SHELL PENETRATION AND FEEDING BY NATICACEAN AND MURICACEAN PREDATORY GASTROPODS: A SYNTHESIS

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ABSTRACT

Predatory gastropod shell borers occur among the Capulidae, Naticacae, Tonnacea, Muricacea, and Vayssiereidae. With the exception of boring nudibranchs, all known gastropod borers are shelled. This synthesis is concerned primarily with naticacean and muricacean borers that excavate smooth, round, beveled holes. They occur in every coastal region of the world that has been examined, and identify prey chemoreceptively. The shell penetrating mechanism includes at least an accessory boring organ (ABO) and radula. The ABO is located in three separate anatomical regions in different groups of borers: in muricaceans, in the sole of the foot anterior to the ventral pedal gland or atop the ventral pedal gland; in naticaceans, under the tip of the proboscis. Studies of the ABO of several species of naticacean and muricacean snails reveal a common ultrastructural form. An acid (possibly HCl) and unidentified chelating agents and enzymes in a hypertonic mucoid secretion released by the ABO are hypothesized to dissolve shell during hole boring. All 33 species of naticacean and muricacean snails examined possess an ABO and are shell borers; the ABO does not appear to have evolved in other shell penetrating molluscs. The role of tubular salivary glands (missing in some muricids and naticids), hypobranchial glands, and anterior pedal mucous glands in shell penetration is uncertain. Borers release paralytic substances from the hypobranchial gland, and possibly also from other glands associated with the proboscis. Gastropods known to bore holes in prey shell date from the Jurassic and perhaps the late Triassic, some two hundred million years ago. Progress is being made in the control of commercially important species of muricaceans, but not of naticaceans.

INTRODUCTION

A notable characteristic of many molluscs is their capacity to secrete a protective calcareous exoskeleton. Another is ironically the ability of some of these same molluscs to bore or burrow into the shells of other invertebrates. A voluminous literature has described the structure and development of molluscan shell (Grégoire, 1972; Wilbur, 1972; Watabe & Wilbur, 1976), but much less is known about processes of shell breakdown by invertebrates and lower plants (Carriker, Smith & Wilce, 1969). Molluscan calcibiocavites (Carriker & Smith, 1969) have been reported in three classes: the Bivalvia (burrowers), Gastropoda (borers), and Cephalopoda (borers). Among the Gastropoda, shell penetrating snails occur in the mesogastropod family Capulidae, mesogastropod superfamilies Naticacea and Tonnacea, neogastropod superfamily Muricacea, and the nudibranch family Vayssiereidae (Carriker, Smith & Wilce, 1969). With the exception of boring nudibranchs, all known shell penetrating gastropods possess a shell.

This review is concerned primarily with the biology of shell penetration and feeding by predatory gastropods in the superfamilies Naticacea and Muricacea.

DISTRIBUTION AND TYPES OF BORING MECHANISMS

Every coastal region of the world that has been examined supports populations of boring gastropods (see representative examples in Table 1). Most species are subtropical or tropical, the number increasing toward the equator (Taylor et al., 1980). It is likely that further zoogeographical investigations will locate them off the shores of most land masses (Sohl, 1969). As suggested by the presence of bore holes in prey shells, boring snails range in depth from intertidal zones to at least 2,700 m (Carriker, 1961), and their numbers decrease into deeper water (Taylor et al., 1980). Clarke (1962) lists several species of Naticidae and Muricidae that occur in abyssal regions of the oceans, but it is not known whether they are borers, or whether

TABLE 1. Species, source of specimens, and comparative anatomy of accessory boring organ (ABO), ventral pedal gland (VPG), and tubular salivary glands of muricacean and naticacean boring gastropods. S, ABO in anterior midventral sole of foot; aVPG, anterior to ventral pedal gland; p, ABO on anterior ventral tip of proboscis; relative size of tubular salivary glands: 0, absent; 1–5, small to large. Nomenclature of North American species based on Abbott (1974).

| Species | Source | Accessory boring organ, location | | Ventral pedal gland | Size tubular salivary gland |
		Male	Female		
Muricacea:					
Bedeva hanleyi	Port Jackson, Australia	S	aVPG	Reduced	1
Eupleura caudata	North Carolina to Massachusetts, U.S.A.	S	aVPG	Large	3
E. caudata etterae	Virginia, U.S.A.	S	aVPG	Large	4
E. sulcidentata	Florida, U.S.A.	S	aVPG	Large	4
Murex brevifrons	Puerto Rico	S	aVPG	Reduced	3
M. cellulosus	Florida, U.S.A.	S	aVPG	Absent	3
M. florifer	Florida, U.S.A.	S	aVPG	Large	2
M. fulvescens	North Carolina, U.S.A.	S	aVPG	Reduced	1
M. pomum	Florida, U.S.A.	S	aVPG	Absent	0
Muricopsis ostrearum	Florida, U.S.A.	S	aVPG	Absent	4
Nucella emarginata	Washington, U.S.A.	S	aVPG	Large	5
N. lamellosa	Washington, U.S.A.	S	aVPG	Large	5
N. lapillus	England; Massachusetts, U.S.A.	S	aVPG	Large	4
Ocenebra erinacea	England	S	aVPG	Large	5
O. inornata (= japonica)	Japan; Washington, U.S.A.	S	aVPG	Large	4
Pterorytis foliata	Washington, U.S.A.	S	aVPG	Large	3
Purpura clavigera	Japan	S	atop VPG	Large	4
Rapana thomasiana	Japan	S	atop VPG	Large	5
Thais haemastoma	Bimini, Bahamas	S	atop VPG	Large	5
T. haemastoma floridana	North Carolina, U.S.A.	S	atop VPG	Large	5
T. haemastoma canaliculata	West coast Florida, U.S.A.	S	atop VPG	Large	5
T. deltoidea	Bimini, Bahamas	S	aVPG	Absent	5
Urosalpinx cinerea	England; Florida to Massachusetts, U.S.A.	S	aVPG	Large	4
U. cinerea follyensis	Virginia, U.S.A.	S	aVPG	Large	4
U. perrugata	Florida, U.S.A.	S	aVPG	Large	3
U. tampaensis	Florida, U.S.A.	S	aVPG	Large	3
Naticacea:					
Lunatia heros	Massachusetts, U.S.A.	p	p	Absent	0
L. lewisi	Washington, U.S.A.	p	p	Absent	0
L. triseriata	Massachusetts, U.S.A.	p	p	Absent	0
Natica severa	Korea	p	p	Absent	0
Neverita didyma	Korea	p	p	Absent	0
Polinices duplicatus	Florida, North Carolina, Massachusetts, U.S.A.	p	p	Absent	0
Sinum perspectivum	Florida, North Carolina, U.S.A.	p	p	Absent	0

members of other families are also shell penetrants. A study of gastropod boreholes from the deep sea could clarify some of these questions.

Naticacean and muricacean boreholes typically possess smooth walls, beveled outer edges, decreasing diameters with depth, and are generally circular and perpendicular to the shell surface. The typical naticid borehole is a truncated spherical paraboloid; muricid holes, on the other hand, although also variously countersunk, are considerably more varied in vertical section than naticid holes (Carriker & Yochelson, 1968). Nudibranchs (*Okadaia elegans*; Young, 1969) also excavate smooth, round, beveled holes, while capulids (*Capulus danieli*; Orr, 1962), and cephalopods (*Octopus vulgaris*; Arnold & Arnold,

1969; Nixon, 1979) excavate asymmetric, sometimes jagged boreholes. Identification of shell-penetrating molluscs on the basis of their boreholes is thus difficult, except possibly for naticids.

Although the anatomy of the shell-penetrating mechanism differs among different species, all 33 naticacean and muricacean species and subspecies that I have examined possess an accessory boring organ (ABO) and excavate boreholes in the shell of their prey (Table 1) (Carriker, 1961). In all muricacean males the ABO is located in the mid-anterior ventral part of the foot (Fig. 1). In most muricacean females the organ occurs in the mid-anterior ventral part of the foot but anterior to the ventral pedal gland (the egg capsule gland of some authors) (Fig. 2) when the gland is present. In a small number of muricean females the ABO lies atop, and is continuous with, the ventral pedal gland, so that during its eversion the ABO passes through the cavity of the gland (Fig. 3). In all naticaceans examined, the ABO is located on the anterior ventral lip of the proboscis (Fig. 4).

In seven of the muricacean species examined, the ventral pedal gland was absent, or present only as a shallow depression, at the time of dissection, but the ABO was fully formed (Table 1). In these species the ventral pedal gland develops and is functional at the time of oviposition.

Fretter & Graham (1962) reviewed hole-boring by the muricids *Nucella lapillus*, *Ocenebra erinacea*, and *Urosalpinx cinerea*, and by the naticids *Natica nitida* and *N. catena*. Radwin & Wells (1968) observed boring in the laboratory by *Murex pomum*, *M. fulvescens*, *M. florifer*, *M. cellulosus*, *Muricopsis ostrearum*, *Urosalpinx perrugata*, and *U. tampaensis*, and Hemingway (1973, 1975a, b) discussed boring by the muricid *Acanthina spirata*. Observations on boring by these species corroborate those for similar species listed in Table 1.

Tubular salivary glands (accessory salivary glands of some authors) occur in most Muricacea (Fretter & Graham, 1962). All the muricaceans listed in Table 1 possess obvious tubular salivary glands except *Murex pomum* in which none was found. The size of the glands relative to the height of each snail varies markedly, being rather small in *Bedeva hanleyi*, *Murex florifer arenarius*, and *M. fulvescens*, and largest in the genera *Rapana* and *Thais*. No tubular salivary glands were
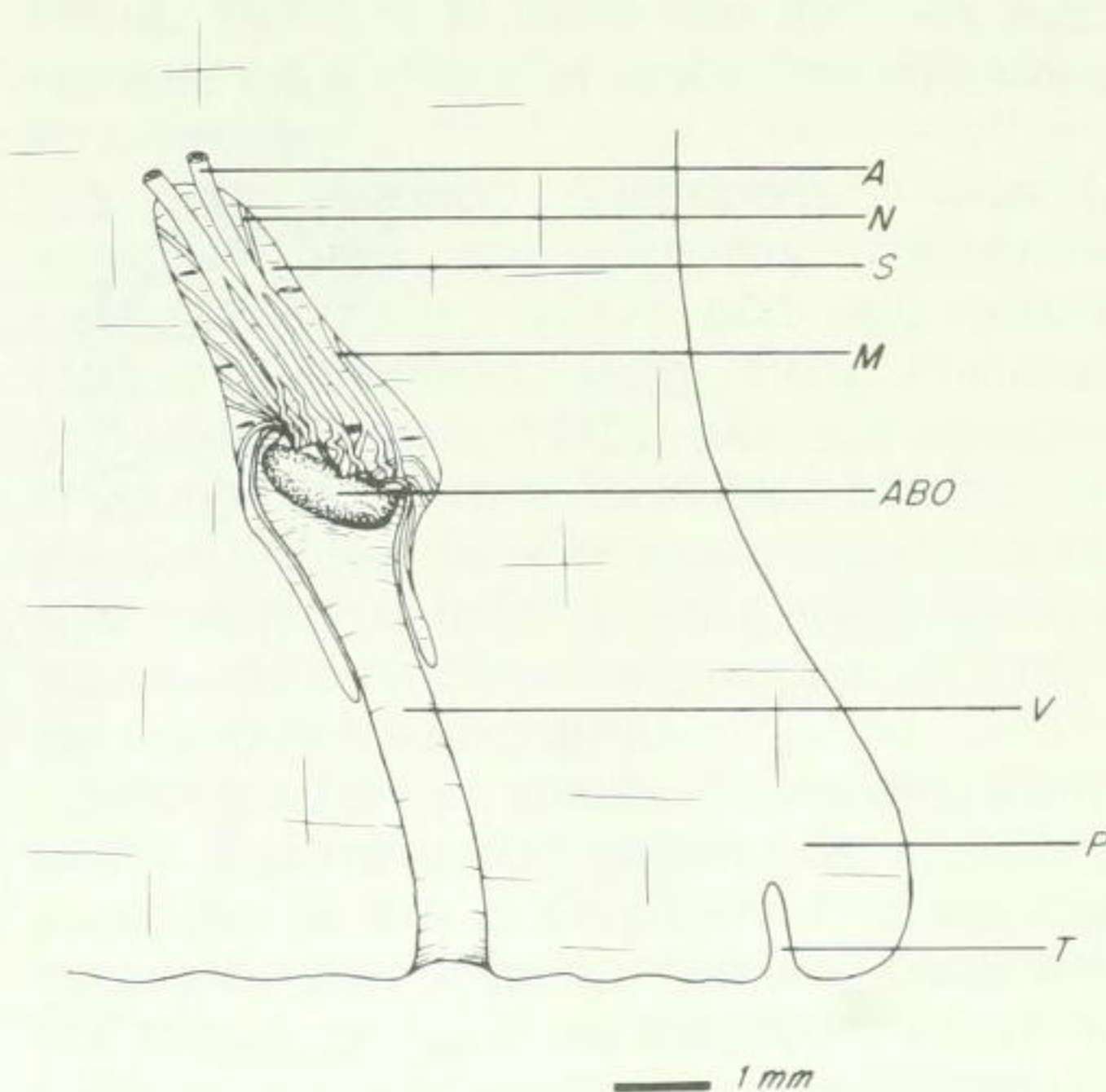

FIG. 1. Drawing of sagittal section of anterior part of foot of a male muricacean, *Rapana thomasiana*, through the accessory boring organ, *ABO*. *S*, ABO sinus containing arteries (*A*), nerves (*N*), and muscles (*M*) passing to back of ABO. *V*, ABO vestibule through which ABO is extended to borehole. *P*, propodium, *T*, transverse furrow.
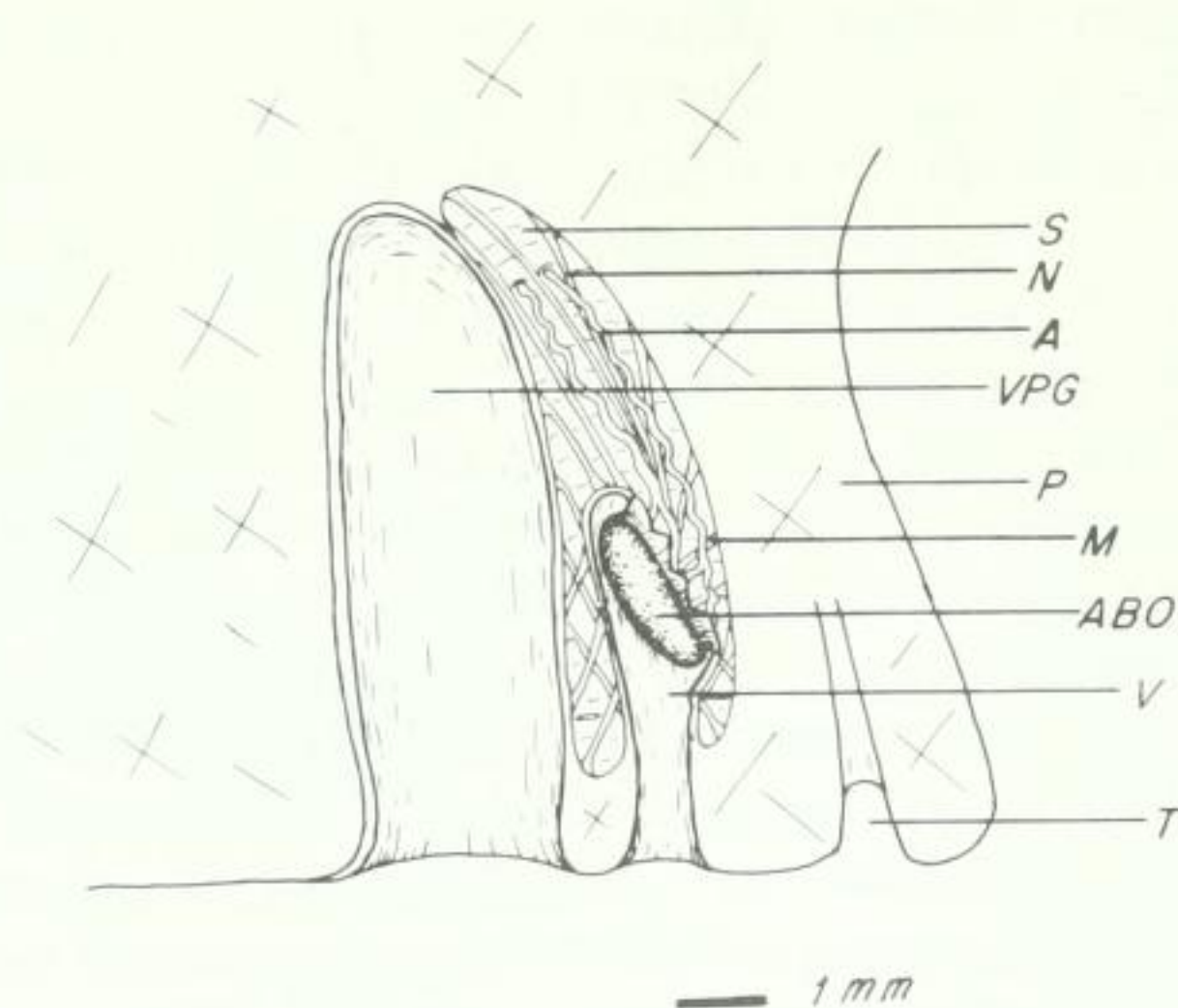

FIG. 2. Drawing of sagittal section of anterior part of foot of a female muricacean, *Urosalpinx cinerea follyensis*, through the accessory boring organ, *ABO*, and ventral pedal gland, *VPG*. *S*, ABO sinus. *V*, ABO vestibule. *P*, propodium, *T*, transverse furrow. *N*, nerve. *A*, artery, *M*, muscle.

found in species of Naticacea. Hemingway (1973, 1975a, b) reported that the tubular salivary glands of *Acanthina spirata* are similar to those of *Urosalpinx cinerea*. The variable size of tubular salivary glands in most muricaceans, and their absence in naticaceans and one species of Muricidae, cast
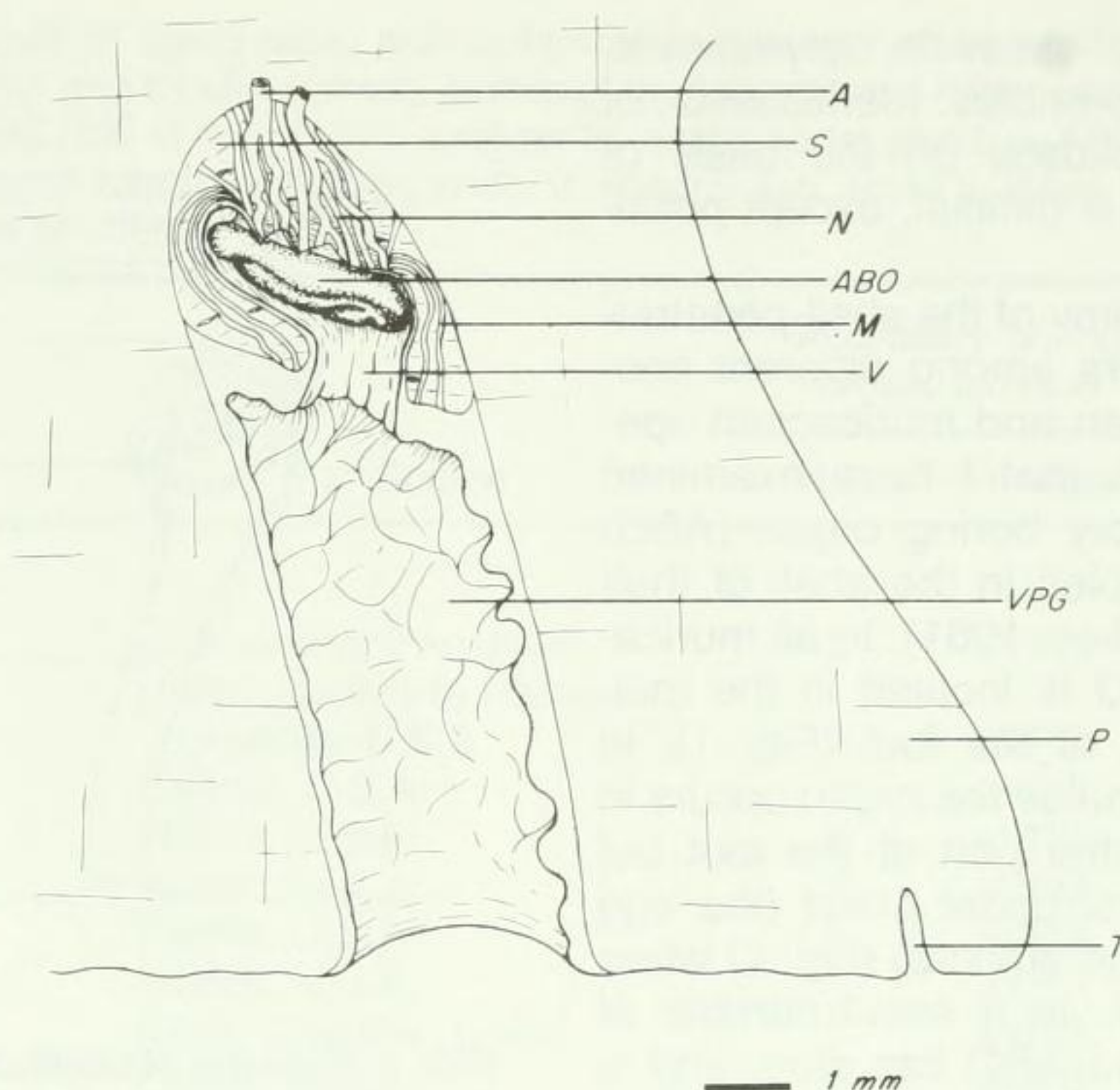
FIG. 3. Drawing of sagittal section of anterior part of foot of a female muricacean, *Rapana thomasiana*, through the accessory boring organ, *ABO*, and ventral pedal gland, *VPG*. The ABO is located atop the ventral pedal gland and in eversion passes through the lumen of the gland. *S*, ABO sinus, *N*, nerve. *A*, artery. *M*, muscle, *V*, ABO vestibule. *P*, propodium. *T*, transverse furrow.
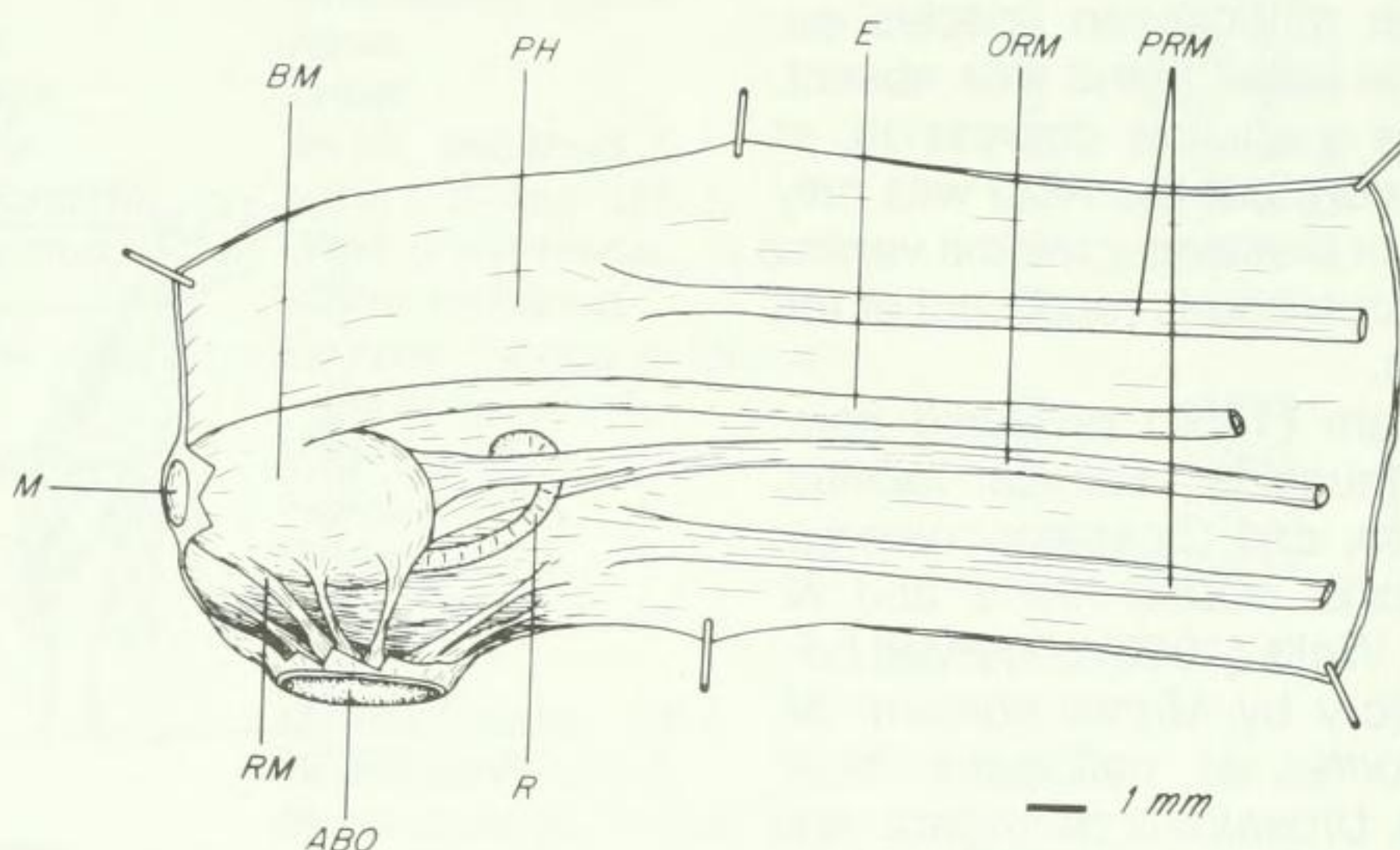

FIG. 4. Drawing of left side of proboscis of a naticacean. *Polinices duplicatus*, opened laterally to illustrate relationship of accessory boring organ, *ABO*, to buccal mass, *BM*, and to proboscidial hemocoel, *PH. RM*, retractor muscle. *M*, mouth. *R*, radular sac. *E*, esophagus. *ORM*, odontophoral retractor muscle. *PRM*, proboscidial retractor muscle.

doubt on the direct functional role of these glands in the shell boring process.

The curious position of the ABO on top of the ventral pedal gland in species of *Purpura, Rapana,* and *Thais* suggests a close affinity of these taxa. Likewise, the absence of this anatomical arrangement in *Nucella lapillus* supports the contention that the species *N. lapillus* does not belong in the genus *Thais* (Abbott, 1974).

RESPONSE TO PREY

Muricaceans feed on a wide variety of bivalves, barnacles, gastropods, small crabs, encrusting bryozoans, and carrion of fish (though they generally select live over dead prey), and may on occasion become cannibalistic (Carriker, 1955; Hanks, 1957; Chew & Eisler, 1958; Fretter & Graham, 1962; Largen, 1967; Radwin & Wells, 1968;

Morgan, 1972; Menge, 1974; Pratt, 1974a; Bayne & Scullard, 1978; Barnett, 1979). Naticaceans, on the other hand, are more restricted in their diet and feed primarily on live bivalves (Hanks, 1952, 1953, 1960; Fretter & Graham, 1962; Franz, 1977; Edwards & Huebner, 1977; Wiltse, 1980). Prey utilization curves of a number of species of small boring gastropods are skewed toward large prey size, and those of large predators are skewed toward small prey size (Sassaman, 1974; but see also Taylor et al., 1980). Boring gastropods feed on the flesh of prey through boreholes excavated by them in the shell of prey, through unbored slits between valves when these are present (as in some bivalves and barnacles), or on gaping prey recently killed by other predators. A curious exception to this is the "commensal" muricid *Genkaimurex varicosa* that bores a hole in the shells of scallops and is thought to "suck juices" from them (Matsukuma, 1977).

Response of boring gastropods to prey has been studied primarily in muricids. Under experimental conditions in the laboratory and in the field, these snails can identify preferred live prey some distance away (Carriker, 1955; Wood, 1968; Carriker & Van Zandt, 1972a; Morgan, 1972; Pratt, 1974a). However, all individuals in a population may not respond at the same time. In the laboratory, for example, only 50 to 80% of a population of *Urosalpinx cinerea* will respond to recently introduced live prey (Carriker, 1957). Nor is preference for prey genetically fixed; existence of prey and predator in similar intertidal zones and relative abundance of prey account for prey selection (Wood, 1968; Pratt, 1974a). *U. cinerea* can be ingestively conditioned in the laboratory, tending to prefer effluents from a given prey species after it has ingested living tissues of that species (Wood, 1968). Starved *U. cinerea* are repelled by effluent from starved oyster drills and attracted to the effluent of satiated oyster drills. These responses probably increase foraging efficiency by directing snails away from unproductive areas and toward their prey (Pratt, 1974a, 1976).

Not all potential prey are attacked by muricids. When, for example, *Urosalpinx cinerea* is confined with a variety of species of bivalves, all are bored except *Anomia simplex* (Pratt, 1974a; Carriker, Van Zandt & Grant, 1978). Since these snails can bore through empty valves of *A. simplex* in laboratory experiments (Carriker, Van Zandt &

Grant, 1978), it is likely that they are suppressed by a chemical associated with living *A. simplex*.

Young boring gastropods, recently emerged from egg capsules (*Urosalpinx cinerea*; Carriker, 1957) and egg collars (*Natica gualtieriana*; Berg, 1976; *Polinices duplicatus*; Wiltse, 1980), also are attracted to young prey, bore holes in them and feed on the soft tissues. To what extent and how soon after initiation of feeding young snails become ingestively conditioned is uncertain. The matter requires investigation.

Most prey are incapable of defending themselves against boring gastropods. A striking exception to this is *Crepidula fornicata* that frequently jabs at an approaching borer with the radula, or dislodges the predator from its valve by pressing the predator against an obstacle (Pratt, 1974b). Apparently passive "retribution" on the part of prey occurs occasionally. There is a report of an oyster that apparently closed its valves on the proboscis of an *Eupleura caudata* that was inserted through a hole bored in the margin of the shell, and held the snail until it died. Shell material was then deposited around the predator's shell, permanently affixing it to the oyster's right valve (Burrell, 1975)! Another example is that of *Urosalpinx cinerea* which in the laboratory can be immobilized by byssi of *Mytilus edulis* at temperatures at which bivalves are active but snails have gone into hibernation. This probably does not occur to any extent in the field, as snails move toward the bottom away from mussels as the temperature of the seawater drops approximately below 15°C (personal observations).

Boring gastropods possess (a) chemoreceptive mechanism(s) for detecting prey and approaching them from a distance. Snails respond to chemical substances characteristic of the effluents of prey species they have eaten (Wood, 1968; Carriker & Van Zandt, 1972b; Morgan, 1972; Pratt, 1974a). Although attractiveness of prey is often marked and responded to by a large proportion of a predator population, the chemical stimulus that guides predators to prey has been identified only as one or more of the metabolic products of prey (Carriker & Van Zandt, 1972b).

Experimentation on carnivorous mesogastropods and neogastropods (Kohn, 1961; Crisp, 1973; Newell & Brown, 1977) suggests that the osphradium plays a primary role in distance chemoreception. The function of the

mantle edge, tentacles, and propodium in sensing chemical cues is probably also important and needs further investigation.

Primary recognition of the immediate presence of prey by muricaceans appears to depend on identification of a chemical cue in the exhalant water of prey. Snails creep over the bottom toward their prey, locating them most rapidly when the prey are on the upstream side of tidal currents (Carriker, 1955). Whether snails respond to the same chemicals from prey at a distance and close to prey, is unclear. When approaching actively pumping prey, Urosalpinx cinerea, for example, often raises the anterior part of the foot, stands on the posterior tip of the foot, propodium and tentacles fully extended, and swings the propodium back and forth in a pattern suggestive of searching. Whether distance or close-range attractant(s), or both, in exhalant seawater is reinforced by a further stimulus associated with the prey is uncertain. Reinforcement might come from valvular movements of the prey, chemical attractant adsorbed to the shell, topography of the prey shell, chemicals in the organic matrix of shell, or even unknown cues from the animal within the shell (Carriker & Van Zandt, 1972b). Pratt (1974a) reported that epibiota on the shell of prey did not play an important role in oyster drills' attacks on Crepidula fornicata. In laboratory experiments, Carriker & Van Zandt (1972b) noted that something on the surface of oyster valves, possibly microorganisms, enriched by effluent from pumping oysters, attracted snails to the oysters, but did not stimulate them to bore the shell. The problem needs clarification.

Very little information is available on the behavior of prey recognition by naticaceans (Kohn, 1961; Fretter & Graham, 1962; Carriker & Yochelson, 1968). The burrowing habit of these snails makes them difficult subjects for this kind of research.

The ability of boring gastropods to detect prey is influenced by environmental factors. For example, response to prey by Urosalpinx cinerea declines as temperature of the seawater drops in the fall from 15 to 7°C, depending on the latitude and other environmental factors (Carriker, 1954; Carriker & Van Zandt, 1972a). A salinity of 12.5 °/oo is near the lower limit for location of prey by both U. cinerea and Eupleura caudata (Manzi, 1970). Feeding activities of Thais haemastoma stop at tempeatures of 10°C and below (Gunther, 1979). Such naticaceans as Polinices dupli-catus in temperate zones cease to identify prey at about 5°C and a salinity of 6 °/oo, whereas Lunatia heros, a species found generally in deeper water than P. duplicatus, continues its activities at temperatures as low as 2°C but to a salinity of only 10 °/oo (Hanks, 1952, 1953; Edwards & Huebner, 1977; Carriker, unpublished observations).

PENETRATION OF PREY

Selection of Borehole Site

Muricaceans

Little is known about borehole site selection by boring gastropods. Urosalpinx cinerea, after crawling onto an epifaunal bivalve, for example, undertakes a series of exploratory activities leading to selection of the penetration site. Exploration can range from a few minutes to half an hour. During the search the proboscis is extended intermittently to the shell surface, and, its tip undulating with minute wave-like movements, is passed slowly over the substratum, stopping now and then to rasp at small, live, sessile organisms (Carriker & Van Zandt, 1972a).

What determines the specific site for boring is unclear. Nor is it known whether individuals express a consistent preference for a particular part of the shell surface of successive prey, or whether an environmental cue plays a part in selection. Urosalpinx cinerea (Carriker & Van Zandt, 1972b) and Nucella lapillus (Morgan, 1972) appear to excavate boreholes randomly on prey valves, though U. cinerea locates its holes primarily away from the edge of the valves, reflecting avoidance of valve edges probably because of valvular motion. Breaks in valves away from valve edges, or along valve edges when valves are held shut by rubber bands, are quickly located and used as penetration sites in lieu of boring through solid shell. It appears that metabolites from active living, non-wounded prey not only trigger the initial attack on prey, but also determine penetration sites when seepage occurs through tiny holes between valve edges. Thus, tightly closed living oysters are not penetrated, nor are empty valves bored even in the presence of attractant from pumping oysters nearby (Carriker & Van Zandt, 1972a). In contrast to U. cinerea, Acanthina spirata bores holes most commonly at the margin of the prey valves (Hemingway, 1973),

and *Dicathais aegrota,* away from the margin of the univalve of the limpet (Black, 1978).

Naticaceans

A series of behavioral patterns involving prey capture and prey manipulation, present upon metamorphosis of the snails, determines the position of the borehole in this group (Berg, 1976). These gastropods, characterized by an exceptionally large, flat foot that facilitates their movements within the sediment and with which they tightly grip their prey, crawl through clean to slightly muddy sand both above and below the sediment-water interface. When infaunal prey are located, probably chemoreceptively, snails burrow rapidly to their level, and generally bore into the shell below the benthic surface.

In the process of prey capture, these naticids secrete copious quantities of mucus. In the laboratory *Lunatia nitida* covers its prey with mucus to help hold the prey closed and prevent it from escaping (Richter, 1962). In some cases, after coating its prey, *L. nitida* tows the bivalve behind it by a rope of mucus, the prey held closed by the mucus sheet until the snail is ready to bore into it. *L. heros,* likewise in the laboratory, sometimes places a bivalve in a pocket formed by underfolding of the posterior part of the foot, and carries the prey there until ready to consume it (personal observation).

Positions for boring seem to be related to the manner in which prey are grasped, and holes are thus usually limited to a small area of prey valves, commonly on one valve more frequently than the other. Position of boreholes appears to vary with the species of predator and prey (Boettger, 1930; Ziegelmeier, 1954; Fretter & Graham, 1962; Carriker & Yochelson, 1968; Taylor et al., 1980). Berg (1976) found that after metamorphosis young *Natica gualtieriana* bored their first prey by a single hole in a stereotyped position. As these snails matured and gained experience at boring, there was no change in the angular distribution of the boreholes in each whorl, but whorl preference changed.

Shell Penetration

Muricaceans

All muricids that have been studied closely employ a similar chemical-mechanical mechanism for penetration of prey valves though the manner of penetration may vary (Carriker & Van Zandt, 1972b; Morgan, 1972; Gunter, 1979). For example, once *Urosalpinx cinerea* has commenced excavation of a borehole, it continues until penetration has been completed. Only dislodgment of the snail by exterior forces or precipitous environmental changes are apt to terminate boring; and even then, many snails, if remaining close by the borehole, will return to the hole. *U. cinerea* can penetrate the shell of its prey in the absence of the live animal, provided boring has been initiated on live whole prey. Thus, boreholes once started can be completed without stimulation of any kind from live prey (Carriker & Van Zandt, 1972a; Carriker, Van Zandt & Grant, 1978). On the other hand a young *Thais haemastoma* bores holes on a valve until it reaches a height of 5 cm; at larger sizes it penetrates at valve edges apparently relaxing prey by a paralytic substance, and in one-third of the oysters consumed, boring no hole (McGraw & Gunter, 1972; Krutak, 1977; Gunter, 1979).

Initial identification of a boring site by *Urosalpinx cinerea* is made by the propodium and by the proboscis tip. In early stages of exploration, the snail frequently extends and passes its proboscis over the spot, and occasionally the mouth opens and the buccal cavity enlarges in what appears to be a "tasting" reaction. Anterior propodial ridges are used only partially, and sometimes not at all, in supporting the proboscis during search for a penetrating site (Carriker, 1943; Carriker & Van Zandt, 1972a).

After the boring site is selected, the snail positions itself on the shell surface with the pore of the retracted ABO located over the prospective boring site. Thereafter the posterior part of the foot remains firmly attached to the shell in the same position. The anterior part of the propodium is then retracted deeply, and the lateral propodial ridges are overfolded, forming a fleshy tube over the borehole site down which the proboscis is extended. Rasping is limited principally to the bottom of the incomplete borehole. The odontophore can rotate on its long axis independent of rotation of the proboscis by at least 180°; thus, by swinging to the left and then to the right in two half turns, the odontophore covers the circumference of the borehole. Rasping over the surface of the incomplete borehole by the radula is uniformly firm, and the pattern of rasping appears random (Carriker & Van Zandt, 1972a).

After the brief rasping period, the proboscis is infolded into the cephalic hemocoel. Simultaneously the mid-anterior part of the propodium, already at the posterior edge of the borehole where it surrounded the proboscis, is extended into the borehole. The propodium then presses the transverse furrow (Fretter & Graham, 1962) closely against the shell, slides it forward across the surface of the incomplete borehole and back onto the surface of the shell to assume a normally extended position and a tight contact between the epithelium of the snail's foot and the prey's shell. In this maneuver the propodium voids seawater from the incomplete borehole prior to entrance of the ABO. The propodium is followed immediately by the ABO which slides gently into position, and presses closely against the shell surface. Once in position, the organ continues to pulsate gently. During its stay in the borehole, the organ secretes solubilizing fluid that removes a thin layer of shell at the bottom and obliterates most of the marks of the previous rasping period. After the period of shell dissolution, the ABO is withdrawn from the borehole. Simultaneously, the propodial tube is formed, the proboscis is extended into the borehole to resume rasping, and a new penetration cycle commences. As soon as the borehole is completed and the break into the extrapallial space of the bivalve is large enough to admit the proboscis, the snail presses the proboscis against the flesh and starts feeding (Carriker & Van Zandt, 1972a). The boring behavior of *Eupleura caudata*, as observed in oyster models (Carriker & Van Zandt, 1972a), is identical to that of *Urosalpinx cinerea*. The boring behavior of *Nucella lapillus* is said to be similar to that of *U. cinerea* (Morgan, 1972). Using a motion picture camera taking single exposures every 1.5 minutes, Morgan showed that in the period of 73.3 hours required to bore, *N. lapillus*, like *U. cinerea*, moved its position on the prey only slightly.

Naticaceans

Because these snails wrap prey in the foot during boring and bore primarily when buried in the sand (Fretter & Graham, 1962), it is difficult to study their shell-penetration process. Ziegelmeier's (1954) account of *Lunatia nitida* is the most detailed. The bivalve is held by the propodium, which overfolds much as does that of muricids, to form a fleshy tube down which the long proboscis is extended

from the cephalic hemocoel to the surface of the prey shell. During penetration the proboscis is rotated a 90° quadrant at a time so that rasping is done systematically sector by sector from the center of the incomplete borehole to the periphery. The center of the hole, where the least radular rasping occurs, thus results in a boss characteristic of incomplete naticacean boreholes. After the rasping of a quadrant, the proboscis is raised from the incomplete borehole and the ABO, located under the ventral lip, is placed in the hole. (Ziegelmeier was not able to see the change in position.) As in muricids, the ABO solubilizes the surface layer of shell in the borehole, and the weakened shell is rasped free by the radula during the next round of mechanical boring. In *Urosalpinx cinerea* the process of hole boring is easily observed in an oyster model (Carriker & Van Zandt, 1972a); no apparatus has yet been devised to permit viewing of the process in naticaceans. Nonetheless, from the information available, and from general observations on feeding by *Lunatia heros, L. triseriata,* and *Polinices duplicatus* in the laboratory (Carriker, personal observations), it appears that the mechanism of shell penetration in muricaceans and naticaceans is similar (see also Fretter & Graham, 1962).

Proboscis and Radula

Proboscis

A long proboscis evolved in prosobranchs that feed on food not immediately accessible to them (Fretter & Graham, 1962; Graham, 1973). In boring prosobranchs, the length of the proboscis is about as long as the height of the shell. This is a distinct advantage because predators can not only bore a hole in the shell of prey, but can also extend the proboscis deep into prey to feed safely within a wide radius of soft tissues until the valves of prey gape. When valves open, nearby predators, especially small crabs, join in feeding. In view of the predatory success of both groups of snails, the muricacean pleurembolic and the naticacean acrembolic types of proboscides appear to be equally effective (Carriker, 1943). After the muricacean proboscis is amputated accidently by being pinched between valves of prey, by small crabs feeding alongside the proboscis in gaping prey, or by experimental procedures in the laboratory, it regenerates rapidly to its former size and

function (*Urosalpinx cinerea, Eupleura caudata*: Carriker, Person, Libbin & Van Zandt, 1972; *Thais haemastoma*: Gunter, 1968). Loss of this important organ is thus not fatal, as the snail possesses enough metabolic reserves to survive until a new proboscis has formed. In the absence of the proboscis the snail is unable to bore, even though the ABO is present. The regenerative capacity of the proboscis of naticaceans has not been tested, but it is likely that it, too, can reform in the event of accidental proboscisectomy.

Radula

Although radulae of muricaceans (rachiglossan, formula 1 + R + 1) and naticaceans (taenioglossan, formula 2 + 1 + R +1 + 2) differ in organization, they are both long, slender structures limited to a few teeth in each transverse row. The narrow radula is admirably adapted to hole boring, the central rachidian tooth in each row bearing the brunt of rasping over the surface of boreholes and the marginal teeth serving synchronously with rachidian teeth in tearing flesh from prey (Carriker, Schaadt & Peters, 1974; Krutak, 1977).

The radula of boring gastropods has been a favorite subject for light (25 species of muricids: Wu, 1965b) and scanning electron microscopy (*Urosalpinx cinerea*: Carriker & Van Zandt, 1972a, Carriker, Schaadt & Peters, 1974; *Nucella lapillus*: Runham, 1969; several species of *Acanthina* and *Eupleura triquetra*: Hemingway, 1975a, b; *Thais haemastoma*: Krutak, 1977). Scanning microscopy shows admirably the successive locking of each tooth over its neighbor, spreading the impact against the shell surface over several rachidian teeth as the radula slides over the tip of the odontophore against the borehole. Independent forward movement of the radula over odontophoral cartilages as the radula scrapes forward against the borehole adds efficiency to the shell-rasping process and spreads the wear of cusp tips over several rows of rachidian teeth (Carriker & Van Zandt, 1972a; Carriker, Schaadt & Peters, 1974). Hole boring wears the teeth down to their base. Gradual replacement of the radula by formation of new teeth in the radular sac insures that a supply of sharp teeth is available for each successive round of shell-boring (Isarankura & Runham, 1968).

Hardness of radular teeth is known only for muricids (Carriker & Van Zandt, 1972b); naticid teeth have not been tested. The mar-ginal teeth of *Urosalpinx cinerea* are about twice as hard as rachidian teeth, and the latter are about the same hardness as oyster shell. Thus, without the aid of the solubilizer secreted by the accessory boring organ, the radula would make little progress into the shell. Calcium is a major chemical element of the teeth of *U. cinerea* and strontium and silicon are present as major to trace constituents (Carriker & Van Zandt, 1972a). Abrasion of radular teeth during boring wears cusps smoothly. No sharpening occurs as it does in teeth of the grazer, *Patella vulgata,* in which the leading edge of each tooth is backed by a softer region that insures self-sharpening of this edge during wear (Runham, Thornton, Shaw & Wayte, 1969).

Unworn teeth of boring gastropods are exceedingly sharp and could readily shred the lining of the buccal cavity during boring and feeding. This is generally avoided by a protective, flexible, cuticularized buccal armature that lines the buccal cavity and prevents damage to buccal tissues. Even so, light abrasion still occurs on the more elevated parts of the buccal lining, but this lining is augmented further by secretion from the buccal epithelia (Carriker, Schaadt & Peters, 1974).

As demonstrated in *Urosalpinx cinerea,* gastropod borers swallow fragments of shell rasped from the borehole during penetration of prey (Carriker, 1977). Depending on their orientation relative to the surface of the incomplete borehole, shell units (prisms, lamellae) are broken off, coated with secretion from the ABO, and further pelleted by mucus on their passage down the alimentary canal to be voided as feces. The envelope of mucoid material undoubtedly reduces or prevents laceration of the epithelium of the alimentary canal. Naticaceans also swallow shell fragments scraped from the borehole (Ziegelmeier, 1954; Fretter & Graham, 1962). These also pass down the esophagus and appear outside the anus as white fecal pellets. Since most shell excavated from boreholes appears to be discharged through the anus, it is questionable that minerals in shell fragments are used metabolically by snails to any extent. The matter should be investigated by tagging shell of prey with radioactive calcium.

Accessory Boring Organ

The ABO is an essential component of the shell penetrating mechanism of boring gastro-
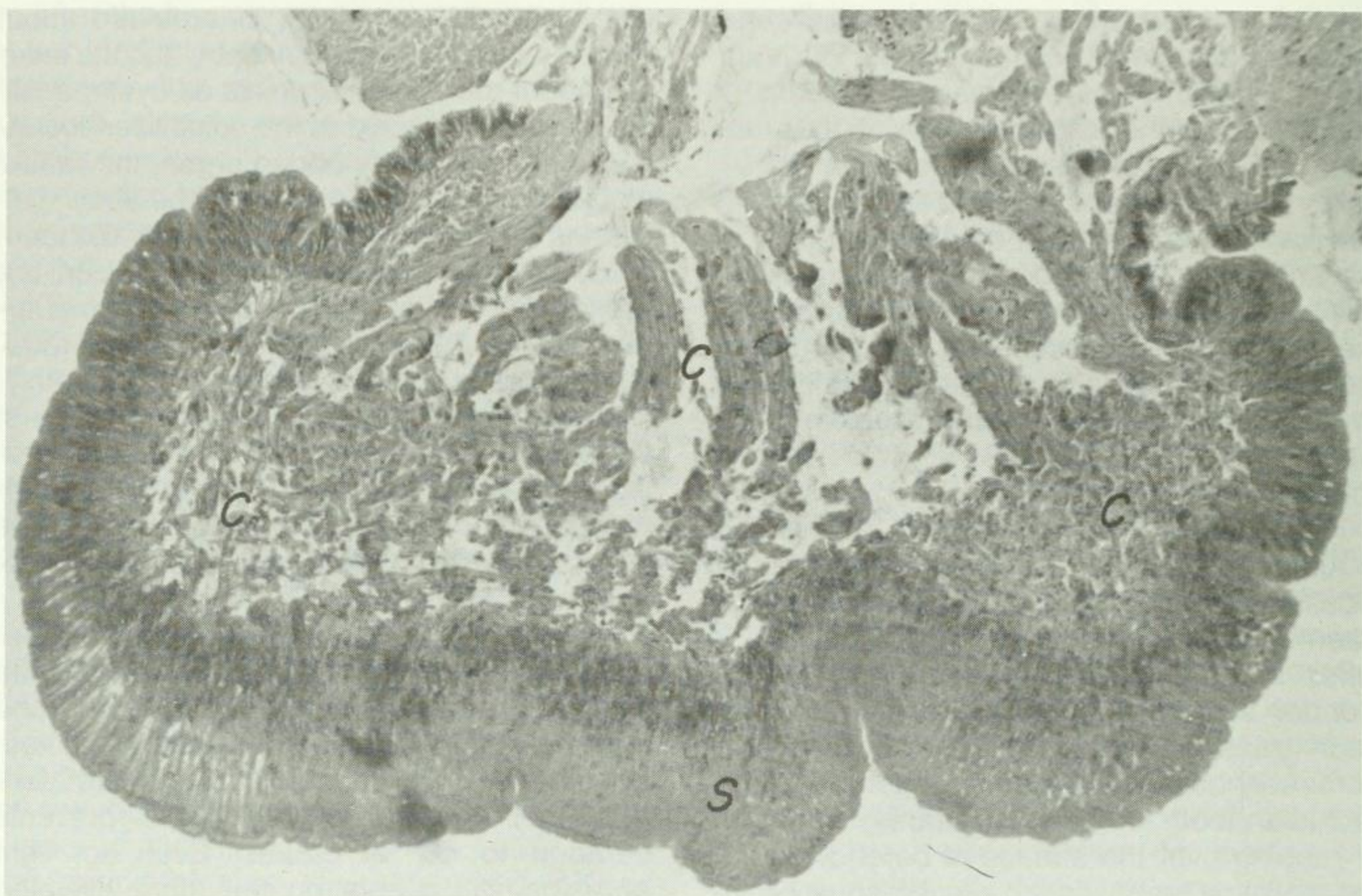
FIG. 5. Light micrograph of histological sagittal section of accessory boring organ of *Urosalpinx cinerea follyensis* extended from foot. *S*, secretory epithelium. *C*, connective tissue in center of organ supporting retractor muscles, capillaries, and nerve fibers. Organ 1 mm in diameter.

pods (Fig. 5). When this organ is removed from, for example, *Urosalpinx cinerea*, by experimental excision, the snail recovers, but is unable to bore, even though the proboscis is present and functional. The organ regenerates relatively rapidly, and the muricid soon resumes boring (Carriker & Van Zandt, 1972a). The effect of removal of the ABO on the shell penetrating capacity of a naticacean has not been determined, but is likely similar to that observed in muricids.

All species of boring muricacean and naticacean gastropods that have been studied to date possess an ABO, but these constitute only a small sample of the large number of species of boring gastropods that exist in the world oceans. Many more species need to be examined before we can generalize on the universality of a shell solubilizing gland in boring gastropods.

Detailed structural studies carried out so far on the ABO of two species of muricids (*Urosalpinx cinerea*: Nylen, Provenza & Carriker, 1969; and *Nucella lapillus*: Chétail, Binot & Bensalem, 1968; Derer, 1975; Webb & Saleuddin, 1977) and one species of naticid (*Polinices lewisi*: Bernard & Bagshaw, 1969)

show that the histology and fine structure of the secretory disc of the organ is similar in the three species. The organ of the naticid differs from that of the muricid organ in possessing a peripheral zone of subdermal mucocytes around the central disc. The peduncle that supports the disc is long and cylindrical in muricids, to accommodate the position of the gland deep within the foot, and short in naticids, in which the organ is attached to the lower lip of the proboscis (Webb & Saleuddin, 1977).

The secretory disc of the muricid and naticid ABO is composed of a single layer of tall columnar epithelial cells arranged in groups. A brush border of unusually long, densely packed microvilli covers the surface of the disc. The center of the organ consists of connective tissue that supports muscles, capillaries, and nerve fiber bundles passing to the base of the secretory epithelium. Dense populations of mitochondria are present near the surface of the epithelium, more abundant in secreting (ABO's of actively boring snails) than in resting (non-boring snails) secreting cells. Dense membrane-bound secretory granules, multivesicular bodies, and single

vesicles are also conspicuous in the cells (Nylen, Provenza & Carriker, 1968, 1969; Chétail, Binot & Bensalem, 1968; Bernard & Bagshaw, 1969; Derer, 1975; Webb & Saleuddin, 1977).

Whereas the mechanical phase of shell penetration by the radula is well understood (Carriker, Schaadt & Peters, 1974), knowledge of the chemical phase is still in a hypothetical state. Earliest physiological research on the ABO of muricids disclosed, a) a pH ranging from 3.8 to 4.1 in the released secretion of a normally functioning gland (Carriker, Van Zandt & Charlton, 1967), b) active aerobic metabolism in the secretory cells (Person, Smarsh, Lipson & Carriker, 1967), and, c) substantial amounts of carbonic anhydrase in the organ (Carriker, Person, Smarsh, Lipson & Chauncey, 1968; Chétail, Binot & Bensalem, 1968). Subsequent research on the chemical phase of penetration was summarized by Carriker & Williams (1978). They hypothesized that a combination of enzymes, an inorganic acid (possibly HCl), and possibly chelating agents is employed in a hypertonic secretion to facilitate dissolution of shell and intracellular transport of calcium during the chemical phase of shell penetration. Secretion granules and vesicles in the secretory epithelium of the ABO and in the released secretion, organic matter in the secretion, and inactivation by heat and papain of the etching capacity of excised ABO's suggest the presence of enzymes. Hydrogen, chloride, and sodium ion concentrations demonstrate the hypertonic and acidic nature of the released secretion. An unidentified chelating agent and a mucoprotein appear to be present in the secretory epithelium; the latter perhaps is the chelator. In a study of lysosomal enzymes, acid phosphatase, and carbonic anhydrase in the ABO of Nucella lapillus, Webb & Saleuddin (1977) concluded that there is minimal involvement of extracellular enzymes in the boring process. They postulated, instead, that hydrogen ions, derived from hydration of metabolic carbon dioxide, are released by the secretory epithelium for dissolution of calcium carbonate of the shell. This supports the earlier findings by Carriker, Van Zandt & Carlton (1967) on the pH of the secretion in Urosalpinx cinerea. However, the findings of Webb & Saleuddin (1977) on extracellular enzymes are at variance with those of Carriker and Chauncey (1973) who reported that released secretion collected from live U. cinerea was positive for carbonic anhydrase.

The similarity determined by scanning electron microscopy of ultrastructural patterns of dissolution etched in the shell of Mytilus edulis by the secretion of the ABO and those produced artificially by HCl and ethylene-diaminotetra-acetic acid, suggest that these chemicals, or similar ones are constituents of the secretion of the ABO. Lactic and succinic acids and a chitinase-like enzyme were also suggested as possible components. However, alteration of shell fracture surfaces by experimental application of these and other chemical agents was not sufficiently comparable to that etched by the secretion of the ABO to support this suggestion.

A marked variation in the rate of dissolution of different ultra-structural parts of the mineral components of shell occurs in shell surfaces when they are etched by the secretion of the ABO (Carriker, 1978). As differential dissolution could result, in part, from variation in the composition of trace and minor mineral constituents of shell, Carriker, Van Zandt & Grant (1978) tested the capacity of Urosalpinx cinerea to penetrate several kinds of non-molluscan minerals commonly present in trace or minor amounts in bivalve shell. The rate of penetration of these minerals decreased in the following order: bivalve (mainly $CaCO_3$) shell, strontianite ($SrCO_3$), anhydrite ($CaSO_4$), witherite ($BaCO_3$), and magnesite ($MgCO_3$), lending support to the original hypothesis of differential dissolution (Carriker, 1978). A variety of biogenically formed calcareous minerals was also tested, and all of these, except the radula of U. cinerea, were penetrated. The relative resistance of radular teeth to dissolution by the secretion is not unexpected, since the radula is exposed to the secretion for a relatively long time during penetration. Clearly, much more research must be carried out on the chemical phase of penetration before the mechanism can be fully understood.

The anatomical location and structure of organs involved in hole boring by other molluscan penetrants such as cymatiid mesogastropods (Day, 1969), vayssiereid nudibranchs (Young, 1969), and octopuses (Nixon, in press) are significantly different from those of the accessory boring organ in muricaceans and naticaceans, yet the shell of their prey is penetrated effectively. Study of the chemical mechanism of shell excavation by these predators should provide a deeper understanding of shell penetration by muricaceans and naticaceans than is now available.

Tubular Salivary Glands

Two kidney-shaped, muscular, tubular salivary glands (also known as accessory salivary glands) discharge through a common duct into the ventral lip of the mouth of most muricaceans (Table 1; Graham, 1941; Carriker, 1943; Fretter & Graham, 1962; Carriker, 1977). These glands are distinctive morphological features of the Muricidae (Ponder, 1973). Four separate functions have been hypothesized for the glands:

Lubrication. Discharge of the secretion of the glands into the path of the functioning odontophore suggests a source (in addition to that from the salivary glands) of lubricant for the radula during the boring process (Fretter & Graham, 1962). This suggestion is supported by the fact that the spongy layer about the mouth and opening of the tubular salivary gland duct in living *Urosalpinx cinerea* stain a deep purple-red color with methylene blue. (The only other external structures in the snail giving a similar staining reaction are the ventral and lateral surfaces of the foot that secrete copious quantities of mucus.) (Carriker, 1943). Furthermore, extracts of the glands of *Nucella lapillus* and *Ocenebra erinacea* have a pH of about 6.0, application of the glands or their extracts to the polished inner surface of mollusc shell leaves no etched mark and no proteolytic or amylolytic enzymes appear to be present (Graham, 1941). In contrast the secretion of the ABO when applied to polished shell does etch (Carriker & Van Zandt, 1964).

Hole boring. That the glands could also be involved in shell penetration may be deduced from their position in the distal end of the proboscis, but there is little else to support this conjecture. These glands are present in most muricaceans (Table 1) in which they vary in relative size, and are absent in naticaceans and apparently also in nonboring gastropods. Conceivably the unexplained role of muricacean tubular salivary glands could be equivalent to that of the mucocytes that surround the naticacean ABO (Carriker, 1977), but there is no information on this. What structure replaces the tubular salivary glands in muricaceans that lack them has not been determined.

Paralysis. The histological resemblance between tubular salivary glands and the poison gland of toxoglossans (Graham, 1941; Fretter & Graham, 1962) suggested to Graham (1941) and to Martoja (1971) that tubular salivary glands could produce some toxic substance. Graham (1941), however, found that their extract has no effect on the heart of *Cardium* sp., and noted that many prey of boring gastropods are sedentary and do not have to be paralyzed before consumption. A further point that might have a bearing on the problem is that salivary glands of stenoglossans (*Ocenebra aciculata,* for example) lack alkaline phosphatase in their cells, while both the tubular salivary glands and the gland of Leiblein are rich in this enzyme (Franc, 1952; Fretter & Graham, 1962).

Because of their intrinsic biological interest, and their possible involvement in shell penetration, tubular salivary glands of muricaceans deserve further attention.

Extracorporeal Enzymes

From experiments on attraction of hermit crabs to simulated gastropod predation sites, Rittschof (1980, in press) suggested that gastropod predators (such as the fasciolariids *Pleuroploca gigantea* and *Fasciolaria tulipa*) release a protease while feeding. Peptides released from gastropod prey while predators consume prey flesh serve as cues that enhance the attractiveness of prey several times over that of prey flesh alone. Rittschof supported his hypothesis by addition of trypsin to prey flesh which in the absence of a predator made the flesh as attractive to hermit crabs as was prey flesh being actively consumed by a gastropod predator.

This finding has significant implications for the study of shell penetration. Boring gastropods possess salivary glands, buccal glands, and in the case of most muricaceans, tubular salivary glands that empty directly into the buccal cavity. Mansour-Bek (1934) reported the presence of proteolytic enzymes including a trypsin-like protease in the saliva (presumably from the salivary glands) of *Murex anguliferus.* Enzymes discharged into the buccal cavity around odontophore and radula could easily trickle into the borehole during the rasping phase of shell penetration, and if a constituent of the secretion were a conchiolinase-type enzyme, attack the organic components of the shell (Carriker, 1969; Travis & Gonsalves, 1969). If the enzymes aid in shell penetration, they should be demonstrable during boring but prior to feeding. Preliminary attempts by Carriker (1978) to identify enzymes that hydrolyze the intercrystalline organic matrix of shell were inconclusive and

should be repeated. Until now, we have hypothesized that shell solubilizing enzymes, if present, are secreted by the ABO (Carriker & Williams, 1978). Identification of hydrolytic enzymes in the buccal region of boring gastropods, and testing of these enzymes on shell preparations should thus provide additional information on the chemical phase of shell penetration.

Anterior Pedal Mucous Gland

This gland is a collection of clusters of subepithelial secretory cells arranged in nests in the anterior part of the foot. The gland discharges into a sagittal canal that empties into the transverse furrow between the propodium and the podium (Fretter & Graham, 1962). The propodium sweeps across the bottom of the incomplete borehole during boring, and the furrow, in an anatomical position to wipe secretion over the surface of the hole, is carried along. Most of the cells of the gland stain so as to suggest that their secretion contains mucoprotein. These constituents, if present, could function as chelating agents in solubilization (Carriker & Williams, 1978). The pH of the secretion in the furrow ranges from 7.0 to 7.8 (Carriker, Williams & Van Zandt, 1978). However, shell etched by the secretion from the ABO in the absence of furrow secretion, revealed the normal pattern of dissolution found in boreholes (Carriker, 1978). The role of the secretion in shell penetration is thus uncertain; at the least the secretion could serve as a lubricant and as a sealant to hold the ABO secretion within the bore hole. Study of the gland needs to be undertaken before the chemical mechanism of shell penetration by boring gastropods can be fully understood.

PARALYSIS OF PREY

That some muricacean gastropods synthesize biotoxins to quiet or kill their prey has been suspected for some time (Gunter, 1968). For example, while most boring gastropods bore a hole large enough to admit the proboscis, adult *Thais haemastoma* bore comparatively small holes at the valve margins that do not admit the proboscis. This fact, together with behavioral observations, suggested to McGraw & Gunter (1972) and Gunter (1968, 1979) that *T. haemastoma* injects a paralytic substance into prey that causes them to gape and die.

Paralytic agents, elaborated in the hypobranchial gland (Whittaker & Michelson, 1954; Whittaker, 1960; Endean, 1972; Hemingway, 1978), have been identified as pharmacologically active esters of choline: urocanylcholine (in *Murex trunculus, M. fulvescens, Ocenebra erinacea, Nucella lapillus,* and *Urosalpinx cinerea*), and senecioylcholine (in *Thais floridana*). Acrylylcholine is present in the nonboring snail *Buccinum undatum*, but no choline esters occur in *Busycon canaliculatum* or in several species of taenioglossans (Whittaker, 1960). The salivary glands of nonboring species of buccinids and cymatiids contain tetramine in addition to choline esters. The hypobranchial gland secretes mucus containing both Tyrian purple and the choline ester that is probably carried to prey by ciliary currents on the surface of the mantle and propodium (Whittaker, 1960; Hemingway, 1978). Urocanylcholine has marked hypertensive as well as a neuromuscular blocking action. Senecioylcholine resembles urocanylcholine but is somewhat less active as a blocking agent, acrylylcholine has only an extremely brief and feeble blocking action (Whittaker, 1960). The first two biotoxins are present in shell boring gastropods and the third in a nonboring gastropod.

A paralytic substance with a high acetylcholine equivalency is also present in the combined salivary and tubular salivary gland complex (as well as in the hypobranchial gland) of the muricid, *Acanthina spirata* (Hemingway, 1973, 1978). As analyses were performed on the combined glands, it is not clear whether one or both of the glands release the biotoxin. Graham's (1941) report, that extract of tubular salivary glands has no effect when injected into the heart of a bivalve, suggests that the acetylcholine is produced by the salivary glands. The matter requires verification.

Hemingway (1978) noted that different choline esters in the hypobranchial glands of predatory gastropods may be as numerous as the species of muricaceans (see also Whittaker, 1960). The apparent specificity of choline esters from these glands led Feare (1971) to make the provocative suggestion that choline esters released by them could also be involved in species recognition or mating behavior! It is understandable that a predator, like *Buccinum undatum*, which attacks bivalve prey without boring through the shell, would be aided in attacking prey by pro-

ducing acrylylcholine, but not why shell-penetrating muricaceans, which prey on bivalves that are generally sedentary (Graham, 1941), release urocanylcholine that has a strong blocking action.

No reports are available on whether glands in the proboscis or mantle cavity of naticaceans emit paralytic chemicals. Since these gastropods bind prey in large quantities of mucus during capture and manipulation prior to boring, the mucus itself, secreted presumably by pedal surfaces, could contain paralytic substances. These interesting possibilities call for attention.

EVOLUTION

The greatest known concentration of muricacean and naticacean borers occurs in shallow water around continents in tropical latitudes (Carriker, 1961; Taylor et al., 1980). Since no boring gastropods have been discovered in freshwater (Carriker & Smith, 1969), and relatively few borers have been reported from the deep-sea (Carriker, 1961; Taylor et al., 1980), it is likely the shell boring habit in prosobranchs evolved in relatively shallow, tropical, marine waters (see also Clarke, 1962).

Gastropods presently known to bore holes in shells of prey date back to the Jurassic and perhaps as early as the Late Triassic, some 200 million years ago (Carriker & Yochelson, 1968; Sohl, 1969; Ponder, 1973; Krutak, 1977; Taylor et al., 1980). Evolution of the shell-penetrating mechanism in muricaceans and naticaceans could have taken place in three major morphological steps in this order in geologic time: a) development of the radula (Firby & Durham, 1974; Krutak, 1977; Taylor et al., 1980), b) elongation of the head to form a proboscis (Graham, 1973), and c) formation of the accessory boring organ (Carriker, 1943; Fretter, 1941, 1946). The mechanism for secretion of paralytic substances could have evolved after the appearance of the radula (Taylor et al., 1980) and could have preadapted snails to become predators of non-shelled prey.

Appearance of the ABO in two separate anatomical locations among muricaceans (in front of the ventral pedal gland, and atop the ventral pedal gland) and in an entirely different region in naticaceans—under the proboscis tip (Carriker, 1961)—is an enigma. Difference in the position of the organ in the two superfamilies might be attributed to the strikingly different epifaunal and infaunal boring behaviors, respectively, of the two groups. However, the general position of the anterior central part of the foot of the predator on its prey, the placement of the organ in the borehole, and alternation of radula and organ in the borehole during penetration are similar in the two superfamiles and within the muricaceans. A comparative embryological study of the development of the ABO in representative muricaceans and naticaceans is urgently needed to determine whether the organ develops anew in its respective anatomical spot in different groups, or is formed in one place and migrates to its definitive position in the adult. In any event, the development of such similar organs as the ABO on different parts of the body is one of the most interesting parallels in molluscan morphology (Bernard & Bagshaw, 1969).

It is curious that the ABO seems to have evolved only in muricaceans and naticaceans, and not in other predatory molluscs. Whether all species of these two distantly related superfamilies possess an accessory boring organ has not been determined. Too few species have been examined to permit a generalization. There is, for example, an omnivorous muricid, *Drupa ricina,* pedal anatomy unknown, that feeds on sponges, holothurians, and carrion, and is not thought to be a typical predator of hard-shelled molluscs (Wu, 1965a). Its tubular salivary glands are fully developed. It will be important to determine whether this snail possesses a fully developed, or a vestigial, ABO, or none at all.

Shell dissolution in muricaceans is not limited to shell boring. The mantle edge of spiny muricids, for example, dissolves spines at their base as the body whorl is deposited from one varix to the next, to eliminate blockage of the aperture (Carriker, 1972). The broad temporal, spatial, and systematic distribution of calcibiocavites, the capacity for dissolution of shell by many invertebrates in noncalcibiocavitic activities, and the prominence of osteoclastic activity in the vertebrates, suggest that calcibiocavitation may be a latent and fundamental characteristic of organisms, expressing itself especially in epithelia, that has appeared from time to time without regard to systematic or morphological position (Carriker & Smith, 1969).

Evolution of the proboscis and the ABO opened to boring gastropods a broad spectrum of prey not otherwise easily available,

and undoubtedly has helped account for the historical longevity and ubiquity of the group (Carriker & Van Zandt, 1972a). In the event of loss of either the proboscis or the ABO, through pinching or amputation during penetration of prey, relatively rapid functional regeneration of both organs occurs (Carriker & Van Zandt, 1972b; Carriker, Person, Libbin & Van Zandt, 1972)—a unique safeguard insuring full replacement of the mechanism and survival of the organism through geologic time.

CONTROL

During the last 50 years shellfish growers and shellfish biologists have devoted considerable time and effort in attempts to control muricacean predators. Examples of better known predators include *Eupleura caudata*, *Ocenebra inornata* (= *japonica*), *Thais haemastoma*, and *Urosalpinx cinerea* in the United States; *Ocenebra erinacea* and *Urosalpinx cinerea* in Great Britain; *Ocenebra inornata*, *Rapana thomasiana*, *Thais bronni*, and *T. tumulosa* in Japan; and *Bedeva hanleyi* and *Morula marginalba* in Australia. There are many other species in other regions of the world.

Efforts to control muricacean borers (also called drills) by physical methods have met only with partial, and then only temporary, success. Hand picking, forks, concrete pillars, oyster dredges, deck screens, drill dredges, drill box traps, and drill trapping of *Urosalpinx cinerea* have all been tried more or less intensively. A more mechanical, less labor intensive method employing a hydraulic suction dredge has been used with some success in the Long Island Sound area (Carriker, 1955). Loose material on the bottom is drawn onto a screened conveyer belt that allows oysters and shell to pass back overboard into the water. Fine materials, including oyster borers, collect in bins under the screen and are later discharged in shallow water to kill the borers by suffocation. The suction dredge is limited to dredging in intermediate depths of water, and on relatively firm bottoms. Invention of a more economical method of disposing of the snails than currently used would significantly reduce the cost of this method of control (Carriker, 1955; Hancock, 1959, 1969). Attempts to trap *Thais haemastoma* on oyster beds have been unsuccessful because no baits more attractive than the surrounding

oysters and mussels have been found (Gunter, 1979).

Efforts to eradicate muricacean predators and their young by desiccation, flaming, fresh and brine waters, magnesium sulfate, copper sulfate, mercuric chloride, formalin, rotenone and chlorinated benzene, and other chemicals have been ineffective on a commercial scale, or effective, but too harmful to other organisms and the environment to be employed (Carriker, 1955; Castagna, Haven & Whitcomb, 1969). Copper barriers have also been suggested by Glude (1956) and Huguenin (1977), but these, like other metals, would contaminate the environment, and their application would be labor intensive and costly. The use of freshwater curtains, created by release of fine streams of fresh water, to control muricacean borers has not been attempted, but merits consideration (D. Rittschof, personal communication).

Naticaceans (moon snails), serious predators of infaunal bivalves, decimate populations of such commercially important species as *Mya arenaria* and *Mercenaria mercenaria* in estuaries and embayments and *Spisula solidissima* on the continental shelf (Franz, 1977). Abortive attempts have been made to control them by manual collecting in the intertidal zone (for example, *Lunatia heros*, Medcof & Thurber, 1958). As with similar attempts at control of muricaceans, this method has serious limitations, primarily because these predators occur subtidally as well and soon replace those removed from the intertidal zone.

The response of boring gastropods to attractive chemical signals from prey, or from female snails during mating, or repulsion of them by unattractive biochemical cues from other organisms, provide the basis for possible ecological control. Attractive or unattractive chemical signals, if they can be identified and synthesized, could possibly be used as bait in trapping, or as dispersive or repelling agents. A great advantage of such signals is that they are biodegradable, and would not contaminate the environment. Ideally they might be species specific.

CONCLUSIONS

Interest in organisms that penetrate hard calcareous substrata dates back many centuries. Aristotle, some 2,300 years ago, is credited for recognizing that predatory marine

gastropods have the capacity to bore holes through shells of prey (Jensen, 1951). Since then advances in the knowledge of shell penetration by boring gastropods has been rapid (Carriker & Smith, 1969; present review). In spite of this progress, however, several important aspects of the biology of shell penetration require further study; these are summarized in this section.

Information on the zoogeographical distribution of boring gastropods is limited, not only in shallow coastal areas but more so in the deep-sea (Clarke, 1962), and is difficult to obtain. Bore holes in prey shell indicate the presence of borers in the geographic vicinity, but provide no clues on the specific identity of the borers. Identification of shell penetrants can be determined by holding snails in aquaria with potential prey, and observing whether hole boring takes place. This procedure generally works well with snails from shallow water, but could be difficult with gastropods from the deep-sea even in pressurized aquaria. A more practical approach would be to examine suspected shell penetrants for the presence of the ABO by anatomical and histological techniques.

All naticacean and muricacean gastropods studied so far possess an ABO and are shell borers, Whether all species of these superfamilies are borers needs to be determined by examination of a wide spectrum of species of these groups, as well as non-naticacean-muricacean predators, from widely different regions of the oceans.

The ABO is known to occur in three different anatomical positions in different species of boring gastropods. However, the number of species that has been examined is small, and it is possible that the ABO could occur in other than the described anatomical locations. The ABO appears to be proportionately larger in young individuals than in adult ones (for example, *Thais haemastoma*; Gunter, 1968, 1979). This condition is not characteristic of most gastropod boring species, and could be interpreted as suggesting that this species has evolved toward a lesser use of the ABO in adults than in the young. On the other hand, species of borers could exist in which the ABO is an incipient organ, and the snails could be evolving either toward or away from the boring habit. A species worth exploring in this regard is *Drupa ricina* (Wu, 1965a). The study of transitional stages of the ABO, as well as the embryological development of the ABO in different anatomical

positions, would be of considerable evolutionary interest.

From an ecological and behavioral point of view it is of interest to know whether the chemical attractant associated with each prey species is a single, or a combination of different molecules, and whether attractants are species specific. This fundamental information is prerequisite to the formulation of a bait for control of these predatory snails.

Although substantial progress has been made in the study of the behavior of shell penetration by boring gastropods and of the gross and fine structure of the ABO, we know rather little about the chemical aspects of shell penetration. Study of the chemistry of the ABO secretion is difficult because the ABO is a relatively small organ, and amounts of released secretion are very small. The presence of a mild acid in the secretion has been verified with pH electrodes, but the composition of the acid, suspected of being HCl, is uncertain. Preliminary observations suggest that an unidentified enzyme(s) and chelator(s) may be components of the active shell solubilizing secretion. This needs confirmation.

The ABO is probably the principal organ involved in the chemical phase of shell penetration. However, close association of duct openings of the salivary glands, buccal glands and tubular salivary glands with the buccal cavity and mouth, and of the anterior pedal mucous gland with the anterior part of the foot, suggests that these glands could play at least a part in the mechanism of shell penetration. Their potential role cannot be discounted until more is known about their functions.

Some boring gastropods appear to be able to quiet or kill their prey by applying a paralytic substance to them through the borehole. Suspected sources of paralytic agents are the hypobranchial gland, salivary glands, and tubular salivary glands. Whether salivary glands can secrete both paralytic and shell solubilizing substances is questionable, but worth exploring. The source of these biotoxins, the method of injection into prey, and the physiological effect on prey also need investigation.

Shell swallowed by boring gastropods apparently passes through the alimentary canal and is voided relatively unchanged in feces. There is the possibility, however, that some nutrients could be extracted from the organic and inorganic components of shell fragments in the stomach of the snail and absorbed. The

metabolic fate of absorbed nutrients, if any, could be tested with radioactive tracers.

Costly depredations by boring gastropods of commercial bivalve populations in all parts of the world confer a high priority on these snails as subjects for the investigations proposed in this synthesis. Especially important would be a search for components of the shell penetrating mechanism that might be blocked in order to control the predators. The results of such a study would benefit not only the shellfish industry but would also contribute new knowledge on the biology of predation by these ubiquitous, refractory—and very interesting—marine snails.

ACKNOWLEDGMENTS

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