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PENETRATION OF MOLLUSCAN AND NON-MOLLUSCAN MINERALS BY THE BORING GASTROPOD *UROSALPINX CINEREA*

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The predatory shell penetrating habit characteristic of the most familiar families of recent boring gastropods, the Naticidae and the Muricidae, probably arose first in the Naticacea during Upper Cretaceous times, some 100 million years ago (Carriker and Yochelson, 1968; Sohl, 1969). During this long geologic history, boring gastropods evolved a unique mechanism for penetration of the exoskeleton of shelled invertebrate prey (Carriker and Williams, 1978).

The exoskeleton of these prey, so far as is known, consists primarily of calcium carbonate in calcitic, aragonitic, or vateritic crystalline form, and, secondarily, of a variety of trace and minor elements and an organic matrix (Carriker and Williams, 1978; Dodd, 1967; Milliman, 1974; Taylor, Kennedy and Hall, 1969). In view of the antiquity of the mechanism, it is tempting to hypothesize that the mechanism is specific for calcium carbonate and that boring snails can penetrate only this substratum. That this may not be the case, however, was suggested by Carriker, Scott and Martin (1963), who obtained faint etchings when accessory boring organs of snails were applied to the polished surface of human dentin and enamel (calcium phosphate in the form of hydroxyapatite). Although probably valid, these tests were carried out with excised accessory boring organs. The tests should be repeated using accessory boring organs of live, normally boring snails.

Recent ultrastructural studies (Carriker, 1978) demonstrated a marked variation in the solubility of different portions of the mineral components of shell units when etched by the ABO secretion. The differential solubilization may have resulted from variation in the solubility of intracrystalline organic components as well as of trace and minor mineral constituents (see also Travis and Gonsalves, 1969). However, no studies have been reported correlating the differential solubility of identified shell constituents. A first step in such an investigation could test the capacity of boring snails to penetrate a variety of isolated non-molluscan minerals which may be present in the shell in trace and minor concentrations (Travis, 1968a, b).

This paper reports the results of an experimental investigation of the capacity of the muricid boring snail *Urosalpinx cinerea follyensis* Baker to penetrate several kinds of molluscan and non-molluscan minerals. The results are discussed with reference to the specificity of the boring mechanism for different substrata and

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differential dissolution of shell by the secretory product of the accessory boring organ.

Materials and Methods

Animals

Actively feeding adult *Urosalpinx cinerea follyensis* ranging in height from 38 to 46 mm were employed in the study. Snails were collected in Wachapreague, Virginia, and maintained in the laboratory in rapidly flowing seawater with oysters (*Crassostrea virginica*) and mussels (*Mytilus edulis*) obtained in the vicinity of Woods Hole, Massachusetts. The laboratory study was begun in 1970 and concluded two years later. During the winter, snails were maintained in seawater warmed to room temperature and allowed to reach gas phase equilibrium in a heat exchanger (Carriker and Van Zandt, 1973). Temperature of the flowing seawater in which the tests were run ranged from 16 to 21.6° C, salinity varied from 30.4 to 32.0‰, and the pH ranged from 8.0 to 8.2.

Mineral samples

Fifteen different biogenic and abiogenic minerals were tested (Table I). Shells of *Spisula solidissima, Crassostrea virginica,* and *Anomia simplex,* used as controls, were obtained from animals in the Woods Hole region. Radulae were extracted from *Urosalpinx cinerea follyensis* collected in Wachapreague. Normal second teeth from young people, extracted for reasons of spacing, provided human enamel and dentine. Fresh beef bone (femur) was purchased at a local meat market. Nine relatively insoluble, inorganically formed minerals were ordered from Ward's Natural Science Establishment.

At least three wafers, approximately 1 mm in thickness and ranging from 5 to 8 mm in broadest dimension, were sawed from each mineral with a diamond wafering blade on a Gillings-Hamco thin sectioning machine. One surface of each wafer was then sanded and polished with alumina (particle size 0.05 m) on a metallurgical lap wheel. Fine scratches remaining on the polished surface of the test samples provided a background and contrast to solubilized surfaces.

Tests

Sample wafers were exposed to penetration by live, normally boring snails in valve models (Carriker and Van Zandt, 1972a). After a snail had bored for a day or two into the valve of a live oyster (approximately 6 cm long), the free (unbored) valve and flesh of the oyster were removed gently under seawater, and the remaining half-shell, boring-snail preparation was placed, inner surface of the valve facing up and the snail suspended underneath, over an oval-shaped opening on a small table-like support. The valve model and support were then positioned on a manipulated stage in gently running seawater under a binocular microscope, the inner surface of the oyster valve slightly above the meniscus of the seawater (see Fig. 1, Carriker, Williams and Van Zandt, 1978). As boring approached the inner surface of the valve, the borehole could be seen through the translucent

calcitostracum. Just before the snail perforated the valve, the surface of the valve around the emerging borehole was rinsed with fresh water, dried, and a thin layer of hot paraffin was applied to the shell surface to prevent possible chemical interaction between the test sample, oyster shell, and seawater. The sample, polished surface in contact with the oyster valve, was then positioned directly over the emerging borehole and cemented in place with Coecal, a slowly hardening calcareous material used for making dental molds. Next, the preparation, with the snail still at the borehole, was submerged in seawater and left there for approximately 24 hr. Borehole sites were chosen on the flat valve of oysters to provide a close contact between the sample and valve surfaces.

In preliminary trials, plaster of Paris was employed to cement the test sample to the oyster valve, but proved less workable than Coecal. Snails abandoned samples which were incompletely cemented to the oyster valve, allowing seawater to enter between the sample and the valve. To insure a water-tight seal, each sample was cemented carefully to the valve surface along its entire perimeter, and an additional thick layer of Coecal was spread over the sample and adjacent valve surface (Fig. 1). Snails bored easily through both plaster of Paris and Coecal without obvious deleterious effects.

Snails enlarged the borehole from the initial break to a diameter which would fully admit the proboscis and the accessory boring organ in about six hours (Carriker and Van Zandt, 1972a, b). Figures for duration of penetration in Table I represent the approximate time that the proboscis and accessory boring organ were in full contact with the surface of the test samples. In several cases, snails abandoned the preparation during the night and it was not possible to determine the actual time of penetration.

At the termination of approximately 24 hr, each snail, if still present, was dislodged from its borehole. The sample and Coecal were removed from the oyster valve, rinsed quickly in distilled water, dried with a current of warm air, and stored in a vacuum desiccator.

Average maximum depth of incomplete boreholes in experimental samples was determined with a Wild M-20 compound microscope provided with incident illumination (epi-attachment) and a scale (each interval = 1 micron) on the fine focus knob for measuring vertical distances.

The effect of secretion of the accessory boring organ on radular teeth was tested as follows. Radulae were excised under a binocular microscope from large adult *Urosalpinx cinerea follyensis,* washed in distilled water, spread between fragments of cover glass, and allowed to dry in the sun. After drying, each radula was mounted on a strip of thin plastic cover glass by application of small drops of Duco cement at the ends and at intervals along the length of the radula. Each radula, still mounted on the plastic strip, was then placed over the open borehole in a valve model just after the proboscis had been retracted and the accessory boring organ was being extended. The preparation was removed from the borehole the instant the accessory boring organ was withdrawn at the termination of the period of chemical activity and before the proboscis was again inserted in the hole. A length of the radula not yet employed in rasping over the bending plane of the odontophore was exposed to the secretion of the

TABLE I

Penetration of molluscan and non-molluscan minerals by Urosalpinx cinerea. *pK_{sp} = negative logarithm of K_{sp}.* ( ) = *snail abandoned bole before the test period ended.*

Minerals			Penetration		
Source of test sample, mineral, major constituents	Hardness, Knoop values (kg/mm²)	Solubility product (as pK_{sp})	Duration (hr)	Depth (μm)	Characteristics, dissolution
Crassostrea virginica shell, calcite: $CaCO_3$ + organic matrix	244[1]	6.2[5]	18.3	230	Shallow borehole
			17.8	210	Shallow borehole
			18.5	180	Shallow borehole
Spissula solidissima shell, aragonite: $CaCO_3$ + organic matrix	—	6.1[5]	20.5	280	Shallow borehole
			19.5	180	Shallow borehole
			20.0	180	Shallow borehole
Anomia simplex shell, aragonite: $CaCO_3$ + organic matrix	—	6.1[5]	18.5	205	Shallow borehole
			18.0	120	Shallow borehole
			(left)	(60)	Shallow borehole
Urosalpinx cinerea, radula[3]: $CaCO_3$, Sr, Mg, Bo, Si, Zn, Fe + organic matrix	200[1]	Practically	0.6	0	No dissolution
	407	insoluble	1.6	0	No dissolution
			2.6	0	No dissolution
Beef bone, hydroxyapatite: $Ca_{10}(PO_4)_6(OH)_2$ + organic matrix	—	54.6[7]	17.0	90	Shallow borehole
			18.0	55	Shallow borehole
			21.0	50	Shallow borehole
Human tooth, hydroxyapatite: $Ca_{10}(PO_4)_6(OH)_2$ + organic matrix—enamel	430[2]	52.2–57.2[6]	17.5	15	Slight depression
			(left)	(10)	Slight depression
—dentine	430[2]		17.5	25	Slight depression
			18.0	5	Slight etching
Strontianite: $SrCO_3$	149	10.0[4]	18.0	110	Shallow borehole
			13 (left)	(40)	Slight depression
			(left)	(10)	Slight depression
Anhydrite: $CaSO_4$	149	4.6[4]	17.0 (left)	(25)	Slight depression
			12.5 (left)	(15)	Slight depression
			(left)	(10)	Slight depression
Witherite: $BaCO_3$	149	9.3[4]	(left)	(20)	Slight depression
			(left)	(5)	Slight etching
			(left)	(?)	Questionable
Magnesite: $MgCO_3$	149–296	5.0[4]	(8.5	Trace	Slight etching
			(left)	(0)	No dissolution
			(left)	(0)	No dissolution
Siderite: $FeCO_3$	163–296	10.5[4]	20.0	0	No dissolution
			(left)	(0)	No dissolution
			(left)	(0)	No dissolution
Smithsonite: $ZnCO_3$	163–296	10.7[4]	(left)	(0)	No dissolution
			(left)	(0)	No dissolution

TABLE I—*Continued*

Minerals			Penetration		
Source of test sample, mineral, major constituents	Hardness, Knoop values (kg/mm²)	Solubility product (as pK_{sp})	Duration (hr)	Depth (μm)	Characteristics, dissolution
Alunite: $KAl_3(OH)_6(SO_4)_2$	149–163	Insoluble?	14.0 (left)	(0)	No dissolution
			18.5	0	No dissolution
			18.0	0	No dissolution
Fluorite: CaF_2	163	10.6[4]	16.0 (left)	(0)	No dissolution
			15.5 (left)	(0)	No dissolution
			13.0 (left)	(0)	No dissolution
Quartz: SiO_2	820		(left)	(0)	No dissolution
		Insoluble	(left)	(0)	No dissolution

[1] Carriker (1969).
[2] Trautz (1967).
[3] Carriker and Van Zandt (1972a).
[4] Kolthoff, Sandell, Meehan and Bruckenstein (1969).
[5] Berner (1976)—calcite and aragonite in seawater.
[6] Patel and Brown (1975).
[7] Brown and Chow (1976).

accessory boring organ. The upper surface of the valve was positioned just above the surface of the seawater so that the radula would be in contact only with secretion of the accessory boring organ. Three radulae were tested, one for 38 min, a second for 97 min, and the third for 154 min. These intervals were chosen because during each normal cycle of rasping and chemical activity the radula is exposed to secretion in the borehole for about one minute, and it takes a snail 150 1-minute rasping periods, or a total of 150 min of exposure to secretion of the accessory boring organ, to penetrate oyster shell 1 mm in thickness (Carriker and Van Zandt, 1972a). After exposure to the secretion for the designated interval, each radula was rinsed in distilled water, dried in a stream of warm air, and stored in a vacuum desiccator.

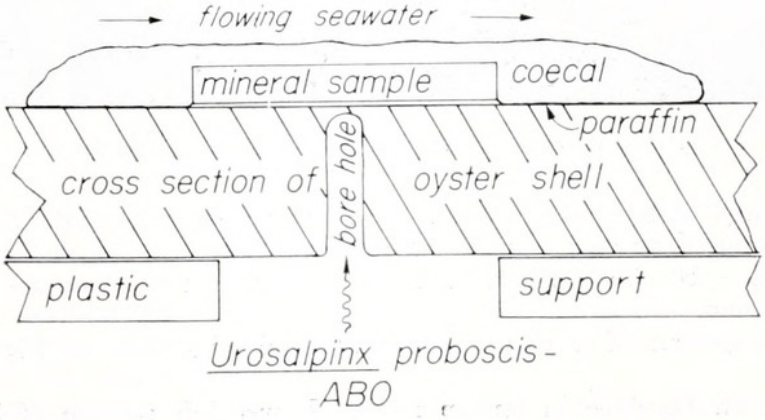
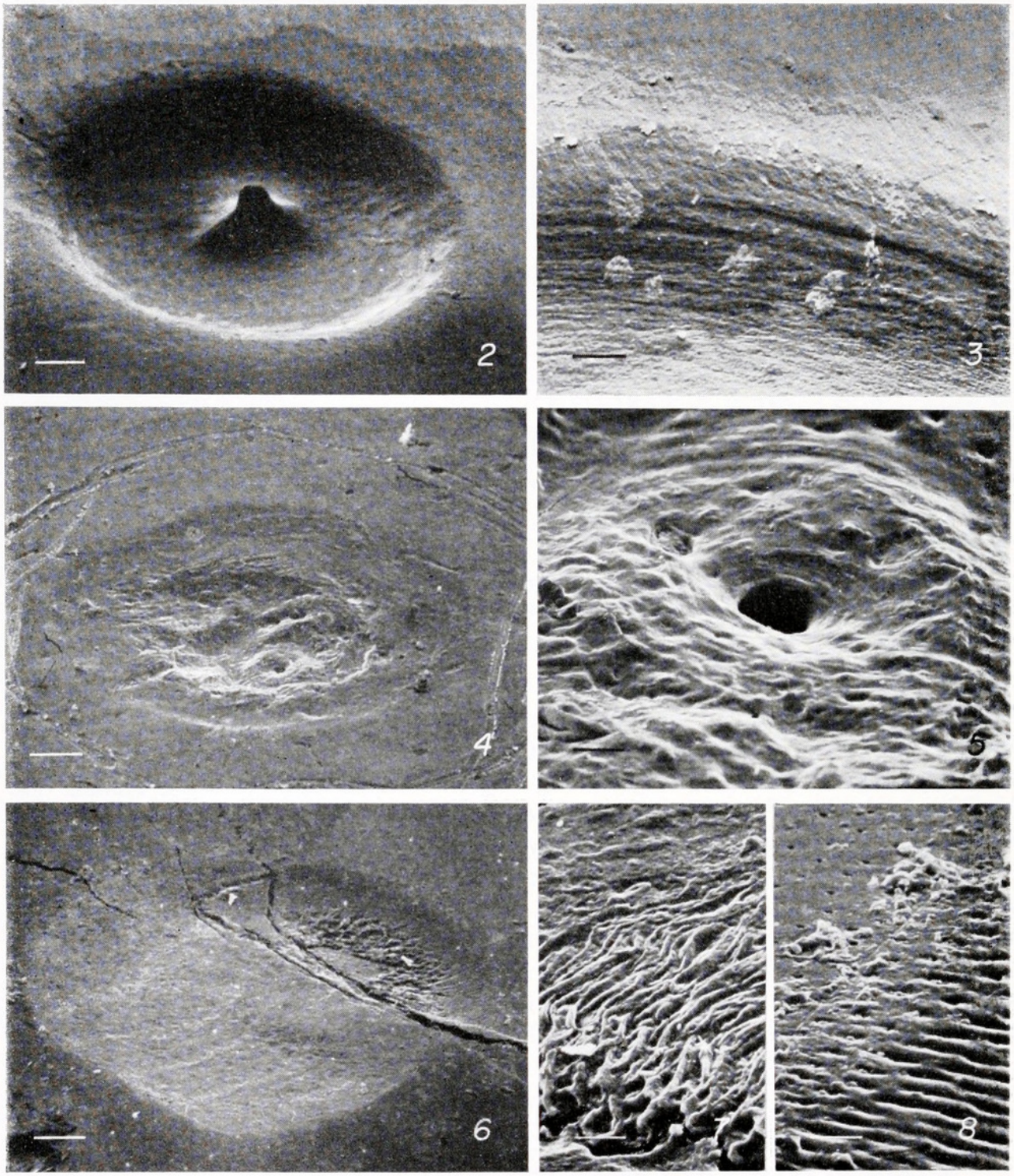


FIGURE 1. Cross sectional diagram of device used to test penetrability of mineral samples by *Urosalpinx cinerea*. Diameter of borehole 1 mm.



Figures 2–20 are scanning electron micrographs.

FIGURE 2. Incomplete borehole in shell of *Anomia simplex*. Scale bar equals 0.2 mm.

FIGURE 3. Portion of beveled edge of borehole in Figure 2. Scale bar equals 0.05 mm.

FIGURE 4. Shallow borehole in beef bone. Small holes in borehole are Haversian canals. Scale bar equals 0.13 mm.

FIGURE 5. Enlargement of a Haversian canal in the borehole in Figure 4. Scale bar equals 20 μm.

FIGURE 6. Shallow borehole in human tooth. Lower left portion of hole is in enamel, and upper right is in dentine. Cracks through wafer resulted from drying. Scale bar equals 0.1 mm.

One of each of the triplicate samples of each test mineral and the three radulae were examined with a scanning electron microscope (Cambridge Stereoscan Mark II) at magnifications ranging from 16 to 2500 ×. Mineral wafers were removed from the Coecal, cemented with silver paint to scanning electron microscope pin stubs 1 cm in diameter, and dried in an oven for about 48 hr before coating with carbon and gold for viewing in the scanning electron microscope. Radulae were removed from the plastic cover glass strips, transferred to double adhesive tape on stubs, and secured at the ends to the tape with silver paint prior to coating with carbon and gold.

Results

All biogenically formed calcareous structures, except radulae, exposed to normally boring *Urosalpinx cinerea* on valve models were penetrated (Table I). The rate of penetration of the mineral wafers decreased in the following order: calcite and aragonite, strontianite, bone and tooth hydroxyapatite, anhydrite, witherite, and magnesite. At least at the magnifications employed with the scanning electron microscope, the abiogenic minerals, siderite, smithsonite, alunite, fluorite, and quartz did not seem to be affected either by radular rasping or secretion from the accessory boring organ. Snails remained on calcitic wafers of *Crassostrea virginica,* aragonitic wafers of *Spisula solidissima,* and hydroxyapatitic wafers of bone for the full 24 hr of the experiment. One snail abandoned an aragonitic wafer of *Anomia simplex,* and another, a hydroxyapatitic wafer of human tooth prior to termination of the testing period. In most cases of abandonment, snails left the preparation during the night or during periods when we were absent, so it was difficult to approximate the amount of time on the wafer. Of the total of 15 tests performed on biogenically formed calcareous minerals, only two (or 13%) of the snails left the sample on the model before the experiment was terminated; whereas of the 25 tests on abiogenically formed minerals, 20 (or 80%) of the snails crawled off the sample before the end of the test.

Shell of *Crassostrea virginica, Spisula solidissima* and *Anomia simplex* was bored to approximately the same average depth (Table I, Figs. 2, 3). The shape and size of incomplete boreholes were characteristic of holes made by *Urosalpinx cinerea* when penetrating normal prey shell (Carriker and Yochelson, 1968). An exception to this was the curious mount left in the center of the borehole in one of the wafers of *Anomia simplex* by one of the snails (Fig. 2). Ultrastructural examination of the fractured surface of the top of the mount showed normal nacreous lamellae; energy dispersive X-ray analysis of the top and sides of the mount disclosed no unusual concentrations of minor or trace elements (at least at the minimal sensitivity of the technique, 500 to 1000 ppm)

FIGURE 7. Enlargement of edge of borehole in enamel in Figure 6. Polished portion of wafer is at upper left. Partly dissolved prism ends and sides shown in lower portion of micrograph. Scale bar equals 9 μm.

FIGURE 8. Enlargement of edge of borehole in dentine in Figure 6. Polished portion of wafer is at upper left; dissolved portion lower right. Cross sections of tubules are visible in polished portion, and oblique sections in the partly dissolved dentine. Scale bar equals 10 μm.

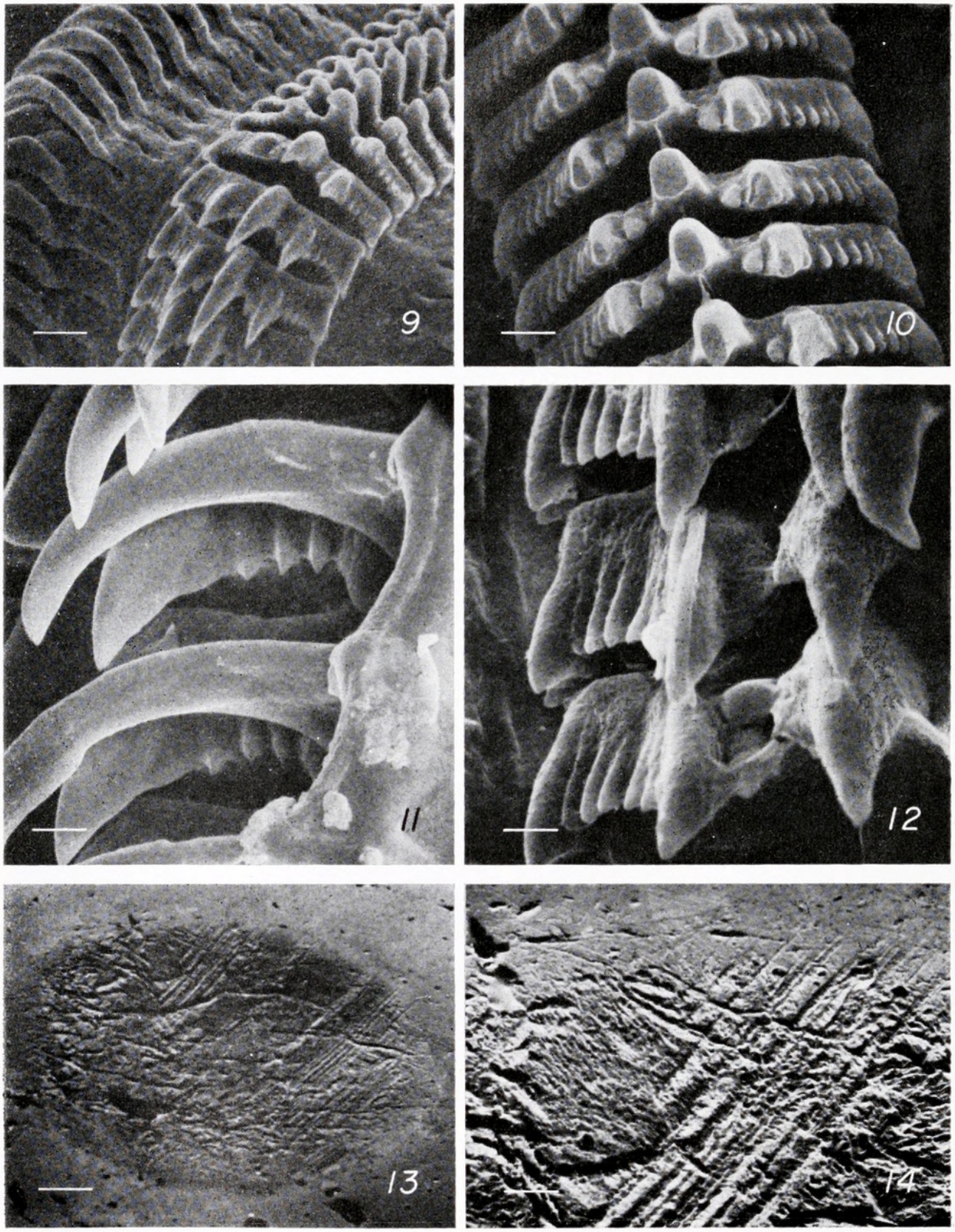


FIGURE 9. Unworn radula of *Urosalpinx cinerea* prior to use by snail for boring hole. Five-cusped teeth are in center row, and marginal teeth in row to either side. Scale bar equals 35 μm.

FIGURE 10. Portion of radula of *Urosalpinx cinerea* taken from anterior end of radula after snail bored a hole, showing extent of abrasion that takes place during shell penetration.

which might have decreased the solubility of shell in that region. Sides of the borehole were characterized by normal bevelling (Fig. 3).

Degree of penetration of beef bone (Fig. 4) was intermediate between that of shell and teeth (Fig. 6, Table I). Dissolution of bone in the borehole was uneven, though conspicuous (Fig. 4), and smoothly bevelled the rim of exposed Haversian canals (Fig. 5). The pattern of concentric rings surrounding the Haversian canal in Figure 5 suggests successive layers of mineral lamellae.

Dentine was penetrated slightly more deeply than enamel (Fig. 6, Table I). The secretion of the accessory boring organ dissolved the edges of tubules in the dentine, making them conspicuous (Fig. 8). Figure 7 suggests that the center of enamel prisms was dissolved more deeply than the perimeter.

Radular teeth of *Urosalpinx cinerea* placed on the secretion of the accessory boring organ were unaffected during exposures ranging from 0.5 to 2.5 hr (Figs. 11, 12; Table I). The wrinkled surface on the cusps of teeth in Figure 12 represents dried secretion; no blunting of cusp points or pitting of the tooth surface was evident. Compare with control radulae in Figures 9 and 10.

Of the abiogenically formed minerals, strontianite was penetrated most deeply (Figs. 13, 14). Incomplete boreholes were quite shallow in witherite (Figs. 15, 16) and in anhydrite, and less noticeable at low (Fig. 17) or higher magnifications (Fig. 18) in magnesite. Rasp marks scraped by the radula during boring were clearly evident in the relatively soft minerals strontianite (Figs. 13, 14) and witherite (Figs. 15, 16).

At magnifications employed with the scanning electron microscope, no obvious dissolution of the surface of the minerals siderite, smithsonite, alunite, and fluorite occurred (Figs. 19–22). The faint half circle in Figures 19, 20, and 22 represents residues left by the secretion at the edge of the accessory boring organ. This interpretation is supported by the persistence of original scratch lines, which are still visible without appreciable disfigurement from dissolution at the site where the accessory boring organ was applied.

The experiments demonstrated that Ca, Sr, Ba, and Mg as carbonates, and Ca both as the phosphate and sulfate, were attacked by the secretion of the accessory boring organ. On the other other hand, Fe and Zn as the carbonates, Ca as the fluoride, Si as the oxide, and K and Al as the sulfate, were unaffected.

Discussion

The capacity of *Urosalpinx cinerea* to penetrate a wide range of types of minerals potentially extends the variety of shelled prey which the snail can

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Denticles between cusps show no dissolution from exposure to secretion of accessory boring organ in borehole. Scale bar equals 15 μm.

Figure 11. Teeth of *Urosalpinx cinerea* exposed experimentally to secretion of accessory boring organ for 0.5 hr. Marginal teeth in foreground and rachidian teeth in background. Scale bar equals 10 μm.

Figure 12. Rachidian teeth of *Urosalpinx cinerea* exposed experimentally to secretion of accessory boring organ for 2.5 hr. Scale bar equals 10 μm.

Figure 13. Shallow borehole in strontianite ($SrCO_3$). Rasp marks are evident on upper right half of borehole. Scale bar equals 0.2 mm.

Figure 14. Enlargement of edge of borehole in Figure 13. Scale bar equals 0.05 mm.

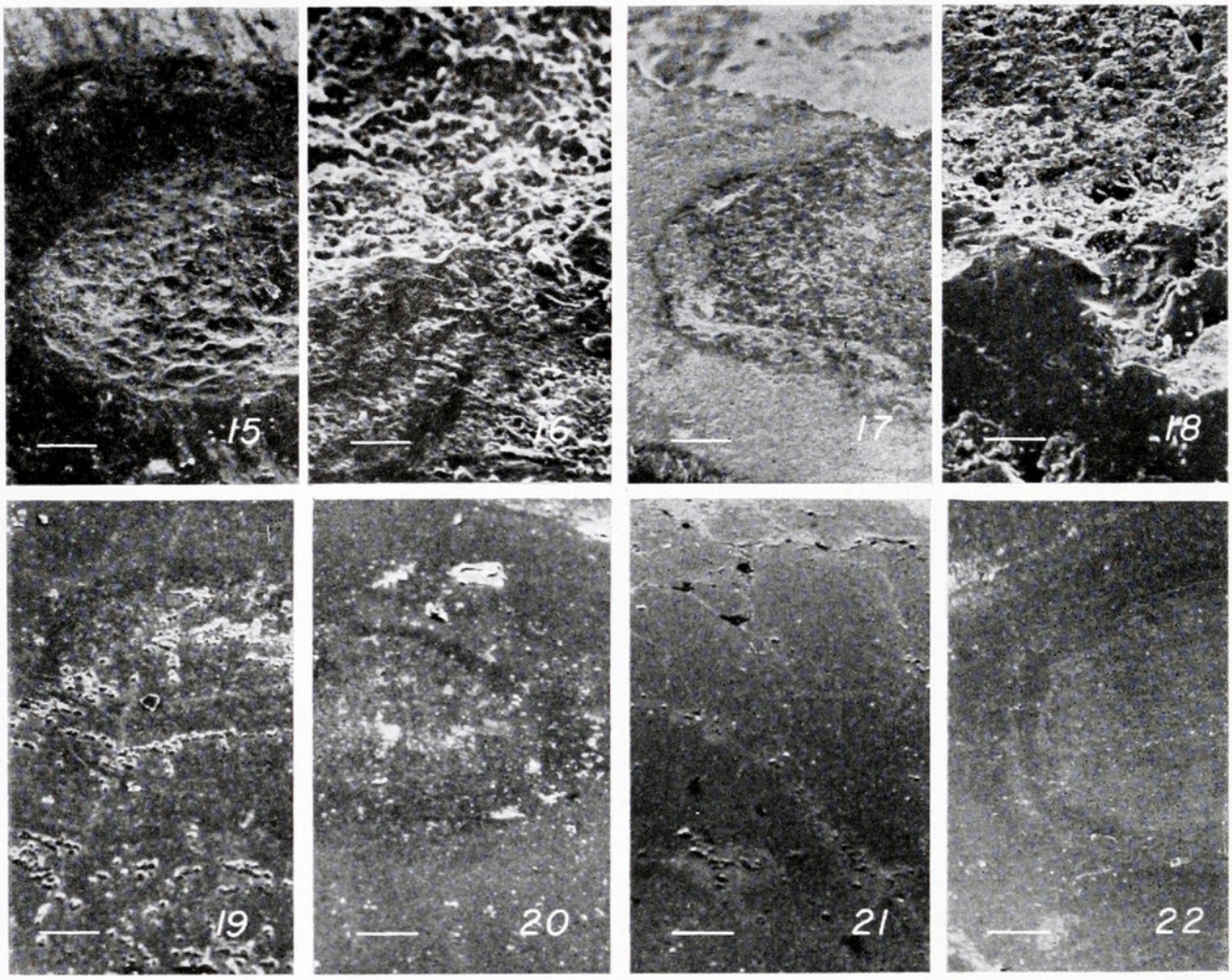

FIGURE 15. Left half of slight depression dissolved by secretion of accessory boring organ in witherite ($BaCO_3$). Rasp marks pass from etched depression onto polished surface of wafer. Scale bar equals 0.15 mm.

FIGURE 16. Enlargement of edge of depression in Figure 15. Scale bar equals 15 μm.

FIGURE 17. Left half of shallow etching made by secretion of accessory boring organ in magnesite ($MgCO_3$). No rasp marks are evident. Silver paint at upper right of micrograph. Scale bar equals 0.3 mm.

FIGURE 18. Enlargement of edge of etching in Figure 17. Scale bar equals 25 μm.

FIGURE 19. Polished surface of siderite ($FeCO_3$) to which snail applied accessory boring organ. Scale bar equals 0.2 mm.

FIGURE 20. Polished surface of smithsonite ($ZnCO_3$) to which snail applied accessory boring organ. Scale bar equals 0.25 mm.

FIGURE 21. Polished surface of alunite $KAl_3(OH)_6(SO_4)_2$ to which snail applied accessory boring organ. Scales bar equals 0.15 mm.

FIGURE 22. Polished surface of fluorite (CaF) to which snail applied accessory boring organ. Scale bar equals 0.2 mm.

penetrate. This accounts, at least in part, for the broad spectrum of species upon which it can prey: its own kind, slipper limpets, cockles, edible and ribbed mussels, soft and hard clams, scallops, oysters, barnacles, and encrusting bryozoans (Carriker, 1955; Hancock, 1959; Wood, 1968). *U. cinerea* may also feed upon small moribund crabs and the carrion of fish, and, in fact, on many other invertebrates whose flesh may be available. There are no reports on whether the snail bores through the exoskeleton of crustaceans. Boring gastropods probably have

the capability to do so, as some species of Naticidae can penetrate the cases of skate eggs (Jensen, 1951), but the motility of crustaceans undoubtedly prevents this. *U. cinerea,* guided by ingestive experience and not by genetic limitation (Wood, 1968) prefers live prey (Federighi, 1931) and subsists generally on oysters, edible mussels, or barnacles as they are available (Carriker, 1955).

Calcitic and aragonitic bivalve shell wafers were penetrated at about the same rate (Table I). *Urosalpinx cinerea* also bores normal holes in the aragonitic shell of the gastropod *Murex fulvescens* (Carriker and Van Zandt, 1972a), and on valve models has excavated shallow boreholes in wafers of abiogenic calcite (Carriker, unpublished data). Because of the reported lack of attractiveness of *Anomia simplex* to *U. cinerea* (Carriker, 1955; Galtsoff, Prytherch and Engle, 1937; Pratt, 1974; Carriker and Van Zandt, unpublished), penetration of the shell wafers of *A. simplex* as readily as those of *Spisula solidissima* was unexpected. Galtsoff, *et al.,* (1937) observed that, of all the food organisms offered to *U. cinerea* in the laboratory, *A. simplex* remained untouched. They concluded that the shell of *A. simplex* affords a barrier to *U. cinerea.* Carriker (1955) in a screened enclosure in the field, found that one *A. simplex* had been partially bored and two others had been completely penetrated, but all three bivalves were still living. Microscopic examination of the completely bored bivalves showed that snails had rasped away some of the flesh but that bivalves had regenerated the mantle and secreted a thin layer of new shell over the perforations. Pratt (1974) confined *U. cinerea* with nine species of potential prey in the laboratory and all but the *A. simplex* were bored. Carriker and Van Zandt (unpublished) observed that ready-to-set larvae of *A. simplex* entered a running seawater laboratory tank in which *U. cinerea* were maintained with oysters and edible mussels, settled on the bottom of the tank and grew to a diameter of about 3.5 cm. None of the dozen *A. simplex* was bored by the 50 adult snails present, whereas oysters and mussels were consumed regularly. The present investigation demonstrated that failure of *U. cinerea* to bore valves of live *A. simplex* was not due to their inability to penetrate shell, but either to the lack of an attractive feeding kairomone, or to the presence of a feeding suppressant in the effluent of the living bivalves. Carriker's (1955) observation that living *A. simplex* were bored but not consumed, and the report by Galtsoff, *et al.,* (1937) that starved *U. cinerea* did not bore the valves of *A. simplex* but did consume the flesh of the shucked individuals, support the tentative conclusion that *U. cinerea* are suppressed by a chemical released by living *A. simplex,* and to a much reduced extent, or none at all, by fluids from shucked *A. simplex.*

Solubility of minor and trace shell minerals in the secretion of the accessory boring organ could facilitate penetration of prey shell by boring gastropods. Travis (1968a, b) found that crystalline "impurities" are present as celestite ($SrSO_4$), strontianite ($SrCO_3$), barite ($BaSO_4$), and witherite ($BaCO_3$) within the mineral cores of single prisms of the shell of *Mytilus edulis.* Two of these minerals, strontianite and witherite, were shown to be soluble in the secretion of the accessory boring organ in the present study; celestite and barite, although not tested, are probably also soluble. Insoluble, or only slightly soluble, minerals present in shell even in small amounts, could slow slightly the rate of penetration of shell,

place a heavier burden than normal on the rasping phase of the shell-boring process (Carriker and Van Zandt, 1972a), and accelerate abrasion of radular cusps (Carriker, 1969; Carriker, Schaadt, and Peters, 1974). In this connection, epidemiological studies have shown that there may be an association between some trace elements, other than fluoride, and human dental caries (Legeros, Miravite, Quirolgico, and Curzon, 1977); that is, some elements, such as strontium, magnesium, and boron, are suspected of being cariostatic, while others, such as manganese, iron, lead, and copper, are suspected of being cariogenic. In the same sense the presence of some trace elements in shell of prey of boring gastropods may retard dissolution and others may accelerate it. This matter has not yet been investigated.

The decreasing rate of penetration of mineral wafers by *Urosalpinx cinerea* was shell, strontianite, bone and teeth, anhydrite, witherite, and magnesite; yet the wide range of solubility products of the minerals, tested in decreasing order, was anhydrite, magnesite, shell, witherite, strontianite, siderite, smithsonite, fluorite, bone and teeth, alunite and quartz (Table I). Thus, rate of penetration was not necessarily greater in the more soluble than in the less soluble minerals. A good example of this was magnesite, which though relatively more soluble than shell, was scarcely penetrated. Another was calcitic and aragonitic shells, which though characterized by different solubilities, were penetrated at about the same rate. The low pH (3.8–4.0) of the secretion of the accessory boring organ (Carriker and Williams, 1978) relative to the composition of the various minerals may offer an explanation. However, pH alone may not be the sole answer, as the secretion of the accessory boring organ appears to be a complex fluid (Carriker, *et al.*, 1978). There is likewise no apparent association between hardness of the mineral wafers and rate of penetration; strontianite, anhydrite, and witherite, for example, although softer than shell, were penetrated considerably less than shell. It is likely that hardness affects only the mechanical aspects of shell penetration by the radula (Carriker and Van Zandt, 1972a).

All abiogenic minerals, which lack the organic framework of molluscan shell, were penetrated slowly, if at all. This observation suggests that the organic matrix, among other possible factors, facilitates penetration of shell by boring gastropods. This suggestion is supported by the fact that in holes bored by *Urosalpinx cinerea,* especially in prismatic and myostracal regions, solubilization of organic matrix noticeably precedes dissolution of the mineral crystals (Carriker, 1978). Differential dissolution of shell is significant because initial solubilization of organic matrix facilitates removal of shell units from the surface of the borehole by the radula (Carriker, 1977), and bares a greater surface area of the calcareous components to the etching action of the secretion than would be the case on a smooth mineral surface. This point is underscored by strontianite, which was penetrated at about one-half the rate of shell. Strontianite, though softer but less soluble than shell, was also the most rapidly penetrated of all the abiogenic minerals tested. This could be explained by the fact that this mineral is mineralogically close to aragonite and could thus be more readily attacked than other abiogenic minerals. Fluorite, also softer and less soluble than shell, is not dissolved at all by the secretion of the accessory boring organ. Possibly this

mineral acts as a depressant. The question might well be posed whether fluorite would be more rapidly attacked by the snail if the mineral were deposited biologically in an organic matrix.

Carriker (1978) hypothesized that differences in distribution and concentration of trace and minor minerals in the cores of shell units, and differential solubility of these minerals in the secretion of the accessory boring organ, could account in part for the various dissolutional patterns observed ultrastructurally in the mineral components of prisms and lamellae exposed in incomplete boreholes excavated by *Urosalpinx cinerea* in the valves of *Mytilus edulis*. The range of variation of solubility of different abiogenic mineral wafers, composed of elements commonly found as trace and minor elements in bivalve shell, in the secretion of normally functioning accessory boring organs, supports this hypothesis.

Snails left insoluble and moderately soluble minerals more frequently than soluble ones. This suggests that they are able to detect, probably by the odontophore, or possibly also with the heavily innervated accessory boring organ (Nylen, Provenza and Carriker, 1969; Carriker and Van Zandt, unpublished), the rate of excavation of the substratum. Thus, it appears that when, after a period of time, slight or no dissolution of the substratum occurs, a snail abandons it. The possibility also exists that some of the substrata could be chemically irritating or depressing, especially the relatively soluble sulfates.

Penetrability of mineral structures seems to bear no relation to hardness (Table I). Molluscan shell, for example, was excavated more deeply than strontianite, anhydrite, and witherite, all of which are softer than shell; and siderite, smithsonite, alunite, and fluorite, softer than shell, or at least about the same hardness as shell, were not penetrated at all.

The relative resistance of radular teeth to dissolution by the secretion of the accessory boring organ is not unexpected. After all, the radula is exposed to the secretion for relatively long periods of time during penetration. Furthermore, the success of boring gastropods over geologic time has unquestionably depended on the effectiveness of radular teeth in shell excavation. Although the radula functions in a secondary role in rasping and shaping the borehole (Carriker and Van Zandt, 1972b), the role is an obligatory one. Radular teeth are composed primarily of calcium, lesser amounts of strontium, and minor quantities of magnesium, boron, silicon, zinc, iron, and a series of trace elements (Carriker and Van Zandt, 1972a). Wafers of minerals containing iron, zinc, and silicon were unaffected by the secretion of the accessory boring organ. The possible insolublility of these minerals in radular teeth as well, and insolubility of the outer coating of the teeth, may contribute to the resistence of teeth to dissolution during the rasping process. An investigation such as carried out by Runham, Thornton, Shaw and Wayte (1969) on the mineralization and hardness of the radular teeth of the limpet could provide some very interesting information on this problem.

There is no association between degree of solubility of minerals in the accessory boring organ secretion and atomic number of the major cations in the minerals. Generally, with an increase in molecular weight of the major constituent, degree of dissolution decreased in the series shell, bone, teeth, strontianite, and witherite

(anhydrite is a partial exception). However, molecular weights of several of the less soluble minerals (for example, magnesite, flourite, quartz) were considerably lower than those of the most soluble minerals.

The fact that beef bone was penetrated more rapidly than human tooth could have resulted from the presence of Haversian canals in the bone, allowing the secretion to penetrate more deeply than on a flat surface. The more rapid penetration of dentine than of enamel could also have been aided by tubules in the dentine (Fig. 7). The solubility product of bone and teeth is roughly comparable (Table I).

Differential dissolution of the core of enamel prisms by the secretion, leaving a substantial portion intact around the outside, suggests that the peripheral part of each prism is less soluble than the center. This is in contrast to dissolution of the shell of *Mytilus edulis,* in which the peripheral area of prisms precedes that of the axial component (Carriker, 1978). Examination of Figure 7 suggests, however, that, as in the case of dissolution of the prisms of *M. edulis,* the thin exterior organic envelope surrounding each enamel prism may also have been dissolved. The present study thus supports the initial results obtained by Carriker, *et al.* (1963), which suggested that excised accessory boring organs etch polished human enamel and dentine.

The capacity of *Urosalpinx cinerea* to penetrate a wider variety of minerals than we anticipated (Carriker and Smith, 1969), extends access to alternate potential foods in times of lack of the common diet, and enhances the probability of survival of the species. The ubiquity and success of the species undoubtedly reflects this capability.

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Summary

1. Results of an experimental study of the capacity of *Urosalpinx cinerea follyensis* Baker to penetrate 15 kinds of molluscan and abiogenic minerals are reported. Minerals, cut into small wafers, and radular teeth were exposed to penetration by normally boring snails in valve models. Depth of incomplete boreholes was measured with a compound microscope. Extent of dissolution was examined with a scanning electron microscope. All biogenically formed calcareous minerals, except radulae of *U. cinerea,* and some abiogenic minerals, were penetrated. Rate of penetration of wafers decreased in the following order: calcite

and aragonite (shell of *Crassostrea virginica, Spisula solidissima, Anomia simplex*), strontianite, bone and tooth hydroxyapatite, anhydrite, witherite, and magnesite. Abiogenic minerals siderite, smithsonite, alunite, fluorite, and quartz were not penetrated. Of the 15 tests performed on biogenically formed calcareous minerals, only two snails (or 13%) left the sample on the model before the experiment was terminated; of the 25 tests on abiogenically formed minerals, 20 snails (80%) crawled off the sample before the end of the tests. Experiments demonstrated that Ca, Sr, Ba, and Mg, as carbonates, and Ca both as the phosphate and sulfate, were attacked by the secretion. Fe and Zn, as the carbonates, Ca as the fluoride, Si as the oxide, and K and Al as the sulfate were unaffected.

2. Degree of penetration of beef bone was intermediate between that of shell and human teeth. Dentine was penetrated more deeply than enamel. The core of enamel prisms was dissolved more deeply than the outer region by the secretion. Radular teeth of *U. cinerea* were unaffected by the secretion during exposures ranging from 0.5 to 2.5 hr.

3. The capacity of *U. cinerea* to penetrate a wide range of types of minerals explains, in part, the large number of different species upon which it can prey.

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