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A SHELL-BORING GASTROPOD IN A DALMANELLA BED OF UPPER CINCINNATIAN AGE.

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ABSTRACT.

First a brief summary is given of present-day knowledge concerning the shell-boring habits of modern gastropods. Then a new, unusually instructive case of shell-boring is described from Upper Cincinnatian (Richmond) beds. Reasons are given for suspecting the boring to have been done by a species of the Genus *Holopea.*

In 1853, Troschel holding a large captured *Dolium galea* in his hand, noted that the liquid which the snail squirted from its long proboscis caused the marble slab of the floor to effervesce. He found that the liquid contained three to four per cent of sulphuric acid, secreted by two large glands which discharge into the buccal cavity.[1] This and other acids have since been found in a number of other marine prosobranchs (e.g., *Tritonium, Mitra, Conus,* etc.). These snails are rapacious carnivores that get hold of their prey by means of the large teeth on the radula within the extensible proboscis. A large *Tritonium nodiferum,* for instance, has been seen to swallow a starfish (*Asterias*) with a disc diameter of 26 cm. and weighing 134 g. "In four hours the starfish had disappeared within the snail with the exception of the tip of one arm, which stuck from the snail's pharynx even after eight hours, but had vanished the next morning."[2] In view of such diet, the physiological significance of the acid secretion is no mystery.

Early the suspicion arose that the same or a more specific

[1] Léon Fredericq: "Handbuch der vergleichenden Physiologie," 2 Bd., 2. Hälfte, pp. 65-75, Jena 1924.
[2] Ibid., 2. Bd., 1. Hälfte, pp. 929-935, Jena 1911.

secretion of acid entered into the process by which some prosobranchiates bore into shells of living animals to feed on their bodies. In the case of *Natica,* a conspicuous disc-shaped body on the underside of the proboscis, directly below the mouth, was suspected to have the function of an acid-producing gland and was so designated by Schiemenz.[3] Yet, while such a function seemed indicated by a number of facts, the actual presence of an acid in or on the "gland" was not demonstrated satisfactorily until very recently.[4]

But other notorious shell-borers such as our own oyster-drill *Urosalpinx cinerea* and its British competitor *Purpura* (*Nucella*) *lapillus* (both of the family *Muricidae*) lack such a visible special organ. Zoölogists are still inclined to believe they actually drill mechanically by means of their radulas. But the reasons given are not convincing. In view of Ankel's experience with *Natica,* the fact that no free acid has been demonstrated[5] in either the buccal cavity or the oesophagus of the oyster drills cannot be considered proof of its absence. More important are the signs of wear seen on the radulas of these forms. In a specimen of *Purpura lapillus,* Sollas found every one of the teeth in the mouth-cavity with cusps broken off.[6] According to Ankel, considerable wear on the first two or more dozens of radula teeth has been observed in both *Urosalpinx* and *Nucella.*[7] While this shows that the radula is used by these forms for scraping, it does not prove that the mechanical action is the sole or even the chief factor in the process of shell boring.

To the writer the remarkable circularity of all drill holes made by snails and the fact that they invariably penetrate the shell at right angles to the surface appear inexplicable as the result of mechanical action alone. The radula is a ribbon,

[3] Schiemenz, K.: "Wie bohrt *Natica* die Muscheln an?" Mitt. Zool. Station, Neapel, Vol. 10, 1891.

[4] Ankel, W. E.: "Wie bohrt *Natica*?" Biol. Zentralblatt, Bd. 57, H. 1-2, 1937. The author produced solution effects on glossy shell fragments by pressing against them such glands freshly cut from the living animal.

[5] E.g., Pelseneer, P.: "Comment mangent divers gastropodes aquatiques?" Ann. Soc. Royal Zool. de Belge, Vol. 55, 1925.

[6] Sollas, I. B. J.: "The Molluscan radula: its chemical composition, and some points in its development." Quarterly Journal of Microscopical Science, N. S., Vol. 51, p. 128. 1907.

[7] Ankel, W. E.: "Prosobranchia," Part IXb of "Die Tierwelt der Nord- und Ostsee." Akad. Verlagsgesellschaft, Leipzig, 1936.

The writer wishes to thank Dr. W. Häntzschel for calling his attention to Ankel's valuable papers and Professor Ankel for reference to Sollas' paper.

narrower than the proboscis and bearing teeth only on one side. Motion is possible only from one side to the other. The snails attack their prey from all sorts of angles. The achievement of perfect circularity and perpendicularity with such a tool would seem almost a miracle. Chemical action, on the other hand, proceeding along the appressed tip of the terete proboscis, would automatically produce a circular hole and would work downward at right angles to the surface. It would also suggest an explanation for the presence, side by side, of drill holes with beveled edges and such without. The beveling, which always converges toward the interior of the shell, seems to indicate that the solvent action continued along the outer surface while the center is being lowered into the shell. In the case of a slender proboscis, with the tip only appressed against the shell, the solvent action of the weak acid aided by the scraping of the radula would sink a hole with nearly vertical walls through the shell.[8] Since the teeth of the oyster drills consist of chitin more or less reinforced along the surface with calcium and iron phosphate,[9] it is to be expected from this auxiliary activity that they should show more or less damage. A thick, fleshy proboscis, on the other hand, would tend to press the sides of the proboscis against the shell over an area wider than the tip and would thereby tend to cause solution to continue along the surface even while the tip is penetrating below the surface. The drill holes which *Natica* produces by means of a gland that is situated on the side of the proboscis, i.e., entirely without the aid of the radula, show exceptionally wide beveling, as is to be expected according to the suggestion here made.

It seems probable, therefore, that when one traces back in geologic time this curious habit of some snails of boring through the shells of lime-secreting organisms,[10] one is actually tracing a peculiar physiological property, that of secreting free acid. As far as the writer knows, the earliest cases of round bore holes made by carnivorous snails have been found in the

[8] The rate of drilling is quite slow. The oyster drill, *Urosalpinx cinerea,* e.g., which is common from Massachusetts to the East Coast of Florida, drills only 0.4 mm. in 24 hours.

Federighi, Henry: "Studies on the oyster drill," U. S. Dept. of Commerce, Bureau of Fisheries, Vol. 47, Bull. 4, p. 110. 1931.

[9] It seems that silica (opal) occurs only in the *Docoglossa,* reinforcing the chitin of the radula teeth. See I. B. J. Sollas, loc. cit.

[10] Our modern borers attack not only pelecypods, but other gastropods amphineurs, and cirrhipeds (*Balanus*) as well.

Upper Cincinnatian. The Fentons[11] have figured three specimens from the Waynesville formation (Lower Richmond) which look typical. One circumstance, however, caused the writer to doubt the nature of these specimens as well as of two

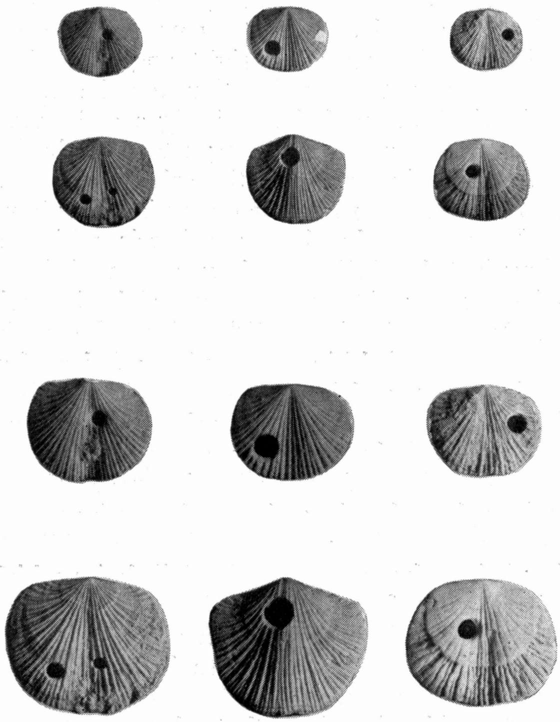

Fig. 1. Six valves of brachiopod shells [*Dalmanella meeki* (Miller)] with holes made by a shell-boring gastropod. The small brachiopod shells at the top of the figure are (a) natural size. The brachiopod shells at the bottom of the figure are (b) enlarged.

From the Waynesville formation of the Richmond Group of the Upper Ordovician, near Oxford, Ohio.

which are in the Geology Department at Cincinnati: They seemed to represent extremely rare finds. These five specimens represent each a unique find of a bore hole for each of the species mentioned (2 species of *Platystrophia,* one each of *Rafinesquina, Dalmanella, Sowerbyella*). These are all species

[11] Fenton, C. L., and Fenton, M. A.: "Some snail borings of Paleozoic age," American Midland Naturalist, Vol. 12, pp. 522-528. 1931.

of which hundreds, if not thousands of specimens were seen annually by the writer and his students in the field, in over twenty years, without a drilled one having been found. Years ago the writer looked through the very large number of Cincinnatian brachiopods in the collections of his department in search of evidence of snail bore holes. Recently one of his graduate students, Miss Lucile Miller, did the same for our (much smaller) collection of Cincinnatian pelecypod shells.[12] Not one shell was found with an undoubted borehole. Such scarcity is entirely contrary to the well-known habits of our modern shell-boring gastropods. A single oyster drill (*Urosalpinx cinerea*) is capable of killing from 30 to 200 oysters in one season, depending on the size of the oysters.[13] Careful studies[14] have shown that in the vicinity of Hampton Roads, Va., about two per cent of the oysters are dead through the activity of *Urosalpinx cinerea,* while under the artificially crowded conditions of planted bottoms the percentage rises to approximately ten per cent.

That the shell-borers were no less hungry in Tertiary times is shown by the abundance of shells with bore-holes.[15] So long as bore holes in Early Paleozoic shells were known to be so rare as to be curios, doubt concerning their origin seemed justified.

At last, however, the writer has come upon a Brachiopod layer in which bore holes occur in relative numbers quite comparable with those of modern days. The specimens, of which six are reproduced in the accompanying figure,[16] were obtained in a small tributary (Bull Run) on the west side of Fourmile Creek which runs approximately in an east-west direction just

[12] Most of these are inner molds and would, therefore, show the bore hole as a round cylinder set on top of the mold.

[13] Federighi, Henry: "Control of the common oyster drill," U. S. Dept. of Commerce, Bureau of Fisheries, Economic circular No. 70, March, 1930. (Oysters to the value of several million dollars are destroyed annually by *Urosalpinx* in the United States alone.)

[14] Federighi, Henry: "Studies on the oyster drill," U. S. Dept. of Commerce, Bureau of Fisheries, Vol. 47, Bull. 4, 1931.

[15] Klähn, Hans: "Der Bohrakt fossiler bohrender Schnecken und das Vernichtungsmass durch räuberische Gastropoden des Sternberger Oligocaen." Sitz. Ber. u. Abh., Naturf. Ges. Rostock, 3, Folge, Bd. 3, pp. 89-103. 1932. Ichiro Hayasaka, "Fossil occurrence of Pelecypod shells bored by certain gastropods." Mem. Faculty of Science and Agriculture, Taihoku Imperial University, Vol. 6, No. 4, 1933. For an excellent general discussion see O. Abel, "Vorzeitliche Lebensspuren," Jena pp. 373-378. 1935. Here also references to Permian (Yakovlev) and Devonian (J. M. Clarke) cases.

[16] The writer wishes to thank Miss Lucile Miller for photographing the specimens for him.

south of Oxford, Ohio. Here, *Dalmanella meeki* (Miller) forms regular banks in the Waynesville formation of the Richmond series. In a thin shale layer from which the shells could be withdrawn freely, about two dozen shells were obtained in a short time, each perforated by circular holes unmistakably like those produced by modern shell-borers. The holes lie anywhere on either valve, a condition to be expected in the case of shells that lay flat on the bottom with valves differing but little in convexity. Most of the holes are not beveled, but a few show moderate beveling, as for instance one of those here figured. Even the comparatively rare case of two holes in one shell was found (see illustration).

A special effort was made to find gastropods in the same bed, but in vain. If the guilty form had a preservable shell—which is probable though not certain—it should be among those recorded from the Waynesville formation. Three clues present themselves. First, none of the species commonly found in brachiopod layers can be held responsible, since otherwise bore-holes should be of common occurrence. This excludes at once all the common species of *Cyclonema, Lophospira,* etc. Second, it is not to be expected that the habit of boring appeared in groups with shells of patelloid or bellerophontoid type, such as for instance *Archinacella* or *Salpingostoma.* Third, the size of the boreholes points to a shell decidedly larger than the common oyster drill. The shell of *Urosalpinx* is typically 28 mm. long and 16 mm. wide (1⅛″ and ⅝″). The holes it drills measure[17] about 0.75 to 1.5 mm. in diameter. This is decidedly less than the dimensions of holes in the *Dalmanella* shells here described, the diameter of which ranges from 1.0 to 2.5 mm. It seems reasonable to assume that the corresponding gastropod was proportionately larger.

The faunas of the horizons of the Cincinnatian formations in the vicinity of Oxford have been studied for many years by Professor W. H. Shideler and his students. When the writer gave the essence of this paper before the Ohio Academy of Science in the spring of 1936, Professor Shideler stated that the only gastropod found so far in the horizon from which the bored shells were collected, is a species of *Lophospira, Lophospira perlamellosa* Ulrich.[18] This species is sufficiently

[17] For good illustrations see Churchill, E. P.: "The oyster and the oyster industry of the Atlantic and Gulf Coasts"; App. VIII to Rept. of U. S. Comm. of Fisheries for 1919, pp. 1-51, esp. pl. 8, opp. p. 38. 1920.

[18] Ulrich, E. O.: "The Geology of Minnesota," Final Report, Vol. III, pt. II, p. 985; p. 73, Figs. 55 and 56, 1897.

different from the common forms of *Lophospira* to fulfill the first of the three conditions listed above. Ulrich's type is, however, much smaller than *Urosalpinx* (13 mm. in height). It should be remembered, however, that other species of *Lophospira* show great variation in size. The closely allied Richmond species, *L. ampla* Ulrich, for instance, varies between 22 and 50 mm. in height.[19] It is not at all impossible that the type specimen lies near the lower limit of size, since no specimens were collected from the particular bed in which the bored shells were found.

It seems possible, therefore, though by no means certain, that this species of *Lophospira* acquired the habit of boring into shells. Whether a single individual now and then hit accidently on this method of feeding, or whether boring had become already an essential habit, can be decided only through a systematic search for evidences of boring in Richmond beds.

[19] Ulrich, E. O.: loc. cit. p. 981; pl. 73, Figs. 52-54, 1897.

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