TAXONOMY AND DISTRIBUTION OF WESTERN ATLANTIC *BITTIUM* (GASTROPODA: MESOGASTROPODA)

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By

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APPROVAL SHEET

This thesis is submitted in partial fulfillment

of the requirements for the degree of

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

The genus Bittium in the Western Atlantic was studied to determine the number and distribution of extant species. Shells of adults and juveniles collected from Brazil to Canada, including the type specimens of B. virginicum, were examined and compared on the basis of length, length-width ratio and varix presence or absence.

Although intergrades of B. alternatum and B. varium probably existed in the middle Chesapeake Bay, along the Atlantic shores of the Delmarva Peninsula and New Jersey, and in western Long Island Sound prior to 1940, B. alternatum is now found from Shark River, New Jersey, northward and B. varium from Chesapeake Bay, southward. There are presently no Bittium between Shark River, New Jersey and Cape Charles, Virginia excepting the B. varium in Chesapeake Bay. Destruction of the eelgrass habitat in the 1930's is the probable cause of the absence of Bittium in the area of former intergradation.

Larger size and lack of a varix distinguish adult B. alternatum from adults of the smaller, more slender B. varium. Juveniles are more difficult to separate since neither species possesses the varix as juveniles, but juvenile B. alternatum are usually wider than juvenile B. varium and attain greater lengths before formation of an apertural canal with maturity. B. virginicum is considered a growth form of B. varium.

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INTRODUCTION

Bittium is a genus of small prosobranch gastropods of the family Cerithiidae. It contains 29 species and is of worldwide distribution (Keen, 1963). In Virginia, representatives of the genus are found on submerged vegetation such as Zostera, Ruppia and benthic macroalgae in the shallow waters of estuaries, sheltered bays and inlets. Three species of Bittium are reported to occur in Virginia: B. alternatum (Say), which has been reported from the Gulf of St. Lawrence to Virginia by Abbott (1954); B. varium (Pfeiffer), which is known from Maryland to Florida, Texas, Mexico, the West Indies (Warmke and Abbott, 1961) and Brazil (Marcus and Marcus, 1963); and B. virginicum (Henderson and Bartsch) reported only from the type locality, Chincoteague Bay, Virginia (Abbott, 1954). For a complete classification of the genus Bittium and for type descriptions of the Western Atlantic species, please see Appendices I and II.

These snails are found on a number of marine plants in different areas. In Puerto Rico, Warmke and Almodovar (1963) observed B. varium more commonly on the red alga Laurencia than on any other alga and found greater numbers on green than on brown algae. Abbott (1958) found B. varium

on turtle grass of Grand Cayman Island. Ladd (1951) collected B. varium from Redfish Bay, Texas in "weed-covered areas." Near Ubatuba, Brazil, Marcus and Marcus (1963) observed B. varium in tufts of Sargassum stenophyllum. Henderson and Bartsch (1914) collected the type specimens of B. virginicum from Zostera in Chincoteague Bay. Nagle (1968) studied the epifauna of Zostera in Hadley Harbor, Massachusetts and discovered that B. alternatum occurs mainly on the outer leaves of the eelgrass, which are highly colonized by epiphytes. Bittium live near the periphery of the epiphytes and appear relatively immune to predation by fish.

Members of the family Cerithiidae are primarily vegetarians (Perry and Schwengel, 1955) though some authorities have concluded that Bittium species are detritus feeders (Fretter and Graham, 1962; Nagle, 1968). Nagle's observation that B. alternatum is never found on the newer, inner leaves of the Zostera supports the latter conjecture, for the outer leaves are usually covered with diatoms and detritus while the inner ones are relatively clean. The preference of Western Atlantic Bittium species for certain marine plants probably is related in part to the detritus trapping abilities of the plants. Intestinal smears of B. eschrichti Middendorf from Boiler Bay, Oregon, which I prepared in September, 1968, revealed numerous diatom frustules. Whether the living diatoms had been consumed by

active feeding or the frustules merely ingested passively with detritus, I did not determine.

Although a detailed anatomical description of B. varium was published in 1963 (Marcus and Marcus), comparable information on B. alternatum and B. virginicum is lacking. From their anatomical studies, Marcus and Marcus considered snails forming shell apertural canals and varices (Fig. 1) to be young adults. This conclusion was of considerable help in determination of adult size for the present study. B. varium and the European B. reticulatum are both known to have planktonic veligers (Marcus and Marcus, 1963; Thorson, 1946), but the length of larval life has not been reported. The breeding season of Bittium in the Western Atlantic is unknown, but in Denmark B. reticulatum larvae are found in the plankton from July to early November (Thorson, 1946). Nagle (1968) stated that B. alternatum has only one brood per year and overwinters in the adult or advanced juvenile stage.

This study was undertaken to determine the taxonomic and distributional status of Western Atlantic Bittium. The shells of the Western Atlantic species of Bittium are quite similar, especially in the juveniles (Figs. 2, 3). Difficulty experienced in distinguishing B. varium from B. alternatum (Wass, 1965) led me to suspect that the reported overlap of range in Virginia had resulted from misidentification. The B. virginicum type description closely fitted

Figure 1. Illustrations of shell features used in comparison of Western Atlantic *Bittium*.

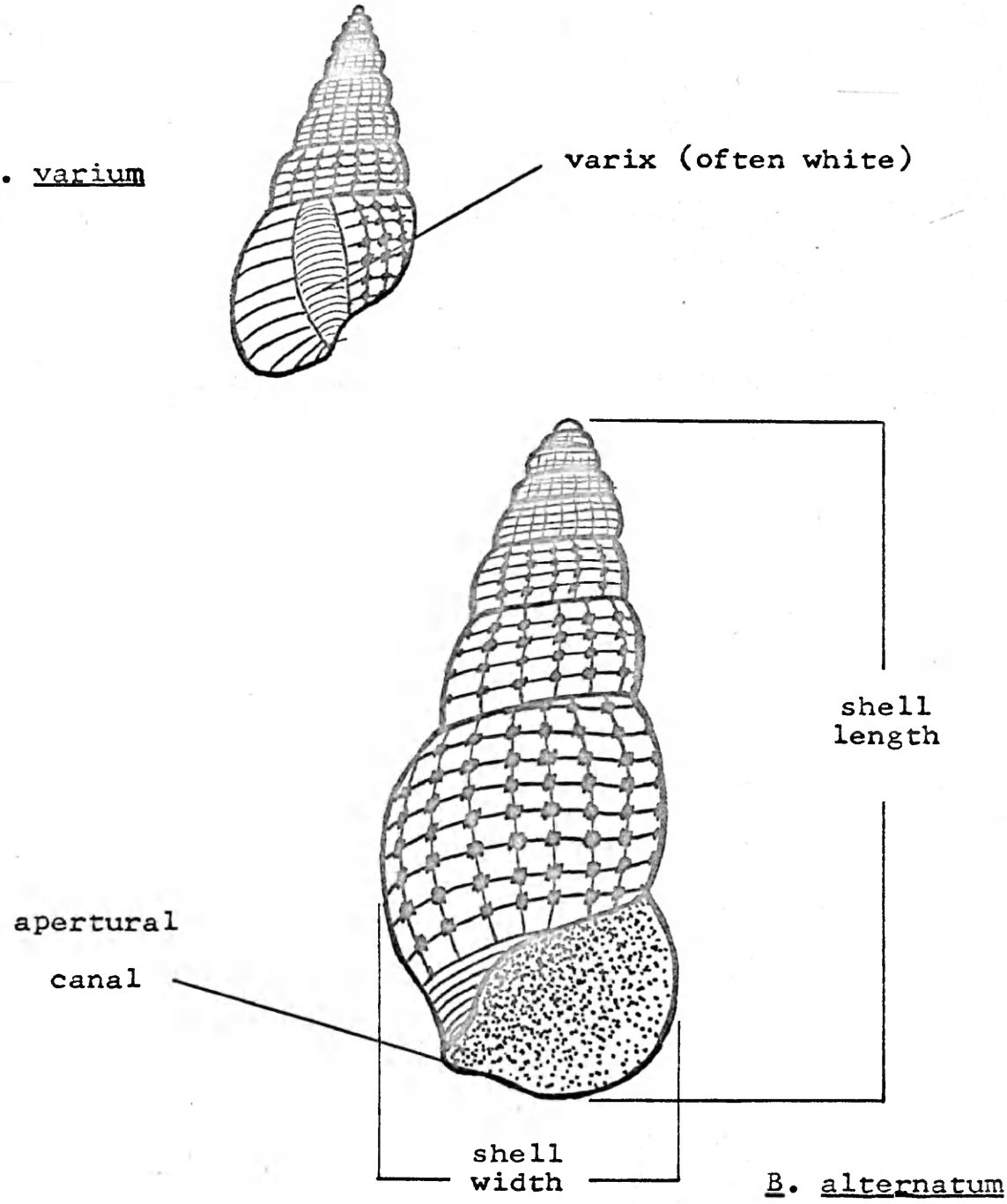
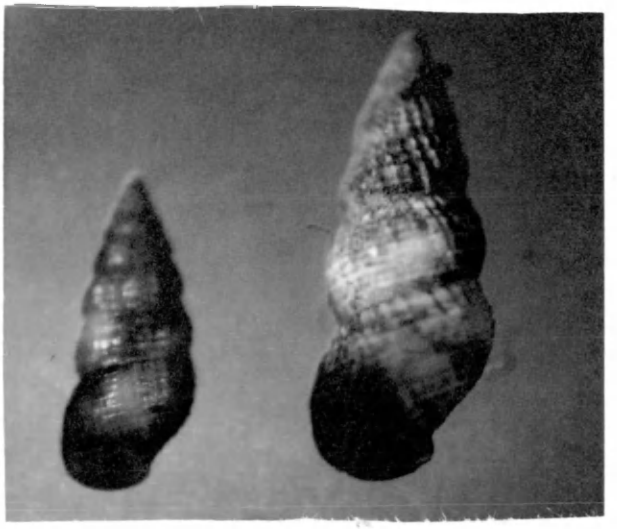
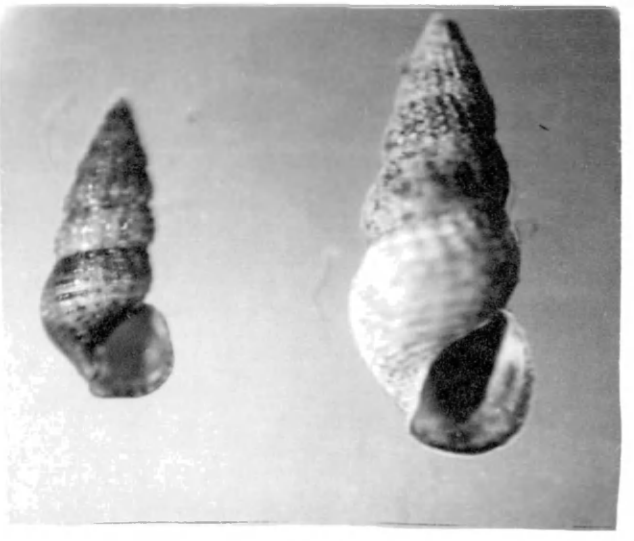


Figure 2a. Dorsal view of B. varium (left) and B. alternatum (right). Actual size of B. varium is 4.6 x 1.8 mm. Actual size of B. alternatum is 6.3 x 2.2 mm.

Figure 2b. Apertural views of B. varium (left) and B. alternatum (right). Sizes same as above.

Figure 2c. Juvenile B. varium (left) and juvenile B. alternatum (right). Actual sizes: B. varium 3.0 x 1.2 mm and B. alternatum 3.4 x 2.0 mm.





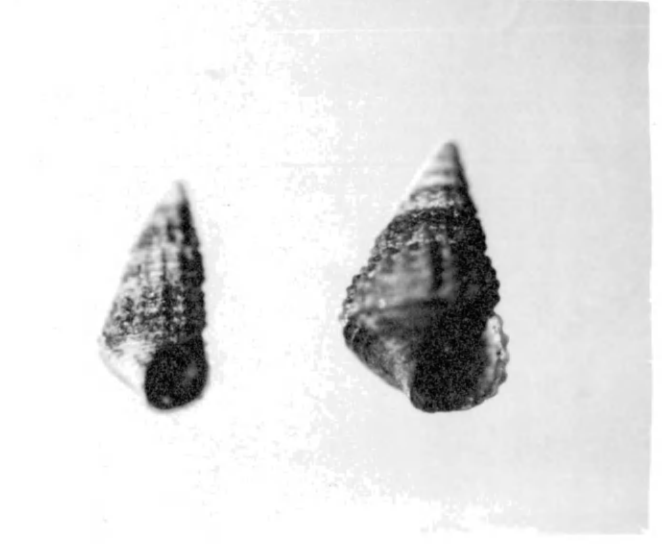
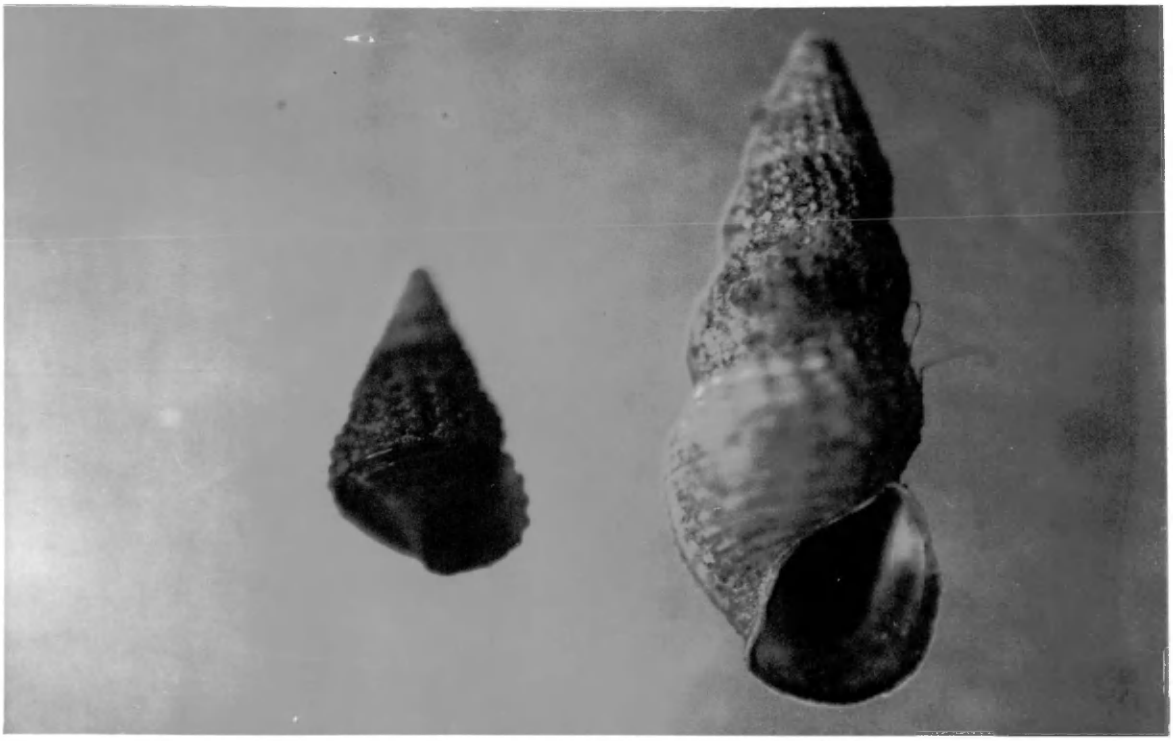


Figure 3a. Mature *B. varium* (extreme left) and three juveniles. Actual sizes, from left to right: 3.2 x 1.3 mm, 3.0 x 1.2 mm, 2.4 x 1.1 mm and 1.6 x 1.0 mm.

Figure 3b. Mature *B. alternatum* (right) and juvenile. Actual sizes: adult, 6.3 x 2.2 mm; juvenile, 3.4 mm.



that of B. varium in aspects other than size.

During the study, it became apparent that fluctuations in distribution and abundance of eelgrass from epizootics since the 1930's may have influenced the distribution of Bittium in the North Atlantic. Therefore, the eelgrass habitat is discussed in this report.

METHODS AND MATERIALS

Collections were made in the Middle Atlantic region of the United States to obtain representative examples of living Bittium species. Since B. virginicum had been reported only from Chincoteague Bay, particular effort was made to secure living specimens of Bittium from that locality. During July and August, 1967, I examined submerged vegetation in much of Chincoteague, Rehoboth and Barnegat Bays without finding any species of Bittium. A similar examination of vegetation in estuaries of Chesapeake Bay (York River, Severn River, Pungoteague Creek) during the same months revealed large numbers of B. varium, from which collections were made. Collecting was easily accomplished by grasping a bunch of eelgrass above the roots and sliding the closed fist along the blades. This stripped Bittium from the plants, usually several for each handful of grass. Additional living B. varium were obtained from Wrightsville Sound, North Carolina in October, 1967. Living B. alternatum were ordered from the supply department of the Marine Biological Laboratory at Woods Hole, Massachusetts in January and March, 1968 and in June, 1969.

To supplement living specimens, shell lots (all specimens collected at the same time and place) of B.

varium and *B. alternatum* and the few available lots of *B. virginicum* were borrowed from the Academy of Natural Sciences of Philadelphia, the American Museum of Natural History, the Chesapeake Biological Laboratory, the Museum of Comparative Zoology of Harvard University, the National Museum of Canada and the U. S. National Museum. Lots borrowed from the National Museum of Canada were not included in the size analysis. The shell apices were severely eroded, rendering accurate length measurements impossible. No varices were present on specimens in these lots, all collected in Canada. Locality and date of collection (where available) for all shell lots used in the size analysis are listed in Table 1.

Shell sculpture, excepting the varix, appeared similar in all specimens examined. Shell color was highly variable, from deep reddish brown to nearly white, and decreased in intensity with increase in size. The shape of the aperture varied with size, also. Therefore, shell characters selected for distinguishing specimens were: (1) presence or absence of a varix, (2) shell length, and (3) shell length-width relationship. Specimens selected from each lot were measured under a dissecting microscope with the aid of an ocular micrometer and were examined for the presence of a varix and an apertural canal. In lots with numerous specimens, 25 or 50 were measured, including the largest and smallest specimens. The samples were divided between

TABLE 1

BITTIUM LOTS USED IN THE SIZE ANALYSIS

Source	Location	Date	Number of Shells
USNM*			
539125	Saceo Sao Francisco, near Nictheroy, Rio de Janeirio, Brazil	April 20, 1935	25
129296	Trinidad, Gulf of Paria	old	6
94122	St. Thomas, Virgin Islands	1888	8
54057	Samana Bay, Dominican Republic	1885	14
434492	Santa Rosa, N.W. Cuba	1933	25
125568	Corpus Christi, Texas	1893	25
408134	Tampa Bay, Florida	1935	25
434523	Bird Key, Biscayne Bay, Florida	1910	25
252569 252569a	Chincoteague, Virginia	1913	26
485390	Magothy Bay, Virginia	July, 1916	23

Table 1. Continued

Source	Location	Date	Number of Shells
516213	Cape May, New Jersey	1924	7
434512	Spray Beach, New Jersey	1933	13
434514	Shark River, New Jersey	1933	16
450147	Canasie, Brooklyn, New York	1934	13
450134	Branford, Connecticut	1934	24
450126	Quonocontans Pond, Westerly, Rhode Island	May, 1897	25
450131	Chatham, Massachusetts	1916	25
450123	Provincetown, Mass.	1916	25
MCZ*			
222533	Beaufort, North Carolina, shore ¼ mile east of hospital	1863	12
198737	Long Island near Hollands Island, Dorchester County, Maryland	January, 1952	25
56477	Tedious Creek, Fishing Bay, Crocheron, Dorchester County, Maryland	1925	25
222532	Greenport, Long Island, New York	old	3
65822	Falmouth, Massachusetts	November 26, 1937	21

Table 1. Continued

Source	Location	Date	Number of Shells
ANSP*			
282231	Mouth of Monkey River, British Honduras	August 21, 1961	4
289797	La Parguera, Puerto Rico	November 29, 1961	25
70379	Beaufort, North Carolina	old	8
150068	Chincoteague Bay, Virginia	1929	1
147824	Cape May, New Jersey	old	1
266125	Shark River, New Jersey	November 15, 1961	10
106658	Point du Chene, New Brunswick, Canada	July, 1912	4
AMNH*	Rockaway, Long Island, New York	new	6
	Mystic River, Connecticut	August, 1945	25
	Woods Hole, Massachusetts	old	16
Supply Dept., MBL*	Woods Hole, Massachusetts	June, 1969	11

Table 1. Continued

Source	Location	Date	Number of Shells
McCrary	Wrightsville Sound, North Carolina	October, 1967	25
Pfitzenmeyer	St. Mary's River opposite Seminary Wharf, Maryland	October, 1965	50
	Holland Straits, Chesapeake Bay	July, 1963	50
Wulff	Clay Bank, Virginia	September, 1967	49
	Gloucester Point, Va.	summer, 1966, 1967	25
	Severn River near Glass, Va.	September 11, 1966	50
	Pungoteague Creek, Va.	July, 1967	25

*Abbreviations: USNM = United States National Museum

MCZ = Museum of Comparative Zoology, Harvard University

ANSP = Academy of Natural Sciences, Philadelphia

AMNH = American Museum of Natural History

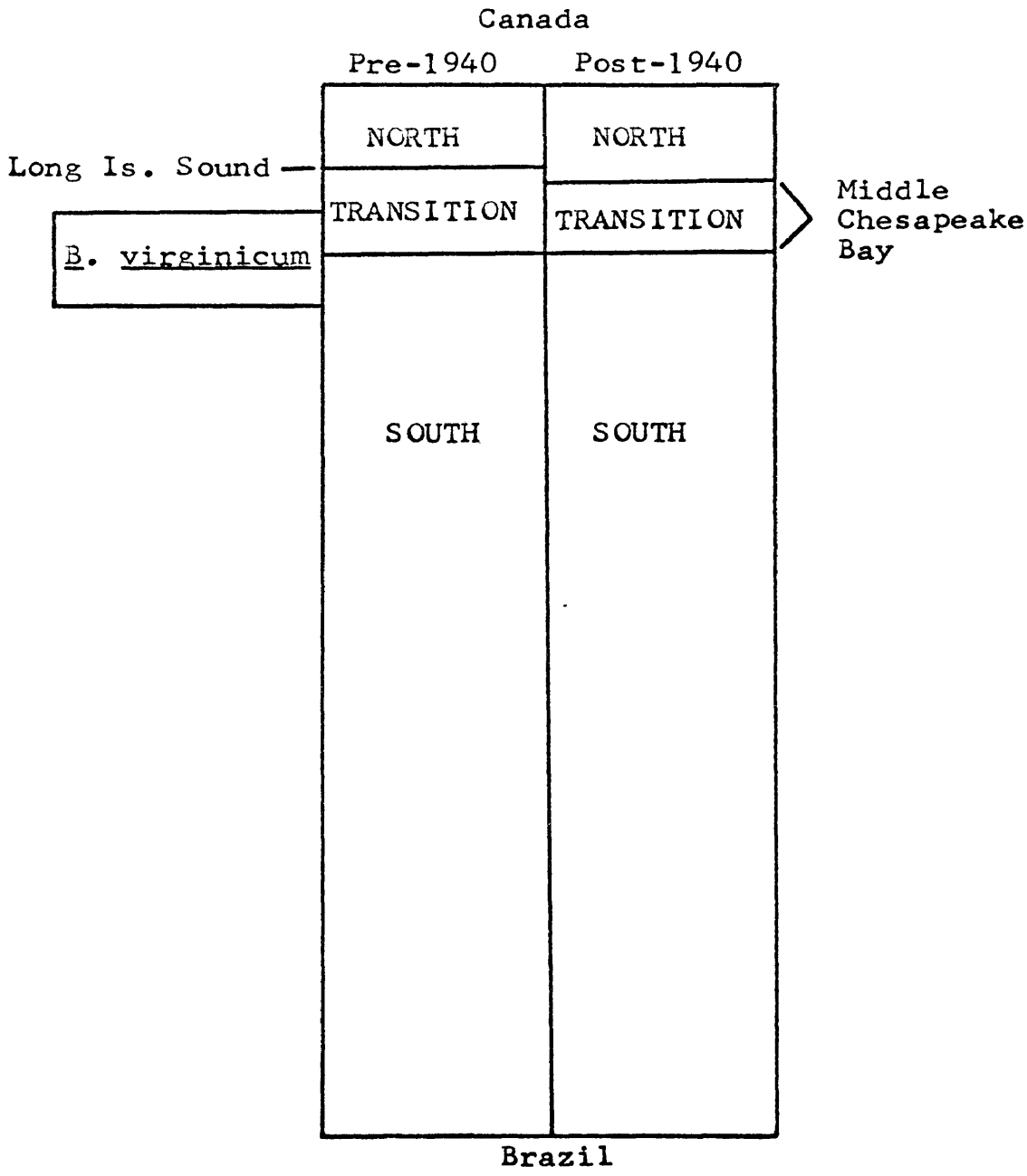
MBL = Marine Biological Laboratory

adults and juveniles when both were present. In lots having fewer than 25 specimens, all specimens in the lots were measured. Length was measured from the apex to the lower edge of the outer lip and width from the extreme lateral edge of the outer lip to the farthest point on the opposite side of the shell, with the aperture up in both cases (Fig. 1).

The means of length and width for adults from each lot were computed. When these means were arranged latitudinally, a strong pattern of mean length distribution related to varix presence emerged. Therefore, lots were grouped as north (no specimens possessing a varix), south (all specimens possessing a varix), or transition (some specimens, but not all, possessing a varix). These groupings were subdivided into lots collected before 1940 (old) and lots collected after 1940 (new) to allow for any changes caused by the eelgrass habitat destruction of the 1930's (see discussion). Because the outstanding feature of B. virginicum was its length, four lots with particularly large mean lengths were grouped separately (USNM 25259, 485390, 434512 and MCZ 222533) and designated B. virginicum in the statistical analysis.

Mean lengths and widths and covariance matrices for all adult specimens in each of the seven groupings (Fig. 4) were computed and compared with each other. Adult mean length was divided by adult mean width to get a ratio

Figure 4. Diagrammatic representation of latitudinal distribution of *Bittium* groupings.



for each group, also for comparison purposes. Linear regressions were computed for juveniles from the seven groups in an attempt to demonstrate different patterns of growth, The regression slopes were compared by means of a Students' t-test.

Since lots in the transition groups had specimens with and specimens without the varix, the transition groups were separated into sublots with and without varices. By use of a multivariate form of the Students' t-test, it is possible to test whether the differences in mean width and length between specimens with varices and specimens without varices in the same lot are significantly different from zero and hence the specimens differ in size (length, width). This test was performed on the four lots in the old transition group which possessed sufficient numbers of specimens in each sublot to be tested.

Radular differences are often used by molluscan taxonomists to distinguish species. Radulae were dissected from mature Bittium specimens collected from the York River, Virginia in September, 1968 and from Woods Hole, Massachusetts in June, 1969. For comparison, radulae from specimens of B. eschrichti collected in Boiler Bay, Oregon in June, 1969 and from specimens of Batillaria minima (Gmelin) collected in Tampa Bay, Florida in the spring of 1968 were also dissected.

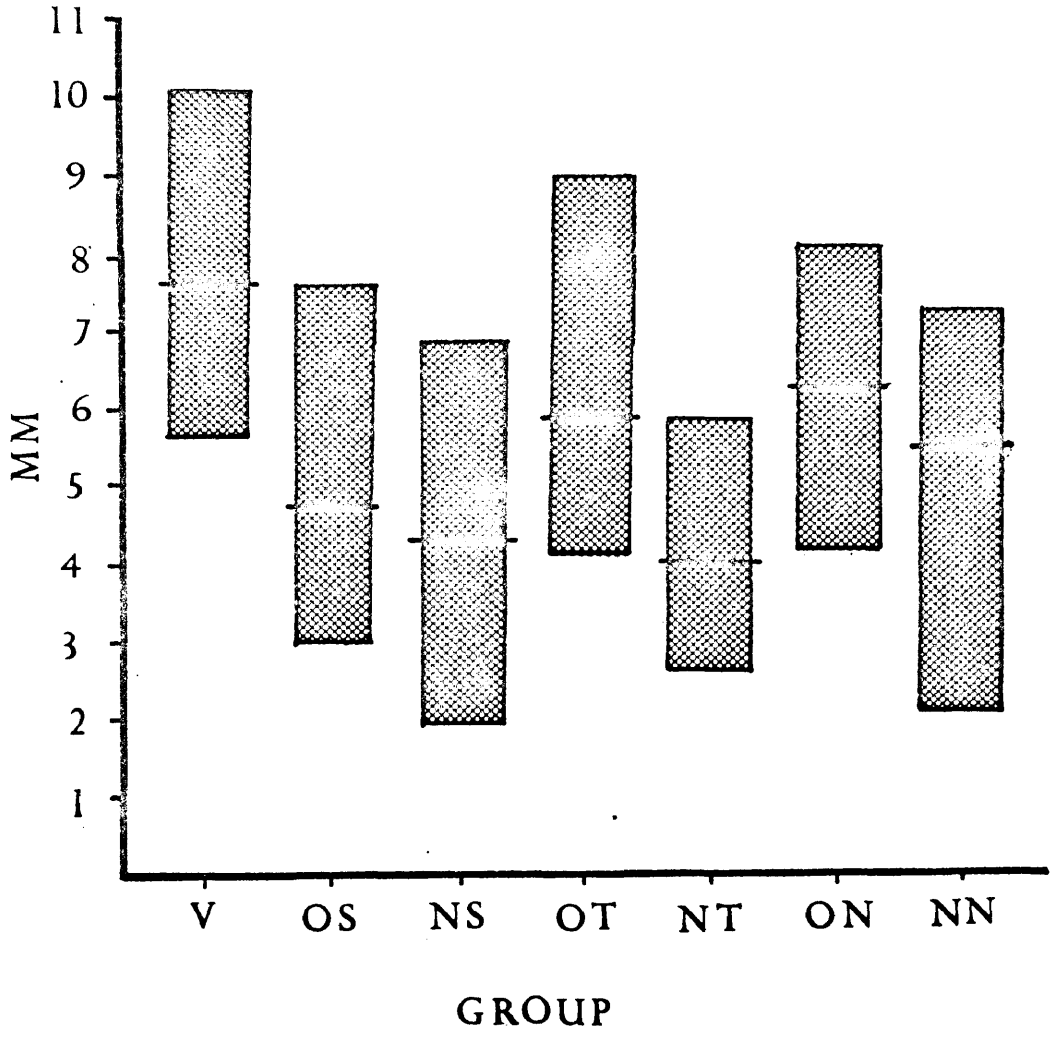
The following procedure was followed with all specimens: The shell was dissolved in hydrochloric acid and the buccal mass then rinsed in water and transferred to a drop of sodium hypochlorite solution (commercial chlorine bleach) to soften the flesh around the chitinous radula. The radula was teased out of the buccal mass, rinsed in water and placed on a slide in a drop of water to which glycerine was added for stability. It could then be mounted under a cover slip, examined under a compound microscope and photographed. A few radulae were mashed to separate the teeth. Photographs were taken with Kodak Panatomic-X 35 mm film at 430x and 1000x magnifications.

RESULTS

The eelgrass in the York River near the Virginia Institute of Marine Science was heavily populated with B. varium throughout the summer of 1967. Only when the air and water began to chill in October did I have difficulty finding the snails. At first I thought they had disappeared completely. A careful search of the eelgrass showed tiny juveniles at the base of the plants, just above the roots in the pockets formed at the attachments of dying outer leaves. There were very few mature specimens remaining. All collecting or attempted collecting in other locations from Virginia to New Jersey was done in midsummer when the snails should have been abundant and easily accessible. It is highly unlikely that the absence of Bittium in Chincoteague, Rehoboth and Barnegat Bays in July and August, 1967 was due to the inadequacy of collecting methods.

The four lots grouped separately because of their excessive lengths included the type specimens of B. virginicum and are henceforth referred to as B. virginicum. Specimens in old and new south lots all had varices and are considered B. varium. No specimens in the old and new north lots had varices. These are considered B. alternatum. Adult length ranges and means are shown in Fig. 5.

Figure 5. Adult length ranges and means of Bittium groups analyzed. (V = B. virginicum, OS = old south, NS = new south, OT = old transition, NT = new transition, ON = old north, and NN = new north.)



The position of the varix on B. virginicum and B. varium varied with respect to the aperture. The most common placement was opposite the aperture so that when the shell was placed aperture up, the varix made a bulge on the left side of the body whorl (see extreme left specimen, Fig. 3).

None of the old transition lots subjected to the multivariate Students' t-test had significantly different mean size differences between sublots at the .05% level. This indicates that size in these lots did not vary with varix presence. Comparison of juvenile regression slopes (Fig. 6) showed that three group pairs were not significantly different: old south, B. virginicum; old north, old transition; new south new north. All other combinations of regression slopes differed significantly (Fig. 7).

Mean lengths, mean widths and mean length/mean width ratios are given in Table 2. B. virginicum mean length was largest. B. virginicum length/width ratio was also largest, indicating that these specimens had the most slender shells for their length. Old north and new north groups had the smallest ratio values (that is, they were widest for their lengths) but were nearly as long as B. virginicum. The new south and new transition groups had the smallest mean lengths. They also had identical length/width ratios. The old south mean length was slightly greater than that of the new south, but the length/width ratio was second in size to

Figure 6. Regressions of juveniles from the *Bittium* groupings.

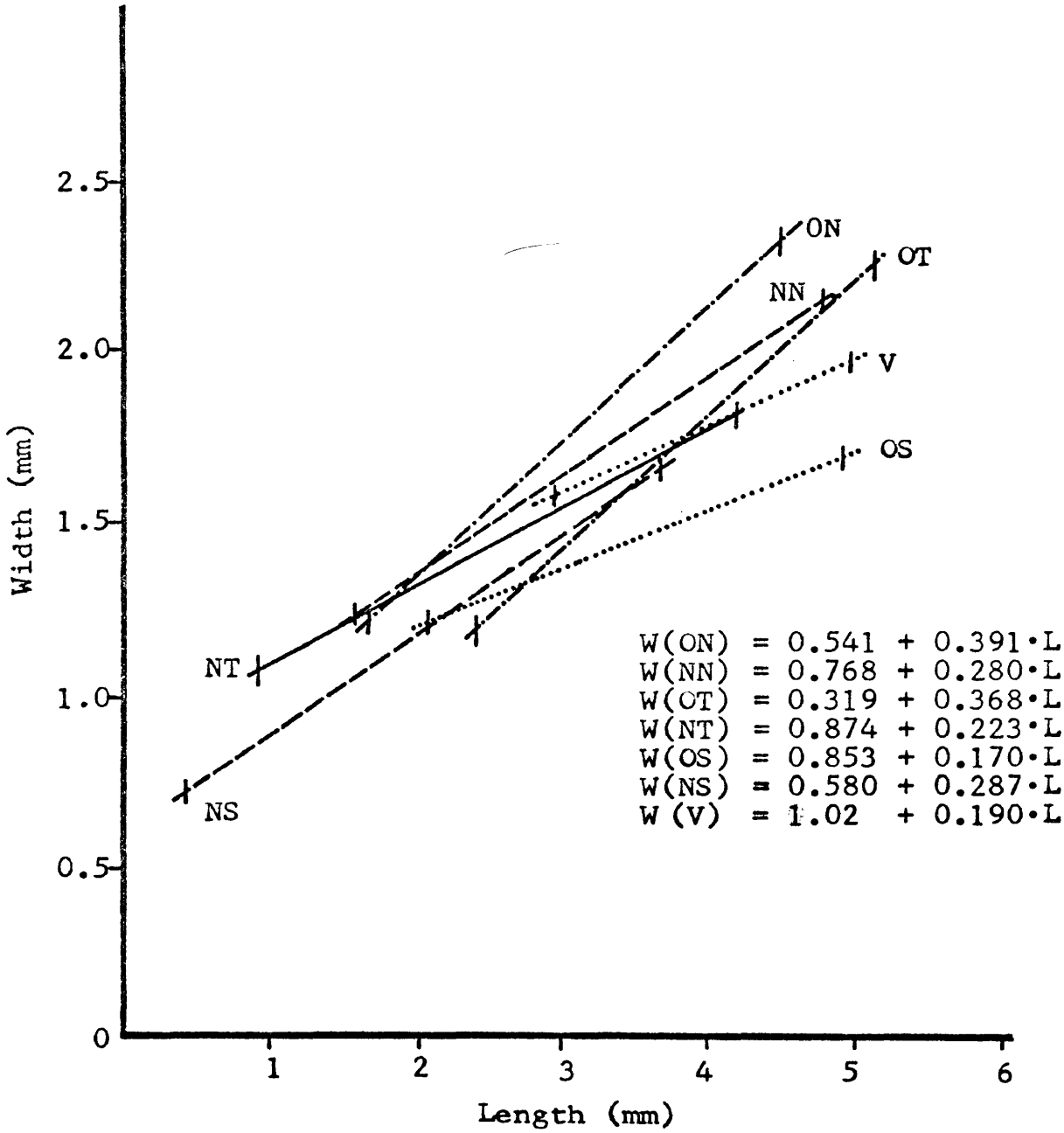


Figure 7. Results of comparing slopes of juvenile *Bittium* regressions by using Students' t-test (+ = significantly different; - = not significantly different at the 0.05% level).

d. f.	Group	OS	OT	ON	V	NS	NT	NN
32	OS		+	+	-	+	+	+
4	OT			-	+	+	+	+
32	ON				+	+	+	+
3	V					+	+	+
90	NS						+	-
17	NT							+
29	NN							

TABLE 2

MEAN SIZE VALUES AND MEAN LENGTH/MEAN WIDTH RATIOS FOR ADULT *BITTIUM* GROUPS

Group	Mean length in mm	Mean width in mm	Mean length / Mean width
New transition	4.15	1.70	2.44
New south	4.35	1.78	2.44
Old south	4.70	1.76	2.67
New north	5.42	2.30	2.36
Old transition	5.94	2.32	2.56
Old north	6.26	2.61	2.39
B. virginicum	7.65	2.77	2.76

that of B. virginicum. The old transition mean length value fell between those of old and new south. Covariance matrices are compared in Table 3.

The Bittium radula is taenioglossate, each row of teeth consisting of a large central tooth flanked on either side by a large lateral tooth and slender, nearly identical inner and outer marginal teeth, all of which overlap slightly so that tooth arrangement is three-dimensional. The radulae of B. alternatum and B. varium appeared to be identical (see Figs. 8, 9). Although B. eschrichti (Fig. 10) lives in rocky areas rather than on marine grasses and macroalgae, and its shell shape and sculpture differ considerably from those of the Atlantic Coast species, I could detect no difference in its radula from those of B. alternatum and B. varium. Examination of the radula of Batillaria minima, a member of the same superfamily as Bittium, revealed a distinctly different tooth structure from that of Bittium.

TABLE 3

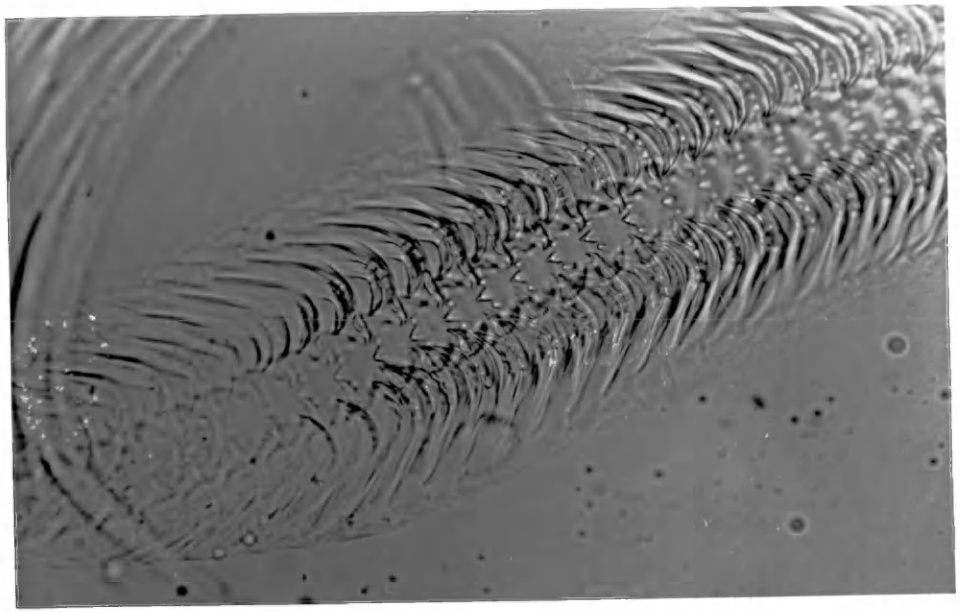
COVARIANCE MATRICES FOR ADULT *BITTIUM* GROUPS

	New		Old		*B. virginicum*	
South	0.9587	0.3669	0.7731	0.2279	1.1063	0.2605
	(110)	0.1642	(131)	0.0816	(64)	0.1307
Transition	0.3617	0.1091	1.1798	0.3335		
	(75)	0.0539	(55)	0.1429		
North	2.0136	0.4874	0.5995	0.1953		
	(21)	0.1525	(108)	0.0927		

Note: Degrees of freedom are in parentheses.

Figure 8a. Details of central and lateral teeth of *B. varium* radula. 430X.

Figure 8b. Details of marginal teeth of *B. varium* radula. 430X.



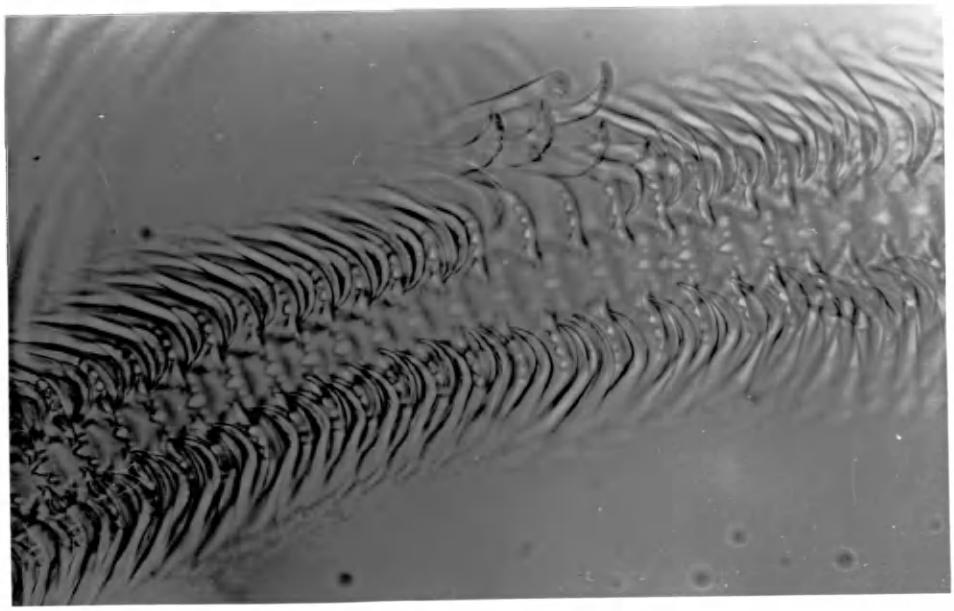


Figure 9a. Portion of *B. alternatum* radula. Marginal teeth turned to show detail. 430X.

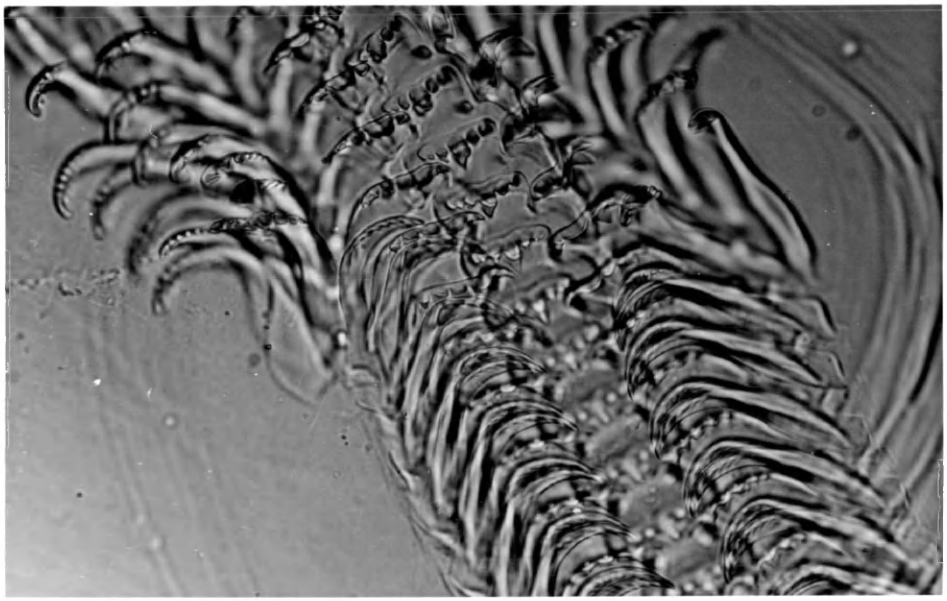


Figure 9b. Portion of B. alternatum radula. Central and lateral teeth. 1000X.

Figure 9c. Portion of B. alternatum radula showing marginal teeth. A few laterals are present on the right side. 1000X.

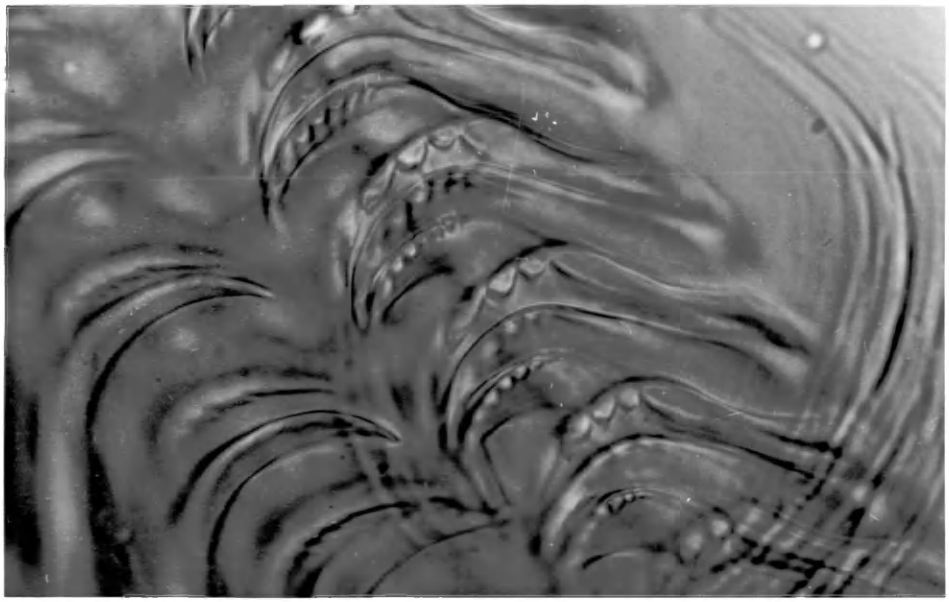


Figure 10a. Portion of *B. eschrichti* radula showing central teeth. 1000X.

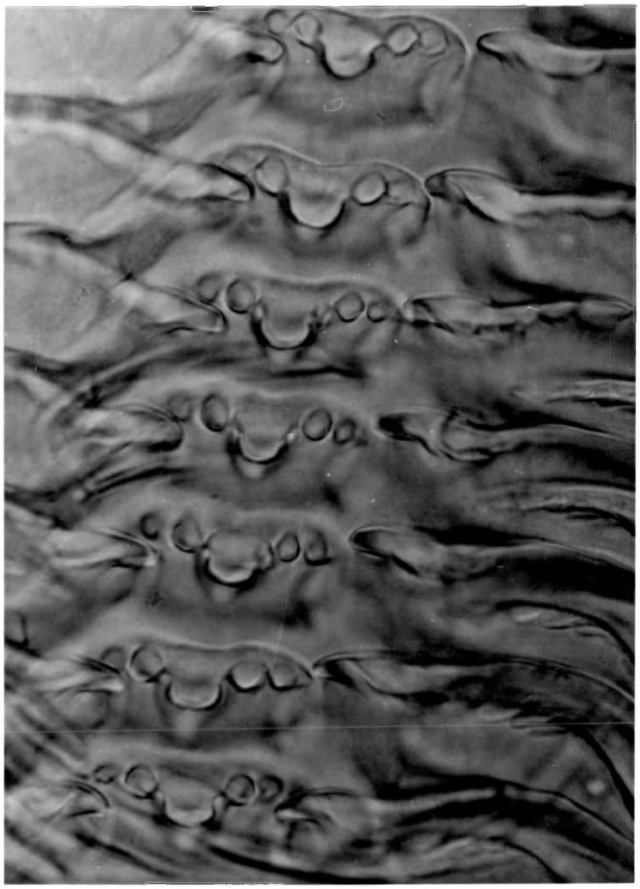


Figure 10b. Portion of *B. eschrichti* radula showing lateral teeth. 1000X.

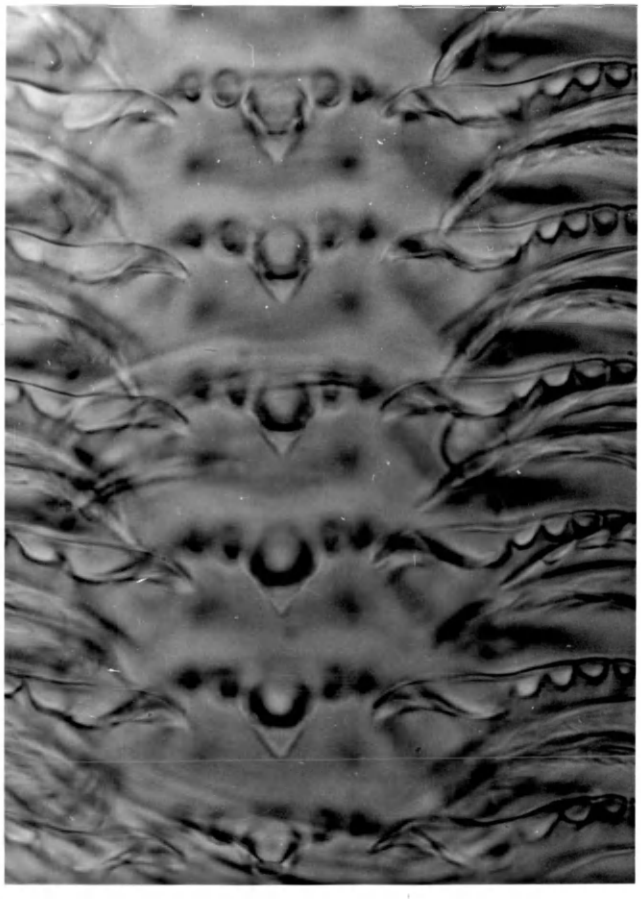


Figure 10c. Portion of B. eschrichti radula showing marginal teeth turned in opposite position from normal direction. 430X.

DISCUSSION

Shells from old and new north groups fit the type description of B. alternatum (Say, 1922). Shells from the old and new south groups fit the type description of B. varium (Pfeiffer, 1840). Although Pfeiffer did not mention the varix in his description of B. varium, subsequent descriptions of this species did (Abbott, 1954; 1968; Marcus and Marcus, 1963; Perry and Schwengel, 1959; Warmke and Abbott, 1963). The type description of B. virginicum (Henderson and Bartsch, 1914) could have been the type description of B. varium except for length and number of whorls.

Examination of the covariance matrices was helpful. Among the old groups, the old transition had the largest covariance. This indicates greater size variability within the group than in the old north or old south groups, which would be the situation if these organisms were intergrades between the northern B. alternatum and the southern B. varium. The old south group had a larger covariance than the old north, but this is reasonable because collections were made over an extensive range, from Virginia to Cabo Frio, whereas the northern lots ranged only from Long Island Sound to southern Canada. The relatively large co-

variance value of the new north group probably resulted from the small sample size. All lots in the new transition group came from the same region of Chesapeake Bay. This accounts for their very low covariance value. Despite the lack of a varix in some specimens from these lots, size measurements and mean length/mean width ratio indicate that they should be considered part of the new south group; these are B. varium.

Comparison of slopes from the regressions of juvenile Bittium showed some interesting results. The old south and B. virginicum group slopes were not significantly different, as was expected from results of other data analyzed. The apparent similarity of slopes of new north and new south was surprising, since the slope gives an approximation of growth in width with growth in length and examination of adult specimens indicated that these two groups differed considerably in this respect. The similarity of slopes of old transition and old north was less surprising, indicating a relationship between the two groups that had already been presumed. The strongest difference in slopes was apparent between old south and old north. I should point out that some lots in each group were composed exclusively of either adults or of juveniles, so all populations analyzed by adult characters were not represented in analysis of the juveniles, and vice versa.

If one considers mean length and mean width, the old transition group falls between the old and new north. With

respect to mean length/mean width ratio, the old transition group falls between the old and new south. It thus belongs with neither north nor south with respect to shell size and shape. Since this group was composed of lots in which some but not all specimens had varices, the varix also will not place it in either species group. In general, lots from the more northern part of the old transition area had a lower proportion of shells with varices than did lots from the southern part of the area. These mollusks must be considered intergrades between the old north and old south, or B. alternatum x B. varium.

It is apparent from the similarity of the radulae of B. alternatum, B. eschrichti and B. varium that radulae do not differ sufficiently to be used in distinguishing among species of the genus Bittium.

All specimens received from the supply department of the Marine Biological Laboratory, Woods Hole which were collected in January and March, 1968 were juveniles, even though I had specified adult specimens in the orders. Specimens collected by the supply department in June, 1969 were evenly divided between adults and juveniles. Although many shell collectors selectively collect the larger specimens, the small size of all Bittium and the aforementioned method of collecting them would insure a random sampling of a population at a given time. From these observations, from the proportion of adults to juveniles in lots collected

during the different months of the year, and from my finding mostly juveniles in the York River during October, 1967, I have concluded that Bittium winters over in the juvenile condition and probably lives for only one year. A few snails spawned late in summer may survive two winters.

The varied position of the varix with relation to the aperture in B. varium and B. virginicum indicates that shell growth occurs after canal formation, probably until the death of the animal. This is not demonstrable in B. alternatum because that species lacks a varix. If shell growth does continue throughout the life of the organism, lots collected in late summer would have slightly larger adults than those collected in spring or early summer. This no doubt contributed to variability between lots of the same species.

In the wasting disease epidemic attributed to Labyrinthula, the eelgrass Zostera marina, which served as a habitat for Bittium on the northern and middle Atlantic Coast of North America, virtually disappeared from this coast in 1932 (Dexter, 1947). Recovery of the eelgrass has been a slow process. In studies of tidal communities at Cape Ann, Massachusetts, Dexter (1947) noticed that more small patches of eelgrass appeared there each succeeding year after 1934, but that no good healthy stands occurred until the summer of 1945. In studies of the Niantic River, Connecticut, Marshall (1960) reported rather thick stands

of Zostera in mid-summer, but these were not as dense as growth had been before the 1930's and were unstable, with large patches dying off from time to time. Cottam and Munro (1955) reported an almost complete recovery of the eelgrass in Chesapeake Bay by 1955 but noted that in other areas the shifting substratum had prevented reestablishment. Marshall (1960), on the other hand, felt that the Zostera epidemic "may have created a shifting, unsettled bottom condition" on the eastern shore of Virginia. Thus, the wasting disease destroyed the eelgrass, creating a shifting bottom which prevented reestablishment of the eelgrass.

The eelgrass in Chincoteague Bay in July, 1967 was sparse and scattered, consisting of patches of no more than a few square yards, interspersed with larger expanses of sandy bottom. I found no Zostera in Rehoboth Bay in July, 1967. Eelgrass in Barnegat Bay during August, 1967 was well established and lined the eastern shore of the bay to a width of at least 10 yards. It appeared to be dying as fast as it grew, for the shore was lined with decaying eelgrass to a width of another six yards and a depth of several feet. New Jersey wildlife officials confirmed that there was no other eelgrass in the state except near Sandy Hook (personal communication). As stated earlier, I found no Bittium in Chincoteague, Rehoboth or Barnegat Bays.

The complete absence of Bittium from Chincoteague Bay, where it was formerly abundant (Henderson and Bartsch col-

lected thousands of specimens there in 1913), may be attributed to the destruction of its eelgrass habitat. Other workers have found that organisms associated with Zostera disappeared or diminished greatly in abundance after the wasting disease epidemic. In 1936, Stauffer (1937) studied the Northwest Gutter near Woods Hole, Mass., an area studied by W. C. Allee in 1923. He found no Bittium there, although during the time of Allee's study there were B. alternatum on the eelgrass at the same location. Many other organisms associated with eelgrass, which had been listed by Allee in 1923, also were not found in 1936. In the Netherlands, Reydon and Visser (1967) discovered that Rissoa membranacea (J. Adams) had become extremely rare since the almost total disappearance of its host plant Zostera marina in 1932.

The Bittium existing today on the Atlantic Coast of the United States and Canada may be descendants of small populations which survived on the few eelgrass beds not totally destroyed in the epidemic. If a region of hybridization between B. alternatum and B. varium existed, as is indicated by measurements of the old transition group, this region was eradicated with the eelgrass during the wasting disease epidemic. Because so little is presently known concerning the length of larval life and the salinity tolerance of Bittium veligers, the possibility of active genetic exchange between widely separated Bittium populations and the pros-

pect of recolonization of areas formerly populated by Bittium can be only speculated. Neither is certain. Ehrlich and Raven (1969) have pointed out that the possibilities of gene flow between natural populations of most species are sharply limited by their wide separation. The "bipolarity" of some species indicates that no constant gene flow is necessary for a species to maintain its integrity in widely separated populations in the absence of disruptive selective pressure on one or more of these populations.

It was previously assumed that a species would vary in a "cline" from one end of the species range to the other. Thus, for instance, one might expect B. varium from Chesapeake Bay to be longer than the same species from Cabo Frio, or vice versa, with intermediate sizes in gradation from north to south. However, this does not hold for B. varium or for B. alternatum, as several lots in each species range averaged longer or shorter than those to the immediate north and south. Since the concept of the cline was based on limited gene flow between adjacent populations, the realization that such gene flow actually exists in very few species of either plants or animals (Ehrlich and Raven, 1969) makes possible explanations for aberrations from the accepted pattern.

Populations which differ slightly from others of the species result from adaptation to local conditions. Whether these adaptations are genetic or merely in response to ex-

tremely favorable or unfavorable conditions may be determined by breeding and transplant experiments. In the case of the extremely long B. virginicum, local conditions very favorable for growth are probably the reason for this "species". The longer specimens were found in several locales (Spray Beach, New Jersey; Chincoteague Bay, Virginia; Magothy Bay, Virginia; Beaufort, North Carolina) at certain times, and normal sized specimens of B. varium from two of those locales (Chincoteague Bay, Beaufort) were collected at other times. Conditions changing with time may be the reason for differences between old and recent Bittium populations.

It is interesting to note that Henderson and Bartsch (1914) reported in their paper which contains the type description of B. virginicum that, of other gastropods collected in or near Chincoteague Bay when the type specimens of B. virginicum were collected: Nassarius vibex belonged to an "exceptionally large race"; Eupleura caudata was "exceptionally large"; and the "enormous size" of Urosalpinx cinereus at first led them to suspect a new species, until they discovered that Say's type

> "came from the Maryland shore and is much larger than the shells of this species from either north or south of this region. These, then, are probably typical cinereus and specimens from Long Island as well as those from Hatteras south belong to a much smaller race.... A few specimens (dead) dredged in the open sea are of the smaller race generally known to collectors...."

This conclusion can be supported by the observation that specimens of B. virginicum have more shell whorls than specimens of B. varium. In other shell characters, the two species appear identical. Shells of B. alternatum attained lengths only slightly shorter than those of B. virginicum but with the same number of whorls as B. varium. Therefore, the length of B. alternatum may be attributed to greater size per whorl, that of B. virginicum to more whorls, both in comparison to B. varium. The greater number of whorls in B. virginicum indicates that more rapid growth occurred before maturity than occurred in normal B. varium, as would be the case under extremely favorable growing conditions.

Mature B. varium may be distinguished readily from B. alternatum by their smaller size (less than 7 mm) and by the varix on the body whorl. Juveniles present more difficulty. Generally, juvenile B. varium are shorter and narrower than juvenile B. alternatum. At present, if specimens were collected from Maryland south, one could be reasonably certain they were B. varium; if collected from New Jersey north, they are probably B. alternatum. The B. virginicum variety of B. varium could be best described as an unusually long B. varium, up to 10 mm in length. I am unaware of the existence of any living B. virginicum.

APPENDIX I

CLASSIFICATION FROM THIELE (1931)

PHYLUM Mollusca

CLASS Gastropoda

SUBCLASS Prosobranchia

ORDER Mesogastropoda

SUPERFAMILY Cerithiacea

FAMILY Cerithiidae

SUBFAMILY Cerithiinae

GENUS *Bittium* (Leach) Gray 1847

SUBGENUS *Bittiolum* Cossman 1906

SPECIES *B. varium* (Pfeiffer) 1840

There is no mention of either *B. alternatum* (Say) 1822 or *B. virginicum* (Henderson and Bartsch) 1914.

APPENDIX II

TYPE DESCRIPTIONS OF WESTERN ATLANTIC BITTIUM

Diastoma virginica (Henderson and Bartsch, 1914)

Shell elongate - conic. Early whorls chestnut-brown, succeeding turns flesh colored, mottled, variegated with brown; some specimens have chestnut brown over entire shell. Nuclear whorls 2½, well rounded, smooth. First 3 post-nuclear whorls rather well-rounded; succeeding turns less so, later ones almost flat. Whorls marked with poorly developed axial ribs, almost obsolete on the early turns. Fourteen ribs on third and fourth, 16 on fifth, 18 on sixth, 20 on the rest. Intercostal spaces twice as broad as ribs, crossed by four low spiral bands between sutures, which are a little wider than spaces which separate them. Axial ribs feebly nodulous at junction with ribs. On the last two turns, the second spiral cord below the summit splits, forming five spiral cords on these whorls. Beginning with the fifth whorl, the cord anterior to the periphery makes its appearance in the suture as a small spiral band, becoming more and more exposed in the succeeding turns. Spaces inclosed between axial ribs and spiral cords are shallow,

impressed, squarish pits on the middle whorls, and elongate pits having their long diameter parallel with the spiral sculpture on the early turns and last two whorls. Suture moderately impressed. Periphery of last whorl well rounded. Base moderately long, well-rounded, marked by feeble continuations of axial ribs and nine spiral cords, which grow successively narrower from the periphery to the umbilical area. These cords are separated by grooves about half as wide as the cords. A strong varix, forming a decided callus, is present diametrically opposite the aperture on the last turn. The spiral cords, preceding and extending partly upon this callus, are tinged with dark chestnut brown. Aperture decidedly patulus, ear-shaped, slightly channeled posteriorly and decidedly anteriorly; outer lip thin, decidedly expanded, evenly rounded, fleshcolored with a checkerboard pattern of brown, when viewed by transmitted light, which is formed by squarish brown spots marking the intercostal portion of the spiral cords; inner lip reflected, somewhat sigmoid; parietal wall covered by a thick callus, rendering peritreme complete.

Type, Cat. No. 252569 in U. S. National Museum, from eelgrass, Chincoteague Bay.

<u>Cerithium</u> <u>varium</u> (Pfeiffer, 1840)

Testa turrita tenue diaphana griseo-fusca, uni-

colore vel nigro-cingulata; anfract. S convexis, plicis longitudinalibus et striis transversis subdecussatis, ultimo varicoso-gibboso; basi concentrice striata; columnella nigra; canali brevissimo, vix recurvo; labro tenui. ___Long. 2½, diam. 4/5 lin.

ENGLISH TRANSLATION

Shell turreted, thin, transparent, dark gray of one color, or black-banded; bent in an S curve and criss-crossed with lengthwise folds and transverse grooves. Apex rounded; bottom whorl with concentric grooves; columella black; canal very short, slightly curved backwards; lip thin.

Turritella alternata (Say, 1822)

Shell dusky; acute at the apex; volutions eight, with about eight unequal, revolving, slightly elevated lines, which are maculated with rufous, and decussated by transverse, elevated, obtuse lines, which are obsolete below the middle of the body whorl and prominent on the spire; labrum not thickened, a slight indentation at its base.

Length 1/5 inch.

Type locality - coast of U. S.

Type - Academy Museum

Animal - Foot longer than the aperture of the shell, rather acute behind, and truncated a little convexly be-

fore; tentacula filiform, cylindrical, obtuse at tip, nearly as long as the foot, white, annulate with brownish lines; eye at the external base of the tentacula, not prominent; rostrum about 1/3 length of the tentacula; operculum blackish.

The shell when taken from the water becomes whitish-cinereous. They abound amongst *Fucus* and sometimes on the shell of *Limulus polyphemus*. Animal considerably resembles that of *Melania virginica* as respects form and, in common with many fresh water shells, possesses the power of gliding along the surface of the water with the shell downward. This shell is somewhat like *T. reticulata*, but the sculpture is less profound, and it never has any appearances of varices or incrassation of the labrum.

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