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VARIATION AND PREDATION OF THE PENNSYLVANIAN GASTROPOD *MICRODOMA CONICUM* MEEK AND WORTHEN[1]

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Abstract. Our study of a large population of the Pennyslvanian gastropod *Microdoma conicum* Meek and Worthen, which appears restricted to the Vanport marine unit of the Allegheny Group in Ohio, showed extreme variation in ornamentation of the shell ranging from essentially smooth to coarsely nodose. Smooth and lightly ornamental forms were more common than previously known. Nearly 38% of the population showed indications of external biological activity of one or a combination of 3 types: (1) small hemispherical pits, 0.1–0.2 mm in diameter, which did not penetrate through the shell material and were formed by an unknown passive epifaunal element while the host was alive; (2) borings, 0.2–0.3 mm in diameter, which passed through the shell and possibly were made by another gastropod (3) shell damage along the margin of the aperture at various stages of growth, which may have been caused by one of the associated faunal elements such as echinoids, fish, or nautiloid cephalopods.

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Our study had 3 main purposes: (1) to illustrate variation in shell ornamentation; (2) to analyze indications of predation and epifaunal relationships; (3) to indicate stratigraphic occurrences of this species. *Microdoma conicum* Meek and Worthen is a distinctive and easily recognized taxon having considerable variation in the ornamentation of the shell. Although Knight (1933) has pointed out some variation in this species, our collections indicated that it is more extensive than has been previously considered. Numerous specimens also showed evidence of predation and attachment of epifaunal elements for which various interpretations could be postulated. The stratigraphic range, which is restricted in Ohio, was compared with other known occurrences in North America.

MATERIALS AND METHODS

Several bulk samples of the Vanport shale lying immediately over the Vanport Limestone were made at a small abandoned drift mine on the north side of Jackson County Rt. 58 along Buffler Run, 2.4 km east of Ohio Rt. 124, S center sec. 24, T. 8 N., R. 16 W., Milton Tp., Jackson Co., Ohio, Mulga 7½' Quadrangle. The shale was processed by boiling in Quaternary 0 to release the fossil content. After drying, the residue was separated by screening and then picked over under a binocular microscope.

Among a great variety of other taxa, several hundred specimens of *Microdoma conicum* were present. These specimens ranged from juvenile forms of only a few whorls to gerontic growth stages. For the purposes of this study, 596 specimens having a length of 3 mm or larger were selected for analysis. The smaller specimens were eliminated because they did not possess the extent of development of the ornamentation to enable us to make a valid comparison with the larger specimens nor did they show evidence, like the larger forms, of epifaunal attachment or predation.

The specimens selected were sorted into 3 categories on the basis of degree of development of ornamentation; (figs. 5, 10) smooth or fine (figs. 1, 2, 4), intermediate (figs. 3, 6), and coarse (figs. 5, 10). Since the population showed considerable variation in the development of ornamentation, these categories were somewhat subjective in nature. The specimens were further categorized on the basis of the presence or absence of epifaunal attachments, the presence of shell damage, and a combination of these factors (table 1). Several of the specimens showing indications of epifaunal attachment were sectioned or acidized to determine the nature of the attachment or boring in relation to the shell wall.

Examination was made of other faunal elements present in the sample to determine whether they also showed the presence of predation or epifaunal attachments. The type specimens of *Cyclopuncta girtyi* Elias were borrowed from the University of Oklahoma for examination and comparative purposes.

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TABLE 1

Population sample of Microdoma conicum categorized on the basis of shell ornamentation, epifaunal elements, and shell damage.

Ornamentation	No Damage	Pits	Shell Damage	Pits Shell Damage	Borings	No. Specimens
Smooth	98	28	7	4	1	138
Intermediate	169	64	38	18	3*	292
Coarse	100	25	30	10	1**	166
Totals	367	117	75	32	5	596

*One specimen also has pits.
**Also has shell damage.

RESULTS

Of the total speciman population, nearly half (49%) were judged intermediate in development of ornamentation with smooth forms making up 23% and coarse forms 28%. Small pits, present on over 25% of the specimens, were circular to sub-circular in surface shape, measuring from 0.1–0.2 mm in diameter, and did not penetrate through the shell material (having a depth of ½ to ⅓ the pit diameter). They were hemispherical in cross section and varied in number with up to at least 70 on individual specimens. Specimens more commonly having pits had intermediate type ornamentation (fig. 6) but those with a coarse ornamentation often had more pits per individual (figs. 5, 10). The pits first occur between the third and fifth whorls of a specimen and then are found throughout the rest of the teleoconch. They normally occurred on the entire teleoconch surface and were restricted to only one side of the shell in 9 specimens. On coarsely ornamented specimens, the pits were often present on the nodes as well as between the nodes, or may be restricted to the nodes (figs. 8, 10) where present. The smoother the ornamentation of the host shell, the more irregular the distribution of pits. Normally, they were spaced 1–3 pit diameters or more apart on smooth shells.

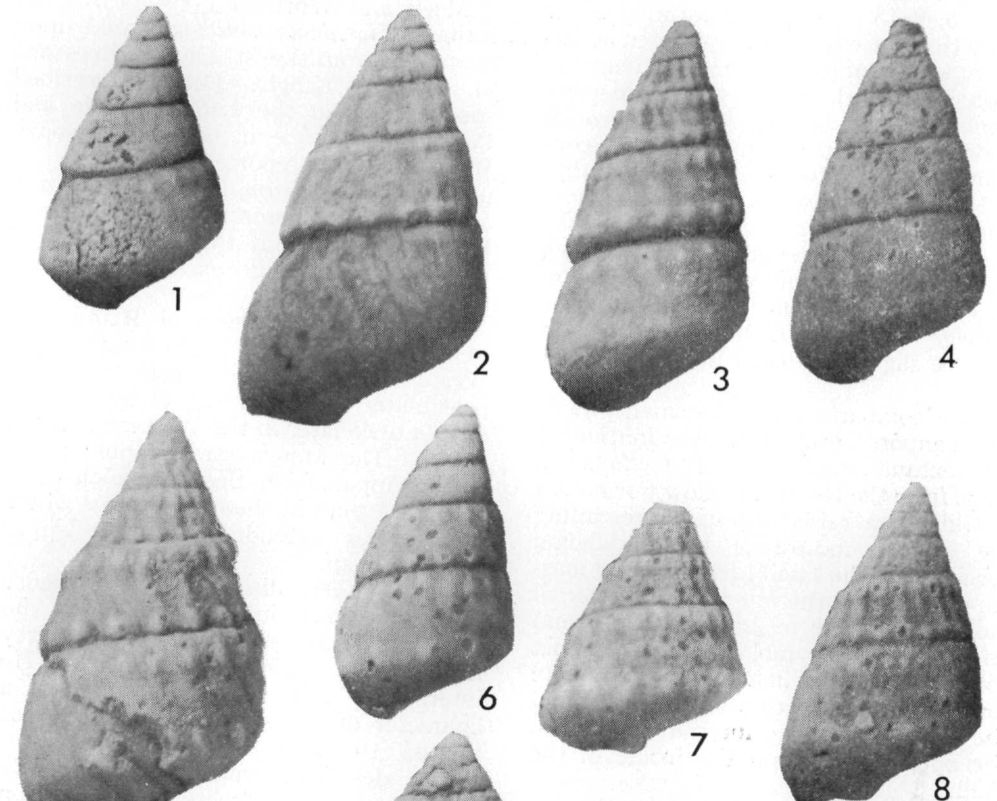
On 5 specimens of *Microdoma conicum*, large borings were present. These had a surface diameter of 0.2–0.3 mm and extended through the shell material with nearly straight sides. One host specimen had 2 such borings; the rest had only one (fig. 9).

Approximately 18% of the specimens showed major shell damage of the margin of the aperture at some stage of growth. This damage was seen as a pronounced line of demarcation, which might be collabral in form and paralleling the normal growth lines, but most often was irregular

FIGURE LEGEND

Microdoma conicum Meek & Worthen, Vanport Shale (all figures x 1).

FIGURE 1. Specimen with nearly smooth shell, OSU-30523.
FIGURE 2. Specimen with intermediate ornamentation, OSU-30524.
FIGURE 3. Specimen with coarse ornamentation, OSU-30525.
FIGURE 4. Specimen with smooth shell and pits, OSU-30526.
FIGURE 5. Specimen with coarse ornamentation, pits, and shell damage, OSU-30527.
FIGURE 6. Specimen with intermediate ornamentation and pits, OSU-30528.
FIGURE 7. Specimen with coarse ornamentation and pits, OSU-30529.
FIGURE 8. Specimen with coarse ornamentation and pits, mainly on nodes, OSU-30530.
FIGURE 9. Specimen with coarse ornamentation, shell damage, and borings, OSU-30531.
FIGURE 10. Specimen with coarse ornamentation which changes to smooth at lines of shell damage and with pits, mainly on nodes, OSU-30532.
FIGURE 11. Specimen with coarse ornamentation and three lines of shell damage, OSU-30533.
FIGURE 12. Specimen with coarse ornamentation and two lines of shell damage, OSU-30534.
FIGURE 13. Specimen with coarse ornamentation, pits, and shell damage, OSU-30535.



FIGURES 1–13

in nature and did not follow growth lines (figs. 5, 9–13). This feature may occur more than once on a host specimen at different stages of growth, with as many as 4 on one whorl, but it was more commonly present on the later teleoconch whorls. Smooth specimens were considerably less affected than those that had intermediate or coarse ornamenttion. The damage did not greatly affect the pattern of shell ornamentation, although the ornamentation may be somewhat reduced in strength on the shell after the damage (fig. 10), and the whorl diameter may be slightly reduced in size (figs. 10, 13).

As a comparison for the small pits in the Vanport specimens, examination of the extant specimens of *Cyclopuncta girtyi* from the Redoak Hollow Formation of Oklahoma raised questions regarding the organic nature of the Oklahoma specimens. The small hemispherical masses occurred on the internal and external molds of septate cephalopod shells and on the external mold of an echinoid tooth. In some instances, they were formed at the junction of a septum and the outer wall on an internal mold with the opening being on the inside of the shell.

In the fauna found associated with *Microdoma conicum*, small pits were found on specimens of the brachiopod *Composita* sp., the cephalopods *Pseudothoceras knoxense* and *Metacoceras* sp., and the gastropods *Shansiella beckwithana* and *Worthenia* sp. *Pseudothoceras* was most commonly affected with 20 specimens showing pits. Borings were present on the bivalve *Astartella concentica* and on numerous specimens of *Composita* sp. Two specimens of *Composita* had both pits and borings.

Besides the forms mentioned above, the associated fauna preserved with *Microdoma conicum* at this locality was large and varied, being comprised of foraminifers, sponges, rugose corals, bryozoans, brachiopods, scaphopods, bivalves, gastropods, cephalopods, polyplacophorans, worms, trilobites, ostracodes, crinoids, echinoids, and fish. Brachiopods, mollusks, and ostracodes were the dominant elements in terms of numbers observed.

DISCUSSION

Meek and Worthen (1867, 1873) described *Microdoma conicum*, based upon specimens from the St. David Limestone in Illinois. Knight (1933) described specimens from the Labette Shale and Pawnee Limestone in eastern Missouri. Wanless (1958) reported *Microdoma* sp. probably *M. conicum*, from the Seahorne and Lonsdale Limestones of Illinois. Hoare (1961) found this species in the Robinson Branch limestone in western Missouri.

The initial occurrences of *M. conicum* in the Appalachian, Eastern Interior, and Western Interior basins seem to be approximately synchronous, although possibly a little later in the Western Interior Basin. The known stratigraphic range in the Appalachian Basin is much more restricted than in the other basins where the species extends into the Upper Desmoinesian.

Girty (1909) discussed the presence of perforations in the shell of the cephalopod *Bactrites smithianus* Girty from the Caney Shale of Oklahoma. He interpreted this structure as being a character of the shell material and not related to a boring organism. Elias (1958) described what was apparently the same type of structure occurring on external and internal molds of the cephalopod *Cravenoceras* from the Redoak Hollow Formation in Oklahoma. His interpretation of the structures, which he named *Cyclopuncta girtyi*, was of an infusorian attached to the shell forming a small pit that did not penetrate through the shell material. Sturgeon (1964) notes and illustrates a specimen of *Shansiella beckwithana* (McChesney) from the Vanport unit with numerous small pits or borings.

Our study indicated that *Microdoma conicum* is a highly variable taxon in terms of its shell ornamentation. Specimens having subdued development of the nodose characteristic were very prevalent and the nondevelopment of this feature on the earlier teleoconch whorls was common. Hence, the degree of variability in ornamentation is greater than had been previously recognized by Meek and Worthen (1867, 1873), Knight (1933), and Hoare (1961).

Nearly 38% of the specimens of the population of *Microdoma conicum* we studied showed some evidence of external biological activity. The pits found on the specimens are believed to be organic structures formed by unknown organisms. The distribution of the pits on all sides of the shell seemed to indicate that the host gastropod was alive at the time of attachment of the epifaunal element; otherwise, the pits would be more commonly restricted to a certain portion of the shell exposed above the substrate. This structure is not the same as *Cyclopuncta girtyi* Elias (1958), which is considered to be an inorganic structure (probably small deposits of an iron compound formed in the cavity between internal and external molds) "and should not be further recognized" as stated by Hantzschel (1962). The unknown epifaunal form that excavated the pits did not attach itself to very youthful shells, either because of the size of the host or possibly, in some cases, because of the development of surface nodose ornamentation, which appears to have had some effect upon the distribution of the location of attachment of the epifauna. Elias (1958) proposed a type of infusoria as the organism responsible for small pits of this type, but another possibility could be hydroid polyps (as illustrated by Plate 1912, fig. 16) on the shell of *Buccinum*.

The borings that penetrated the shell were similar to those made by modern gastropods. They differed in not being as distinctly chamfered as in many modern forms. One specimen of *Composita* sp., having two borings just below the beak of the brachial valve, had blister-like secondary deposits of carbonate covering the holes on the inner surface, indicating that the brachiopod was alive at the time of predation. Other specimens of *Composita* and a specimen of *Microdoma*, cut to examine the borings, did not show secondary deposits over the boring, making it difficult to know whether or not the host was alive at the time of boring.

Specimens of *Microdoma conicum* showing shell damage to the margin of the aperture at various stages of growth definitely were alive at the time of predation. In all cases, the specimens showed continued shell growth after the damage had taken place. In those few instances where the major growth line was a smooth curve paralleling other growth lines, it appeared to represent only a minor cessation of growth and not predation. Smooth major growth lines occurred most commonly on the earlier teleoconch whorls whereas the irregular lines, showing shell damage, occurred most often on the later whorls. Although many of the specimens had been crushed during compaction, the fractures formed by this process were distinct from those being described as the result of predation. The latter structures could be traced across one whorl and did not extend into adjacent whorls. Because of the irregularity of the damaged margin, we propose that some element or elements of the associated fauna that used *Microdoma* as a food source caused the shell damage. Of the known associated elements, the echinoids, fish, and nautiloids would appear to have been the most likely predators. The irregularity of shell damage would seem to lend more credence to an organism with teeth or a beak-like structure rather than a radular structure. The presence of the unknown epifaunal element, which formed the pits, did not serve as camouflage or protection from the predator causing shell damage since the shells with pits were damaged as often as those without pits.

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