

**Predation in the Paleozoic: Gastropod-Like Drillholes in  
Devonian Brachiopods**

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**Abstract.** Middle Devonian articulate brachiopods (Ludlowville and Moscow Formations, Hamilton Group, New York) have external tapered holes with a central boss that are indistinguishable from drillholes of naticid gastropods that are known from the Triassic and later. Drillholes are specific to prey (ribbed shells were avoided) and specific to sites on prey. Healed drillholes suggest penetration of live prey. As many as 44 percent of the preferred prey are drilled, indicating a level of predation that has been reported only from post-Paleozoic strata.

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Predation is an important agent of natural selection and a major determinant of ecologic structure. Drilling of shelled prey has attracted attention because there is a well-preserved fossil record. The oldest convincing gastropod drillholes that have been reported are of Late Triassic age (1, 2), part of the Mesozoic "revolution" in predation (3). We now describe drillholes that are approximately twice as old (Middle Devonian) and indistinguishable from those of naticid gastropods. We report that (i) live prey were drilled and that drilling was (ii) prey specific as well as (iii) site specific on prey. Only the latter two features were described for the Triassic drillholes (1), but quantitative evidence was not reported.

The Devonian drillholes occur on brachiopods (Articulata) from the Ludlowville and Moscow Formations of the Hamilton Group, New York (4). These are shallow-water, near-shore marine deposits that contain diverse bottom-dwelling invertebrates. We examined the Fall Brook coral bed in the Windom Shale, Moscow Formation, and used articulated specimens, unless otherwise specified. There are several distinct types of

borings. Bryozoan and sponge borings parallel the hosts' surface and usually are reticulate. Polychaete borings (5) are roughly cylindrical, generally longer than they are wide, and usually oblique to the hosts' surfaces. In contrast, the naticid-like drillholes have features characteristic of those made by modern naticids (6): they are perpendicular to shell surface, the sides are tapered (parabolic) inward, there is a central boss in incomplete drillholes (preserved in 6 of 48; Fig. 1), and the size is similar [mean maximum outside diameter,  $1.18 \pm 0.55$

(standard deviation) mm; range, 0.20 to 3.08 mm;  $n = 126$ ] (7). Other reported Paleozoic borings are much smaller (8) and lack boss and taper (9, 10).

The distribution of drillholes suggests behavior like that of modern naticids, but is characteristic of other predators as well. First, drillholes are prey-specific. At all ten localities sampled, they were found only on brachiopods and were most frequent in certain genera (Table 1). Although these preferences changed little during the estimated 2 to 3 million years spanned by our samples (Table 1), different predators may have been responsible. Second, drillholes are concentrated over the relatively "meaty" apical half of the shell (11) (Fig. 2). Third, drillholes were made in live brachiopods, because (i) the taper shows all but one of 126 were made from the exterior of the shell; (ii) although 10 of 21 drilled brachiopods had multiple drillholes, only a single *Athyris* had two complete drillholes (12); (iii) complete drillholes penetrate only one valve of articulated brachiopods (13); and (iv) there are calcareous blisters healing the inside of drillholes (Fig. 3). Eight of 12 incomplete drillholes were sealed by blisters (14).

We cannot identify the predators. All drilled brachiopods lived on the sediment surface, but recent drilling naticids are infaunal. The gastropod taxa that today include shell-drilling genera are not known as fossils before the Triassic

Table 1. Brachiopods (Articulata) with naticid-like drillholes, from the Middle Devonian Hamilton Group, New York (for articulated specimens only). Stratigraphic units are numbered from oldest to youngest: 1, Centerfield Limestone; 2, Wanakah Shale; 3, Jaycox Shale; 4, Kashong Shale; 5, Windom Shale, Fall Brook coral beds; and 6, Windom Shale, Taunton beds.

Species	Number bored/total by stratigraphic unit					
	1	2	3	4	5	6
<i>Athyris spiriferoides</i>	3/14*	21/298	2/34	2/81	6/39	4/26*
<i>Camarotoechia</i> spp.	0/1			0/252		0/3
<i>Cyrtina hamiltonensis</i>	1/87			0/1	2/21	
<i>Delthyris</i> cf. <i>D. sculptilis</i>	0/9		0/8	0/19		
<i>Devonochonetes coronatus</i>	0/1			0/5		
<i>Douvillina inequistriata</i>	1/8	1/1	6/21*	0/2		0/5
<i>Elita fimbriata</i>		0/1	0/4	0/2	0/2	
<i>Mediospirifer audaculus</i>	0/3	0/9	1/56	0/7	3/17	0/12
<i>Megastrophia concava</i>		0/2	1/6			0/3
<i>Meristella</i> cf. <i>M. haskinsi</i>	1/11		0/8	2/60		
<i>Mucrospirifer mucronatus</i>	0/3	0/7	0/56†	0/31	0/7	0/1
<i>Nucleospira concinna</i>	1/15	0/4	0/6	5/180		1/2
<i>Parazyga hirsuta</i>	1/3		4/41		3/9	
<i>Pentamerella pavilionensis</i>	0/6				0/8	
<i>Pholidostrophia naerea</i>	4/18*	0/4	8/18*			
<i>Pseudoatrypa</i> cf. <i>P. devoniana</i>	2/82				5/86	1/109
<i>Rhipidomella</i> spp. (29)	5/47	3/15	8/84		7/27*	0/6
<i>Schuchertella arctostriata</i>		0/1?		0/2		
<i>Spinatrypa spinosa</i>					5/50	0/9
<i>Spinocyrtia granulosa</i>	0/2	0/3	0/6		0/1	0/11
<i>Strophodonta demissa</i>	0/8	0/2	0/6			
<i>Tropidoleptus carinatus</i>		0/2	0/100†	0/150		1/3

\* Species that were significantly preferred. Chi-square values (and ratios) for units 1 through 6, respectively: 24.0 (19/319), 5.6 (25/349), 80.4 (30/469), 15.8 (10/835), 17.0 (32/276), and 19.8 (7/190) (28). † Species that were avoided.

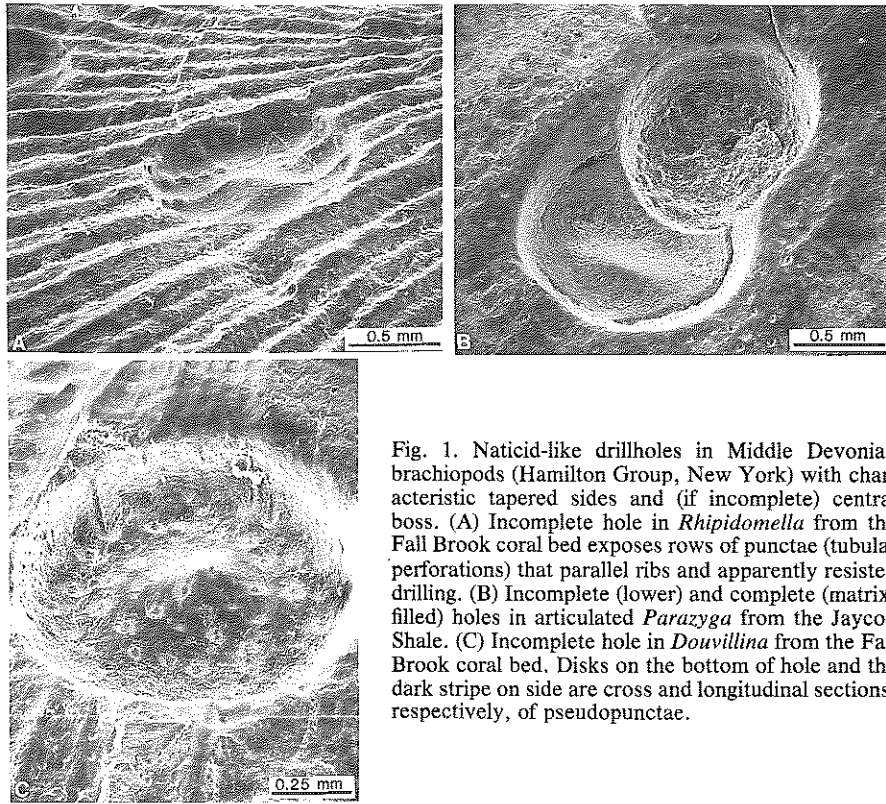


Fig. 1. Naticid-like drillholes in Middle Devonian brachiopods (Hamilton Group, New York) with characteristic tapered sides and (if incomplete) central boss. (A) Incomplete hole in *Rhipidomella* from the Fall Brook coral bed exposes rows of punctae (tubular perforations) that parallel ribs and apparently resisted drilling. (B) Incomplete (lower) and complete (matrix-filled) holes in articulated *Parazyga* from the Jaycox Shale. (C) Incomplete hole in *Douvillina* from the Fall Brook coral bed. Disks on the bottom of hole and the dark stripe on side are cross and longitudinal sections, respectively, of pseudopunctae.

or Jurassic (1, 15). The most likely drillers among our gastropods are *Glyptotomaria* and *Naticonema*, both Archeogastropoda; although no living member of this order drills shells, some are carnivorous (15, 16).

These Devonian drillholes are evidence of predation, with as many as 44 percent of preferred prey being drilled—a frequency not surpassed until the Cretaceous (Table 1) (17). Eleven percent of the brachiopods in the Fall Brook coral bed are drilled. When disturbed, modern gastropods often do not reoccupy their drillholes (11). These early predators

may have been relatively inefficient; there were 21 incomplete and 24 complete drillholes. The high incidence of completed but healed drillholes is consistent with this interpretation and with the possibility of repellent brachiopod tissue, such as is found in living articulates (18).

Punctae are minute organic-bearing perforations in brachiopod shells (19). The resistance of these punctae to drilling (Fig. 1A) implies that the Devonian predator drilled by solution, as do modern gastropods (20). Pseudopunctae are calcite (19) and were not resistant (Fig.

1C). Punctata shells were not avoided, but Strophomenida and relatively smooth shells were preferred ( $P < 0.05$ ) (21). Although ribbing does not deter Cenozoic gastropods (22), it may have hindered adhesion by these early predators and increased their drilling effort by making drillholes oblique to the local shell surface. Ribbing strengthens shells against crushing (23) and may deter predation by starfish (24), so that ribbing may have evolved in concert with predation.

Fürsich and Jablonski (1) proposed a dual origin of shell-drilling among the Naticidae; a Triassic "failure" and a Cretaceous radiation. We suggest a previous origin among unidentified predators (possibly soft-bodied and molluscan) in the early to middle Paleozoic. The different locations of accessory boring organs in living naticids and muricids (20) suggest several successful origins of drilling; perhaps there was more than one failure as well. Following Gould, Fürsich and Jablonski (1) explained the Triassic failure in terms of unspecified "fortuitous" phylogenetic constraints. We now propose that there were at least two evolutionary failures of the highly adaptive drilling habit and offer an explicit deterministic hypothesis to explain them.

During the slow drilling process (11), gastropods are vulnerable. Only a few living shell-less gastropods drill holes (15, 20); although many are repellent to predators, shells mitigate other disturbances (for example, turbulence, suspended sediment, and salinity fluctuations). Perhaps Paleozoic predators evolved a drilling apparatus but lacked shells. This might explain the frequent occurrence of incomplete and healed drillholes in our sample. The repeated evolutionary "failures" could then be

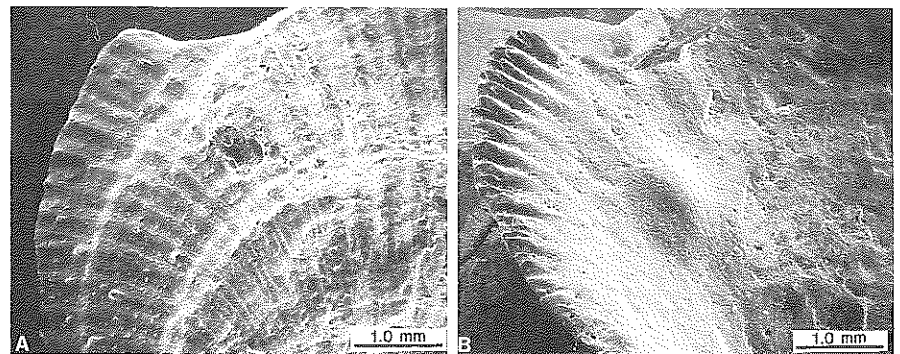
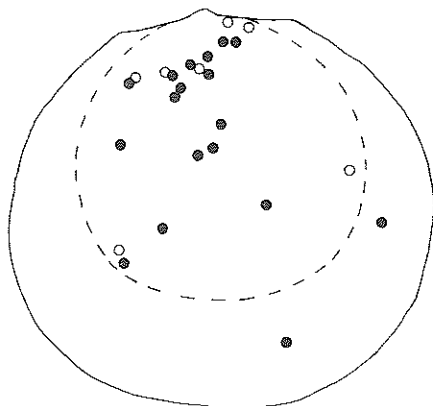


Fig. 2 (left). Naticid-like drillholes in *Rhipidomella* (both articulated and disarticulated) are concentrated in relatively meaty apical half of shell (27). Dashed growth-line delimits equal areas. There are 18 complete (●) ( $P < 0.0025$ ) and 7 incomplete (○) ( $P < 0.005$ ) borings from 24 valves 8.8 to 32.0 mm wide enlarged to standard width. Fig. 3 (right). Naticid-like drillhole on (A) exterior of Middle Devonian brachiopod *Rhipidomella* healed with shell blister on (B) interior. Negative reversed in (A) to facilitate the comparison.

24 valves 8.8 to 32.0 mm wide enlarged to standard width. Fig. 3 (right). Naticid-like drillhole on (A) exterior of Middle Devonian brachiopod *Rhipidomella* healed with shell blister on (B) interior. Negative reversed in (A) to facilitate the comparison.

explained by the fact that fitness is not determined by an isolated organ or system. This hypothesis would predict that late Paleozoic radular teeth may be found as isolated microfossils (for example, in conodont concentrates) and in soft-bodied fossils. Radula-like structures are known from unskeletonized nonmollusks of Cambrian age (25). The naticid-like drillholes that we have described in Devonian brachiopods contribute to growing evidence (26) of a long prelude to the Mesozoic revolution in predation.

#### References and Notes

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14. This observation is based on examination of naturally disarticulated specimens. One blister had flaked away, revealing a complete but repaired drillhole.
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18. C. W. Thayer, *Science* **228**, 1527 (1985). Healing and repellency might have evolved in response to previous predation or boring parasites.
19. M. J. S. Rudwick, *Living and Fossil Brachiopods* (Hutchinson, London, 1970).
20. Modern gastropods also use abrasion [M. R. Carriker, *Malacologia* **20**, 403 (1981)]. Punctae also repel boring parasites (C. W. Thayer, *Lethaia*, in press).
21. Result based on two-by-two contingency table of number drilled versus not drilled,  $\chi^2$  (with 1 df), for units with most selective boring (that is, largest total  $\chi^2$ ) = (unit 1) 0.3 (punctate versus impunctate and pseudopunctate), 4.6 (Strophomenida versus other orders), 16.9 (costate versus costellate and smooth; (unit 3) 0.8, 34.2, and 25.8, respectively. Smooth shells preferred in units 4 and 5.  $\chi^2$  = 13.6 and 7.9, respectively. Punctate shells preferred in units 2 and 5,  $\chi^2$  = 14.6 and 6.6, respectively (both due to *Rhipidomella*). All other  $\chi^2 < 2$  [R. R. Sokal and F. J. Rohlf, *Biometry* (Freeman, San Francisco, 1969), p. 589]. Taxonomy and punctuation are from R. C. Moore, Ed. [*Treatise on Invertebrate Paleontology*, part H, *Brachiopoda* (Geological Society of America and Univ. of Kansas Press, Lawrence, 1965). Small spines (for example, *Nucleospira*) were not a deterrent.
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27. The  $\chi^2$ , expected distribution is 50 percent:50 percent [R. R. Sokal and F. J. Rohlf, *Biometry* (Freeman, San Francisco, 1969), p. 552].
28. That is  $\chi^2 > 3.8$  and  $n < 10$ ;  $\chi^2$  for units [W. G. Cochran, *Biometrics* **10**, 431 (1954)] pools species with  $n \leq 3$ . In addition, the following occurred in the specified unit only: unit 1, *Productella spinulicosta* 0/1; unit 3, *Longispina mucronatus* 0/15; unit 4, *Ambocoelia* undescribed sp. 0/5, *Cryptonella rectirostra* 1/19, *Eosyringothyris asper* 0/1, *Pustulatia pustulosa* 0/12, and *Trematospira gibbosa* 0/6; unit 5, chonetid 0/4 and unidentified 1/5.
29. The species are *R. penelope*, *R. vanuxemi*, and *R. leucosia*.
30. We thank R. Alexander, R. Bambach, J. Jablonski, J. Kitchell, V. Maes, R. Robertson, N. Sohl, G. Vermeij, and E. Yochelson for comments; T. Lutz for statistical analysis; D. Ricketts for micrographs; and Sigma Xi for a grant-in-aid to S.A.S.

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