

Predatory drill holes and partial mortality in Devonian colonial metazoans

Mark A. Wilson*

Department of Geology, College of Wooster, Wooster, Ohio 44691, USA

Paul D. Taylor*

Department of Palaeontology, The Natural History Museum, London SW7 5BD, UK

ABSTRACT

Elliptical holes ~0.2–0.3 mm in diameter with beveled edges have been found penetrating the zooids of encrusting hederellids (colonial metazoans of uncertain affinity) from several localities in the Middle Devonian (Givetian) of North America. These are the first known predatory drill holes in pre-Cretaceous colonial animals and a key addition to the record of Paleozoic predation. Some drill holes were subsequently patched from within by new skeletal material, proving that the drilling occurred during the life of the colony. These drill holes are analogous to predatory drill holes in some modern cheilostome bryozoans, which can be similarly patched, in this case by the intramural budding of a new zooid into the empty chamber of the old zooid. A drilling predator of unknown affinity evidently consumed hederellid zooids one at a time, inflicting partial mortality on the colonies. The mode of drilling suggests that the predator specialized in this type of colonial prey, and the repaired drill holes show that the hederellids had a response to such damage. Reports of small circular holes interpreted as predatory drill holes are becoming more common in noncolonial shelled invertebrates from the Paleozoic, notably brachiopods, bivalves, and crinoids. These drill holes are far less frequent than in post-Paleozoic shells (where most are the work of gastropods), and many are of questionable origin, with some representing the traces of parasites and others postmortem domichnia.

Keywords: Devonian, predation, drill holes, hederellids.

INTRODUCTION

The ecological and evolutionary history of predation in Paleozoic marine invertebrates has been the subject of several recent studies (see, for example, Kowalewski et al., 1998, 2000, 2005; Harper et al., 1999; Baumiller et al., 1999; Leighton, 2001, 2003; Harper, 2003; Baumiller and Gahn, 2004; Cosma and Baumiller, 2005). Our increasing abilities to analyze the fossil record and to search the literature more effectively have shown that predation on shelled organisms in the Paleozoic may have been uncommon but was widespread and possibly exerted significant selective pressures (Harper, 2003). At issue is the validity of predator-prey evolutionary escalation hypotheses (i.e., Vermeij, 1977, 1987; Signor and Brett, 1984) to the Paleozoic marine realm.

Unequivocal evidence for predation is difficult to find in the Paleozoic, and it is even harder to sort out the responses of prey to specific modes of predation. Drill holes in shells are probably the best indicators of predation. Unfortunately, though, there are many nonpredatory mechanisms that can produce holes in

shells, from parasitism (Baumiller, 1990) to postmortem boring (Wilson and Palmer, 2001), and workers often have to rely on the statistics of stereotypy to demonstrate that a set of holes in a shell was likely produced by a predator. In addition, the number of drill holes in Paleozoic shells is very low, making the statistical argument for boring stereotypy even more problematic.

We present here new evidence for predatory drilling in the Middle Devonian, a crucial time in marine community evolution representing the “mid-Paleozoic precursor to the Mesozoic marine revolution” (Signor and Brett, 1984, p. 229). In addition, this is the first record of pre-Cretaceous drilling predation on a colonial metazoan, and the only known fossil example where the prey responded by plugging the holes with skeletal “patches.”

MATERIAL AND METHODS

Approximately 350 hederellid colonies from the Silurian through the Pennsylvanian were microscopically examined from the paleontological collections of the Natural History Museum, London (NHM); one colony was studied from the University of Michigan Museum of Paleontology (UMMP). The col-

onies were found encrusting a variety of hard substrates, including coral skeletons, brachiopod shells, stromatoporoids, and hardgrounds. Of the colonies studied, six showed two or more drill holes, with two others possessing single drill holes, yielding a drilling frequency of ~2% of colonies. All of the drilled colonies were collected from Givetian (Middle Devonian) units. Six are from the Widder Formation (Hungry Hollow Member) of Arkona, Ontario, Canada; one is from the Ludlowville Formation (Centerfield Member) of East Bethany, New York; and one is from the Silica Formation of Sylvania, Ohio. (See GSA Data Repository¹ for further locality and specimen information.)

Colonies with two or more drill holes were studied using a low-vacuum scanning-electron microscope. Twenty-five drill holes from one Widder Formation colony (NHM D30066) were preserved well enough to be measured and described with an optical microscope.

¹GSA Data Repository item 2006108, Appendix (drilled hederellids), is available online at www.geosociety.org/pubs/ft2006.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

*E-mails: mwilson@wooster.edu; pdt@lbnhm.ac.uk.

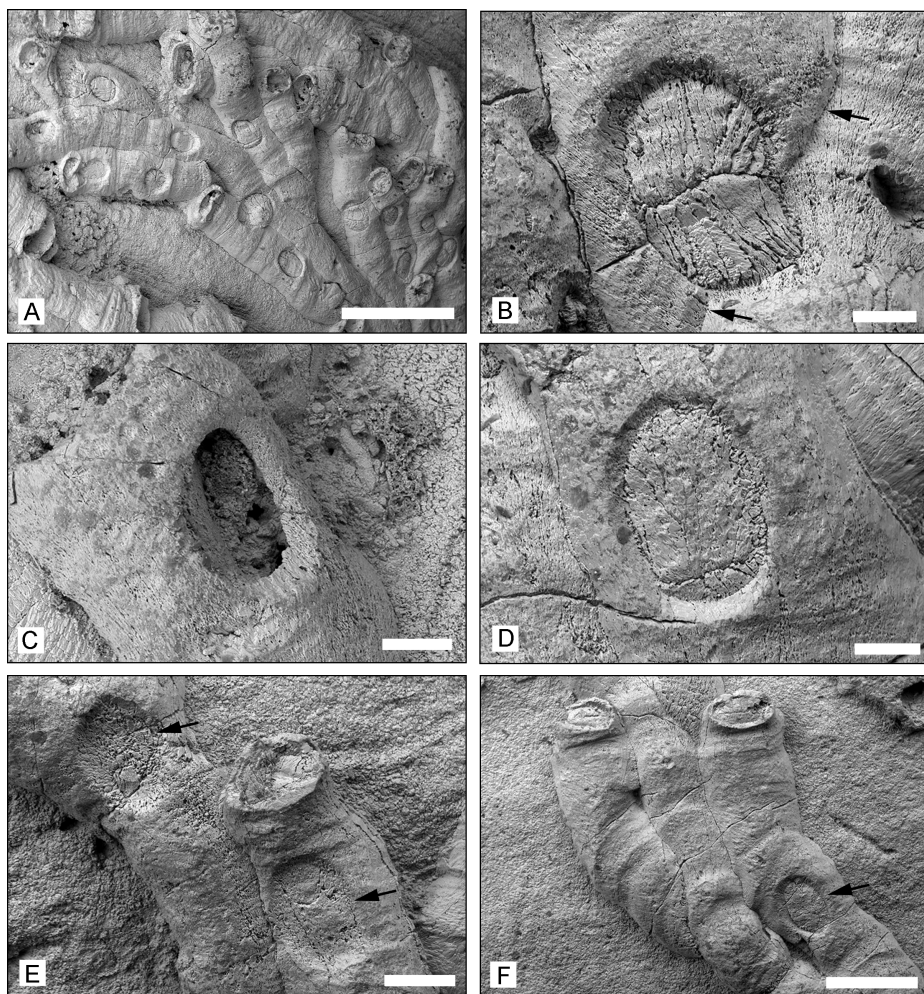


Figure 1. Inferred predator drill holes in colonial metazoan *Hederella thedfordensis* Bassler, NHM D30066, Middle Devonian, Hamilton Group, Arkona, Ontario. **A:** Group of zooids containing numerous patched drill holes. **B:** Patched drill hole crossing boundary (arrows) between two zooids. **C:** Beveled drill hole positioned slightly off midline of zooid. **D:** Patched drill hole showing sloping edges. **E:** Scoop-like incomplete drill holes (arrowed) in two zooids. **F:** Zooids with apertures sealed by diaphragms that, on right, contain patched drill hole (arrow). Scale bars: A = 1 mm; B–D = 100 μm ; E = 200 μm ; F = 500 μm .

THE ENIGMATIC HEDERELLIDS

Hederellids are a diverse group of colonial encrusting metazoans found from the Silurian (Bassler, 1939) into the Permian (Lisitsyn, 1998). Their ramifying colonies have long, tubular, generally vermiform, zooids, which are nonporous and terminate with elliptical apertures sometimes closed by diaphragms (Fig. 1F). Bassler (1939), who produced the most definitive work to date on their taxonomy, considered them to be a suborder of cyclostome stenolaemate bryozoans. This placement has been followed by most other workers (e.g., Kiepora, 1973; Sparks et al., 1980), even though some have expressed doubts about the cyclostome or even bryozoan affinities of hederellids. Brood (1975, p. 71), for example, wrote, “It may even be doubted if the hederellids are bryozoans at all, since the reasons for regarding them as bryozoans are few, except for their general shape as small,

colonial animals with a calcareous skeleton.” We also believe that the hederellids were not bryozoans because maximum zooidal diameter (1.5 mm) is considerably larger than in bryozoans (~ 0.5 mm), the zooids often bud from the sides of a continuous stolonal tube, and their fibrous wall structure is unknown among Paleozoic bryozoans (Wilson and Taylor, 2001).

Like most other encrusters, hederellids would have been suspension feeders, presumably employing a tentacular organ to entrain and/or capture plankton. The fact that the predators here drilled through skeletal walls shows that the feeding organ of hederellids could be retracted and predator access through the aperture blocked.

THE DRILL HOLES

Almost all the drill holes in the hederellid zooids are situated along their upward-facing

midlines, usually one drill hole per zooid but sometimes two in a single zooid (Fig. 1A). In five cases, a single drill hole penetrates the sides of two adjacent zooids (Fig. 1B). The drill holes are mostly elliptical, always oriented with their long axes parallel to the long axes of the bored zooids (compared to the hederellid apertures, which are oriented transversely to the long axis of the zooid, Fig. 1F). (The elliptical nature of these excavations is unusual for predatory drill holes. It appears to be a function of drilling an upward-facing hole on a narrow tube.) The exterior opening is larger than the interior opening, giving them beveled margins (Figs. 1B–1D). The outer width of the drill holes averages 0.24 mm (range 0.15–0.30 mm; standard deviation 0.04 mm; $N = 25$), and the outer length averages 0.31 mm (range 0.15–0.36 mm; standard deviation 0.05 mm; $N = 25$). Of the 25 drill holes measured on one colony, 21 were repaired by skeletal “patches” apparently secreted from within the skeleton and emplaced flush with the inner margins of the drill holes (Figs. 1A, 1B, 1D, and 1E).

These drill holes generally fit the ichnological description of *Oichnus ovalis* Bromley 1993 (p. 170–171) in that they are oval to circular and “taper subparabolically” from a larger external opening to a smaller internal hole. However, Bromley (1993) specifically excluded submillimeter-sized drill holes from his ichnotaxon. We suggest that the size of a drill hole is not a useful ichnotaxonomic character, so the definition of *O. ovalis* should be later revised to include these smaller drill holes and others.

Three drill holes were found that did not penetrate the skeletal wall of the hederellid zooids (Fig. 1E). These incomplete drill holes have the same outline shape as completed drill holes but are circular to elliptical shallow scoops. Scoop surfaces are not preserved well enough to show any striations or other marks to indicate the drilling mechanism.

Thus far, only three species of *Hederella* have been found with drill holes: *H. thedfordensis* (the Widder Formation colonies), *H. magnum* (Silica Formation), and *H. delicatula* (Ludlowville Formation). Other species of hederellids are found on the same substrates as the drilled colonies but show no drill holes themselves.

We are convinced that these are predatory drill holes because they: (1) were excavated from the outside, as shown by the existence of incomplete drill holes; (2) damaged the living hederellid, as shown by the existence of patch-like repairs; (3) always penetrated directly into the zooidal chamber, with the only “edge drillings” occurring when the drill hole overlapped two adjacent zooids; and (4)

showed a preference for particular hederellid species, despite the availability of other hederellid species encrusting the same substrates. The drill holes thus fit the criteria for recognizing predatory boreholes outlined by Carrier and Van Zandt (1972), Harper (2003), and others. The occasional set of two drill holes in a single zooid may represent drilling into zooids that had been previously drilled and repaired.

We can only speculate about the identity of the drilling predator. It was likely very small in size, no longer than a few millimeters in length, and it may have scraped the beveled holes with a radula-like device. It probably moved along the branches of the hederellid colony, drilling into and consuming one zooid at a time, while the hederellid repaired the damage behind it.

DRILLING PREDATION AND PARTIAL MORTALITY IN COLONIES

Colonial metazoans differ from unitary species in exhibiting partial mortality—the death of some but not all of the modular zooids that make up the colony. Partial mortality can often be due to predators attacking single zooids one at a time (McKinney et al., 2003). Colonies as a whole are able to survive partial mortality, and therefore predation on colonies is akin to grazing by herbivores on plants. In bryozoans, regeneration of new zooids may occur into the skeletal chambers of zooids damaged by predation, a process termed intramural budding (Taylor, 1988).

Drilling predation has seldom been recorded from colonial metazoans. However, colonies belonging to a clade of Late Cretaceous–Paleocene cyclostome bryozoans called meliceritids frequently contain circular and oval drill holes 40–90 μm in diameter (Taylor, 1982) that are inferred to have been made by small predators. Drill holes of similar morphology are known from other Jurassic–Holocene bryozoans, but not all are necessarily the work of predators (McKinney et al., 2003).

Drill holes made by an unknown predator into the zooids of a Holocene bryozoan species are commonly associated with reparative budding and provide a good analogue to the patched drill holes reported here in Devonian hederellids. The South Atlantic cheilostome *Microporella hyadesi* Jullien contains multiple drill holes that are 60–65 μm in diameter, circular, straight-edged, and numerous but show a low degree of stereotypy in penetrating various locations on the autozooidal frontal shield as well as ovicells (Fig. 2A). In many cases, a patch of new skeleton plugs the hole from within (Fig. 2B). The patch is part of the skeleton of an intramural reparative bud,

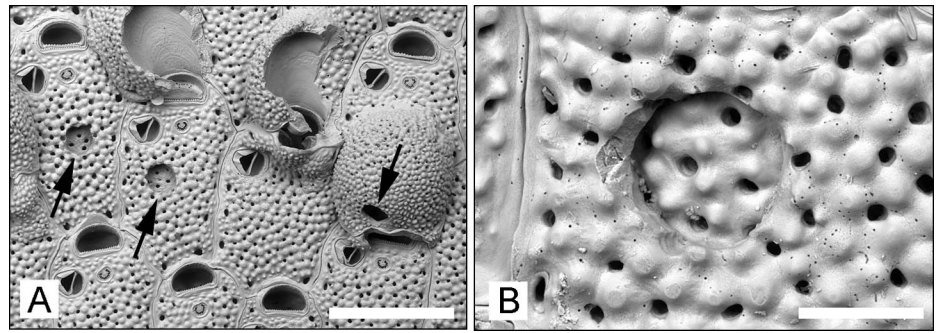


Figure 2. Drill holes in Holocene bryozoan *Microporella hyadesi* (Jullien) from South Atlantic, Discovery Station WS 84, NHM 1990.10.22.14 pt. **A:** Part of colony showing patched drill holes in two zooids (left arrows) and unrepaired drill hole in ovicell (right arrow). **B:** Detail of patched drill hole; pustulose and porous frontal shield of this bryozoan contrasts with smooth, nonporous wall of hederellids, but patching of drill holes from underneath is similar. Scale bars: **A** = 500 μm ; **B** = 100 μm .

which also secretes a new orificial rim concentrically within that of the old drilled zooid.

DRILL HOLES IN THE CONTEXT OF PALEOZOIC PREDATION

The drill holes in Devonian hederellids are the earliest unambiguous examples of selective predation on a colonial metazoan, and these may be the most ancient examples of a prey organism successfully repairing drilling damage to its skeleton (see Harper, 2003; McKinney et al., 2003, for reviews of drilling predation in the fossil record). One of the primary reasons to study predation in the fossil record is to ascertain whether predators were a significant selective force in the evolution of prey organisms, and vice versa (Vermeij, 1977, 1987; Signor and Brett, 1984; Kowalewski et al., 2005). It is critical when evaluating potential escalatory predator-prey relationships to be certain that the evidence for predation is clear-cut and to account for taphonomic biases in the fossil record (Harper, 2003). The drill holes show a true Devonian predator-prey relationship, albeit one between an unknown predator and a prey metazoan that has not yet found its systematic home.

Hederellids had the ability to repair their skeletons after they had been damaged. This skeletal repair mechanism may have evolved in response to predation, or it may have been present before predation evolved to simply fix broken zooidal walls. The latter is more likely, since the level of predation on these colonies was no more than 2% in the 350 colonies we examined. In any case, we see here a successful response of a prey species to the attention of predators.

It may be significant that the drilled hederellids are of Devonian age, even though this is the period of greatest diversity in the group. Signor and Brett (1984, p. 229) suggested that there was a “mid-Paleozoic marine revolution” driven by an increase in predators and

the consequent adaptation of prey. Kowalewski et al. (1998) showed a significant increase in drilling predation during the Devonian, and Leighton (2001, 2003) suggested that brachiopod prey, at least, had evolved responses to drilling predation by the Middle Devonian. This was a time when “high-energy” predators were surpassing “low-energy” predators, according to Bambach (1999, p. 136), establishing a pattern that continued through the Carboniferous. We do not know if the hederellid predators were high or low energy, but they can nevertheless be viewed as part of an escalating regime of predation in the Devonian.

ACKNOWLEDGMENTS

We are grateful for the very useful reviews of this manuscript by Lindsey Leighton, Liz Harper, and Franz Fürsich, and for stratigraphic advice from Carl Brett. We also thank The College of Wooster for supporting this research through the Luce Fund for Distinguished Scholarship.

REFERENCES CITED

- Bambach, R.K., 1999, Energetics in the global marine fauna: A connection between terrestrial diversification and change in the marine biosphere: *Geobios*, v. 32, p. 131–144.
- Bassler, R.S., 1939, The Hederelloidea, a suborder of Paleozoic cyclostomatous Bryozoa: *Proceedings of the United States National Museum*, v. 87, p. 25–91.
- Baumiller, T.K., 1990, Non-predatory drilling of Mississippian crinoids by platyceratid gastropods: *Palaeontology*, v. 33, p. 743–748.
- Baumiller, T.K., and Gahn, F.J., 2004, Testing predator-driven evolution with Paleozoic crinoid arm regeneration: *Science*, v. 305, p. 1453–1455.
- Baumiller, T.K., Leighton, L.R., and Thompson, D.L., 1999, Boreholes in Mississippian spiriferide brachiopods and their implications for Paleozoic gastropod drilling: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 147, p. 283–289.
- Bromley, R.G., 1993, Predation habits of octopus past and present and a new ichnospecies, *Oichnus ovalis*: *Bulletin of the Geological Society of Denmark*, v. 40, p. 167–173.

- Brood, K., 1975, Cyclostomatous Bryozoa from the Silurian of Gotland: Stockholm Contributions in Geology, v. 28, p. 45–119.
- Carriker, M.B., and Van Zandt, D., 1972, Predatory behavior of a shell-boring muricid gastropod, in Winn, H.E., and Olla, B.L., eds., Behavior of marine animals, current perspectives in research, Volume 1: Invertebrates: New York, USA, Plenum Press, p. 157–244.
- Cosma, T.N., and Baumiller, T.K., 2005, A trace fossil on a Silurian bivalve: Evidence of predatory boring?: *Ichnos*, v. 12, p. 135–139.
- Harper, E.M., 2003, Assessing the importance of drilling predation over the Paleozoic and Mesozoic: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 201, p. 185–198.
- Harper, E.M., Forsythe, G.T.W., and Palmer, T.J., 1999, A fossil record full of holes, the Phanerozoic history of drilling predation: Comment and reply: *Geology*, v. 27, p. 959–960.
- Kiepara, M., 1973, Devonian bryozoans of the Holy Cross Mountains, Poland. Part II. Cyclostomata and Cystoporata: *Acta Palaeontologica Polonica*, v. 18, p. 323–400.
- Kowalewski, M., Dulai, A., and Fürsich, F.T., 1998, A fossil record full of holes, the Phanerozoic history of drilling predation: *Geology*, v. 26, p. 1091–1094.
- Kowalewski, M., Simões, M.G., Torello, F.F., Mello, L.H.C., and Ghilardi, R.P., 2000, Drill holes in shells of Permian benthic invertebrates: *Journal of Paleontology*, v. 74, p. 532–543.
- Kowalewski, M., Hoffmeister, A.P., Baumiller, T.K., and Bambach, R.K., 2005, Secondary evolutionary escalation between brachiopods and enemies of other prey: *Science*, v. 308, p. 1774–1777.
- Leighton, L.R., 2001, New example of Devonian predatory boreholes and the influence of brachiopod spines on predator success: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 165, p. 53–69.
- Leighton, L.R., 2003, Morphological response of prey to drilling predation in the Middle Devonian: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 201, p. 221–234.
- Lisitsyn, D.V., 1998, The first Permian find of the genus *Hederella* (Bryozoa): *Paleontological Journal*, v. 32, p. 589–591.
- McKinney, F.K., Taylor, P.D., and Lidgard, S., 2003, Predation on bryozoans and its reflection in the fossil record, in Kelley, P.H., Kowalewski, M., and Hansen, T.A., eds., Predator-prey interactions in the fossil record: New York, Kluwer Academic–Plenum Publishers, p. 239–261.
- Signor, P.W., and Brett, C.E., 1984, The mid-Paleozoic precursor to the Mesozoic marine revolution: *Paleobiology*, v. 10, p. 229–245.
- Sparks, D.K., Hoare, R.D., and Kesling, R.V., 1980, Epizoans on the brachiopod *Paraspirifer bownockeri* (Stewart) from the Middle Devonian of Ohio: *University of Michigan Papers on Paleontology*, no. 23, p. 1–105.
- Taylor, P.D., 1982, Probable predatory borings in Late Cretaceous bryozoans: *Lethaia*, v. 15, p. 67–74.
- Taylor, P.D., 1988, Colony growth pattern and as-togenetic gradients in the Cretaceous cheilostome bryozoan *Herpetopora*: *Palaeontology*, v. 31, p. 519–549.
- Vermeij, G.J., 1977, The Mesozoic marine revolution: Evidence from molluscs, predation, and grazing: *Paleobiology*, v. 3, p. 245–258.
- Vermeij, G.J., 1987, Evolution and escalation: Patterns of marine life: Princeton, New Jersey, Princeton University Press, 544 p.
- Wilson, M.A., and Palmer, T.J., 2001, Domiciles, not predatory borings: A simpler explanation of the holes in Ordovician shells analyzed by Kaplan and Baumiller, 2000: *Palaaios*, v. 16, p. 524–525.
- Wilson, M.A., and Taylor, P.D., 2001, “Pseudo-bryozoans” and the problem of encruster diversity in the Paleozoic: North American Paleontological Convention 2001 (Berkeley, California): *PaleoBios*, v. 21, no. 2, supplement, p. 134–135.

Manuscript received 27 November 2005

Revised manuscript received 23 February 2006

Manuscript accepted 28 February 2006

Printed in USA

Geology

Predatory drill holes and partial mortality in Devonian colonial metazoans

Mark A. Wilson and Paul D. Taylor

Geology 2006;34;565-568
doi: 10.1130/G22468.1

Email alerting services click www.gsapubs.org/cgi/alerts to receive free e-mail alerts when new articles cite this article

Subscribe click www.gsapubs.org/subscriptions/ to subscribe to *Geology*

Permission request click <http://www.geosociety.org/pubs/copyrt.htm#gsa> to contact GSA

Copyright not claimed on content prepared wholly by U.S. government employees within scope of their employment. Individual scientists are hereby granted permission, without fees or further requests to GSA, to use a single figure, a single table, and/or a brief paragraph of text in subsequent works and to make unlimited copies of items in GSA's journals for noncommercial use in classrooms to further education and science. This file may not be posted to any Web site, but authors may post the abstracts only of their articles on their own or their organization's Web site providing the posting includes a reference to the article's full citation. GSA provides this and other forums for the presentation of diverse opinions and positions by scientists worldwide, regardless of their race, citizenship, gender, religion, or political viewpoint. Opinions presented in this publication do not reflect official positions of the Society.

Notes