of the Ravens Throat River Lagerstätte near the headwaters of Ravens Throat River, Mackenzie Mountains, northwestern Canada. **B**) Topographic map of the area of the Lagerstätte (63º10'N, 127º 55'W). **C**) Generalized stratigraphy of the Rockslide Formation in the Ravens Throat River area. Green-colored intervals comprise the Lagerstätte exhibiting Burgess Shale-type preservation. The coprolites are restricted to the lower of the two intervals (denoted by black dots).
FIG. 2.—Arthropod valve clusters. **A**) TMP 2013.101.0313: view from below showing irregularly shaped cluster of at least 17 disarticulated valves. **B**) Outlines of the valves in A. **C**) TMP 2013.101.0324: view from above showing nested pair of articulated valves, with a smaller pair at lower left. **D**) Outlines of the valves in C. Views A and B photographed under ethanol. Scale bars = 5 mm.
FIG. 3.—Bioclast clusters. **A**) TMP 2013.101.0109: view from above showing four hyolith conches (in ventral view) and one operculum (in ventral view). **B**) TMP 2013.101.0339a: view from above showing one articulated hyolith (dorsal side up), three conches in ventral view, and one operculum (in dorsal view); a helen appears to be present (upper right). **C**) TMP 2013.101.0477: view from above showing disarticulated ptychoparioid sclerites (many of which are pyritized) with two corynexochid sclerites (large ones in upper right and lower left). All dusted with ammonium chloride sublimate. Scale bars = 5 mm.
FIG. 4.—Spreiten-burrows associated with coprolites. **A**) TMP 2013.101.0298a: view from below of type 1 containing hyolith operculum (not discernible); see also Figure 12A and 12B. **B**) TMP 2013.101.0342: view from above of type 2 containing an arthropod valve (or valves) and a hyolith with slightly offset operculum (dorsal side up) (none discernible), and showing deviations in the direction of lateral migration. **C**) TMP 2013.101.0405: view from below of type 2 containing worm cuticle and an arthropod valve (or valves; not discernible). All photographed under ethanol. Scale bars = 5 mm.
FIG. 5.—Spreiten-burrows associated with coprolites. **A**) TMP 2013.101.0436, type 2: view from above containing valve (or valves) under worm cuticle (not discernible), with spreiten to the lower right. **B**) Sawn surface parallel to bedding 8 mm below coprolite, oriented as if viewed from above; bright speckles are pyrite cubes. **C**) Sawn surface perpendicular to bedding, at the lower edge where it intersects burrow. **D**) TMP 2013.101.0362: sawn surface perpendicular to bedding, at the edge where it intersects the burrow; edge is the right side of Figure 10D. Scale bars = 5 mm.
FIG. 6.—Histogram showing the diameter frequency of the circular coprolite specimens belonging to types 1 and 2.
FIG. 7.—Coprolites of type 1 that have been subsequently disturbed. **A**, **B**) TMP 2013.101.0446: view from above showing 1 mm thick lens with flakes sloughed off the upper surface. **C**) TMP 2013.101.0416b: view from below showing flakes and flake fragments forming a ring around a vertical spreiten-burrow. **D**) TMP 2013.0101.0312: view from above showing dispersed flakes; an outstretched agnostoid is also present (not discernible). A, C and D photographed under ethanol; B dusted with ammonium chloride sublimate. Scale bars = 5 mm.

FIG. 8.—Coprolites of type 2 containing arthropod valves. **A**, **B**) TMP 2013.101.0452: view from above showing a pair of butterflied valves, with one partly articulated hyolith (oriented ventral side up) and one conch (both barely discernible) are present in the upper right, surrounded by a carbonaceous halo; there is a narrow area of indistinct spreiten to the right. **C**) TMP 2013.101.0458: view from above showing a pair of superimposed valves (the upper one mostly broken off), with a patch of shiny carbonaceous matter preserving part of the valve; spreiten are visible in C. **D**) TMP 2013.101.0418: view from above showing valve (or valves) having a diameter slightly less than that of the spreiten. **E**) TMP 2013.101.0378: view from above showing a pair of compacted 'butterflied' valves under flakes; the hinges are oriented diagonally from the lower left to the upper right and slightly separated. **F**) TMP 2013.101.0357: view from above showing a valve (or valves) under flakes; a small articulated hyolith (not discernible) is present in the upper left (oriented ventral side up). A, C, D, and F photographed under ethanol; B dusted with ammonium chloride sublimate; E photographed dry. Scale bars = 5 mm.

FIG. 9.—Coprolites of type 2 containing 'worm' cuticle. **A**) TMP 2013.101.0425: view from above showing coiled cuticle. **B**) TMP 2013.101.0459b: view from above showing coiled cuticle. **C**) TMP 2013.101.0397: view from above showing cuticle fragments. **D**) TMP 2013.101.0443: view from below showing coiled and fragmented cuticle. **E**) TMP 2013.101.0451: view from above showing cuticle fragments and a patch (left of center) of elongate pellets. **F**) TMP 2013.101.0470: view from above showing cuticle fragments. All dusted with ammonium chloride sublimate. Scale bars = 5 mm.

FIG. 10.—Coprolites containing consumed bioclasts. **A**, **B**) TMP 2013.101.0298a, type 1: view from below showing a hyolithid operculum (in ventral view); see also Figure 5B. **C**) TMP 2013.101.0203a, type 2: view from above showing at least five overlapping hyolith conches and two opercula (one in dorsal and one in ventral view). A photographed under ethanol; B and C dusted with ammonium chloride sublimate. Scale bars = 5 mm.

FIG. 11.—Coprolites containing consumed bioclasts. **A**) TMP 2013.101. 0447, type 2: view from above showing an enrolled agnostoid, a hyolith conch, and an arthropod valve (or valves); scratches are artefacts. **B**) TMP 2013.101.0432, type 2: view from below showing an enrolled (but slightly displaced) agnostoid and an arthropod valve (or valves); scratches are artifacts. **C**) TMP 2013.101. 0084, type 2, view from below showing an enrolled agnostoid and an articulated hyolith (oriented ventral side up). All dusted with ammonium chloride sublimate. Scale bars = 5 mm.

FIG. 12.—Coprolites with detritivores. TMP 2013.101.0376, type 2: view from below, showing three articulated hyoliths (all oriented dorsal side up), one (at lower right) without the operculum (possibly having been split off), and arthropod valve (or valves) and possibly worm cuticle (at lower left). The three are crudely radially arranged with the conchs partially overlapping but the opercula not. **A**) Photographed under ethanol. **B**) Dusted with ammonium chloride sublimate. Scale bar = 5 mm.

FIG. 13.—Coprolites with detritivores. **A**) TMP 2013.101.0377, type 2: view from above showing a complete trilobite (oriented dorsal side up). **B**) TMP 2013.101.0472a, type 2: view from above showing an outstretched agnostoid and two complete ptychoparioids (all oriented dorsal side up), and a hyolith conch (to the right of the larger ptychoparioid). **C**) TMP 2013.101.0091, type 2: view from above showing an articulated hyolith (oriented ventral side up), three complete ptychoparioids (the lower left and upper right ones oriented dorsal side up; the upper left one is uncertain), and an enrolled agnostoid (partially under the right side of the ptychoparioid at the lower

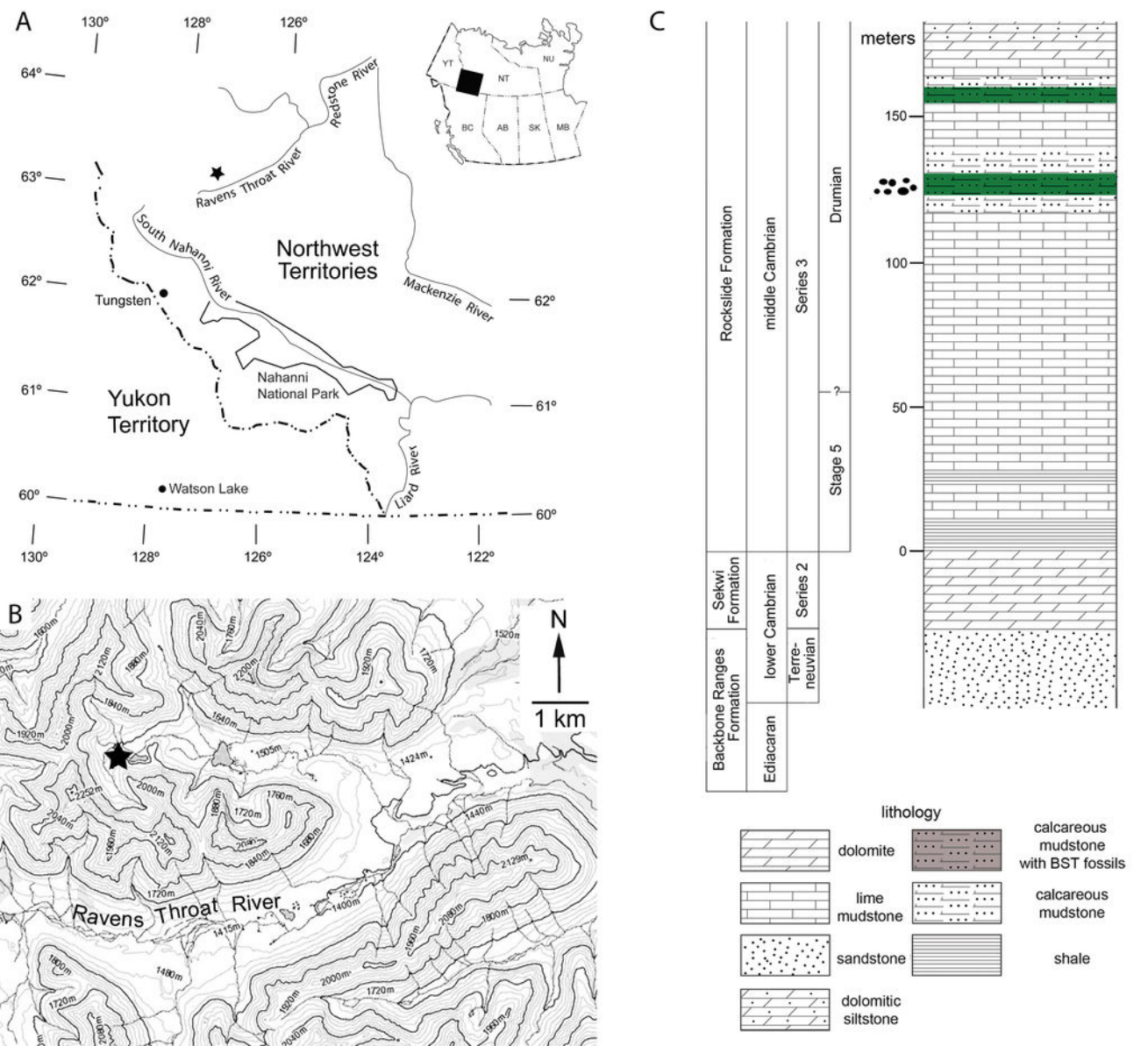
left). **D)** TMP 2013.101.0367, type 2: view from below showing an outstretched agnostoid (oriented dorsal side up). All dusted with ammonium chloride sublimate. **E**) TMP 2013.101.0382, type 1: view from above showing an outstretched agnostoid (oriented dorsal side up), a hyolith operculum (in ventral view), and an agnostoid pygidium (in ventral view). **F**) TMP 2013.101.0372, type 2: view from above showing a complete ptychoparioid (oriented dorsal side up); pits in the axial lobe are due to neomorphic calcite crystals. Scale bars = 5 mm.

FIG. 14.—Coprolites with detritivores. **A**) TMP 2013.101.0113, type 2 with carbonaceous halo (not discernible): view from above showing an arthropod valve (at lower right) and two hyoliths side by side plus one at right angles under it (all oriented dorsal side up). **B**) TMP 2013.101.0472b, type 2: view from below showing three subparallel articulated hyoliths (all oriented dorsal side down); a fourth (oriented dorsal side up) lies under the one at right (only the operculum is visible). **C**) TMP 2013.101.0110, type 2: view from below showing an articulated hyolith (oriented dorsal side up); a pair of butterflied bradoriid valves (not visible) is located to the lower right of the conch. All dusted with ammonium chloride sublimate. Scale bars = 5 mm.

FIG. 15.—Coprolites with detritivores. **A**) TMP 2013.101.0075, type 2: view from below showing an articulated hyolith and complete ptychoparioid (both oriented dorsal side up). **B**) TMP 2013.101.0060, type 2: view from above showing an articulated hyolith (oriented dorsal side up) with complete ptychoparioid meraspide located (oriented ventral side up) on the conch; the apex of the hyolith extends beyond the periphery of the coprolite. **C**) TMP 2013.101.0320, type 2 with carbonaceous halo (not discernible): view from above showing articulated hyoliths (oriented dorsal side up), outstretched agnostoid (oriented ventral side up), and a ptychoparioid cranidium. All dusted with ammonium chloride sublimate. Scale bars = 5 mm.

FIG. 16.—Coprolites with detritivores. TMP 2013.101.0315, type 1 showing bioclasts and agnostoids. **A**) View from below of the largest aggregate containing a bradoriid arthropod valve (dark patch at middle bottom) and around a dozen agnostoids. **B**) Close-up showing the bradoriid valve, several outstretched agnostoids (oriented dorsal side up), an enrolled agnostoid (next to the lower right corner of the bradoriid), and an agnostoid pygidium (oriented ventral side up, under the lower right corner of the bradoriid). **C**) Close-up showing numerous outstretched agnostoids that are mostly aligned upper-left/lower-right but facing both directions, with a subordinate alignment upper-right/lower-left. **D**) Close-up (rotated) of several aligned agnostoids. A and D photographed under ethanol; B and C dusted with ammonium chloride sublimate. Scale bars in A and B = 5 mm, C and D = 1 mm.

FIG. 17.—Cartoon depicting the benthic dynamics indicated by the coprolites. 1, the worm-like predator occupies a shallow vertical burrow but extends from it in order to hunt prey, in this case the nektobenthic arthropod *Perspicaris*?; the burrow shifts laterally during this activity and spreiten are produced. The feeding/grasping apparatus is conjectural. 2, the predator has caught its prey and is in the process of digesting it; it is hypothesized that the burrow continues to shift laterally, producing more spreiten. The predator may continue to hunt and consume further prey. 3, the predator abandons its burrow and deposits a single fecal mass near its entrance; mud has sloughed into the burrow during this process. 4, opportunistic coprovores, in this case hyoliths, are drawn to the fecal mass.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124°
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Redstone River
Ravens Throat River
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Northwest Territories
Mackenzie River
Tungsten
Nahanni National Park
Yukon Territory
Liard River
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Rockslide Formation
middle Cambrian
Series 3
Drumian
Stage 5
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Sekwi Formation
lower Cambrian
Series 2
Terre-neuvian
Backbone Ranges Formation
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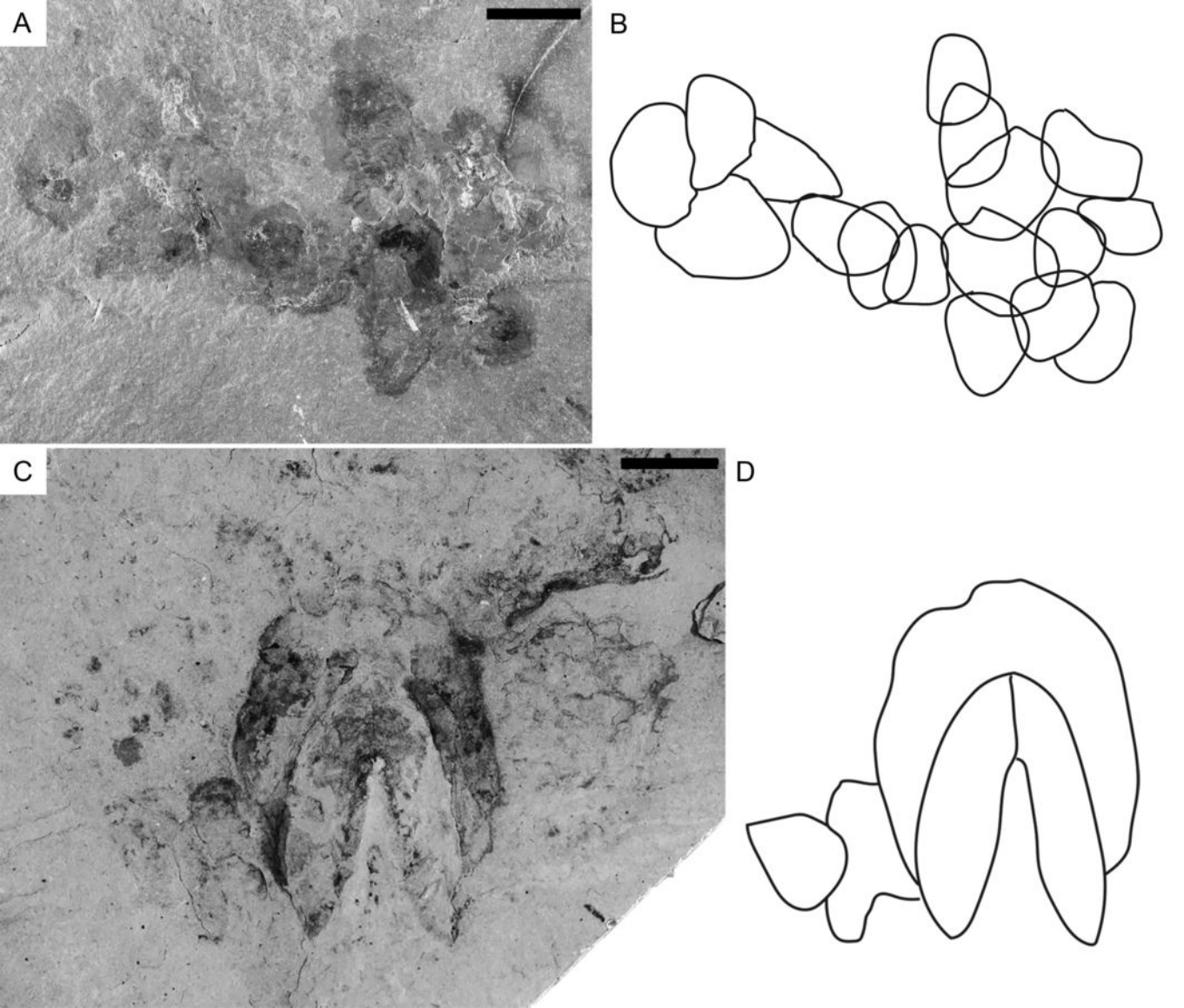
calcareous mudstone
shale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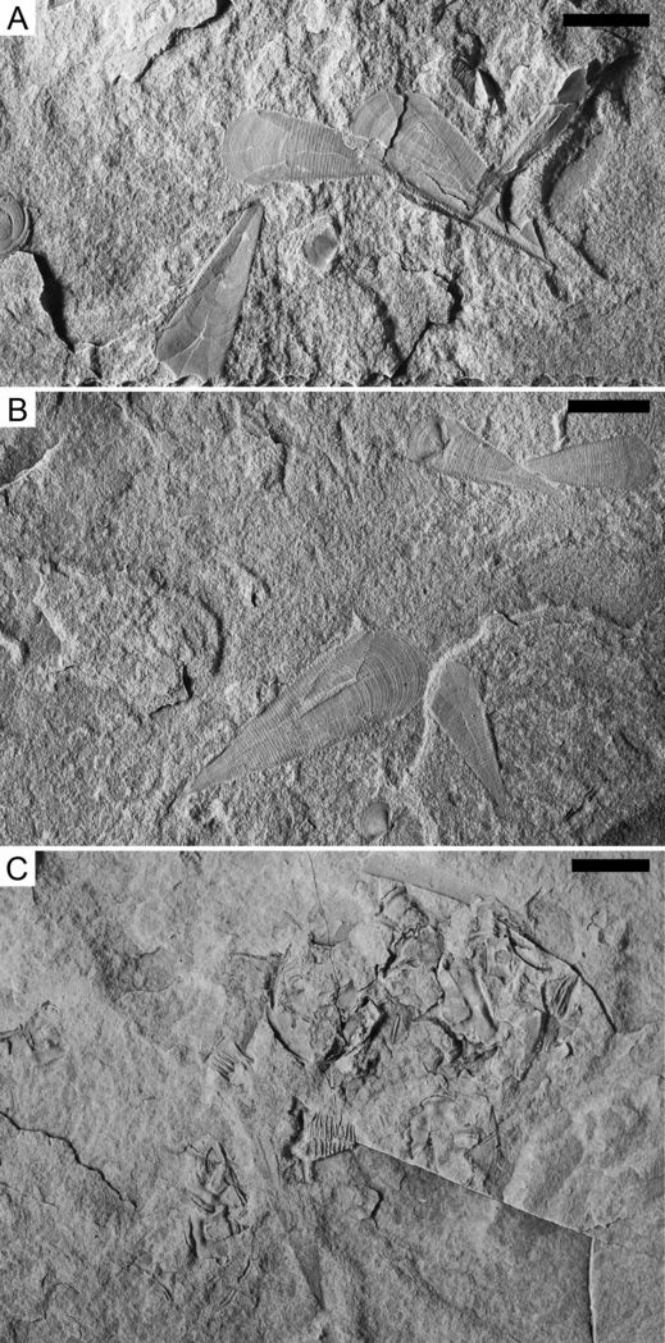
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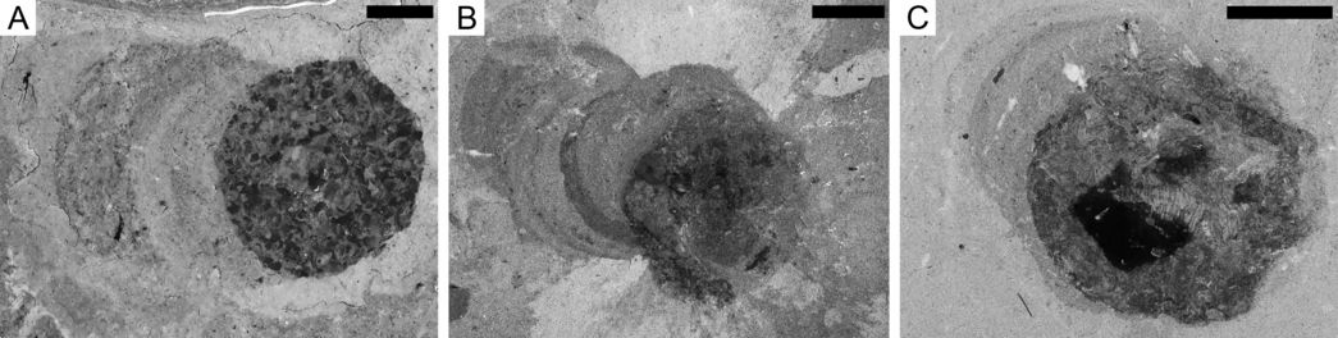
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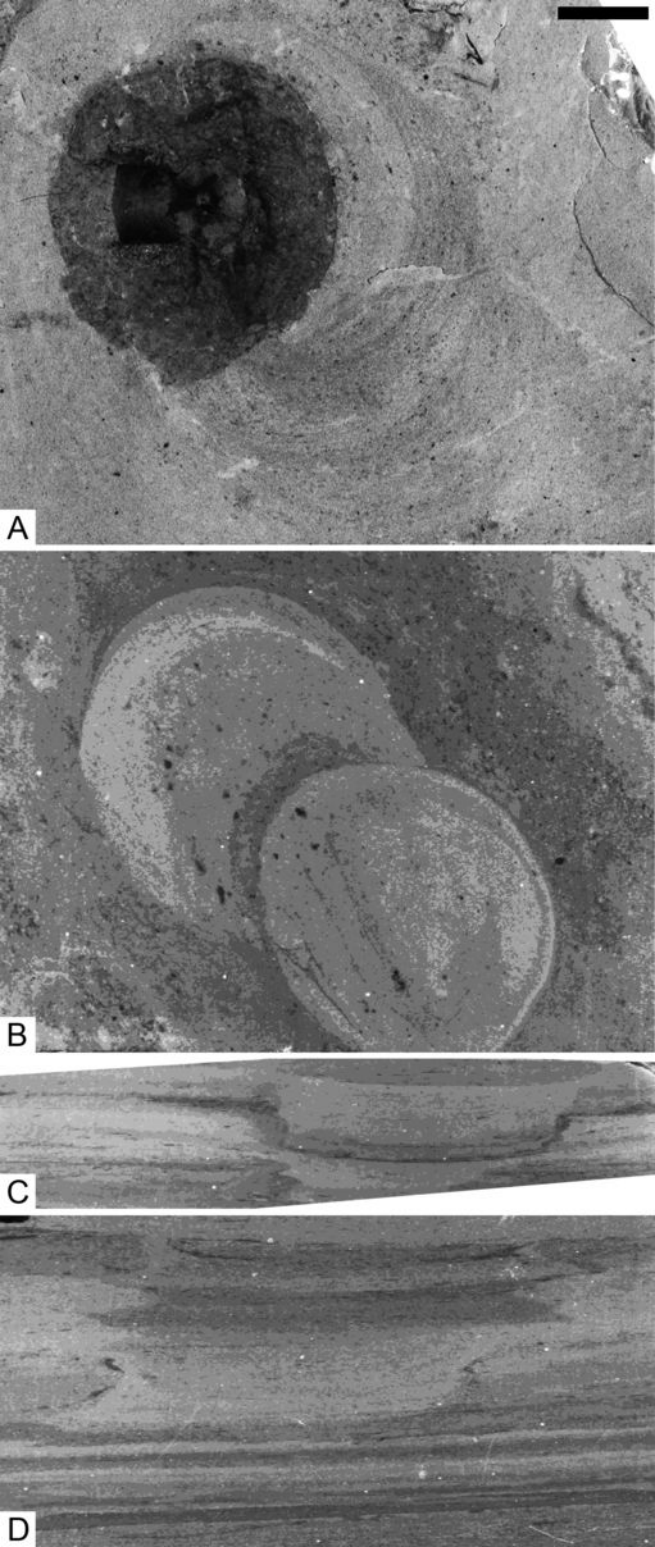
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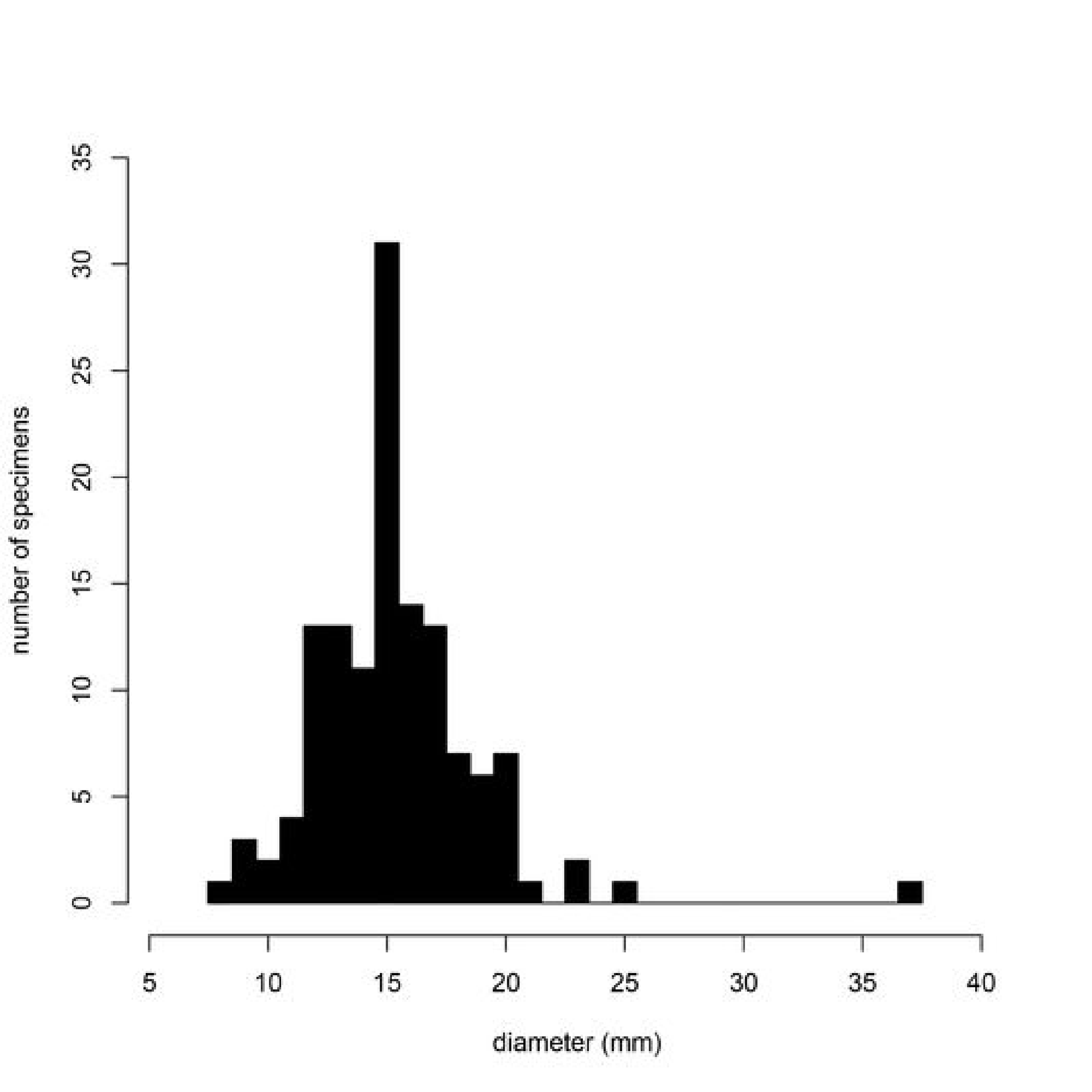
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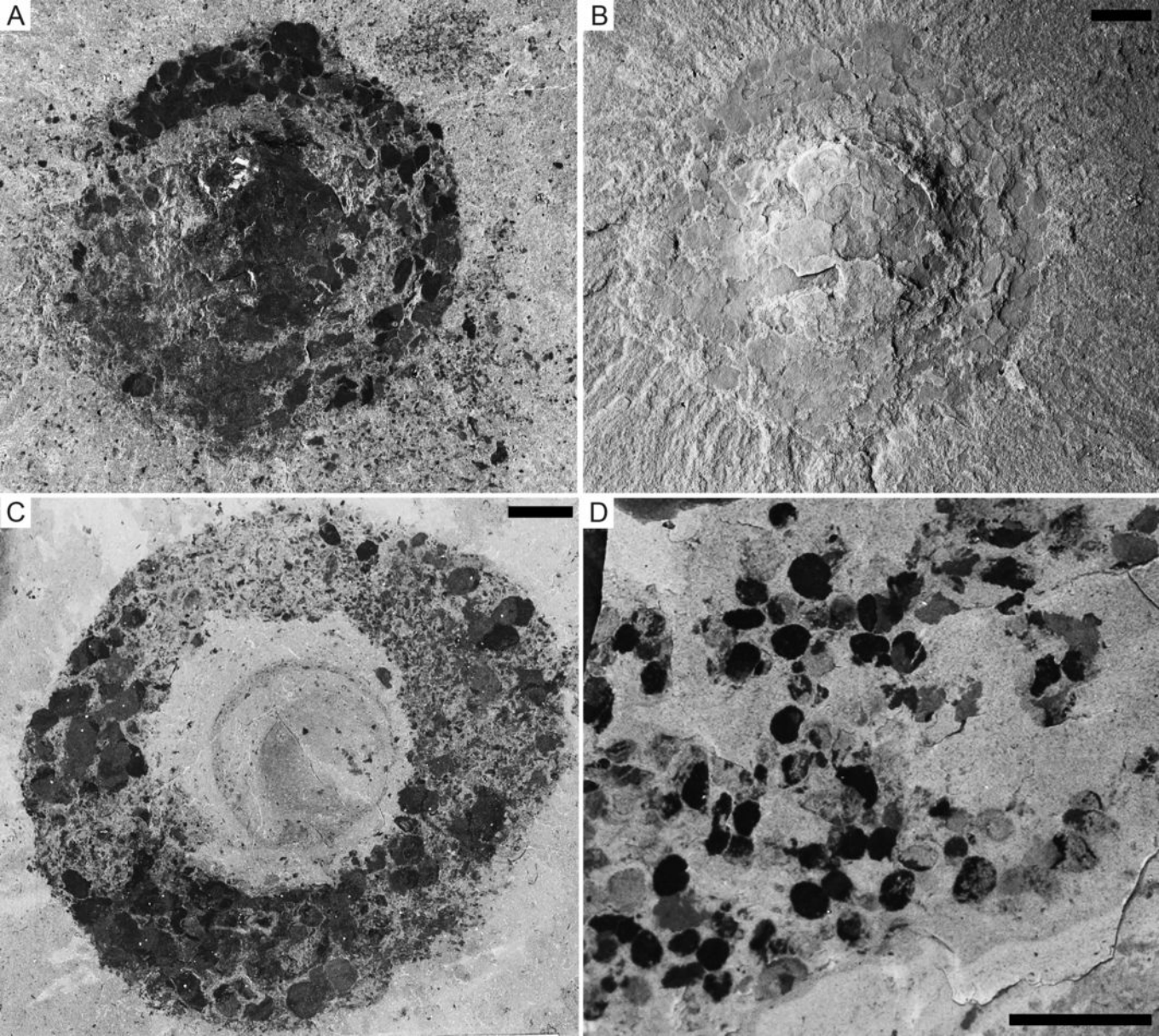
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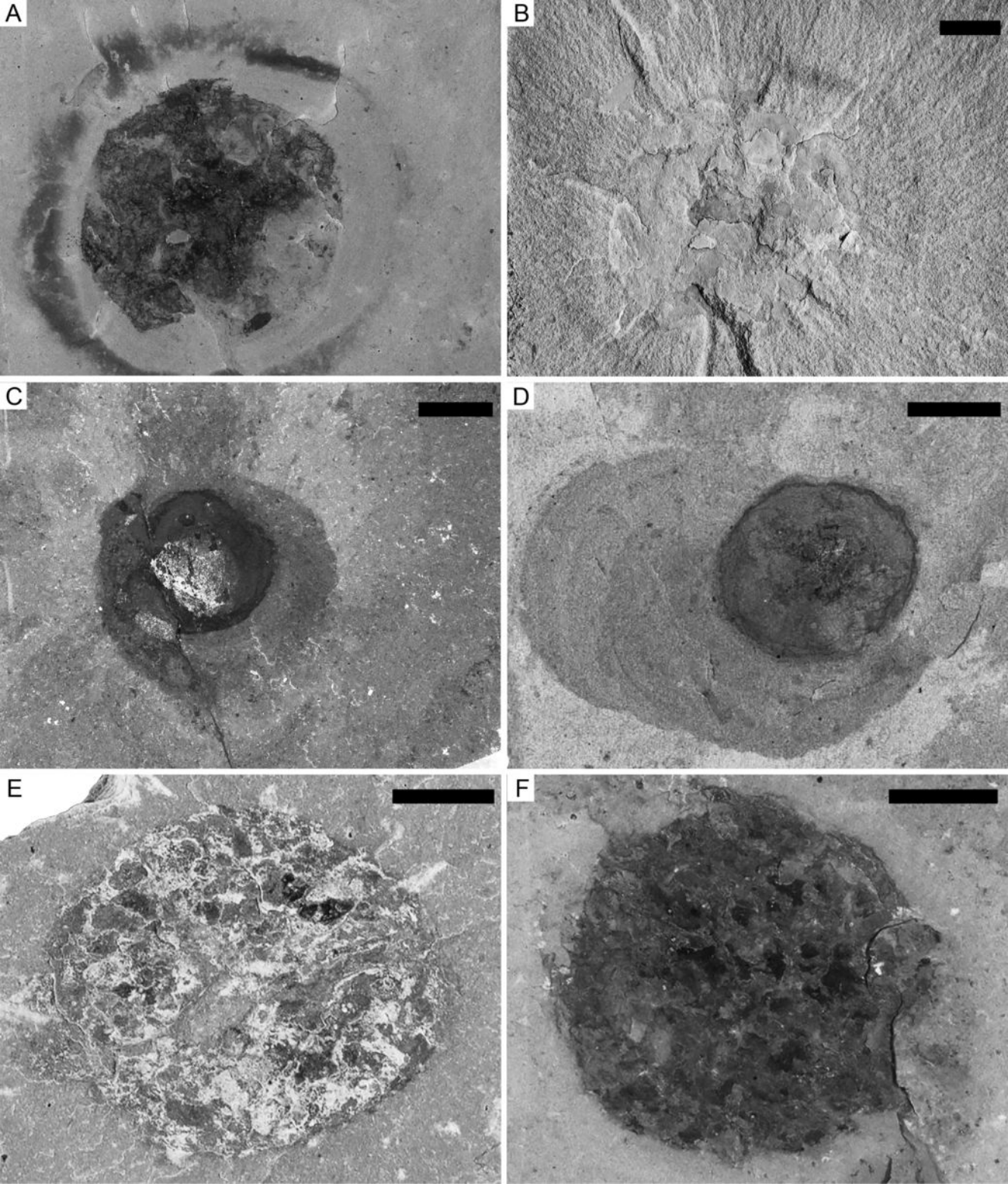
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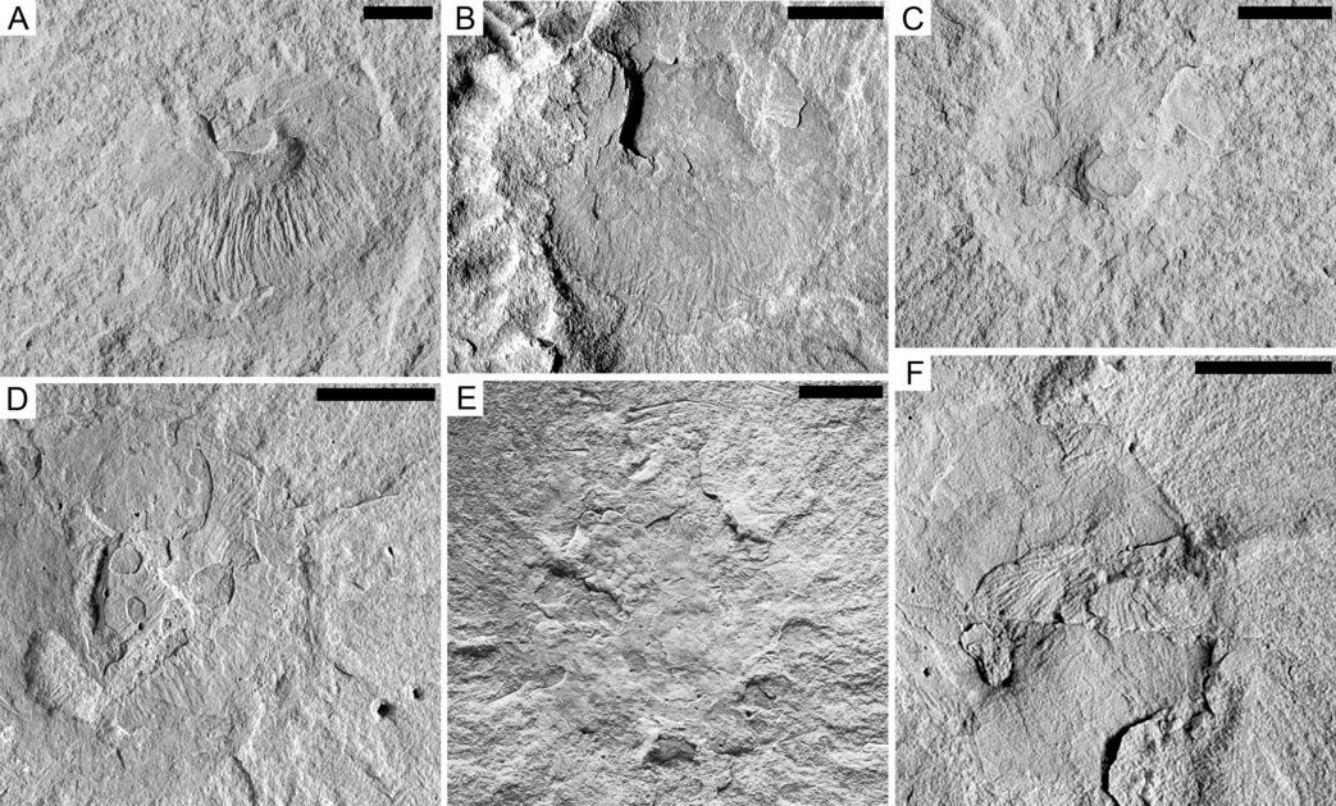
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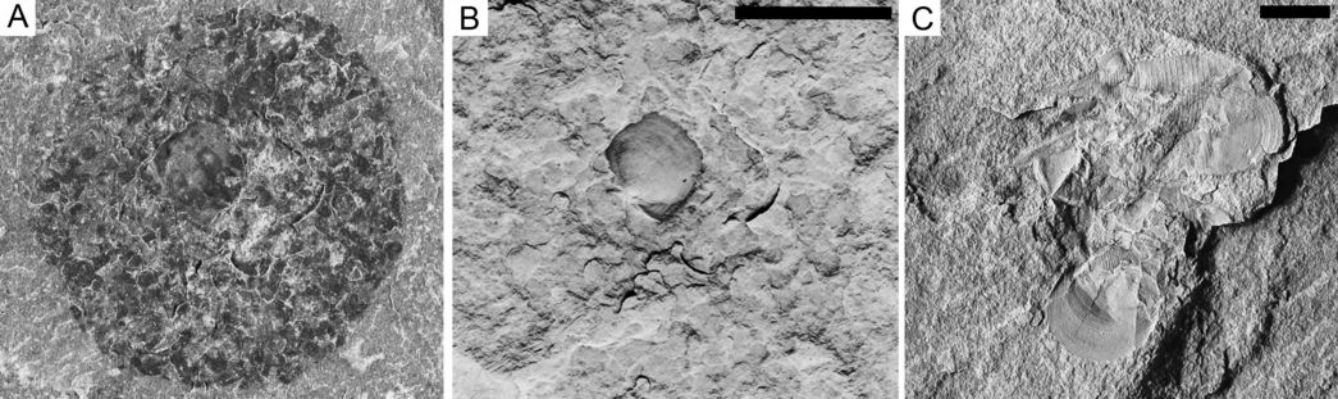
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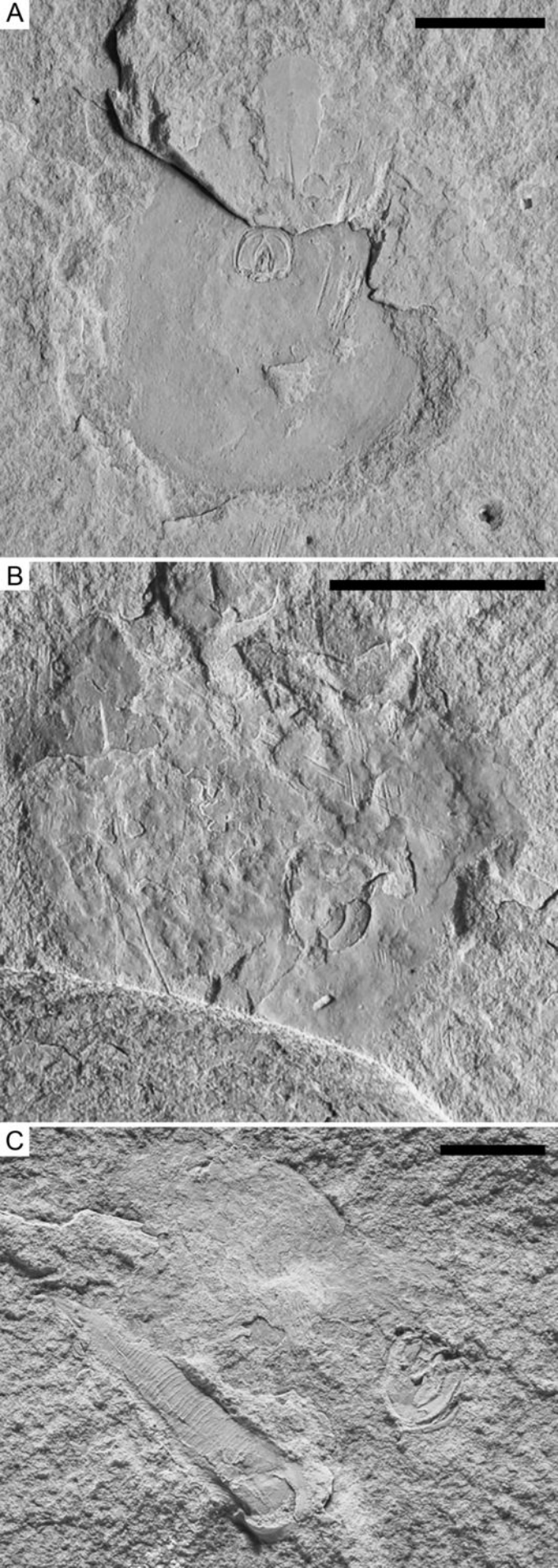
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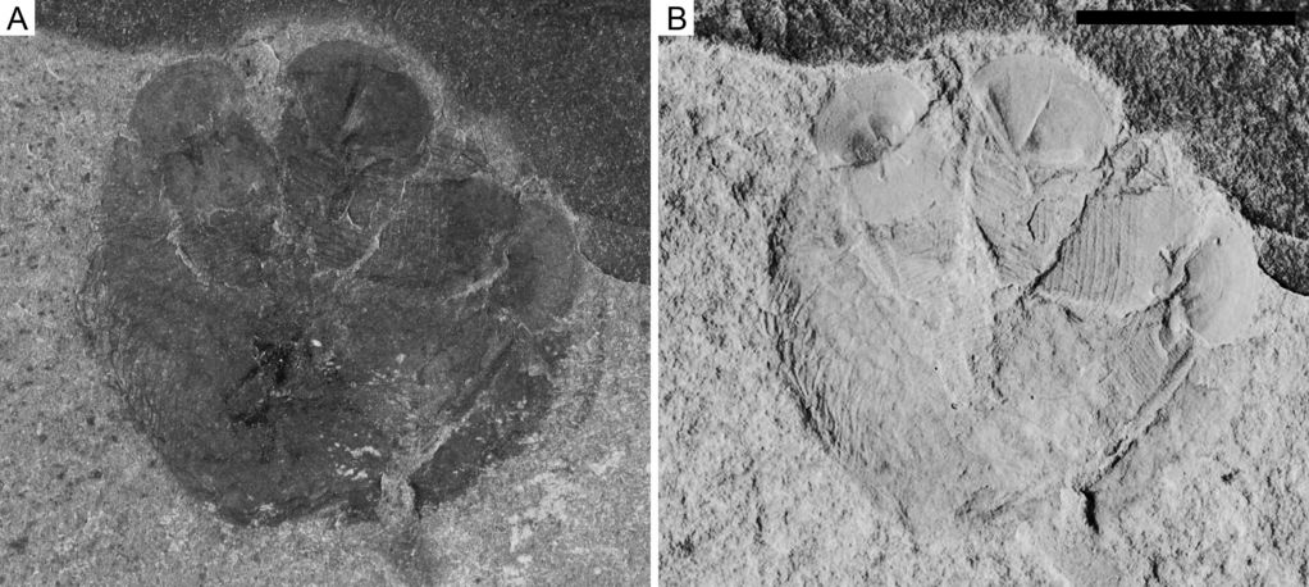
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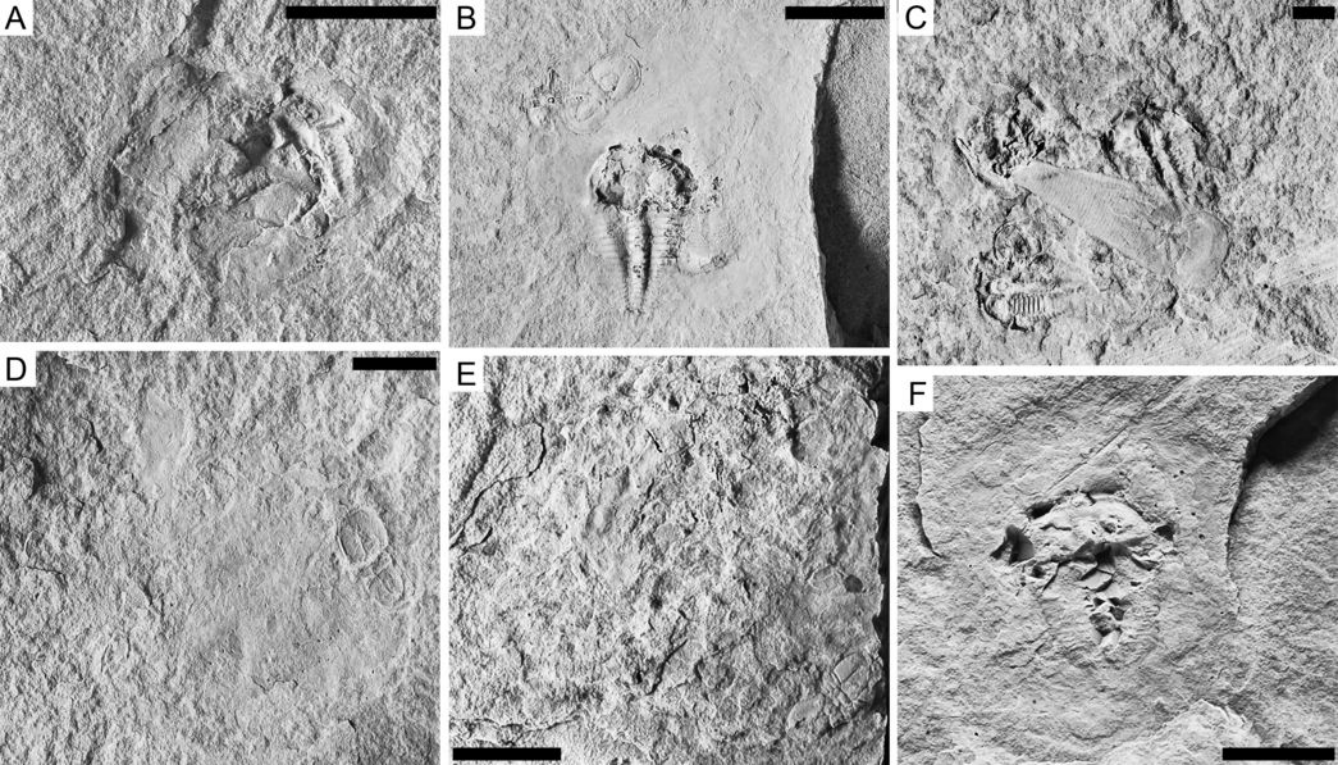
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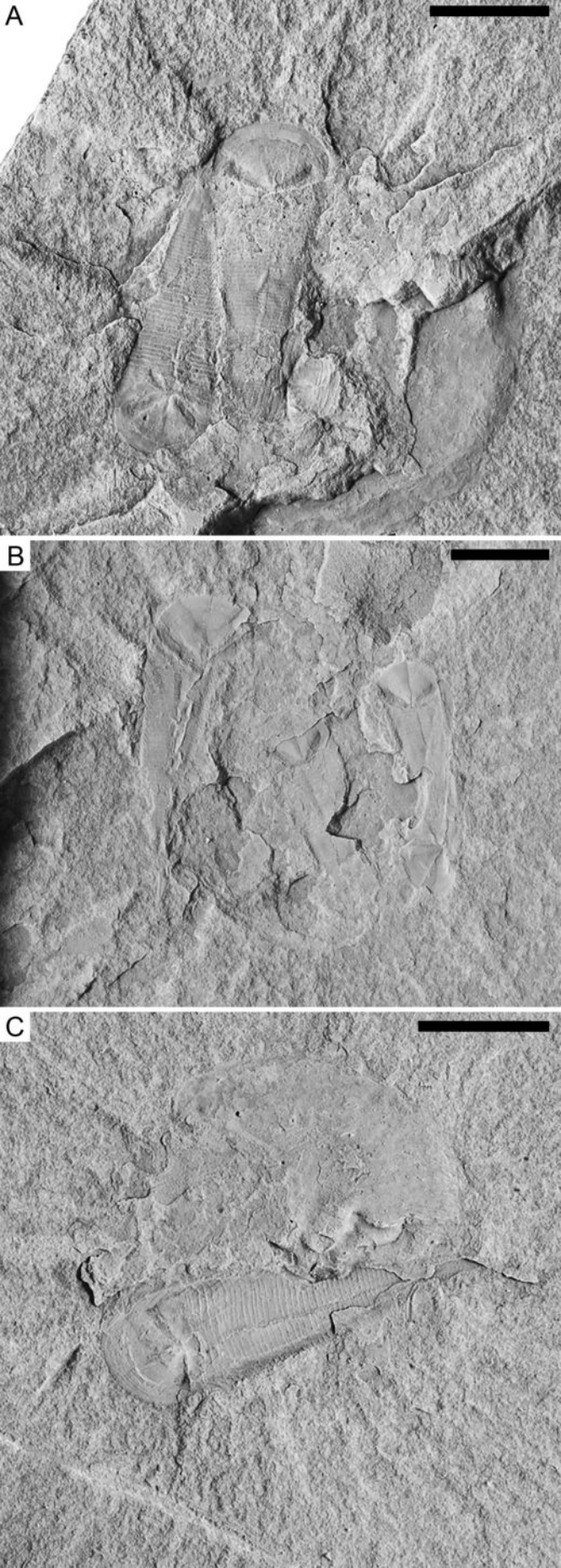
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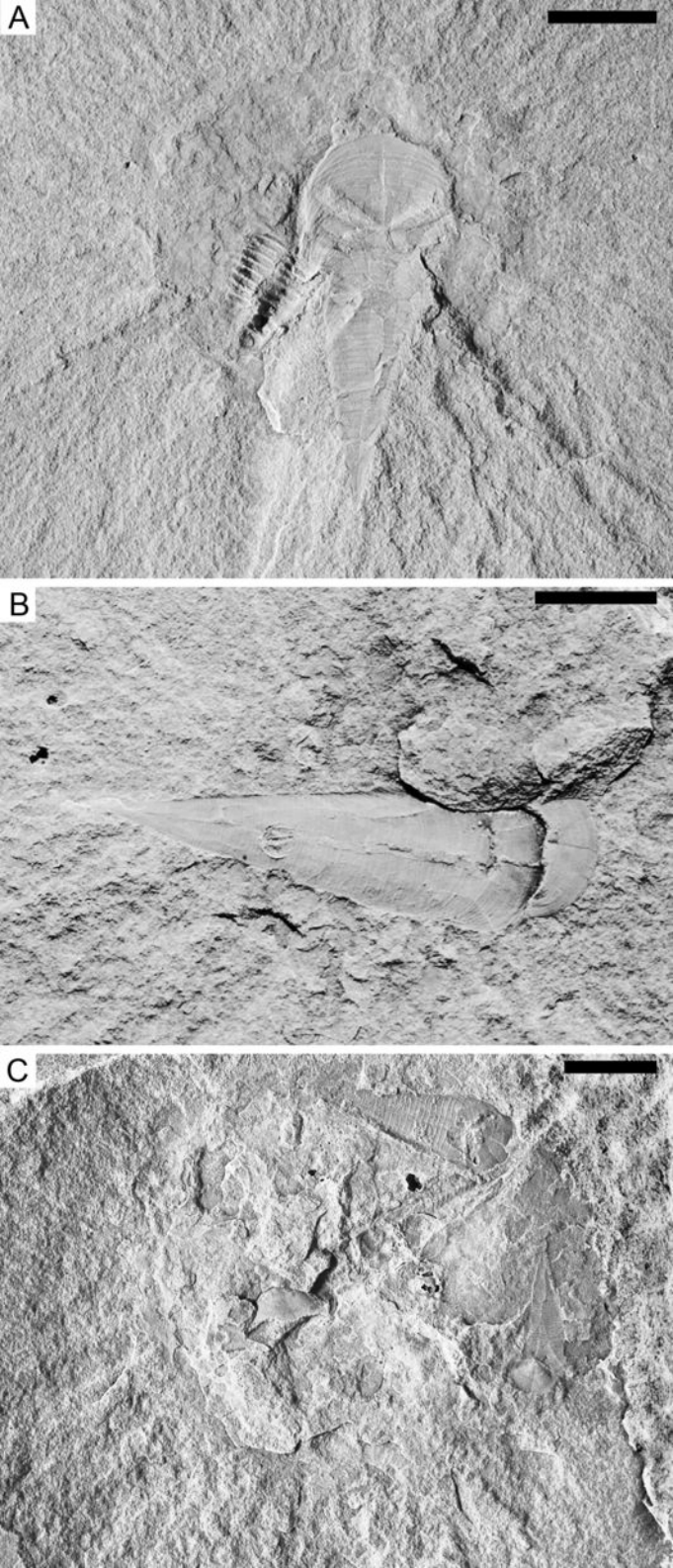
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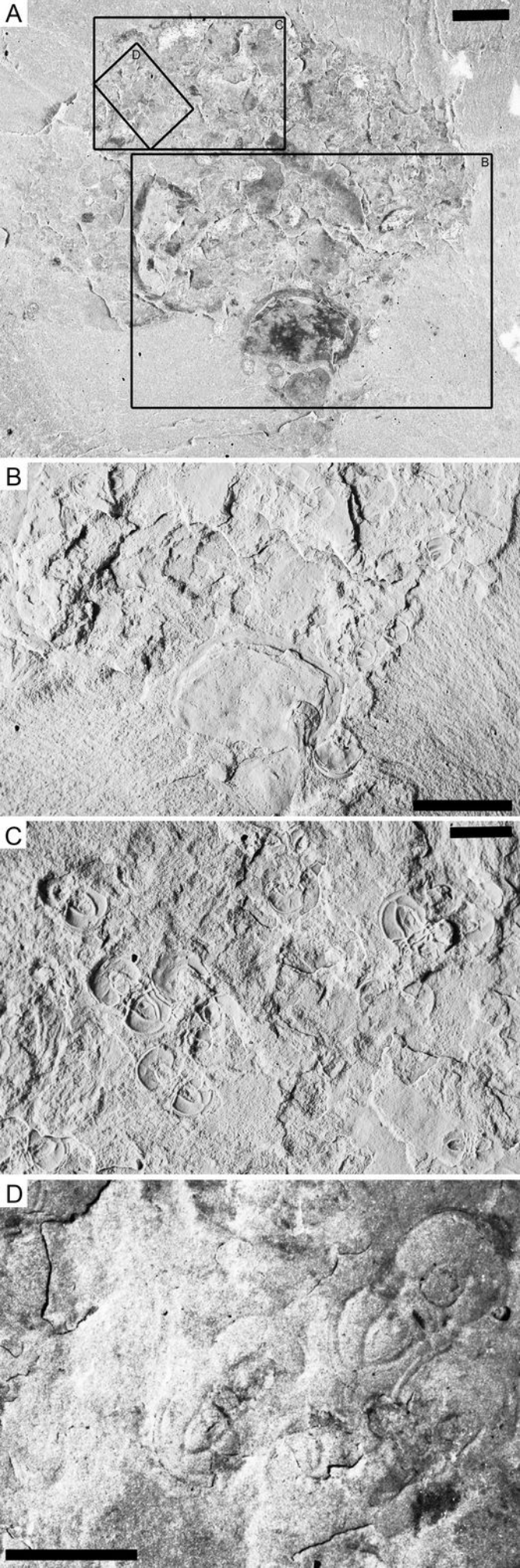
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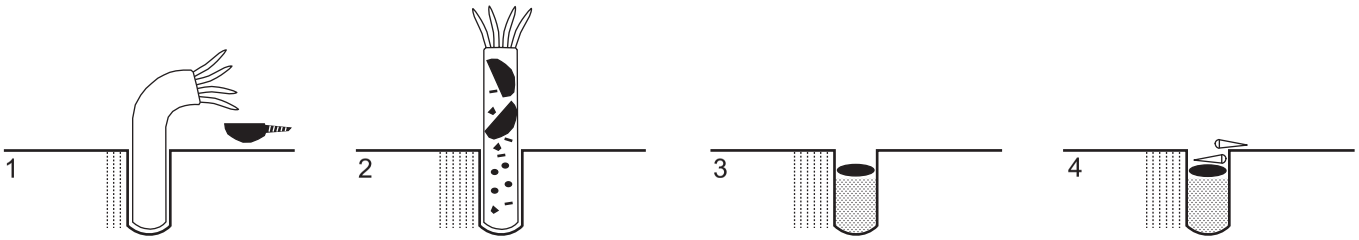
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