ISSN 2642-1550, Volume 5, 2023

Noteworthy Taphonomic Attributes of a Nautiloid Cephalopod from the Middle Silurian (Wenlock) Massie Formation of Southern Indiana

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Received 5/27/2022
Accepted for publication 6/23/2023
Published 10/2/2023

Suggested citation: Thomka, J. R., Bantel, T. E., and Gunderson, L. K., 2023, Noteworthy taphonomic attributes of a nautiloid cephalopod from the middle Silurian (Wenlock) Massie Formation of southern Indiana: Indiana Geological and Water Survey, Indiana Journal of Earth Sciences, v. 5. doi: 10.14434/ijes.v5i1.34564

ABSTRACT

A specimen of the nautiloid cephalopod *Dawsonoceras annulatum* from the middle Silurian (Wenlock) Massie Formation of southeastern Indiana, USA, is herein described because of its suite of uncommon taphonomic characteristics. Three noteworthy features are observable. First, an articulated calymenid trilobite is preserved in the sediment infill of the cephalopod, having been either swept into the open shell post-mortem or rapidly buried alive while sheltering inside the hollow cavity. Second, a series of small (pinhole-sized) borings, identifiable as the ichnogenus *Ropalonaria* and potentially produced by ctenostomate bryozoans, is present on the upward-facing and lateral surfaces of the cephalopod shell—a feature that is otherwise unreported in the fauna of the Massie Formation. Borings appear to occur preferentially in raised portions of the shell. Third, tightly coiled microconchids are encrusting the exterior of the shell, representing an association that had been previously documented in this unit, but using incorrect identities of the encrusting organism. The trilobite within the nautiloid shell is the first example of this rare biotic association from the Massie Formation, and the other two features, although not rare, have been either incorrectly documented or left undocumented in reports on the Massie Formation. Given that this fossil fauna occurs in a region strongly affected by dolomitization, these features are worthy of description on that basis alone. However, their co-occurrence on a single specimen highlights the fact that relatively common taxa such as cephalopods are still capable of yielding rare and/or significant taphonomic and paleoecological data.

INTRODUCTION

Cephalopods are a fairly ubiquitous component of Paleozoic sedimentary rocks, perhaps especially so in the extensive carbonate and calcareous mudrock strata of middle Silurian age (Brett, 1991; Ferretti and Kříž, 1995; Holland, 2014). In spite of the abundance of cephalopods as bioclasts in rocks and as fossil specimens in faunal collections, these organisms should not be ignored, even if the particular taxa are relatively common and geographically widespread. Occasionally, specimens are discovered that are particularly informative, shedding light on taphonomic and/or paleoecological patterns that may be significant to interpreting the stratigraphic unit or region from which the material was collected. In some cases, specimens of common cephalopod taxa that may easily go unnoticed or uncollected due to their commonness lead to improved understanding of broader paleontological phenomena (Donovan, 1989). The present contribution is a description of one such specimen: a nautiloid cephalopod displaying several taphonomic features that are sufficiently rare to warrant documentation and interpretation.

The purpose of this report is to describe three taphonomic and, in the context of taphonomic feedback (Kidwell and Jablonski, 1983), ecological phenomena on an otherwise unremarkable nautiloid cephalopod specimen from the middle Silurian of the eastern midcontinental United States. Documentation of these features not only increases knowledge of the paleontology of an important Paleozoic fossil-bearing unit, but also provides an encouraging case study in the value of detailed taphonomic investigation of fossils that would be overlooked or left uncollected in many instances.

Lithostratigraphic nomenclature

Shaver and others (1986)			Brett and others (2012)
Salamonie Formation	Laurel Member		Laurel Formation
Salamonie Formation	Osgood Member	Upper Shale	Massie Formation
Salamonie Formation	Osgood Member	Middle Limestone	Lewisburg Formation
Salamonie Formation	Osgood Member	Lower Shale	Osgood Formation

Figure 1. Lithostratigraphic nomenclature of the region containing the study locality. The traditional system is that of Shaver and others (1986). This has been updated to the terminology of Brett and others (2012), which is employed here. The studied material was collected from the Massie Formation, formerly the Upper Shale of the Osgood Member of the Salamonie Formation. Modified from Brett and others (2012, Fig. 11).

LOCALITY AND STRATIGRAPHY

Studied material was collected from the active New Point Stone quarry outside of Napoleon, north-central Ripley County, southeastern Indiana (N39°12′31.39′′, W85°18′53.74′′), a site that is famous for exceptionally diverse, abundant, and well-preserved echinoderms and trilobites (Frest and others, 1999, 2011; Thomka and others, 2016). The fossil fauna is all the more remarkable because it occurs in strata that were moderately to strongly affected by late-diagenetic dolomitization, which left most equivalent exposures throughout the region largely devoid of calcareous macrofossils (McLaughlin and others, 2008; Brett and others, 2012; Thomka and Brett, 2015b).

The most prolific fossil-bearing unit at the Napoleon quarry is the middle Silurian (Wenlock: Sheinwoodian) Massie Formation. This formation consists of a basal bioclastic carbonate unit capped by a microbiohermal hardground (Thomka and Brett, 2015a, 2015b), an overlying, highly fossiliferous siliciclastic mudstone interval which has yielded the vast majority of spectacular specimens (Frest and others, 2011; Thomka and others, 2016), and an upper unit composed of dense, sparsely fossiliferous calcisiltites (Brett and others, 2012). Recent stratigraphic studies (Brett and others, 2012) have resulted in revisions to the traditionally held lithostratigraphic terminology for the region containing the Napoleon quarry, specifically the nomenclature of Shaver and others (1986). The relevant changes to the stratigraphy of the study site are summarized in Figure 1. The former "Lower Shale," "Middle Limestone," and "Upper Shale" units of the Osgood Member of the Salamonie Formation are now recognized, respectively, as the Osgood Formation, Lewisburg Formation, and Massie Formation (Fig. 1). The former Laurel Member of the Salamonie Formation is now recognized as the Laurel Formation (Fig. 1).

The specimen described in this study was collected from the lower decimeter of the siliciclastic mudstone lithofacies, where the poorly lithified mudrock matrix

DOI 10.14434/ijes.v5i1.34564

allowed the cephalopod shell to be weathered free and examined with very little preparation. Nautiloid cephalopods are moderately common macrofossils in the mudstone lithofacies of the Massie Formation, occurring in a low-diversity assemblage composed of, in decreasing rank abundance, *Dawsonoceras annulatum*, indeterminate orthoconic forms, and *Michelinoceras* sp. (Gunderson and others, 2022).

DESCRIPTION OF SPECIMEN

The studied specimen is a partial orthoconic nautiloid cephalopod phragmocone (Fig. 2), most likely the anterior to middle portion based on the degree of tapering and the fact that neither the body chamber nor the apical termination are preserved. This specimen is reposited at the Cincinnati Museum Center (Cincinnati, Ohio) under specimen number CMC IP 95633. It measures 85 mm in length, 38 mm in maximum width, and 25 mm in maximum thickness; it is moderately intact and minimally compressed compared to most cephalopod fossils recovered from the Massie Formation. The shell material is pale brownish-gray, which is typical for cephalopods not preserved as internal molds at this locality. The infilling sedimentary material is a well-lithified, light gray, argillaceous biomicrite (Fig. 2).

This specimen can be reliably identified as *Dawsonoceras annulatum* (Kröger and Isakar, 2006), the most abundant cephalopod taxon within the mudstone lithofacies of the Massie Formation at the Napoleon quarry and a taxon that is common in middle Silurian carbonates in multiple continents (Foerste, 1928; Holland, 2002; Manda and Turek, 2015). Based on preliminary data pertaining to the taphonomy of *D. annulatum* from the study site, this specimen is fairly typical with respect to dimensions and degree of surface feature visibility relative to other material recovered from this interval (Gunderson and others, 2022).

Figure 2. Nautiloid cephalopod (*Dawsonoceras annulatum*) partial phragmocone (CMC IP 95633) from the lower decimeter of the mudstone lithofacies of the Massie Formation, collected at the Napoleon quarry, northern Ripley County, southeastern Indiana. View of upper surface, where encrusting organisms and bioerosion structures are located; adapical end of phragmocone to the bottom of the image. Scale bar = 5 cm.

TAPHONOMIC FEATURES

Three features observed on this specimen are worthy of comment, either because they are features that are relatively uncommon among Silurian cephalopods in general, features that are known from faunas elsewhere but not previously documented from the Massie Formation, and/or features that were noticed in previous studies of material from the Napoleon quarry but not given sufficient or accurate descriptions. Specifically, these significant features are: (1) an articulated trilobite inside the cephalopod phragmocone, (2) microconchid tentaculitoid mollusks on the exterior of the shell, and (3) shallow bioerosion structures penetrating the shell structure. As noted above, all of these features reflect taphonomic feedback, a concept centered around the presence of dead skeletal remains affecting the ecology of organisms subsequently occupying the environment in which the bioclasts accumulated (Kidwell and Jablonski, 1983).

Articulated trilobite inside cephalopod shell

The cephalopod specimen is completely filled with well-lithified sedimentary material consisting of light gray argillaceous micrite and bioclastic material (Fig. 3). Given the relatively uncompressed dimensions of

DOI 10.14434/ijes.v5i1.34564

the nautiloid shell, it is apparent that this material was swept into the empty chambers of the phragmocone after the decay of soft tissues but before burial. Along with the fine, light gray infilling sediment is a series of articulated, dark brown trilobite thoracic segments (Fig. 3). This articulated trilobite—clearly a calymenid and probably the genus *Calymene*—is entirely contained within the conch of the cephalopod. Unfortunately, weathering has destroyed the posterior portion of the trilobite and the anterior portion is embedded within the lithified infilling sedimentary material. Consequently, an obliquely cross-sectional view of the thorax is all that is visible for this specimen, but this is sufficient to demonstrate the articulated state of the thorax (Fig. 3). The trilobite is located left of center and in the upper portion relative to the body walls of the cephalopod, with the long axis of the trilobite (that is, the plane of bilateral symmetry) oriented approximately 20º from the long axis of the cephalopod.

Occurrences of articulated trilobites inside nautiloid cephalopod conchs are rare but not unknown, as reviewed by Davis and others (2001) and Fatka and others (2021). Sheltered preservation of articulated trilobites within cephalopods has been interpreted

Figure 3. **Oblique view of the adapical end of CMC IP 95633, showing cross-sectional view of articulated calymenid trilobite thorax segments found within the *D. annulatum* shell. The posterior end of the trilobite has been weathered away, and the anterior end is embedded within the well-lithified infilling sedimentary material, so the degree of completeness of the trilobite (*Calymene* sp.?) is impossible to assess. Hence, it is unclear whether this represents a dead individual or part of a molted exoskeleton. Scale bar = 2 cm.**

as reflecting three potential phenomena: sweeping of fresh trilobite carcasses into open cephalopod shells by currents, burial of living trilobites that had voluntarily entered an open cephalopod shell to avoid predators and/or undergo molting, and burial of living trilobites that had voluntarily entered an open cephalopod shell to scavenge upon organic tissues within (Davis and others, 2001; Fatka and others, 2021). Of these options, Fatka and others (2021) found post-mortem transportation of trilobite skeletons to be least likely for most occurrences and hiding from predators (during molting or otherwise) to be the most typical cause of sheltered trilobite preservation. Unfortunately, the incompleteness of the trilobite in this cephalopod prevents assessment of the origin of this faunal association; indeed, it is not possible to even discern whether the trilobite material represents a dead individual or a discarded exoskeleton (see discussion in Fatka and others, 2021). Nevertheless, it is worth documenting this occurrence, as it provides an additional example of an intriguing taphonomic phenomenon and one not previously known from the Massie Formation. It also serves as another example of sheltered preservation of calymenids, as this trilobite group seems prone to enter into nautiloid shells (Davis and others, 2001).

Encrusting microconchids

Abundant encrusting organisms on macrofossils from the Massie Formation have been extensively documented (Paul, 1971; Frest and others, 2011; Thomka and others, 2016). Among the most common encrusters are minute, calcareous, tubular structures most famously found on articulated or partially articulated diploporitan thecae (Bassler, 1915; Boyce, 1956; Paul, 1971), but also readily observed on other shelly macrofossils (Frest and others, 2011). Although commonly identified as generalized "worm tubes" (Paul, 1971; Frest and others, 2011) or ascribed to *Spirorbis* (Brett, 1991), these tightly coiled structures (Fig. 4) are now known to represent microconchids, an unusual form of probable tentaculitoid mollusk (Taylor and Wilson, 2003; Vinn and Mutvei, 2009; Zatoń and others, 2011; Thomka and Eddy, 2018). Microconchid encrustation of Paleozoic calcareous macrofossil bioclasts is increasingly recognized as a very common occurrence, but a biotic association that remains relatively rarely or inaccurately reported.

The *D. annulatum* specimen is encrusted by at least four microconchid tubes that are relatively uniform in dimension, all being 1-2 mm in maximum diameter (Fig. 4). All microconchids are present on the exterior of the non-moldic cephalopod shell, occurring on the upper surface (that is, the surface in which the dorsal surface of the enclosed trilobite is exposed)

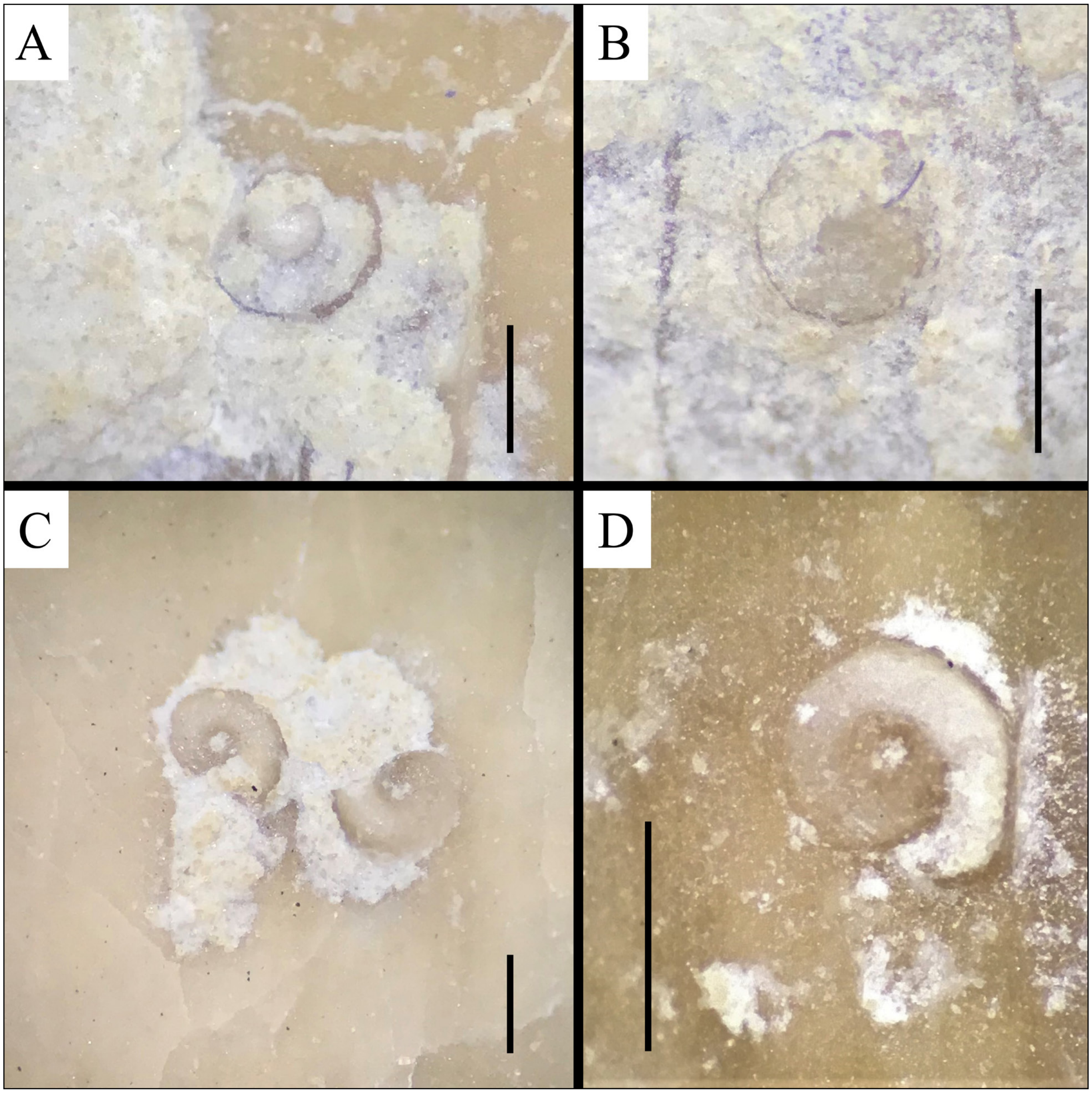

Figure 4. Microconchid "tubeworms" (tentaculitoid mollusks) encrusting *D. annulatum* shells from the Massie Formation. A) Moderately well-preserved specimen from the upper surface of CMC IP 95633. Note the tight planispiral coil in continuous contact with the substratum. B) More poorly preserved specimen from the upper surface of CMC IP 95633. It has been weathered away to a nearly two-dimensional structure showing the coiled microconchid morphology. C-D) Examples of better-preserved microconchids from other *D. annulatum* shells recovered from the Napoleon quarry. C shows two specimens in close proximity to one another with apertures facing different directions. D shows a well-preserved microconchid with nice three-dimensionality. All scale bars = 1 mm.

and preferentially occur on the topographically positive ridges of the annulated phragmocone (Fig. 4). This distribution suggests a restriction to settlement areas that were elevated and therefore more likely exposed to stronger currents for the suspension-feeding microconchids. Abrasion of the upper surface resulted in relatively poor preservation of the microconchids (Fig. 4), but their presence is clearly identifiable. Examination of other *D. annulatum* shells revealed the presence of numerous encrusting microconchids showing a similar pattern, although shells with more pristine surface textures may contain a few microconchids in the depressed valleys in addition to the ridges (Gunderson and others, 2022). The microconchids are tightly spiraled in a planispiral orientation parallel to the encrusted shell surface, maintaining constant contact with the substrate; this morphology is discernable in spite of the effects of abrasion (Fig. 4). The shells are cylindrical tubes, with a circular aperture and no visible accretionary growth lines (Fig. 4), seemingly primarily as a consequence of surficial biostratinomic degradation rather than recrystallization, as *D. annulatum* is one of the rare cephalopods that precipitated a shell that was not entirely aragonitic (DeBaets and Munnecke, 2018). It is unclear whether the cephalopod was encrusted while alive or after death, but post-mortem encrustation seems more logical given the apparent restriction of encrusters to one side of the shell and the random orientation of microconchid apertures. As all of the cephalopod shells collected from the Massie Formation at the Napoleon quarry were recovered as material weathered free from poorly lithified mudrocks, it is impossible to relate the orientations of microconchid apertures and cephalopod long axes to primary compass direction(s).

Encrusting microfossils have not previously been reported from cephalopod substrata in the Massie Formation, and other fossils from the Napoleon quarry that have been analyzed for encrusters have resulted in these minute, tightly coiled cylindrical tubes being reported using inaccurate names (Paul, 1971; Brett, 1991; Frest and others, 2011). Hence, even though microconchids are commonly encountered on cephalopods at this site (Gunderson and others, 2022) and elsewhere in the Silurian (DeBaets and Munnecke, 2018, Fig. 1b), formally recording the presence of microconchids on this cephalopod specimen is important not only for improving the completeness of the record of organisms collected from the Napoleon quarry locality, but also for encouraging other researchers to identify and label these encrusters correctly. Outdated terms such as "tubeworms" and *Spirorbis* are terms that are still occasionally encountered in literature describing microconchids—although neither tube-secreting serpulid worms nor *Spirorbis* were actually alive during the Silurian (Taylor and Wilson, 2003; Vinn and Mutvei, 2009)—and revisions to documented fauna, such as this study, are needed to formally revise and update faunal lists. In addition, to our knowledge, the only published description of encrusting organisms using cephalopods from the Massie Formation as substrata is the recent study by Thomka and Bantel (2021), who recorded multiple echinoderm attachment structures on the shell of an indeterminate orthoceratid. Additional studies of cephalopod fossils from the Napoleon quarry—which include ongoing research by one of us (LKG)—are needed to document the full extent of cephalopod encrustation and diversity of encrusters on cephalopod substrata in the Massie Formation. However, recording the presence of microconchids is an important step toward this objective.

Bioerosion structures

Borings have not previously been reported from nautiloid cephalopod shells recovered from the Massie Formation of southeastern Indiana. More broadly, this occurrence also contributes to the record of bioerosion in bioclastic substrata through the early Silurian, which is increasingly recognized as an important interval in the history of endolithic borings (Taylor and Wilson, 2003; Tapanila, 2005). Numerous pinhole-sized borings are present on the upper surface (in the context of position on the seafloor, defined by the dorsal side of the trilobite) and one lateral surface of the *D. annulatum* specimen (Fig. 5). They are more common and display a maximum spatial density toward the adapical region of the partial phragmocone, perhaps indicating the upcurrent direction at the time the bioerosion structures were produced.

Borings appear circular to slightly irregular in plain view and appear to be relatively straight-sided and primarily

Figure 5. Bioerosion structures (*Ropalonaria* isp.) on the upper and lateral surfaces of the *D. annulatum* shell (CMC IP 95633). These mesoborings are most likely produced by ctenostomate bryozoans and the clustered, "pinprick" structures visible on the shell exterior are accessory tubules associated with a horizontally oriented structure formed within the shell substratum. *Ropalonaria* borings are smaller, more discrete, and more densely spaced on the lateral surface of the phragmocone, and larger, less densely spaced, and characterized by more gradational or overlapping borders on the upper surface of the phragmocone, seemingly reflecting the influence of abrasion. Scale bar = 2 cm.

DOI 10.14434/ijes.v5i1.34564

vertical in cross section (Fig. 5). Borings typically have non-overlapping edges, but in the areas of greatest boring concentration, adjacent borings may display borders in immediate contact with one another (Fig. 5); whether this reflects taphonomic modification of boring margins by weathering is unclear but seems likely. The greatest density of borings is 24 borings per cm^2, occurring on the lateral surface of the phragmocone. Boring intensity was documented as 11-12 borings per cm^2 on the central portions of the ridges situated toward the adapical end of the specimen, where borings were larger and may have been affected by abrasion (resulting in widening of openings and coalescence of adjacent borings). Despite being characterized by a circular opening to the surface, they are too shallow to represent the common cylindrical, vertical boring *Trypanites*, which is among the most abundant of bioerosion structures in early-middle Paleozoic carbonate substrata (Bromley, 1972; Taylor and Wilson, 2003; Wilson and Palmer, 2006). Rather, these represent the ichnogenus *Ropalonaria* (Pohowsky, 1978), with the "pinpricks" constituting apertural openings of a shallow, primarily horizontally oriented structure consisting of interconnected tubes (not visible on the shell exterior) penetrating the shell, with multiple disconnected openings to the surface. These more complex mesoborings are commonly produced by ctenostomate bryozoans, which produced *Ropalonaria* borings manifesting externally as closely spaced "pinprick" openings on calcareous bioclasts (Pohowsky, 1978). These organisms, known to produce bioerosion structures in calcareous substrates since the Ordovician (Pohowsky, 1978; Wilson and Palmer, 2006), generate borings in which multiple accessory tubules connected by a stolon open up to the shell-water interface in a manner that is highly consistent with the mesoborings observed on this nautiloid (Pohowsky, 1978; Olempska, 2012, Fig. 2a).

Similar to the encrusting microconchids described above, *Ropalonaria* borings are restricted to the raised ridges of the cephalopod shell, being present only on the upper surface of the shell (Fig. 5). This almost certainly reflects preferential occupation of regions exposed to stronger and/or more persistent currents for the suspension-feeding bryozoan tracemakers occupying the dead cephalopod shell. Based on preliminary data, these mesoborings occur relatively frequently on *D. annulatum* shells from this locality and their distribution is consistent with the observations made on CMC IP 95633 (Gunderson and others, 2022). Thus far, these are the only bioerosion structures present on cephalopods in the Massie Formation (Gunderson and others, 2022); they are not rare, but have not hitherto been reported from cephalopod (or other) substrata in the Massie Formation or other fossiliferous units at the Napoleon quarry. Their occurrence and ubiquity most likely reflect the lack of attention historically paid to cephalopods as substrata in the middle Silurian of southeastern Indiana.

DISCUSSION

Nautiloid cephalopods are relatively common macrofossils in middle Silurian carbonate deposits and comprise a relatively low-diversity assemblage within the Massie Formation of southeastern Indiana. Study of the presently considered specimen highlights the fact that their skeletal remains were important in affecting encrusting and bioeroding organismal communities, as well as providing an empty cavity that could shelter trilobite remains from biostratinomic and/or compactional disarticulation. The specimen described herein belongs to a common and widespread taxon, one whose occurrence is unremarkable in Wenlock-age strata of the greater Cincinnati Arch region; however, it is preserved in a manner that is noteworthy. This taphonomic significance may reflect exceptional events that produced a truly unique specimen, but it is equally likely—if not more likely—that the features highlighted in this paper are more common than the current literature suggests. It is hoped that continued collection of, and attention to, ubiquitous Paleozoic cephalopods will result in discovery of additional noteworthy specimens. This extends to specimens that have been collected previously and never given serious study and/or specimens that are characterized by features that are not traditionally considered to represent exceptional preservation.

ACKNOWLEDGMENTS

The Wanstrath family of Napoleon, Indiana, generously allowed access to the collection locality. Our knowledge of the stratigraphy and fossil fauna of the Napoleon quarry has been significantly increased by discussion and fieldwork with Carlton E. Brett (University of Cincinnati) and Donald L. Bissett (Dry Dredgers). Our understanding of the nature of the bioerosion structures was improved by comments by Timothy J. Palmer (Aberystwyth University). Cameron E. Schwalbach (Cincinnati Museum Center) facilitated repository of the studied specimen. The constructive reviews provided by Benjamin F. Dattilo (Purdue University-Fort Wayne) and Olev Vinn (University of Tartu) improved previous versions of this paper.

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