

BIOGENIC SHELL DAMAGE IN THE SMALL
GASTROPOD *ODOSTOMIA IMPRESSA* (SAY)WILLIAM MILLER, III
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I. ABSTRACT

Nearly every shell and fragment of the small pyramidellid snail *Odostomia impressa*,* occurring in very large numbers in and around modern intertidal oyster banks in coastal Georgia, shows evidence of biogenic shell damage. Almost all of the shells have repaired or unrepaired fractures caused by crabs; most of the shell fragments

also appear to be the result of attack by crabs, rather than physical breakage by waves or compaction. Most of the specimens are infested by an algal microborer, which gives shells a chalky, excoriated appearance. Gastropod borings in the Georgia odostomes were very rare. In a comparison with *O. impressa* shells from subtidal oyster banks in Virginia, it was found that crab damage in the Georgia sam-

*The generic label *Odostomia* will be used in this paper, although it should be pointed out that Robertson (1978) has recently proposed that American odostomes be separated into two genera: *Boonea* Robertson, 1978 (which includes *Odostomia impressa*), and *Fargoa* Bartsch, 1955. For the present, I prefer to retain the traditional name *Odostomia* for three reasons: 1) for the

sake of simplicity, as the present study is not a taxonomic treatment; 2) because the revision begun by Robertson, although it represents a step in the direction of a more realistic supra-specific grouping of the odostomes, is preliminary and not exhaustive; and 3) because paleontologists like myself cannot employ the sexual anatomical criteria used to allocate species to *Boonea* or *Fargoa*.

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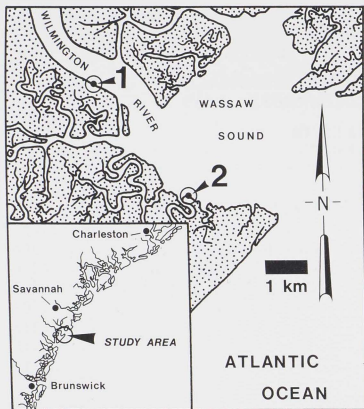


Figure 1. Map showing general location of the study area (inset) and the lower Wilmington River-Wassaw Sound estuary. Locality 1, just upstream from Sister Island; samples H-1 through H-4. Locality 2, near mouth of Blue Bank Creek; samples W-1 through W-5 (see Table 2). (Based on N.O.A.A. Savannah River and Wassaw Sound Map, 1980.)

ples was much more extensive, but that many of the Virginia shells had been bored by the bryozoan *Electra*.

A conservative estimate of the average frequency of fatal attacks on Georgia oostomes from intertidal oyster banks is about 25 percent, using samples from time-averaged shelly deposits. The predator on *O. impressa* in this setting is probably the xanthid crab *Panopeus herbstii*, which is in turn preyed upon by raccoons, birds, and fish. The algal microborer responsible for microscopic holes and striations in oostome shells appears to be a cyanophyte typical of lower intertidal zones.

II. INTRODUCTION

Over the past two decades a large literature has accumulated on the varieties and ecologic significance of biogenic shell damage in fossil mollusks. This type of shell damage is caused largely by predatory

attacks (e.g., snail borings in bivalve shells, crab damage inflicted upon snail shells), by endolithic organisms exploiting mollusk shells as habitats (e.g., boring algae and fungi in various types of mollusk shells, polydorid worm borings in bivalve shells), and by shell-growth adjustments to infestation by parasites (e.g., pyramidellid infestation of oysters). Skeletal overgrowths by epilithic organisms represent a special category of biogenic shell damage affecting both living and abandoned mollusk shells. (Good summaries of the literature dealing with the interpretation of shell damage are found in the following sources: Reyment, 1971; Bishop, 1975; Golubic *et al.*, 1975; Vermeij, 1978; Boucot, 1981; Dodd and Stanton, 1981.)

Nearly all of the studies of shell damage inflicted by the activities of predatory organisms on mollusks focus on large prey species. With the exception of a study of the frequency of crab predation on minute cerithiaceous gastropods by Dudley (1980), I know of no studies that make use of small mollusks. The purpose of the present study is to describe the varieties and significance of shell damage in a diminutive pyramidellid snail, *Odotostomia impressa* (Say, 1821), from intertidal oyster banks in the Wassaw Sound area of coastal Georgia. *Odotostomia impressa* was used because of its abundance in modern shell deposits along the margin of the sound, and because nearly every specimen examined showed some form of biogenic shell damage.

During a survey of the environmental distribution of pyramidellid snails from Wassaw Sound (Miller, in press), it was discovered that the most common and easily detected form of damage evidenced by *O. impressa* had been inflicted by predatory crabs; many of the shells had been infested by algal microborers, and a few had been attacked by boring gastropods. Because all of these forms of shell damage caused by predators (or potential predators) and endolithic associates leave a more or less indelible trace in the carbonate substrate of *O. impressa* shells, all are potentially preservable as trace fossils. Moreover, the traces of predation on *O. impressa* give an indication of the position of this abundant and widely distributed gastropod in the trophic structure of intertidal oyster bank communities.

TABLE 1. Sample station data. The location of the two oyster banks sampled is shown in Fig. 1.

SAMPLE NUMBER	ENVIRONMENTAL SETTING	SAMPLE VOLUME
WASSAW SOUND		
W-1	high intertidal rubble flat behind oyster bank	1.00 liter
W-2	low intertidal slope in front of oyster bank	1.00
W-3	shallow tidal slough near oyster bank	1.00
W-4	high intertidal sediment pond within oyster bank	1.00
W-5	high intertidal sediment pond within oyster bank	0.75
WILMINGTON RIVER		
H-1	shelly bar in tidal creek near oyster bank	1.00
H-2	middle intertidal oyster bank (dead)	0.75
H-3	low intertidal rubble slope in front of oyster bank	0.75
H-4	high intertidal shell-armored levee	1.00

III. METHODS

Nine bulk samples of shelly sediments were collected from two oyster banks located along the edge of the lower Wilmington River and Wassaw Sound (Fig. 1). A variety of intertidal to very shallow subtidal environments was sampled representing a cross-section of estuarine margin settings (Table 1). Samples were wet-sieved on a screen having 1 mm openings, dried, and picked for specimens of *Odostomia impressa*. All shells and fragments were carefully examined using a dissecting microscope for signs of predation and endolithic infestation, and selected typical specimens

were examined using a scanning electron microscope. An inventory of the condition of shells is shown in Table 2.

In addition, two samples collected from subtidal "oyster rocks" in the lower James River, Virginia, by Mr. James P. Whitcomb, were used in comparisons with the intertidal material from Georgia. These samples were collected from Brown Shoal (V-1) and Wreck Shoal Rock (V-2) by dredging 30 and 22 liters, respectively, of oyster shells and sediments. The 1 to 5 mm sediment fraction was dried and picked for *O. impressa*; all specimens were examined for shell damage using a dissecting microscope.

TABLE 2. Condition of *Odostomia impressa* shells from Wilmington River and Wassaw Sound oyster banks. Sample numbers are keyed to Table 1; percentages are given in parentheses. An asterisk indicates a percentage used in a statistical test for significant difference between W-1 and H-3, the largest samples from Georgia (see text).

SAMPLE NUMBER	Whole Shells	Apical Fragments	Decollate Shells	Apertural Fragments	Whorl Shards	TOTAL SPECIMENS
W-1	234 (32.4)	171 (23.7)*	74 (10.2)	172 (23.8)	71 (9.8)	722
W-2	0	0	0	1 (50.0)	1 (50.0)	2
W-3	5 (83.3)	0	1 (16.7)	0	0	6
W-4	37 (46.3)	15 (18.8)	0	24 (30.0)	4 (5.0)	80
W-5	166 (30.0)	129 (23.3)	35 (6.3)	124 (22.4)	99 (17.9)	553
H-1	6 (27.3)	7 (31.8)	2 (9.1)	7 (31.8)	0	22
H-2	9 (69.2)	4 (30.8)	0	0	0	13
H-3	73 (33.6)	59 (27.2)*	18 (8.3)	60 (27.6)	7 (3.2)	217
H-4	53 (57.6)	24 (26.1)	5 (5.4)	9 (9.8)	1 (1.1)	92

IV. VARIETIES OF BIOGENIC DAMAGE

Crab-Inflicted Damage. — Shells damaged by crab predation occur in three forms: 1) whole shells with minor apertural damage, caused by an unsuccessful attack (Pl. 1, fig. 1); 2) various kinds of shell fragments, suggesting in some cases the death of the prey (Pl. 1, figs. 2, 3, 4, and 5); and 3) shell damage that was repaired by the would-be victim (Pl. 1, fig. 6; Fig. 2). Almost every specimen of *Odostomia impressa* from the Wassaw Sound area showed signs of breakage or peeling caused by crabs; crab damage was far less ubiquitous in the Virginia samples (Table 3).

Many of the whole shells had chipped outer lips on the body whorl. Shell breaks resulting from apertural chipping, or desquamation, are usually arcuate in outline and do not extend back along the body whorl more than one-half volution (Pl. 1, fig. 1). The edges of the breaks are normally sharp and fresh in appearance. There was no statistically significant difference in the proportion of shells with unrepaired apertural damage between the lower Wilmington River and Wassaw Sound sample localities, considering only the largest samples ($z = 1.297, \alpha = 0.05$).

Crabs peel the odostomes by holding the spire with one cheliped and chip away frag-

ments of the outer lip with the other (Bishop, 1975, Fig. 12.2), the by-products of which are the numerous whorl shards found in some samples (Pl. 1, fig. 2; Table 2). Chipped apertures represent unsuccessful predation attempts that have been repaired in some specimens by new shell growth (Pl. 1, fig. 6). Repaired peeling is distinguished from other cracks and shell blemishes by the following characteristics: 1) newly formed shell appears imbricated beneath older shell below the repaired fracture; 2) the spiral cords forming the surface ornamentation of *O. impressa* are offset slightly at fracture lines; and 3) the arcuate outline of the fracture line separating the pre-attack from the post-attack portions of the shell (Schindel *et al.*, 1982). Fig. 2 shows a close-up view of a repaired fracture.

Other specimens are indicative, at least in part, of fatal attacks on the odostomes by crabs. These include decollate shells with the apical and apertural areas broken off, probably by the scissor-like pinching action of chelipeds (Pl. 1, fig. 3); apertural fragments (Pl. 1, fig. 5); and apical fragments (Pl. 1, fig. 4). It is not known if all decollate shells should be regarded as evidence of fatal attacks, and some individuals loosing apertural fragments in attacks may have been able to repair the damage. However, an unrepaired apical fragment, wherein the

TABLE 3. Predation traces on *Odostomia impressa* shells. Only whole shells are considered; percentages are given in parentheses. An asterisk indicates a percentage used in a statistical test for significant difference between W-1 and H-3 (see text).

SAMPLE NUMBER	Completed Borings	Damage Inflicted by Crabs				TOTAL WHOLE SHELLS EXAMINED	
		Unrepaired Apertural Damage	Shell Repair Frequency				
			1	2	3		4
W-1	11 (4.7)	218 (93.2)*	103 (44.0)*	21 (9.0)	5 (2.1)	1 (0.4)	234
W-3	0	2 (40.0)	2 (40.0)	1 (20.0)	—	—	5
W-4	0	27 (73.0)	18 (48.6)	4 (10.8)	—	—	37
W-5	7 (4.2)	159 (95.8)*	58 (34.9)	7 (4.2)	3 (1.8)	—	166
H-1	0	6 (100.0)	2 (33.3)	—	—	—	6
H-2	0	9 (100.0)	2 (22.2)	—	—	—	9
H-3	3 (4.1)	71 (97.3)*	29 (39.7)*	1 (1.4)	—	—	73
H-4	2 (3.8)	51 (96.2)	14 (26.4)	8 (15.1)	—	—	53
V-1	0	4 (25.0)	3 (18.8)	—	—	—	16
V-2	0	16 (22.2)	11 (15.3)	1 (1.4)	—	—	72
Grand Total =							671

shell has been peeled back into the penultimate whorl or even farther up the spire, is taken as a strong indication that the predator was successful in attacking and extracting enough of the soft parts to cause the death of the snail. A count of apical fragments in a sample from a time-averaged shell accumulation, then, can be regarded as an average minimum estimate of the frequency of successful attacks by predatory crabs. In the Georgia samples (Table 2), it appears that the average frequency of successful attacks was around 25 percent, with no statistically significant difference between the lower Wilmington River and Wassaw Sound localities (comparing proportion of apical fragments in the largest samples; $z = 0.513$, $\alpha = 0.05$).

Figure 2. Repaired shell fracture in immature *Odostomia impressa*. Notice offset spiral cords and imbrication of younger portion of shell beneath older portion at the break. (Both bar scales represent 200 μm .)

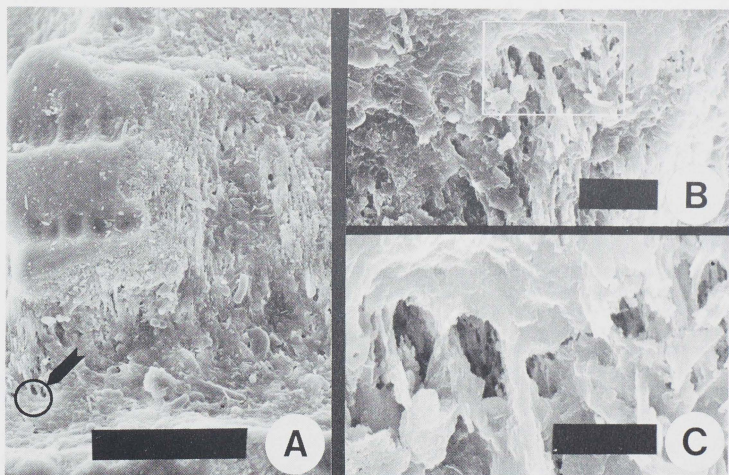
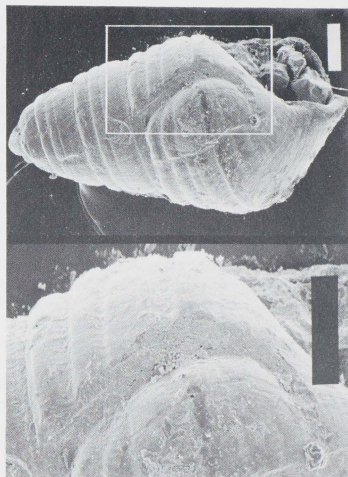


Figure 3. A, Excoriated shell surface surrounding an island of undamaged surface. Arrow indicates area shown in B. (Bar scale represents 100 μm .) B, Close-up view of microborings typical of excoriated surfaces. (Bar scale represents 20 μm .) C, Area shown in B under higher magnification. Notice that borings enter shell surface at oblique angle, and the smaller microborings in lower left-hand corner. (Bar scale represents 10 μm .)

Interestingly, the samples from subtidal oyster banks in the James River, Virginia, contained only slightly damaged or repaired whole shells, with no specimens indicative of fatal attacks. Caution must be taken in interpreting this comparison because of different methods of collecting specimens (bulk sediment samples in Georgia vs. dredge samples in Virginia) and because the Georgia samples come from time-averaged shelly deposits containing several generations of odostomes, whereas the Virginia shells contained the retracted soft parts of snails and seem to represent cohorts of living populations. Crab predation on *O. impressa* appears to be an important cause of mortality in intertidal settings, at any rate, and is unreported in the literature.

Finally, some of the individuals of *O. impressa* with repaired fractures appear to have been attacked several times (Table 3). It is not known if each fracture repair is indicative of a separate unsuccessful attack or if the fractures are repaired multiple shell injuries in some cases inflicted during the same attack, with the fractures located high on the spire indicating accessory damage rather than previous episodes of attempted predation. Although there was no statistically significant difference in the proportion of shells with at least one repair between the lower Wilmington River and Wassaw Sound localities (considering only largest samples; $z = 0.648$, $\alpha = 0.05$), the shells from the sound margin oyster bank did exhibit more examples of multiple repairs. The highest number of multiple repairs observed was four (Table 3).

Algal Microborers. — The second most frequent form of shell damage in the Georgia samples was excoriation, mainly of apical areas, by endolithic or semi-endolithic microborers (Fig. 3, A). At low magnification, shell surfaces damaged by microborers appear chalky and hummocky; at higher magnifications these irregular chalky surfaces are in fact bored and pitted. Where excoriation fields extend axially down the surface of the spire, a trench is formed which superficially resembles a repaired fracture (see center of specimen in Pl. 1, fig. 3). In the tabulation of the frequency of repaired crab damage, care must be exercised not to confuse repairs with excoriation trenches.

Microborings in the odostomes from Georgia are usually subcircular to elliptical holes, 1 to 6 μm in diameter, which enter the shell surface in most cases at oblique angles (Fig. 3, B). The microborings are associated with elongate striations having about the same range of diameters as the holes (Fig. 3, A and C). This may indicate that the microborer organism was in fact semi-endolithic, with part of the creature anchored within the shell surface and part lying on the surface of the shell. These attributes suggest that the microborer responsible for these holes and striations was an alga (see Boekschoten, 1966, 1967). In fact, some odostomes observed under low magnification in reflected light were covered with green material reminiscent of algal coatings on stone walls. Although the identity of the microborer is undetermined, similarities in size and morphology between these traces and the straight microborings made by endolithic cyanophytes, such as *Hyella*, are

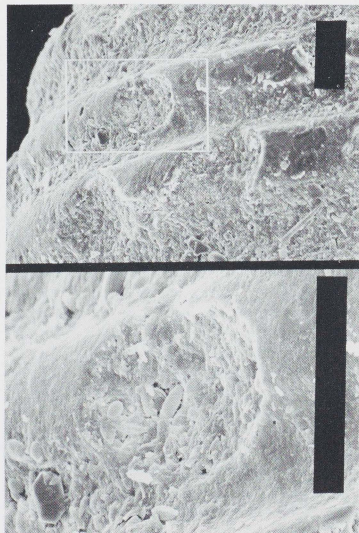


Figure 4. Rimless microscopic pit on *Odostomia impressa* shell. Notice hummocky floor of pit and lack of bordering rim (cf. Fig. 5). (Bar scale represents 100 μm .)

noteworthy (see Golubic *et al.*, 1975, Fig. 12.5).

A second population of microborings with much narrower openings, about $0.5 \mu\text{m}$ in diameter, was observed under the highest magnifications used in scanning the surface of shells. A small cluster of these borings and pits can be seen in the lower left-hand corner of Fig. 3, C. These extremely small microborings may be attributable to endolithic fungi that are in some way associated with the boring algae described earlier (see Golubic *et al.*, 1975, Fig. 12.4, A).

Tabulation of the frequency of microborers in *O. impressa* was not possible. However, it is estimated that over one-half of all specimens, including fragments, from the two largest samples from Georgia had more than half of their surface areas infested with microborers, as evidenced by chalky, pitted microtopography observed at low magnification using a dissecting microscope.

Gastropod Borings. — Signs of predation caused by gastropods in odostome shells from Georgia were very rare; no examples of such borings were found in the Virginia samples. Many of the borings are not unlike miniature versions of the holes made by naticid snails (see Boucot, 1981, Figures 181, 182), but are only about 0.25 to 0.5 mm in outer diameter. Some of the holes counted as gastropod borings, however, departed significantly from the well developed para-

bolic configuration of true naticid borings in having rather irregular shapes, perhaps due to boring through thin shell substrates. Some of these holes actually may have been caused by non-biogenic processes, such as the chemical dissolution of the shell, so that the counts tabulated in Table 3 should be regarded as liberal estimates. The identity of the predatory snail responsible for the unequivocal borings has not been established, but juvenile naticids may be the culprits. However, owing to the oyster bank habitat, epifaunal muricids should not be ruled out (Robert Robertson, person. comm., 1982). There seems to be little difference in the frequency of bored shells between the lower Wilmington River and Wassaw Sound localities, considering the largest samples only.

Bryozoan Borings. — Whereas none of the odostomes from Georgia showed signs of having been bored by bryozoans, many of the Virginia specimens had been infested on their apical regions by *Electra* sp., a boring cheilostome (see Boekschoten, 1967, Fig. 34). Odostome spires heavily pitted with *Electra* borings superficially resemble spires with extensive algal excoriation damage. In a few of the specimens from Virginia, *Electra* zotaria were still adhering to the shells, thereby allowing the definite identification of this source of shell damage in the subtidal samples.

Pits of Unknown Origin. — A number of the odostomes from Georgia featured microscopic pits located on the surfaces of whorls above the body whorl. Two varieties were observed: 1) subcircular to elliptical pits lacking rims and having hummocky floors (Fig. 4); and 2) circular to subcircular pits with rims and more or less smooth, parabolic floors (Fig. 5). Rimless pits are about 80 to 100 μm in diameter, and grade into trench-like excoriated areas; the pits with rims seem to be slightly smaller in average diameter.

Although the origin of the pits is unknown, there are two possible causes. The microtopography within the rimless pits is very similar to that of shell surfaces infested with algal microborings, and the same endolithic organisms may be responsible for these circular traces. The rim-bearing pits, however, may result from the handling of the spire of *O. impressa* during crab attacks, with the pits representing the points of im-



Figure 5. Rim-bearing microscopic pit on *Odostomia impressa* shell. Arrows point to powdered shell material forming the discontinuous rim. (Bar scale represents 20 μm .)

pact of serrations located along the inner edges of endopodites and dactylopodites of a cheliped with the shell surface. This would account for the rim of powdered shell material surrounding this type of pit (see Fig. 5). No attempt was made to measure the frequency of pits or pitted shells.

V. DISCUSSION AND CONCLUSIONS

The study of biogenic shell damage is one of the only methods available to the paleo-synecologist that can be used in establishing the kinds of ecological associations which existed among fossil species within paleo-communities. Inferential methods, such as deducing the presence of algal-covered substrates from the presence of the shells of grazing gastropods, are much less reliable owing to dependence on taxonomic uniformitarianism and absence of physical evidence in the form of traces (e.g., "addition by inference" in analysis of paleo-communities described by Kauffman and Scott, 1976, p. 17). Evidence of predation, parasitism, post-mortem infestation of skeletons, and competition for space among epilithic organisms may be obtained by carefully observing the condition of fossil shells in the course of assemblage analysis (see Boekschoten, 1967; Bishop, 1975; Golubic *et al.*, 1975; Liddell and Brett, 1982; Schindel *et al.*, 1982). Traces on shells may in some instances be the only surviving evidence of predators or encrusters that lacked skeletal hardparts (e.g., *Polydora* borings in Neogene bivalves). Notwithstanding, problems arise even when traces are plentiful in the identification of ecological associations within very old paleo-communities, wherein

shell damage cannot be related with certainty to the predators or encrusters responsible by making a direct comparison with modern community structure. The best evidence of ancient ecological associations will always come from the observation of organisms in physical contact in fossil assemblages directly indicating an interrelationship (Ager, 1963, Chapt. 15).

Not only are large shells of fossil mollusks useful in establishing the existence of ecological associations in ancient communities, but so are the typically more numerous shells of small sizes. Because smaller shells often occur in very large numbers in marine and estuarine fossil deposits (e.g., *Gemma gemma* (Totten) in sandy paralic Pleistocene deposits in North Carolina, described by Miller, 1982), they are more useful than larger, less abundant fossils in statistical analyses of predation or infestation frequency. Through studies of shell damage in modern mesoscopic mollusks, the interpretation of such damage in fossil material can be advanced, at least in Cenozoic examples.

Odostomia impressa is a well known ectoparasite on *Crassostrea virginica* (Gmelin) (Allen, 1958; Wells, 1959, 1961; Robertson, 1978). It occurs in large numbers in shelly sediments surrounding modern oyster banks in coastal Georgia. Nearly all of the shells studied from the Wassaw Sound area showed signs of repaired or unrepaired damage caused by crabs, and most fragmental specimens and shell shards are the result of predation by crabs. At least 25 percent of odostomes in this area of the Atlantic Coast are successfully attacked and killed by crabs. This im-

PLATE 1

Condition of shells and fragments of *Odostomia impressa* from the lower Wilmington River-Wassaw Sound estuary, Georgia (see Table 2).

Figures

1. Whole shell showing unrepaired damage to the outer lip of the body whorl. Notice arcuate outline of the fracture. (Bar scale represents 1 mm.)
2. Oblique view of a whorl shard. (Bar scale represents 400 μ m.)
3. Decollate shell with both the apical and apertural areas broken away. (Bar scale represents 400 μ m.)
4. Apical fragment showing peeling beyond the penultimate whorl. This degree of damage was almost certainly fatal to the snail. (Bar scale represents 1 mm.)
5. Apertural fragment. (Bar scale represents 400 μ m.)
6. Repaired apertural damage, of the type shown in fig. 1. Arrows point to the fracture line. (Bar scale represents 400 μ m.)

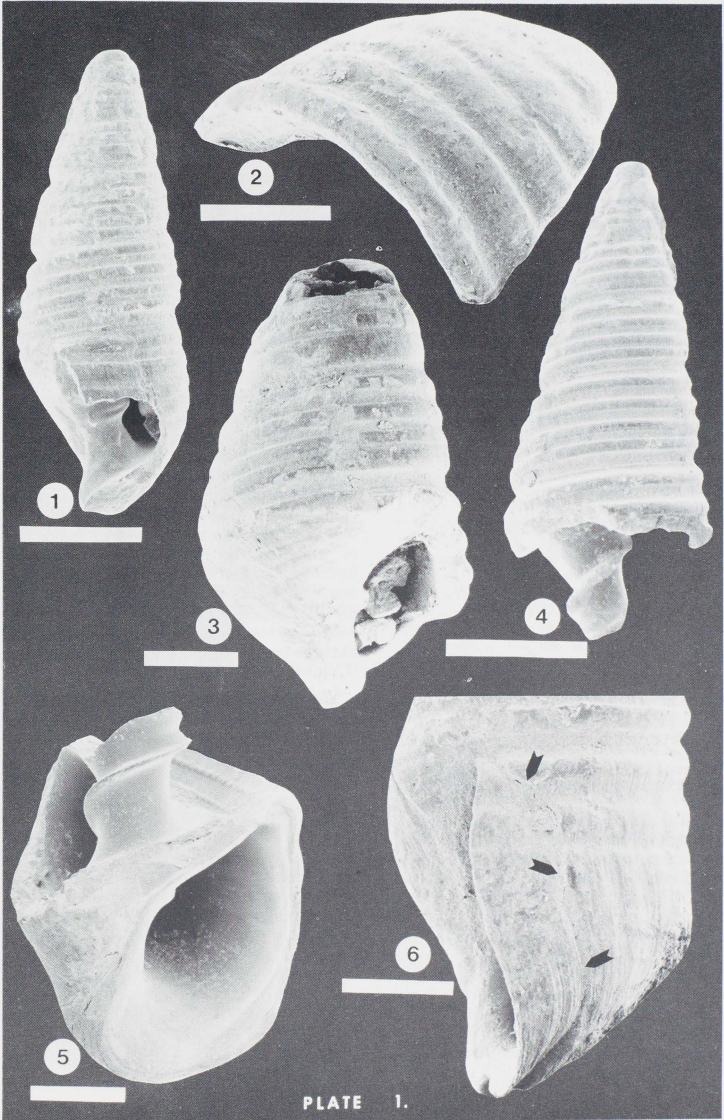


PLATE 1.

portant source of mortality in intertidal populations of *O. impressa* has not been previously reported in the literature on pyramidellids. The likely predator on *O. impressa* is the mud crab *Panopeus herbstii* H. Milne-Edwards, 1834 (R. W. Frey, person. comm.). This small, secretive xanthid is very abundant in oyster banks in Georgia, and is associated with the crabs *Sesarma* and *Uca* near the landward edges of the banks. *Panopeus herbstii* is a trophic generalist, feeding upon a wide range of intertidal organisms including young oysters, barnacles, and odostomes; it is in turn preyed upon by raccoons and fish, and probably by birds (see Williams, 1965, p. 196-198). The discovery that a xanthid, probably *P. herbstii*, preys on odostomes is of ecological

interest as it demonstrates for the first time how *O. impressa* fits into the food chain of intertidal oyster banks: *O. impressa* and *C. virginica* are associated in a parasite-host relationship, and *P. herbstii* and *O. impressa* appear to be linked in a loose predator-prey association (Fig. 6). Scavengers and decomposers, as usual, reclaim the leavings. Although a few individuals of *O. impressa* in the Virginia samples had been nipped by crabs, it appears that crabs may be far less important as predators on odostomes in subtidal environments than on intertidal banks. This preliminary finding could be tested by comparing relative incidence of predation by crabs within the same locality along a bathymetric gradient.

The chalky appearance of many of the odostome shells from Georgia is the result of algal excoriation. It is probable that much of the shell damage in estuarine fossil deposits usually attributed to chemical dissolution of CaCO_3 (Wiedemann, 1972) is actually caused by infestation by endolithic and semi-endolithic algae, both during life and following the death of the host mollusks. It is now known that microboring organisms and their traces can be used as indicators of paleodepths, bathymetric distribution being controlled by light penetration and water supply. The microborings in the odostomes from Georgia are morphologically very similar to the straight cyanophyte borings typical of the lower intertidal zone (Golubic *et al.*, 1975, p. 234-242).

Minor traces in the samples from the Wasaw Sound area included rare gastropod borings and microscopic pits. The pits are of two varieties with two different possible origins: 1) rimless pits with hummocky floors, which may be caused by algal microborers in the early stages of shell surface infestation; and 2) slightly smaller pits having rims made of powdered shell material, which could have been made by the impact of strongly-toothed crab claws with the surface of odostome shells during attacks.

Many of the Virginia specimens, used as comparative material, also had what appeared to be excoriated spires. On close inspection it was found that this was the result of borings by the cheilostome bryozoan *Electra*. None of the specimens from intertidal banks in Georgia featured this type of shell damage.

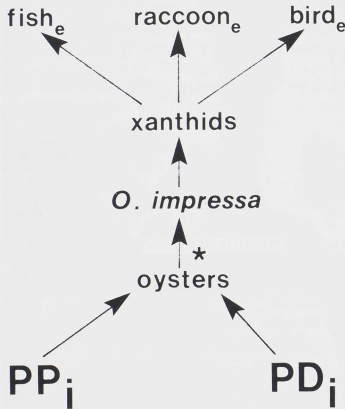


Figure 6. Idealized branch of an intertidal consumer food chain showing the position of *Odostomia impressa* in the trophic structure of oyster bank communities. PP_i = imported phytoplankton from the open estuary and ocean; PD_i = imported plant detritus from salt marshes; $fish_e$ = export in form of fish predator feeding on oyster bank at high tide; $raccoon_e$ = export in form of raccoon feeding at low tide; $bird_e$ = export by birds feeding probably at low tide; * = parasitic relationship. Recuperator organisms are not shown.

In conclusion, mesoscopic shells represent an abundant but little used paleoecologic resource for studies of biogenic shell damage both in modern shelly deposits and in fossil assemblages. The large numbers in which these small mollusks sometimes occur make them particularly useful in statistical comparisons between localities along environmental gradients within the same general area, in comparisons between different major environments, and in comparisons of fossiliferous beds stacked in stratigraphic sections. Biogenic shell damage provides evidence of the ecological interactions between species and may afford the only clues as to the existence of soft-bodied organisms in ancient communities. Traces of predation and parasitism in shells also should be of interest to the neontologist because they provide evidence of the position of mollusks in the trophic structure of modern communities by indicating interactions between species that are very rarely observed by the field ecologist. Just as in Sherlock Holmes' admonition of Dr. Watson, in which the master of deduction demonstrates to his colleague the means of reading a man's profession from the condition of his hands, trouser-knees, and shirt-cuffs, ecologists and paleoecologists should learn to "read" something of the ecologic role of mollusks from the condition of their shells.

VI. ACKNOWLEDGMENTS

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VII. LITERATURE CITED

- AGER, D. V., 1963, Principles of Paleocology. McGraw-Hill, New York, 371 p.
- ALLEN, J. R., 1958, Feeding habits of two species of *Odostomia*: *Nautilus*, v. 72, p. 11-15.
- BISHOP, G. A., 1975, Traces of predation, in FREY, R. W. (ed.), *The Study of Trace Fossils*; Springer-Verlag, New York, p. 261-281.
- BOEKSCHOTEN, G. J., 1966, Shell borings of sessile epibiontic organisms as paleoecological guides (with examples from the Dutch coast): *Palaeogeog.*, *Palaeoclimatol.*, *Palaeoecol.*, v. 2, p. 333-379.
- BOEKSCHOTEN, G. J., 1967, Palaeoecology of some Mollusca from the Tielrode Sands (Pliocene, Belgium): *Palaeogeog.*, *Palaeoclimatol.*, *Palaeoecol.*, v. 3, p. 311-362.
- BOUCOT, A. J., 1981, Principles of Benthic Marine Paleocology. Academic Press, New York, 463 p.
- DODD, J. R., and R. J. STANTON, 1981, Paleocology, Concepts and Applications. John Wiley and Sons, New York, 559 p.
- DUDLEY, E. C., 1980, Crab predation on two small marine gastropods (Cerithiacea): *Nautilus*, v. 94, p. 162-164.
- GOLUBIC, S., R. D. PERKINS, and K. J. LUKAS, 1975, Boring microorganisms and microborings in carbonate substrates, in FREY, R. W. (ed.), *The Study of Trace Fossils*; Springer-Verlag, New York, p. 229-259.
- KAUFFMAN, E. G., and R. W. SCOTT, 1976, Basic concepts of community ecology and paleoecology, in SCOTT, R. W., and R. R. WEST (eds.), *Structure and Classification of Paleo-communities*; Dowden, Hutchinson and Ross, Stroudsburg, Penn., p. 1-28.
- LIDDELL, W. D., and C. E. BRETT, 1982, Skeletal overgrowths among epizoans from the Silurian (Wenlockian) Waldron Shale: *Paleobiology*, v. 8, p. 67-78.
- MILLER, W., III, 1982, The paleoecologic history of late Pleistocene estuarine and marine fossil deposits in Dare County, North Carolina: *Southeastern Geol.*, v. 23, p. 1-13.
- MILLER, W., III, *in press*, Survey of the pyramidelid gastropods in the Wassaw Sound area, coastal Georgia: *Nautilus*.
- REYMENT, R. A., 1971, Introduction to Quantitative Paleocology. Elsevier, Amsterdam, 226 p.
- ROBERTSON, R., 1978, Spermatophores of six eastern North American pyramidelid gastropods and their systematic significance (with the new genus *Boonea*): *Biol. Bull.*, v. 155, p. 360-382.
- SCHINDEL, D. E., G. J. VERMEIJ, and E. ZIPSER, 1982, Frequencies of repaired shell fractures among the Pennsylvanian gastropods of north-central Texas: *Jour. Paleontology*, v. 56, p. 729-740.

- VERMEIJ, G. J., 1978, Biogeography and Adaptation. Harvard Univ. Press, Cambridge, Mass., 332 p.
- WELLS, H. W., 1959, Notes on *Odostomia impressa* (Say): *Nautilus*, v. 72, p. 140-144.
- WELLS, H. W., 1961, The fauna of oyster beds, with special reference to the salinity factor: *Ecol. Monographs*, v. 31, p. 239-266.
- WIEDEMANN, H. U., 1972, Shell deposits and shell preservation in Quaternary and Tertiary estuarine sediments in Georgia, U.S.A.: *Sedimentary Geol.*, v. 7, p. 103-125.
- WILLIAMS, A. B., 1965, Marine decapod crustaceans of the Carolinas: U.S. Fish and Wildlife Serv., *Fish. Bull.*, v. 65, 298 p.

REVIEW

THE ABYSS OF TIME: Changing Conceptions of the Earth's Antiquity after the Sixteenth Century, by Claude C. Albritton, Jr. Published by Freeman, Cooper and Company, San Francisco, California, 1980, 251 pp., 29 figs., \$12.75

Professor Albritton opens this volume with the statement: "I am confident that someday the concept of geological time will be acclaimed as one of the more wonderful contributions from natural science to general thought." Thus, he introduces his fascinating history of Man's search through the centuries for the answer to the fundamental question "How old is the Earth?"

In his own pursuit of the concept of geological time, Claude accompanied by his wife Jane (to whom this book is dedicated) has sought to retrace the footsteps of the classic writers who have observed the rocks of the crust and have recorded their thoughts on the antiquity of these rocks. His travels have taken him throughout the world and have added much to his insight about his subject. Included are such diverse places as Cretaceous outcrops near Glen Rose, Texas, the Isle of Malta, and the railway station at Capri.

Professor Albritton traces the changing perspective of geological time from Nicolaus Steno to Arthur Holmes. Among those whose contributions to the temporal history of the Earth are discussed are

Robert Hooke, Thomas Burnet, Benoit de Maillet, the Comte de Buffon, James Hutton, John Playfair, William Smith, Johann Gottlob Lehmann, Giovanni Arduino, Abraham Gottlob Werner, Adam Sedgwick, Roderick I. Murchison, Georges Cuvier, Charles Lyell, George Poulett Scrope, Louis Agassiz, Charles Darwin, Lord Kelvin, Alfred R. Wallace, Thomas C. Chamberlin, Ernest Rutherford, John Joly, and others. This is far more than merely a history of geological time. The work of each individual is treated in clear, readable prose with a modern, fresh evaluation of his contributions. The book serves as a thorough review of the history of historical geology from the mid-seventeenth century to the mid-twentieth century. Thus, it is a valuable resource and reference for all geologists and historians interested in the development of historical geology.

In his concluding chapter, Professor Albritton considers the current movement to force our preparatory schools to teach evolution theory and creation theory with "reasonably equal emphasis". He observes, "One can only conclude that some creationists, recoiling from the fearsome prospect of time's abyss, have toppled backward into the abyss of ignorance."

This masterful work is highly recommended reading for all geologists. Surely the *Abyss of Time* could not be surpassed as an answer to the "abyss of ignorance."

—H.C.S.