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PALEOECOLOGICAL IMPLICATIONS

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AMERICAN MUSEUM OF NATURAL HISTORY  
VOLUME 159 : ARTICLE 3      NEW YORK : 1977





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**BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY**

**Volume 159, article 3, pages 87-128, figures 1-29, tables 1-9**

**Issued December 22, 1977**

**Price. \$2.80**

**ISSN 0003-0090**

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## ABSTRACT

Intertidal environments of St. Catherines Island, Georgia are diverse and include exposed sand beaches, sandy tidal flats, relict salt marsh deposits (mud and peat) on exposed beaches, and salt marsh complexes. Nine localities from the northern half of St. Catherines Island were selected for study because they displayed a wide variety of intertidal habitats and organism associations. No attempt was made to describe the entire spectrum of intertidal associations on St. Catherines Island.

The bulk of study was made on the relict salt marsh deposits. Besides representing unique modern habitats for infaunal and epifaunal bivalve-dominated associations, the salt marsh deposits gave us valuable paleoecological insights. The organism groupings recognized in the present study are associations in the sense of Kauffman and Scott (1976), but communities in the usage of most workers. One relict mud occurrence contained an assemblage of six distinct associations. The fidelity of replication of these associations in the fossil record depends, in part, upon the steepness of the intertidal environmental stress gradients and the resultant spatial and temporal environmental heterogeneity. The infaunal bivalves of the relict muds showed expected trends of size distribution with depth, the larger individuals occupying the greater depths. It is suggested that the lateral transportation of dislodged mud clasts has an analog in the geological past in the occurrence of "exotic" fossiliferous pods and steinkerns.

Association boundaries were sharp only where spatial heterogeneity was pronounced, such as within salt marsh complexes. The polychaete associations along sandy tidal flats were less clearly bounded and were often marginally intergradational.

Many observations on the intertidal associations of St. Catherines Island were in disagreement with observations made on similar associations elsewhere. Contrary to the conclusions of Woodin (1976), dense infaunal bivalve populations (*Petricola pholadiformis*) did coexist with dense epifaunal bivalve populations (*Brachidontes recurvus*). Also, repeated observations of dense tube-building polychaete populations failed to show epifaunal bivalves as predominant co-occurring forms.

Polychaete associations along a narrow tidal flat displayed onshore-offshore distributional trends that may have paleoecological utility in the resolution of transgression-regression sequences.

Tidal creek populations of *Ilyanassa obsoleta* have a narrower aperture relative to total height than similar populations from more open sand flats. It is suggested that this is correlated with the greater duration of intertidal exposure in the tidal creek habitat. Study of another intertidal snail, *Littorina irrorata*, demonstrated considerable lateral as well as vertical motility in that species.

## INTRODUCTION

It is often said that one approach toward better understanding of the fossil record is through the study of living organisms and organism communities in their normal habitats (the "transferred ecology" approach, Lawrence, 1971). The converse should be equally apparent, because, as expressed in terms of the Gestalt metaphor of figure-ground (McLuhan and Nevitt, 1972), every situation is a figure for a ground of events and relationships. A figure can only be understood in terms of its ground (context) and the ground is

constantly changing. However, both ecologists and paleoecologists often study figure minus ground.

This study should not be viewed as an attempt to completely describe the intertidal communities of St. Catherines Island, Georgia. Rather, emphasis is on selected aspects of the intertidal associations; in particular, those aspects that have paleoecological impact. Intertidal associations were studied in the following environments: exposed sand beach, protected sand beach, sandy

tidal flat, relict salt marsh (mud and peat) deposits on exposed beach, and salt marsh complex.

To date, the nearshore marine organisms of St. Catherines Island have never been the subject of any published study. To our knowledge, the only previous work on the subject is an unpublished report (Feinberg and Old, 1972), that listed the marine organisms, mainly molluscs, collected during a short visit to the island. However, several excellent studies have been published concerning the intertidal and subtidal faunas and sediments of nearby Sapelo Island (Frey and Howard, 1969; Howard and Dörjes, 1972; Howard and Reineck, 1972; Howard and Frey, 1973; Dörjes, 1972; Hertweck, 1972; Wiedemann, 1972). In addition, studies of nearshore marine molluscan communities (Bird, 1970) and biogenic sedimentary structures (lebensspuren) made by benthic organisms (Frey, 1970) in the Beaufort, North Carolina, area have proved quite helpful in this investigation.

Because the term "community" is constantly used by both ecologists and paleoecologists in a variety of ways, any ecological study should, at the onset, attempt to clearly state the manner of use of the community concept. We adopt the "holistic" community approach discussed by Kauffman and Scott (1976). This concept considers a community to be "ecologically defined on the basis of all component organisms: their diversity characteristics; the uniqueness of their composition (including normal variations in time and space); the sum total of their interactions with each other (trophic, food chain, and behavioral relations) and with the containing environment. . . ." This view of a community is in sharp contrast to that of most workers; for example, Mills (1969, p. 1427), who considered a

community to be simply "a group of organisms occurring in a particular environment, presumably interacting with each other and with the environment, and separable by means of ecological survey from other groups." The intertidal organism groups recognized in this study are best described as associations, following the approach of Kauffman and Scott (1976), since no attempt was made to deal with all the component species of a particular environmental setting. An association is a group of organisms derived from a single community (Kauffman and Scott, 1976, p. 19).

#### ACKNOWLEDGMENTS

The present paper gives some of the results of investigations conducted on St. Catherines Island during a two-week period (June 23-July 7) in 1975 and a three-week period (June 7-June 28) in 1976. We are very grateful to the Edward John Noble Foundation for providing the funds and opportunity that made this study possible, as well as for permission to visit the island and use its facilities. We are also indebted to the American Museum of Natural History for administering the research program on St. Catherines Island. We also acknowledge support from NSF grant BNS74-13381. We acknowledge the aid of Mr. John Harper, who measured some of the gastropod populations included in this study, Mr. Bruce Cain, who prepared the statistical program for treatment of some of the measured data, and Mr. John Fierstien, who assisted in the field collecting. Finally, we thank Mr. John Tobey Woods, caretaker of St. Catherines Island, for his invaluable help in transportation of equipment and personnel and for sharing his vast knowledge of the island's environments and history.

#### LOCATION AND SETTING

St. Catherines Island is one of the Georgia Sea Islands, a chain of coastal islands extending from Charleston, South Carolina, southward along the entire Georgia coast. The island is about 40 miles due south of Savannah, Georgia, and is separated from the mainland by about 5 miles of salt marshes, intersecting tidal channels, and estuaries. About 10 miles long and up to 2 miles wide, St.

Catherines Island is separated by St. Catherines Sound from Ossabaw Island to the north and by Sapelo Sound from Blackbeard and Sapelo islands to the south (fig. 1). The island consists of a variety of environments ranging from densely forested areas supporting many different floral associations to widespread tidal (salt) marshes, tidal flats, and open sandy beaches. Be-



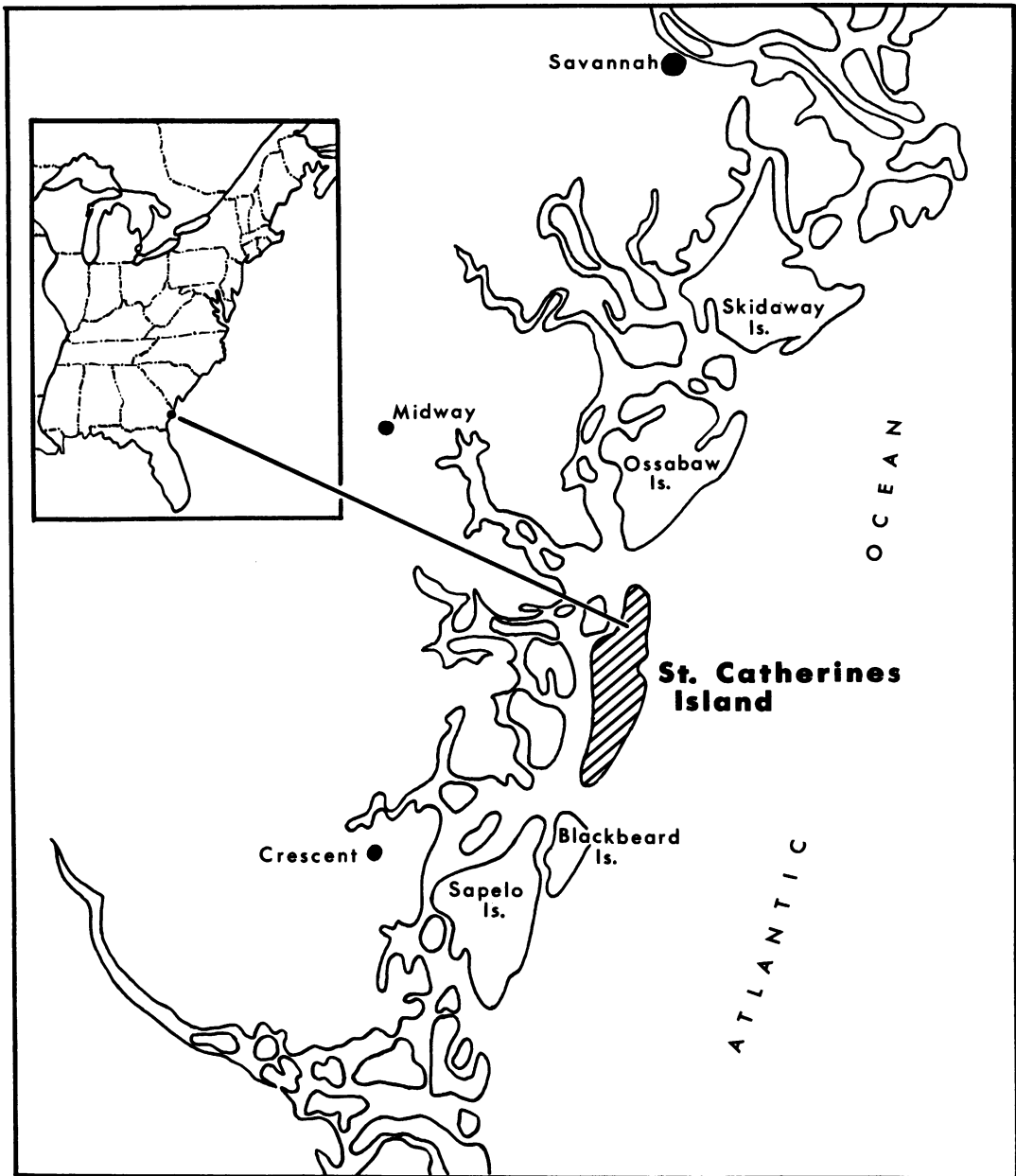


FIG. 1. Map showing the location of St. Catherines Island, Georgia.

cause our investigation focused mainly on intertidal organisms and their habitats, we concentrated our study on the various littoral zone environments. Open sand beaches extend the full length of the island along its eastern (seaward)

shore and sand spit complexes are found at both the northern and southern tips of the island. Some shoreline areas are represented by extensive sandy tidal flats which are exposed at low tide and support several organism communities.

Another commonly encountered intertidal environment is the salt marsh, dominated by *Spartina* grass, which comprises 80 percent of the western shoreline and occupies a very large portion of the east central region immediately behind the sand beach complex.

#### DESCRIPTION OF FIELD STATIONS

Following a reconnaissance survey of the island's intertidal environments, several localities were selected on the basis of diversity of habitat and accessibility for detailed study. We decided that it was feasible to examine all the major intertidal habitats by restricting our detailed field work to the northern portion (fig. 2).

Stations 1 and 2, situated on North Beach, were studied in greatest detail. North Beach is a long, slightly arcuate sand beach on the eastern (seaward) shore of St. Catherines Island. It stretches from the large sand spit which forms the Northeast Point of the island southward approximately 2.6 miles to Seaside Inlet, a moderate-sized tidal channel that drains the northern portion of a large salt marsh complex forming the east central portion of the island. North Beach is an open beach and represents the highest energy environment we studied on St. Catherines Island. However, it does not normally possess the high energy surf and large breakers typical of many Atlantic coast beaches. The majority of North Beach sand is fine-grained quartz. In some places obvious depositional features, such as the sand spit at Northeast Point, are being constructed by means of the longshore transport system moving sand along the surf zone and the lower foreshore portion of the beach. Also evident along a portion of North Beach is a steep sand bluff, ranging from 20 to 25 feet in height. This bluff well illustrates the ongoing effects of coastal erosion since, at high tide, the waves slowly undercut the base of the bluff causing slumping and sliding of sand onto the beach where it is carried away by the longshore transport system. Progressive erosion in this manner creates the steep erosional face of the sand bluff and undercuts numerous trees which subsequently fall onto the beach surface below (figs. 3, 4). The portion of North Beach that best illustrates this phenomenon extends from the Picnic Area south to the area adjacent to Station 1.

Stations 1 and 2 are representative of the several relict salt marsh deposits along North Beach. These relict deposits are currently being exhumed, in part, by normal beach erosion processes in the foreshore area of the beach. It appears that through time longshore transport of sand along the seaward shore of St. Catherines Island has slowly buried the northeastern fringe of the large salt marsh, which occurs along the east central portion of the island. Visible remnants of this marsh complex in the form of salt marsh peat and mud deposits are evident on North Beach in several places due to removal of overlying quartz sand. Station 1 is situated approximately 1.4 miles south of Northeast Point adjacent to the southern end of the aforementioned sand bluff. Station 2 is approximately 0.3 mile south of Station 1, also in the foreshore portion of the beach.

A totally different type of intertidal environment is represented by Stations 3 and 4 (fig. 2). These stations are situated along the northwestern tip of the island and represent a protected sandy beach environment along St. Catherines Sound and adjacent Walburg Creek, a very large tidal channel which opens into St. Catherines Sound at the northwestern point of the island. At high tide, this area represents a moderate to low energy, narrow sand beach; however, at low tide a relatively narrow sandy tidal flat ranging from 100 to 150 feet in width is exposed. Station 3 is situated on the beach approximately 100 feet west of Engineer Point—West, where the west (left) fork of Engineer Road intersects the northwestern shore of the island (see fig. 2). At this locality, a transect across the narrow sand flat was made in order to study the distribution and abundance of the dominant epifaunal and infaunal organisms.

Station 4 is approximately 0.4 mile south and west of Station 3 on the same narrow sand flat, which forms the northwestern shore of St. Catherines Island. This portion of the sand flat is also a protected, rather low energy intertidal environment and forms the eastern bank of Walburg Creek. Station 4 harbors several large populations of *Ilyanassa obsoleta*, a common intertidal snail.

The northern shoreline of St. Catherines Island fronts on St. Catherines Sound, a large inlet separating Ossabaw Island from St. Catherines



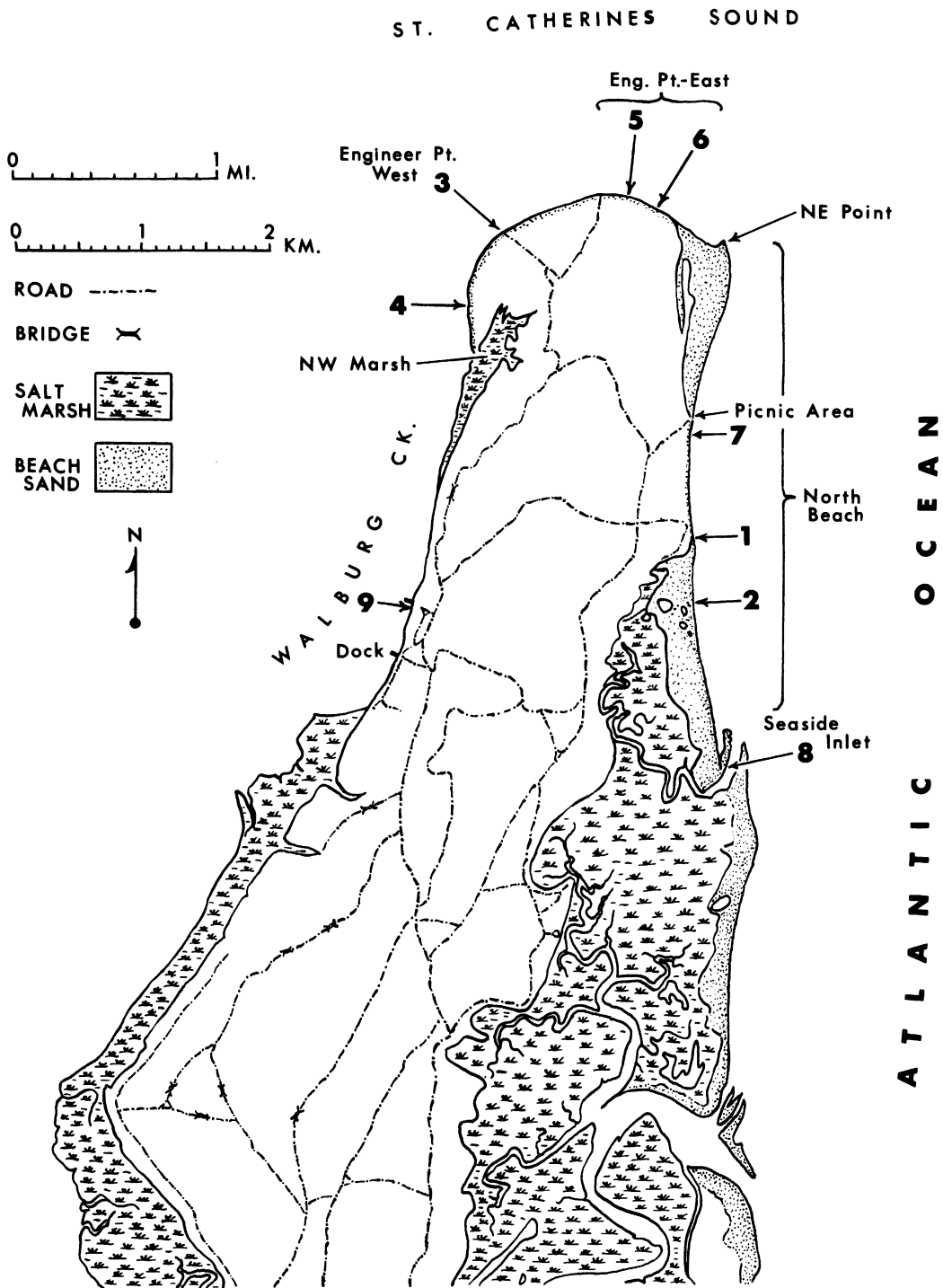


FIG. 2. Map of northern half of St. Catherines Island. The numbers refer to sample stations discussed in text.



FIG. 3. North Beach, St. Catherines Island, at low tide. View to north with Northeast Point in background. Dark area on beach in distance is a relict peat and mud deposit (Station 7)



FIG. 4. View to south, along North Beach, at low tide. Note erosional bluff and two deposits of relict peat and mud; Station 7 near center of photograph and Station 1 in background.

Island. Stations 5 and 6 are in an area herein called Engineer Point—East, which incorporates a

wide sandy tidal flat at low tide. The western end of this sand flat is 0.15 mile east of the shoreline



terminus of the east fork of Engineer Road. The shoreline between Station 3 (Engineer Point—West) and the western end of this wide sand flat illustrates the ongoing effects of a high rate of coastal erosion. Over the years significantly large amounts of sediment have been removed from this stretch of shoreline by the tidal currents surging in and out of St. Catherines Sound. Numerous effects of this erosion can be seen in the form of undermined and toppled trees along the beach, as well as standing trees and palmetto clusters with several feet of their root systems exhumed and exposed.

The wide sandy tidal flat at Engineer Point—East presents yet a different type of intertidal environment. It is a low energy environment situated in a somewhat protected position behind the sand spit forming Northeast Point. At high tide, the sand flat is submerged and a narrow sand beach stretches along the shore; however, at low tide a sand flat approximately 500 to 600 feet wide becomes emergent. This sand flat appears to be quite comparable in size and other characteristics to Nannygoat and Cabretta tidal flats on Sapelo Island (Howard and Dörjes, 1972). The tidal flat is entirely composed of

quartz sand. However, significant amounts of dark fecal pelletal muds are in the troughs of the ripple marks that cover nearly the entire flat surface at low tide (fig. 5). Station 5, near the western end of the flat, denotes an area where a mixed association of several different species of intertidal snails was observed and collected. Station 6 is situated near the center of the flat approximately 0.3 mile east of the terminus of Engineer Road (east fork) and 0.4 mile west of Northeast Point and is the site of a transect measured across the flat perpendicular to shore. The purpose of the transect was to determine the presence, distribution, and abundance of the common epifaunal and infaunal organisms in this habitat. Data from Station 6 and from Station 3 were compared with similar data reported by Howard and Dörjes (1972) from nearly Sapelo Island.

Station 7, about 125 yards south of Picnic Area, represents the northernmost relict mud deposit on North Beach (fig. 6). This station was selected because it presents a low relief of mud deposits which are frequently buried by thin sheets of quartz sand.

Station 8, on North Beach adjacent to Seaside

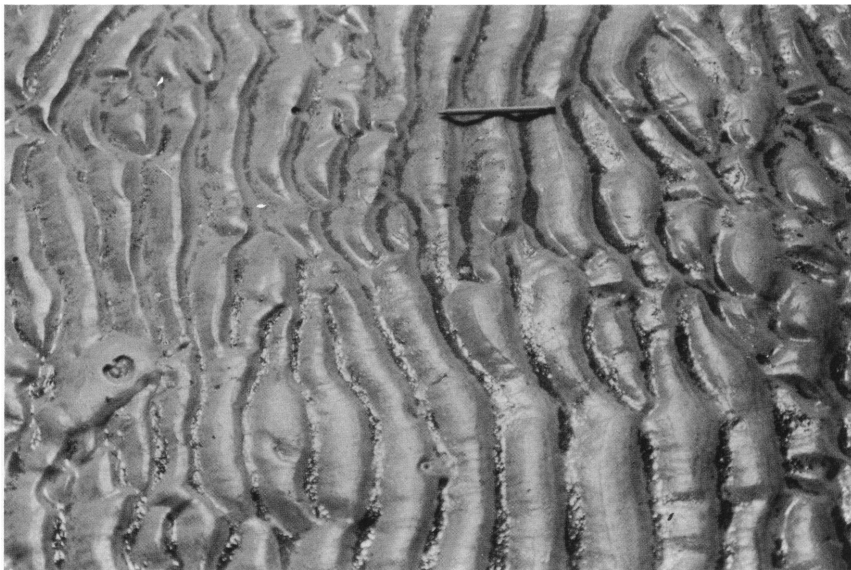


FIG. 5. Ripplemarks on Engineer Point—East sand flat at low tide. Note fecal pellets concentrated in troughs of ripples.

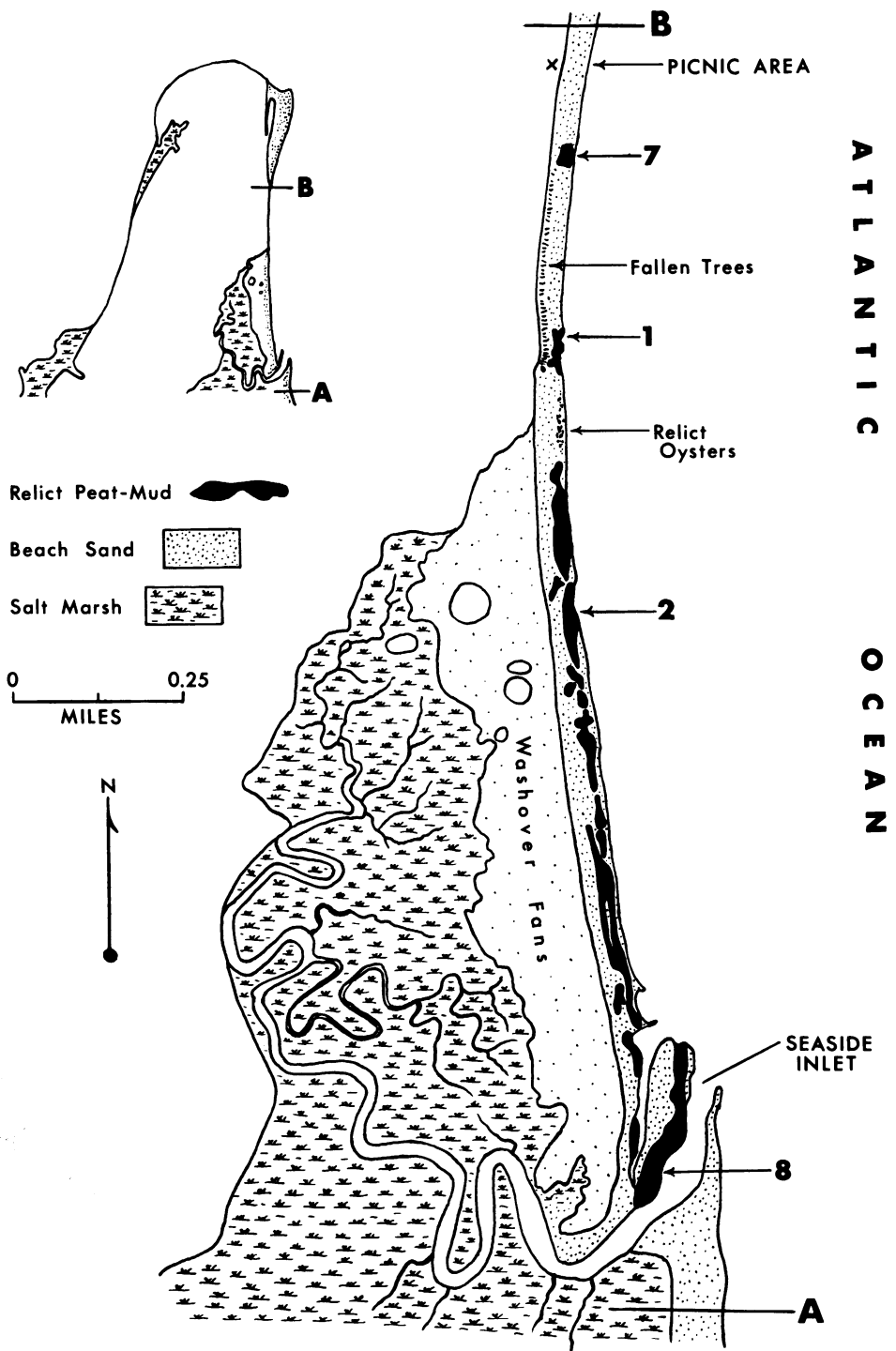


FIG. 6. Map showing location and distribution of relict peat and mud deposits along North Beach, St. Catherine's Island. Numbers refer to locations of sample stations.

Inlet, portrays yet another variation of relict mud deposits. Here the mud deposit presents a wide tidal flat at low tide and is partially covered by thin but widespread sheets of wave- and current-rippled sand.

Station 9 is situated on the western side of the

Island, adjacent to the Manor House Dock. A narrow fingering *Spartina* marsh extends along the shore of Walburg Creek at this point and contains large populations of the common periwinkle *Littorina irrorata* and the mussel *Geukensia demissa*.

## METHODS AND PROCEDURE

The variety of littoral environments investigated prevented any single or uniform procedure of study. The methods employed proved very appropriate in some cases, but less so in others.

As mentioned above, North Beach Stations 1 and 2 are similar in faunal communities, type of substrate, and distribution. Also, both contain abundant infaunal bivalve populations. Sampling, at these sites, was designed to provide detailed information on the abundance and distribution of the densely packed epifauna and infauna inhabiting the relict marsh deposits. Therefore, the study quadrants were restricted to a small size in order to carefully tabulate and collect the entire biota for later morphometric study. At each station, two different sites were sampled at low tide; one at the seaward edge of the deposit (designated A), the other near the midpoint of the deposit (designated B). At each of these sampling sites, a 2 feet by 2 feet quadrant was set up. Surface and subsurface counts to a depth of from 6 to 8 inches were made of the infaunal bivalves and associated organisms in each quadrant. This permitted not only comparisons between stations but also between seaward and backshore portions of each station. The organism counts made at these four sites are very accurate, as extreme care was taken to remove complete blocks of the substrate to be broken down by hand for tabulations and collection of the entire faunal association. These specimens were preserved in a formalin solution for later size-frequency measurements. During extraction of the substrate and fauna, orientation and characteristics of the burrows were noted, as well as data concerning numbers of living and dead bivalves in the sample. Substrate samples were collected at various levels at each site for detailed microfaunal and sediment analysis. Those results, however, are not included in this paper.

Different study techniques were employed at Stations 3 (Engineer Point—West) and 6 (Engineer Point—East). Our emphasis was to ascertain onshore-offshore variation in the epifauna and infauna over a considerable expanse of tidal flat. Regular spacing of relatively large quadrants provided extensive coverage of the tidal flat. In contrast to Stations 1 and 2, our concern here was quick tabulation of abundance and distributional data. No effort was made to study the infauna in detail, nor to effect total recovery of contained fauna for subsequent study. These stations are similar in that both represent semiprotected sandy tidal flats along the shore of St. Catherines Sound. At both stations 15 feet by 15 feet quadrants were set up at low tide on the tidal flat surface. These quadrants were spaced along a transect line across the tidal flat perpendicular to the shore face and extending from the low to high tide marks. In each quadrant, we made detailed surface counts not only of all the epifaunal organisms, but also the surface tubes, trails, and traces made by infaunal and epifaunal organisms. This method provided fairly accurate abundance data on species in each 225-square-foot quadrant. However, since the sediment substrate of the entire quadrant was not sieved, abundance data for all infaunal species could not be tabulated. Sediment samples were taken from the quadrant and sieved in order to obtain a general overview of the contained infauna. At Station 3, the tidal flat is relatively narrow, about 115 feet in width from the low to high tide marks. Two 15 feet by 15 feet quadrants were set up at this station. Station 6 represents a very wide tidal flat, 500 to 600 feet wide at low tide. Here, five 15 feet by 15 feet quadrants were set up along the line of transect at intervals of 100 feet. Data from these two localities were compared with one another as well as with that reported by Howard and Dörjes

(1972) from two similar tidal flats on Sapelo Island, Georgia.

Stations 4 and 5 are situated on narrow and wide sandy tidal flats, respectively, and represent sites where populations of intertidal gastropods were observed and collected. Our field procedure was designed to provide a large and random sample of the intertidal gastropod population. The high density of gastropods at Station 4 determined the size of the quadrant. At Station 4, the sand flat exposed at low tide measured approximately 105 feet in width. A 10 feet by 10 feet quadrant was set up in the middle of a population of *Ilyanassa obsoleta*, on the lower portion of the flat about 10 feet from the low tide water line. The surface behavior and distribution of the snails were observed and the entire population sample within the quadrant was collected and preserved in formalin for later study. Station 5, near the inner western end of the extensive Engineer Point—East tidal flat, represents the site where a random sample of intertidal gastropods of several species was collected. No quadrant was established because the snails were sparsely distributed over a broad area of the flat surface. Sampling was accomplished during the outgoing tide while the snails were continuously emerging onto the tidal flat surface from below.

The procedure of study at Stations 7 and 8 was similar to that employed at Stations 1 and 2. Two 2 feet by 2 feet quadrants were established in each case in order to assess the nature and abundance of both epifaunal and infaunal organisms.

At Station 9, a 5 feet by 10 feet grid was established in order to monitor the populations of *Littorina irrorata* and *Geukensia demissa*. The size of the grid was determined by the density of individuals at this locality. A larger grid would have made the counting of specimens impossible in the time available at each intertidal interval.

Sediment samples and observations were taken at several additional intertidal localities on both the northern and southern portions of St. Catherines Island. The *Spartina* marsh—mud flat areas of Northwest Marsh and the complex of subenvironments in Seaside Inlet were the subjects of considerable investigation (fig. 2). The *Littorina irrorata* populations of the various *Spartina* marshes are part of an extensive ongoing study and will be discussed in a later published report. Wherever appropriate in succeed-

ing sections of this paper, supplemental data from other intertidal localities will be mentioned.

## RESULTS

*Stations 1 and 2—North Beach.* The peat and mud deposits of Stations 1 and 2 are clearly interpretable as the remnants of a salt marsh environment since careful examination of the muds yielded numerous roots and fragments of *Spartina* sp. (marsh grass) and other associated reeds and marsh flora, as well as shells of *Littorina irrorata*, the common salt marsh gastropod. Occasional articulated valves of *Geukensia* (= *Modiolus*) *demissa* and fragments of *Uca* sp., the marsh fiddler crab, were also found. Interspersed among and adjacent to the mud deposits are relict shell banks composed of valves of the common oyster, *Crassostrea virginica* (figs. 7, 8). In this area, living oyster banks are commonly developed in an intertidal position along the banks of tidal channels and creeks in or near salt marshes. The abundance of these mud deposits and their present location on North Beach indicates that the large salt marsh complex comprising the east central portion of the island probably extended farther seaward than its present limits. Extensive coastal marshes formerly occupied large portions of the continental shelf during periods of lowered sea level. As sea level rose, these low coastal environments were inundated by the transgressing nearshore marine environment. Subsequently, beach sands and marginal marine sediments were transported and deposited over these marsh muds by active longshore currents and high storm tides.

Another example of relict marsh deposit was mentioned by Frey and Howard (1969) and Howard, Frey and Reineck (1973). They reported relict marsh deposits being exposed by active erosion on the foreshore of Cabretta Beach in the nearby Sapelo Island—Blackbeard Island complex. As the old marsh deposits are exhumed and eroded on the seaward foreshore of the beach, beach sand is being processed landward forming washover fans which build westward over the present (live) marsh. Similar washover fans and conditions exist on North Beach between Station 1 and Seaside Inlet, as well as numerous sites along the middle and southern portions of the Island's eastern shore. The nature



FIG. 7. Relict oyster bank (*Crassostrea virginica*) and associated mud deposit. Station 2 area on North Beach. View to northeast, at low tide.



FIG. 8. Portion of the same oyster bank (fig. 7) showing dead individuals of *C. virginica* oriented in life position.

of the relict deposits on Cabretta Beach (including the preserved organisms) seem nearly identical with the North Beach deposits of this study.

Schäfer (1972) reported the similar formation of relict peat deposits in coastal portions of the North Sea. These extensive deposits are also in-



habited by boring infaunal bivalves as are those on St. Catherines Island. In fact, Schäfer (1972, p. 355) reported that he observed, in 1958, thick *Spartina*-rich clays on the Georgia coast bored by *Petricola*, an infaunal bivalve.

Station 1 exposes a brownish peat overlying dark gray muds. The surface of the peat, at its northern end, stands approximately 32 to 40 inches above the beach surface and, at the southern end, 12 to 16 inches above the beach surface. This peat-mud deposit is entirely exposed at low tide and has a highly serrated seaward face caused by erosional surge channels cut perpendicularly into the deposit (fig. 9). A shallow sand runnel extends along the back and north end of the deposit where the outgoing tide collects in tidal pools and slowly drains off. In June, 1975, the peat-mud deposit measured approximately 260 feet in length (north-south) and from 59 to 84 feet in width. The deposit was remeasured in June 1976, and found to be only 200 feet long and from 33 to 44 feet wide. This size reduction was due to the encroachment and partial burial by shifting foreshore beach sands. In vertical section, the deposit displays a dense, spongy mat of medium brownish peat that extends from the

surface to a depth that varies from 1 to 11 inches and consists almost entirely of plant remains. Underlying this peaty layer is a homogeneous deposit of medium to dark gray mud which contains sporadic *Spartina* and other plant fragments. Coring and probe work at different locations around the periphery of the deposit indicate the gray mud extends from 8 inches to more than 6½ to 7 feet in depth below the beach surface. Detailed probe work at many locations reveal that beach sands completely underlie the deposit and that the peat/mud complex varies in total thickness from 5 to 6 feet in the northern portion to 8 or more feet in the central portion, and 2 to 5 feet in the southern portion.

The dominant macro-organisms of the intertidal community of Station 1 (herein named the *Brachidontes*-*Petricola* Association) can be subdivided into epifaunal and infaunal components and are listed, along with relative abundance data, in table 1. Figures 10 and 11 depict the general organization of the *Brachidontes*-*Petricola* Association.

In the shallow tidal pool and adjacent sand runnel area behind the peat deposit, we periodically observed *Polinices duplicatus* and *Busycon*



FIG. 9. North end of Station 1 peat and mud deposit, North Beach. View to the east at low tide.

TABLE 1  
Station 1 — *Brachidontes-Petricola* Association

EPIFAUNAL ORGANISMS		
<i>Brachidontes recurvus</i> (bivalve)	—	V A <sup>a</sup>
<i>Lyonsia</i> sp. (bivalve)	—	C - R
<i>Balanus</i> sp. (barnacle)	—	R
<i>Ulva</i> sp. (green alga)	—	R
polychaete worms (unidentified)	—	V R
hermit crabs (unidentified)	—	R - C
<i>Terebra dislocata</i> (gastropod)	—	V R
INFAUNAL ORGANISMS		
<i>Petricola pholadiformis</i> (bivalve)	—	V A
<i>Barnea truncata</i> (bivalve)	—	R
<i>Cyrtopleura costata</i> (bivalve)	—	V R
polychaete worms (unidentified)	—	C

<sup>a</sup>Abundance in terms of abundant (A), common (C), and rare (R).

*carica*, both predatory gastropods, and numerous hermit crabs inhabiting a variety of discarded gastropod shells. One curious occurrence of a hermit crab occupying a fragment of *Juncus* reed was noted.

Quadrant 1A of Station 1 was close to the seaward edge of the peat deposit near a small surge channel which received periodic pounding by the surf, as well as the movement of water from swashing waves. Quadrant 1B was situated on the upper surface of the peat deposit, about 48 feet behind the seaward edge. At low water, most of the deposit is exposed in the littoral zone, whereas at high tide, the deposit is entirely submerged. Quadrant 1B would receive nearly continuous turbulence during high water, since the high-tide waves break across the upper surface of the deposit.

The distribution of epifaunal and infaunal components of the *Brachidontes-Petricola* Association coincides with distribution of substrate type. The epifaunal organisms, dominated by byssally attached *Brachidontes recurvus*, are found entirely on the surface of the peat deposit.

In quadrant 1A, *B. recurvus* numbered 217 individuals (54% of the epifauna) and averaged 54 individuals per square foot (table 3). In marked contrast, near the middle of the peat deposit individuals of *B. recurvus* were so densely

packed they formed a resistant "pavement" across the surface of the deposit (figs. 10 and 12). Quadrant 1B is typical of the upper surface of this peat deposit and 3979 individuals of *B. recurvus* were counted. They represented 83 percent of the epifauna and averaged 995 individuals per square foot.

*Lyonsia* sp., another tiny epifaunal clam, often occurs in clusters within the *Brachidontes* "pavement." Also associated are scattered clumps of the green alga, *Ulva* sp. and clusters of *Balanus* sp.

Much of the peat deposit has been bored and infiltrated by infaunal clams and burrowing worms. The dominant boring clam is *Petricola pholadiformis*. *Barnea truncata* is present, but much less common (table 1). The infaunal clams live in vertical to steeply inclined tubes which have been bored into the dark gray muds underlying the peat layer (figs. 13, 14). Stanley (1970, p. 8) stated that *P. pholadiformis* normally lives as a borer in hard substrates but some individuals live as burrowers in soft sediment; and this is, therefore, one of those interesting species utilizing more than one life habitat. Schäfer (1972) characterized *P. pholadiformis* and *Barnea candida* as boring bivalves which mechanically drill into hard substrates, namely wood and peat, by use of denticles and anterior filing ridges as well as by chemical techniques. However, Purchon (1955) stated that *P. pholadiformis* is adapted for burrowing in soft substrates only, since it lacks the specialized boring devices of the pholads. In areas of the peat deposit where some of the peat layer has been eroded (quadrant 1A), the clam borings penetrate either the mud or 1 to 6 inches of peat and mud. In other areas, the borings often penetrate peat, a peat/mud mixture, or entirely mud.

At quadrant 1A, the peat deposit was examined for infauna at two successive 9-inch thick levels. *P. pholadiformis* comprised 68 percent of the total infauna in the upper 9-inch interval, compared with 10 percent for *B. truncata* (table 2). This interval contained a total of 617 individuals (bivalves and polychaete worms) and averaged 206 individuals per cubic foot of substrate. Infaunal abundance sharply declined in the lower 9-inch interval and *P. pholadiformis*

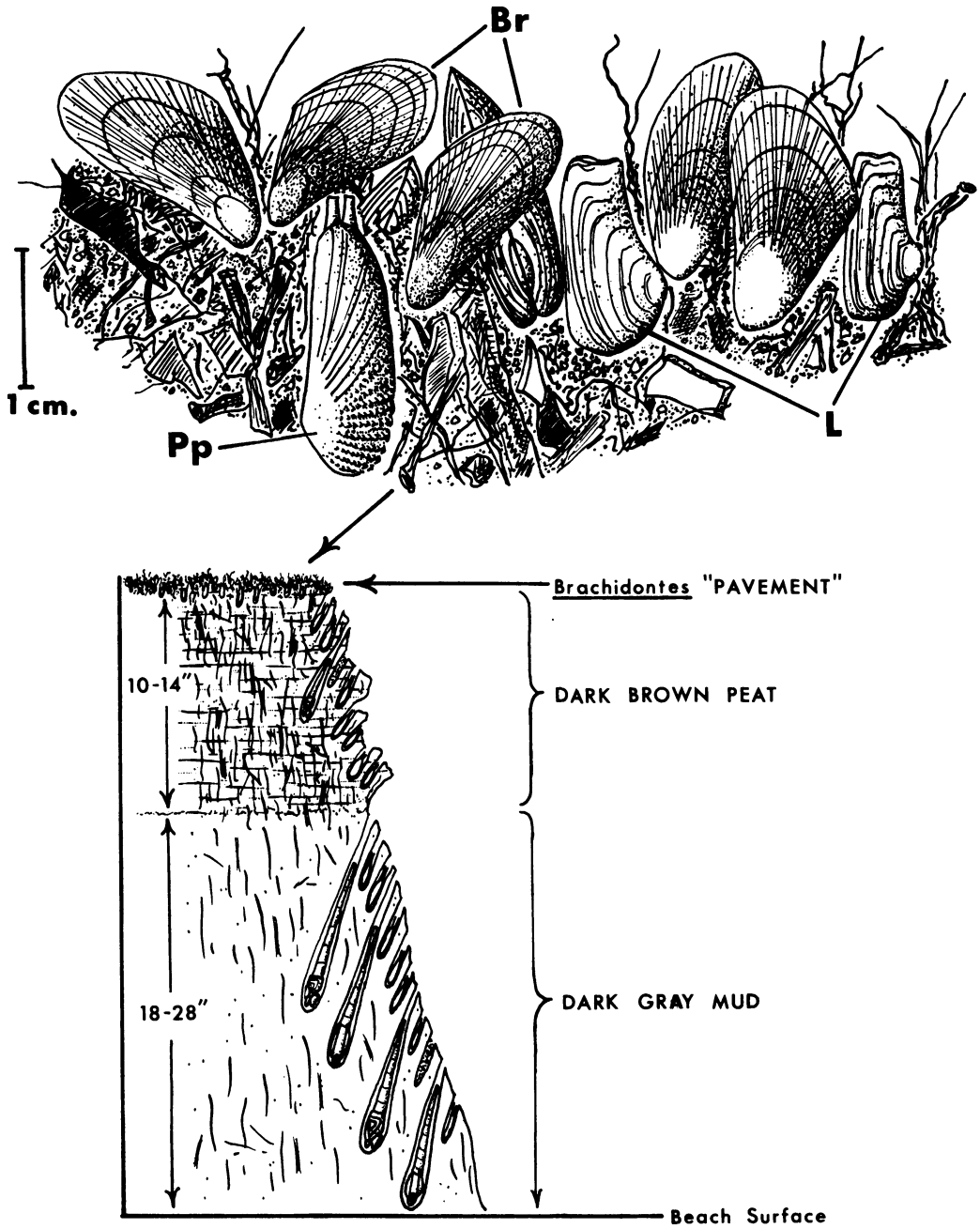


FIG. 10. Vertical profile of the peat-mud deposit at Station 1, including an enlarged cross-sectional diagram of the *Brachidontes* "pavement". Br, *Brachidontes recurvus*; L, *Lyonsia* sp.; Pp, *Petricola pholadiformis*.

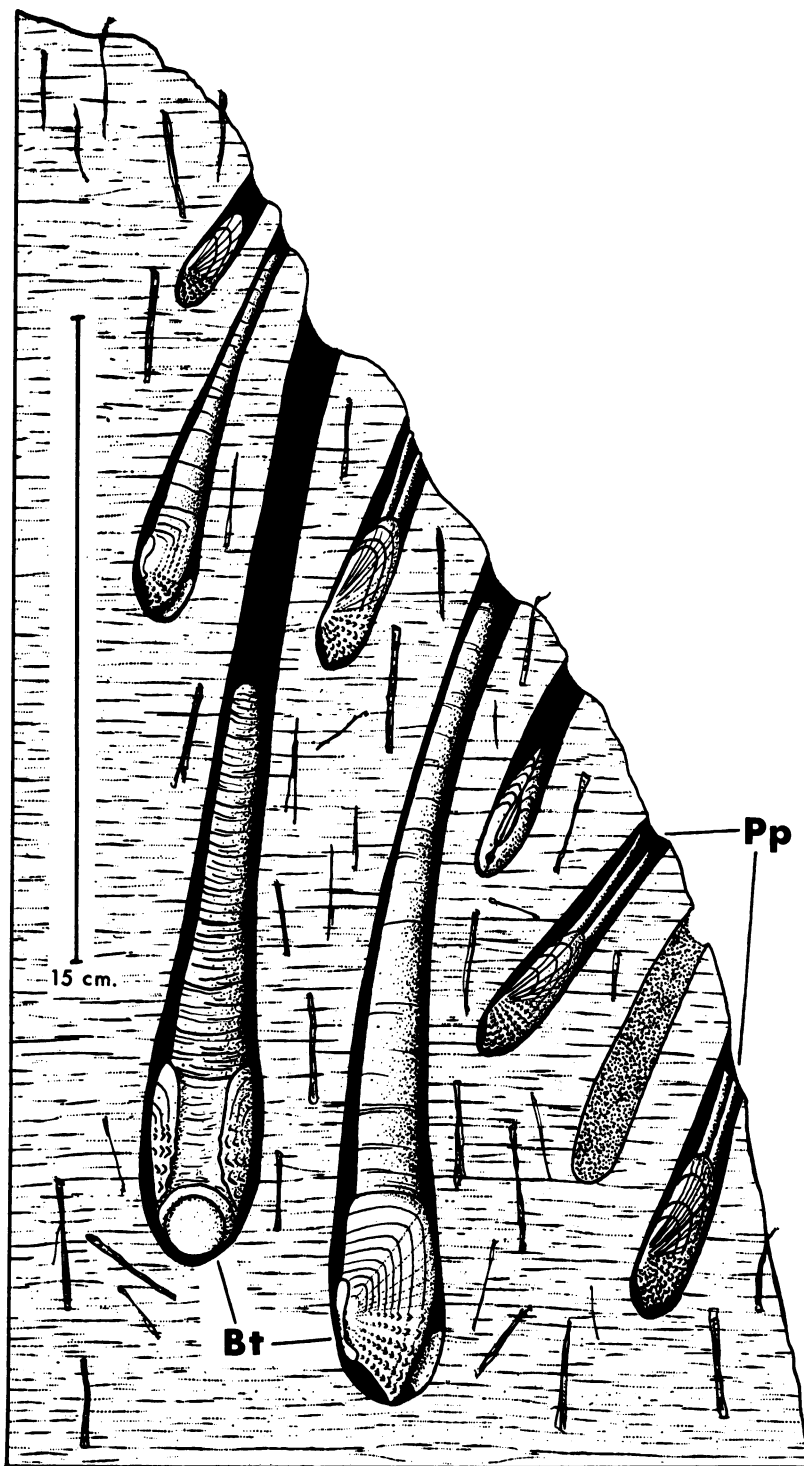


FIG. 11. Enlargement of a portion of figure 10 illustrating the distribution of *Barnea truncata* and *Petricola pholadiformis* in the Station 1 deposit. The dark gray mud contains plant fragments. Pp, *Petricola pholadiformis*; Bt, *Barnea truncata*.



FIG. 12. Surface of peat layer at Station 1 showing the "pavement" of living *Brachidontes recurvus*.



FIG. 13. Typical infaunal bivalves of the relict peat and mud deposits on North Beach. Top row, *Barnea truncata*; Bottom row, *Petricola pholadiformis*.

made up only 39 percent of the total infauna whereas *B. truncata* increased to 32 percent. The total abundance in this lower interval was only

28 individuals (9.3 individuals per cubic foot of substrate).

Observations of these two bivalves indicate



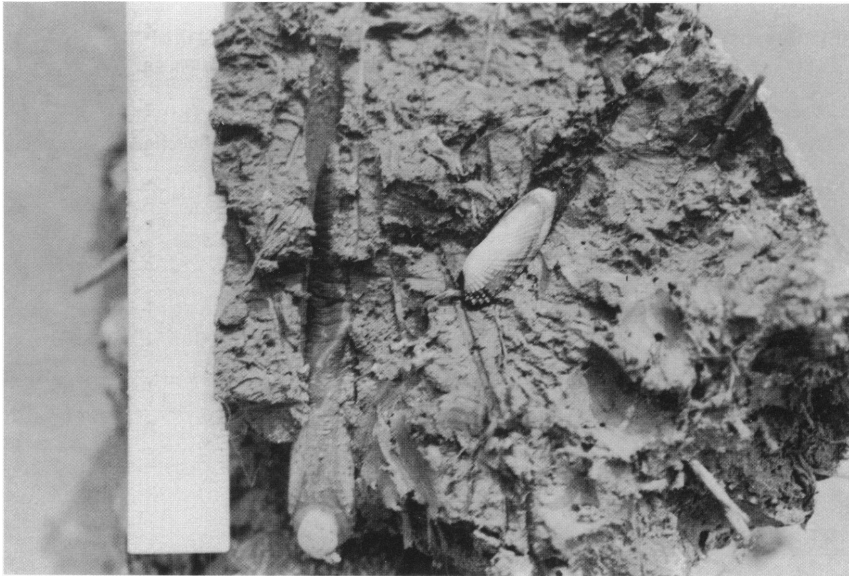


FIG. 14. Station 1. Cross-sectional view through mud deposit showing *Petricola pholadiformis* (shorter boring) and *Barnea truncata* (longer boring).

that *B. truncata* is generally a deeper borer (or burrower) than *P. pholadiformis*. The latter was observed in borings to a maximum depth of 4.5 to 5 inches, whereas *B. truncata* was noted at depths of less than 5.5 inches to a maximum of 11 or 12 inches below the surface. Correspondingly, *B. truncata* has a relatively longer siphon than that in *P. pholadiformis*. The greatest density of *B. truncata* occurred in the upper 9-inch interval along the seaward portion of the peat deposit and, in general, individuals of this species normally occur slightly deeper in the substrate than similar sized individuals of *P. pholadiformis* in the same deposit.

Also, in quadrant 1A the majority of errant polychaetes occurred in the upper 9-inch interval, compared with only eight worms in the lower interval.

In quadrant 1B, the infaunal association was studied only to a depth of 6 inches below the surface. This marked the total depth of infaunal habitation in quadrant 1B, and was therefore considerably less than the penetration observed in Station 1A. However, distribution and abundance data were gathered for two different intervals: the uppermost 1-inch layer and the suc-

cessively lower 5-inch interval. As in quadrant 1A, *P. pholadiformis* dominated the infauna, comprising 58 percent of total individuals. Polychaetes equaled 41 percent (table 2). Total infaunal abundance averaged 140.5 individuals per cubic foot. A significant aspect of the infaunal distribution in quadrant 1B is that 97.5 percent of the total infauna occurred within the upper 1 inch of substrate, immediately below the *Brachidontes* "pavement." In this quadrant individuals of *Brachidontes recurvus* form an extremely dense, resistant surface which impedes wave erosion of the peat deposit. The *B. recurvus* individuals are firmly attached by byssal threads to the peat surface, to each other, and to occasional individuals of *Lyonsia* sp. This resistant mat forms a hardground-type surface upon which larval spat of several organisms can settle and attach. Examples include encrusting individuals of *Balanus* sp. and clusters of *Ulva* sp. Only 83 *P. pholadiformis* individuals were found living in the substrate of quadrant 1B, compared with 347 living individuals in quadrant 1A. However, 80 of these individuals occurred in the upper 1 inch of the substrate, immediately below and closely associated with the *Brachi-*

TABLE 2  
 Statistical Census of the Intertidal Fauna from Quadrants 1A and 1B of Station 1 Peat/Mud  
 Deposit on North Beach, St. Catherines Island, Georgia<sup>a</sup>

QUADRANT 1A (upper 9" layer)	No. living specimens	No. articulated valves	No. single valves	Total no. specimens	% of total fauna	No. spec./cu. ft.
<i>Petricola pholadiformis</i>	337	54	57	420	68	140
<i>Barnea truncata</i>	46	—	34	63	10.2	21
<i>Cyrtopleura costata</i>	2	—	—	2	0.3	0.6
polychaete worms (unident.)	132	—	—	132	21.4	44
TOTALS				617		205.6
QUADRANT 1A (lower 9" layer)						
<i>Petricola pholadiformis</i>	10	—	1	11	39	3.6
<i>Barnea truncata</i>	5	4	—	9	32	3
polychaete worms (unident.)	8	—	—	8	29	2.6
TOTALS				28		9.3
QUADRANT 1B (upper 6" layer)						
<i>Petricola pholadiformis</i>	83	76	6	162	57.6	81
<i>Barnea truncata</i>	3	—	—	3	1.1	1.5
polychaete worms (unident.)	116	—	—	116	41.2	58
TOTALS				281		140.5

<sup>a</sup>Represents 2 feet by 2 feet quadrants sampled to depths stated.

*dontes* zone. In fact, small individuals of *P. pholadiformis* were observed living among and serving as attachment sites for *B. recurvus*. Thus *P. pholadiformis* can occupy situations not only variable in type of substrate but also ranging from very shallow, near surface borings to deeper cylindrical, tubular borings in mud deposits. Small individuals of *P. pholadiformis* and *Lynsia* sp. were often found with distorted valves, presumably due to the dense packing within the *Brachidontes* mat.

The co-occurrence of dense populations of *P. pholadiformis* with *B. recurvus* would appear to violate the postulate of Woodin (1976, p. 34) that "No infaunal forms should consistently attain their highest densities among densely packed suspension-feeding bivalves." Although it is true that higher densities of *P. pholadiformis* were attained in quadrant 1A, individuals were distributed over a depth of 5 inches. In quadrant 1B, *P. pholadiformis* was virtually limited to the upper 1 inch, coincident with the *Brachidontes* "pavement." Certainly, quadrant 1B would have to be viewed as containing dense assemblages of infaunal and epifaunal bivalves!

In these peat deposits, the distribution of surface boreholes (openings) is not very representative of the distribution and abundance of infaunal bivalves. In quadrant 1B, no boreholes were observed in the dense *Brachidontes* mat; however, 83 living and 79 dead specimens of *P. pholadiformis* were collected from the substrate. In quadrant 1A, where exposed gray muds and portions of the *Brachidontes* mat were present, a total of 151 surface boreholes of *P. pholadiformis* were counted (table 3). Analysis of the substrate revealed a total of 347 living and 83 dead *P. pholadiformis* individuals as well as 46 living specimens of *B. truncata* (table 2).

Observations of a vertical profile of the peat deposit displayed a definite pattern of size distribution within the *P. pholadiformis* and *B. truncata* populations. As might be expected, the smallest individuals occurred in the upper 1 or 2 inches, while progressively larger individuals occurred at correspondingly greater substrate depths. Larger (older) individuals obviously possess longer, more well-developed inhalant and exhalant siphons and are able to live in deeper, more well-protected borings. As the individuals

TABLE 3  
Surface Census of the Intertidal Fauna of Quadrants 1A and 1B at the Station 1 Peat/Mud Deposit on North Beach, St. Catherines Island, Georgia<sup>a</sup>

	QUADRANT 1A (Seaward Edge)			QUADRANT 1B (Middle Portion)		
	No. living specimens	% of total fauna	No. specimens/sq. ft.	No. living specimens	% of total fauna	No. specimens/sq. ft.
<i>Brachidontes recurvus</i>	217	54	54.2	3979	83	994.7
<i>Lyonsia</i> sp.	142	35	35.5	259	5.4	64.7
<i>Petricola</i> boreholes	151	—	37.7	— none visible	—	—
algal clumps ( <i>Ulva</i> sp.)	29	7	7.2	255	5.3	63.7
<i>Balanus</i> sp.	14	3	3.5	289	6	72.7
polychaete worms (unident.)	— none visible	—	—	1	—	—
TOTALS	402		100.5	4783		1195.7

<sup>a</sup>Represents surface counts of 2 feet by 2 feet quadrants.

grow, they bore deeper into the deposit. Schäfer (1972) reported that when a substrate surface became too heavily infested with borings, secondary settlement was impossible. Some juveniles might bore into the rim area between existing boreholes, but further progression of boring activity would intersect an existing borehole and the individuals would probably be washed out. This usually results in death because a bivalve would not be able to use its specialized foot for orientation and reborings.

From a paleoecological viewpoint, the observed size distribution of these infaunal bivalves might be useful in recognition of a "paleosurface" and permit discrimination between top and bottom in a sedimentary sequence.

*Station 2—North Beach.* Station 2, approximately 1.7 miles south of Northeast Point and 0.3 mile south of Station 1, conforms to the majority of the relict mud deposits along North Beach in that it rises only several inches to a foot above the normal beach surface and is almost entirely composed of medium to dark gray mud. The upper peat layers typical of Station 1 are lacking. This mud deposit covers a larger overall area than the Station 1 deposit, extending in irregular patches for hundreds of yards along the foreshore of the beach (figs. 2 and 6). Quartz beach sands are often found washed over portions of the mud deposits. In other places, small remnants of relict oyster banks protrude upward in the foreshore area adjacent to the muds. The surface of the muds is liberally bored by *P.*

*pholadiformis* and other infaunal organisms, occasionally resulting in extreme bioturbation. A nodular texture of gray mud lumps intermixed with quartz sand and sandy mud is found in some surficial portions of the deposit where beach sands have either been washed into boreholes in the mud or the mud layers are thin and the boreholes intersect intercalated lenses of sand. This further demonstrates mixture of different lithologies by extensive bioturbation.

In places where *Petricola* boreholes intersect sand lenses or receive surface sands washed in from above, an interesting biogenic structure is often formed at the surface of the borehole. The structure appears superficially as a small, rounded "button-like" mound of sand penetrated vertically by two distinct holes (fig. 15). These *Petricola* "buttons" are semiconsolidated rounded masses of sand which form a cap at the top of some *Petricola pholadiformis* boreholes with the two holes permitting inhalant and exhalant water flow via the siphons of the bivalve. *Petricola* "buttons" are common in relict mud deposits supporting *Petricola* populations, especially in areas where beach sands have been washed across and into available boreholes. If preserved and indurated, these structures might form recognizable trace fossils.

Wave action along this and other such relict mud deposits on St. Catherines Island continually dislodges mud in chunks of various sizes. These mud clasts, when caught in the longshore transport system, are often moved considerable

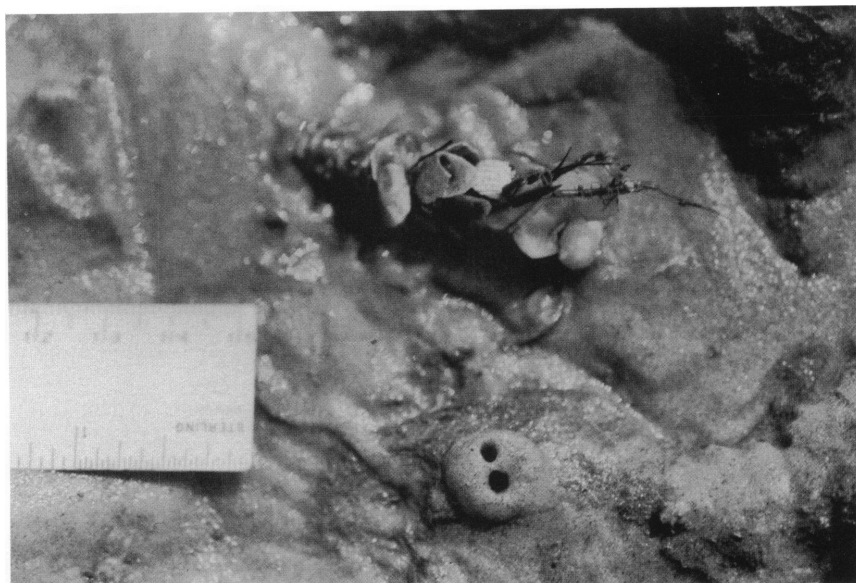


FIG. 15. Station 2, relict mud deposit on North Beach. Note the *Petricola* sand mound ("button") in lower portion of photograph. The top portion of a *Diopatra cuprea* tube can be seen in the upper center of the photograph.

distances from their dislodgment sites and, as such, display remarkable durability. Similar phenomena can be presumed to have occurred in the geological past and might explain some of the "exotic" fossiliferous pods sometimes reported in lithic sequences. For example, the Upper Pennsylvanian Ames Limestone in the Appalachian Basin commonly contains bituminous mud clasts that preserve a fauna not indigenous to the limestone. Most likely, these represent dislodged portions of colateral lagoonal or swamp deposits that have been transported into foreshore and sublittoral depositional environments. Even if the transport of these clasts destroys their integrity, the matrix infilling of the contained fauna (e.g., bivalves and gastropods) which is protected in part by the presence of the shell may escape destruction. The result would be "exotic" steinkerns—not an uncommon occurrence in the fossil record.

The mud deposits of Station 2 contain the same infaunal association as Station 1. *P. pholadiformis* comprises virtually the entire bivalve population. Burrowing polychaetes are also abundant. Living individuals of *B. truncata* are rare. A

noticeable difference between this deposit and Station 1 is the total lack of an upper peat layer and, thus, the upper epifaunal elements. The only surface elements occurring at Station 2, as well as Station 1, are the ubiquitous hermit crabs and the surface portions of the tubes of *Diopatra cuprea*, a tubicolous worm restricted to small tidal pool areas (fig. 15).

Two separate sample quadrants were studied at Station 2: Quadrant 2A, situated on the exposed seaward edge of the mud deposit and quadrant 2B, approximately 40 feet behind the seaward site near the middle of the deposit on a transect of N83°W. Quadrant 2B is situated 52 feet east of the back edge of the deposit and 152 feet seaward of the berm. At low tide, quadrant 2A is at the seaward edge of the deposit; however, the surface of the mud deposit extends seaward for an additional 48 feet.

Both Station 2 quadrants were sampled to a depth of 9 inches in order to obtain a quantitative census of the contained infauna. Once again, the sampled depth marked the extent of infaunal penetration. The diversity and abundance of the total collected infaunal sample is recorded in

table 4. Diversity was low on both quadrants but quadrant 2B contained many more individuals of *P. pholadiformis* (751 individuals comprising 93% of the total fauna as compared with 93 individuals and 52% of the fauna at Station 2A). Quadrant 2B had a density of 270 individuals per cubic foot of sediment, whereas 2A contained only 59 individuals per cubic foot. Polychaete worms were more abundant and comprised a greater proportion of the total fauna in the seaward portion of the deposit (quadrant 2A).

Analysis of the substrates in quadrants 2A and 2B provided evidence for interpretation of these mud deposits as former salt marsh sediments. In addition to grass and root remains of *Spartina*, fragments of reeds up to one-half inch in diameter were observed in the mud. Also, fossil *Littorina irrorata* shells, articulated valves of *Geukensia (=Modiolus) demissa* infilled with mud, and fiddler crab claws were found in the muds. All of these organisms are good indicators of present-day salt marsh environments. The relict peat and mud deposits of St. Catherines Island do not always contain all of the above-mentioned salt marsh indicators. This may reflect differential preservation or perhaps patchiness and heterogeneity of the original (primary) salt marsh environment.

The living infaunal bivalves discussed earlier are rather narrowly adapted to ephemeral "fos-

sil" mud and peat deposits that, in turn, accumulated in old salt marshes during sea-level fluctuations. The ancient salt marsh deposits sporadically become available for colonization (i.e., exposed) by boring bivalves as part of the changing erosional configuration of the coastline. However, the same coastal processes continually destroy, by erosion or deposition, the exhumed relict deposits. An almost identical situation was reported by Schäfer (1972) for the southern portion of the North Sea where bivalves such as *P. pholadiformis* (introduced from North America), *Barnea candida*, and *Zirfaea crispata* have bored into extensive subtidal and intertidal peat deposits. The peat beds provide the necessary substrate for survival of these specific bivalves and were also formed during postglacial sea level lows. Although *P. pholadiformis* apparently prefers relict mud deposits along open beaches, it has been reported from other habitats. Connell (1955) noted the species living with the soft clam *Mya arenaria* in muddy sand on an intertidal beach at Eel Pond, Woods Hole, Massachusetts. Density at this site was, however, much less than the relict muds of St. Catherines Island. Connell (1955, p. 21) reported a maximum density of 4.3 living clams per square foot. Also, the percentage of dead to living valves of *P. pholadiformis* was much higher at Woods Hole than that on St. Catherines Island. The percentage of dead

TABLE 4  
Statistical Census of the Intertidal Fauna from Quadrants 2A and 2B of Station 2 Mud  
Deposit on North Beach, St. Catherines Island, Georgia<sup>a</sup>

QUADRANT 2A (Seaward Edge)	No. living specimens	No. articulated valves	No. single valves	Total no. specimens	% of total fauna	No. spec./cu. ft.
<i>Petricola pholadiformis</i>	73	17	5	93	52.2	31
<i>Barnea truncata</i>	2	—	—	2	1.1	0.6
polychaete worms (unident.)	83	—	—	83	46.6	27.7
TOTALS				178		59.3
QUADRANT 2B (Middle Portion)						
<i>Petricola pholadiformis</i>	680	61	19	751	92.6	250.3
<i>Barnea truncata</i>	2	—	—	2	0.2	0.6
polychaete worms (unident.)	58	—	—	58	7.1	19.3
TOTALS				811		270.3

<sup>a</sup>Represents 2 feet by 2 feet quadrants sampled to 9-inch depth.



specimens at Woods Hole ranged from 39 to 74 percent, whereas comparable data at St. Catherines Island ranged from 9 to 49 percent.

Some other relict mud deposits of St. Catherines Island present high densities of *P. pholadiformis*. For example, a census taken at a mud deposit 1 mile north of Beach Pond, along the southeastern shore of the island, revealed an average of 228 individuals per cubic foot in a 2 feet by 2 feet quadrant.

From a paleoecological viewpoint, the relict peat and mud deposits of St. Catherines Island represent a curious spatial and temporal mixture of environments and communities which could only be sorted out in the ancient geologic record with the greatest difficulty, if at all. This was clearly shown by observations made in July 1976, at another relict mud deposit on the southeastern shore of St. Catherines Island, about 1 mile north of Beach Pond. At this site, a small tidal pool situated within the relict mud deposit was carefully examined as a potential fossil assemblage. In a surface area of only a few square feet, faunal elements of six different associations were found. This mixed assemblage and environmental interpretations of the contained faunal elements are summarized in table 5. Only thorough knowledge of the microhabitat preferences of the taxa involved could have resulted in reconstruction of the various spatial and temporal components of this thanatocoenose. Faunal elements 1 through 4 are all represented as fossil shell material (indicated only, however, by slight discoloration of some of the shells). Each of these four faunal elements is found today in a distinct and specific salt marsh habitat, although the spatial distance between some of the habitats may only be a few feet (for example, between *I. obsoleta* and *M. mercenaria*). Most likely, therefore, elements 1 through 4 reflect previous contemporary salt marsh communities. At this locality, articulated valves of fossil *M. mercenaria* could be seen in living orientation meandering in a narrow zone for about 50 yards. This may reflect the exact position of the center of an ancient tidal creek! Faunal element 5 (*Petricola* borings) reflects a much later (Recent) inhabitation of the ancient salt marsh mud. This situation was discussed at some length in a previous section of this paper. Element 6 is a current postmortem accumulation

TABLE 5  
Mixed Assemblage, Relict Mud, Southeastern  
St. Catherines Island

FAUNAL ELEMENT	ENVIRONMENTAL INTERPRETATION
1. <i>Littorina irrorata</i> & <i>Geukensia (=Modiolus) demissa</i>	Tall <i>Spartina</i> , creek-head marsh areas (Kuenzler, 1961)
2. <i>Ilyanassa obsoleta</i>	Tidal creek muds
3. <i>Crassostrea virginica</i>	Tidal creek banks or tidal creek mouth (lives in sporadic patches)
4. <i>Mercenaria mercenaria</i>	Center of tidal creek channels, at interface of mud and moving sand.
5. <i>Petricola pholadiformis</i> borings	Intertidal relict muds, open beach.
6. <i>Mulinia lateralis</i> , <i>Donax</i> sp., <i>Ensis directus</i>	Subtidal to intertidal marine, open to semi-protected sand beach.

in the tidal pool as a result of wave action washing the empty bivalve shells over the top of the mud deposit.

The type of mixed assemblage described above is, fortunately, the exception rather than the rule in the fossil record. Were this not the case, the plethora of fossil community studies of the last few years would be on very shaky ground, to say the least. Several workers (e.g., Peterson, 1976; Warme, 1971) have demonstrated fidelity between living and dead species, even in relatively high energy environments such as coastal lagoons. Amount of postmortem transport is usually negligible. Other factors, such as differential preservation and solution of shell material, are still significant potential causes of bias in fossil community studies. In fact, differential shell dissolution achieves special significance in salt marsh environments where low pH muds often quickly destroy calcitic shell material (Wiedemann, 1972). The fidelity between fossil and living species at a particular site is partially reflective of the degree of spatial and temporal environmental heterogeneity (Peterson, 1976). The extreme spatial heterogeneity of salt marsh

environments, coupled with rapid temporal adjustments in micro-habitats, largely predetermines the type of mixed assemblage shown by faunal elements 1 to 4. Furthermore, pronounced spatial heterogeneity is correlated with a high environmental stress gradient, which, in turn, promotes organism communities that are strongly habitat-controlled with sharply defined boundaries (Rollins, Carothers, and Donahue, In press). Such is typical in estuarine and rocky intertidal environments. In contrast, level-bottom intertidal and subtidal environments usually have lower environmental stress gradients, lower spatial and temporal heterogeneity, and poorly defined community boundaries. These communities consequently display the greatest replication between living and dead species.

*Stations 3 and 4—Engineer Point—West.* Station 3 is typical of much of the protected sound shoreline along the northwestern portion of the island. At high tide it is a very narrow protected beach, but, at low water, a narrow sandy tidal flat is exposed. The dominant sediment is fine-to-medium quartz sand with local accumulations of organic detritus and grayish mud in the form of fecal pellets.

At Station 3, a transect was measured at low tide perpendicular to the shoreline across the sand flat. Two 15 feet by 15 feet quadrants (3A and 3B) were established for the purpose of assessing organism abundances. Several random quadrants were also set up and studied along this stretch of sand flat. Distribution and abundance studies of the intertidal organisms were limited to epifaunal species and those infaunal forms which either leave a visible activity track or trail on the surface or construct a structure (e.g., tube) denoting their presence. More deeply burrowing infaunal species were not studied because accurate quantitative data could not be gathered for these forms.

The two most conspicuous species of intertidal organisms present in this area are the tubicolous polychaete worms, *Diopatra cuprea* and *Onuphis microcephala* (fig. 16). Discussion of these and associated intertidal species in the Sapelo Island area can be found in Frey (1971), Howard and Dörjes (1972), and Howard and Frey (1973). These tubicolous worms live in nearly vertical tubes which they construct from

available sedimentary materials. *Diopatra cuprea*, the larger of the two polychaetes, constructs a tube 1/2 to 3/4 inches in diameter and often 1 to 2 feet in length. The tube has a distinctive upper portion which often protrudes from 1 to 2 inches above the sand surface. The tube is usually constructed of small molluscan shells or shell fragments, sedimentary grains, vegetation fragments, and other debris which the worm utilizes in a shingle-like, overlapping manner as the wall of the tube. The material utilized for tube construction by *D. cuprea* varies according to availability. Individuals of *D. cuprea* at Station 3 and along the shore as far as Station 6 primarily construct tubes of shells and shell debris, whereas those near Northwest Marsh and other salt marsh areas incorporate much more *Spartina* and other vegetative fragments. The polychaete *Onuphis microcephala* constructs a "soda straw-like" tube, approximately 1/8 or 1/4 inch in diameter, with a wall consisting almost entirely of cemented sand grains.

Both of these worms are common in the lower intertidal zone along the northern shore of St. Catherines Island (figures 17 and 18). *Diopatra cuprea* is abundant along the low water line, and *O. microcephala* is more widely distributed across the lower and middle portions of the intertidal sand flat, although in places it is extremely abundant along the low water line. The location and distribution of intertidal associations along the stretch of narrow sand flat from east of Engineer Point—West westward to the oyster banks on Walburg Creek was mapped (fig. 20). Along certain sections of the lower intertidal zone populations of *D. cuprea* and *O. microcephala* are intergradational. More often, either *D. cuprea* or *O. microcephala* is the dominant species in the lower intertidal zone and forms a very recognizable, high density association. Abundance of *D. cuprea* in two different sample quadrants at Station 3 ranged from 3.2 to 8.2 tubes per square yard. The highest density of *D. cuprea* observed on St. Catherines Island was in the lower intertidal zone slightly east of Station 3 and averaged 14.2 tubes per square yard. *Onuphis microcephala* tubes, since they are smaller, occur in greater numbers and higher densities. Abundance of *O. microcephala* near Station 5 (west end of Engineer Point—East sand flat) ranged from 20.5

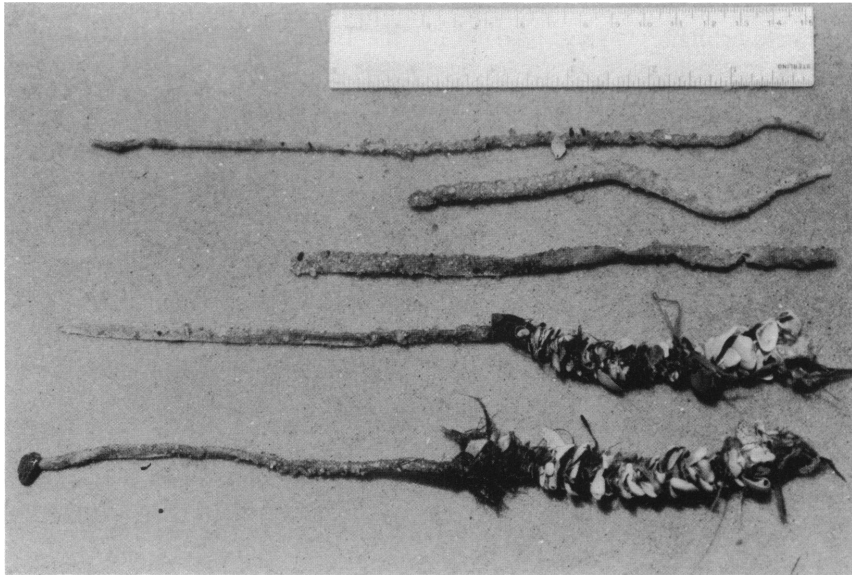


FIG. 16. Comparison of intertidal worm tubes from the Engineer Point area, St. Catherines Island. The three sand grain tubes are *Onuphis microcephala* and the two tubes agglutinated with shell fragments, etc., are *Diopatra cuprea*.



FIG. 17. *Diopatra* zone at Engineer Point—West (Station 3). The view is to the northeast and encompasses the lower foreshore at low tide.

to 34 tubes per square foot (184.5 to 306 tubes per square yard).

Another common infaunal organism with a very distinctive surface feature is the hemi-

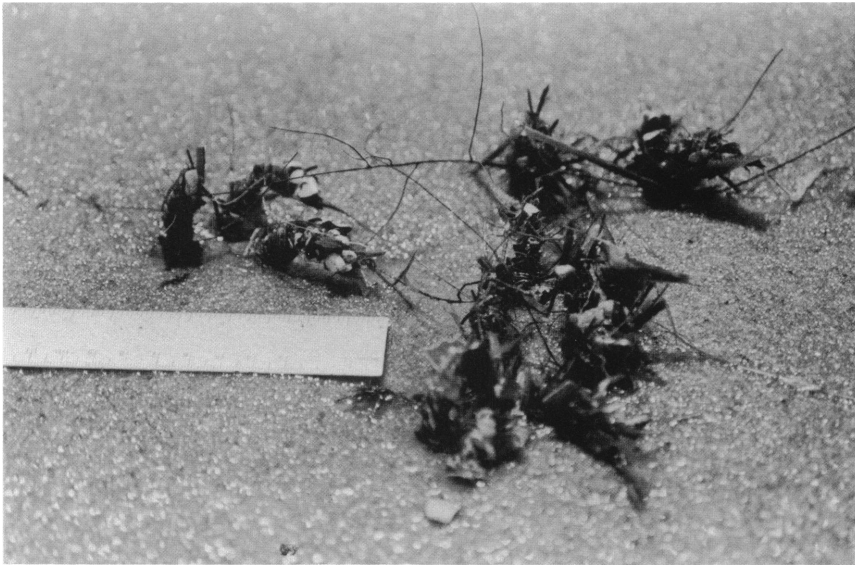


FIG. 18. Engineer Point—West (Station 3). Cluster of *Diopatra cuprea* tubes. Foreshore portion of intertidal zone.

chordate *Balanoglossus* sp. This species of acorn worm resides in a U-shaped burrow in the sand. The surface ends of the burrow are marked by a shallow, funnel-like depression at one opening and a small convoluted pile of sand at the other opening. The pile of sand represents fecal castings or sediment that has been passed through the gut and ejected out onto the tidal flat surface at the posterior (anal) opening of the burrow (fig. 19). At Station 3 and along much of the adjoining narrow sand flat, *Balanoglossus* sp. occurs in a linear pattern along the middle intertidal zone, parallel to the more seaward *Diopatra* zone. The contact between the *Diopatra* and *Balanoglossus* associations is gradational. In most areas studied, individuals of *Balanoglossus* sp. are not so numerous as those of *D. cuprea* and at Station 3 range from 0.8 to 1.7 individuals per square yard (see table 6).

Other organisms observed on the Engineer Point—West sand flat are the shallow burrowing gastropods *Ilynaea obsoleta* and *Terebra dislocata*, hermit crabs occupying shells of *Busycon* and other snails, and numerous juvenile individuals of *Limulus polyphemus*, about 1/4 to 1/2 inch in diameter, which create abundant mean-

dering surface trails as a result of their shallow burrowing activities.

The transect measured at Station 3 consists of two quadrants in which counts were made of organism surface abundance. Quadrants 3A and 3B were respectively situated 128 feet and 160 feet seaward of the back edge of the beach. Quadrant 3A was approximately 42 feet from the low tide mark and 3B about 10 feet from the low tide mark. The relative abundance of organisms in these two quadrants is summarized in table 6.

Howard and Frey (1973) discussed the preservation of *Diopatra* and *Onuphis* tubes in the fossil record. We agree with their conclusion that the sand grain tubes of *O. microcephala* and the tubes of *D. cuprea* might well be preserved as the trace fossil *Skolithos* (= *Scolithus*), often preserved in quartzites as nearly vertical tubes. They also suggested that *Diopatra* tubes might be represented as the tubelike trace fossil *Monocraterion* or *Terebellopsis*. It appears that the tubular trace fossils *Sabellarifex* and *Sabellarites* might also result from *Onuphis* and *Diopatra* preservation in the geologic record. The U-shaped dwelling burrows of *Balanoglossus*, if preserved in the sedimentary record, might well resemble



FIG. 19. Engineer Point—West (Station 3). Fecal castings of the acorn worm *Balanoglossus*.

the U-shaped trace fossil *Arenicolites*, especially since the tubes are simple and often have a funnel-shaped opening.

From a paleoecological standpoint, preservation of *Onuphis* and *Diopatra* as *Skolithos* and *Balanoglossus* as *Arenicolites* might provide a tool for locating and orienting paleo-shorelines, since they occur different distances from shore as lateral facies of the same sedimentary unit. Based on observations made along the narrow tidal flat on the northern shore of St. Catherines Island, *Diopatra* and *Onuphis* associations seem most characteristic and dominant in the lower intertidal zone along the low water line. *Balanoglossus*, however, usually occupies a linear zone in the middle to lower intertidal zone behind and landward of the *Diopatra* and *Onuphis* zone. If this distribution pattern can be applied to *Skolithos* and *Arenicolites*, then vertical sedimentary sequences bearing these trace fossils (often to the exclusion of any other fossils) might be meaningfully viewed in terms of transgression and regression events. For example, *Skolithos* or similar trace fossil tubes preserved in arenaceous sediments overlying layers containing U-shaped *Arenicolites*-type tubes might be interpreted as evidence for a transgressive sequence.

At Station 4, a large, patchy population of the

omnivorous mud snail *Ilyanassa obsoleta* was observed. At low tide, individuals of *I. obsoleta* emerge in abundance to feed on the organic detritus and algae exposed on the narrow sand flat and in the shallow tidal pools. In one instance large numbers of *I. obsoleta* were observed aligned in broad parallel bands on the shoreface with an orientation perpendicular to the shoreline. This pattern reflected the distribution of concentrations of surface algae and points out the food gathering prowess of *I. obsoleta*.

A 10 feet by 10 feet measured quadrant was established at random in the midst of the *I. obsoleta* population. All the specimens of *I. obsoleta* emergent within the quadrant at that time were collected—a total of 1692 individuals (16.9 individuals per square foot). This does not, however, represent the total population of *I. obsoleta* within the quadrant since numerous individuals escaped collection because they were submerged. Tide, at the time of sampling, was past dead low and many of the snails were beginning to burrow into the substrate. The only additional macrofaunal elements observed within the quadrant were eight tubes of *Diopatra cuprea*.

Station 4 does not reflect a typical habitat for *I. obsoleta* on St. Catherines Island. Commonly, this snail is found more closely associated with



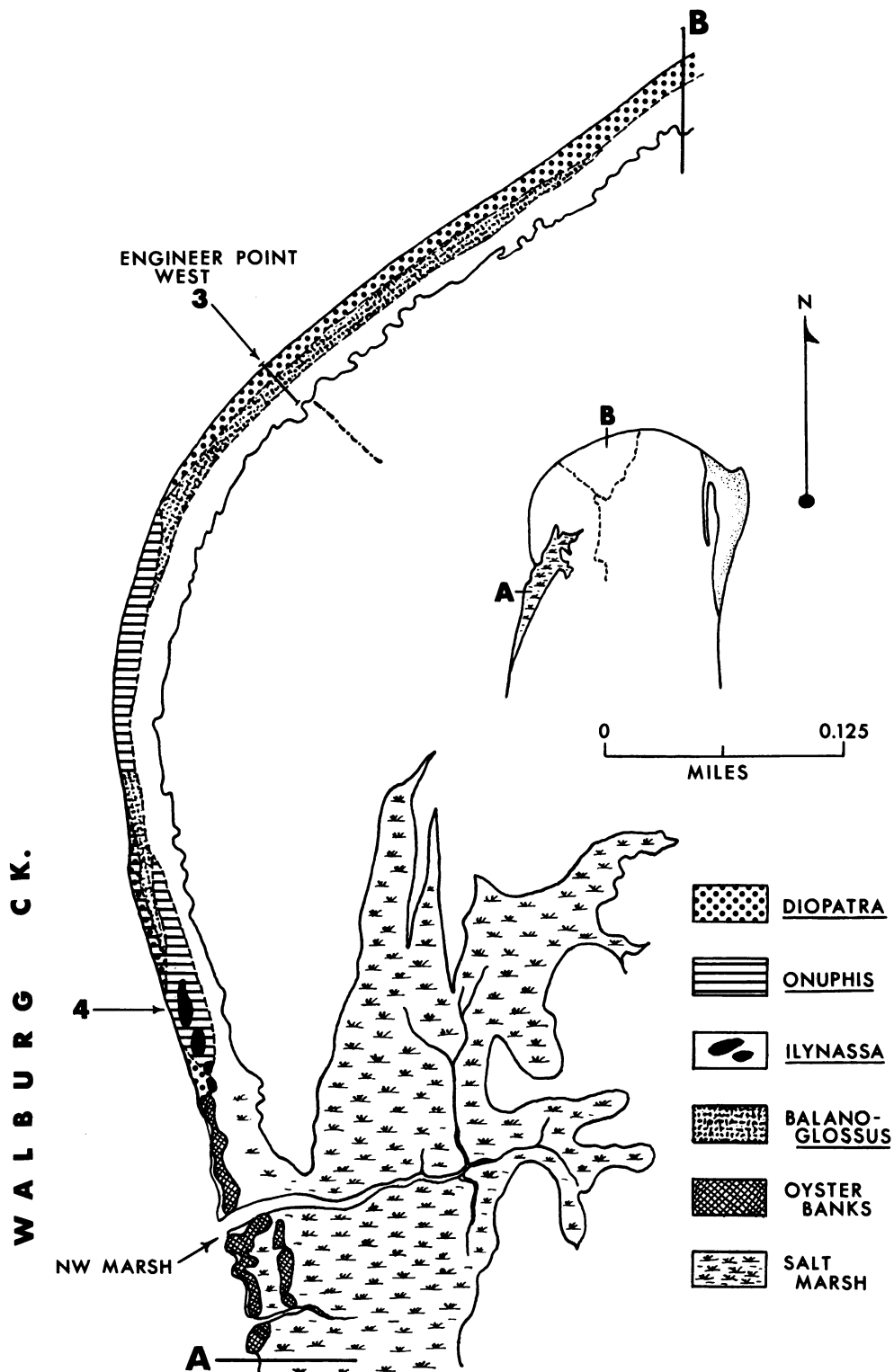


FIG. 20. Map of the northwestern shoreline of St. Catherines Island from east of Engineer Point—West to Northwest Marsh showing the location and distribution of the major intertidal associations. The salt marsh is not divided into associations.

TABLE 6  
Surface Census of the Intertidal Fauna of Quadrants 3A and 3B at Station 3  
(Engineer Point — West) Sand Flat, St. Catherines Island, Georgia<sup>a</sup>

	QUADRANT 3A			QUADRANT 3B		
	No. living specimens	% of total fauna	No. specimens/sq. yard	No. living specimens	% of total fauna	No. specimens/sq. yard
<i>Balanoglossus</i> sp.	43	58	1.7	21	21	0.8
<i>Diopatra cuprea</i>	8	10.8	0.3	79	78	3.2
<i>Limulus polyphemus</i> (juveniles)	20	27	0.8	—	—	—
<i>Ilynessa obsoleta</i>	2	2.7	—	—	—	—
<i>Terebra dislocata</i>	—	—	—	1	0.9	—
Hermit crab trail	1	1.3	—	—	—	—
TOTALS	74			101		

<sup>a</sup>Represents surface counts of 15 feet by 15 feet quadrants.

salt marsh tidal creeks where it burrows into organic-rich muds instead of sand. Comparison of the sample of living *I. obsoleta* from Station 4 with other samples collected in salt marsh environments shows pronounced differences in the overall physical condition of the shells. The former display clean, unabraded or undissolved shells, whereas the ones from organic muds are usually pitted and broken. Apparently, either the physical or chemical condition of the marsh mud environment is responsible for pronounced attrition of the shell of this species. According to Wiedemann (1972), the surface muds in *Spartina* marshes at Sapelo Island are quite strongly acidic (pH of 6.85 and 6.2 for two measured sites). Even the pH of more typical mudflat sediments averaged 7.3 (Wiedemann, 1972, p. 117). Since the equilibrium pH for calcium carbonate is about 8.0, neither of the previously mentioned habitats could be considered to be conducive to long-term shell preservation. However, the marsh muds should cause particularly rapid dissolution of the shells of *I. obsoleta*, especially in view of the fact that these snails spend the bulk of their lives below the sediment-water interface.

Bivariate analysis of *Ilynessa obsoleta* populations collected in various environments on St. Catherines Island show still other differences in shell morphology relative to habitat. In bivariate plots of apertural width vs. total height the *Ilynessa obsoleta* population sample taken at Station 4 displays a relatively wider aperture than a sample taken from the bank of a salt marsh tidal creek at

English Cut on the west central shore of the island (see figs. 21, 22). The salt marsh locality, since it is topographically higher, has longer periods of intertidal emergence than the protected beach area of Station 4. Also, Station 4 is subjected to a moderate amount of wave action, whereas the marsh locality receives no wave action at all. These snail populations appear to demonstrate a phenotypic response to some environmental factor(s); most likely to the varying degree of desiccation in the two environments. This type of phenotypic variation is quite common among intertidal organisms and has been demonstrated for other snails, such as *Littorina saxatilis* (Newkirk and Doyle, 1975) and *Thais lapillus* (Kitching, Muntz, and Ebling, 1968).

*Stations 5 and 6—Engineer Point—East.* The wide tidal flat designated Engineer Point—East is quite similar to Nannygoat flat, described by Howard and Dörjes (1972), on Sapelo Island. Nannygoat flat is situated in a similar semi-protected site around the southern tip of Sapelo Island, facing south on Doboy Sound and inlet. The two tidal flats are comparable in terms of sediment type, sedimentary and biogenic features, and general faunal composition. Both flats are predominantly composed of quartz sand, but fine muds are also common, mainly in the form of green-gray fecal pellets that tend to concentrate in ripple troughs and depressions across the surfaces of the tidal flats. Extensive tidal creek and channel systems transport the suspended fine muds and organic detritus from the salt marsh

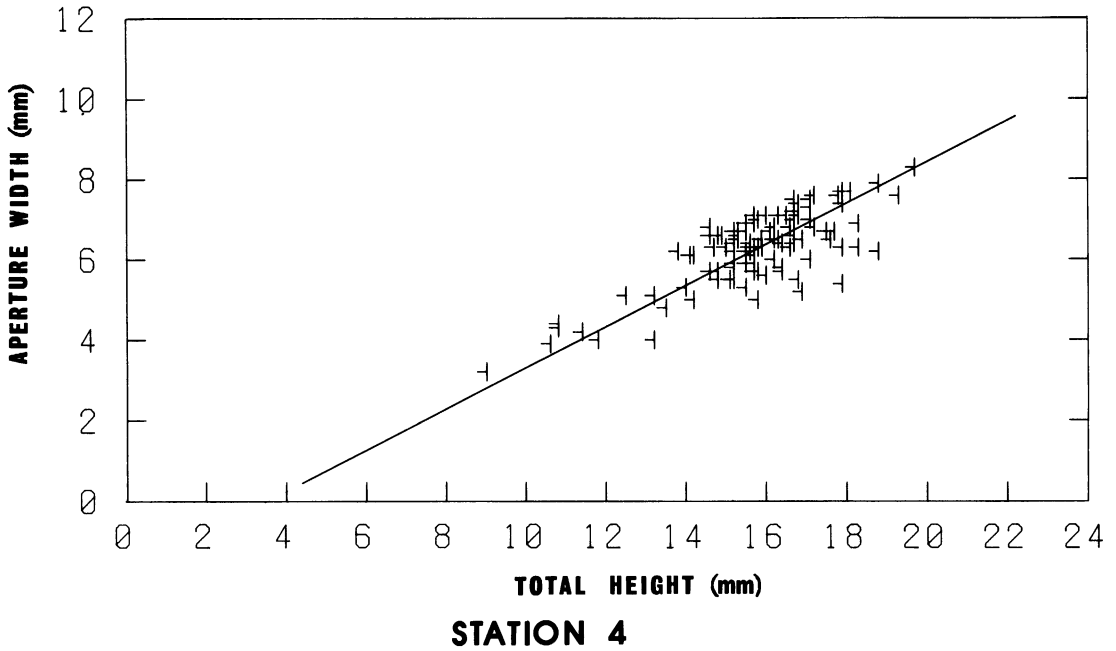


FIG. 21. Bivariate plot of apertural width vs. total height for a sample of *Ilyanassa obsoleta* collected from Station 4. N = 104.

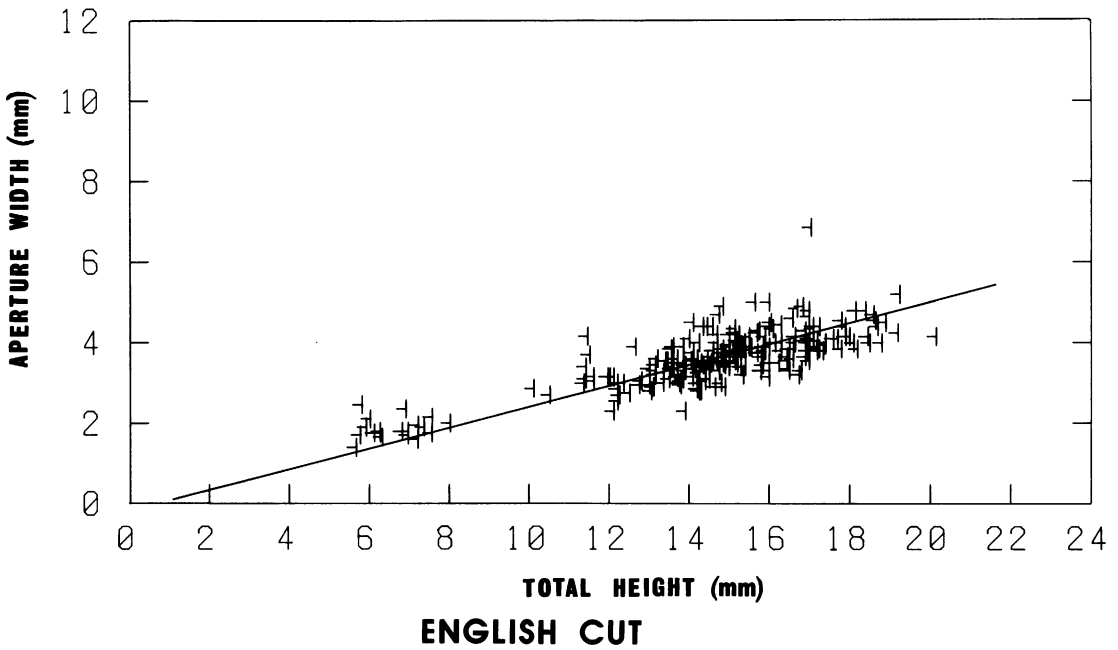


FIG. 22. Bivariate plot of apertural width vs. total height for a sample of *Ilyanassa obsoleta* collected from a small tidal creek in English Cut marsh. N = 240.

complexes to these and other fringing tidal flats. Tidal channel waters are nearly always highly turbid, indicating that large amounts of fine sediment are constantly in transit within this coastal area.

The surface of Engineer Point—East flat, as well as those of Nannygoat and Cabretta flats (Howard and Dörjes, 1972), is covered at low tide with abundant, low amplitude ripple marks (fig. 23). The elongated ripples on Engineer Point—East flat have an amplitude of 1/2 to 1 inch from trough to crest and include both asymmetrical and symmetrical types. Three different forms of ripples have been directly observed in the Station 6 area during low tide: As the tide recedes, asymmetrical ripples form in some places from currents slowly draining off the flat toward the sound. Asymmetrical ripples oriented in the opposite direction form at the same time in adjacent areas through the action of small waves washing shoreward across the shallow flat. Finally, large areas of the flat surface are covered by symmetrical ripples with low rounded crests formed by a combination of the dominant water movements (currents receding off the flat and small waves moving landward across the flat).

The sandy tidal flat at Station 6 is approximately 500 feet wide at low tide. The five 15 feet by 15 feet study quadrants were aligned along a north-south transect with quadrant 6A approximately 100 feet shoreward from the outer edge of the flat and quadrant 6E situated at the inner edge of the flat. All quadrants were spaced about 100 feet apart. A narrow sandy beach, 116 feet wide, with a 2 to 4 degree slope toward the sand flat, occurs between quadrant 6E and the back edge of the beach. Abundance and distribution of the observed intertidal faunas within the five quadrants are presented in table 7.

Howard and Dörjes (1972) stressed the abundance of biogenic sedimentary structures on the surface of the Sapelo Island tidal flats. Biogenic activity was observed nearly everywhere on the Engineer Point—East flat and the resultant bioturbation was very noticeable. The quadrant studies, coupled with numerous additional observations along many portions of the flat, indicate that the Engineer Point—East flat supports virtually the same intertidal fauna (infaunal and epifaunal) as Nannygoat flat on Sapelo Island. Three of the most readily apparent organisms popu-

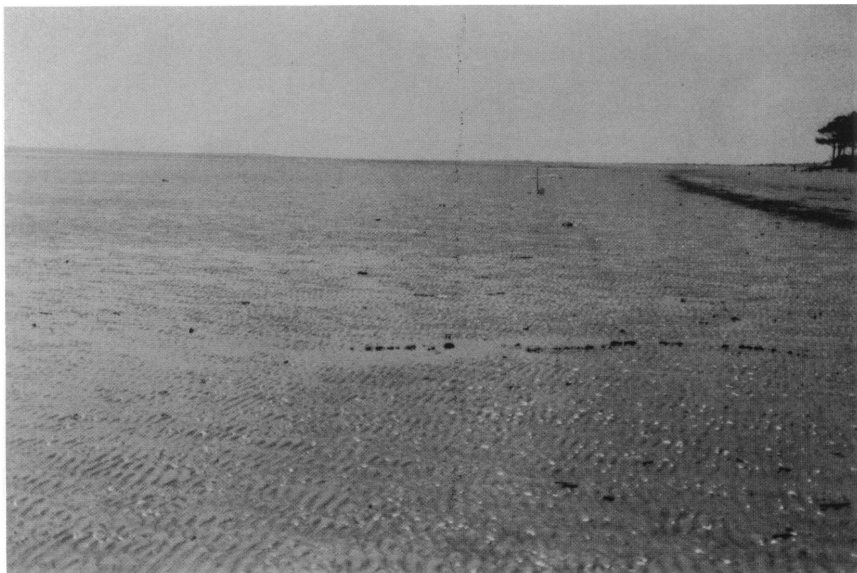


FIG. 23. Ripplemarks on Engineer Point—East (Station 6) tidal flat. View to the east across the flat toward the northeast point of the island (low tide).

TABLE 7  
Surface Census of the Visible Intertidal Fauna of Quadrants 6A-6E at Station 6  
(Engineer Point - East) Sand Flat, St. Catherines Island, Georgia<sup>a</sup>

	QUADRANTS				
	6A	6B	6C	6D	6E
<i>Diopatra cuprea</i> (tubes)	4	9	—	4	4
<i>Onuphis microcephala</i> (# tubes per square yard)	30	32	8	7	7
<i>Balanoglossus</i> sp.	12	24	16	6	8
meandering surface traces created by <i>Terebra dislocata</i> (mid-outer flat) and <i>Limulus</i> <i>polyphemus</i> juveniles (inner flat)	12	22	50	v. abund.	v. abund.
<i>Nassarius vibex</i>	—	—	2	3	—
small mound with central hole (unidentified)	—	—	40	50 - 60	45
shallow surface depressions, probably by sting-rays	—	—	7	—	—
				SHOREWARD →	

<sup>a</sup>Represents surface counts of 15 feet by 15 feet quadrants along a transect across the tidal flat.

lating Station 6 were also common at Station 3. These are the onuphid tubicolous polychaetes *Diopatra cuprea* and *Onuphis microcephala*, and the hemichordate *Balanoglossus* sp. The agglutinated tubes of *Diopatra* seem rather evenly distributed across the flat, whereas *Onuphis* is most abundant in the outer (soundward) portion of the flat and is significantly less common in the middle and inner areas (figs. 24, 25). The outer sectors of the flat averaged 30 to 32 individuals of *O. microcephala* per square yard but extremely high densities of *O. microcephala* (306 individuals per square yard) were observed at the western end of the flat. Howard and Dörjes (1972) reported a similar low, but even, distribution of *Diopatra* across Nannygoat flat. However, the number of *O. microcephala* individuals was higher in the middle to inner portions of Nannygoat flat than in the comparable regions of Engineer Point-East flat. In the Station 6 area, the acorn worm, *Balanoglossus* sp. occurs across the entire flat, but is most abundant in the middle sector (approximately 200 to 300 feet shoreward of the outer edge of the flat). This is markedly different from Nannygoat flat where *Balanoglossus* sp. was reported to be much less

abundant and limited to the extreme inner edge of the flat and the foreshore face of the beach.

Several species of intertidal gastropods were observed to cause numerous meandering tracks, trails and surface bioturbation effects on the Engineer Point-East flat. Large numbers of *Terebra dislocata* were observed shallowly burrowing through the upper few centimeters of sediment in the middle to outer portions of the flat. *Nassarius vibex*, another intertidal snail, was frequently observed feeding on the inner to middle portions of the tidal flat surface, especially during the outgoing and incoming tides. *Nassarius vibex* burrows below the surface during the period of maximum exposure at low tide. Finally, *Polinices duplicatus* was observed leaving its distinctive shallow burrowing trace along the inner edge of the flat and foreshore beach area. Howard and Dörjes (1972) reported similar occurrences for *Nassarius* and *Polinices* on Nannygoat flat.

A cursory survey, at low tide, along the quadrant transect 6A to 6E displayed a noticeable shoreward increase in the degree of biogenic traces, presumably a reflection of the greater intertidal exposure time of that portion of the flat as well as variation in faunal distribution. Such a



FIG. 24. Western end of Engineer Point—East sand flat (Stations 5 and 6) showing low tide distribution of *Onuphis microcephala* association. Note the upper portions of *O. microcephala* tubes protruding above tidal flat surface.



FIG. 25. Engineer Point—East sand flat (Station 6). Close-up of upper portions of *O. microcephala* tubes.

directional trend in the development of tracks and trails parallel to an onshore-offshore transect might have paleoecological application for loca-

tion of the shoreward margins of ancient tidal flats.

Other intertidal organisms observed on



Engineer Point—East contributing to the bioturbation of surficial sediments and leaving obvious biogenic traces are: the common horseshoe crab, *Limulus polyphemus* (abundant juveniles); the sea pansy, *Renilla reniformis* (rare); hermit crabs and sting-rays (both common). Large numbers of juvenile limulids, measuring about 1/4 inch to 1/2 inch across the cephalothorax, are quite active on the inner portion of the flat as the tide recedes. Their shallow burrowing activity produces extremely abundant meandering surface trails, similar to those produced by *Terebra dislocata* further seaward on the flat. Distinctive tracks and trails of hermit crabs are also abundant at low tide on the flat surface. Finally, shallow depressions presumably excavated by sting-rays are quite common in places. Our study did not include sampling of the infauna of each quadrant, so we are unable to make comparisons with the infaunal analyses of Howard and Dörjes (1972).

Station 5 represents the only area on St. Catherines Island where we observed a co-occurrence of *Ilyanassa obsoleta* and *Nassarius vibex*. These two species usually occupy distinct habitats, tidal creek muds and sandy tidal flats, respectively. At Station 5, a localized patch of exhumed marsh mud harbored a small, but dense, colony of *I. obsoleta*.

*Station 7—North Beach.* Station 7, situated about 125 yards south of the Picnic Area, represents the northernmost relict mud deposit on North Beach (see fig. 6). The exposure consists of dark gray mud which has a low profile, rising only from 1 to 6 inches above the beach surface (fig. 26). In this respect, the Station 7 deposit resembles that of Station 2. The deposit is about 210 feet long and 90 to 120 feet wide. Due to its low relief, beach sands are continually shifted on and off large portions of this deposit. Deposition and removal of the fine quartz beach sand is a common occurrence along most beaches and affects all relict peat/mud deposits along North Beach. At any given time, the shifting beach sands are largely controlled by the active long-shore current system and the surf energy.

As at the previous North Beach stations, a 2 feet by 2 feet quadrant was sampled to a depth of 9 inches (fig. 27). The quadrant was located 20 feet behind the seaward edge and 70 feet south of the northern edge of the deposit (low

tide). The quadrant was purposely selected in a low relief section of the deposit where shifting sands had covered much of the mud surface. More than half of the quadrant was covered by a veneer of quartz sand varying from 1/2 to 2 inches in thickness. This particular area was selected primarily in order to note the effects of sand burial on the infaunal bivalve populations. Abundant boreholes of *Petricola pholadiformis* were visible on the exposed mud surface and numerous boreholes could be detected below the sand which covered portions of the mud.

The dominant infaunal species at this station was *Petricola pholadiformis*. In fact, this species comprised 70 percent of the total recovered fauna of 867 individuals (both infauna and epifauna). The tiny epifaunal bivalve *Brachidontes recurvus* accounted for 23 percent of the total fauna (see table 8). The density of the total fauna at Station 7 was 289 individuals per cubic foot. This compares closely with the density recorded for quadrant 2B (Station 2). Burrowing polychaetes were uncommon and individuals of *Barnea truncata* were quite rare.

In the half-quadrant where the mud surface was exposed or covered by only a very thin sand veneer, 87 to 93 percent of *P. pholadiformis* individuals were alive. In the other half quadrant, where 1 to 2 inches of quartz sand entirely covered the mud surface, 85 to 90 percent of the specimens of *P. pholadiformis* were alive. Although no continuing record was kept of the duration of sand burial at this station, it appears that the beach sands are constantly shifted across the low mud deposits, covering portions of the deposit at one tide and uncovering them on the next tide. These short-term burial events have little, if any, detrimental effect on the *Petricola* association. Long-term burial, however, might well have adverse effects. Several large, similar sized *P. pholadiformis* specimens were found dead in their burrows at this station and might have succumbed to some previous episode of prolonged burial.

An interesting aspect of the Station 7 deposit is the relatively large number of living *B. recurvus* individuals found in small clusters attached to the surface of the deposit. Although significant in number, these *Brachidontes* clusters are by no means as abundant or densely packed as those forming the *Brachidontes* "pavement" of Station



FIG. 26. Surface view of the relict mud and peat deposit at Station 7, North Beach. Note the beach sand covering low portions of the mud.



FIG. 27. Station 7, relict mud deposit on North Beach. Close-up view of the 2 feet by 2 feet quadrant prior to sampling. Note the beach sand covering the mud surface.

1. They form a sporadic epifaunal association at Station 7. Most low relief mud deposits along North Beach (e.g., Station 2) lack the epifaunal

*Brachidontes* association. This station demonstrates that the *Brachidontes* association can settle, populate, and survive on a low relief mud

TABLE 8  
 Statistical Survey of the Intertidal Fauna from Station 7 Mud Deposit  
 on North Beach, St. Catherines Island, Georgia<sup>a</sup>

	No. living specimens	No. articulated valves	No. single valves	Total no. specimens	% of total fauna	No. spec./cubic ft.
<i>Petricola pholadiformis</i>	542	47	39	609	70.2	203
<i>Barnea truncata</i>	4	—	19	14	1.6	4.6
<i>Brachidontes recurvus</i>	202	—	—	202	23.3	67.3
polychaete worms (unident.)	42	—	—	42	4.8	14
TOTALS				867		289

<sup>a</sup>Represents a 2 feet by 2 feet quadrant sample to 9-inch depth.

surface even if it lacks a well-developed upper peat layer. *Brachidontes recurvus* requires some type of secure substrate for attachment. These small clusters at Station 7 mainly utilized the posterior ends of vertically oriented *Petricola* valves, both living and dead, for byssal attachment. Fewer individuals were found byssally attached to dead, but articulated valves of *B. truncata*, as well as various plant and shell fragments embedded in the mud.

This occurrence affords another example of the utilization of shells and other hard substrate materials as points of attachment for settling larvae, enabling epifaunal organisms to populate soft sediment environments. This is common in the fossil record, as well as the modern marine environment, and involves many types of benthic organisms. The skeletal structures of many Paleozoic brachiopods, molluscs, etc., served as points of attachment for the settling larvae of many bryozoans, corals, barnacles, worms, and other sessile organisms. Succession of marine benthic communities, both past and present, has often been due to the sporadic presence of valves and shell fragments on a soft substrate, providing initial sites for settlement and subsequent colonization. Continual accumulation of skeletal debris through time often has resulted in the formation of a "hardground," populated by yet a different association of organisms. Examples of such from the fossil record can be found in Kauffman (1974), Walker and Alberstadt (1975), and Rollins, Carothers, and Donahue (In press).

*Station 8—North Beach at Seaside Inlet.* The portion of North Beach adjacent to Seaside Inlet (fig. 2) presents a large variety of marginal

marine environments intimately associated in a small area. A large relict mud deposit, in part covered by variable thicknesses of quartz sand, occurs on the north side of Seaside Inlet and superficially resembles the relict mud deposits of Stations 2 and 7 (fig. 28). It is a broad, low relief deposit of dark gray mud which, when exposed at low tide, forms an extensive tidal flat. Thin sand deposits overlie the mud in places and commonly show elongated current and symmetrical ripple marks formed during the receding tides. Patches of dead *Crassostrea virginica* valves, most still articulated and cemented virtually in life orientation, occur sporadically on the flat. The muds of this deposit contain large numbers of dead, articulated *Geukensia demissa* valves, the majority of which are infilled with mud and many are in life orientation.

The mud surface at Station 8 shows extreme bioturbation in the form of very abundant boreholes and burrow openings, as well as a nodular, rubbly texture. Moderate amounts of fine quartz beach sands, which are periodically swept across this intertidal deposit, have accumulated in many of the borings and burrows. This mode of sand deposition combined with the large number of borings and burrows has resulted in a near-surface mixture of nodular masses of mud almost "floating in" a sandy mud matrix.

Analysis of a 2 feet by 2 feet quadrant to a depth of 12 inches in a highly bioturbated portion of this deposit revealed a much different faunal association than the typical *Petricola* association. The burrowing shrimp *Upogebia* sp. was the dominant infaunal organism of this deposit and comprised 54 percent of the total recovered



FIG. 28. Station 8, Seaside Inlet. View to the northwest at low tide. Vehicle is parked on backshore of beach. The shovel and pail denote location of sample station. Dark areas are highly bioturbated gray muds.

fauna (see table 9 and fig. 29). The fauna contains several crustacean species but *Upogebia* appears to be primarily responsible for the major bioturbation. The crustaceans collected in this sample were *Upogebia*, the burrowing shrimp *Alpheus*, the snapping shrimp *Uca*, the fiddler crab, and some small crabs. All the collected faunal elements are infaunal, except for the crabs which are both infaunal and epifaunal. Although other portions of the Seaside Inlet deposit may support typical *Petricola* associations, this *Upogebia* association is typical of the highly bioturbated areas.

The overall intertidal zone at Seaside Inlet represents, at low tide, a very extensive flat that contains a greater number of intertidal habitats than other North Beach mud deposits. This might explain the presence of *Uca* sp. and the tubicolous worm, *Diopatra cuprea*, generally not present along the more open, seaward shoreline.

*Station 9—Manor House Dock.* In June 1976, a 5 feet by 10 feet sample quadrant was established in the fringing salt marsh along Walburg Creek (fig. 2). The quadrant was positioned near the middle of the narrow marsh in the midst of dense *Spartina* grass. The *Spartina* grass was less

than 0.5 meter high and thus conforms to Kuenzler's definition of short *Spartina* (Kuenzler, 1961). At this locality, the *Spartina* is exposed except at high tide when it is covered by several inches to a few feet of water.

The dominant macroinvertebrates at Station 9 are the common intertidal snail, *Littorina irrorata*, which grazes mainly on the grass blades and other vegetation, and *Uca* sp., a fiddler crab that emerges from its burrow when the mud surface of the marsh is exposed.

This station was established to determine the average abundance and density of *L. irrorata* and *Geukensia demissa* in this fringing marsh environment. The population of *L. irrorata* was extremely dense and a total of 809 individuals of that species were collected from the quadrant (50 square feet). In the same area, approximately 12 to 15 specimens of *Geukensia demissa* were counted. An accurate count of *G. demissa* could not be made due to that species' habit of living almost completely buried in the mud substrate. Also, accurate counts of *Uca* sp. were not obtainable since that species is highly motile and can readily escape down burrows. The repopulation potential of *L.*

*irrorata* was tested by completely removing all individuals from the 50 square feet and recollecting the area 24 hours later. One hundred eighty-six individuals had repopulated the area, concentrating in the boundary regions of the quadrant. Ten days later, the quadrant was again harvested, providing 194 individuals. Repopulation involved, in both instances, a large number of juveniles, compared with the original undisturbed population. We conclude that *Littorina irrorata* is a moderately motile snail, readily moving from

one *Spartina* plant to another, in addition to its well-known vertical tidal migration.

The density of *L. irrorata* in the fringing marsh of Station 9 is higher than in other marsh areas that we examined on St. Catherines Island. In June 1976, three other 5 feet by 10 feet sample quadrants were set up in different marsh regions of the island for the purpose of studying *L. irrorata* populations. This ongoing study involves assessment of population dynamics and life histories as well as motility and recoloniza-

TABLE 9  
Statistical Survey of the Intertidal Fauna from Station 8 Mud Deposit on North Beach near Seaside Inlet, St. Catherines Island, Georgia<sup>a</sup>

	No. living specimens	% of total fauna	No. specimens/cubic foot
<i>Upogebia affinis</i>	13	54.2	3.2
<i>Uca</i> sp.	4	16.6	1
<i>Petricola pholadiformis</i>	3	12.5	0.7
<i>Alpheus</i> sp.	2	8.3	0.5
<i>Sesarma</i> -type crabs	2	8.3	0.5
TOTALS	24		6

<sup>a</sup>Represents a 2 feet by 2 feet quadrant sampled to 12-inch depth.

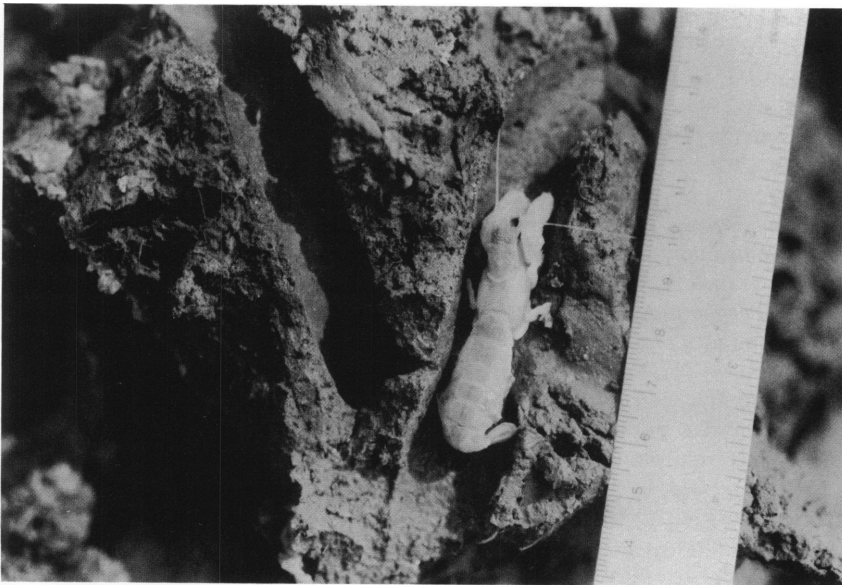


FIG. 29. Station 8, Seaside Inlet. Block of gray mud showing burrows and the burrowing shrimp *Upogebia* sp.

tion potential. The detailed results will be presented in a subsequent publication. One of these quadrants is situated in English Cut marsh (west-central portion of island) where the number of *L. irrorata* individuals ranged from 19 to 41 over a two-week period. Another site, Hoke's Landing, situated in a large marsh on the east-central portion of the island, provided 306 to 448 indi-

viduals over the same time span. In the third marsh locality, Northwest marsh (fig. 2), 53 to 136 specimens of *L. irrorata* were counted in the two-week span. All three sample quadrants are control quadrants from which no specimens were collected. The data therefore reflect variation in standing crop over a two-week period.

## SUMMARY AND CONCLUSIONS

St. Catherines Island, Georgia, has a large number of distinct intertidal environments and communities. The intertidal habitats include exposed sand beaches, sandy tidal flats, relict salt marsh deposits (mud and peat) on exposed beaches, and salt marsh complexes. Nine localities on the northern half of the island were selected for study as examples of the main types of habitats and organism associations. Many of the environments described in this study have counterparts on nearby Sapelo Island.

The organism groupings recognized in this study are actually associations in the sense of the "holistic" community approach of Kauffman and Scott (1976), but are communities in the usage of many other workers, such as Mills (1969).

The relict salt marsh deposits (Stations 1, 2, 7, and 8) received the most attention in this study. These exhumed marsh deposits serve as unique modern environments for an infaunal *Petricola* Association, dominated by burrowing and boring bivalves, and a *Brachidontes* Association composed of epifaunal clams, barnacles, and algae. In some places, such as Station 1, the *Brachidontes* Association and the *Petricola* Association occur within the same community, an apparent violation of the conclusion of Woodin (1976) that dense infaunal bivalve populations do not coexist with dense epifaunal bivalve populations. These relict marsh deposits receive pronounced physical punishment by waves and currents and are often the sites of sudden deposition of sand. However, the *Petricola* and *Brachidontes* associations appear little affected by short-term disruptions of this sort. In addition to the living associations, the relict marsh muds preserve several fossil associations. At one locality on the island we ob-

served a mixed assemblage of six distinct associations in time and space. Observations of vertical sections of relict peat deposits displayed an expected trend of size distribution of contained infaunal bivalve specimens; the smallest individuals occurred in the upper 1 or 2 inches, whereas progressively larger individuals were found at greater substrate depths. Mud clasts are continually dislodged from the relict marsh deposits by wave action and are sometimes transported considerable distances by longshore currents. It is suggested that certain "exotic" fossiliferous pods reported in the geological literature might have similar origin. Even when the transport of the clasts destroys their integrity, the matrix infilling of the contained fauna may be protected by presence of the shell, resulting in "exotic" steinkerns.

Association boundaries were sharp only where spatial heterogeneity was pronounced, as in salt marsh complexes. Polychaete associations along sandy tidal flats, although densely populated, were less clearly bounded and were often marginally intergradational.

Observations on polychaete associations along the narrow tidal flat of the northern shore of St. Catherines Island (Station 3) showed an onshore-offshore distributional trend with possible paleoecological utility in the recognition of ancient transgression and regression events. If *Onuphis* and *Diopatra* have distributional as well as structural analogs in the trace fossil genus *Skolithos* and if *Balanoglossus* is similarly related to the fossil *Arenicolites*, then the latter would represent a middle- to lower-intertidal zone behind and landward of the *Skolithos* zone.

Morphometric comparison of populations of *Ilyanassa obsoleta* from a sand flat (Station 4) and from a tidal creek displayed differences in aper-

tural shape, presumably correlated with differences in time of intertidal exposure. Specifically, the tidal creek population had a narrower aperture relative to total height. The tidal creek population of *I. obsoleta* also displayed much more shell damage and dissolution, possibly due to the increased acidity of tidal creek muds.

A wide tidal flat (Engineer Point—East) on the northern tip of St. Catherines Island is similar in

physiography and organism content to Nannygoat and Cabretta flats on Sapelo Island, described by Howard and Dörjes (1972).

A fringing salt marsh, on the western side of the island, was selected for a study of the abundance and repopulation potential of the intertidal snail *Littorina irrorata*. In addition to its well known vertical tidal migration, *L. irrorata* demonstrated rather high lateral motility.

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