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THE BIOLOGY OF MARINE TARDIGRADA AT WOODS HOLE, MASSACHUSETTS

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THE BIOLOGY OF MARINE TARDIGRADA
AT WOODS HOLE, MASSACHUSETTS

by

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B. S., Bates College, 1964
M. S., University of New Hampshire, 1966

A THESIS

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ABSTRACT

THE BIOLOGY OF MARINE TARDIGRADA AT WOODS HOLE, MASSACHUSETTS

by

LELAND W. POLLOCK

While intertidal marine areas are easily accessible to study, the ecology of the interstitial environment of sandy beaches is poorly understood. Nevertheless, an abundant and diverse microscopic community is described from this area. I used a biological study of one group from this fauna, the Tardigrada, as an introduction to a thorough understanding of this environment.

I selected a transect perpendicular to the water-line at Crane's Beach in Woods Hole, and studied environmental parameters and populations of tardigrades for nearly two years. My objective was to define important abiotic conditions surrounding an interstitial community and to examine the biology of one constituent group. Results are reported in four separate but related parts.

In Part I, MARINE INTERSTITIAL TARDIGRADA FROM WOODS HOLE, MASSACHUSETTS, I described species of tardigrades encountered during this study, including *Stygarctus* ~~*granulatus*~~ n. sp., *Batillipes* ~~*dicrocercus*~~ n. sp., *B. pennaki*, *B. bullacaudatus*, *B. mirus*, and single specimens of two others. I discussed morphological and anatomical features along with

aspects of natural history. I found that patterns of toe length represent a useful taxonomic character for distinguishing species of the most abundant and diverse genus, Batillipes.

In Part II, REPRODUCTIVE ANATOMY OF SOME MARINE HETEROTARDIGRADA, based on observations of Batillipes and Stygarctus, I revised limited information available at present. Here, I observed that flagella of spermatozoa represent the first cilium-like structure described from this phylum. I noted differences in size, shape, number, and maturity of summer versus winter ova in Batillipes and described similar dimorphism in the shape and location of gonopores of Stygarctus and Batillipes. The significance of the latter in deciphering systematic relationships within Heterotardigrada is explored, and its utility in determining sex ratios of populations is demonstrated in Part IV.

An intertidal beach is subject to seasonal, spring- versus neap-tidal, and semi-diurnal tidal changes in parameters. In Part III, SEASONAL AND TIDAL CHANGES IN THE MARINE INTERSTITIAL ENVIRONMENT, I examined Crane's Beach as a dynamic region influenced by characteristics of the atmosphere, land, and seawater. I applied Salvat's classification of similarity in parameters along the surface of fine sand beaches to both superficial and depth axes of a coarse grain beach. Superficial sediment in upper portions of the intertidal area became severely depleted of water especially during neap tides. Deepest layers of sand remained saturated and consequential stagnation was apt to cause anaerobic conditions. Meiofauna occupied zones between these extremes. In my brief study of tidal changes in pH, oxygen content, and salinity, and from extensive observations on changes in temperature, interstitial water table, and water content, I found that conditions here remained nearly as stable as in nearshore, subtidal superficial sediments.

I studied composition, distribution, and dynamics of populations of tardigrades in ASPECTS OF THE ECOLOGY OF MARINE INTERSTITIAL TARDIGRADA AT WOODS HOLE, MASSACHUSETTS. An assemblage of tardigrades in typically low diversity, four species, dominated Crane's Beach. While co-occurrences exist, each species occupied a specific volume within the beach. Seasonal environmental changes affect the location of concentrations in populations. During colder months, some populations shifted parallel to the surface of the beach along the high to low tidal axis or toward greater depth in sand. Others simply remained deep in sand throughout the year. Year-round reproduction and availability of tardigrades occurred, although I found maximal desnsities either in spring and fall or throughout the summer and fall. The sequence of progressive growth, inferred from changes in abundance of size classes in each population, suggests a life-span of two to four months. Sex ratios of the population of _S_. _granulatus_ were nearly equal. Apparently overall distribution of tardigrades was limited by availability of substratum, presence of sufficient interstitial water, and adequate circulation of water to permit oxygenation. Specific differences in distribution were related to seasonal changes in temperature, possible intrageneric competition, and a combination of local biotic and abiotic conditions the definition of which will provide challenging material for subsequent research.

INTRODUCTION

The Tardigrada comprise a small phylum of microscopic invertebrate animals. Their presence in water films surrounding leaves of lower plants has been noted since the eighteenth century. Freshwater and semi-terrestrial forms have received much taxonomic attention, and although precise definition of specific characters remains unclear (Ramazzotti, 1962), 350-400 species have been described (see Ramazzotti, 1962, 1965, for a recent review). Most ecological observations on these animals relate to their ability to enter a "cryptobiotic" state of inactive subsistance in the presence of unfavorable surroundings. May (1948) has reviewed the literature on this phenomenon and Marcus (1936) summarizes available information of other aspects of anatomy and biology of freshwater tardigrades.

The first marine form was described from algal washings by Schultze (1867). Although species living in beach sand have been known since the first decade of this century, two-thirds of the 29 described species have been reported since 1950. Ecological studies of marine interstitial tardigrades are especially scarce.

Kowalevsky (1901a and b) and Giard (1904) drew attention to the abundance of marine interstitial fauna. Since then, interest in this environment and fauna has remained primarily European, and only recently interest has become world-wide.

By necessity most work on these animals has consisted of faunal surveys in various geographical locations. Interstitial species include members of nearly every invertebrate phylum (with the exception of Porifera, Ctenophora, Onychophora, Phoronida, Pogonophora, and Hemichordata). Since most interstitial species are specifically adapted to this environment and are found nowhere else, preliminary studies have presented a tremendous task for taxonomists who must deal with microscopic, transparent forms that are difficult to collect. In most taxa this initial descriptive phase remains far from complete.

Comprehensive study of interstitial meiofauna in the 1930's and 1940's was localized at Kiel University in Germany at the laboratory of Remane. Accomplishments of Remane's group inspired many preliminary investigations in other localities. The French contributed significantly during most of the 1950's by producing numerous faunal surveys and initiating studies of environmental ecology of sandy beaches. A summary of this early work in interstitial biology, particularly the French effort, may be found in Delamare Deboutteville (1960).

In the present decade, interest has become world-wide. Today, areas studied by meiobenthologists include all of Europe, Scandinavia, the British Isles, the east coasts of North and South America, Malaysia, New Caledonia, India, Australia, Africa and Madagascar.

While interest in marine interstitial biology is young in the United States, scattered studies have appeared in the literature. In 1917, Cobb located vast numbers of nematodes in sand flats of Barnstable Harbor on Cape Cod in Massachusetts. Also Wilson (1932) published a lengthy work including descriptions of several interstitial copepods. The most comprehensive ecological work on American meiobenthos is Pennak's studies (1939, 1940, 1942, and 1951) of freshwater and marine interstitial fauna.

As a contribution toward understanding the interstitial ecosystem, I have chosen an ecological approach to study of a single meiofaunal group - the Tardigrada. For this purpose I selected a transect along a beach at Woods Hole and examined populations of tardigrades in detail for over one year. This project includes a systematic survey of the species, a series of observations on natural history and comparative anatomy, a detailed ecological study of important abiotic aspects of this tidal beach environment, and a continuous survey of structure and dynamics of three abundant populations of tardigrades.

Part I of this dissertation, MARINE INTERSTITIAL TARDIGRADES FROM WOODS HOLE, MASSACHUSETTS, is a systematic survey including two species new to science and observations regarding their anatomy and natural history. Paper II, THE REPRODUCTIVE ANATOMY OF SOME MARINE HETEROTARDIGRADA, is prerequisite to interpretations made in following parts of the dissertation. SEASONAL AND TIDAL CHANGES IN THE MARINE INTERSTITIAL HABITAT (Part III) described parameter composition and variations on the beach and provides a frame of reference for understanding the interstitial environment of a tidal beach as a living place for interstitial tardigrades. Year-round data (March, 1968 - May, 1969) on three populations of tardigrades is presented and discussed in relation to observations on parameters and to pertinent literature in ASPECTS OF THE ECOLOGY OF MARINE INTERSTITIAL TARDIGRADA AT WOODS HOLE, MASSACHUSETTS (Part IV). I plan to submit each of these parts as separate papers for publication in appropriate journals.

Part I

MARINE INTERSTITIAL TARDIGRADA FROM WOODS HOLE, MASSACHUSETTS[1]

While interstitial tardigrades from the United States remain poorly known, their occurrence has been noted in three regions along the Atlantic shore: Cape Cod (Marcus, 1946; McGinty and Higgins, 1968), the mid-Atlantic states (Hay, 1917; McGinty and Higgins, 1968), and on the east coast of Florida (Riggin, 1962; King, 1962). Eight of the 29 species of marine tardigrades have been reported from North America; of these, six represent range extensions while two are descriptions of new species of _Batillipes_.

The first species described from the United States, _Batillipes_ _caudatus_ Hay, 1917, later was placed in synonomy with _B_. _mirus_ Richters, 1909 (Marcus, 1927). However, Hay's description remained the only study on marine tardigrades from America for 29 years. _B_. _pennaki_ Marcus, 1946, was described from material supplied by Pennak from Woods Hole, Massachusetts, as well as from specimens Marcus found in Brazil. More recently _B_. _friaufi_ Riggin, 1962 and the unusual _B_. _bullacaudatus_ McGinty and Higgins, 1968 have been described from Florida and Virginia, respectively. _Stygarctus_ _bradypus_ Schulz, 1951 was reported by Uhlig (1968) from Woods Hole and by McGinty and Higgins (1968) from York River, Virginia and Woods Hole. McGinty and Higgins (1968) found a single _Halechiniscus_ _remanei_ Schulz, 1955 at York River, Virginia.

The tardigrades discussed here were encountered during a year long ecological study on Crane's Beach, Woods Hole, Massachusetts. Crane's Beach (lat. 41° 31' 41" N, long. 70° 40' 41" W) is on the Buzzards Bay side of the neck connecting Penzance Point to Woods Hole. Most observations were made on living animals at 430 X or 930 X (oil immersion) of a light microscope. Permanently mounted specimens were prepared by the method outlined in McGinty and Higgins (1968).

FAMILY BATILLIPEDIDAE Riggin, 1962

Discopodidae Marcus, 1934, p. 862.

DIAGNOSIS: Arthrotardigrada with median cirrus present; on each leg four to six adhesive toes on pedestals of unequal length; claws absent.

TYPE GENUS: Batillipes Richters, 1909.

DISCUSSION: Members of this family are distinguished by toes each composed of an expanded, adhesive surface attached to the leg by a tubular pedestal. The family includes two genera, Batillipes and Orzeliscus Bois-Reymond Marcus, 1952, both of which typically are found in the marine interstitial habitat.

GENUS BATILLIPES Richters, 1909

DIAGNOSIS: Batillipedidae with four to six toes composed of tubular pedestals terminating in disc-shaped adhesive expansions.

TYPE SPECIES: Batillipes mirus Richters, 1909.

DISCUSSION: The nine species in this genera are distinguished primarily by caudal appendage shape, relative length and shape of cephalic appendages, and size of lateral body projections. Patterns of toe pedestal length, compared in Fig. 1, differ among *Batillipes* species. As more species are encountered, foot patterns may be useful taxonomic indicators.

Two species, *B. mirus* and *B. pennaki*, apparently have a wide geographic range. Most of the other species have been recorded only at or near their type localities.

Batillipes pennaki Marcus, 1946

Table I

DIAGNOSIS: *Batillipes* with single, pedunculate, heavy caudal spike; short, constricted clavae; short leg spines on all legs. Toe pattern, group A1 (Fig. 1).

DISTRIBUTION: Woods Hole, Massachusetts (Marcus 1946); Ipanema, Rio de Janeiro, and Guaruja near Santos, Brazil (Marcus, 1946); several beaches in Bassin d'Arcachon, France (Renaud-Debyser, 1959a); Siponto and Aloisa (near Foggia), Trani, Capitolo, and Cozze (near Bari), Torre dell'Orso and S. Catoldo (near Lecce), and Torre Canne (near Brindisi) all on the Adriatic coast of Italy (DeZio, 1962, 1964); Lawson's bay near Waltair, India (Rao and Ganapati, 1968); and I have found them in Hampton Harbor, Seabrook, New Hampshire.

DISCUSSION: Observations are presented here to supplement the brief original description (Marcus, 1946) and more encompassing anatomical discussions of the genus (Marcus,1927). *B. pennaki* from Crane's Beach is heavy-set with short cephalic appendages, including medially constricted clavae. Body width uniform anterior to posterior. Lateral projections between the third and fourth pair of legs more pointed than originally described by Marcus (1946). Terminal spike prominent; inserted on large basal peduncle (one animal out of several thousand examined possessed a two pointed, pedunculate spike). Cuticle with evenly distributed pores; eyes absent. Morphometry of three size groups of _B_. _pennaki_ from Crane's Beach appears in Table I.

The mouth opening is ventral and leads directly to a tubular mouth canal. Both the opening and canal are heavily cuticularized; canal flanked by a pair of strong stylets. Using a fulcrum at the point of attachment of short stylet supports to the mouth canal, stylets can be extruded through the mouth opening. Canal and associated stylets of all specimens have a distinct right hand bend.

Mouth canal penetrates a short distance into a subspherical pharyngeal bulb. The terminus of the canal is surrounded by bifurcate ends of three solid placoids whose distal ends diverge outwardly and posteriorly through the body of the pharyngeal bulb. The bulb lumen is symmetrically tri-radiate and "Y" shape in cross-section. During pumping, the outer shape of the bulb remains unchanged as its lumen expands in anterior to posterior peristolic waves. Expanded, the bulb lumen is equal in width to the mouth canal.

The bulb lumen is connected by a short flexible esophagus to a saccate gut. In starved or recently molted animals, the gut is cylindrical, tapering posteriorly to a ventral anus between the hind legs. In well fed animals, the gut expands into six pairs of lateral diverticulae and a trefoil-shaped terminal diverticulum. As the diverticulae develop, the gut lumen is reduced.

The animals defecate only during molting, expelling dark colored material into the old cuticle. Many small, irregular granular bodies, presumably inclusions within the gut cells, remain in fixed positions in the gut after defecation.

Noncontractile ligaments, leading from diverticulae to legs, cause movements of the gut during locomation. Leg movements thus transferred to gut contents, and probably to contents of the pseudocoel as well, provide a rudimentary circulatory mechanism. Agitation decreases with decreasing leg activity from the anterior pair toward posterior pairs (the fourth pair seldom moving at all.)

Reproductive systems of both sexes have been examined in detail and are to be discussed elsewhere (Part II).

Animals of less than 75 µm length encountered in this study differ from mature animals in possessing four toes per leg and disproportionately large feet, cephalic appendages, and caudal spike. Apparently the middle two adult toes are the last to be formed.

Molting occurs throughout spring, summer, and fall. Although I have not observed animals in the "simplex state" or expelling their buccal apparatus (described for eutardigrades by Marcus, 1929), several individuals with partially resecreted stylets have been found. Stylets form progressively backward from their anterior tips, while placoids reform concurrently. Stylets are completed and functional before molting occurs.

As a new cuticle forms, the animal contracts away from its old cuticle, the last connections being points of muscle attachment. A molting animal moves with difficulty and measures about three fifths the length of its old cuticle. When new feet become functional, detachment from the old cuticle can occur. The old cuticle adheres to the substratum while the animal crawls about inside, occasionally jabbing at it with its stylets. The search for an escape opening is slow, but once located, the exit is rapid and generally through a rectangular panel of cuticle posterio-ventral to the mouth.

The pedunculate single caudal spike, short cephalic appendages, and constricted clavae distinguish _B_. _pennaki_ and _B_. _annulatus_ DeZio, 1962 from other species of _Batillipes_. _B_. _annulatus_ differs from _B_. _pennaki_ only in the number of claval constrictions. Other distinguishing characters mentioned in the original description (DeZio, 1962) include the absence of sessile digits on the fourth legs and the shape of lateral body projections between the third and fourth pair of legs. However, _B_. _pennaki_ from Woods Hole resemble _B_. _annulatus_ in both of these features.

Batillipes _mirus_ Richters, 1909

DIAGNOSIS: _Batillipes_ with simple caudal spine inserted directly on body. Toe pattern, group A1 (Fig. 1).

DISTRIBUTION: Near Kiel, Germany (Richters, 1909); North Sea, Germany (Schulz, 1950); Julebaek Beach, Helsingør, Denmark (Fenchel, Jansson, and Thun, 1967); Herdla, Norway (Tambs-Lyche, 1939-40); coast of Sweden (Jagersten, 1952); Henriksberg, Finland (Purasjoki, 1953); Tvarminne, Finland

(Karling, 1955); Roscoff, France (Swedmark, 1951, 1955, 1956b); L'Aber, Roscoff, France (Guérin, 1960); Eyrac Beach, Bassin d'Arcachon, France (Renaud-Debyser, 1956); Graveyron, Bassin d'Arcachon, France (Renaud-Mornant and Jouin, 1965); Rochefort, France (Baudoin, 1952); Marseilles, France (Swedmark, 1956a); near Fortullino, Italy (Papi, 1952); Franta, Bulgaria (Valkanov, 1950, 1954); in the Black Sea (Plesa, 1963); Afifea, Mangalia, Constanta, and Iarna, Romania (Rudescu, 1964); several beaches at Anglesey and the Lleyn Peninsula, Wales (Boaden, 1963); Strangford Lough, Northern Ireland (Boaden, 1966); several beaches between Kuantan and Tregganou, Malaysia (Renaud-Mornant and Serène, 1967); Beaufort, North Carolina, USA (Hay, 1917); Alligator Harbor, Florida (King, 1962); York River, Yorktown, Virginia (McGinty and Higgins, 1968); and I have found them on several beaches in Woods Hole, Massachusetts.

DISCUSSION: _B_. _mirus_ from Woods Hole is slender with a single non-pedunculate caudal spike and narrow, unconstricted clavae. Body width is uniform anterior to posterior with lateral body spine between third and fourth pair of legs just posterior to lateral body projection. Cuticle is transparent with evenly distributed pores. Leg spines are short.

Richters (1909), Hay (1917), and Marcus (1927) describe eye spots in this species. However, McGinty and Higgins (1968) were unable to distinguish them in preserved specimens from Virginia, although eyes of freshwater tardigrades are seen clearly in similarly prepared specimens. A pair of concave bodies can be seen laterally within the head of living _B_. _mirus_ from Woods Hole. If these internal, unpigmented, granular bodies represent the eye spots described by earlier workers, they are entirely different from eye spots found in other tardigrades.

While B. mirus is rare at Crane's Beach, larger populations are found at nearby beaches in Woods Hole, particularly at Wood Neck Beach (about six km north of Crane's Beach on the Buzzards Bay coast).

B. carnonensis Fize, 1957 may be separated from B. mirus by the shape of the external median cirri, absence of spines on first three pairs of legs, and more prominent lateral body projections (Fize, 1957). Constricted clavae distinguish B. pennaki and B. annulatus from B. mirus, while the nonpedunculate single caudal spike separates B. mirus from all other species.

Batillipes bullacaudatus McGinty and Higgins, 1968

Table II

DIAGNOSIS: Batillipes with caudal spine terminating in bulbous structure; spines of fourth leg long; median, internal, and lateral cirri and fourth leg spines frayed at tip, generally trifid. Toe pattern, group A1 (Fig. 1).

DISTRIBUTION: York River, Yorktown, Virginia (McGinty and Higgins, 1968) and Crane's, MBL, and Nobska Beaches at Woods Hole, Massachusetts.

DISCUSSION: B. bullacaudatus is smaller and more delicate in appearance than other species of Batillipes at Crane's Beach. Cephalic appendages are long; clavae are narrow and unconstricted. Lateral projections are especially prominent between third and fourth pairs of legs. Lateral body spine and leg spines are long. Cuticle is transparent with uniformly arranged pores. Caudal appendage is an elongate spine terminating in membranous bag. Eyes are absent. Morphometric data on three size groups of B. bullacaudatus from Crane's Beach are shown in Table II.

Although all species of Batillipes from Crane's Beach possess some adhesive capabilities, B. bullacaudatus is most broadly adhesive over its body surface. Commonly members of this species are covered dorsally by debris. However, they possess weakly adhesive toes and can be dislodged from substratum more easily than other species of Batillipes.

The caudal appendage of B. bullacaudatus is unique. Although the terminal membrane is occasionally absent, the long, vertically directed caudal spike remains distinctive. The function of the "balloon" tail remains unclear. I never have observed the bulbous portion "inflated", even during changes in salinity (10 - 60 $^{o}/oo$) and temperature (15 - 35^{o}C). Individuals may hang suspended in the medium, attached to the substratum only by the adhesive caudal appendage. A vertical orientation of the caudal spike aids in the accumulation of debris on the back of animals. Such a covering of debris undoubtedly provides some protection from drying conditions high on Crane's Beach, where B. bullacaudatus typically is found.

Batillipes dicrocercus n.sp.

Fig. 2

Table III

DIAGNOSIS: Batillipes with furcate caudal appendage and prominent fourth lateral body projections. Toe pattern, group A1 (Fig. 1).

HOLOTYPE: Adult; collected by L. W. Pollock, 19 March 1968; deposited in the U. S. National Museum.

TYPE LOCALITY: Crane's Beach, on the Buzzards Bay side of Penzance Point, Woods Hole, Massachusetts; lat. 41° 31' 41" N. long. 70° 41' 41" W; medium-coarse sand of poor sorting; lower one quarter to mid-tide beach level, 5 - 25 cm depth in sand.

DESCRIPTION OF THE HOLOTYPE: Body length, from base of cephalic appendages to base of caudal process, 130.9 µm (µm = mirometer); head width, between bases of lateral cirri, 52.2 µm; dorsal median cirrus, 16.3 µm, pedestalate; external cirri, 14.7 µm, pedestalate; clavae, 14.7 µm; lateral cirri, 26.0 µm on common base with clavae.

Cuticle transparent with prominent, uniformly arranged pores of approximately 1.5 µm diameter. Pharynx sub-spherical, 15 x 13 µm. Eyes absent.

Head limited by constriction posterior to lateral cirri; body width increasing posteriorly; prominent, acute lateral body projections anterior to fourth pair of legs. Lateral body spine, dorsal and posterior to body projection, 16.3 µm in length.

Leg spines increasing in length from the first to the fourth pair of legs; spines on fourth pair, 21.1 µm. Legs slightly telescopic distally; six disc-shaped toes per leg (four in juveniles); toe shape as described for _B_. _bullacaudatus_ (McGinty and Higgins, 1968).

Caudal appendage two branched from slightly swollen base; each branch 13.0 µm in length.

Table III shows morphometric characters from 14 *B. dicrocercus*.

ETYMOLOGY: The specific name has been proposed on the basis of the forked caudal appendage of these animals. (L. *Batillum* - shovel + L. *pes* - foot; G. *dicro* - forked + G. *cercus* - tail).

DISCUSSION: Although *B. dicrocercus* resembles *B. littoralis* Renaud-Debyser, 1959 and *B. similis* Schulz, 1955 in general body shape, the relative lengths of cephalic appendages, and presence of lateral body projections, the shape of its caudal process distinguishes *B. dicrocercus* from these species.

This new species can be separated on morphological and ecological grounds from both *B. bullacaudatus* and *B. pennaki*, which are common in the type locality. *B. bullacaudatus* has a distinctive "balloon" caudal appendage, a generally smaller adult size, and more delicate appearance. *B. pennaki* may be distinguished from *B. dicrocercus* by its single caudal spike on a large pedunculate base, short cephalic appendages and leg spines, stout, constricted clavae, a body shape of even width, and less prominent lateral body projections.

These three species generally have different distributional patterns at Crane's Beach. *B. dicrocercus* occurs in the lower half of the intertidal beach, usually at a 5 - 25 cm depth in sand in the quarter to mid-tide region. While its population density in this region was measured at 0.2 - 0.5 animals per cm^3 of sand during the spring, no individuals were encountered in summer collections. *B. bullacaudatus* usually occurs from the three-quarter tide level to sandy areas several meters beyond the mean high tide line, at depths of 20 - 40 cm in the sand. Densities of 0.6 - 1.0 animals per cm^3 are common for this species. The *B. pennaki* population is widespread throughout the beach, though areas of maximum density are usually in the mid-tide region and are often much greater than 3.0 animals per cm^3.

FAMILY STYGARCTIDAE Schulz, 1951

EMENDED DIAGNOSIS: Heterotardigrada with median cirrus and five pairs of cephalic appendages; cuticle formed into unpaired dorsal thickenings or plates; in adults, four claws on each leg; in some, claws attached with brief basal membrane to distal extreme of non-digitate foot; middle two claws on each leg possess filimentous extensions; lateral body spines present.

TYPE GENUS: *Stygarctus* Schulz, 1951.

DISCUSSION: This family includes two genera, *Stygarctus* and *Parastygarctus* Renaud-Debyser, 1965. All known members of this family are marine, interstitial forms.

GENUS *STYCARCTUS* Schulz, 1951

EMENDED DIAGNOSIS: Stygarctidae with cuticle thickened to form three unpaired body plates between a one-piece cephalic plate and a caudal plate; caudal spikes present; legs bend only at junction with body and at foot.

TYPE SPECIES: *Stygarctus bradypus* Schulz, 1951.

DISCUSSION: The genus *Stygarctus* has remained monotypic since the description of *S. bradypus* Schulz, 1951 from

"Küstengrundwasser". Nonetheless, S. bradypus has a wide geographical distribution. Schulz originally collected it in beach sand near List on the North Sea coast of Germany. Renaud-Debyser has reported this species from numerous beaches in Bassin d'Arcachon (Renaud-Debyser, 1956, 1959a) on the Atlantic coast of France and from coralline sand at Bimini in the Bahamas (Renaud-Debyser, 1959b). More recently Rao and Ganapati (1968) reported it from the Waltair coast, India. McGinty and Higgins (1968) extended its known distribution along the east coast of North America including Woods Hole, Massachusetts; York River, Virginia; Atlantic Beach, North Carolina; and Ocho Rios, Jamaica. Uhlig (1968) also noted its presence in a Woods Hole beach.

There are no morphological observations in any of these range extension reports. The only available illustration of S. bradypus is Schulz' original set of figures (Schulz, 1951, p. 90, Fig. 1-5). Unfortunately the small size of these illustrations cannot adequately portray the morphological detail of this unusual animal. Consequently it is possible that morphological differences between S. bradypus and animals reported as this species have gone unnoticed.

Stygarctus granulatus n. sp.

Figs. 3 & 4

Table IV

DIAGNOSIS: Stygarctus with small refringent bodies scattered over cuticular plates, particularly dorsally; two pairs of acute processes along posterior rim of cephalic plate;

11 cephalic appendages including four clavae of approximately equal size; anal region surrounded by cuticular plates; caudal processes one-half the length of fourth pair of legs in all but smallest juveniles; lateral body cirri with thickened basal section, basal section smooth or annulate; lacking posterior accessory projections from body plate II.

HOLOTYPE: Adult; female; collected by L. W. Pollock, June, 1968; deposited in U. S. National Museum.

TYPE LOCALITY: Crane's Beach, Buzzards Bay side of Penzance Point, Woods Hole, Massachusetts; lat. 41° 31' 41" N, long. 70° 40' 41" W; medium well sorted sand; mid-tide to high tide area, 20 - 40 cm depth in sand.

DISTRIBUTION: Woods Neck, MBL, Crane's and Nobska Beaches in Woods Hole, Massachusetts.

DESCRIPTION OF HOLOTYPE: (See Figs. 3 and 4 of composite and Table IV for morphometric data). Body length from anterior rim of cephalic plate to base of caudal processes, 130.2 µm; head width, between bases of lateral cirri, 49.0 µm; dorsal median cirrus, not visible; lateral cirri, 14.7 µm; lateral clavae, 6.5 µm; external median cirri, 11.4 µm; anterior clavae (or cephalic papillae), 7.2 µm; internal median cirri, 8.2 µm. Bases of all cephalic cirri enclosed within tiny cups (Figs. 3 and 4).

Mouth subterminal at tip of retractable mouth cone; pharynx sub-spherical 9 x 10 µm; mouth tube and stylets, 27.0 µm; stylet supports absent; eyes absent.

Cuticle transparent and formed into a series of dorsoventrally flattened bands, appearing as unpaired dorsal and ventral plates (one around head; three around trunk; body plates I - III; and one around caudal portion). Small thickenings intermediate between dorsal body plates I and II, and II and III. Dorsal plates thick, with scattered small refractile bodies; ventral plates thinner, with few refractile bodies. Cephalic and body plates expanded ventro-laterally forming acute processes posteriorly at lateral extremes. On the dorsal cephalic plate only, a second set of acute processes located on posterior rim just above the two posterio-lateral projections described above. Caudal plate with two prominent terminal spikes, 16.3 µm or 0.417 times the length of the fourth pair of legs. A pair of lateral body spines, 30.4 µm, with thickened (and in some specimens, annulate) base (3.9 µm in length) inserted on tubercles near anterior extreme of caudal body section.

The first three pairs of ventrally directed legs insert in round spaces located in anterior corners of ventral body plates I - III. These legs equal in length, ca. 25 µm. The fourth pair of legs insert latero-terminally in spaces located in posterior corners of ventral caudal plate. Fourth legs longer (39.2 µm in length) than anterior legs. Four simple terminal claws with basal connections on each leg. Foot non-digitate. Each of the middle two claws of every leg with a filimentous process, appressed along dorsal surface of claw to its midpoint, then diverging slightly and extending 13.0 µm beyond end of claw. Claws of fourth pair of legs longer, 10.0 µm, than those of anterior three pairs of legs, 6.5 µm. Single small papilla lateral on hind legs near junction with body. Small blunt projection on internal surface of fourth legs. The first three pairs of legs without papillae or spines.

Anal apparatus ventral between fourth pair of legs (Fig. 4). Sinuous tube, 9.8 µm in length, leads caudally to terminal anus between bases of caudal spikes. A partial enclosure of cuticular plates surrounds the tube. Two rhomboidal lateral plates (8.5 µm long by 2.0 µm in height) bow outward on either side of the tube and at their posterior extremes flank the anal opening. These plates arch inwardly as if to form a "capsule" but terminate pre-apically leaving a gap 1.5 µm wide. A small square plate (2.0 µm on a side) lies erect at right angles to the body axis in an anterior gap between the lateral plates.

Holotype, female. Six small plates surround mid-ventral gonopore; gonopore located in anterior portion of caudal plate. Reproductive anatomy of S. granulatus will be discussed in greater detail elsewhere (Part II).

ETYMOLOGY: The specific name is derived from refractile granules scattered over the cuticular plates. (G. Stygo - cave + G. arctus - bear, L. granul - little grain + L. atus - to possess).

DISCUSSION: A comparison of specimens of S. granulatus and the original description of S. bradypus (Schulz, 1951) reveals several distinguishing characters. The second set of acute processes on the posterio-dorsal border of the cephalic plate of S. granulatus are absent on S. bradypus, as are scattered refractile bodies on dorsal and ventral plates, papillae on the fourth pair of legs, intermediate thickenings between the trunk plates, and cuticular elaborations around the anus. It is not clear from Schulz' figures (1951, Fig. 1 and 2) whether or not S. bradypus has the thickened basal section of the lateral body spines seen in S. granulatus (Fig. 3 and 4)

On the other hand S, bradypus has a pair of processes along the posterior edge of body plate II. According to Schulz (1951) these processes pass posterio-laterally towards the anterior edge of body plate III, where they are distally bifurcate. No such structure is found in S. granulatus. The recurved "cephalic papillae" or anterior clavae in S. bradypus are more than twice the length of the lateral clavae - a feature stressed in the original description (Schulz, 1951). In S. granulatus the anterior clavae are only slightly longer (see Table IV). Schulz indicates that the caudal spikes of S. bradypus measuring 90 - 130 μm are three-quarters the length of the fourth legs, while in S. granulatus of comparable size, they are approximately one-half the length of the fourth legs (see Table IV). The stylets of S. granulatus are much longer than those of S. bradypus (Schulz, 1951, Figs. 4A and B). They are equal in length to the mouth tube, and extruded they project up to one-half their length beyond the mouth opening. Stylets extend from a dorsal placement on the pharynx bulb to their point of entry, via small lateral sheaths, into the mouth tube near its origin.

The peculiar perianal cuticular morphology in this family is unique in known tardigrades. Although no such configuration is described for S. bradypus, the anal region of Parastygarctus higginsi, "...entoure d'un repli de la cuticle.." (Renaud-Debyser, 1965b, p. 34), is probably similar. A sinuous anal tube has been described from P. higginsi (Renaud-Debyser, 1965a) and for Styraconyx sargassi Thulin, 1942 (Renaud-Mornant, 1967b).

A reduced number of toes or claws on juvenile tardigrades has been observed in marine forms (Marcus, 1927; McGinty and Higgins, 1968). The interior two adult claws, distinguished by filamentous extentions, are first to develop in S. granulatus, since they are the only claws present in the smallest juveniles.

AFFINITIES OF THE STYGARCTIDAE: While our understanding of heterotardigrade relationships is far from complete, the systematic position of the Stygarctidae is more problematic than that of most other families. Schulz (1951) and Renaud-Debyser (1965a and b; Renaud-Mornant, 1967a) have commented on the intermediate position of this family between the two heterotardigrade suborders, the Arthrotardigrada Marcus, 1927 and the Echiniscoidea Marcus, 1927. On the basis of an unpaired median cirrus, absence of eyes, placement of clavae and dorso-lateral cirri, and slightly telescoping extremities, Schulz (1951) placed the Stygarctidae within the Arthrotardigrada.

While the anterior clavae of stygarctids (termed "cephalic papillae" by Schulz, 1951 and Renaud-Debyser, 1965a) are located in a position approximately corresponding to the cephalic papillae of echiniscoids, they are morphologically identical to lateral clavae, and therefore "anterior clavae" is a more accurately descriptive term for them. However, they do represent a possible homology to cephalic papillae of echiniscoids, as do the external and internal median cirri to echiniscoid cephalic appendages.

All instances of cuticular thickening to form well defined plates are described from those heterotardigrades which Ramazzotti (1962) groups within the Echiniscoidea. Such formations in the stygarctids appear most similar to the series of unpaired dorsal plates found in the echiniscoid genus *Oreella* (specifically *O. mollis* Murray, 1910 and *O. vilucensis* Rahm, 1931).

The morphology of the distal portion of the legs in both *S. granulatus* and *P. higginsi* is more similar to that of several echiniscoids than to any group within the arthrotardigrades. The basal connections between the ends of the legs and the claws are nearly identical to those shown for *Oreella minor* Ramazzotti, 1964 (p. 349, Fig. 2B). The feet of this species of *Oreella* suggest further evidence of the close affinity between this genus and the stygarctids, as indicated originally by Schulz (1951) on other grounds. Legs of *S. granulatus* are slightly telescopic distally.

The presence of a median cirrus and slightly telescoping legs represent the only major arthrotardigrade features of *S. granulatus*. The reliability of these characters are systematic guidelines must await clarification by much more information on heterotardigrade morphology.

Renaud-Debyser (1965a and b) lists eight characters in which Parastygarctus differs from Stygarctus. These features include the arrangement of cephalic appendages, the possession of articulate cirri, flexible dorso-lateral cirri, claws with basal membranes, two lateral projections from each side of every body plate, the absence of caudal spikes, unique cephalic papillae, and a cephalic plate composed of two pieces. If characters of S. granulatus are included in this comparison, only the final four items in this list remain distinctive.

ECOLOGY: At Crane's Beach the population center of the population of S. granulatus remains at 20 - 40 cm depth in the sand between mid- and high-tideal levels. During periods of maximum growth of populations, I measured densities higher than 30 animals per cm^3 of sand, although densities of 5 - 10 animals per cm^3 are more common. For further details see Part IV.

Deprived of their natural substratum, S. granulatus appears clumsy and sluggish. However, animals active in the interstices of sand grains are capable of surprisingly rapid movement. The filamentous projections from the interior two claws of each leg are adhesive. This feature as in the adhesive toes of Batillipes, produces forward progress with nearly every leg movement. The anterior three pairs of ventrally directly legs move as alternate tripods, and allow S. granulatus to progress nearly as rapidly as can Batillipes.

The fourth legs are oriented in opposition to the anterior legs and are infrequently used. As the animals crawl forward, the fourth legs are held posteriorly in a "V" (approximately as they appear in Figs. 3 and 4). If anterior legs lose contact with the substratum, the animal slowly swings these long fourth legs laterally forward and then rapidly back to the "V" position until they catch on some object to the sides and "vault" the animal ahead.

[1] This paper, Contribution No. 160, Systematics-Ecology Program, Marine Biological Laboratory, Woods Hole, Massachusetts, has been submitted for publication to the *Transactions of the American Microscopical Society*.

TABLE I. MEASUREMENTS (µm) of *BATILLIPES PENNAKI* MARCUS, 1946. MEAN ± STANDARD DEVIATION.

Character Size Groups (Individuals studied)	50–99 µm (10 individuals)		100–149 µm (10 individuals)		150–199 µm (10 individuals)	
Body length	86.9	12.35	127.5	12.90	169.7	11.39
Lateral cirri	18.5	1.85	22.0	4.05	27.1	3.47
Clavae	7.3	1.83	9.5	1.51	9.7	1.61
External cirri	9.0	1.89	11.5	2.58	13.9	2.69
Internal cirri	9.8	1.56	11.8	2.24	14.6	1.88
Median cirrus	6.9	1.89	8.4	1.34	12.5	0.92
Caudal spike	13.9	2.03	19.7	4.12	22.1	3.52
Fourth leg spines	4.6	1.57	9.7	1.90	14.1	1.81
Dorso-lateral spine	17.3	2.33	16.8	2.62	20.2	8.40
Stylets & placoid length	20.5	3.81	30.2	5.13	24.3	2.26

TABLE II. MEASUREMENTS (µm) of *BATILLIPES BULLACAUDATUS* McGINTY and HIGGINS, 1968. MEAN ± STANDARD DEVIATION.

Character						
Size Groups (Individuals studied)	50–99 µm (2 individuals)		100–124 µm (10 individuals)		125–149 µm (10 individuals)	
Body length	81.5	18.46	115.6	6.69	135.4	6.12
Lateral cirri	27.2	3.81	29.8	6.07	35.7	3.19
Clavae	8.2	0.00	13.9	2.54	15.8	2.67
External cirri	6.5	0.00	12.2	2.05	13.8	1.23
Internal cirri	17.5	1.58	19.9	2.85	22.8	3.12
Median cirrus	17.1	5.73	20.9	4.91	23.7	5.73
Caudal spike	29.3	9.19	44.6	3.01	50.8	10.61
Bulbous portion	missing		42.7	11.16	52.8	10.11
Fourth leg spines	19.5	2.26	28.2	4.23	30.1	3.46
Dorso-lateral spine	14.6	2.33	17.6	2.59	13.0	0.00
Fourth lateral projection	8.2	0.00	7.6	1.70	8.7	1.70

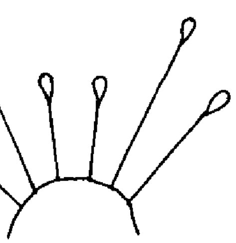
TABLE III. MEASUREMENTS (µm) of <u>BATILLIPES DICROCERCUS</u> n. sp. MEAN ± STANDARD DEVIATION.

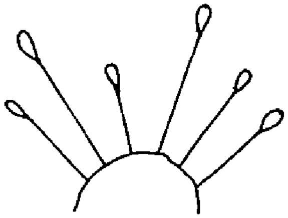
Character						
Size Groups (Individuals studied)	50–99 µm (2 individuals)		100–149 µm (5 individuals)		150–199 µm (7 individuals)	
Body length	82.0	0.71	134.7	14.56	167.5	9.06
Lateral cirri	26.4	5.46	25.8	4.46	33.0	9.07
Clavae	8.7	1.68	12.5	0.77	15.0	2.07
External cirri	9.2	0.69	12.6	2.38	13.7	2.44
Internal cirri	16.7	0.50	20.4	3.02	22.2	1.73
Median cirrus	15.3	1.41	23.1	6.11	23.7	5.40
Caudal spike	obscured		14.1	2.05	17.3	2.79
Fourth leg spines	15.8	3.88	17.5	2.72	23.3	3.69
Dorso-lateral spine	19.6	4.60	16.8	3.60	17.9	3.67
Fourth lateral projection	10.0	0.00	8.3	1.90	7.9	1.32

TABLE IV. MEASUREMENTS (µm) of *STYGARCTUS GRANULATUS* n.sp. MEAN ± STANDARD DEVIATION.

Character						
Size Groups (Individual studied)	50-99 µm (9 individuals)		100-124 µm (10 individuals)		125-149 µm (7 individuals)	
Body length	72.1	15.51	115.6	4.65	133.5	7.27
Head width	34.7	7.62	41.7	2.71	43.9	6.47
Caudal section width	24.2	2.65	33.9	3.25	35.9	2.59
Lateral cirri	10.7	1.86	13.0	2.66	12.9	2.25
Lateral clavae	4.9	1.62	6.9	1.09	7.2	1.19
External cirri	6.9	1.30	9.3	2.01	9.5	2.28
Internal cirri	7.6	1.78	9.7	1.79	10.0	1.51
Anterior clavae	5.4	1.21	6.9	1.23	8.3	1.18
Median cirrus	9.1	3.08	10.5	2.07	11.4	2.26
Stylet length	19.6	3.78	24.6	3.07	26.1	6.50
Lateral body spine	23.6	2.85	26.4	3.03	24.4	3.23
Fourth leg length	23.0	4.50	31.2	4.08	36.0	2.56
Claw length	5.8	1.92	9.3	0.71	10.3	0.64
Claw projection	9.3	3.02	12.3	1.89	12.9	2.38
Caudal body spike	14.4	2.61	17.6	3.19	18.7	2.79
Caudal spike/ Fourth leg length	.6260		.5641		.5194	

Fourth Foot Patterns


A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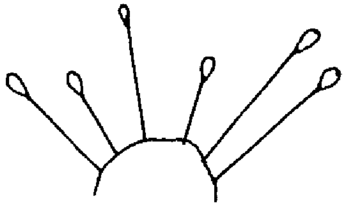
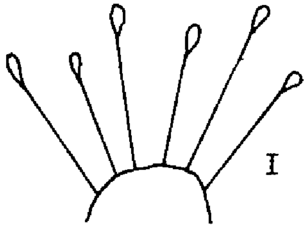
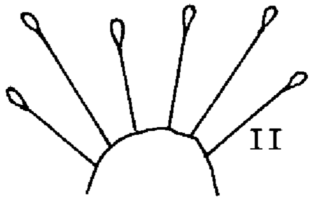

C

First Foot Patterns


I


II

	A	B	C
I	B. annulatus DeZio, 1962 B. bullacaudatus McGinty & Higgins, 1968 B. dicrocercus n. sp. B. mirus Richters, 1909 B. pennaki Marcus, 1946	B. phreaticus Renaud-Debyser, 1959a B. similis Schulz, 1955	B. friaufi Riggin, 1962 B. littoralis Renaud-Debyser, 1959a
II	B. carnonensis Fize, 1957		

FIG. 1. Toe length patterns of first and fourth foot of described species of Batillipes. Illustrations are dorsal views of feet on animal's right side.

FIG. 2. Batillipes dicrocercus n. sp. from Woods Hole, Massachusetts. Composite illustration of adult (dorsal view).

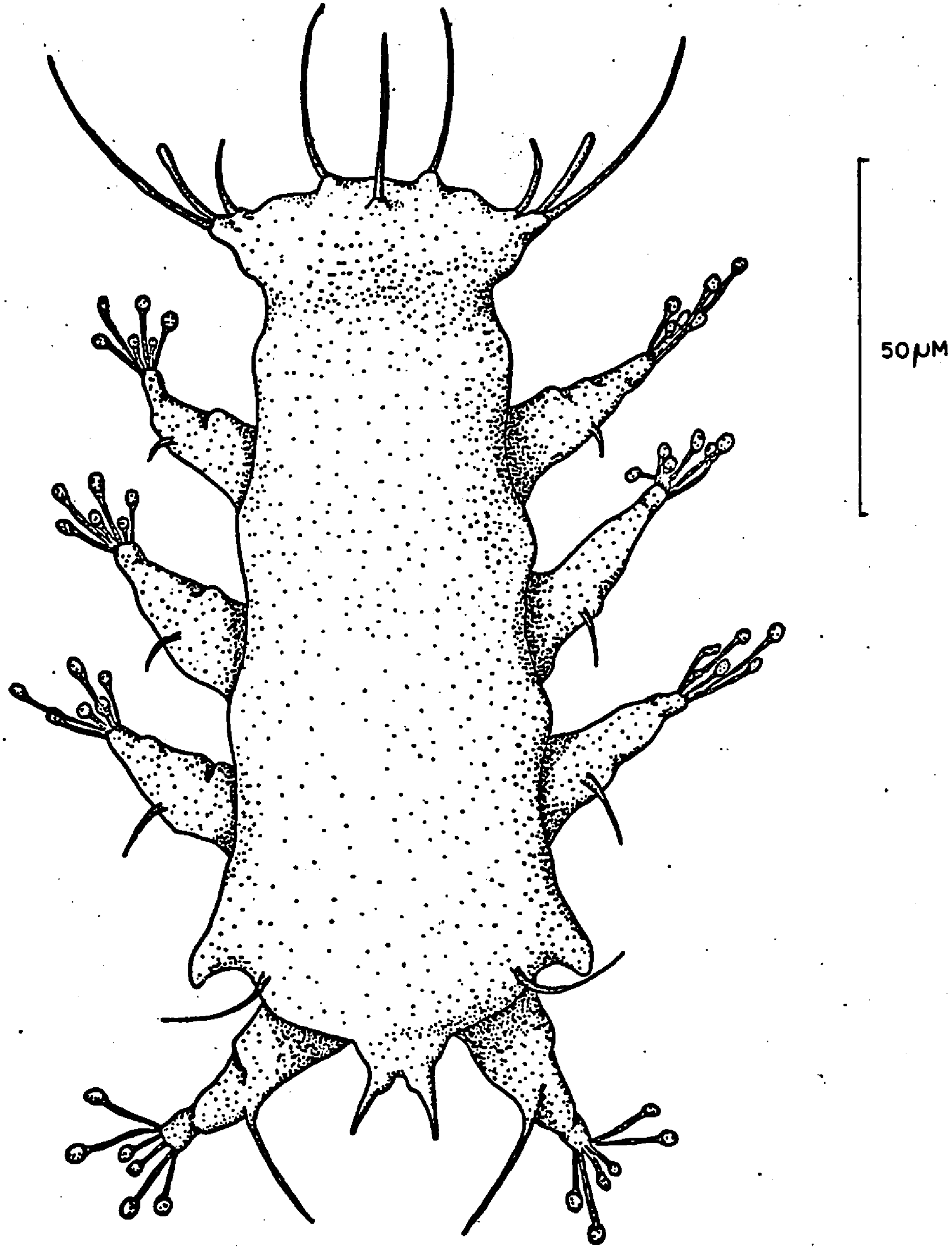


FIG. 2

FIG. 3. Stygarctus granulatus n. sp. from Woods Hole, Massachusetts. Composite illustration of adult female (dorsal view).

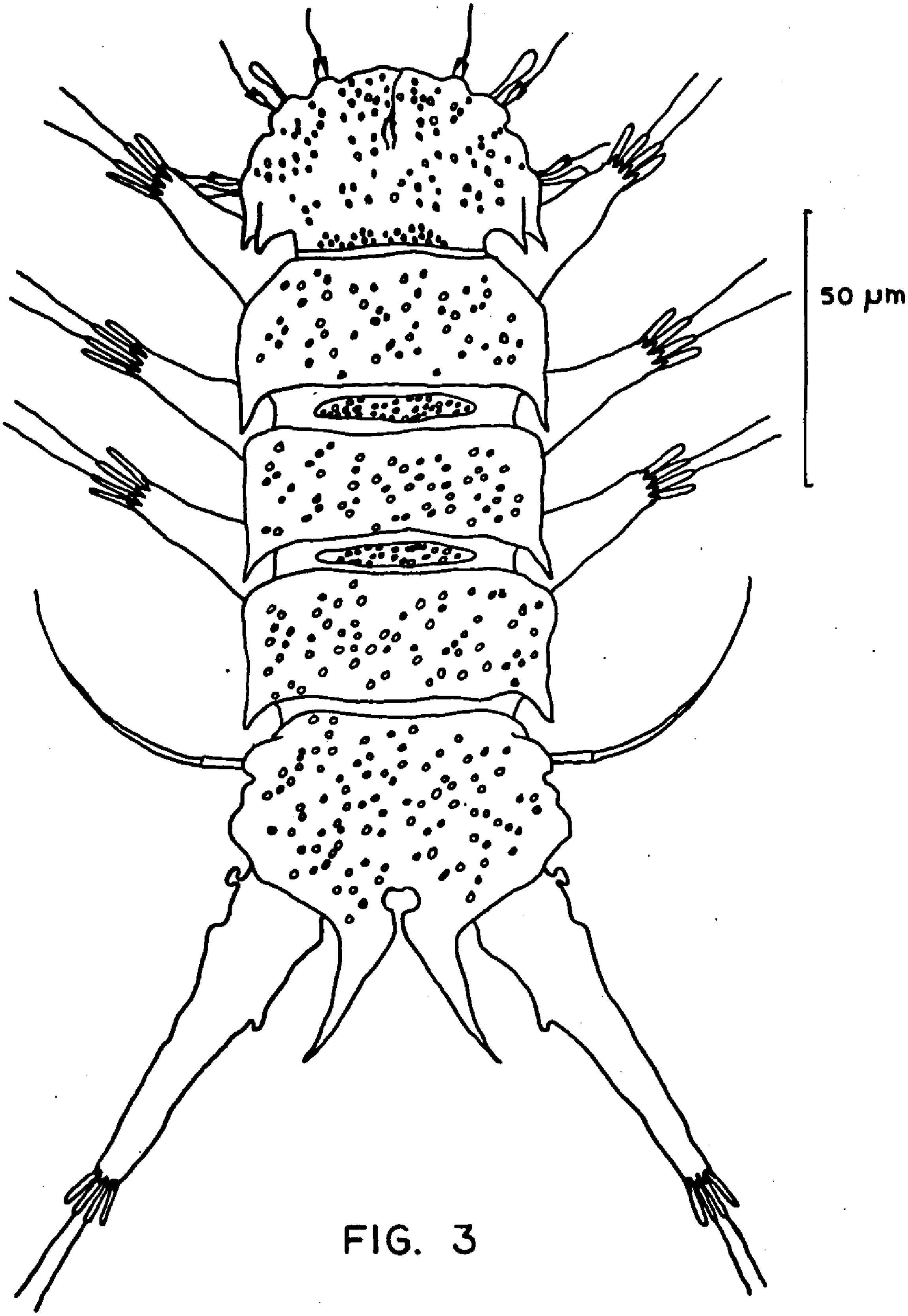


FIG. 3

FIG. 4. *Stygarctus granulatus* n. sp. from Woods Hole, Massachusetts. Composite illustration of adult female (ventral view).

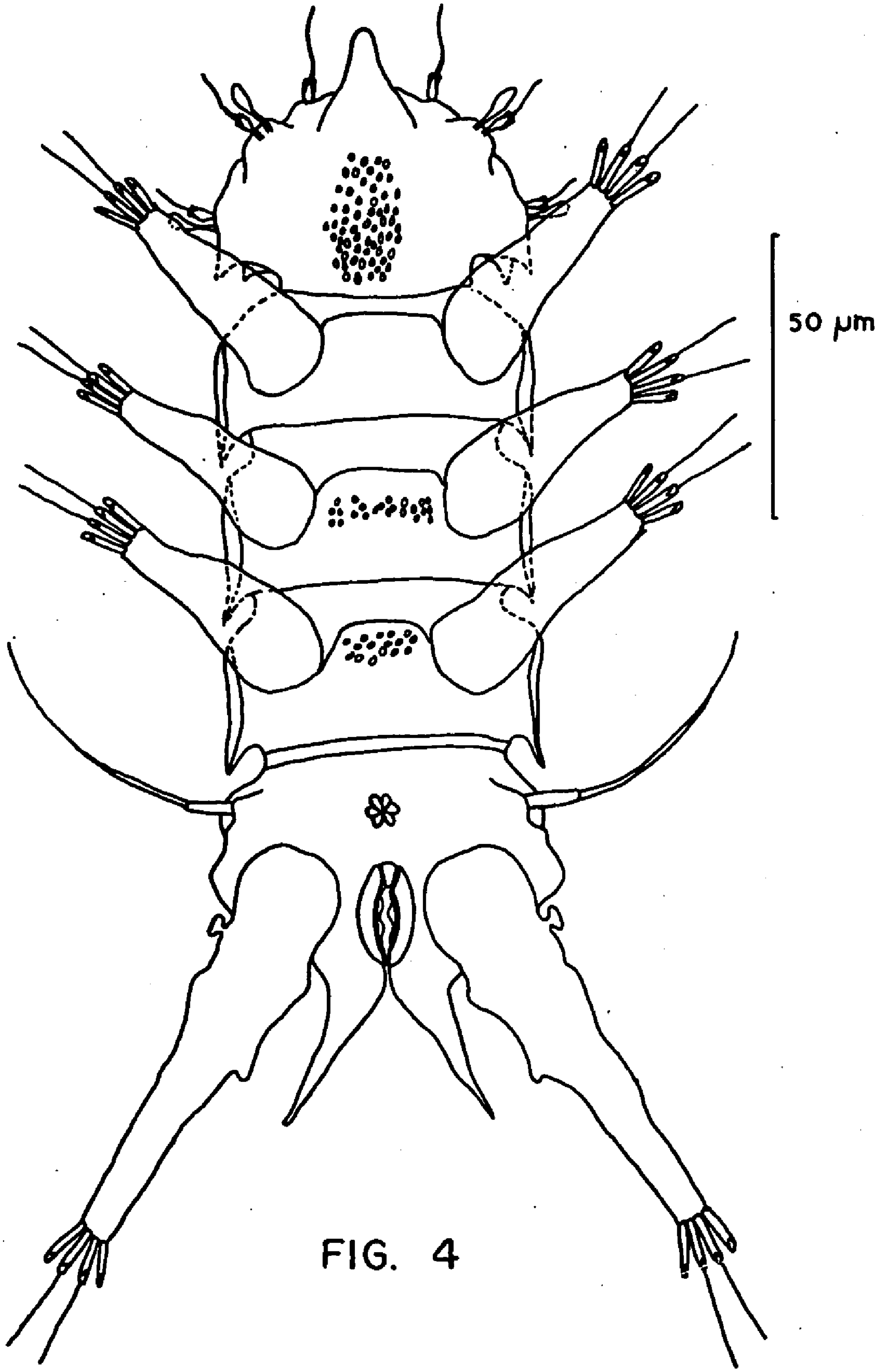


FIG. 4

Part II

REPRODUCTIVE ANATOMY OF SOME MARINE HETEROTARDIGRADA

Sex distinctions in the Tardigrada are recognized primarily by dimorphism of gonoducts. Mature tardigrades possess a sac-like gonad, suspended by ligaments dorsally in the pseudocoel. A single oviduct in females or two vasa deferentia in males lead from the gonad and either enter the hind gut (in the order Eutardigrada Marcus, 1927) or exit via a separate ventral gonopore anterior to the anus (in the order Heterotardigrada Marcus, 1927). The anus is ventral between the fourth pair of legs in both orders.

Richters (1908) and Schulz (1955) describe examples of dimorphism in lateral clavae (characteristic cephalic appendages in heterotardigrades). Males of *Halechiniscus guiteli* Richters, 1908 and *H. perfectus* Schulz, 1955 possess clavae at least as long as the adjacent lateral cirri, while clavae of females are shorter. Ramazzotti (1964) suggested that a similar situation may exist in *Oreella minor* Ramazzotti, 1964.

Dimorphism in the shape of claws and fourth pair of legs, known only from several species of eutardigrades, is discussed in detail by Ramazzotti (1962), Rudescu (1964), and Baumann (1966).

Renaud-Mornant (1967a and b) has demonstrated dimorphism in both shape and location of gonopores in *Parastygarctus* higginsi Renaud-Debyser, 1965 and Archechiniscus marci Schulz, 1952. While some individuals possess a ventral tubular gonopore slightly anterior to the anus, a six-leaved rosette of plates surrounds the more anterior gonopore of others. Only members of the latter group possess a pair of "glandes annexes", consisting of laterally located bulbs connected to medially curving tubules, which terminate in the vicinity of the gonopore (Renaud-Debyser, 1965b, Renaud-Mornant, 1967a).

In the present study the reproductive anatomy of two genera of marine heterotardigrades, Batillipes Richters, 1909 and Stygarctus Schulz, 1951, from Woods Hole, Massachusetts is described. My observations, using oil immersion (930 X) with a light microscope, were of living animals either active in seawater or anesthetizied in a 6.5% (w/v) $MgCl_2$ solution.

OBSERVATIONS

Batillipes pennaki Marcus, 1946 and Batillipes mirus Richters, 1909

Figs. 1A, 2A, & 3

The testis (Fig. 1A) is a large, flattened sac suspended dorsally in the pseudocoel by ligaments to the body wall. It bifurcates posteriorly and recurves ventrally forward on either side of the body, forming lateral bulbes. Dur-periods of reproductive activity, these sperm-producing lateral bulges (mistakenly termed "vesicula seminalis" by Marcus, 1927, p. 532) occupy most of the pseudocoelomic space created by lateral outpocketings of cuticle between the third and fourth pair of legs. From the anterior tip of each lateral bulge, vasa deferentia pass diagonally posteriad, (Fig. 3a), join together mid-ventrally, and as a single common duct continue posteriorly to the ventral gonopore. The male gonopore (Figs. 1A, and 3B) is a slightly raised, oval-shaped opening just anterior to the anus.

Motile spermatozoa are visible in the testis and vasa deferentia of mature animals. Active spermatozoa possess a rounded anterior portion and a long flagellum which constitutes the only demonstrated occurrence of a cilium-like structure in the phylum. Mature spermatozoa move along the periphery of the testis, down and around the lateral bulges, to collect in, and eventually distend the vasa deferentia. Although in some cases the entire testis appears as a mass of agitating spermatozoa, more frequently such activity is confined to the vasa deferentia and lateral bulges.

The ovary (Fig. 2A) in both species of <u>Batillipes</u> is similar to the testis in position and shape. From the ovary a single oviduct descends dextrally between the sixth and terminal diverticulae of the gut, and then medially toward the mid-ventral line. Ova are forced through the oviduct by a combination of back-arching and movements of the fourth leg. Once an ovum has entered the oviduct, the line of contraction of this right hind leg forces it medially and slightly anteriad toward the mid-ventral gonopore. The female gonopore (Figs, 2A and 3C) is surrounded by a six-leaved rosette of small plates. A thin cuticular fold of unknown function extends from the gonopore nearly to the anus.

The finely granular ova include a clear nuclear area. They are extremely pliable during deposition and become grossly distorted and elongate as they are forced through the stretched but narrow oviduct.

Mature females collected in spring and summer carry as many as eight ova, all of which are approximately the same size and appearance. These irregularly rounded ova are packed tightly within the distended ovary (Fig. 2A). Females collected during fall and winter rarely possess more than four developing ova, arranged linearly in the ovary. In animals of the latter group, the most posterior ovum is largest, suggesting that it is most mature. Fall and winter ova are more resistant to changes in their rounded shape than are spring and summer ova. This suggests the differences in egg types reported for freshwater rotifers and gastrotrichs (Hyman, 1951) and proposed for freshwater tardigrades by Pennak (1953).

In male and female _Batillipes_, the anus is ventral between the fourth pair of legs, frequently in a slight depression in the cuticle. The anus appears in the form of the letter "I", as in Figs. 1A and 2A, or as three pursed lines.

Stygarctus _granulatus_ n. sp.

Figs. 1B, 2B, & 4

In reproductively mature males of _S_. _granulatus_, a flattened saccate testis occupies the entire dorsum from the base of the brain to the terminus of the body (Fig. 1B) and includes several large rounded bodies. Vasa deferentia (Fig. 4B) pass ventrally from either side of the posterior end of the testis, near the junction of the fourth legs to the body, and then ventro-anteriorly. These ducts join medially and form a common duct which extends posteriorly along the mid-ventral line. The common duct exits via a rounded gonopore located just anterior to the anal apparatus. The male gonopore (Figs. 1B and 4C) is surrounded by a tubular collar. Motile spermatozoa of S. granulatus have a narrow anterior piece and a long flagellum. Within the testis and vasa deferentia they undulate very slowly, often in waves of several spermatozoa in unison.

The saccate ovary (Fig. 2B) extends from the base of the pharynx, along the dorsum and swells posteriorly to fill most of the terminal section of the body. Although many ova (as many as 30) may be found in various stages of development in the ovary, one or two large, fine-granular ova occupy much of the terminal portion of the ovary. Whether or not Stygarctus possesses differences in egg types as described above for Batillipes is unknown.

Although the oviduct was not observed, it must be short, since terminal ova lie close to the gonopore. A thin tubule leads dorsally from the pore into the pseudocoel, but its path can be traced only a short distance in optical section. The mid-ventral female gonopore (Figs. 2B and 4E) is anterior in the terminal body section, and is surrounded by a rosette of six small plates. Six small saccate bodies, reminiscent of the vulvar glands of some nematodes (Hyman, 1951, p. 281, Fig. 135B) are subcuticular to the rosette of plates and lie in a similar pattern. Their function is unknown.

A pair of "annex glands" (Fig. 2B and 4E), similar to those described from P. higginsi (Renaud-Debyser, 1965b, Renaud-Mornant, 1967a), are found in females of S. granulatus. These glands consist of rounded bulbs located in the lateral extremes of the anterior portion of the terminal body section, and are connected by coiled tubules to distinct pores on either side and slightly posterior to the rosette gonopore. No connection to the internal genital system was observed. Comparable structures were not found in females of Batillipes or in males of either genus.

The anal apparatus (Fig. 1B and 2B) is similar in both sexes of S. granulatus. A sinuous tube leads caudally along the ventral body surface between the fourth pair of legs. A terminal anus lies between the bases of two caudal spikes. A partial enclosure of cuticular plates surrounds the tube. Two rhomboidal lateral plates bow outward on either side of the tube, and flank the anal opening at their posterior extremes. These plates arch inwardly as if to form a capsule, but terminate pre-apically leaving a gap. A small square plate lies erect at right angles to the body axis in the anterior gap between the lateral plates.

I have seen no indication of diminutive size or scarcity of male Batillipes or Stygarctus, although both phenomena are described in Eutardigrada (Pennak, 1953). On the contrary, reproductively mature males occasionally outnumbered reproductive females, and some of the largest specimens of both genera were male.

DISCUSSION

Distinctions in gonopores of four heterotardigrade genera are now clear. From the study of mature, living Batillipes, aided by their transparent cuticle and large size, it is clear that an oval, slightly raised, posteriorly positioned gonopore is associated with the male system, while a six-leaved rosette of plates surrounds a more anterior female gonopore. Gonopores in S. granulatus are similar, with the exception that a tubular collar surrounds the male pore. In her further description of P. higginsi (Renaud-Mornant, 1967a) and in her redescription of A. marci (Renaud-Mornant, 1967b), Renaud-Mornant described a rosette pattern for males and a tubular gonopore in females. Since that time she has discovered this error and agrees with sex determinations as presented here (Renaud-Mornant, personal communication).

"Annex glands" exit via distinctly separate pores near the gonopore, presenting a problem in interpretation of their function. Presumably they are involved in reproduction or oviposition, despite their isolation from the rest of the female genital system. The conformation of the connecting tubules may provide an internal specific character. In P. higginsi, the tubules connect the bulb directly to the median pores. In S. granulatus, tubules form a distinct convolution, curling back over the laterally placed bulb before passing medially to pores. Tubules in S. bradypus possess a convolution medially between the bulb and the pores.

Copulation in marine tardigrades has never been described and was not observed during this study. Whether fertilization is internal (suggested by the presence of seminal receptacles in some female eutardigrades) or external (observed to occur within the shed cuticle of some female eutardigrades) is unclear.

Two patterns of oviposition have been described from the phylum. In some groups (most macrobiotids and a few echiniscoids) a small number of eggs are deposited freely and become attached to substrata either by cuticular elaborations or by adhesive surfaces. Other groups (most hypsibiids, *Milnesium*, and echiniscids) deposit a larger number of eggs within the old cuticle at ecdysis. The absence of eggs in many carefully examined shed cuticles of *S. granulatus* and *Batillipes*, the small number of mature ova present, and the ability to produce adhesive substances suggest that freely deposited eggs are probably produced by both of these genera.

Since gonoducts connect directly to the hind gut in the orders Eutardigrada and Mesotardigrada Rahm, 1937, separate pores occur only in the order Heterotardigrada. A summary of gonoporal morphology in this order appears in Table I. Distinctions in gonopores are not expected in the fresh- and moss-water genera *Echiniscus* and *Pseudechiniscus* in which males have never been observed (Ramazzotti, 1962; Rudescu, 1964). Gaps in this information relate to several monotypic genera known only from incompletely described collections. Nevertheless, distinctive patterns are indicated within familial groupings of Ramazzotti (1962).

All female heterotardigrades on which information is available, have either a rosette shaped gonopore or a pore in a similar forward location the detail of which is unknown. In addition most described male gonopores are also anterior rosettes.

The only known differences in gonopore shape and location occur within the families Batillipedidae Riggin, 1962 (in Batillipes), Stygarctidae Schulz, 1951 (in Stygarctus and Parastygarctus) and Oreellidae Ramazzotti, 1962 (in Archechiniscus). The occurrence of these distinctions suggests a closer affinity between these genera than might be indicated by other morphological features.

Within the Halechiniscidae Thulin, 1928 rosette gonopores have been described from both sexes of Florarctus and Tetrakentron. These genera also represent two distinct groups within this family based on claw characteristics (considered to be important indicators of relationships between tardigrades by Thulin, 1928; Marcus, 1929; Schulz, 1963; and Renaud-Mornant, 1967b). Florarctus resembles Halechiniscus, Tanarctus, Actinarctus, and Plecola in having simple or single spurred claws on each toe, while Tetrakentron and Styraconyx (including the former genus Bathyechiniscus) have more complex claw shapes on each toe. As representatives of these groups, the lack of gonoporal dimorphism in Florarctus and Tetrakentron, and the presence of rosette gonopores in males of Halechiniscus suggest that the same may prove true within remaining genera of this family.

Discrepencies in the occurrence of gonoporal dimorphism exist within the Oreellidae. Female Oreella possess anteriorly positioned pores, which are probably rosettes. While pores in both sexes of Echiniscoides are rosette, dimorphism has been shown in gonopores of Archechiniscus.

Once again, if characteristic claw shapes constitute a reliable guide to relationships between tardigrades, genera of this family are related distantly at best. The comparative consistancy of basic claw shapes in all other families suggests that a reorganization of the Oreellidae eventually will be required. Preliminary information here indicates that presence or absence of dimorphism in gonopores may represent another consistant familial character. That discrepency in dimorphism is found in this group is further evidence of the possibly artificial grouping of the Oreellidae as a single family.

Although in the past, sexes of tardigrades have been recognized on the basis of difficult-to-distinguish gonoducts or on the presence of mature gametes, species in four genera of Heterotardigrada display dimorphism in the shape and position of gonopores. Although such dimorphism is absent in the Eutardigrada and probably in most other Heterotardigrada (though probably it exists in Orzeliscus), its occurrence in the Stygarctidae, in Batillipes, and in Archechiniscus should provide a valuable asset to studies of systematics, population structure, sex ratios, and culture experiments.

TABLE I. GONOPORE SHAPES IN GENERA OF THE SUBORDER HETEROTARDIGRADA. Rosette = pore located forward, surrounded by six platelets; oval = posterior rounded pore without platelets; forward pore = gonopore located forward, its structural details are unknown; ? = undescribed.

TAXON	MALE PORE	REFERENCE	FEMALE PORE	REFERENCE
Suborder ARTHROTARDIGRADA				
Batillipedidae				
Batillipes	oval	present study	rosette	present study
Orzeliscus	?		?	
Stygarctidae				
Stygarctus	oval	present study	rosette	present study
Parastygarctus	" *	Renaud-Mornant, 1967a	rosette*	Renaud-Mornant, 1967a
Halechiniscidae				
Halechiniscus	rosette	Renaud-Mornant, 1967b	?	
Florarctus	rosette	Delamare Deboutteville & Renaud-Mornant, 1965	rosette	Renaud-Mornant, 1967b
Tanarctus	?		?	
Actinarctus	?		?	
Plecola	?		?	
Styraconyx	?		forward pore	Thulin, 1942 and Renaud-Mornant, 1967b
Tetrakentron	rosette	Marcus, 1929	rosette	Marcus, 1929
Suborder ECHINISCOIDEA				
Oreellidae				
Oreella	?		forward pore	Ramazzotti, 1964
Echiniscoides	rosette	Marcus, 1936	rosette	Marcus, 1936
Archechiniscus	oval *	Schulz, 1953	rosette*	Renaud-Mornant, 1967b
Echiniscidae (no males in Echiniscus and Pseudechiniscus; females with rosette, Marcus, 1936).				
Parechiniscus	rosette	Rudescu, 1964	rosette	Marcus, 1936
Mopsechiniscus	?		?	

* see correction in text.

FIG. 1. Diagrammatic illustration of male reproductive systems (ventral view). A. Composite *Batillipes mirus* and *B. pennaki*. B. *Stygarctus granulatus*. A - anus; G - gonopore; LB - lateral bulge; T - testis; VD - vasa deferentia.

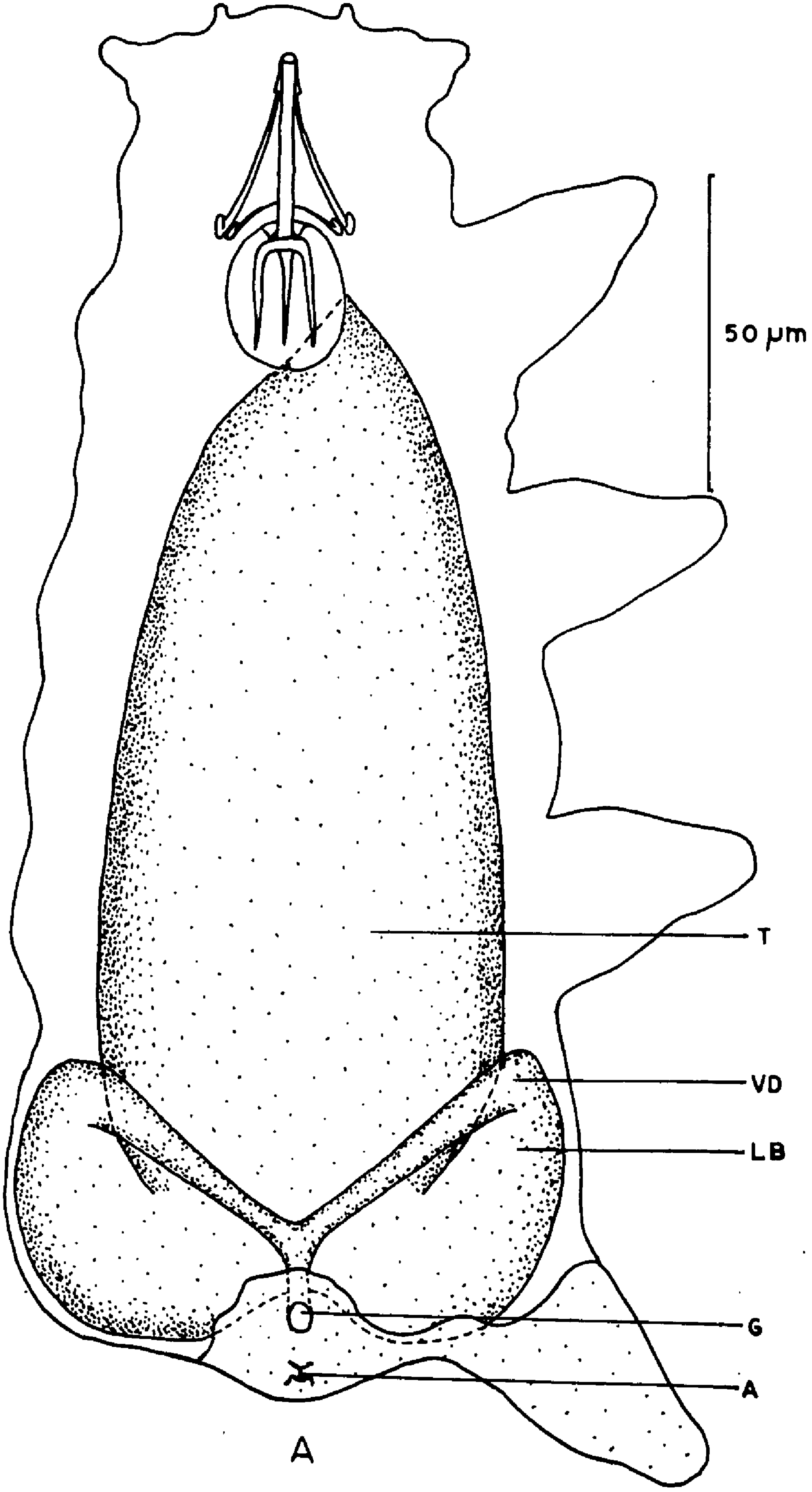


FIG. 1

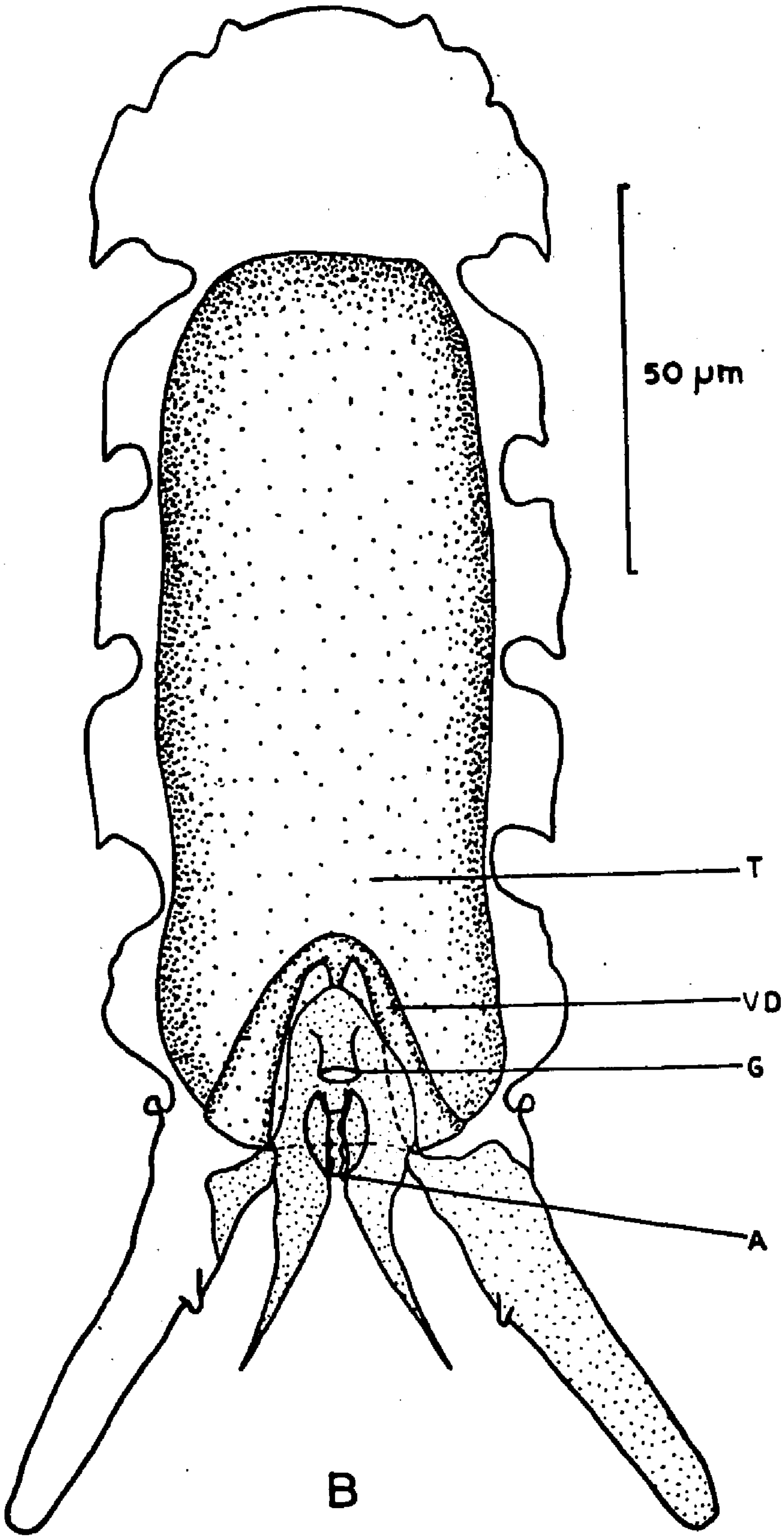


FIG. 1

FIG. 2. Diagrammatic illustration of female reproductive systems (ventral view). A. Composite B. mirus and B. pennaki. B. Stygarctus granulatus. A - anus; AG - "annex gland"; G - gonopore; O - ovum; OD - oviduct; OV - ovary; P - rosette plate.

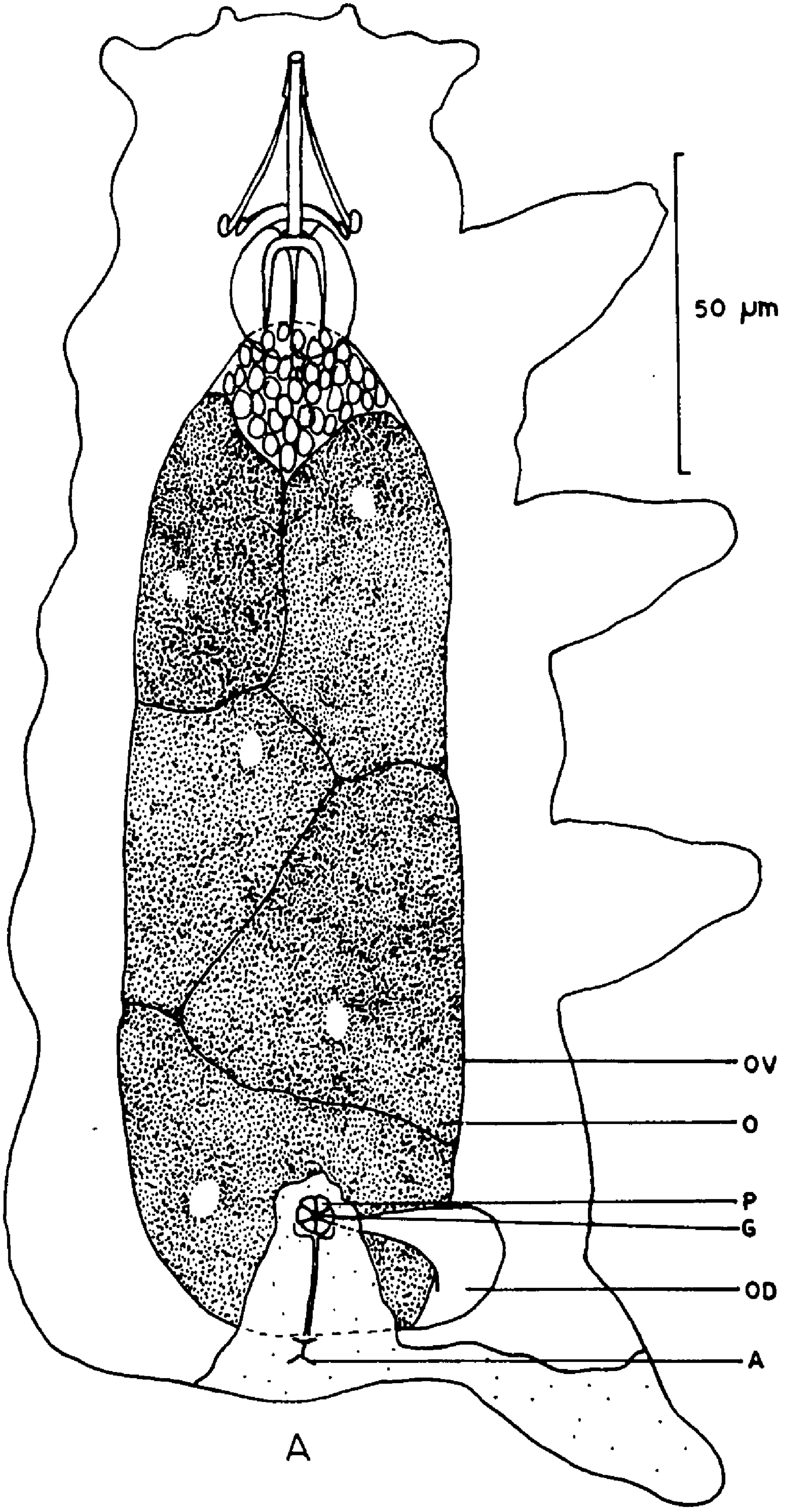


FIG. 2

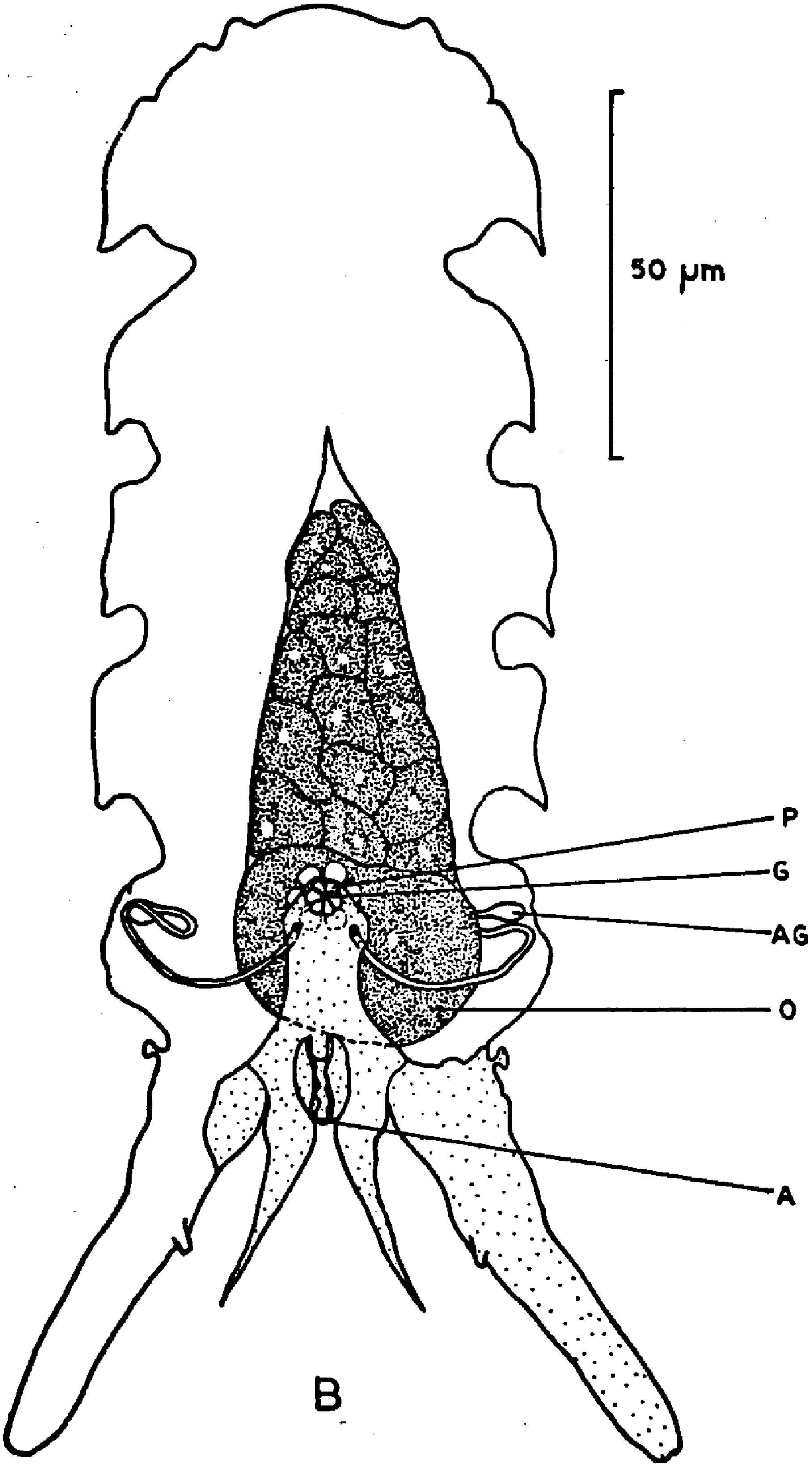


FIG. 2

FIG. 3. Gonopore shapes and location in _Batillipes_.

A. Ventral view of living male of _B_. _mirus_ showing lateral bulges (LB) and vas deferens (VD) containing motile spermatozoa.

B. Surface view (ventral) of same animal showing oval male gonopore (G) just anterior to anus (A).

C. Ventral view of female of _B_. _mirus_ showing rosette gonopore (G) located more anteriorly to anus (A).

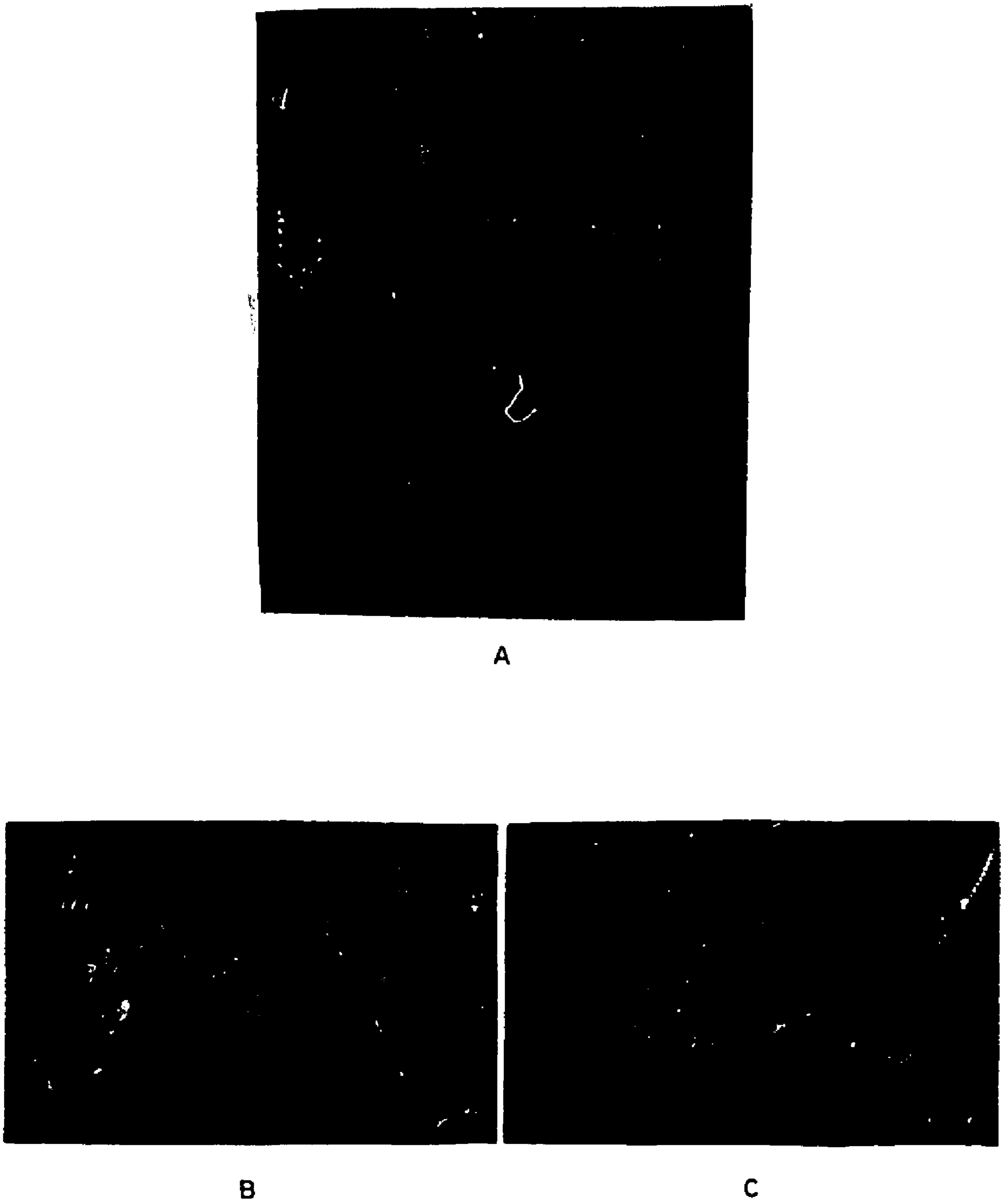


FIG. 3

FIG. 4. Gonopore shapes and location in _Stygarctus granulatus_.

A. Dorsal view of living male showing clusters of motile spermatozoa.

B. Ventral view of same animal showing vas deferens (VD) containing motile spermatozoa.

C. Surface view (ventral) of same animal showing tubular male gonopore shape (G).

D. Dorsal view of living female showing ova (O) in ovary.

E. Three quarter ventral view of same animal crushed by coverslip pressure but showing ova (O), rosette female gonopore (G), and lateral "annex glands" (AG).

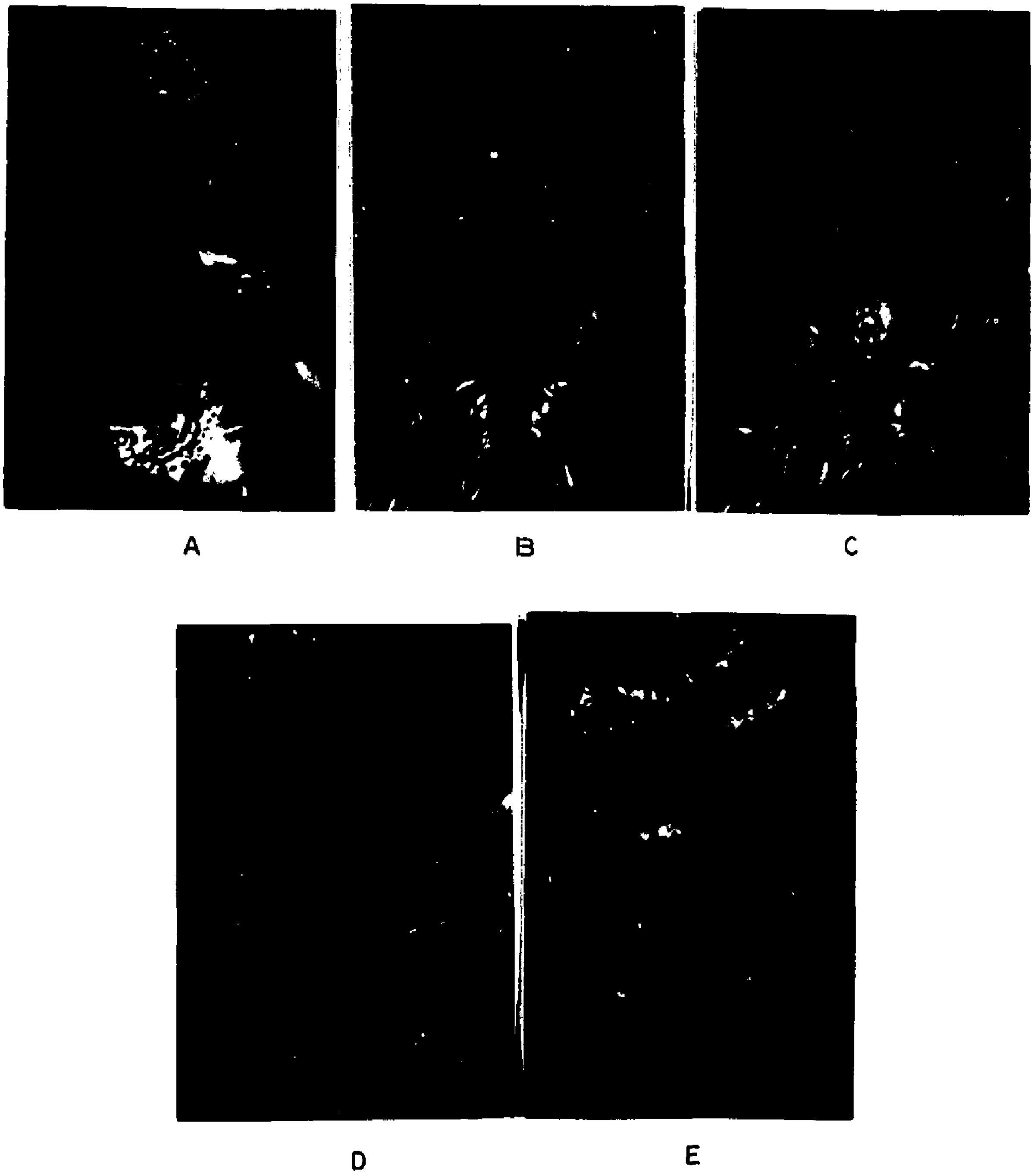


FIG. 4

Part III

SEASONAL AND TIDAL CHANGES IN THE MARINE INTERSTITIAL ENVIRONMENT

Intertidal areas experience cyclic patterns of environmental changes as a result of tides. A comprehensive study of intertidal parameters must incorporate a tidally related dimension. Major determinants of environmental conditions during ebb tide, and in the case of porous sediments, runoff from precipitation, and seepage of ground water.

Basic components and influences derived from these sources are subject to further modification by the physical composition of the substratum. Within sandy beaches, a labyrinthine system of capillary spaces exists, the dimensions of which are determined by size, shape, packing, and sorting (i.e. degree of homogeneity) of the sedimentary particles, as well as the quantity of organic or shell debris present (Fraser, 1935; Ruttner-Kolisko, 1956; Callame, 1963). The extent and depth to which tidally active water can circulate is determined by slope of the beach, amplitude of tidal changes, and dimensions of the interstitial spaces (Callame, 1963). Thus beaches range from relatively impermeable, flat, fine grain size habitats (mean grain diameter less than 0.25 mm), where water circulation is restricted to surface areas, to porous, steeper, larger grain size habitats, allowing circulation to depths exceeding one meter at the high tidal line

(Renaud-Debyser, 1963).

While reports of ecological studies on beaches of low porosity are numerous (for recent reviews see McIntyre, 1969 and Salvat, 1967, comprehensive information on conditions within porous beaches is scarce. Surveys combining studies of interstitial fauna with ecological data on porous tidal beaches are available from Ganapati and Rao (1962) on several beaches along Waltair coast of India, and Renaud-Debyser (1963) and Renaud-Debyser and Salvat (1963) from beaches in France. Despite the lack of tides and low salinity in the Baltic Sea and Øresund, the detailed ecological studies of porous Scandinavian beaches by Jansson (1967a - c, 1968a - c), Fenchel and Jansson (1966) and Fenchel, Jansson, and Thun (1967) are valuable to compare to data from tidal regions.

Differences in habitat and faunal composition exist between fine and coarse sand beaches (Renaud-Debyser and Salvat, 1963; McIntyre, 1969). In general, macrofauna are able to burrow into superficial layers of fine sand beaches, whereas in coarser beaches, burrowing is more difficult and they are less abundant. On the other hand, most members of the interstitial meiofauna (animals less than two mm in length) generally are flat or vermiform and can pass through capillary spaces without moving sand grains themselves. The richest variety of these are found in porous beaches.

This paper reports a general survey of conditions within the interstitial habitat of a porous tidal beach, conducted in conjunction with a study of its interstitial meiofauna.

Since most published information on intertidal parameters only consider conditions measured during low tide, I shall explore the role of seasonal changes in temperature and cyclic variations in water content, atmospheric exposure, temperature, and salinity as they are imposed on a beach by tides. Where differences between spring and neap tidal amplitude are large, patterns of parameter change may become more complex. Although other sources of variability may also be involved (e.g. day versus night changes), seasonal, tidal, and spring versus neap tidal changes were selected for detailed study.

Following a qualitative survey of interstitial animals in beaches at Woods Hole, Massachusetts, I selected Crane's Beach (41° 31' 41" N, 70° 40' 41" W) on Penzance Point for further study. Penzance Point (Fig. 1), a peninsula extending westward one quarter mile from Woods Hole, is bordered on the north by Buzzards Bay and on the south and east by Great Harbor. Crane's Beach faces Buzzards Bay at the narrowest portion (100 m wide) of the neck joining Penzance Point to Woods Hole.

Crane's Beach (Fig. 2) measures 150 m in length along the head of a cove. A series of sea walls provide shelter towards the west, while the east end of the beach blends into a rocky point. A sand bar covers the mouth and much of the interior of the cove, protecting lower portions of the 20 m wide beach (mean low water to supralittoral fringe) from severe surf.

My study was confined to a transect two m wide, located 20 m from the west end of the beach. The transect extended from mean low water to above spring high water and from the sand surface to the level of the water table at low tide (i.e., the lowest depth reached by interstitial space water saturation). The resultant triangular prism was 18 m along the sand surface and approximately one m deep at the highest station (Fig. 3).

MATERIALS AND METHODS

Nine stations were placed at elevations of 8, 31, 54, 69, 85, 107, 130, 153, and 176 cm above mean low water and are termed stations A - I respectively. In this manner, tidal exposure (i.e., elevations above mean low water) remained constant for each station. At each station, samples were taken from the surface of the sand to the low tidal level of the water table at depths of 1, 4, 8, 14, 22, 27, 32, 38, 44, 51, 58, 65, 72, and 80 cm. Maximal depths sampled ranged from 14 cm at station A to 80 cm depth at station H. Asymmetry in this sampling pattern resulted from stratified sampling used in concurrent analyses of faunal distribution (discussed in Part IV). Stations were located in the field by sightings with a hand level to a surveyor's range pole calibrated in centimeters of elevations above mean low tide and placed at a supralittoral reference point. Horizontal distances between stations were measured for construction of beach profile diagrams.

A granulometric study was made by analyzing samples collected at ten cm intervals of depth from the surface of the sand to the level of the ground water at stations B, D, F, and H. The 20 cm^3 samples were dried thoroughly and sieved on U. S. Standard Screens at increments of 2.0, 1.5, 1.0, 0.5, 0.0, -1.0, and -2.0 Ø (representing mesh openings of 0.25, 0.35, 0.50, 0.71, 1.00, and 2.00 mm respectively). Granulometric composition was estimated as the percentage of the total sample weight represented by each size fraction. Results are presented in terms of phi mean diameter (84 Ø - 16 Ø/ 2) and phi deviation measure (= sorting) (16 Ø + 84 Ø/ 2 after Inman (1952). Analyses were limited to particles less than two mm in diameter in order to compensate for the incommensurate importance of larger (heavier) sediments in composition-by-weight analysis and in the production of interstitial space (a point raised by Boaden, 1966). While a distinction of two mm is arbitrary, functional "living area" for epizoic meiobenthos generally consists of sand and spaces lying between these larger particles.

Estimates of pore volume were made on the same samples used in granulometric analyses. Following granulometric studies, all fractions of each sample were recombined (with a mean loss of 0.58% from original samples) and mixed thoroughly. Re-mixed dry sediment was placed in a graduate and agitated to simulate natural packing until a volume of ten cm^3 was reaches. Then, while holding the graduate at an angle to prevent entrapment of air bubbles within sand spaces, I added water quantitatively to the dry sand. The amount of water required to saturate interstitial spaces in ten cm^3 of dry sand (multiplied by ten) is an estimate of the volume of interstitial spaces in the sediment (± 0.5%).

Emery and Foster (1948) demonstrated a progressive delay in the occurrence of low tide in the water table from the low water line toward landward stations. A preliminary observation at Crane's Beach revealed the importance of compensating for this time lag if true low tidal conditions were to be measured throughout the beach. As a result, landward stations were sampled up to two and one quarter hours after seaward stations. While potential error from not sampling precisely at low tide in the water table at each station must be recognized, to have failed to compensate at all would have been to sample conditions and faunal distributions considerably before true low tide was reached at landward stations, and thereby introduce a potentially serious source of error. Generally, collections were scheduled during afternoon low tides of predicted elevations of less than 0.0 cm above mean low water (U. S. Coast and Geodetic Survey, Tide Tables, 1968 and 1969).

Seasonal changes in interstitial water were assessed from data on temperature and water content gathered at intervals of approximately two weeks from mid-March, 1968 through late July, 1968. Temperatures were also recorded at intervals of two weeks from late August, 1968 through April, 1969. Temperature was measured with a portable thermister (Yellow Springs Instrument Co., Yellow Springs, Ohio) inserted at appropriate depths into the walls of excavations at each station. Readings are accurate to ± 0.25 °C. Records of air temperature, levels of precipitation, and the temperature and salinity of seawater in Buzzards Bay, were supplied generously by R. Alexander and J. Chase of the Woods Hole Oceanographic Instütution.

Water content of samples of sand was estimated by the field method of Hummon (personal communication). In this method, five cm^3 of sand (packed by agitation to simulate natural packing) were added to five cm^3 of seawater in a ten cm^3 graduate cylinder. The difference between the level of displaced water and the ten cm^3 line was used to indicate the volume of air within the five cm^3 sample of "naturally packed" sand.

In general, a given volume of beach sediment contains approximately 60 ± 2% sediment and 40 ± 2% air-water (Graton and Fraser, 1935). A fully water saturated sample of sand of five cm^3, added to a water volume of five cm^3 gives a total volume of ten cm^3. On the other hand, if the sample were totally devoid of water, the combined volume would be five cm^3

of water + 60% of five cm^3 of sand (three cm^3) = eight cm^3. The actual amount of water displacement for each sample therefore will lie between eight (devoid of water) and ten cm^3 (fully saturated) marks on the graduate and may be determined proportionately as a part of the two cm^3 difference. For example, a reading of 9.5 cm^3 indicated a sample of 75% water saturation. Estimations of water content expressed as percent total saturation are accurate to ± 2.5%. A subsequent study of pore volume of Crane's Beach sediments indicated a grain to space ratio of 64 : 36% was more accurate. The error introduced by a 4% difference in volume used to calibrate this system is considered to lie within the already broad limits of accuracy of this technique.

To study changes in interstitial conditions during tidal cycles, I measured sand temperatures, water content, pH, salinity, oxygen content, and depth of the water table and seawater periodically at several stations throughout a complete spring tidal cycle (13 May 1968) and again throughout a neap tidal cycle one week later. At each half hour, depth of the water table was recorded in excavations at stations A - I. Every one and one half hours temperature and water content of unsaturated portions of stations B, D, F, and H were measured at intervals of ten cm in depth. Concurrently, pH, oxygen content, and salinity of adjacent seawater and the water table at stations B, D, F, and H were recorded. Temperature and water content were measured by methods described above. Water table and seawater chemistry was determined by microtitration using Hach chemical kits (Hach Co., Ames, Iowa) (oxygen ± 0.25 ppm;

pH ± 0.05 units; and salinity ± 0.5 ppt). Water samples were taken by a 20 cm^3 syringe inserted four cm into the sediment below the water table in freshly dug excavations. Water for oxygen determinations was drawn slowly into the syringe to avoid contamination by air bubbles. Oxygen content measurements require 15 cm^3 of water left from over-flowing the 20 cm^3 gathered. Salinity and pH measurements each use five cm^3 of water.

RESULTS

PHYSICAL ENVIRONMENT

Crane's Beach measures 150 m along the water line and 20 m perpendicular to the water. The average slope of the beach is 11°. Portions of the beach profile are subject to modification by sea and wind erosion. Slight variations in horizontal distance between stations occur regularly. An overall loss of sand during the fall and winter coincides with prevalent on-shore winds (i.e. from the north- west). Apparently sand is re-deposited during the spring and summer.

Sand at Crane's Beach is coarse and poorly sorted. The mean grain diameter (Fig. 4A) decreases with distance from the water line and ranges from 1.50 - 2.25 mm diameter at station B to 0.25 - 0.75 mm at station H (except for a band of extremely large sand at ten cm depth). Sorting (Fig. 4B) is generally poor although it also becomes more homogeneous with distance from the water line. In Fig. 4C, an inverse relationship between pore volume and landward distance is less clear but is suggested.

The diurnal tidal pattern influencing seawater at Crane's Beach produces high tidal elevations ranging from 2.6 feet (neap) to 5.2 feet (spring) with a mean amplitude of 3.5 feet. A graph of predicted high tidal elevations (Fig. 5) illustrates the pattern of spring-neap tidal alternations in this area. Vertical lines superimposed on this graph represent approximate dates of each collection.

Sources of freshwater at Crane's Beach are few. Since this survey is restricted to sand above the low tidal water table, the depth and chemistry of the continental ground water was not studied. Its influence on conditions within the transect studied is apparently unimportant since little dilution of interstitial water by freshwater occurred at the low tidal water table. Precipitation in the Woods Hole region is not excessive, 55.34" from January, 1968 through April, 1969, mostly occurring late in winter and early spring (February through June) and late fall through early winter (November through December). Less than 1" of precipitation per month was recorded in July, August, and September, 1968. Since the beach is located on a neck of land 100 m wide, precipitation runoff was minimal.

WATER CONTENT

Crane's Beach is a porous sandy area and a large portion of the beach drains during each tidal cycle. Nearly all sites within the transect lose 50% of their saturation water content during each ebb tide, while only surface sand in the high tidal region drains and evaporates below 10% of its full water saturation.

Important seasonal difference in water circulation are not expected here. Should extensive freezing of interstitial water occur, such as described from a tidal Scandinavian beaches by Jansson (1967c), circulation certainly would be affected adversely. However, tidal water movements and milder winters prevent such an occurrence at Crane's Beach. Two feet of snow and ice regularly cover Crane's Beach in midwinter. However, during this study layers of frozen sand were confined to the surface 10 - 20 cm in the high water region of the beach.

Spring and neap tidal changes in elevations of the seawater and water table at stations A - L are shown in Fig. 6A and B. Curves indicating stations are identified by letter and depict changes in the water table from first exposure by ebbing spring tide (Fig. 6A) through the low tide at mid-day, and then until stations were again covered by flooding seawater; and from neap low tide (Fig. 6B) through the afternoon high tide and then past the night low tide.

Differences between spring and neap tidal circulation of water are illustrated in Fig. 7. Lines at intervals of three hours indicate the approximate period within a 12 hour tidal cycle that portions of the beach remained less than 50% saturated by interstitial water. The two regions of the beach most affected were shallow depths at higher stations and deeper portion of all stations. Although during the neap tidal cycle the upper 30 cm at station H never exceeded 30% satuuration, greater depths at the same station were able to fill and drain to some extent. All depths in remaining stations lost less water in the neap cycle than they did during spring tides. The range of water table amplitude throughout the beach was generally less in a neap tide than in a spring (see Table I).

The progressive delay in movements of the water table from the low water region towards the landward interior of the beach is illustrated in Fig. 6A and B, where letters along the ordinate indicate the approximate times at which deepest water table levels (= "station low tides") were reached at each station and for the adjacent seawater. Low tide at stations H and I occurred four hours after the seawater reached its nadir during the spring tidal series (Fig. 6A). In contrast to progressive delays in movement of the water table from seaward to landward during the spring cycle, only the high tidal region of the beach (stations G, H, and I) was affected during the neap cycle (Fig. 6B). Throughout the rest of the beach, low tide in the water table co-occurred with low tide in seawater.

Although in nature sandy soil rarely becomes totally devoid of water (Kramer, 1949), a tidal range in water content from 100% saturation to less than 10% was a frequent occurrence near the sediment surface in high water regions of the beach. An estimate of the lower limits of water depletion, including compensation in field sampling for lags in water movement, is averaged from measurements of low tidal water

7

content from April through July, 1968. Although variations are expected to result from alternations of spring-neap tidal cycles, Fig. 8 indicates the relative severity of water depletion expected within the beach transect. Average lowest water contents reached at depth intervals of ten cm at each station appear along the right side of each graph. Since at high tide, stations are flooded with seawater, vertical lines on the left indicate high tidal water saturation. The black area between represents the tidal range in water content expected at each station. From this graph we see that the upper half of the beach lost more than 80% of its water saturation while nearly all of the beach lost over 50%.

However, as important as minimum saturation levels attained at given sites, is the rate of water loss and duration of exposure to low saturation. Changes in water content measured through spring and neap tidal cycles in depth intervals of ten cm at three stations (D, F, and H) are shown in Fig. 9A and B. Patterns of spring and neap tidal drainage were generally similar.

Although porous sand has a very low water retention capacity (Kramer, 1949), it apparently drains much more slowly than it fills. Surface layers drained nearly completely upon emmersion and filled quickly, while deeper layers drained far more slowly than they filled. Left-hand skewness of graphs from greater depths illustrate this phenomenon (Fig. 9).

A time gradient of immersion-emersion exists from superficial sediments high on the beach to greater depths toward the low tidal area. While porosity of Crane's Beach permitted extensive drainage, this time gradient was reflected in the duration of exposure to a given level of water content. Fig. 7, described above, represents the duration of exposure to 50% saturation throughout the beach during a spring and a neap tide. The portion of the beach which was less than 50% saturated for more than one half of each 12 hour cycle included the uppermost third of the beach at spring tide and the uppermost half at neap tide.

TEMPERATURE

Although temperatures in the water table remained slightly higher than in adjacent seawater, both showed similar seasonal changes (Fig. 10). Water table temperatures ranged from - 2.0°C during the winter to 22.3°C during midsummer, with an average rate of change of about 1°C per week. Although air temperature was more variable, the pattern of seasonal change was similar to that of the seawater. Meanwhile temperatures at the water table lay between those of open seawater and the atmosphere, reflecting sensitivity to both of these influences.

Tidal ranges in temperature fluctuation are illustrated in Fig. 11. With characteristics of seawater dominating conditions at flood tide, vertical lines to the left represent temperatures at high tide. Extremes in temperature at low tide are indicated on the right side of each station graph. Once again, the black area represents the range of temperatures expected to occur during a full tidal cycle.

Changes in temperature throughout the year may be grouped into one of these three general patterns - although the actual values differed with seasonal conditions.

The three illustrated patterns of increasing severity in fluctuations of temperature (Fig. 11, patterns A - C) have been selected as representative of annual trends in tidal variations of temperature. Annual occurrence of these patterns is shown in Fig. 12. Although the range of temperatures between the sand surface and low tidal water table at any station was narrow in fall and winter, but large during spring and summer. The difference was less than 3°C between depths of 20 cm and the water table at all seasons.

Daily changes in temperature at stations D, F, and H, shown in Fig. 13A and B, indicate that large temperature differences were limited to surface ten cm of sediment. Temperatures at greater depths remained within a few degrees of the temperature of the water table throughout spring or neap tidal cycles.

The range of temperature increase during daytime low tides was directly related to duration of exposure to harsh atmospheric conditions. The fact that lowest spring low tides in Buzzards Bay occurred near mid-day during the summer increased the severity of exposure. In addition, the lag in drainage of the water table within the beach (discussed above) prolonged exposure to atmospheric conditions. Surface temperature of exposed sediments continued to increase regardless of local low tide and dropped only as flooding tidal waters approached closely.

SALINITY

Except for infrequent and local salinity changes caused by unusually heavy rainfall or by melting snow and ice, salinities in Buzzards Bay remained stable. Records of salinity here showed a mean of 32.0 ± 0.2 °/oo throughout this study. Salinity of intertidal seawater was more variable (28.5 ± 1.5 °/oo) during a tidal cycle. Salinity of the water table was somewhat lower, reflecting limited landward influence of freshwater.

OXYGEN ABUNDANCE

Measurements were made from the water table to ascertain minimum values of oxygen during tidal cycles. Oxygen content ranged from 3.0 - 6.0 ppm through a cycle, as compared to 4.5 - 9.0 ppm in adjacent seawater. From lowest values toward the end of the high tidal portion of the cycle, oxygen content of the water table increased slightly during the low tide. At no time was H_2S smell or a "black layer", indicating anaerobic conditions, located within the transect at Crane's Beach.

pH

pH showed little variation within a tidal cycle. Values ranged from 8.5 at seaward stations and in adjacent seawater, to 7.5 farther landward.

DISCUSSION AND CONCLUSIONS

WATER CONTENT

The composition of water in intertidal sediments is derived from tidally moving seawater and freshwater from precipitation and ground water. Beach slope, porosity and grain size of the sediment, capacity for water retention of different sedimentary types and sizes, tidal and wave activity of seawater, abundance of precipitation, and evaporative power of the atmosphere all determine the specific amount of water in intertidal sediments (Bruce, 1928a; Fraser, 1935; Gerlach, 1954; Rullier, 1957; Callame, 1963; Jansson, 1967b; and Johnson, 1967).

With diurnal flow and ebb of tidal water to counter pervasive atmospheric influence, the latter two factors may be important only at the surface of the sand in high beach regions. Evaporation undoubtedly draws some interstitial water regularly from the high tidal region and more broadly over superficial few centimeters of sand during mid-summer. Crane's Beach experiences little run-off from rain water other than that falling directly onto the beach at low tide.

Movement of water through an interstitial network is restricted by the permeability of the sediment (Emery and Foster, 1948; Ruttner-Kolisko, 1961). More confined dimensions of capillary spaces result in increasingly limited water movements (Ruttner-Kolisko, 1962). Brafield (1964) has related circulation within sand directly to the proportion of the sediment less than 0.25 mm in diameter. Although fine sediments lose little more than surface water at low tide (Callame, 1963), coarser sediments, such as those at Crane's Beach, undergo extensive drainage to depths exceeding one meter in the high tidal region. Despite this, movements of water within the beach still are restricted to some extent and lag behind movements of adjacent seawater.

The degree and rate at which portions of the beach fill during tides is related to the amount of time overlaying seawater remains at a higher elevation. Flooding spring tidal seawater rose quickly at Crane's Beach (ca. 24 cm per hour). As a result, inward water pressure caused saturation of even the most interior portion of the beach. Both the rate and magnitude of change in amplitude was reduced during neap tides (ca. 15 cm per hour). With the consequent reduction in water pressure, interior sections filled and drained much less than during spring tides.

A gradient from overlying seawater into the beach filled interstitial spaces rapidly. In drainage however, flow resulted from gravity pressure. Drainage "suction" of the falling water table was countered by capillary retention of water within interstitial spaces. Therefore while 50% of the interstitial water was lost quickly, it took far longer for much of the remaining water to be lost. As a result, drainage was accomplished much more slowly than filling (see Fig. 6).

Kramer (1949) described four conditions in which water may be found in soils. Gravitational water drains by gravitation alone and hence is lost and regained quickly. Capillary water held around and among particles moves far more slowly. Hygroscopic water forms very thin films (perhaps only 15 - 20 molecules thick) around sediment particles and is extremely difficult to remove. Finally water can exist in the soil as a vapor.

From these generalizations, I would hypothesize that the water lost quickly from beach sediments represented gravitational water, while loss of capillary water produced the gradually diminishing levels below 50% saturation. Interstitial water losses even at the sand surface seemed to stabilize at levels of 10% saturation (Fig. 9), which probably represented an approach to minimal, tightly-held films of hygroscopic water. As the water table rose, pore spaces became filled quickly so that interstitial spaces at all stations filled within a fraction of the time it took for them to drain.

TEMPERATURE

Temperature of seawater, the water table, and deeper portions of the interstitial habitat were similar and showed little daily or tidal variation. They followed gradual seasonal thermal changes in the atmosphere and were dominant in determining temperatures throughout the beach during flood tide. Approximately 12 hours of each day (i.e. while the beach is filled with flood tidal water), temperatures at all beach sites lay close to those of the low tidal seawater. Jansson (1967c) indicated that in tideless Scandinavian beaches, temperatures in sand approximate or fall lower than those of seawater each night. On intertidal beaches therefore, increased temperatures probably occur only during daytime portions of low tides. An underlying pattern of temperature change within the beach during the night and high tide period follows a curve of seasonal change similar to that shown in Fig. 10.

The temperature difference between the atmosphere and the water table and the period of exposure during low tide determine extremes in variations of beach temperatures. During low tide, thermal insulation and evaporative cooling dampen significant influence of even the most extreme atmospheric conditions below a depth of 10 - 20 cm (below five cm in fine-grain beaches).

In early spring, fall, and winter, when temperatures of the sea and air were similar, the interstitial habitat remained at nearly constant temperature during the day-time regardless of tidal exposure. As day-time air temperature rose in late spring and summer, a lesser but proportional rise in interstitial temperature occurred at low tide. In winter when air temperatures were lower than that of seawater, temperature of superficial sand in the high tidal region dropped several degrees below that of seawater. At such times, the upper 15 - 20 cm of the beach may freeze. From spring through fall, atmospheric influence is strongest during day-time low tides. In winter, night-time low tide conditions may be more severe.

Decreased amplitude of the water table during neap cycles affects temperatures throughout the beach. Surface layers of sand high on the beach are exposed to the atmosphere for several days at a time, which allows temperatures there to reach extremes. On the other hand, at neap tides, temperatures in deeper portions of the beach remain under the moderating influence of seawater temperatures longer. Thermal conditions within an intertidal beach depend upon the extent to which atmospheric conditions outweigh ordinarily dominant sea and interstitial water temperatures. The pattern of tidal variations in temperature is closely related to water content changes.

SALINITY

In tidal beaches the chemistry of seawater dominates the chemistry of interstitial water (Kuhl and Mann, 1966). Except in areas of unusually concentrated precipitation (Govindankutty and Nair, 1966), interstitial salinity remains approximately comparable to that of the seawater (Ganapati and Rao, 1962; Johnson, 1967) in a few cases, slightly higher (Fenchel and Jansson, 1966) and in most slightly lower (Renaud-Debyser, 1963; Jansson, 1966; Kuhl and Mann, 1966). Gradients in salinity exist horizontally between the seawater and shoreward areas where freshwater may be important (Brinck et al, 1955) and between the sediment surface where evaporation may increase salinity (Gerlach, 1954) and ground water dilutions at greater depths (Jansson, 1968c). Salinity gradients are steep and variable in atidal areas (Jansson, 1967c) but less so on tidal beaches where flooding and draining seawater reduce dilution from freshwater. In addition, poor mixing of rain or freshwater with seawater (Reid, 1930) decreases pervasive influence by freshwater still further. Salinity variations are great high on sandy beaches and low towards the water line (Johnson, 1967; McIntyre, 1969).

OXYGEN

In an oversimplified sense, oxygen is present within interstitial spaces in decreasing abundance from the water's edge toward the shore (Pennak, 1942; Jansson, 1968a) and from the sand surface towards greater depths (Bruce, 1928a; and many others since). However patterns are frequently irregular and difficult to distinguish (Jansson, 1968a). In some cases increased oxygen levels are found in the vicinity of the ground water table (Jansson, 1966, 1968a). The quantity of oxygen within the beach is generally less than that of adjacent seawater (Ganapati and Rao, 1962; Gordon, 1960; Renaud-Debyser, 1963).

The abundance of oxygen within a beach is apparently related to the permeability of the sediment to water (Brafield, 1964, 1965). In beaches containing large quantities of clay or silt, organic debris, very fine-grain sand, or where ice cover prevents exposure to air and waves, oxygen becomes limited (Ruttner-Kolisko, 1956, 1961; Brafield, 1964; and Jansson, 1967a, 1968b). Often in these situations, a black layer of ferrous or hydrogen sulfide forms close to the surface of the beach and indicates the depth at which anaerobic conditions prevail (Bruce, 1928b; Brafield, 1964, for a review).

In beaches of large sized sediment (including Crane's Beach), oxygen content is often low but is seldom zero (Ganapati and Rao, 1962; Renaud-Debyser, 1963; Amoureaux, 1963;

Jansson, 1968a). Renewal of interstitial water during tidal ebb and flow is important to maintaining high concentrations of oxygen in intertidal beaches (Pennak, 1951, Gordon, 1960).

Levels of oxygen in interstitial water should be maximal as supersaturated intertidal water percolates into interstitial spaces during flood tide, and again as decreased water content allows air to penetrate deep into the beach at low tide. However the longer a site within the beach remains saturated with stagnant water, the lower is the level of oxygen expected (Gordon, 1960; Jansson, 1968a). Enckell (1968) found no change in the oxygen diffusion rate in water 2.5 cm below the lowest point reached by changing water level in an experimental sand chamber. Oxygen diffusion rates increase rapidly with increasing temperature (2 - 3% per degree C, Odén, 1962) and with increasing current speed (Enckell, 1968). As a consequence oxygen abundance is dependant directly on water movements within the beach.

pH

Several investigators have measured pH of interstitial water and found it similar to that of adjacent seawater (Bruce, 1928b; Pennak, 1951; Ganapati and Rao, 1962; Renaud-Debyser, 1963; Salvat, 1967; Jansson, 1968c). From these studies, and mine at Crane's Beach, it is apparent that variation in pH is not great and that interstitial water in most marine beaches is slightly more acid than the seawater. Bruce (1928b) observed that pH changes, resulting from gaseous exchange of animals and plants, are moderated by an alkali-reserve buffering effect of calcareous materials in beach sand.

ORGANIC DEBRIS

Organic debris is generally available in small quantities in sandy beaches (Renaud-Debyser, 1963; Ganapati and Rao, 1962), although quantitative measurements of debris were not made at Crane's Beach. Accumulation of debris in an intertidal area depends upon wave exposure, water currents, the slope of the beach and coarseness of the sand, and the amount of vegetation in nearby areas (Dahl, 1953). The importance of this material to intertidal meiofauna is physical, chemical, and biological. As small particulate matter, debris is apt to accumulate and clog interstitial spaces, sometimes limiting space severely (Pennak, 1951) and often changing its permeability and capacity for water retention (Jansson, 1966). In addition its presence is important to the formation of a ferrous sulfide layer in sand an through byproducts of its biodegredation to the general chemistry of interstitial water (Bruce, 1928b). Finally organic debris contributes an important source of food to intertidal communities (Perkins, 1958; Remane, 1952; Renaud-Debyser and Salvat, 1963).

THE INTERSTITIAL ENVIRONMENT AS AN INHABITABLE REGION

Conditions within the interstitial framework of intertidal beaches results from influences of seawater, atmosphere, and ground water. Seawater provides the aqueous medium during flooding tide. During this period, interstitial temperatures, oxygen availability, salinity, and pH levels are similar to those of overlying seawater. At this time, atmospheric influence results from its effect on seawater conditions. Likewise the effect of ground water, a basically freshwater source with poor mixing potential with seawater, is minimal. As seawater drains during ebb tide, atmospheric influences can become important in terms of temperature, water content, and modifications in salinity through evaporation and/or precipitation, and in penetration of oxygen. Effects of strong ground water influx on oxygen and salinity are also greatest during decreasing abundance of seawater during ebbing tide.

Through a combination of sedimentary characters and topographical features, the dimensions of the interstitial system plays its own role in determining interstitial conditions. The extent and speed of water circulation within the beach is the major functional product of this physical framework. Freely flowing interstitial seawater insures tidal replenishment of water, availability of adequate oxygen (Brafield, 1964), and prevention of accumulations of space-clogging debris (Ganapati and Rao, 1962). However stagnation results in rapidly diminished oxygen (Gordon, 1960), accumulation of debris, and frequently in the production of toxic decomposition products (Bruce, 1928b).

Most interstitial conditions and cyclic changes in relative importance of external influences are related intimately to water movement and changes in the abundance of interstitial water. Therefore distinctions in beach parameters may be broadly represented by a generalized pattern of water conditions within the beach.

Salvat (1964, 1967) provided a useful classification of environmental zones along the surface of fine-grain beaches. He described four distinctive areas along a low to high tide axis, which he characterized in the following manner (paraphrased from Salvat, 1967):

Zone of Dry Sand - sediment above the level of neap high tides which is emergent during several successive tidal cycles. Under the effect of meterological conditions, this sediment, which loses its gravitational water upon emersion, also may lose its capillary water (or retention water). It sustains strong thermal variations. It is distinguished from other areas by non-regular immersion.

Zone of Retention - sediment reached by all tides. While it loses gravitational water at emersion, it conserves water of retention. Sediment in this zone displays an absence of very fine sedimentary fractions, weak accumulation of organic materials, and relatively loose settling. Consequently, great porosity and significant permeability cause excellent circulation and replenishment of interstitial water. Thermic variations can be significant during emersion.

Zone of Resurgence - the site of intensive circulation of interstitial water during high tide as well as low. During ebb tide, gravitational water from the Zone of Retention drains through this zone and appears at the sand surface to stream towards lower levels. Such "resurgence" continues as long as the level of interstitial water lies above the level of tidal water. Circulation is inverse when height of tidal water exceeds that of interstitial water. During emersion the lowering level of interstitial water causes a similar lowering in the level of resurgence, and so superficial sediments in this area lose their gravitational water. This part of the Zone of Resurgence is visible on the beach surface at spring tides as riverlets of outflowing water. Sediments here are characterized by little accumulation of very fine fractions and organic materials. Porosity is reduced by a more compact arrangement of sand grains. Oxygenation is excellent when water from rising tides penetrates the sediment, but at low tide, as undersaturated gravity water from the Zone of Retention reaches the level of resurgence, oxygenation is diminished.

<u>Zone of Saturation</u> - sediment continually saturated by water and shown weak porosity and permeability. Water circulation is greatly reduced because interstices are clogged by very fine particles and a large accumulation of organic material.

To explain the situation at Crane's Beach, I have extended Salvat's classification by dividing the <u>Zone of Dry Sand</u> into the <u>Zone of Extensive Drying</u> and the <u>Zone of Dry Sand</u>. <u>The Zone of Extensive Drying</u> is distinguished by irregular water replenishment during spring high tides or during storms, while the <u>Zone of Dry Sand</u> is restricted to regions almost never receiving seawater.

This sequence of environmental zonation can be applied successfully not only to horizontal vectors but along vertical axes of intertidal conditions at Crane's Beach as well. In fact so well do Salvat's definitions of regions along the sand surface of fine-grain beaches apply to depth zones in larger-grain beaches that changes in the terminology used above are not required. Characterizations vertically at stations along the low to high tide axis of Crane's Beach are shown in Fig. 14 and differ from one another primarily in proportions of each of these five zones. Low tidal elevations vary through spring and neap cycles as well as with local weather conditions, so resurgence and saturation predominate in low tidal areas. Decreased fluctuations in the amplitude of the water table at low tide within the beach confine the extent of the Zone of Resurgence at landward stations. The Zone of Retention dominates the entire beach but becomes diminished sharply above the high tidal line. The area of extensive drying conforms to the range of variation between spring and neap high tidal levels, while dry sand areas occur only above the spring high tides. Table II is a summary of ecological conditions including water content, temperatures, salinity, oxygen abundance, and the general habitability associated with each of these zones within the porous, intertidal, interstitial habitat at Crane's Beach.

The Zone of Retention and the Zone of Resurgence are most heavily populated by meiofauna. In terms of the range of conditions facing faunal elements, these sections of a porous, intertidal beach are probably not much more severe environments than are shallow subtidal areas. At the same time, the capillary network of interstitial spaces provides a tremendously expanded intertidal surface area for meiofaunal activity. A cross-section through coastal region of porous sediments would reveal that potential meiofaunal areas are limited to the surface few centimeters of subtidal sediments (McIntyre, 1969), expand to occupy large areas and depths within an intertidal area (Renaud-Debyser, 1963; Part IV), and then plane off to a limited area surrounding the region of continental ground water (Delamare Deboutteville, 1960).

TABLE I. TIDAL RANGES OF WATER TABLE AMPLITUDE (in cm).

	Sea	D	E	F	G	H	I
May 13, 1968 Spring Tide	166	31	37	54	67	85	75
May 20, 1968 Neap Tide	108	26	32	49	72	60	45

TABLE II. ENVIRONMENTAL ZONES AT CRANE'S BEACH.

ZONE		WATER CONTENT	TEMPERATURE	SALINITY	OXYGEN	"HABITABILITY"
Dry Sand		Almost never gets seawater; high content from precipitation; low content usually.	highly variable; great atmosphere influence. High in summer; low in winter.	Local extremes thru evaporation and precipitation.	Well aerated.	Poorly populated.
Extensive Drying		Low and irregular; long drying times. Capillary water lost; holds hygroscopic water.	Wide variations.	Local, infrequent lowering from freshwater sources.	Well aerated.	Requires adaptation for strong variability.
Retention	Upper	Tidally varying; 100-15% saturation. Some capillary water lost at low tide.	Variations can be great in summertime low tides during day.	Little variation.	Well aerated.	Often densely populated. Comparable variability to adjacent subtidal.
	Lower	100-40% saturation. Gravitational water lost at low tide.	Little tidal variation.	Little variation.	Well aerated.	
Resurgence		High saturation. Some gravity water lost at spring low tides.	Nearly constant. Follows gradual seasonal cycle.	Locally variable due to ground water sources.	Aerates in water flow and waves. Often low.	Low density due to oxygen variability.
Saturation		Saturated.	No variation.	Variable with ground water.	Usually anaerobic.	Poorly populated; oxygen limited.

FIG. 1. The region surrounding Woods Hole, Massachusetts.

FIG. 2. Location of Crane's Beach on Penzance Point, Woods Hole, Massachusetts.

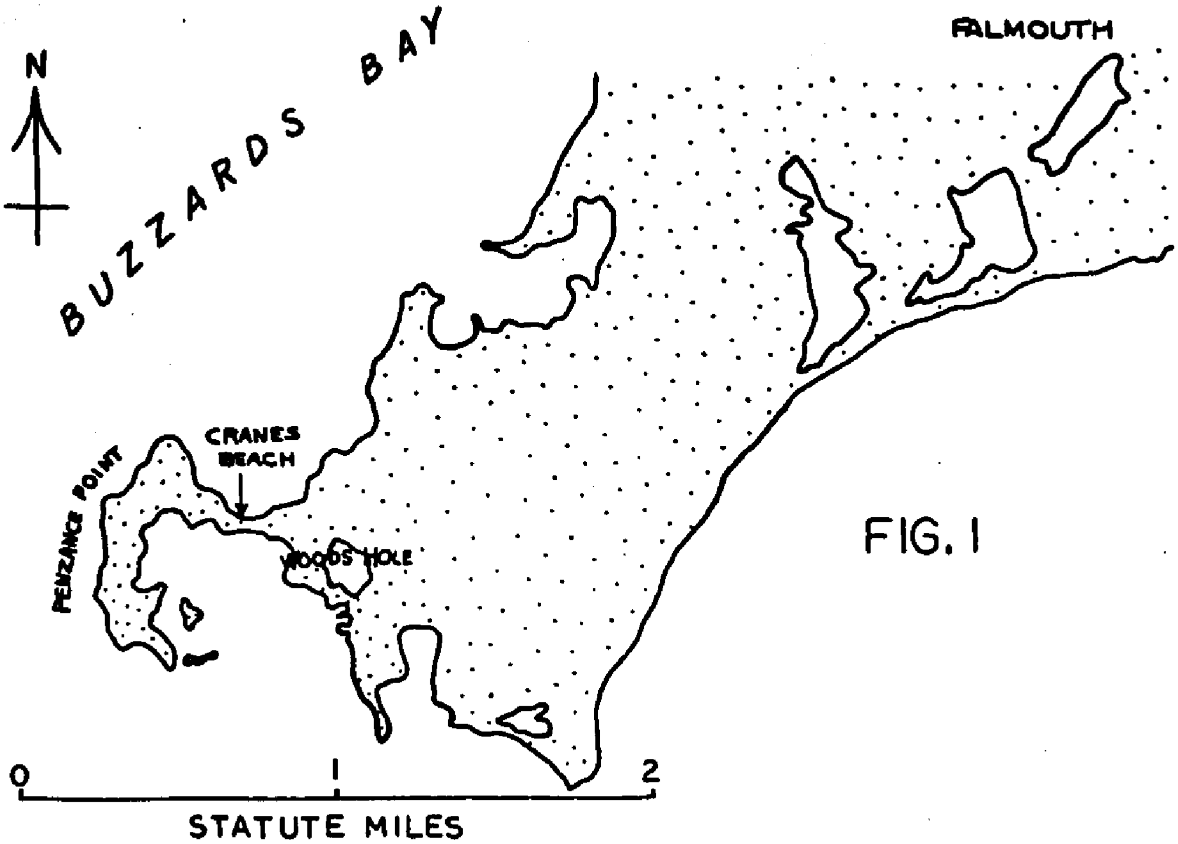

N
BUZZARDS BAY
FALMOUTH
CRANES BEACH
PENZANCE POINT
WOODS HOLE
0
1
2
STATUTE MILES

FIG. 1

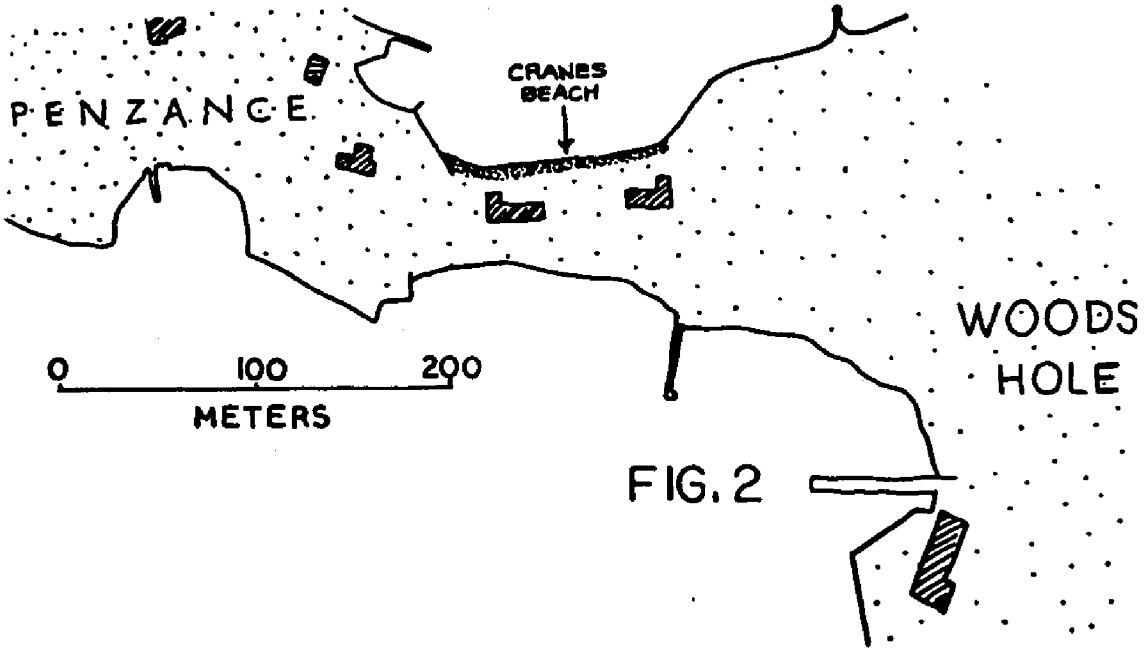
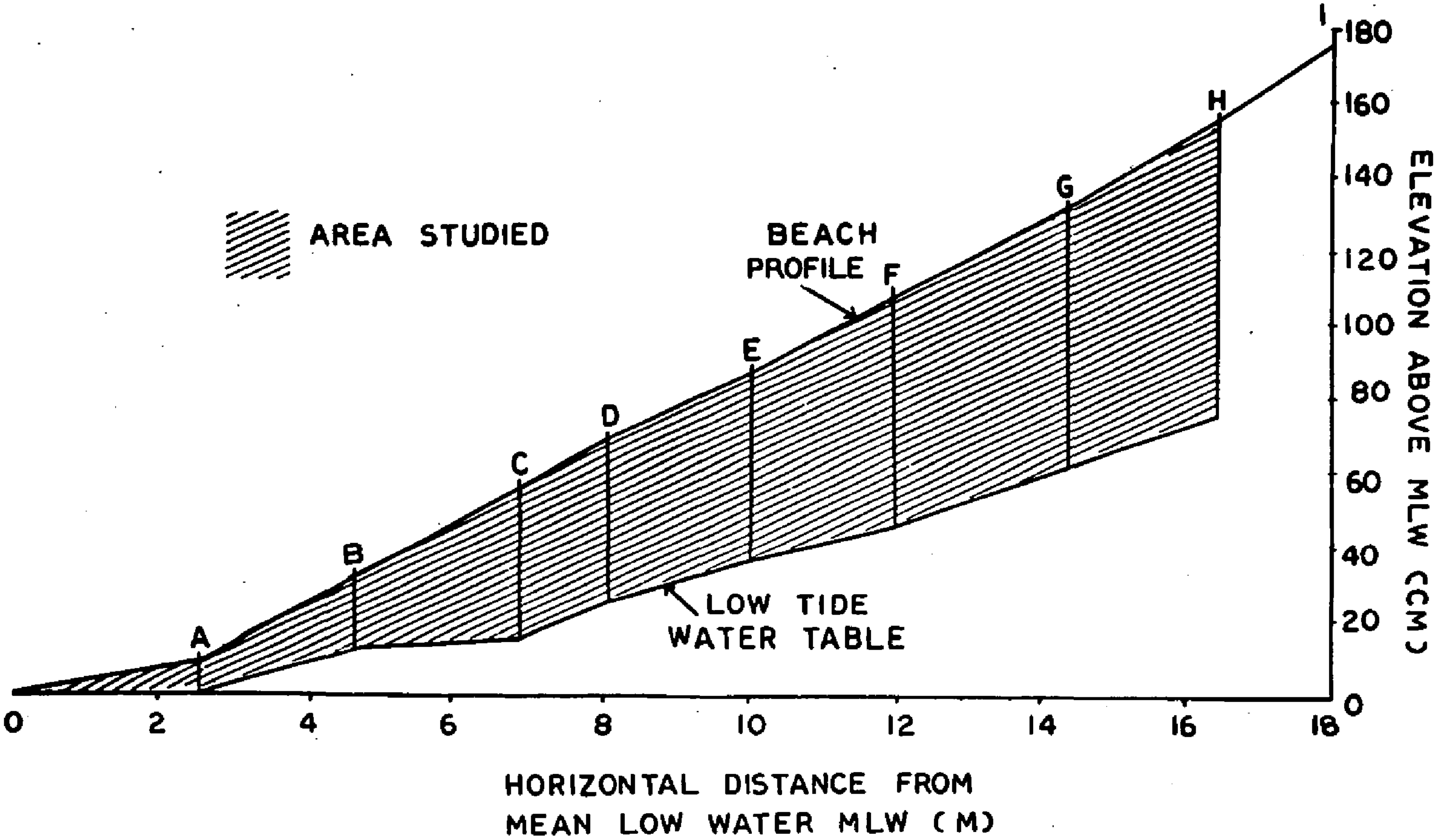

PENZANCE
CRANES BEACH
WOODS HOLE
0
100
200
METERS

FIG. 2

FIG. 3. The Crane's Beach profile showing study transect, including stations A - 1.



▨ AREA STUDIED
BEACH PROFILE
LOW TIDE WATER TABLE
A
B
C
D
E
F
G
H
I
0
2
4
6
8
10
12
14
16
18
0
20
40
60
80
100
120
140
160
180
ELEVATION ABOVE MLW (CM)
HORIZONTAL DISTANCE FROM MEAN LOW WATER MLW (M)

FIG. 3

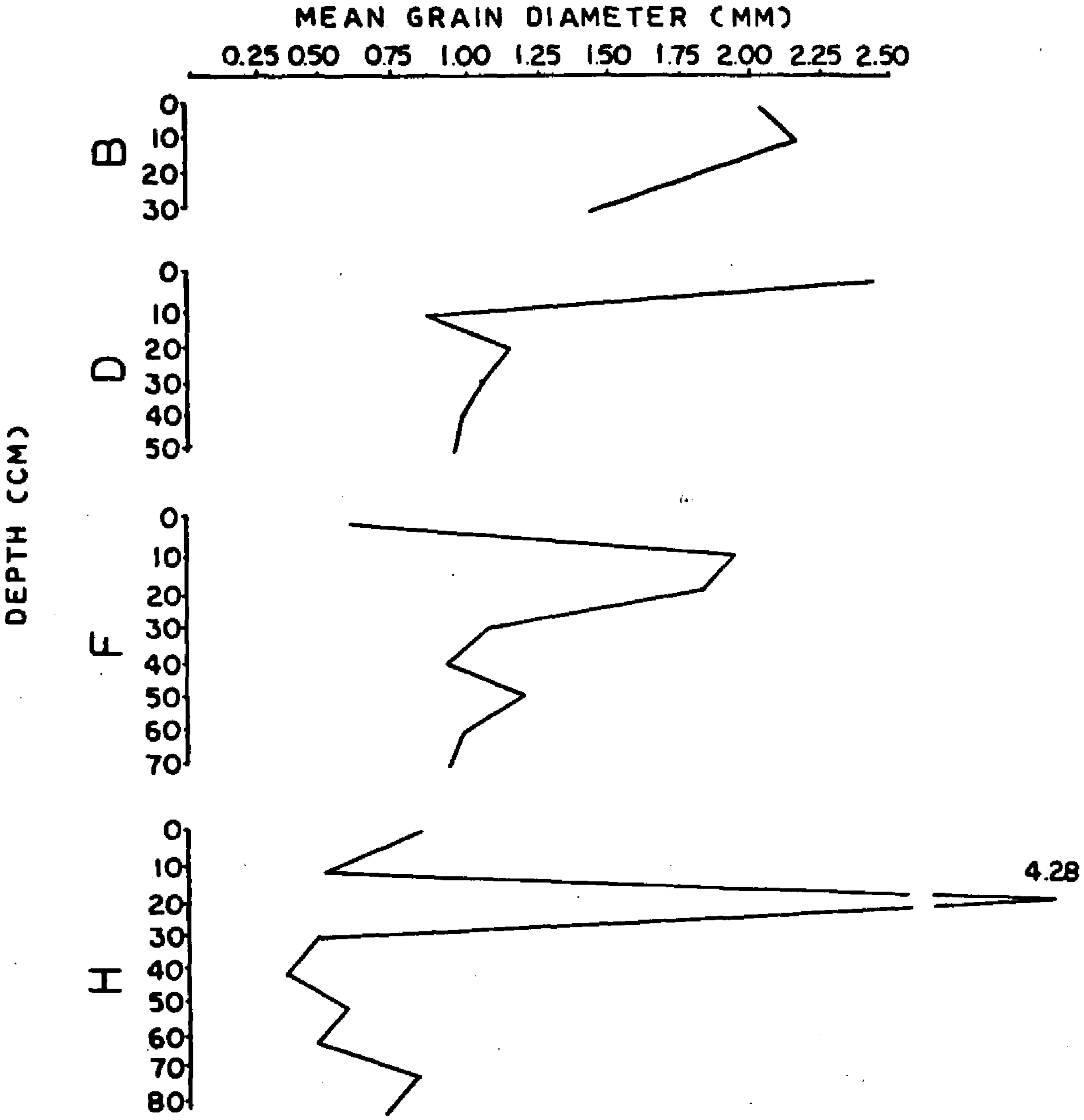
FIG. 4. Sedimentary characteristics of Crane's Beach stations B, D, F, and H at ten cm depth intervals.

A. Mean grain diameter (mm).

B. Sorting (Ø units).

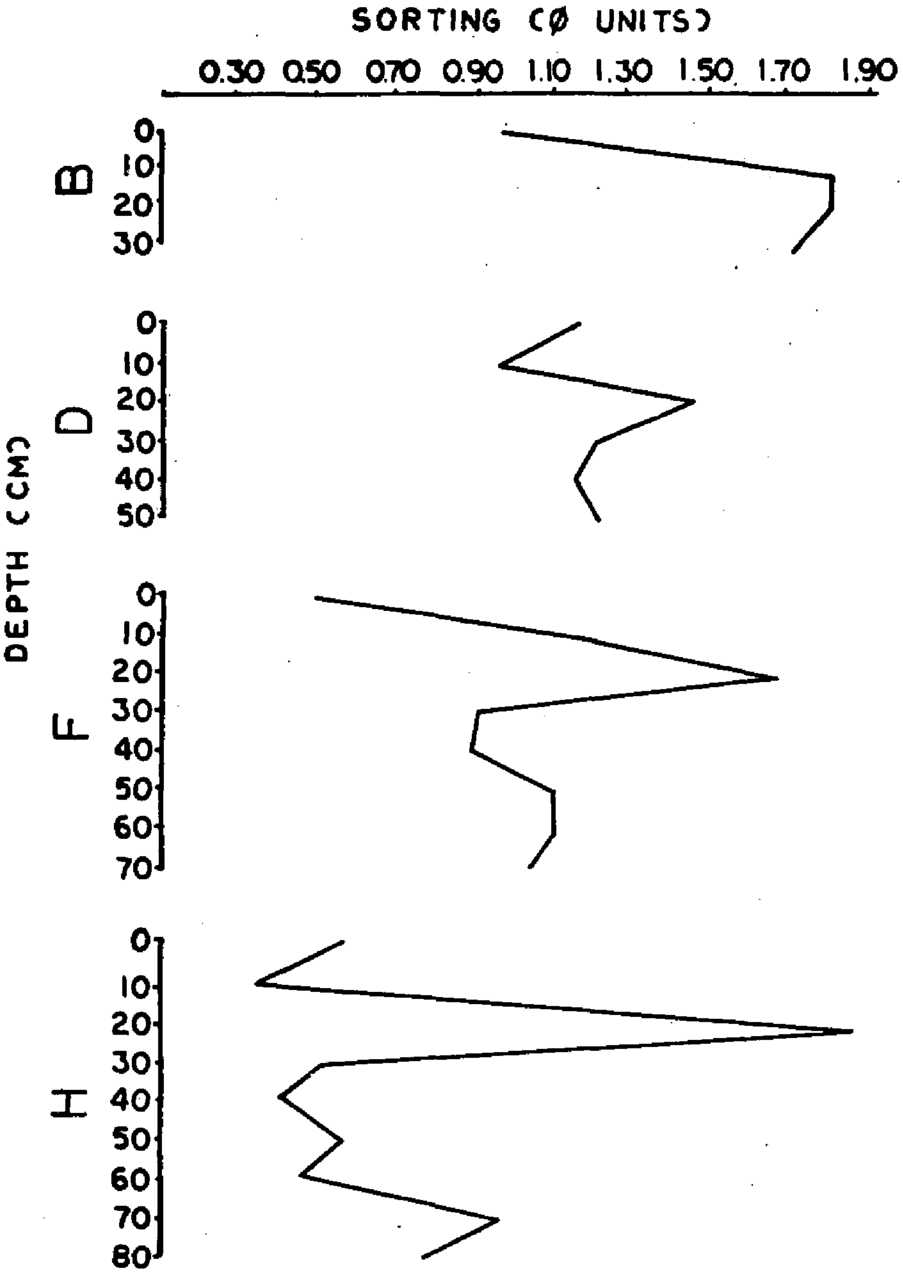
C. Pore volume (% total sample volume).

FIG. 4


MEAN GRAIN DIAMETER (MM)
0.25
0.50
0.75
1.00
1.25
1.50
1.75
2.00
2.25
2.50
DEPTH (CM)
B
0
10
20
30
D
0
10
20
30
40
50
F
0
10
20
30
40
50
60
70
H
0
10
20
30
40
50
60
70
80
4.28

A

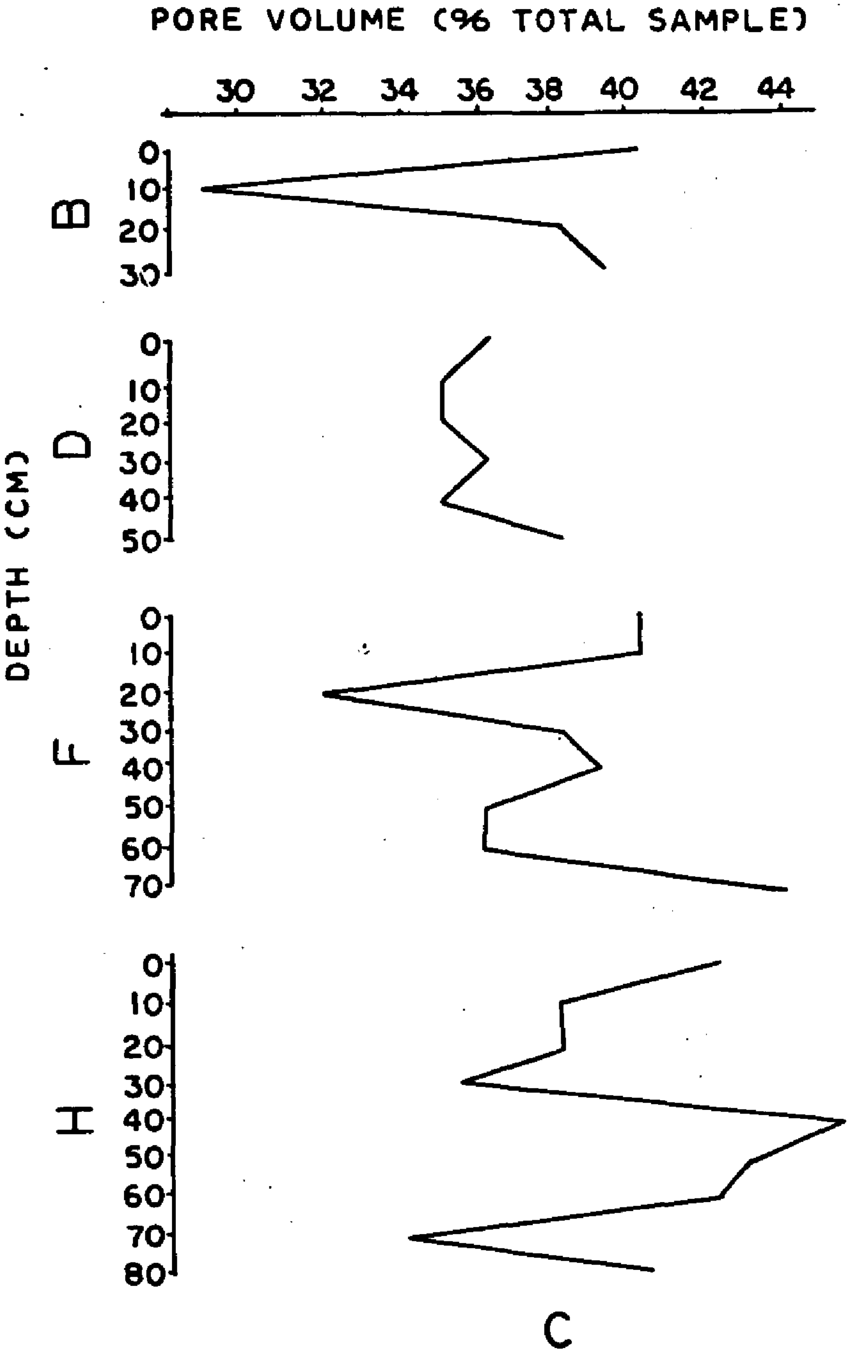
FIG. 4



SORTING (Ø UNITS)
0.30 0.50 0.70 0.90 1.10 1.30 1.50 1.70 1.90
DEPTH (CM)
B
0 10 20 30
D
0 10 20 30 40 50
F
0 10 20 30 40 50 60 70
H
0 10 20 30 40 50 60 70 80

B

FIG. 4



PORE VOLUME (% TOTAL SAMPLE)
30
32
34
36
38
40
42
44
DEPTH (CM)
B
0
10
20
30
D
0
10
20
30
40
50
F
0
10
20
30
40
50
60
70
H
0
10
20
30
40
50
60
70
80
C

FIG. 5. Tidal pattern at Woods Hole shown by monthly changes in high tide elevation (from U. S. Coast and Geodetic Survey, Tide Tables, 1968 and 1969). Collection dates are indicated by vertical lines.

FIG. 5

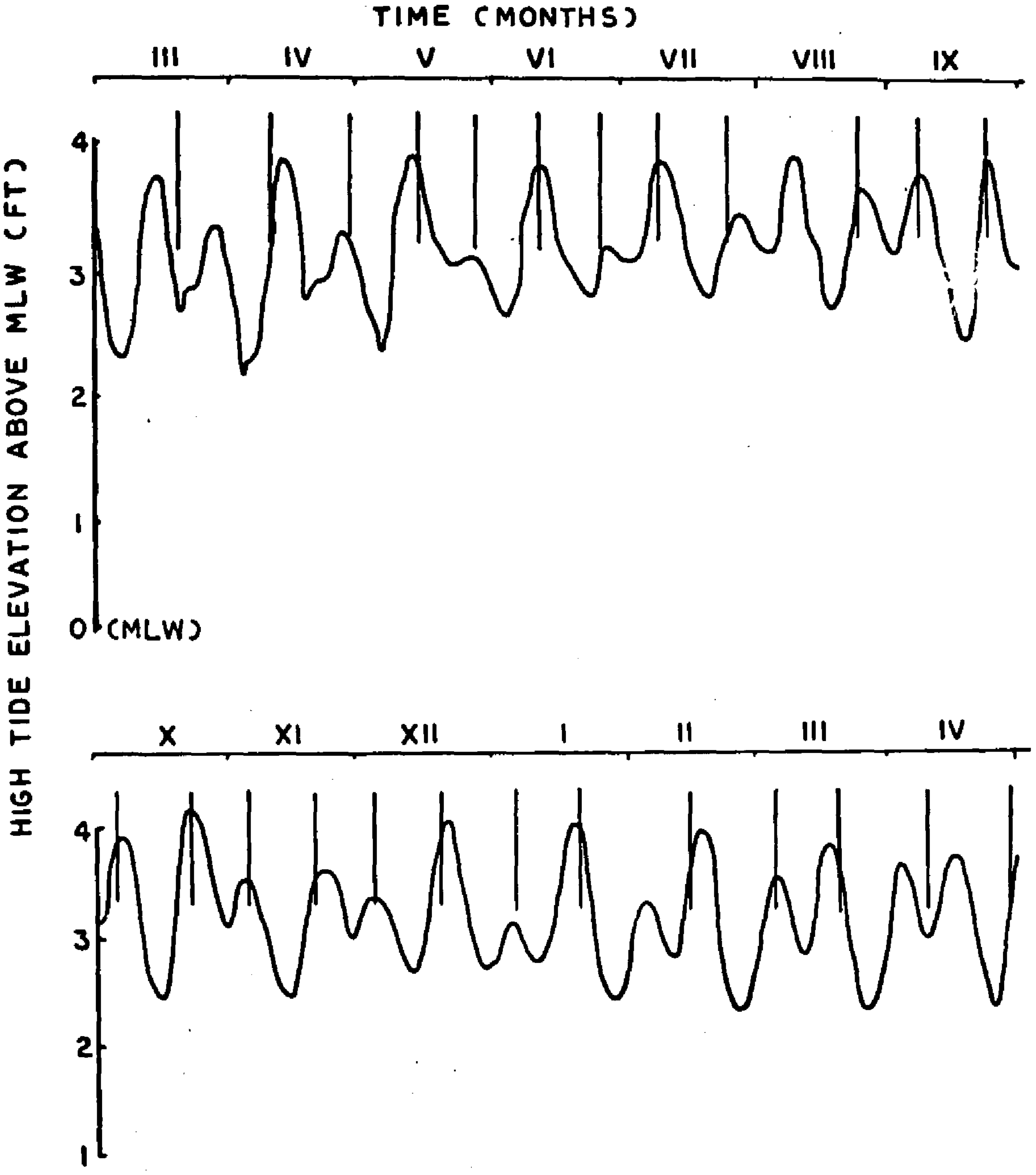

TIME (MONTHS)
III
IV
V
VI
VII
VIII
IX
HIGH TIDE ELEVATION ABOVE MLW (FT)
4
3
2
1
0 (MLW)
X
XI
XII
I
II
III
IV
4
3
2
1

FIG. 6. Tidal changes in elevation of seawater and the water table at stations A - I.

A. Spring tide cycle, 13 May 1968.

B. Neap tide cycle, 20 May 1968.

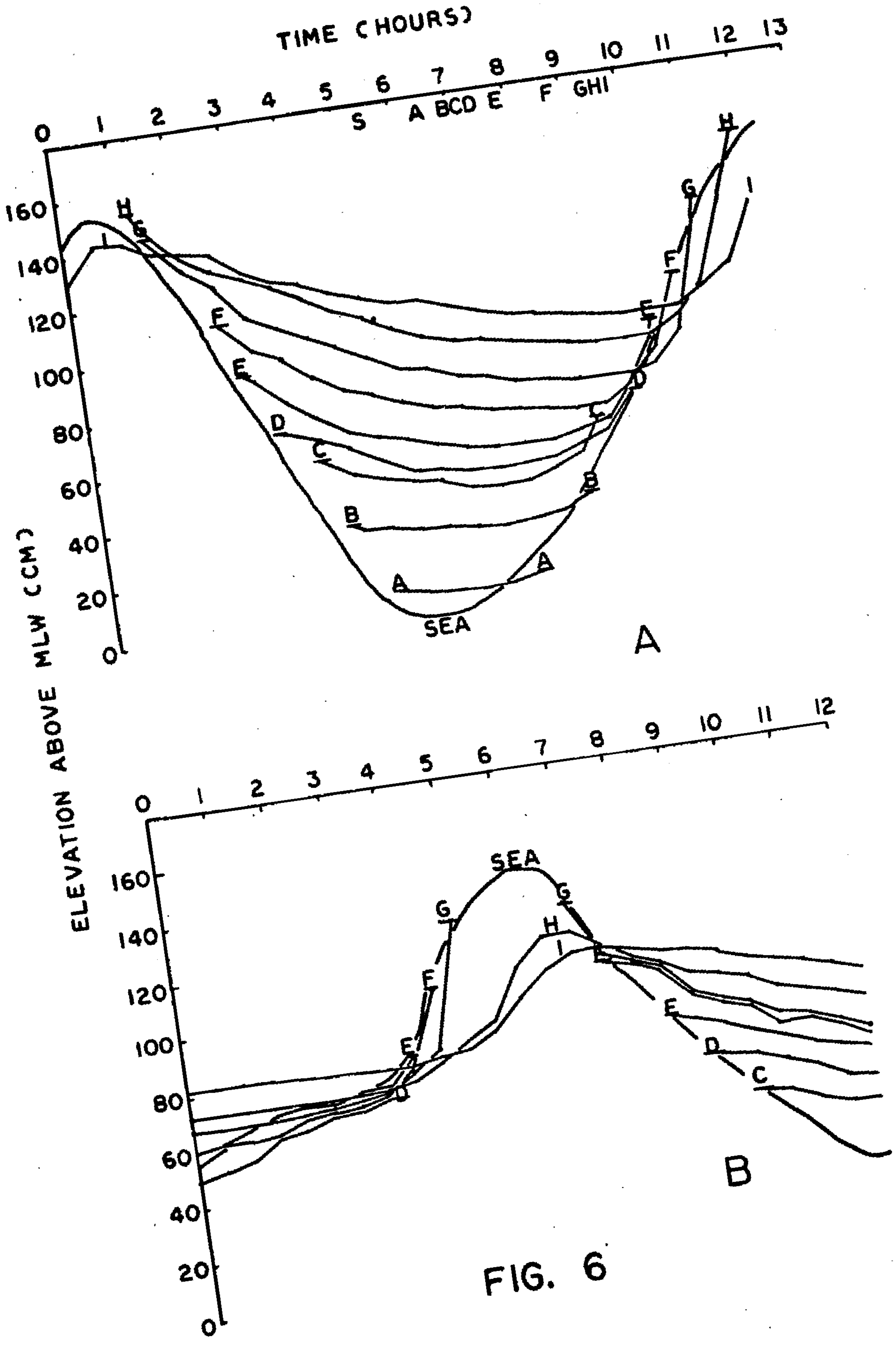

TIME (HOURS)
0 1 2 3 4 5 6 7 8 9 10 11 12 13
S A BCD E F GHI
ELEVATION ABOVE MLW (CM)
0 20 40 60 80 100 120 140 160
H G I F E D C B A SEA
A
0 1 2 3 4 5 6 7 8 9 10 11 12
SEA G H I F E D C
B

FIG. 6

FIG. 7. Comparison of spring and neap tide drainage patterns throughout the transect. Lines indicate hours of exposure to less than 50% saturation.

FIG. 7

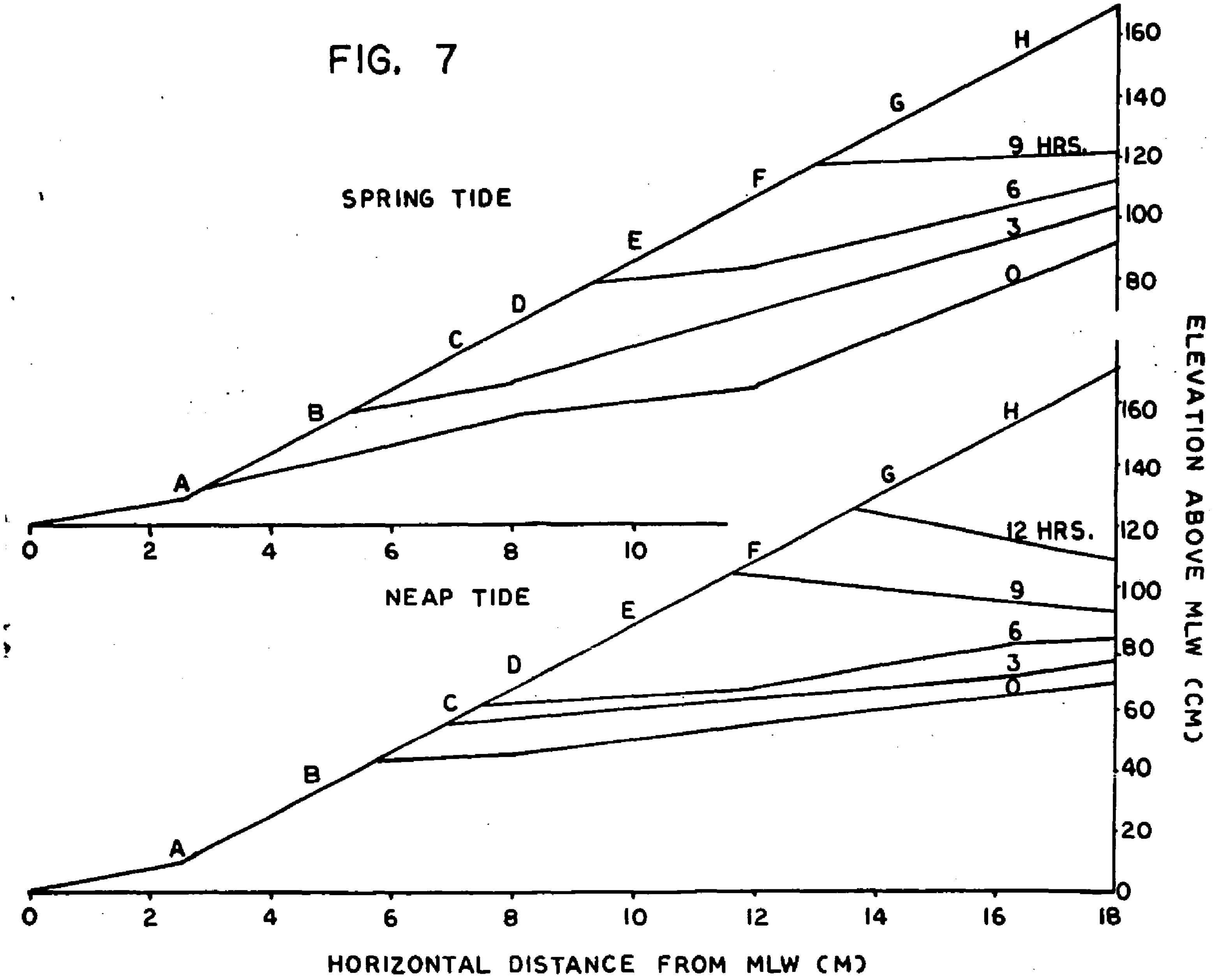
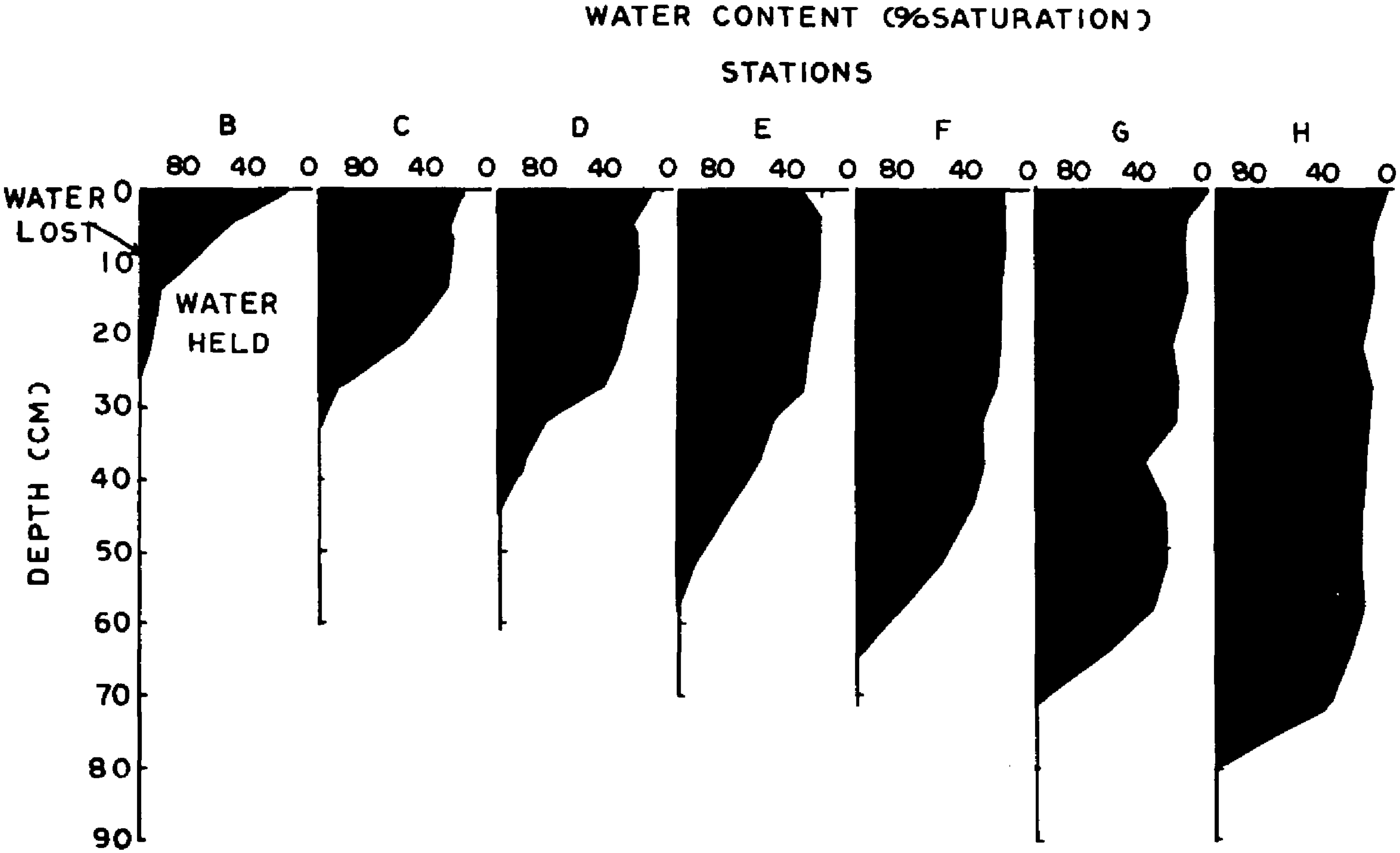

SPRING TIDE
A
B
C
D
E
F
G
H
9 HRS.
6
3
0
160
140
120
100
80
0
2
4
6
8
10
NEAP TIDE
A
B
C
D
E
F
G
H
12 HRS.
9
6
3
0
160
140
120
100
80
60
40
20
0
0
2
4
6
8
10
12
14
16
18
HORIZONTAL DISTANCE FROM MLW (M)
ELEVATION ABOVE MLW (CM)

FIG. 8. Average range of tidal change in water content expected at ten cm depth intervals at stations B - H, Crane's Beach, 1968. Low tide depletion on right side of each graph, and high tide saturation on left.



WATER CONTENT (%SATURATION)
STATIONS
B
C
D
E
F
G
H
80
40
0
WATER
LOST
WATER
HELD
DEPTH (CM)
0
10
20
30
40
50
60
70
80
90

FIG. 8

FIG. 9. Tidal changes in water content at ten cm depth intervals at stations D, F, and H.

A. Spring tidal cycle, 13 May 1968.

B. Neap tidal cycle, 20 May 1968.

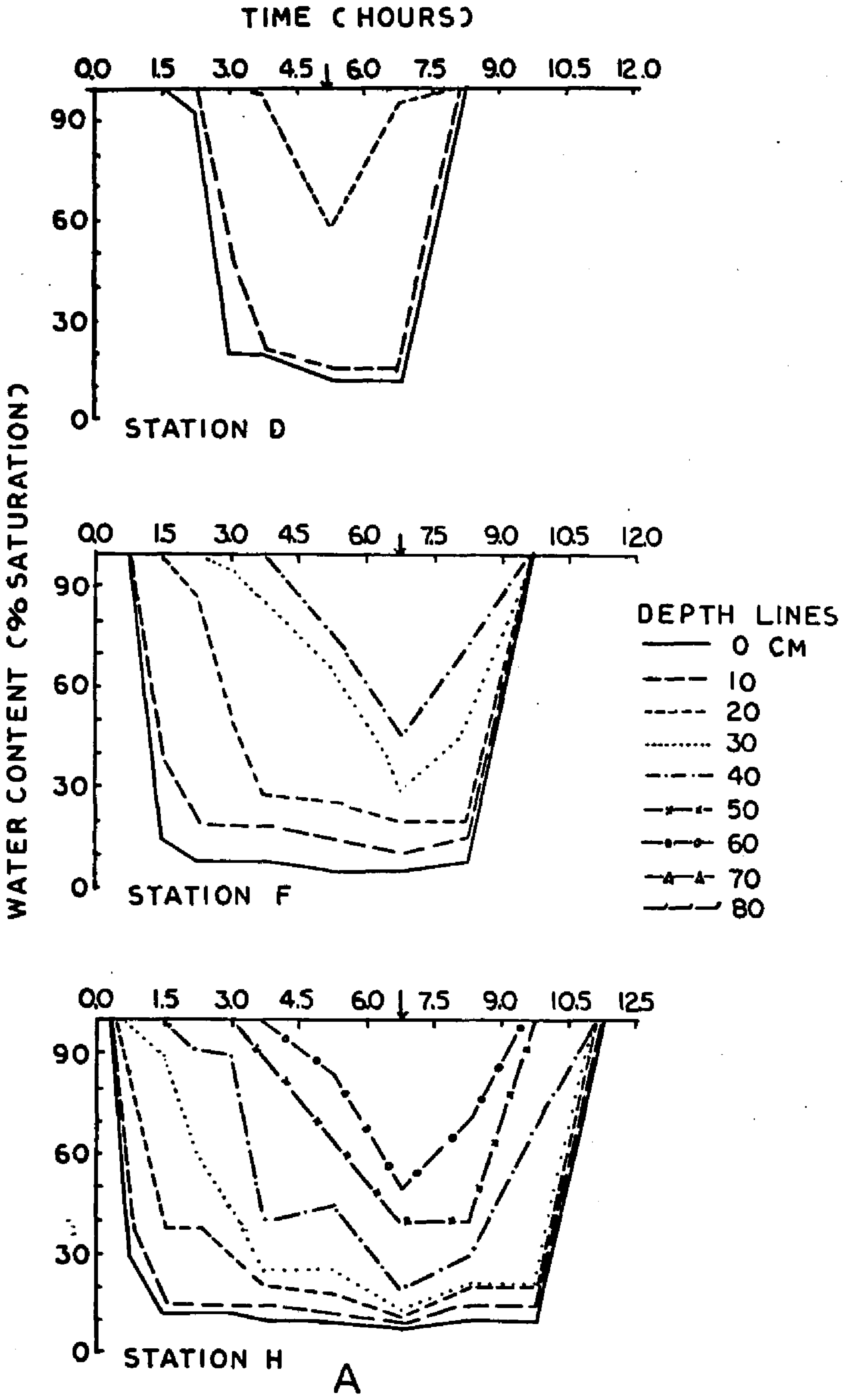
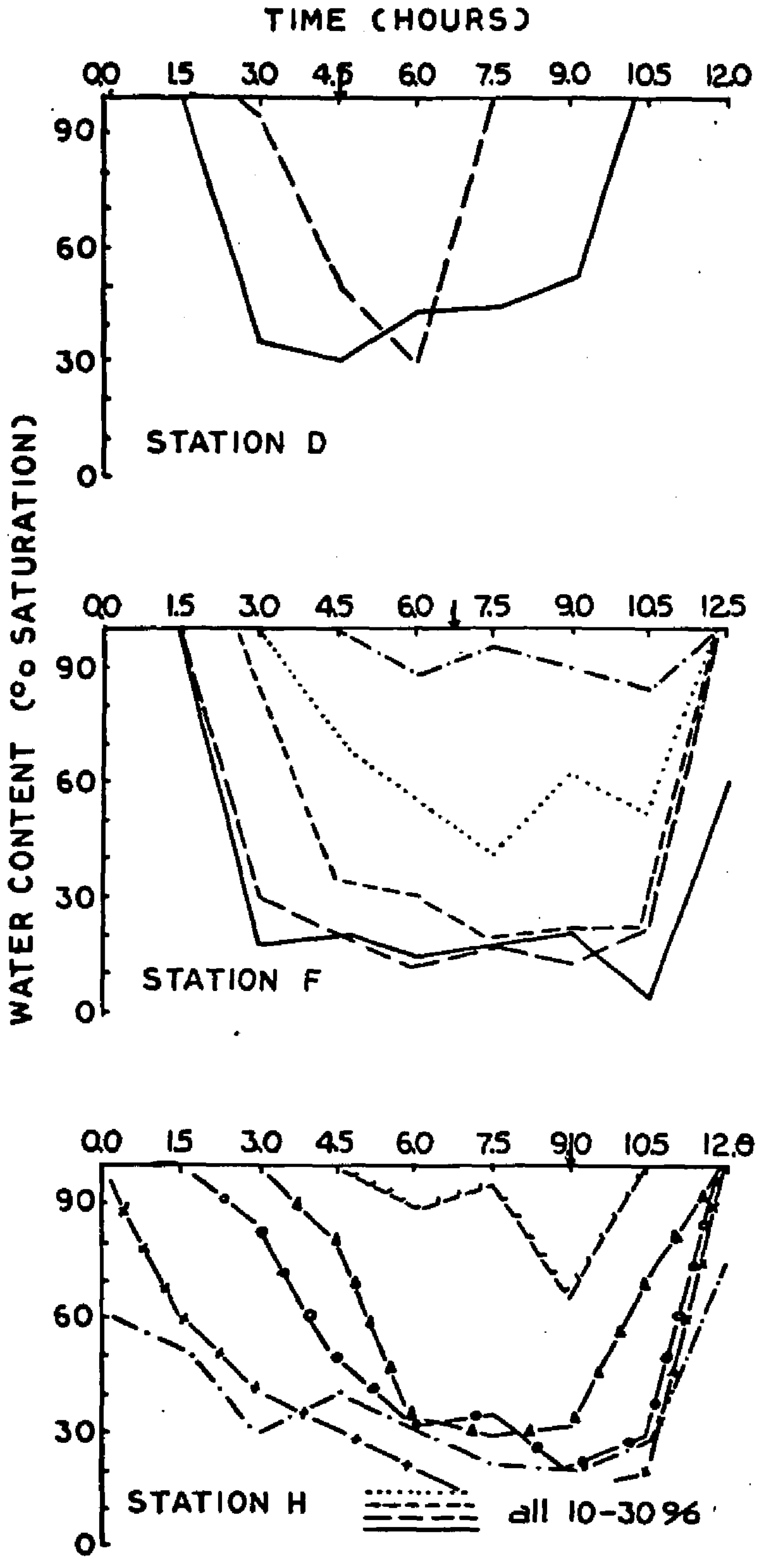

TIME (HOURS)
0.0
1.5
3.0
4.5
6.0
7.5
9.0
10.5
12.0
12.5
90
60
30
0
WATER CONTENT (% SATURATION)
STATION D
STATION F
STATION H
DEPTH LINES
0 CM
10
20
30
40
50
60
70
80
A

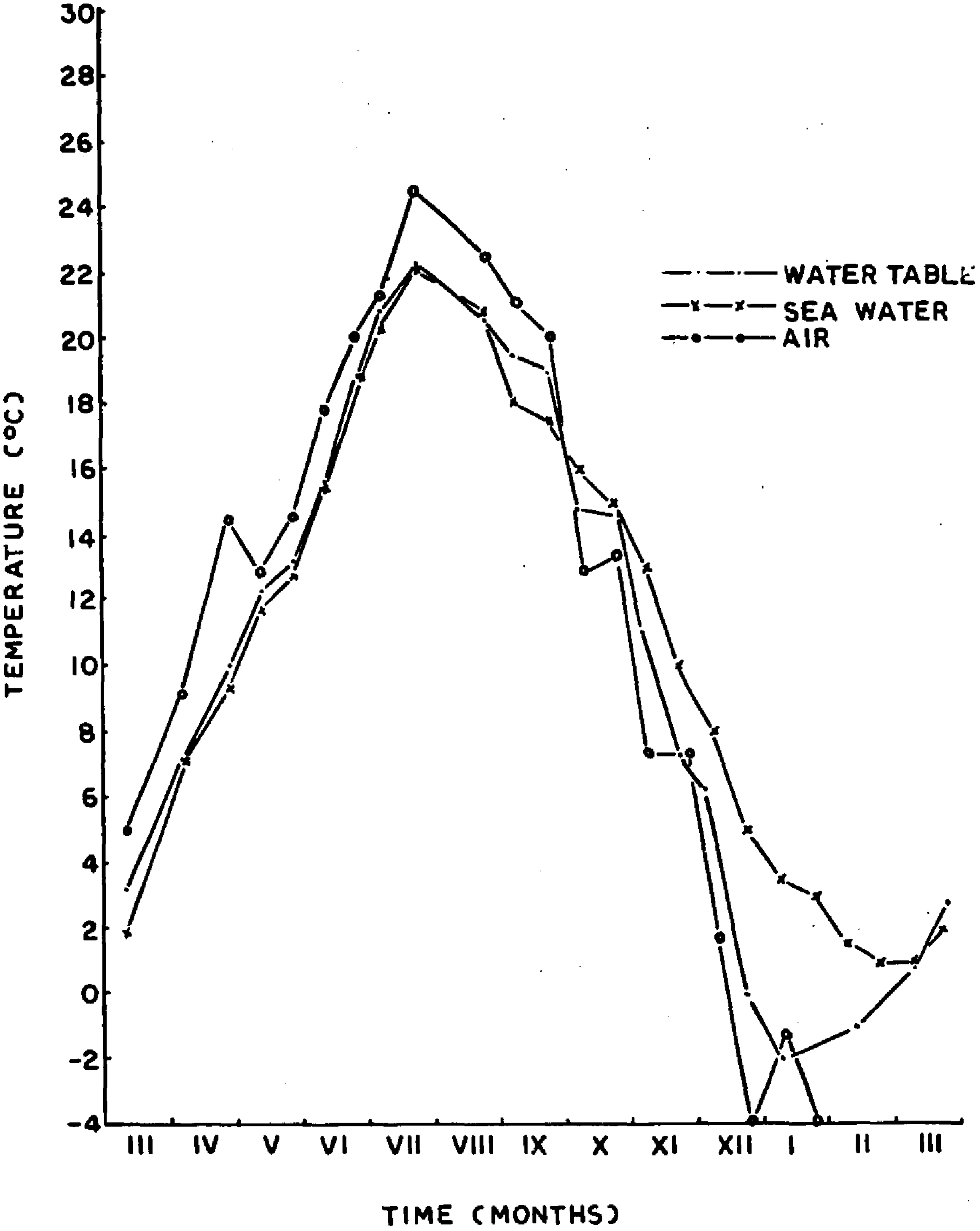
FIG. 9


TIME (HOURS)
0.0
1.5
3.0
4.5
6.0
7.5
9.0
10.5
12.0
90
60
30
0
STATION D
WATER CONTENT (% SATURATION)
0.0
1.5
3.0
4.5
6.0
7.5
9.0
10.5
12.5
STATION F
0.0
1.5
3.0
4.5
6.0
7.5
9.0
10.5
12.8
STATION H
all 10-30 96

B

FIG. 9

FIG. 10. Annual temperature changes in atmosphere, seawater, and Crane's Beach water table, 1968 - 1969.



30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
-2
-4
TEMPERATURE (°C)
III
IV
V
VI
VII
VIII
IX
X
XI
XII
I
II
III
TIME (MONTHS)
WATER TABLE
SEA WATER
AIR

FIG. 10

FIG. 11. Three patterns (A - C) of tidal variation in temperature at ten cm depth intervals at stations B - H. Low tidal extremes in temperature on right side of each graph; high tidal temperatures on left.

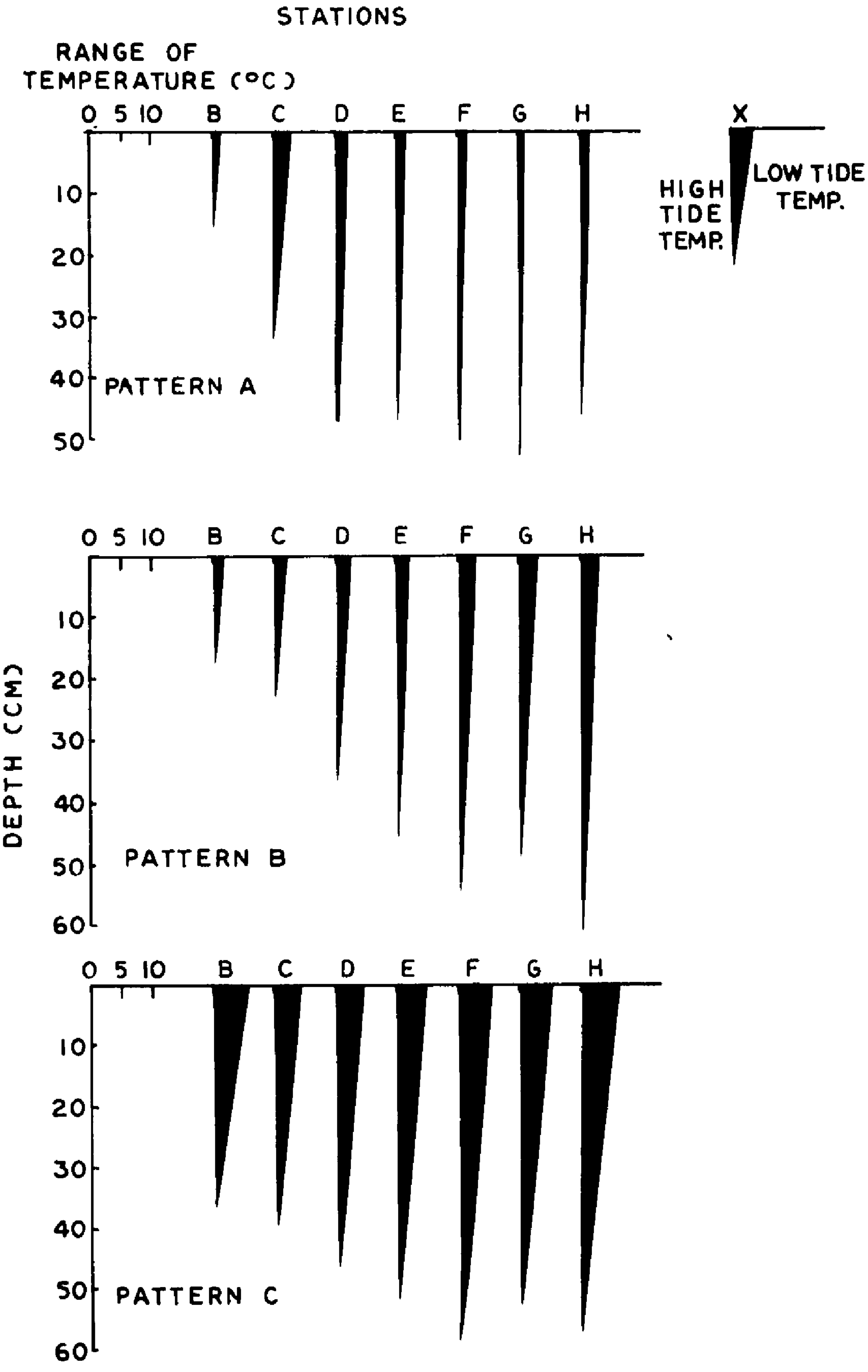

STATIONS
RANGE OF TEMPERATURE (°C)
0 5 10
B
C
D
E
F
G
H
X
HIGH TIDE TEMP.
LOW TIDE TEMP.
DEPTH (CM)
10
20
30
40
50
60
PATTERN A
PATTERN B
PATTERN C

FIG. 11

FIG. 12. Annual temperature patterns (A - C, Fig. 11) at Crane's Beach, 1968 - 1969.

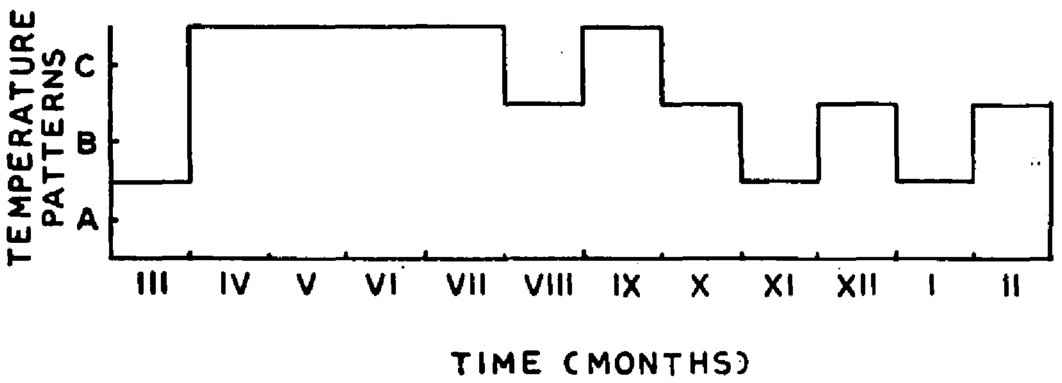

TEMPERATURE PATTERNS
A
B
C
III
IV
V
VI
VII
VIII
IX
X
XI
XII
I
II
TIME (MONTHS)

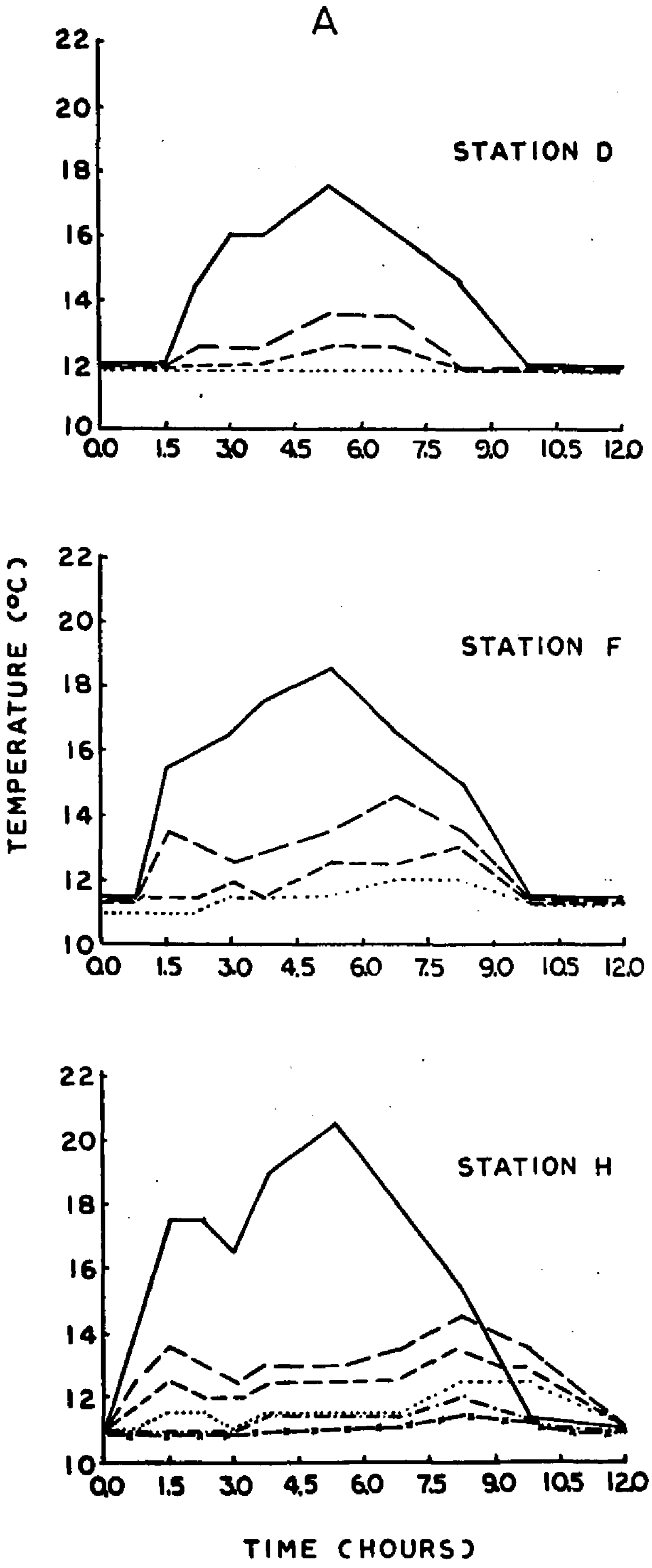
FIG. 12

FIG. 13. Tidal changes in temperature at ten cm depth intervals at stations D, F, and H. Legend to depth lines in Fig. 9A.

A. Spring tidal cycle, 13 May 1968.

B. Neap tidal cycle, 20 May 1968.

FIG. 13


A
STATION D
STATION F
STATION H
TEMPERATURE (°C)
TIME (HOURS)
22
20
18
16
14
12
10
0.0
1.5
3.0
4.5
6.0
7.5
9.0
10.5
12.0

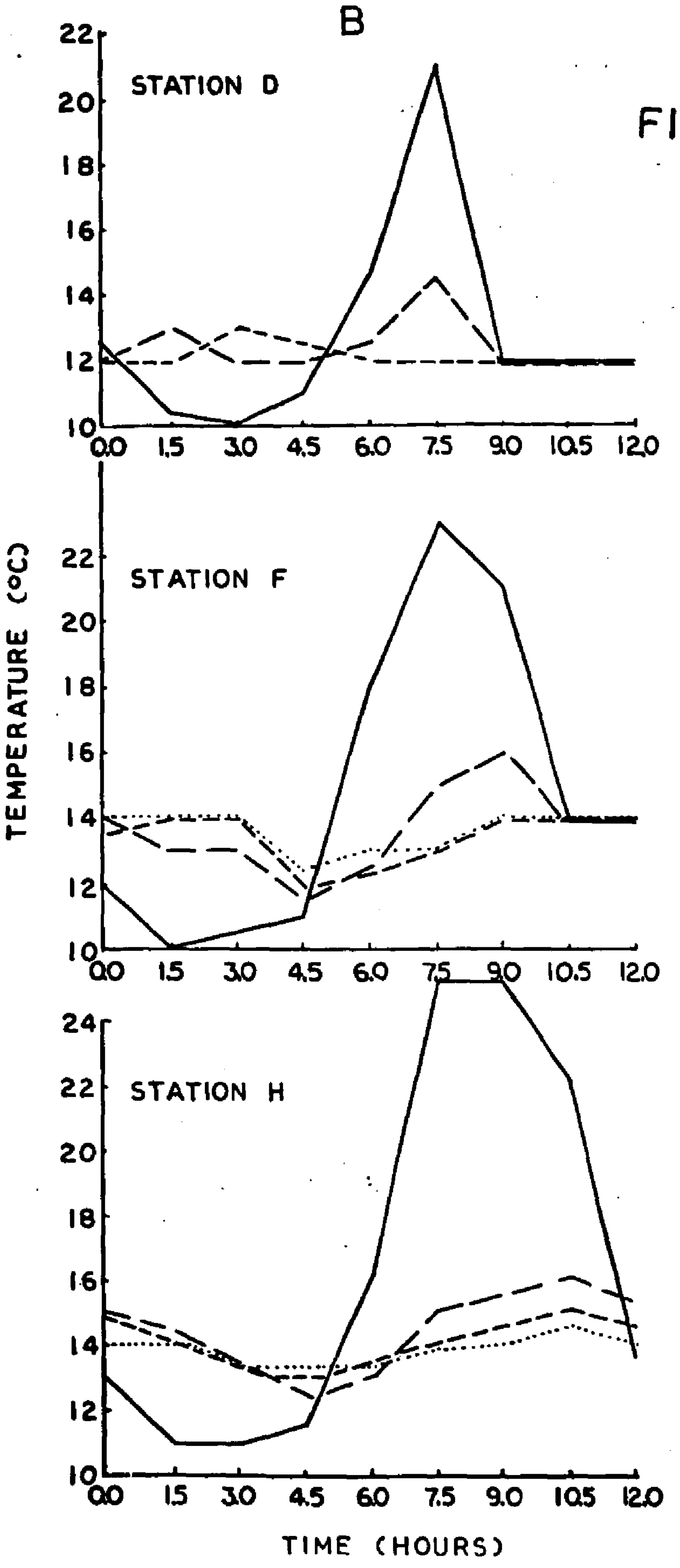
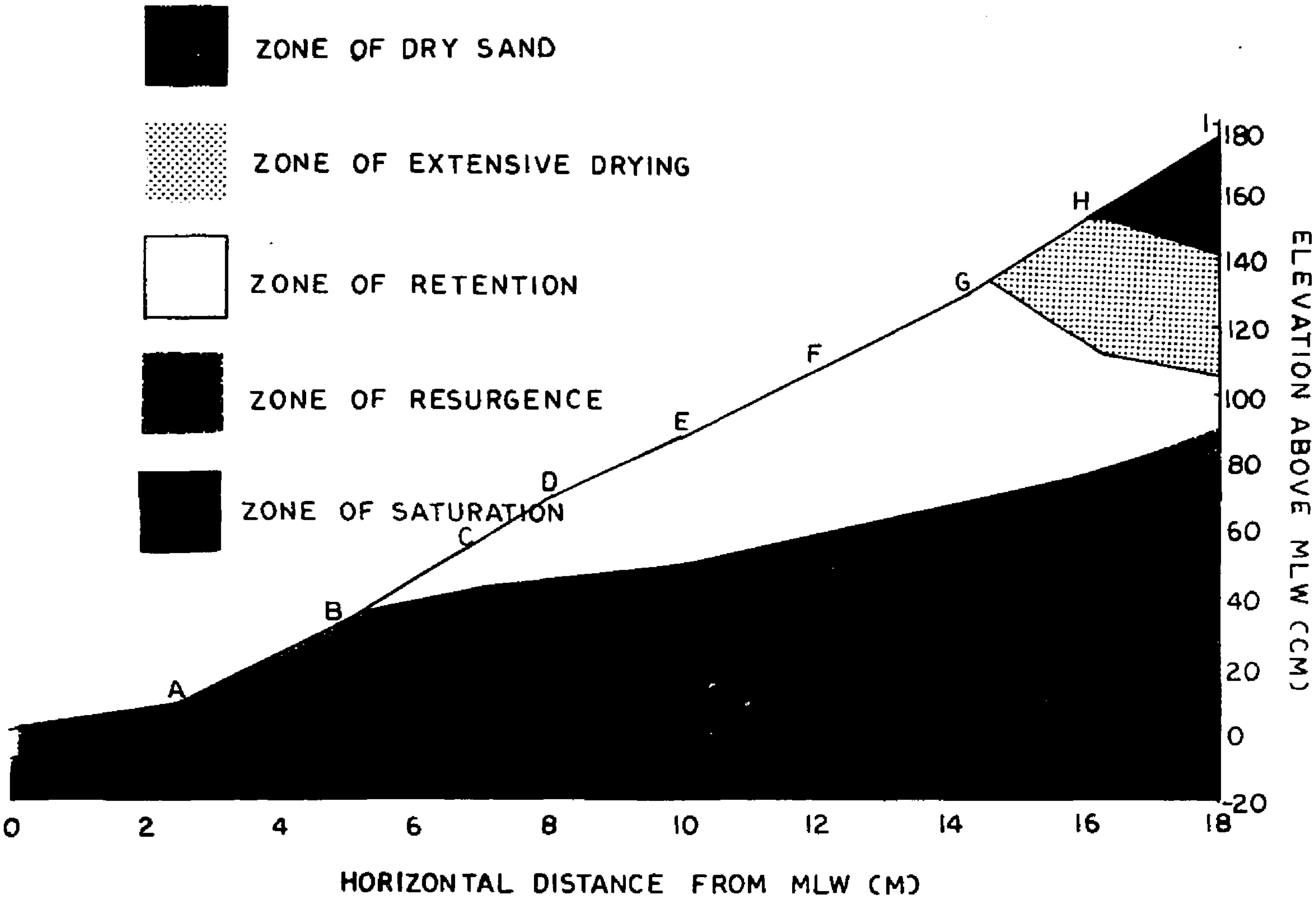

B
STATION D
STATION F
STATION H
TEMPERATURE (°C)
TIME (HOURS)
22
20
18
16
14
12
10
24
0.0
1.5
3.0
4.5
6.0
7.5
9.0
10.5
12.0

FIG. 13

FIG. 14. Environmental zones at Crane's Beach.


ZONE OF DRY SAND
ZONE OF EXTENSIVE DRYING
ZONE OF RETENTION
ZONE OF RESURGENCE
ZONE OF SATURATION
A
B
C
D
E
F
G
H
I
180
160
140
120
100
80
60
40
20
0
-20
ELEVATION ABOVE MLW (CM)
0
2
4
6
8
10
12
14
16
18
HORIZONTAL DISTANCE FROM MLW (M)

Part IV

ASPECTS OF THE ECOLOGY OF MARINE INTERSTITIAL TARDIGRADA AT WOODS HOLE, MASSACHUSETTS

Although scattered references to microscopic sand dwelling animals appeared prior to 1900, Kowalevsky (1901a and b) and Giard (1904) drew attention to the abundance of marine interstitial fauna. Since then, work has been largely taxonomic, as faunal surveys in a variety of geographical locations mostly in Europe. Nearly every phylum of invertebrates is represented in the interstitial meiofauna (see Swedmark, 1964; and Ax, 1966 for reviews). Most species are highly adapted to this environment (Remane, 1952; Swedmark, 1964), and are found nowhere else. Taxonomists face the difficult task of working with microscopic, thigmotactic, and transparent forms. The systematics of most taxa remains far from complete, and as a result, there are few detailed studies of the ecology and distributions of interstitial meiofauna.

The Tardigrada comprise a phylum of metazoan invertebrates including several marine, interstitial representatives (see Ramazzotti, 1962, 1965 for general review, and Renaud-Mornant and Pollock, 1970 (in press) for review of marine forms). As an occasionally abundant interstitial group, they lend themselves particularly well to ecological study since most of the thirty one known species are easily distinguished. Renaud-Debyser (1956, 1959a, and 1963) studied interstitial tardigrades and related environmental parameters at several beaches in France. She gathered data over an extended period on the distributions of _Batillipes mirus_ Richters, 1909, _Stygarctus bradypus_ Schulz, 1951, and several other species of _Batillipes_ at Bassin d'Arcachon. DeZio (1964, 1965) and DeZio and Grimaldi (1964a and b, 1966) contributed a study of tardigrade distribution at atidal beaches along the Adriatic coast of Italy. They discussed correlations between tardigrade frequency and several environmental parameters. Ganapati and Rao (1962) surveyed the fauna and ecology of beaches along the Waltair coast of India where they encountered several species of tardigrades.

Two brief ecological observations on tardigrades in United States beaches have appeared also. King (1962) discussed the relation between occurrence of tardigrades and severity of waves on Florida beaches, while McGinty and Higgins (1968) presented ecological observations made during their morphological study of two species of _Batillipes_ from Virginia.

Information on structure and dynamics of tardigrade populations is limited. Length-frequency analyses were made on natural populations of moss-dwelling tardigrades (Higgins, 1958; Ramazzotti, 1962; Franceschi Crippa and Lattes, 1967) to determine the number of instars occurring during a lifetime. Franceschi et al (1962-63) observed changes in the structure of a population for a period of six months. Information regarding the composition of populations of marine tardigrades is entirely lacking.

During this study, I recorded year-round distributions of marine interstitial tardigrades at a single beach and will describe general patterns in their distributions and structure of their populations. Also I shall attempt to correlate their distributions with environmental parameters discussed in Part III.

Following a qualitative survey of interstitial tardigrades in the vicinity of Woods Hole, Massachusetts, I selected Crane's Beach (41^{0} 31' 41" N, 70^{0} 40' 41") on Penzance Point for detailed study. Penzance Point (Fig. 1) is a peninsula extending westward one quarter mile from Woods Hole. Crane's Beach (Fig. 2) faces Buzzards Bay at the narrowest portion of the neck joining Penzance Point to Woods Hole.

I determined the extent of tardigrade distribution from low tide towards the high tidal region by preliminary surveys of Crane's Beach. A transect (Fig. 3) was selected 20 m from the west end of the beach. This transect consisted of a strip two m wide extending perpendicularly from the water's edge to a point above that reached by spring high tides, and in depth from the surface of the sand to the level of interstitial space saturation at low tide (=water table). This transect measures 18 m along the beach and nearly one m in depth in the high tidal region. In general, this volume sampled all of the intertidal beach normally drained of water during ebb tide, including the Zone of Extensive Drying, Zone of Retention, and Zone of Resurgence, described in Part III.

MATERIALS AND METHODS

Nine stations were established along the transect at elevations of 8, 31, 54, 69, 85, 107, 130, 153, and 176 cm above mean low water (MLW) and are referred to as stations A - I respectively. Elevations were located at each collection by sightings with a hand level from a surveyor's range pole placed at a supralittoral reference point. By this technique, elevations of stations and consequent tidal exposure remained constant throughout the study.

At each station, samples were collected from the sand surface to the level of the low tide water table, at depth intervals of 1, 4, 8, 14, 22, 27, 32, 38, 44, 51, 65, 72, and 80 cm. Maximal depths sampled ranged from 14 cm at station A to 80 cm depth at stations H and I. Every depth interval at each station represented a "sample site".

Initially (March, 1968 - July, 1968), 71 sample sites were studied in bi-weekly collections by gathering triplicate subsamples of ten cm^3 volume each. The usual number of subsamples taken per collection was 213, requiring approximately two and one-quarter hours to take in the field.

While triplicate subsampling yielded potentially useful data on patterns of micro-distribution within a small area, such information lies beyond our present capability for accurate correlation with "micro-habitat" parameters. Since the primary objective of this study was to survey generally environmental conditions and tardigrade distributions throughout an intertidal beach, data of this detailed nature was unusable. To derive a representative estimate of population parameters at each sample site later in this study (August, 1968 - May, 1969) I gathered single samples at each sample site. Ten cm^3 of sand were scraped as a thin layer of sediment from a 100 cm^3 area. This procedure averaged differences in micro-distribution within that area during the collecting procedure. Previously, the same averaged estimation resulted from calculations of mean representation of the composition of populations gathered in triplicate subsamples.

To analyze populations of tardigrades from triplicate subsamples (March, 1968 - July, 1968), I employed a variation of Uhlig's seawater-ice extraction technique (Uhlig, 1964, 1968). Subsamples were collected in open plastic cylinders (two cm diameter) which, when capped at one end, held ten cm^3 of sediment. In the laboratory, a piece of filtering screen (No. 6 plankton netting) was secured over the uncapped end of the cylinder. The cylinder was then inverted, the cap removed, and a second uncapped cylinder was taped end to end to the first. Crushed seawater-ice (about 32 $^o/oo$ salinity) was packed tightly into the top cylinder and the entire apparatus was suspended with the filtered end touching the surface of 20 cm^3 seawater in a 60 mm Petri dish. While periodically adjusting this apparatus to maintain only surface contact between the filetering cloth and seawater, I allowed one and one half hours for extraction.

Areas of high population density and proportional changes in population abundance from collection to collection were clearly indicated. A series of efficiency tests on this modified technique showed that of the total tardigrades extracted by this method and by subsequent rinses with $MgCl_2$ and formalin, only 20% were removed by the seawater-ice technique alone. Consequently application of these data to strictly quantitative analyses was unwarranted. Later (August, 1968 - May, 1969) I analyzed the structure and dynamics of populations by more accurate procedures. The initial survey indicated that three species of tardigrades were present in adequate numbers for continued study, Batillipes pennaki Marcus, 1946, B. bullacaudatus McGinty and Higgins, 1968, and Stygarctus granulatus n. sp. Since the three occurred within central portions of the total transect, the sampling pattern was modified. Station A was omitted since it never contained significant numbers of individuals of these three species. Likewise, animals found below 50 cm depth throughout the beach constituted an insignificant portion of the populations and consequently, sample sites at deepest levels of the remaining stations were abandoned also.

Extraction with $MgCl_2$ was substituted for the seawater-ice technique. Ten cm^3 of sediment in a 50 cm^3 beaker were flooded with 3.5% $MgCl_2$ in seawater solution. After standing for eight to ten minutes, the beaker was agitated thoroughly and the $MgCl_2$, containing the anesthitized meiofauna, was decanted into a 60 mm Petri dish. The sediment was rinsed three times with filtered seawater, and each rinse was decanted into the Petri dish. After the tardigrades had settled to the bottom and revived, they were counted at 50 X magnification.

In several samples subsequently flooded with 10% formalin and washed three times with seawater, no additional tardigrades were found. Direct counts of subsamples of sediment so treated failed to reveal additional specimens. This technique provided nearly complete extraction of interstitial tardigrades and since no damaged specimens were encountered following this treatment, losses due to abrasion were few.

Unfortunately, this technique also removed interstitial detritus, which was particularly plentiful in the portion of the transect occupied by S. granulatus. Since this was the most abundant tardigrade in the transect, and exhibited uniform density and size composition within a small area, a smaller sample volume provided adequate material for assessing its abundance and composition.

As a result, samples from sites deeper in the sand than 27 cm were subsampled in the laboratory. Sand from the ten cm^3 field sample was mixed in a Petri dish. From this a subsample of two cm^3 was removed and treated as described above. Replicate subsamples yielded highly comparable data. To standardize results from all of these procedures, results were recorded as the number of individuals of each species present in one cm^3 of sediment.

Examination and enumeration were made at 50 X with a dissecting microscope. Petri dishes containing extracted material were placed on a grid and living animals within each section of the grid were counted. Error from individuals of more mobile species (e.g., Batillipes pennaki or B. bullacaudatus) being counted more than once by virtue of their movements must be recognized. However, since this effect is random, it was probably equalled by animals moving in such a pattern as to be missed entirely. Error due to examination inefficiency because of debris in the counting dish may be important particularly for small animals. However, the use of 50 X for examination minimized this effect.

A correction factor (5 X) was applied to data collected between March, 1968 - July, 1968 to compensate for the estimated 20% efficiency of the modified seawater-ice technique. Totals in individual collections were expressed as a percent of the cumulative total. In this manner, changes in abundance of the three populations could be compared without regard for the actual numbers of animals in each population.

Sources of error in this study were many and severely restricted application of quantitative techniques of analysis. Although observed frequencies of individuals at least indicated minimal values of natural populations, sample sites separated from one another by a horizontal distance of two meters and a vertical distance of about seven cm can provide only limited data concerning localized populations of microscopic animals. In addition, inaccuracies in collecting, extracting, and examining have been discussed and are also important sources of error. Nevertheless, I have assumed that data from procedures described above incorporating corrections as indicated above, were comparable with one another at least. Interpretations of these data which are to follow were based on proportional abundance and composition without assigned quantitative dimensions.

Records of frequency of animals falling into arbitrary size classes were kept from May, 1968 - April, 1969. Length limits to each class were derived from arbitrary scale divisions of an ocular micrometer used at 50 X magnification (Table I). Rapid and erratic movements of B. pennaki prevented accurate measurements of individuals and consequently its size class frequencies were grouped to include classes 2 and 3, 4 and 5, and 6 and 7. Individual size classes could be distinguished in the other two species. Size class composition was determined at every collection and was expressed as the percentage of the total population collected falling into each class.

Using 430 X or 930 X oil immersion of a compound microscope to distinguish sexes by characters described in Part II, I observed sex ratios without dependence on mature gametes. Sex ratios of the population of S. granulatus were observed from November, 1969 - April, 1969 by recording sexes of the first 30 individuals encountered on re-examination of subsamples from the area of maximal density at each collection. Ratios express the number of females found for each male (i.e., one male : "X" females).

To survey the degree of homogeneity in populations within a small area, I collected 16 immediately adjacent ten cm^3 subsamples in a square pattern, four samples on each side. In this manner the entire population within the boundaries of this square (about ten cm per side) was collected in ten cm^3 units. Animals were extracted by the $MgCl_2$ technique and both gross numbers and size class composition were recorded.

These studies were applied to S. granulatus at Crane's Beach and a large population of B. mirus from nearby Wood Neck Beach in Woods Hole.

From collection data, a general analysis of co-occurrences between populations was derived. At each collection I recorded the percentage of the total of each population found co-occurring in subsamples with another species of tardigrade. Animals occurring at less than 0.5 animals per cm^3 of sand were considered present in insufficient numbers to warrant inclusion. In such low densities, animals occupying the comparatively spacious labyrinth of interstitial spaces are not likely to infringe directly upon one another.

RESULTS

In two years of sampling at Crane's Beach, I encountered seven species of marine tardigrades. In Part I, I discussed observations on several tardigrades from Crane's Beach, including descriptions of two new species. The species found include B. pennaki, B. bullacaudatus, B. mirus, B. dicrocerus n. sp., and S. granulatus. Single individuals of two additional species were encountered. Of these, Echiniscoides sigismundi (Schultze, 1867), associated with algae growing on barnacles, is assumed to be accidental in Crane's Beach. The second species was an unidentified heterotardigrade. Although B. mirus is abundant elsewhere in Woods Hole, too few individuals were encountered in the Crane's Beach transect to be considered further. B. pennaki, B. bullacaudatus, and S. granulatus (Fig. 4A, B, and D) were selected for detailed study. B. dicrocercus (Fig. 4C) will be discussed briefly but its abundance was never great enough to permit thorough study.

These four species of tardigrade inhabited nearly all of the transect. While distributions are widespread, distinct areas of maximum density were present in a consistent pattern for each population (Fig. 5). They partitioned the beach in depth and in elevation. The population of S. granulatus was usually the most abundant and remained at depths of 30 - 50 cm from the mid- to high-tidal region. The three Batillipes populations were more superficial in the sediment. B. pennaki ranked second in overall abundance and although it was widespread throughout the transect, population maxima occurred in the mid-tidal region. B. dicrocercus (not shown in Fig. 5) was never observed in summer collections, but in winter the population generally occupied a small area along the sand surface between the one-quarter and mid-tidal line. The general pattern of distribution of B. bullacaudatus showed low but consistent concentrations high along the beach above the Stygarctus population. At seaward stations this species was found at greater depth in the sand, slipping below the area occupied by B. pennaki.

Seasonal changes were observed in locations of population centers (Fig. 6). Roman numerals indicate the approximate locations of maximal concentrations of populations (averaged from bi-monthly collections) at alternate months, and dots represent locations during intervening months. As suggested by Renaud-Debyser (1956), shifts in these positions do not necessarily reflect a physical movement of individual animals, but rather represent a statistical difference in the location of maximal densities at each collection. Marked distributional changes occurred during coldest months when populations adjusted to extreme atmospheric conditions by moving from landward to more seaward locations (Fig. 6B, B. bullacaudatus), to greater depths in the sand (Fig. 6A, B. pennaki), or by remaining deep within the sand (Fig. 6C, S. granulatus). By January, maximal concentrations of the three populations were located to the seaward of mid-tide.

Widely ranging individuals of one species frequently were found in subsamples containing larger numbers of a second species. However more numerically extensive co-occurrences were limited to the periphery of distributional ranges. S. granulatus and B. bullacaudatus were found together in mid- to late-summer as both populations moved deeper into the sediment at station E (Fig. 6B and C). During the winter when B. bullacaudatus occurred much further toward the low tidal region, more than 60% of its population overlapped the distribution of S. granulatus. While these co-occurrences never involved more than 30% of the S. granulatus population, they included more than 50% of the population of B. bullacaudatus.

B. pennaki and B. bullacaudatus usually remained separated. However the incidence of co-occurrence increased as B. bullacaudatus shifted toward the low tide area at mid-summer and again at mid-winter. This overlap in distribution involved more than 40% of the *B. bullacaudatus* population but never included more than 10% of the *B. pennaki* population.

Co-occurrence between *S. granulatus* and *B. pennaki* was observed along the upper seaward portion of the *Stygarctus* population and deeper landward portions of the population overlapped from September through January when *S. granulatus*, moving seaward at deep levels in the sand, encountered the descending population of *B. pennaki* (Fig. 6A, C).

Changes in density of populations at each collection are shown in Fig. 7. In the three cases, the percentage of the cumulative total population occurring at any single collection was low (maximum of 13.0% of *B. bullacaudatus*; 9.0% of *B. pennaki*; and 7.25% of *S. granulatus*).

The three populations were least abundant during winter. *B. bullacaudatus* (Fig. 7B) reached maxima in April and May and again in August and September. Both *B. pennaki* and *S. granulatus* were abundant throughout the summer and fall (*B. pennaki* (Fig. 7A) from late June through early October and *S. granulatus* (Fig. 7C from early July through November). In addition, *B. pennaki* was abundant in April, 1968 but not in April, 1969.

Although I have discussed reasons limiting quantitative treatment of these data, records of maximal densities observed are valid as minimal estimates. Largest concentrations of both *Batillipes* populations occurred on 10

April 1968. _B_. _pennaki_ was found at 20.5 individuals per cm^3 of sediment near the surface of the sand at station D, while _B_. _bullacaudatus_ reached a density of 10.0 individuals per cm^3 at 14 cm depth at station F. On November 20, 1968, _S_. _granulatus_ at 32 cm depth at station F occurred at a concentration of 99.0 animals per cm^3 of sand.

The size class composition of the populations is shown in Fig. 8A – C. From these graphs, peaks in the abundance of each size class can be detected and are indicated in Fig. 9A – C. A possible progression through successive size classes is suggested by connecting lines in Fig. 9. While other relationships are inferable, this pattern suggesting a growth period of three to four months seems most consistent with abrupt variations in size composition over short periods (seen in Fig. 8A – C). Should growth progressions require a longer period, size composition measured in bi-monthly collections would change more gradually than shown in Fig. 8. A shorter growth period, however, should produce more frequent peaks in abundance of each size class than were observed.

In the population of _S_. _granulatus_ from Crane's Beach, the average sex ratio from November, 1968 through May, 1969 was nearly equal, 1,000 males : 1,054 females. Increased numbers of males were evident in the fall (up to 1 : 0.5) and an approximately equal dominance of females was recorded in spring (1 : 1.42).

An analysis of population distributional homogeneity in a small area is shown in Fig. 10A – D for _S_. _granulatus_ and B. mirus. The total number of indivuals (N) in each ten cm^3 subsample comprising a collection of 16 subsamples appears in the upper left hand corners of Fig. 10A and C. Size class data in this study are treated as the percentage of total populations gathered at each collection, so size class composition of each subsample is presented numerically in Fig. 10A and C and as composition by percent in Fig. 10B and D.

Since in each case the ratio of the variance to the mean is greater than one, both of these distributional patterns are positively contagious. The C_x coefficient of Green (1966) was applied to estimate the randomness of these distributions:

$$C_x = \frac{\frac{S^2}{m} - 1}{X - 1} .$$

For positively contagious distributions, C_x values range from 0 (= random) to +1 (=maximum positive contagion). C_x for the Stygarctus population was 0.00055, indicating nearly random distribution, while C_x for B. mirus population, 0.017, was less even but only weakly contagious. Mean densities ± one standard error of the mean were: S. granulatus, 34.13 ± 1.85 and for B. mirus, 53.63 ± 29.88.

DISCUSSION AND CONCLUSIONS

Marine interstitial tardigrades have been reported from relatively few locations throughout the world. Their small size, relatively strong thigmotaxis, and tendency to accumulate detritus over their bodies by adhesive secretions account for their apparent scarcity.

While morphological diversity in marine tardigrades is great, with nearly one half of the known species in mono- or di-typic genera, species diversity on a single beach apparently is low. DeZio (1964) reports three species of interstitial tardigrades occurring in several beaches along the Adriatic coast of Italy. Rao and Ganapti (1968) found four species in beaches on the Waltair coast of India, as did McGinty and Higgins (1968) at a beach on the Atlantic coast of North America. From studies in Bassin d'Arcachon on the Atlantic coast of France, Renaud-Debyser (1959a, 1963) listed seven species of interstitial tardigrades, of which six occurred on a single beach (1959a). Therefore seven species occurring at Crane's Beach, including one accidental species, would appear to represent ordinary diversity.

A pattern of "typical" composition of tardigrade species at a single beach in temperate regions may be derived from similarities in all of these studies. This assemblage includes a common species of _Stygarctus_ (present in all but the study of DeZio, 1964), extremely rare _Halechiniscus_ and two to four species of _Batillipes_, of which one or two are abundant and the remainder are in much lower density. The species composition of Crane's Beach was similar. _S_. _granulatus_ replaced _S_. _bradypus_ reported elsewhere. The single specimen of an unidentified heterotardigrade, tentatively a halechiniscid, corresponded to species of

Halechiniscus reported in other studies. Remaining tardigrades at Crane's Beach, all in the genus *Batillipes*, included abundant *B. pennaki*, less abundant *B. bullacaudatus*, uncommon *B. dicrocercus*, and a few individuals of *B. mirus*.

B. mirus or *B. pennaki* occur in nearly all beaches where the tardigrade fauna has been reported. Although neither species was recorded by Renaud-Debyser (1963) from coralline sand at Bimini in the Bahamas, I have located abundant *B. mirus* in coralline sand from another small Bahaman island. Fize (1957) reported a single species, *B. carnonensis*, from the coast of France. Rao and Ganapati (1968) also recorded *B. carnonensis* as the dominant *Batillipes* species in Indian beaches of the Waltair coast.

Scattered citations on tardigrades (see comprehensive bibliography in Renaud-Mornant and Pollock, 1970, in press) suggest that some interstitial species are broadly distributed throughout the world (e.g., *B. mirus*, *B. pennaki*, *S. bradypus*, *H. remanei*, *B. carnonensis*, and *O. belopus*). Others show restricted tropical distributions (e.g., *Archechiniscus marci*, *Parastygarctus higginsi*, and members of the genus *Florarctus*). Still others range along smaller coastal regions (e.g., *Arctinarctus doryphorus*, *B. bullacaudatus*, and *S. granulatus*). Most remaining interstitial species are restricted to the vicinity of the type locality.

Renaud-Debyser reported tardigrade distributions at beaches in Bassin d'Arcachon in France. At Camp Américaine (Renaud-Debyser, 1959a) in spring, *S. bradypus* occurred in a homogeneous population throughout the beach, rare *H. remanei* was found in the high tidal region at 20 - 40 cm depth, and three species of Batillipes partitioned the remainder of the beach. At Eyrac Beach (Renaud-Debyser, 1963), populations of B. mirus and S. bradypus were studied in detail. In April, S. bradypus concentrated at 20 - 40 cm depth at the three quarter tidal elevation. Although B. mirus occurred in greatest abundance in the same region of Eyrac Beach in April, by May this population was most dense within 20 cm of the sand surface lower on the beach. Since her faunal survey followed an unusually cold winter, early spring distributions may not be representative.

Distribution of S. granulatus from Crane's Beach and S. bradypus from Eyrac Beach and the Waltair coast of India (Rao and Ganapati, 1968) is similar, with concentrations deep in the upper one half of the beach. However, at Eyrac, maximal densities of S. bradypus occur near high tidal levels, while S. granulatus at Crane's Beach is most abundant between three quarter tidal and mid-tidal levels. Rao and Ganapati (1968) found maximal densities of S. bradypus deep in sand at mid-tide.

Renaud-Debyser (1959a) recorded populations of B. pennaki deep in the sand along the level of the low tidal water table. DeZio and Grimaldi (1964b), studying atidal Cozze Beach on the Adriatic coast of Italy, indicated that B. pennaki occurred at increasing depth in sand with increased distance from the water line. Maximal numbers were found at 20 - 30 cm depth five to eight meters from the water line. The distribution of B. pennaki from Crane's Beach (Fig. 5) was more similar to the pattern shown for *B. mirus* at Eyrac Beach (Renaud-Debyser, 1963).

B. bullacaudatus and *B. dicrocercus* occupied peripheral locations at Crane's Beach. *B. bullacaudatus* was found usually in the upper portion of the beach (Fig. 5), as in the type locality (McGinty and Higgins, 1968), although regular small numbers occurred in samples lower on the beach as well. *B. dicrocercus* was limited to the upper 20 cm of sand in the seaward portion of Crane's Beach. These distributions were similar to tardigrade repartition at Camp Américaine, Bassin d'Arcachon (Renaud-Debyser, 1959a), where *B. littoralis* Renaud-Debyser, 1959 was restricted to samples high on the beach and *B. phreaticus* Renaud-Debyser, 1959 occurred in samples from the low tidal region. Although this sort of characterization is difficult to apply to atidal beaches, the occurrence of *B. annulatus* DeZio, 1962 to the seaward of *B. pennaki* may represent a similar phenomenon (DeZio, 1965).

From these observations it appears that tardigrades inhabit the region from one quarter tidal level to above the high tidal line, and from the sand surface to the low tidal water table or "nappe phreatique". However, species are apparently most typical in specific areas within the beach. Fig. 11 summarizes published reports of the location within an intertidal beach generally occupied by several interstitial tardigrades. Differences in beach location reflect specific distinctions in ecological and biological responses, suggesting a relatively low degree of niche diversity.

Seasonal changes in locations of maximal density were described for *B. mirus* and *S. bradypus* over six months at Eyrac Beach, Bassin d'Arcachon (Renaud-Debyser, 1963) and through a full year for a population of *S. bradypus* (Renaud-Debyser, 1956) and *B. pennaki* (DeZio and Grimaldi, 1964b). From a March-April location at 20 cm depth in the high tidal to three quarter tidal region of Eyrac Beach, *B. mirus* shifted toward the sand surface in the mid-tidal area by mid-summer. During the same time period, *S. bradypus* remained within the three quarter tidal to high tidal region. In winter however, Renaud-Debyser (1956) indicated that the latter population shifted slightly seaward. DeZio and Grimaldi (1964b) found that *B. pennaki* drew nearer to the water line during hottest months but moved shoreward during coldest months. In addition they report that *B. pennaki* performed daily vertical migrations which they feel were related to increased evaporation and elevated temperatures during late afternoon when the population was found deepest in sand. Renaud-Debyser (1963) attributed a semi-daily shift of 15 cm in the location of the *S. bradypus* population at Eyrac Beach largely to impassive transport in circulating tidal water.

Tardigrades show three types of distributional responses to seasonal changes in the environment (Fig. 6A - C). *S. granulatus* and *S. bradypus* remained deep in sand where temperature changes are minimal, and both species shifted to seaward in winter. A vertical shift in the *B. pennaki* population at Crane's Beach resulted in animals close to the sand surface in summer and at greater depths in winter. In an area of limited temperature variation and absence of tides, B. pennaki drew nearer the water line in summer and thereby closer to the sand surface, but further to the landward and deeper in winter (DeZio and Grimaldi, 1964b). While shifts in the population of B. pennaki in a tidal beach were essentially vertical, B. bullacaudatus ranged parallel to the sand surface along the high to low tidal axis of the beach, moving closest to the water line in January, farthest away in fall and intermediate in summer.

Co-occurrences recorded between interstitial tardigrades are difficult to interpret. DeZio's (1965) quantitative observations on distribution of B. pennaki and B. annulatus at an Adriatic beach reports similar results to those found here. Some distributional overlap occurs between species, but in general, species remain separated. Apparently intrageneric co-occurrence is lower than intergeneric co-occurrence. This fact may reflect an active form of competitive avoidance, species differences in ecological preferences or tolerances, or differences in food preferences and its distribution.

Occurrence of tardigrades, especially young individuals and egg-bearing females, in nearly every collection demonstrated that year-round reproduction existed, as is typical of interstitial meiofauna generally (Swedmark, 1959). Amidst this continuing availability of tardigrades, spring and fall maxima in populations were reported by Renaud-Debyser (1956), DeZio and Grimaldi (1964b), and McGinty and Higgins (1968). Renaud-Debyser (1956) found maximal densities of S. bradypus at Arcachon in May through June and again during the winter. Lowest numbers occurred in March and April. B. mirus at Arcachon was far less abundant but showed maximal frequency in May. Populations of B. pennaki in the Adriatic were most abundant in November and once again in May (DeZio and Grimaldi, 1964b).

At Crane's Beach, spring and fall periods of maximal frequency occurred in numbers of B. bullacaudatus but not in the other two populations. Both B. pennaki and S. granulatus were abundant throughout the summer and fall. Lowest numbers in all populations occurred during the winter. Possibly a colder climate at Woods Hole accounts for the absence of maxima in spring and fall in thw two populations found lower and deeper on the beach. Farther south on the Atlantic coast at York River, Virginia, McGinty and Higgins (1968) reported fall and spring maxima in interstitial tardigrade abundance.

Changes in population density can be abrupt. Renaud-Debyser (1956) reported an increase in the population of S. bradypus from almost no individuals per collection to a total of 700 per collection in about three weeks. In one case, DeZio and Grimaldi (1964b) recorded an increase in the abundance of B. pennaki from 125 animals to 975 animals in a collection only three days later.

Changes in population density of species at Crane's Beach were less dramatic (Fig. 7). A decreasing incidence of abrupt changes in population numbers in the following sequence, B. bullacaudatus, B. pennaki, and S. granulatus, coincides with an increasing degree of environmental stability (i.e., a decreased range of parameter variation). Hence strongly fluctuating numbers within populations of tardigrades may result from opportunistic population growth during favorable periods in a variable environment. Greater population stability of S. granulatus may be related to greater environmental stability deep within the beach (see Part III).

Measurements of maximal concentration may indicate comparative species abundance, patterns of food distribution, or reproductive behavior. Interstitial tardigrades at Crane's Beach formed comparatively dense groups. I have compared their abundance with quantitative data from other studies in Table II.

Several investigators have considered size composition in populations of fresh- and moss-water dwelling tardigrades to determine the number of instars produced by various species. Marcus (1929), Higgins (1959), Ramazzotti (1962), and Franceschi Crippa and Lattes (1967) estimated numbers of instars ranging from six to twelve, perhaps differing among species and with environmental conditions (Ramazzotti, 1962). McGinty and Higgins (1968) discussed morphological changes accompanying growth in B. mirus but did not examine size composition of natural populations.

Franceschi et al (1962-63) observed the size class structure of a population of the moss-water dwelling tardigrade, Macrobiotus hufelandii Schultze from December, 1962 through March, 1963. They divided members of the population into four size classes and expressed the contribution of each as a percentage of the total population collected at each of several samples per month (Fig. 8D).

A comparison between their findings and data on tardigrade populations from Crane's Beach shows several similarities. In both cases, middle sized animals (including sexually mature individuals) dominated every collection, while largest and smallest sizes were least abundant. Although scarcity of larger size animals probably represents higher mortality in that group, low numbers in smallest sizes may reflect a selective sampling error against small animals. More likely however, it indicates more rapid progression into middle size classes than out of them.

Franceschi et al (1962-63) recorded an overall increase in the proportion of smaller size classes in spring as compared to winter. However at Crane's Beach, the highest proportion of small B. pennaki were found in mid-summer, smallest B. bullacaudatus in the fall, and smallest S. granulatus in mid-winter and early spring. The reason for these differences is not clear, although presumably it relates to species differences in environmental responses as well as to local conditions surrounding each population and collection.

The occurrences of peaks in frequency of each size class from data of Franceschi et al (1962-63, p. 85, Fig. 5) are indicated in Fig. 9D. Peaks connected in the growth progression suggested by Franceschi et al, produce a pattern similar to that shown for tardigrades from Crane's Beach (Fig. 9A - C). In contrast to previous estimations of the active life-span of moss-water dwelling species (e.g., 15 - 30 months, Ramazzotti, 1962), results of Franceschi et al (1962-63) and the present study suggest that life-spans may be of much shorter duration (i.e., from 2¼ - 4 months).

Rudescu (1964) calculated the ratio of females to males in several species of fresh- and moss-water dwelling tardigrades from Rumania. He estimated that the ratio of males : females is about 1 : 10 - 15 for most species of _Hypsibius_; 1 : 20 for species of _Macrobiotus_; and 1 : 25 in the genus _Milnesium_. While he did not suggest estimates of sex ratio for marine species, he mentioned that male _B. mirus_ were most abundant during June and July. The ratio of _S. granulatus_ at Crane's Beach is nearly equal, with males slightly dominant in fall and females in spring.

Recently Jansson (1968b) reviewed the few attempts to correlate field distributions of specific interstitial meiofauna with environmental parameters. Among those considered to be potentially significant are oxygen availability, grain size, detritus, water content, salinity, and temperature.

Undoubtedly meiofauna, including tardigrades, possess physiological and morphological limits of tolerance to extremes of each of these parameters. However the tolerances of interstitial tardigrades are broad. They were found in beaches of homogeneous fine sand (0.25 mm diameter, Fenchel, Jansson, and Thun, 1967) and also in coarse sand as in Crane's Beach where mean diameter exceeded one mm. I have recovered living tardigrades from samples at 30°C as well as from frozen sand at - 5°C, and from frozen seawater at - 8°C in the laboratory. While their presence in full strength seawater (35 °/oo) has been well documented (e.g., Renaud-Debyser, 1963), Riemann

(1966) found species of Batillipes in portions of the Elbe Estuary in less than 5 ^{o}/oo salinity.

Seasonal and tidal variations in environmental parameters at Crane's Beach were monitored concurrently with this study and were discussed in Part III. General zones of similarity in parameters were distinguished by applying Salvat's (1964, 1967) characterizations of surface areas on fine sand beaches to surface and depth related areas of similarity within the transect at Crane's Beach. Table III and Fig. 12 summarize general environmental characteristics from this study.

The area of Crane's Beach inhabited by interstitial tardigrades was limited to the Zone of Retention and the Zone of Resurgence by three important parameters. As meiobenthic animals, tardigrades are restricted in their activities to contact with substratum. Since their larval development is direct, their presence in seawater overlying beach sand must be accidental. To the landward, they are limited by lack of adequate interstitial water in the Zones of Extensive Drying and of Dry Sand. Finally, tardigrade distribution is confined to areas where sufficient water circulation permits oxygenation of interstitial water, i.e., the region above the Zone of Saturation.

Within broad limits of Zones of Retention and Resurgence, however, specific differences in distribution are much more difficult to explain. Perhaps subsequent determinations of preference ranges within tolerable extremes of these parameters will help to explain distributions.

As the only dramatically changing parameter on a seasonal basis, temperature must have been an important influence on tardigrade distributional shifts recorded in winter at Crane's Beach. Although Enckell (1968) feels that daily temperature variations probably exert very little influence on microdistribution of interstitial species, animals living in surface areas (including the species of Batillipes at Crane's Beach) must withstand regular and greater temperature variations than deeper dwelling species, such as Stygarctus, do. On the other hand, deeper sediments are more apt to become anaerobic from stagnation during saturation than are surface areas.

While salinity gradients may be strong and important in the ecology of atidal beaches (Jansson, 1967c, 1968b), at Crane's Beach variations were slight (Part III). As a result, the influence of salinity on distributions of tardigrades at Crane's Beach must have been weak.

Sand grain size and sorting are important determinants of pore spaces, which may be limiting to larger interstitial animals relying on a thrashing or "sliding" type of locomotion (Jansson, 1967b; Wallace, 1958; and Wieser, 1959). However, small body size and a "ventral creeping" locomotion in interstitial tardigrades is much less reliant upon pore sizes directly (Renaud-Debyser, 1963; Jansson, 1967b).

Interstitial tardigrades have been recorded from subtidal areas at constant saturation of pore spaces by seawater.

In atidal beaches, DeZio and Grimaldi (1964b) and Fenchel, Jansson, and Thun (1967) found that most tardigrades of the genus <u>Batillipes</u> occurred in sand of 50 - 75% saturation by water, based on Fenchel's et al (1967) calculation that sediment with water content equal to 20% of the sample weight is saturated. Some surface areas at Crane's Beach, however, experienced tidal fluctuations in water content from saturation at high tide to less than 10% saturation at low tide (Part III). While it is possible that tardigrades exposed to extensive variations in water content do not remain in an active state throughout the entire period, they survive exposure in areas which lose up to 90% saturation with each ebb tide. The suggestion that 10% saturation limits meiofaunal habitability (Enckell, 1968; Pennak, 1940) applies to tardigrades at Crane's Beach as well.

As I have suggested in Part III, extremes of parameters measured at day-time low tidal exposure represent a brief portion of each twelve hour tidal cycle. Considering the much milder ranges of variations in parameters existing throughout the remainder of the tidal cycle, the importance of momentary low tidal conditions in shaping meiofaunal responses may be overestimated easily. Comparison between the low tidal temperature and ranges in water content selected by each population of tardigrades (Fig. 13 and 14) reveals little difference in the chosen extremes of these two variables. <u>B</u>. <u>pennaki</u> occurred more frequently at slightly higher temperature than did <u>B</u>. <u>bullacaudatus</u> and <u>S</u>. <u>granulatus</u>, while <u>S</u>. <u>granula-</u>

tus was found in areas of somewhat higher water content than were the species of *Batillipes*.

Time limitations permitted only a superficial examination of the role of biotic factors in determining distributions of tardigrades at Crane's Beach. Factors such as nutritional requirements, competition, and predation all are likely to be important considerations.

The specific food preferred by tardigrades at Crane's Beach was not determined, although a puncture-suction type of feeding on diatoms and other plant materials has been described for similar marine forms (Marcus, 1927). However, their feeding apparatus and gut contents are clues to similarities in feeding habits. Mouth parts (Fig. 15A and B) include a rounded mouth connected by a tubular canal to a bulbous, muscular pharynx. Flanking the canal are stylets which can be extruded through the mouth. In species of *Batillipes* (Fig. 15A), stylets are stout and strong and include accessory members called stylet supports. Such an apparatus is capable of powerful thrusts extending a short distance through the mouth. In *Stygarctus* however (Fig. 15B), stylets are long, thin, and stylets supports are absent. They are not adapted to powerful jabs although they can be extruded up to one half their length. The canal of *Stygarctus* is much longer and narrower than that of *Batillipes*. With such dissimilar feeding apparatus, *Stygarctus* must feed in a manner very different from *Batillipes*, reducing the chance of direct competition between individuals of these two genera. On the other hand, similarity in buccal apparatus of Batillipes species suggests that their methods of feeding are similar.

Specific differences in gut contents among the species of Batillipes reflect possible differences in food materials selected. B. pennaki, B. dicrocercus, and B. mirus commonly possessed contents ranging in color from yellow-orange to dark brown. The gut of B. bullacaudatus however, always ranged from light yellow to greenish --- never orange or brown. Some difference in food selection or digestion may exist between B. bullacaudatus and the other species.

Similarities in feeding parts and gut contents, as well as in general distributional patterns, suggest a greater likelihood that B. pennaki, B. dicrocercus, and B. mirus compete. Such a phenomenon would help to explain the fact that B. pennaki and B. mirus are both abundant and widespread geographically but seldom co-occur in large numbers on a single beach. Also such possible competition might explain why B. dicrocercus is most abundant only during winter when B. pennaki is least abundant.

Until more is known about feeding by interstitial tardigrades, it is impossible to predict the likely degree of competition with other members of the meiofauna. Several species of nematodes, similarly equipped with strong stylets and a muscular pharynx, represent the most likely compeditors. Indeed, DeZio and Grimaldi (1964b) suggested possible competition between tardigrades and nematodes at Cozze Beach in Italy.

In two years of sampling at Crane's Beach, I encountered almost no macrofauna (i.e., animals over two mm in length). Feeding on tardigrades must be limited primarily to meiofaunal predators since nearly all populations of tardigrades remained too deep in sediment to be exposed to surface feeding macrofauna. Most likely meiofaunal candidates in this poorly studied feeding category include larger Protozoa, Turbellaria, Nematoda, Rotifera, harpacticoid Copepoda, and possibly other Tardigrada.

Broadly tolerant interstitial tardigrades are capable of colonizing large portions of porous tidal beaches. While niche diversity is lower for this group than for several others (e.g., Protozoa, Nematoda, Gastrotricha), year-round abundance of populations indicates their success as meiofaunal inhabitants. With indications that resistance to most environmental parameters individually is great, presumably a combination of biotic and interrelated abiotic influences are responsible for consistant distinctions in distributional patterns of species at Crane's Beach. For example, among the parameters reviewed here, seasonal changes in temperature produce alterations in distribution and possibly in growth of populations. Co-occurrences and similarities in feeding capability suggest that intrageneric competition may be responsible for some modification in patterns. While understanding of interstitial ecology is embryonic, thorough biological studies of individual taxa eventually will provide data by which the importance of environmental parameters can be discerned.

Inevitably, an introductory study uncovers more questions than it answers. While that is true of this thesis as well, several contributions have been made to the field of interstitial biology. I have explored the role of important parameters of the intertidal, porous beach environment, accumulated considerable morphological, anatomical and ecological information regarding the Tardigrada, and described basic elements of population structure and dynamics of this abundant meiofaunal group.

TABLE I. LENGTH EQUIVALENTS FOR ARBITRARY SIZE CLASSES.

Size class lower limit (in micrometer units)	Actual length (in µm)
2.0	56.0
3.0	84.0
4.0	112.0
5.0	140.0
6.0	168.0
7.0	196.0
8.0	224.0
9.0	252.0

TABLE II. COMPARISON OF MAXIMUM CONCENTRATIONS OF CRANE'S BEACH TARDIGRADA WITH QUANTITATIVE DATA IN THE LITERATURE.

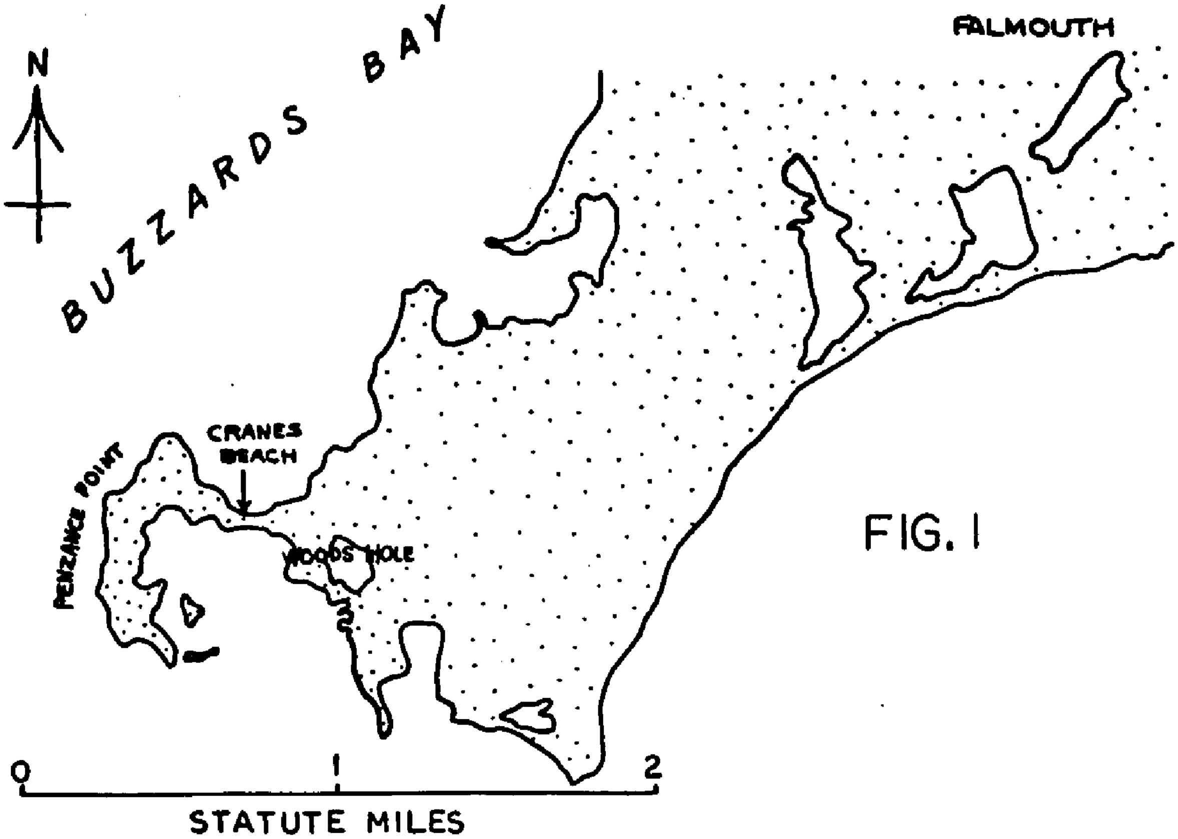
Species	Concentration (individuals/ cm^3)	Reference
Stygarctus bradypus	5.0	Renaud-Debyser, 1963
Stygarctus bradypus	1.0	Renaud-Debyser, 1959a
Stygarctus bradypus	0.1 - 1.0	Renaud-Debyser, 1959b
Stygarctus granulatus	99.0	Present study
Batillipes mirus	225.0	King, 1962
Batillipes mirus	30.0	McGinty and Higgins, 1968
Batillipes mirus	4.75	Renaud-Mornant and Serène, 1967
Batillipes pennaki	40.0	DeZio and Grimaldi, 1964b
Batillipes pennaki	20.5	Present study
Batillipes pennaki	0.2	Renaud-Debyser, 1959a
Batillipes bullacaudatus	10.0	Present study
Batillipes phreaticus	0.4	Renaud-Debyser, 1959a
Batillipes littoralis	0.2	Renaud-Debyser, 1959a

TABLE III. ENVIRONMENTAL ZONES AT CRANE'S BEACH (From Part III).

ZONE	WATER CONTENT	TEMPERATURE	SALINITY	OXYGEN
Zone of Dry Sand	Almost never gets seawater. Affected by precipitation but usually very low.	Highly variable due to strong atmosphere influence. High in summer, low in winter.	Locally extreme through evaporation and/or precipitation.	Well aerated always.
Zone of Extensive Drying	Extensive periods of drying. Low & irregular. Capillary water usually lost. Hygroscopic water retained.	Wide variations.	Local but infrequent lowering from fresh water sources.	Good aeration always.
Zone of Retention: Upper	Tidally or regularly varying; 100-15% saturation. Some capillary water lost at low tide.	Can be great in summertime low tides.	Little variability.	Good aeration.
Zone of Retention: Lower	Tidally or regularly varying; 100-40% saturation. Gravitational water lost at low tide.	Little tidal variation.	Little variability.	Good aeration.
Zone of Resurgence	High saturation. Some gravitational water lost at spring low tides.	Nearly constant. Follows gradual seasonal cycle.	Locally variable to landward due to ground water sources.	Good aeration with water flow and in seaward portions where waves spread oxygen.
Zone of Saturation	Saturated; no variation.	No tidal variability.	Apt to be variable due to ground water.	Usually anaerobic.

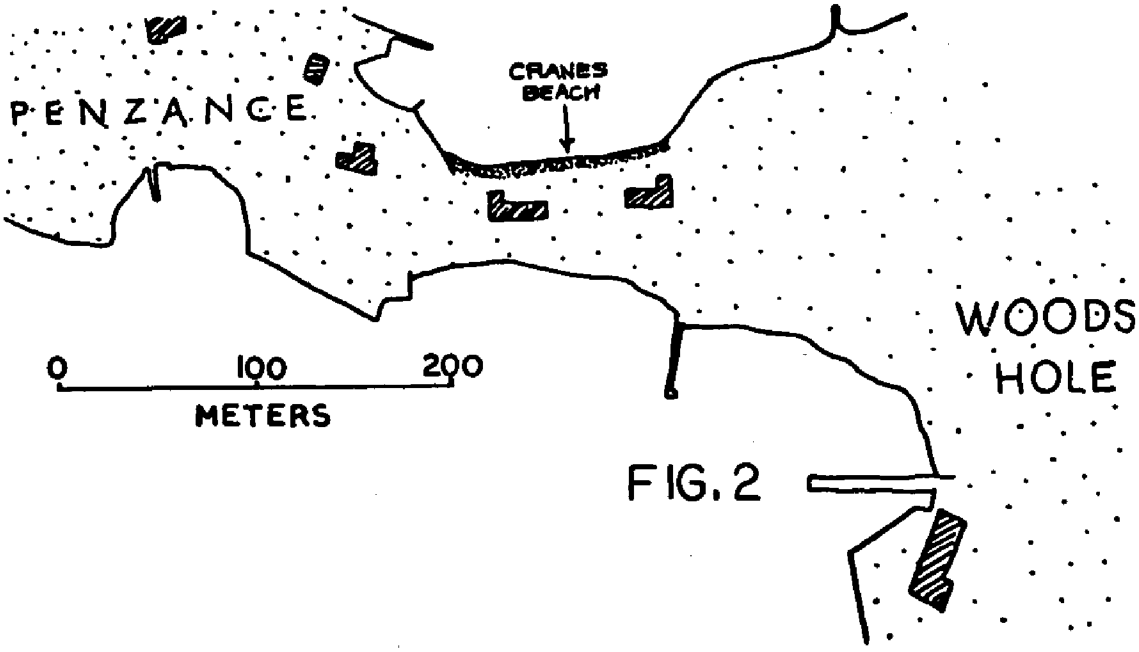
FIG. 1. The region surrounding Woods Hole, Massachusetts.

FIG. 2. Location of Crane's Beach on Penzance Point, Woods Hole, Massachusetts.



N
BUZZARDS BAY
FALMOUTH
CRANES BEACH
PENZANCE POINT
WOODS HOLE
0
1
2
STATUTE MILES

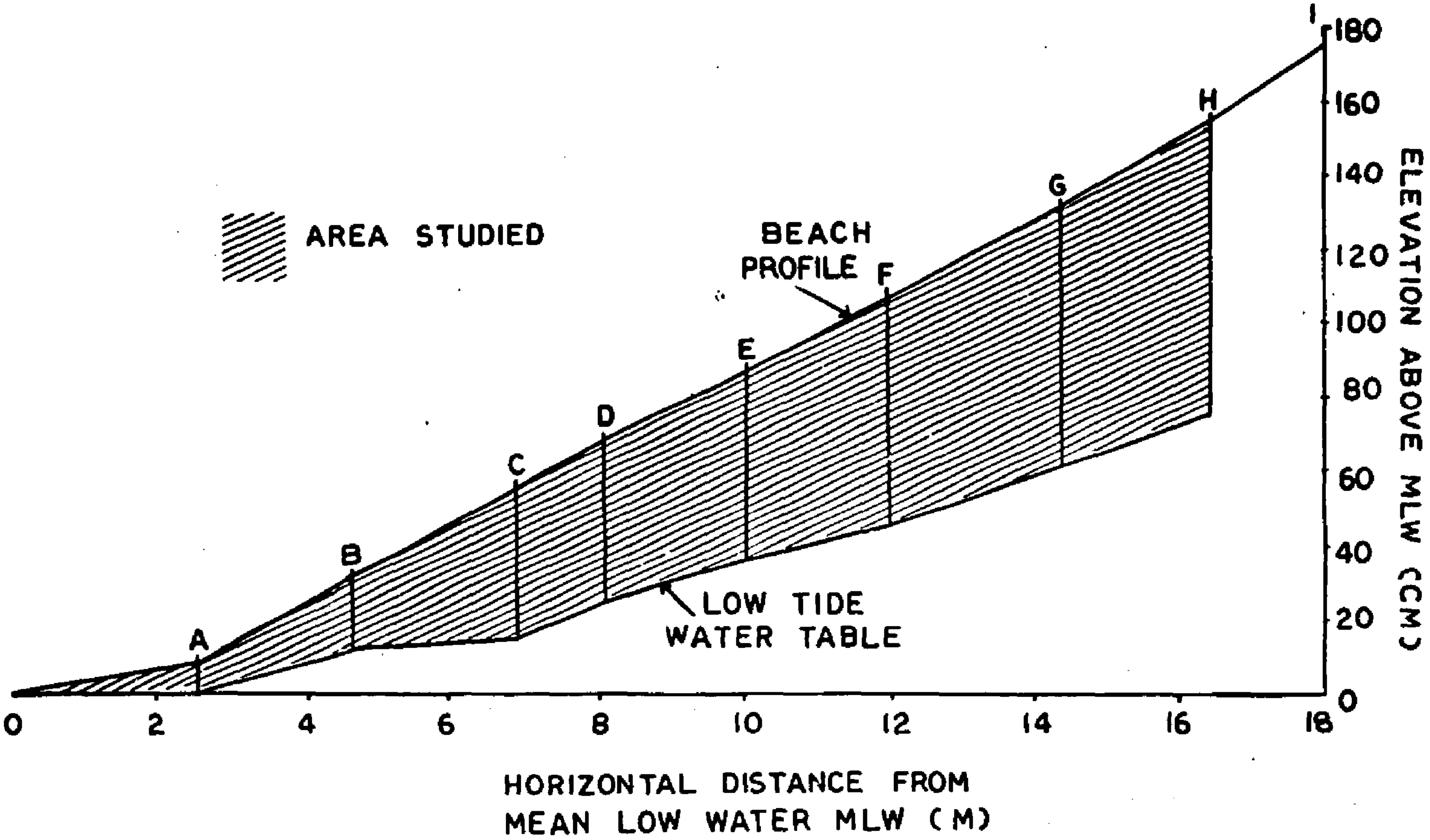
FIG. 1



PENZANCE
CRANES BEACH
WOODS HOLE
0
100
200
METERS

FIG. 2

FIG. 3. Crane's Beach profile showing study transect, including stations A - 1.



▨ AREA STUDIED
BEACH PROFILE
LOW TIDE WATER TABLE
A
B
C
D
E
F
G
H
I
0
20
40
60
80
100
120
140
160
180
ELEVATION ABOVE MLW (CM)
0
2
4
6
8
10
12
14
16
18
HORIZONTAL DISTANCE FROM MEAN LOW WATER MLW (M)

FIG. 3

FIG. 4. Interstitial Tardigrada from Crane's Beach.

A. *Batillipes pennaki* Marcus, 1946.

B. *Batillipes bullacaudatus* McGinty and Higgins, 1968.

C. *Batillipes dicrocercus* n. sp., (Part I).

D. *Stygarctus granulatus* n. sp., (Part I).

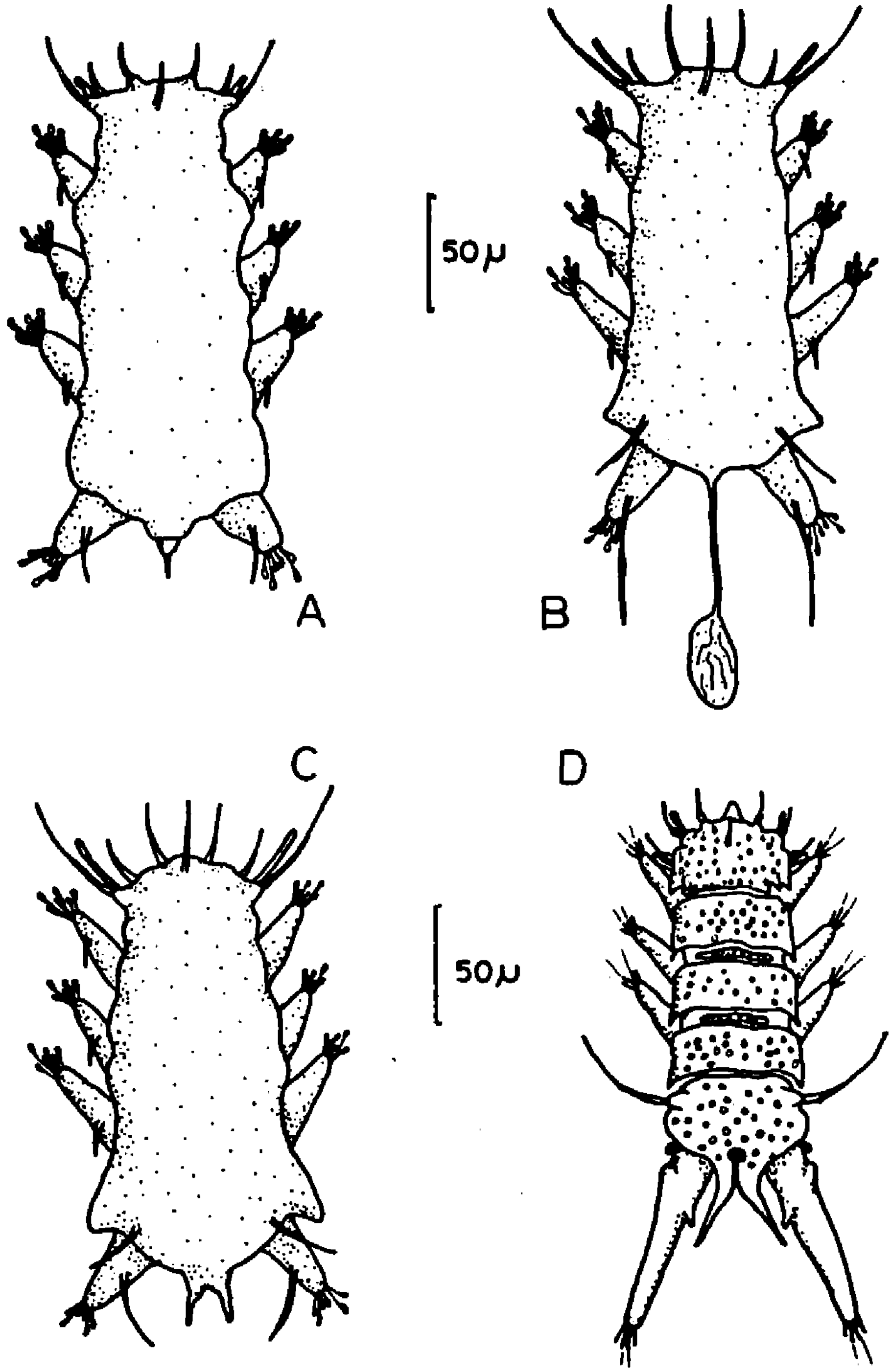


FIG. 4

FIG. 5. General distributional patterns of tardigrades at Crane's Beach.

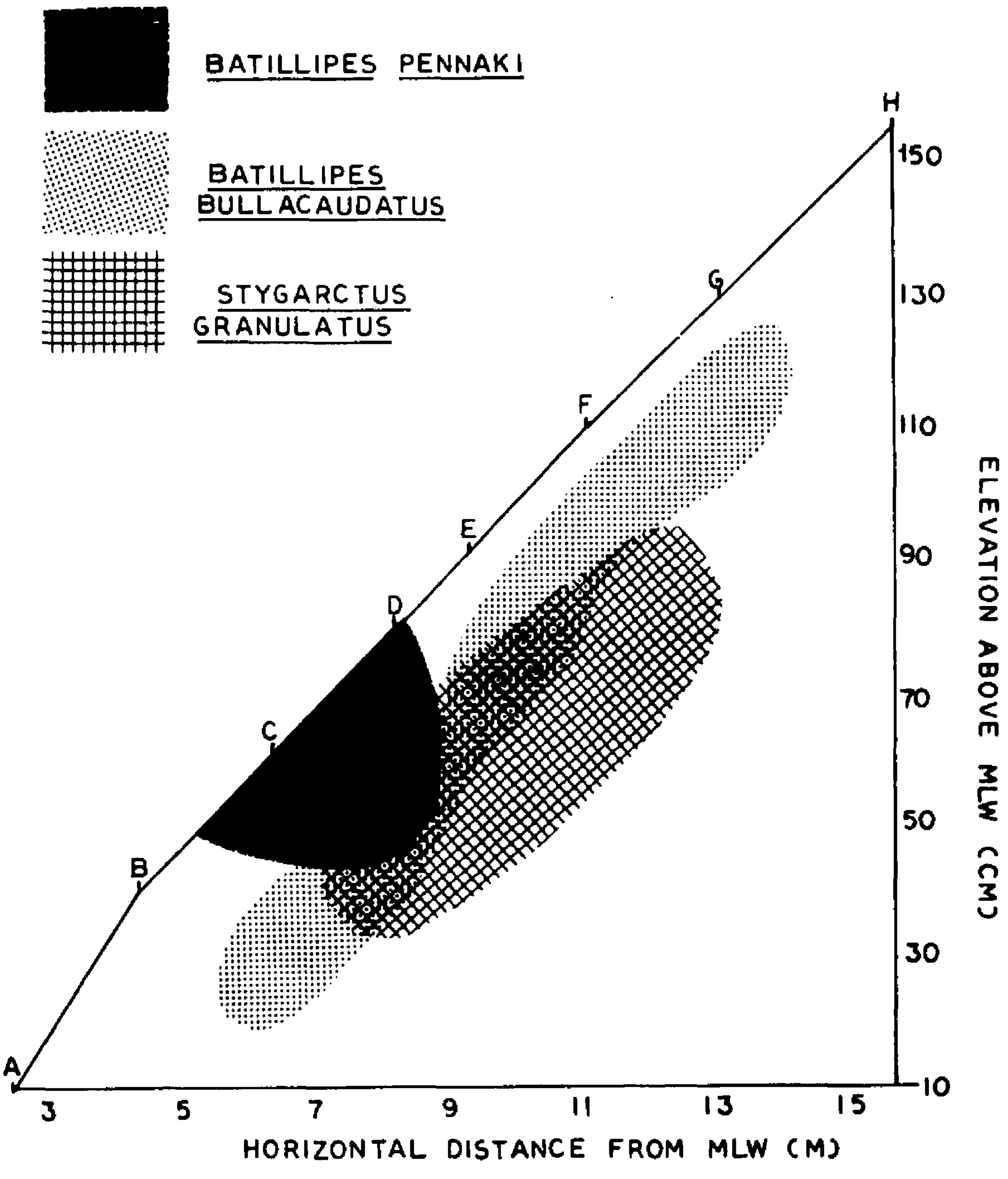

BATILLIPES PENNAKI
BATILLIPES BULLACAUDATUS
STYGARCTUS GRANULATUS
A
B
C
D
E
F
G
H
150
130
110
90
70
50
30
10
ELEVATION ABOVE MLW (CM)
3
5
7
9
11
13
15
HORIZONTAL DISTANCE FROM MLW (M)

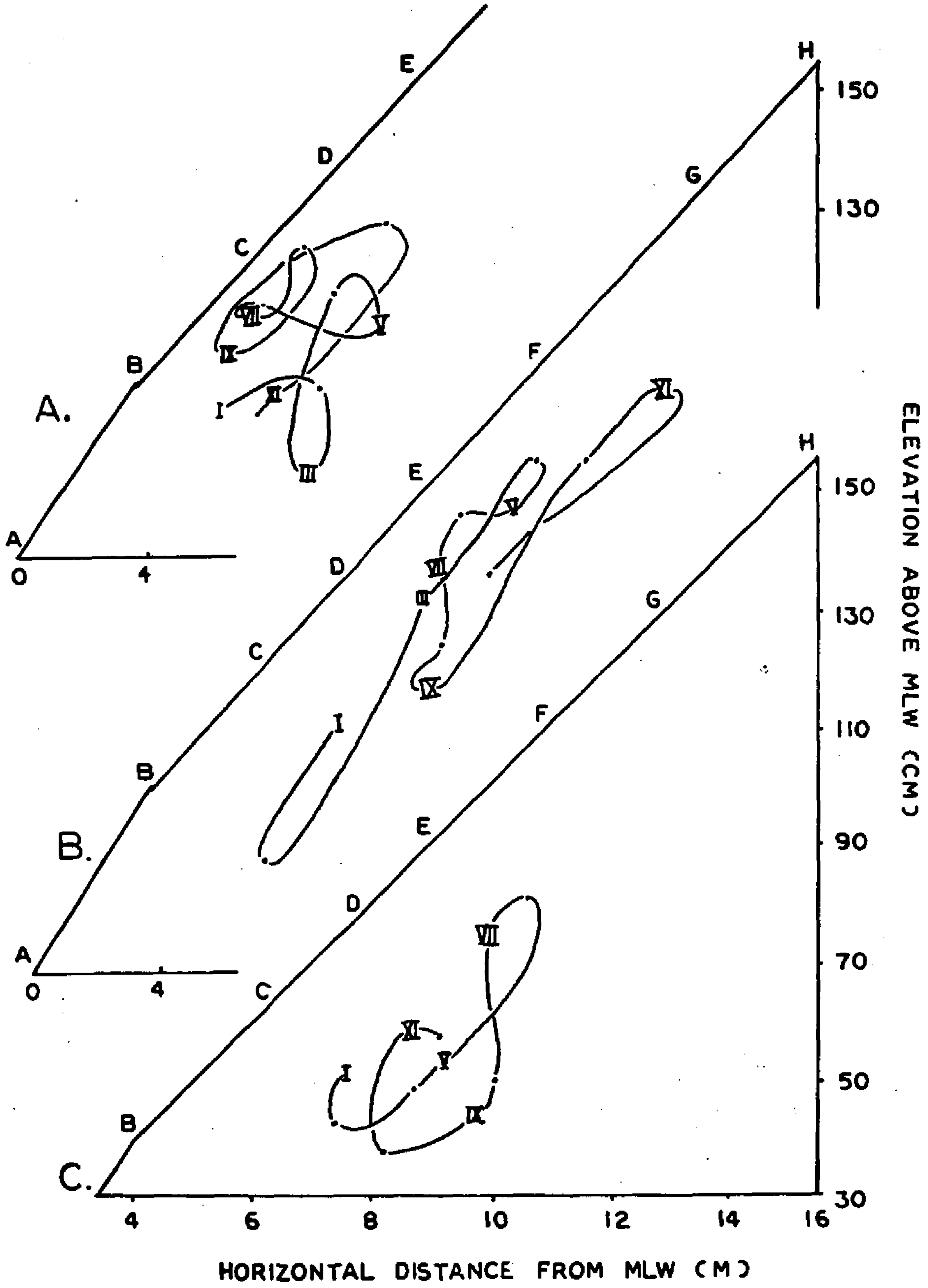
FIG. 5

FIG. 6. Seasonal shifts in areas of maximal population density, 1968 - 1969. Locations in alternate months indicated by Roman numerals; intervening months by dots.

A. *Batillipes pennaki*.

B. *Batillipes bullacaudatus*.

C. *Stygarctus granulatus*.



A.
B.
C.
A
B
C
D
E
F
G
H
0
4
I
XI
III
V
VII
IX
150
130
110
90
70
50
30
4
6
8
10
12
14
16
ELEVATION ABOVE MLW (CM)
HORIZONTAL DISTANCE FROM MLW (M)

FIG. 6

FIG. 7. Patterns of annual change in population abundance, Crane's Beach, 1968 - 1969.

A. *Batillipes pennaki*.

B. *Batillipes bullacaudatus*.

C. *Stygarctus granulatus*.

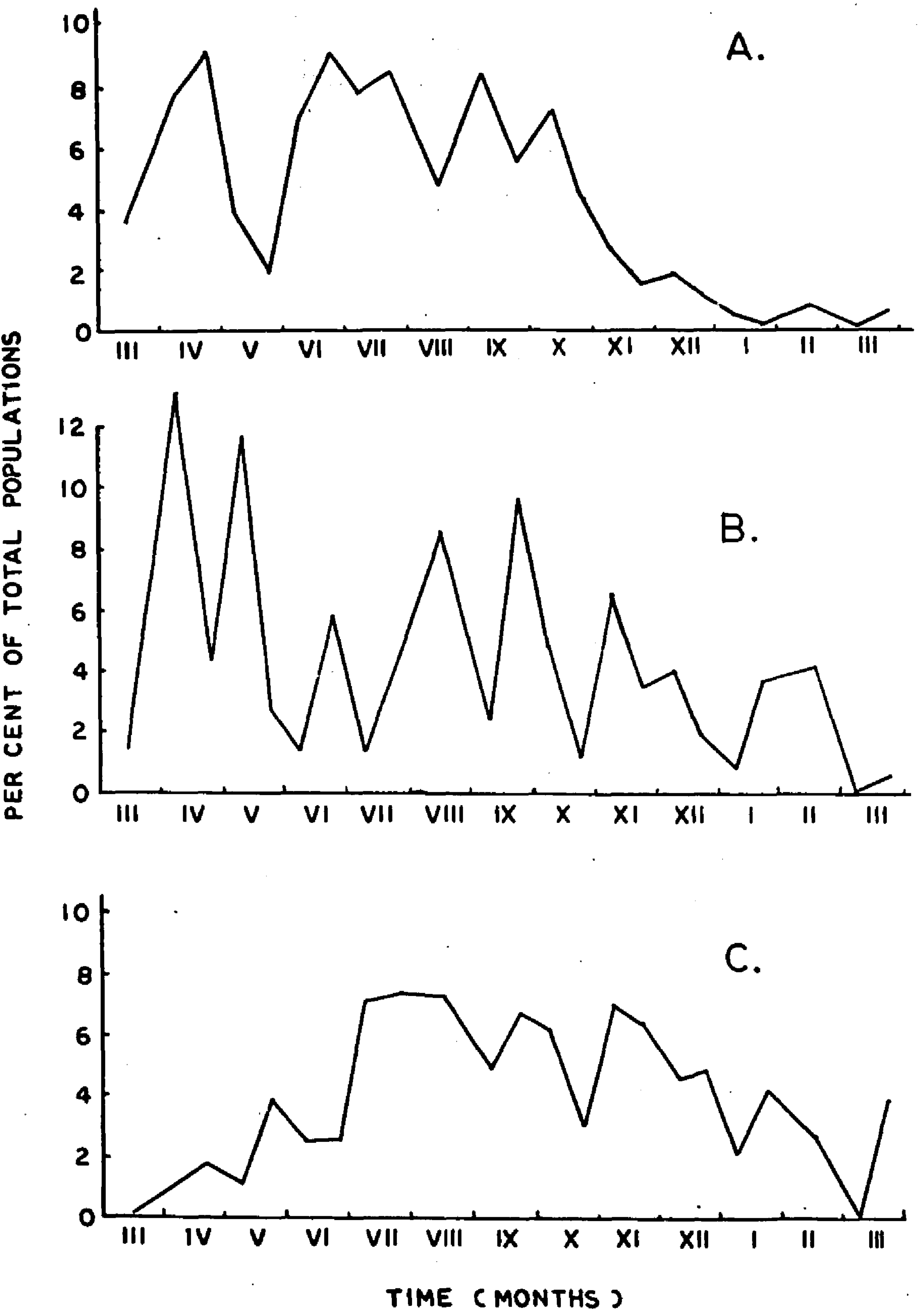

A.
B.
C.
PER CENT OF TOTAL POPULATIONS
0
2
4
6
8
10
12
III
IV
V
VI
VII
VIII
IX
X
XI
XII
I
II
III
TIME (MONTHS)

FIG. 7

FIG. 8. Changes in composition of size classes of tardigrades at Crane's Beach, 1968 - 1969 (A - C) and from data of Franceschi et al, 1962 - 1963 (D).

A. *Batillipes pennaki*.

B. *Batillipes bullacaudatus*.

C. *Stygarctus granulatus*.

D. *Macrobiotus hufelandii* Schultze.

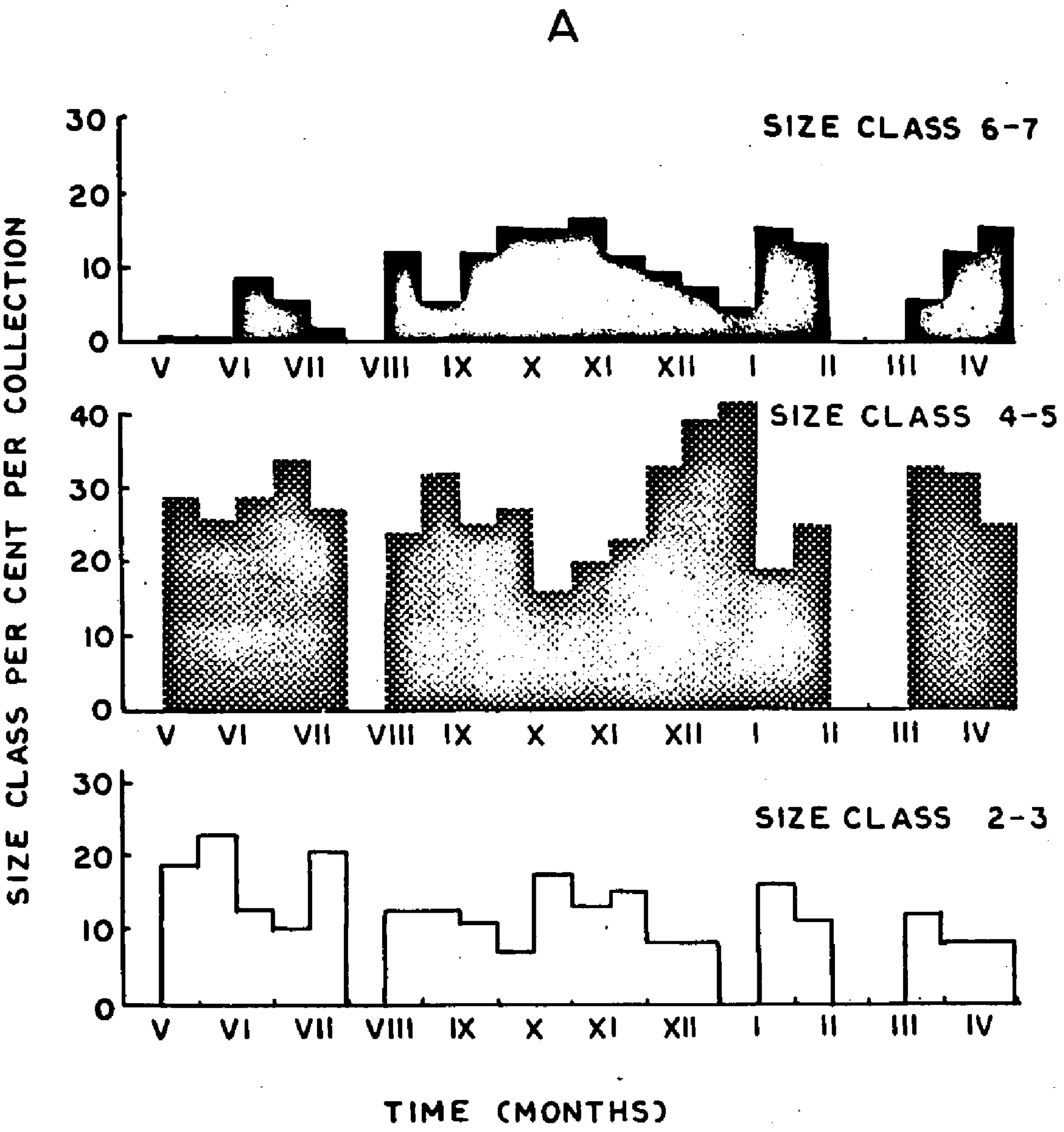

A
SIZE CLASS 6-7
SIZE CLASS 4-5
SIZE CLASS 2-3
SIZE CLASS PER CENT PER COLLECTION
30
20
10
0
40
V
VI
VII
VIII
IX
X
XI
XII
I
II
III
IV
TIME (MONTHS)

FIG. 8

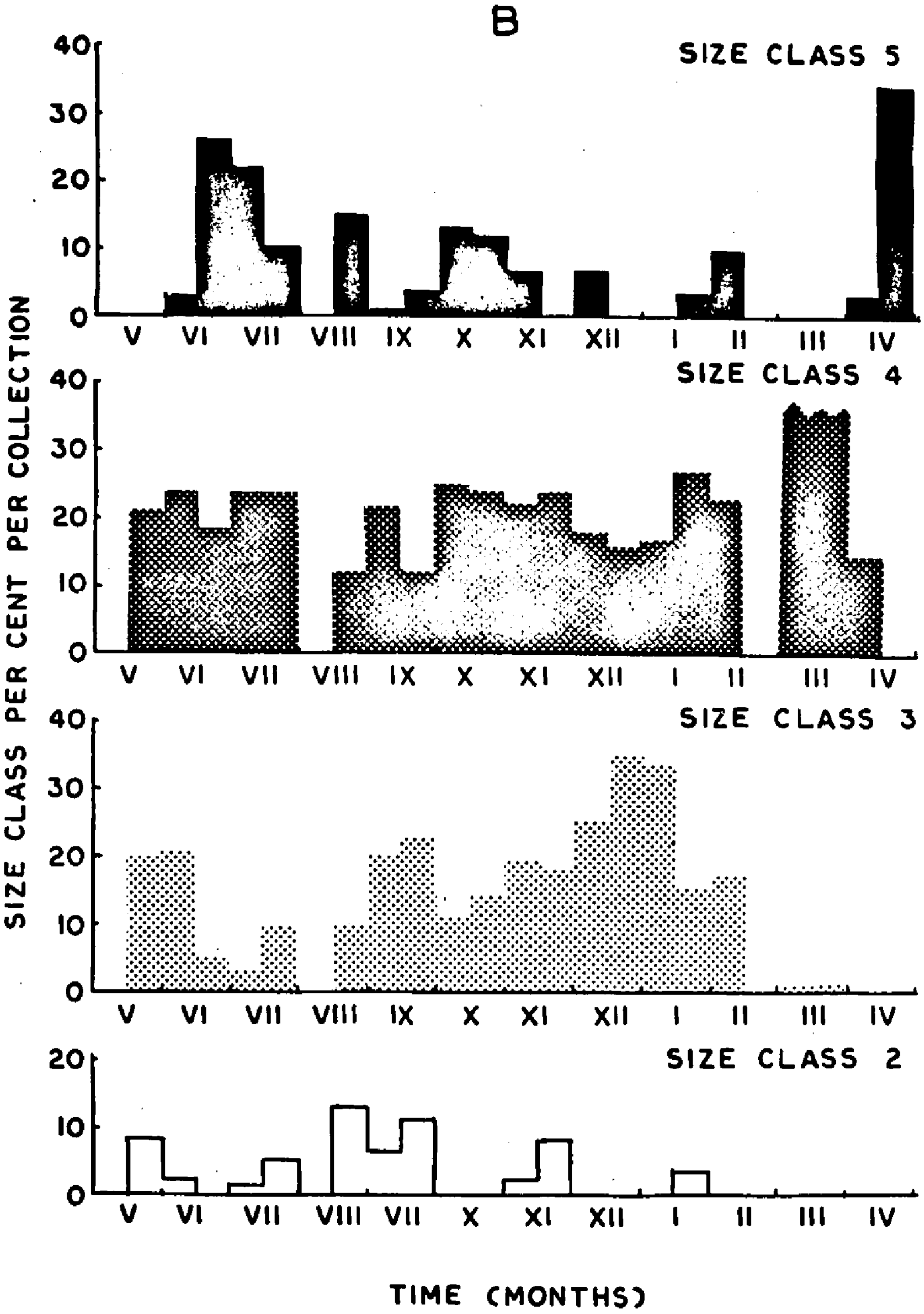

B
SIZE CLASS 5
SIZE CLASS 4
SIZE CLASS 3
SIZE CLASS 2
40
30
20
10
0
20
10
0
V
VI
VII
VIII
IX
X
XI
XII
I
II
III
IV
V
VI
VII
VIII
VII
X
XI
XII
I
II
III
IV
SIZE CLASS PER CENT PER COLLECTION
TIME (MONTHS)

FIG. 8

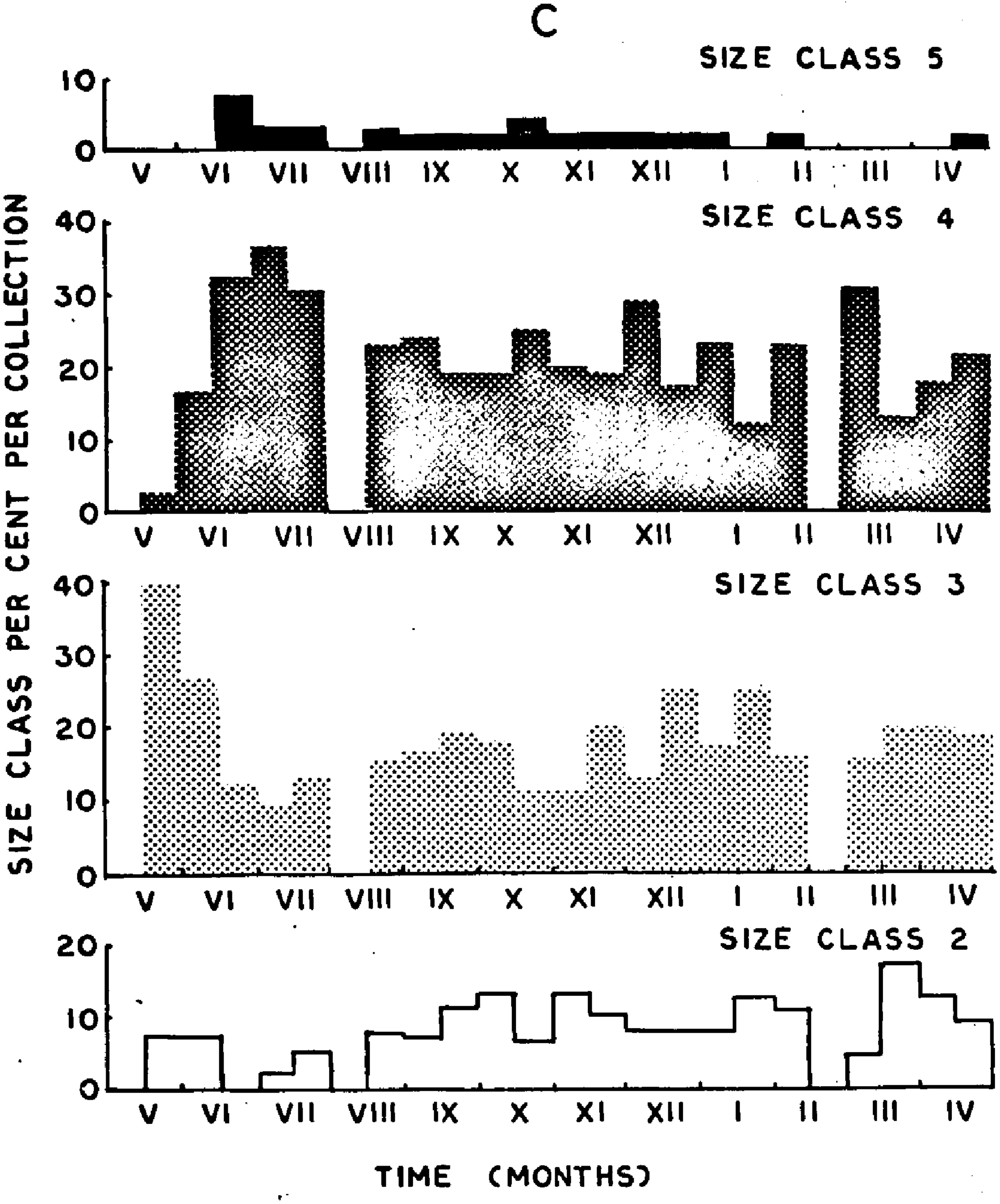

C
SIZE CLASS 5
10
0
V
VI
VII
VIII
IX
X
XI
XII
I
II
III
IV
SIZE CLASS 4
40
30
20
10
0
SIZE CLASS 3
SIZE CLASS 2
SIZE CLASS PER CENT PER COLLECTION
TIME (MONTHS)

FIG. 8

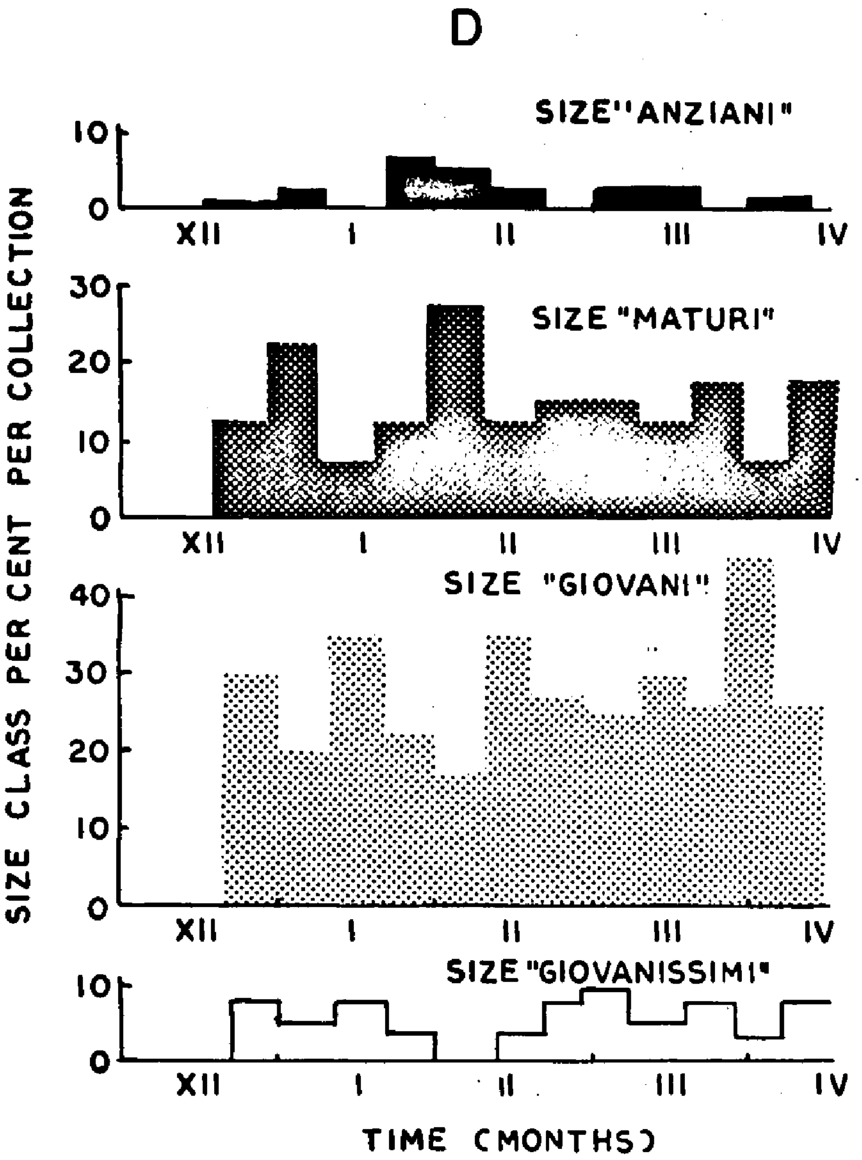

D
SIZE "ANZIANI"
SIZE "MATURI"
SIZE "GIOVANI"
SIZE "GIOVANISSIMI"
SIZE CLASS PER CENT PER COLLECTION
TIME (MONTHS)
XII
I
II
III
IV
0
10
20
30
40

FIG. 8

FIG. 9. Calendar location of peaks in each size class from data in Fig. 8A - D. Connecting lines suggest most likely growth progressions.

A. *Batillipes pennaki*.

B. *Batillipes bullacaudatus*.

C. *Stygarctus granulatus*.

D. *Macrobiotus hufelandii*.

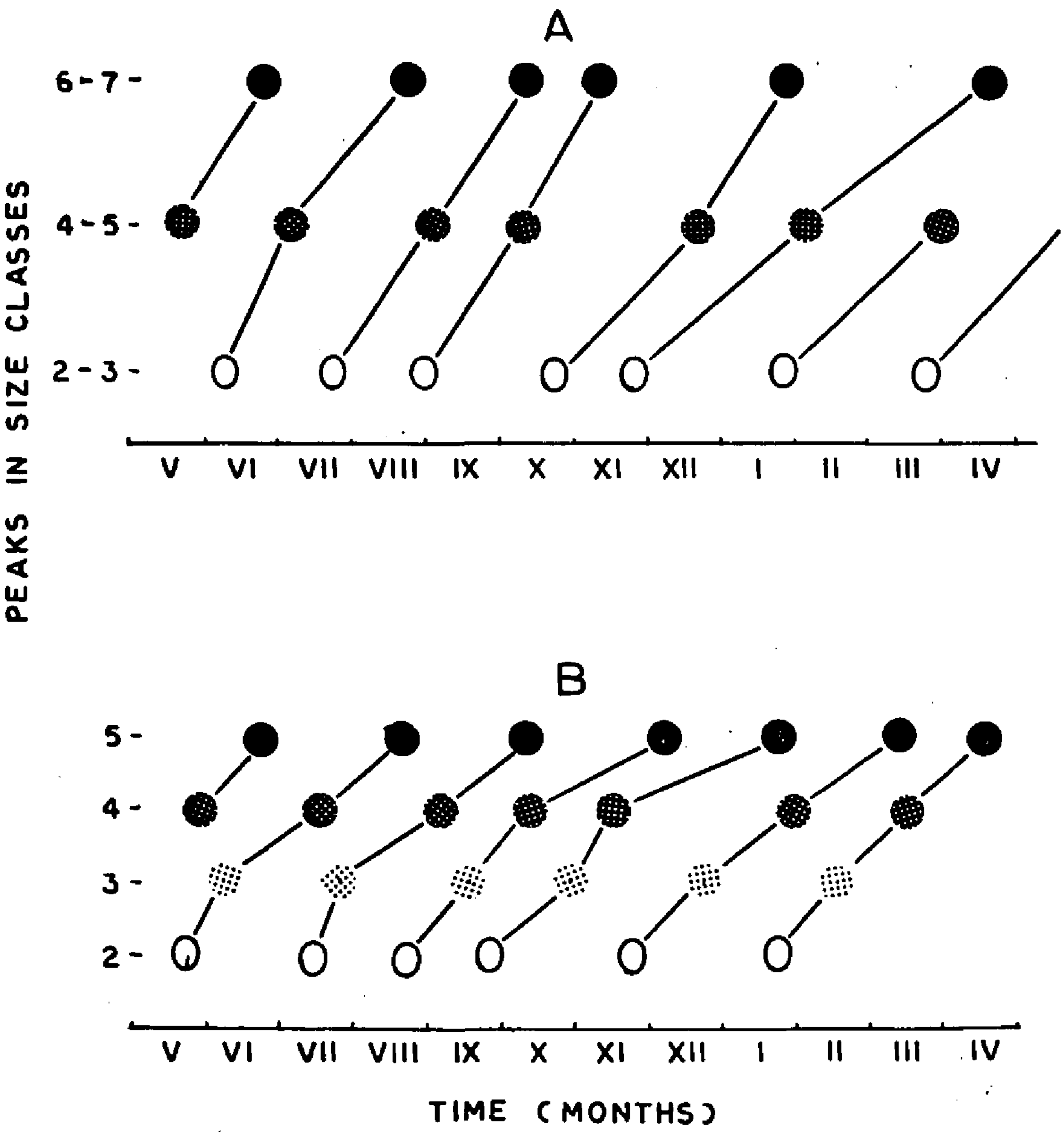

A
6-7
4-5
2-3
PEAKS IN SIZE CLASSES
V
VI
VII
VIII
IX
X
XI
XII
I
II
III
IV
B
5
4
3
2
TIME (MONTHS)

FIG. 9

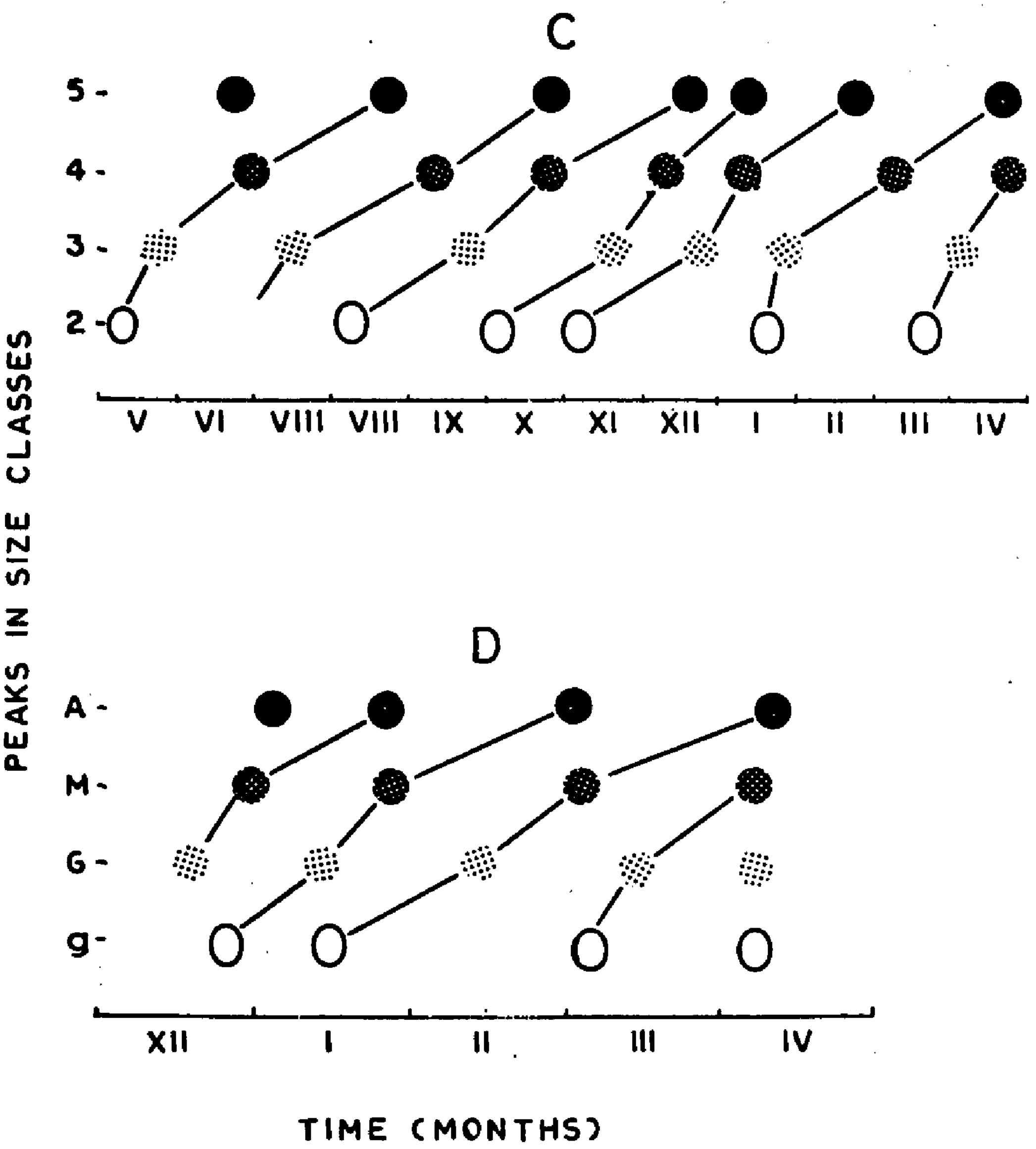

C
5 -
4 -
3 -
2 -
V
VI
VIII
VIII
IX
X
XI
XII
I
II
III
IV
PEAKS IN SIZE CLASSES
D
A -
M -
G -
g -
XII
I
II
III
IV
TIME (MONTHS)

FIG. 9

FIG. 10. Distributional patterns in 16 adjacent subsamples collected in square pattern as shown.

A. *Batillipes mirus* Richters, 1909 from Wood Neck Beach, Woods Hole. N = individuals in each subsample; graphs depict numerical proportions of "small" and "large" size classes in each subsample.

B. *B. mirus* - size class data from A shown as per cent composition in each subsample.

C. *Stygarctus granulatus* from Crane's Beach: as in A.

D. *S. granulatus* - as in B.

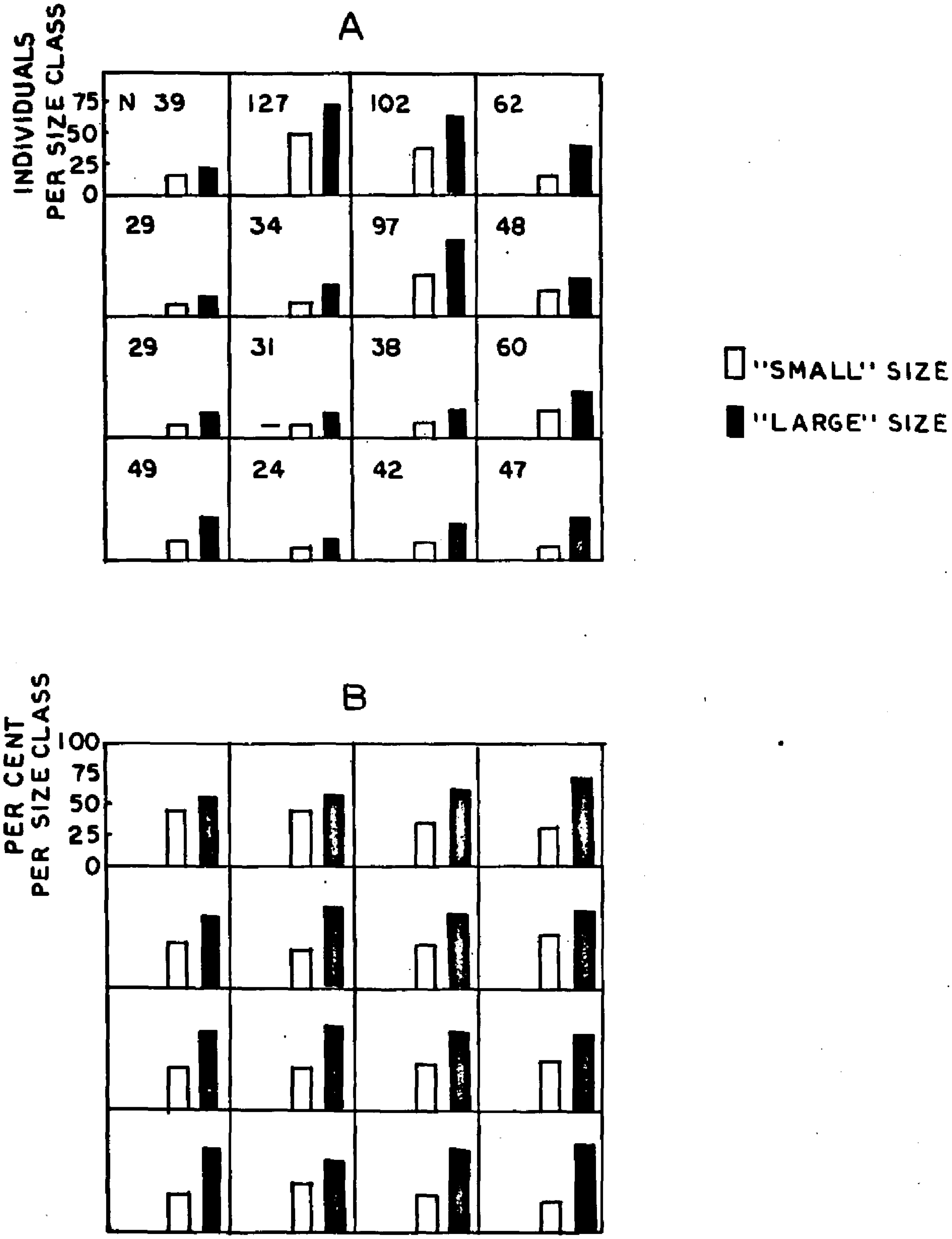

A
INDIVIDUALS PER SIZE CLASS
75
50
25
0
N 39
127
102
62
29
34
97
48
29
31
38
60
49
24
42
47
"SMALL" SIZE
"LARGE" SIZE
B
PER CENT PER SIZE CLASS
100
75
50
25
0

FIG. 10

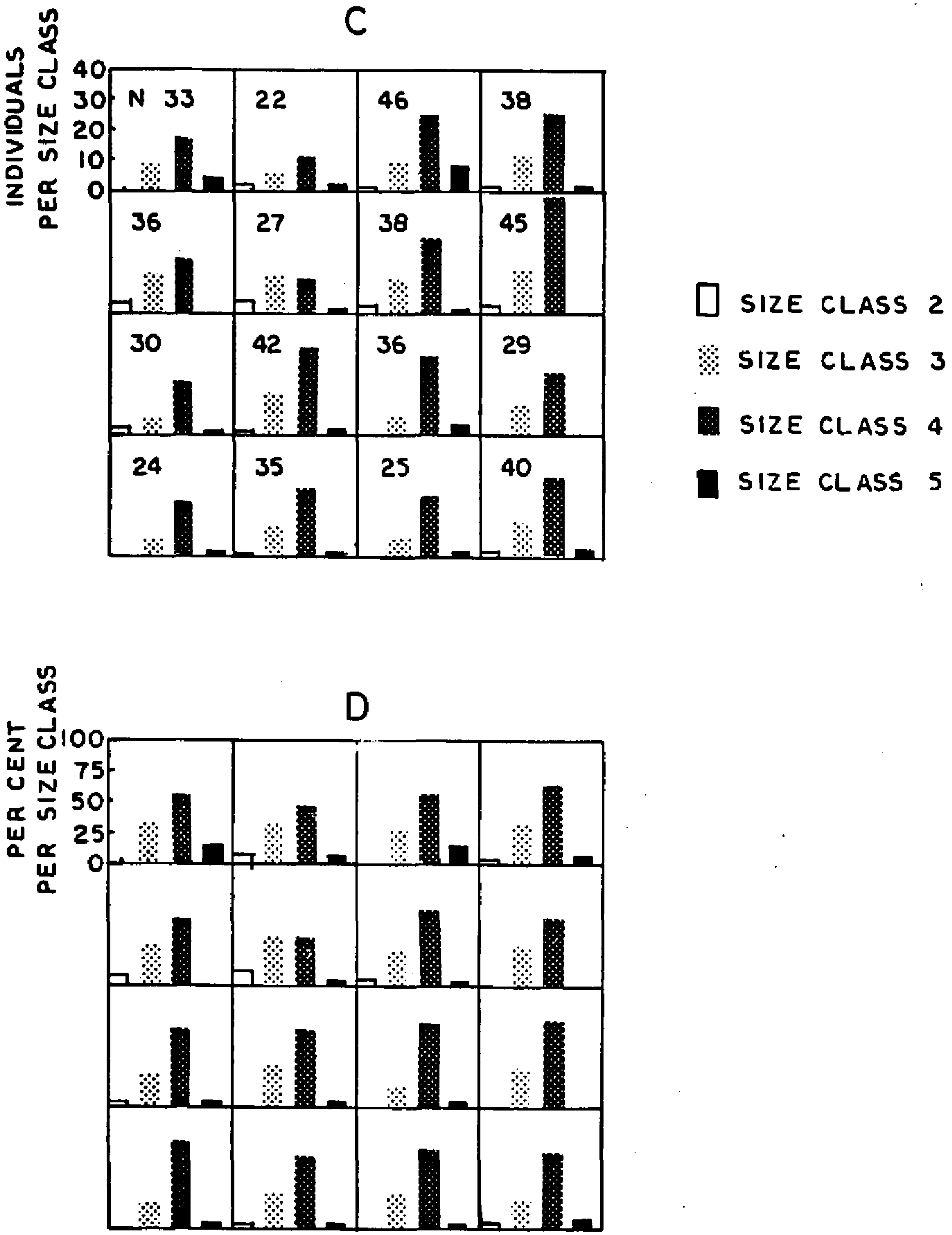

C
INDIVIDUALS PER SIZE CLASS
0
10
20
30
40
N 33
22
46
38
36
27
38
45
30
42
36
29
24
35
25
40
SIZE CLASS 2
SIZE CLASS 3
SIZE CLASS 4
SIZE CLASS 5
D
PER CENT PER SIZE CLASS
0
25
50
75
100

FIG. 10

FIG. 11. Beach distribution typical of several characteristic interstitial tardigrades from Crane's Beach and as reported in the literature.

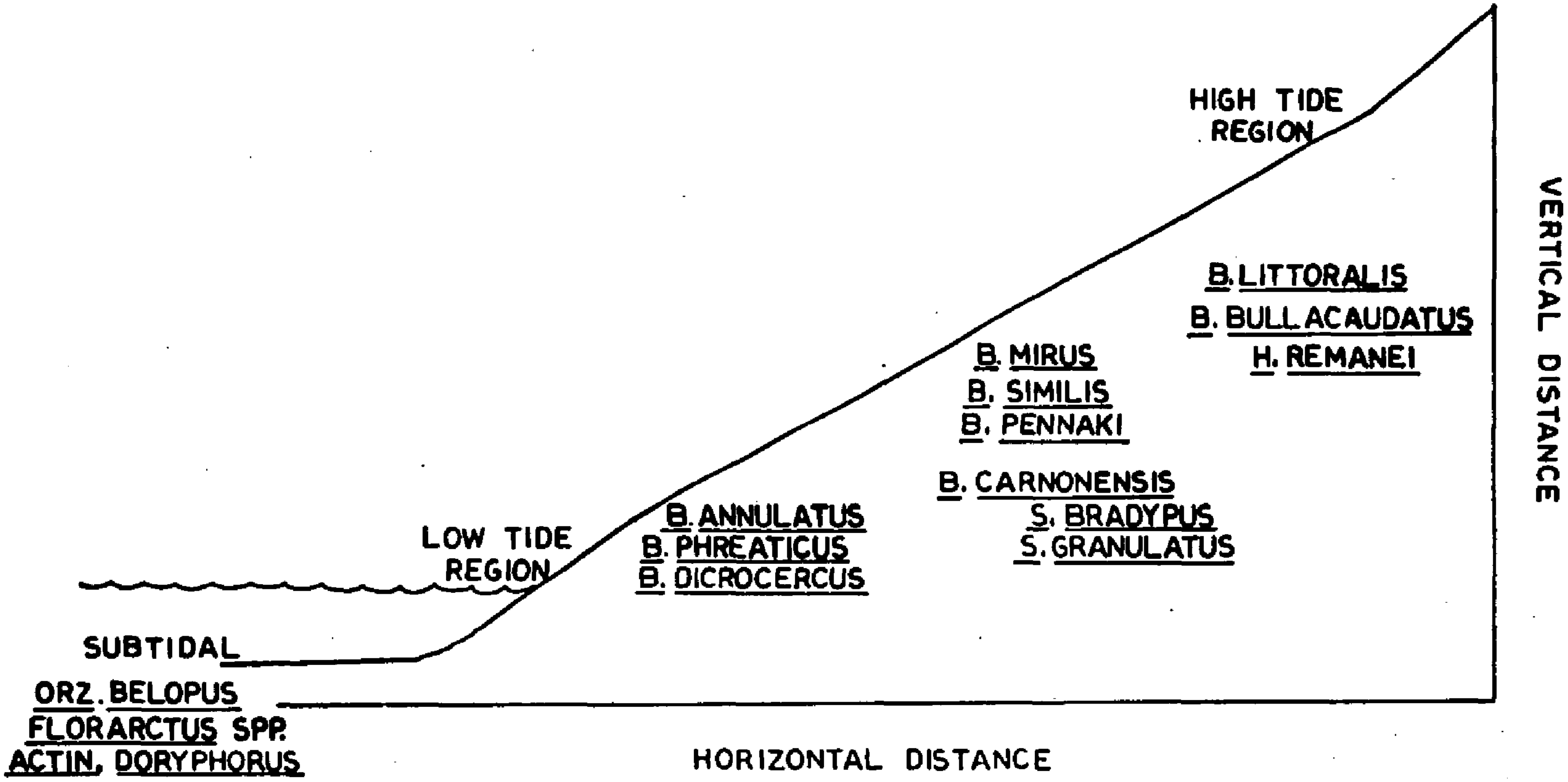
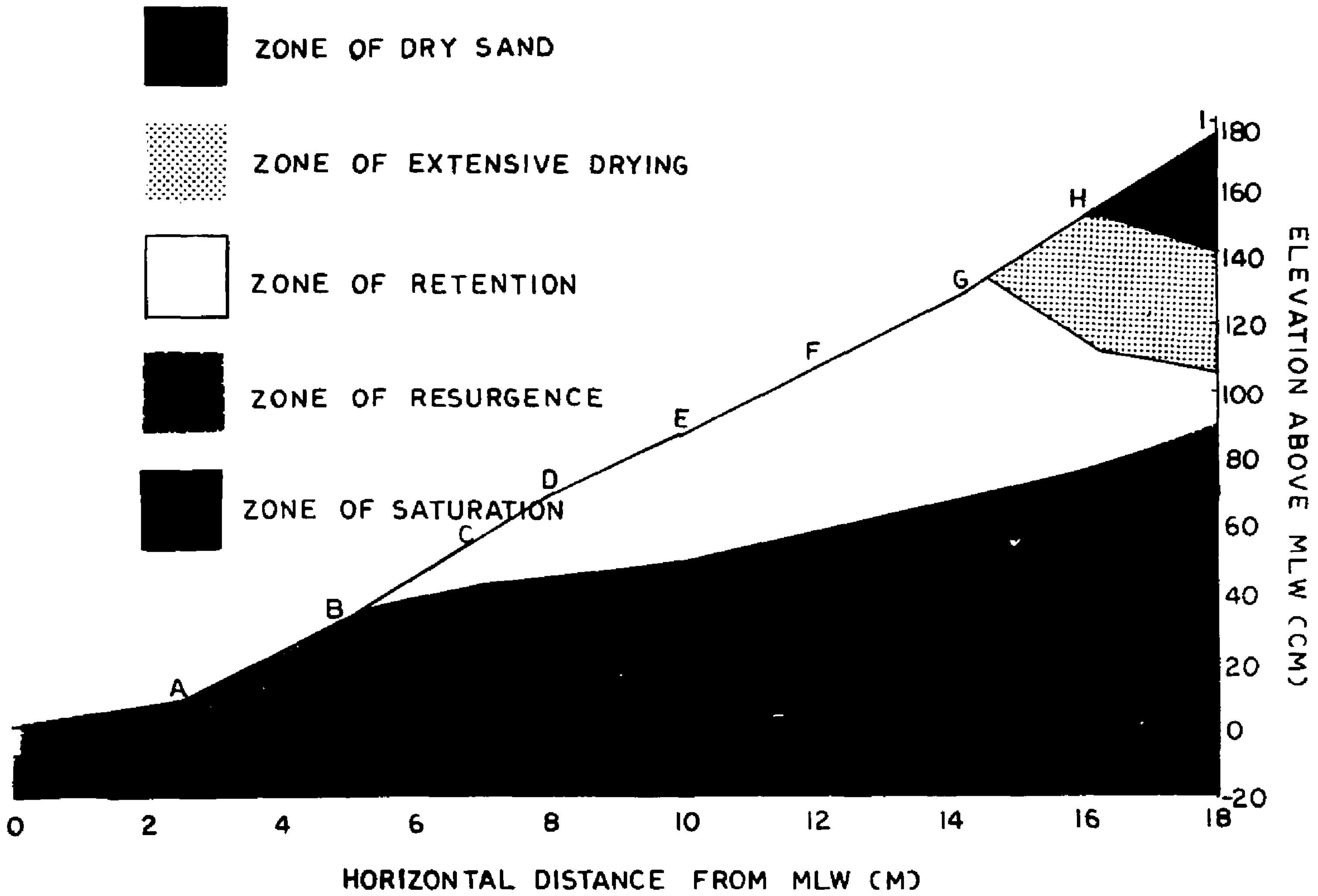

HIGH TIDE REGION
VERTICAL DISTANCE
B. LITTORALIS
B. BULLACAUDATUS
H. REMANEI
B. MIRUS
B. SIMILIS
B. PENNAKI
B. CARNONENSIS
S. BRADYPUS
S. GRANULATUS
LOW TIDE REGION
B. ANNULATUS
B. PHREATICUS
B. DICROCERCUS
SUBTIDAL
ORZ. BELOPUS
FLORARCTUS SPP.
ACTIN. DORYPHORUS
HORIZONTAL DISTANCE

FIG. 11

FIG. 12. Environmental zones at Crane's Beach (from Part III).



ZONE OF DRY SAND
ZONE OF EXTENSIVE DRYING
ZONE OF RETENTION
ZONE OF RESURGENCE
ZONE OF SATURATION
A
B
C
D
E
F
G
H
I
180
160
140
120
100
80
60
40
20
0
-20
ELEVATION ABOVE MLW (CM)
0
2
4
6
8
10
12
14
16
18
HORIZONTAL DISTANCE FROM MLW (M)

FIG. 13. Frequency of occurrence of population at local temperatures, Crane's Beach, 1968 - 1969.

A. *Batillipes pennaki*.

B. *Batillipes bullacaudatus*.

C. *Stygarctus granulatus*.

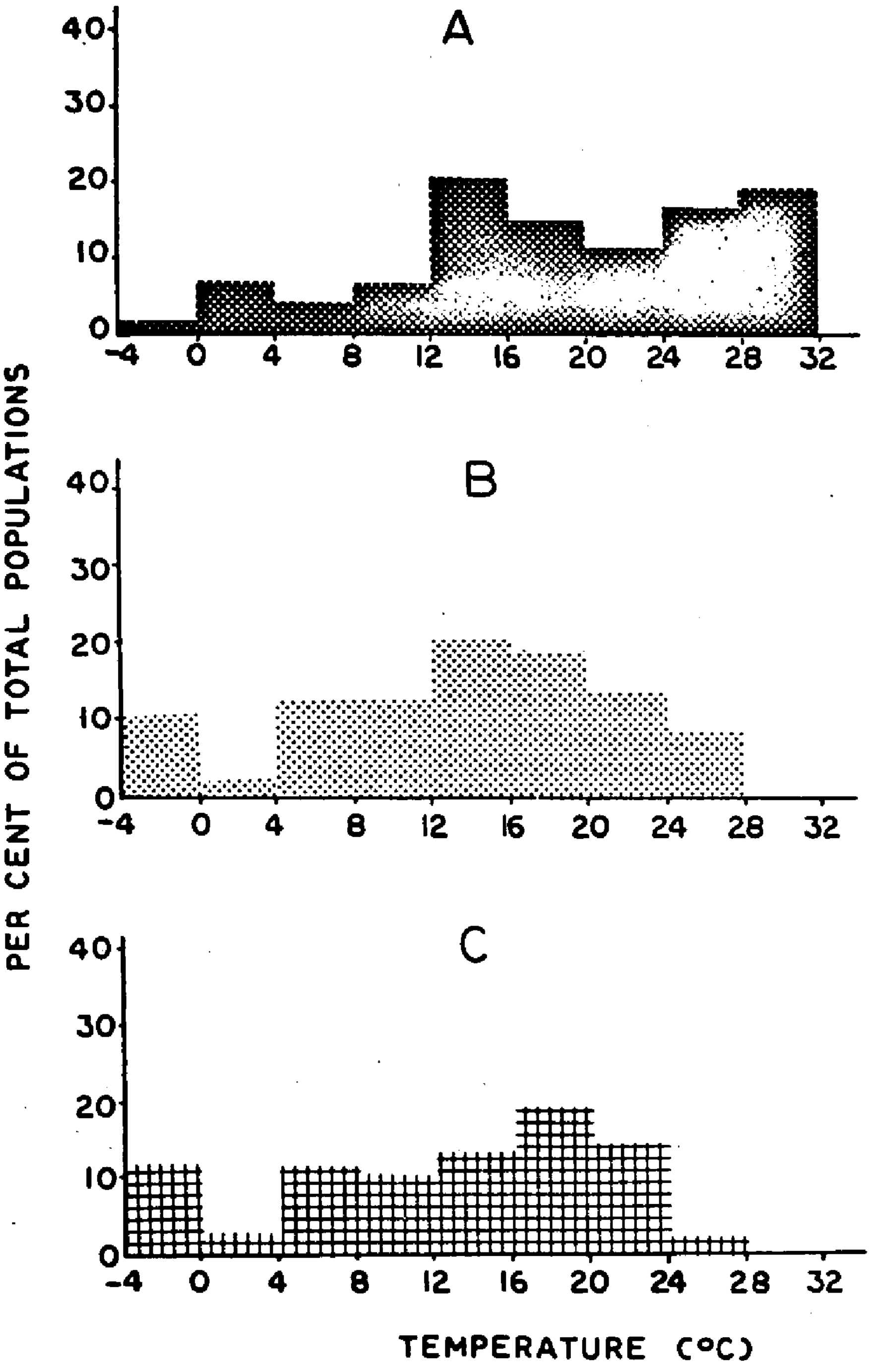

A
B
C
PER CENT OF TOTAL POPULATIONS
0
10
20
30
40
-4
0
4
8
12
16
20
24
28
32
TEMPERATURE (°C)

FIG. 13

FIG. 14. Frequency of occurrence of populations at extremes in low tide water depletion, Crane's Beach, 1968.

A. *Batillipes pennaki*.

B. *Batillipes bullacaudatus*.

C. *Stygarctus granulatus*.

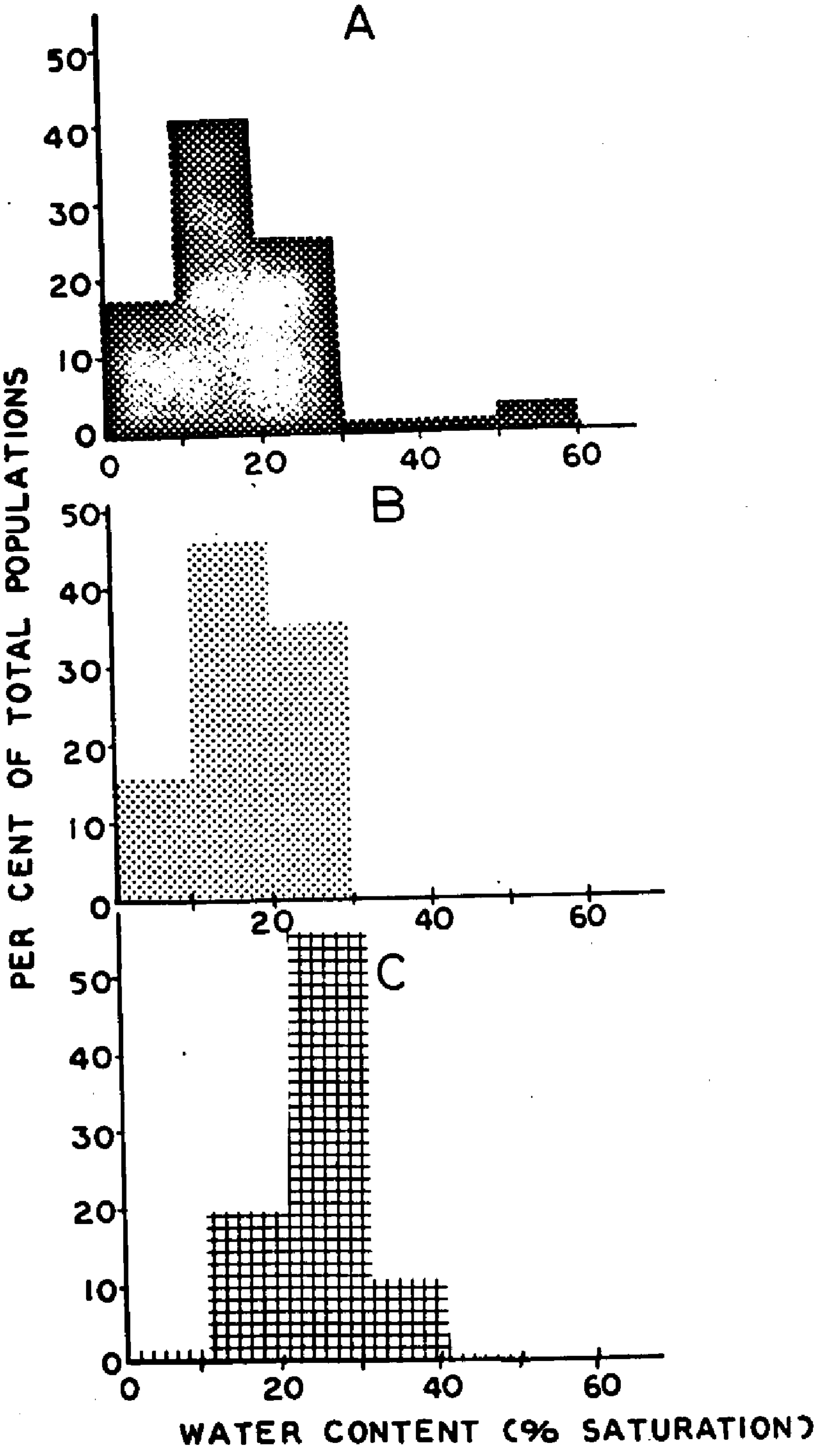

A
B
C
PER CENT OF TOTAL POPULATIONS
0
10
20
30
40
50
0
20
40
60
WATER CONTENT (% SATURATION)

FIG. 14

FIG. 15. Diagrammatic illustration of buccal apparatus of interstitial heterotardigrades. MC - mouth canal; MO - mouth opening; PH - pharyngeal bulb; PL - placoid; SS - stylet support; ST - stylet.

A. *Batillipes* sp.

B. *Stygarctus granulatus*.

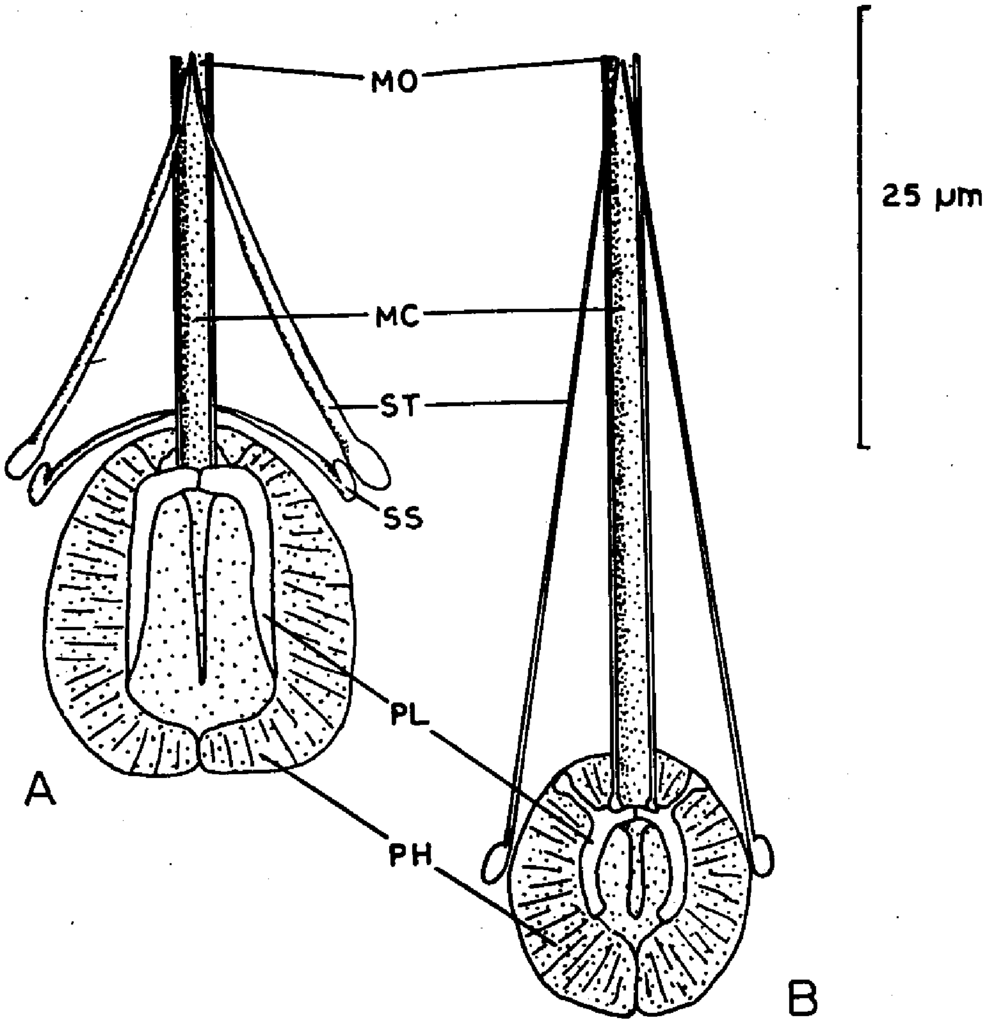


FIG. 15

LITERATURE CITED

Amoureux, L. 1963. Étude des teneurs en oxygène dissous dans les eaux interstitielles de l'Aber de Roscoff. Cah. Biol. mar., 4: 23-32.

Ax, P. 1966. Die Bedeutung der interstitiellen Sandfauna fur allgemeine Probleme der Systematik, Ökologie und Biologie. Veröffentlich. Inst. Meeresforsch. Bremerh., Sonderbd. II: 15-65.

Baudoin, R. 1952. Contribution à l'écologie et à la biogéographie de la zone intercôtidale des Charentes. Compt. Rend. Som. Soc. Biogéogr., 251: 72-82.

Baumann, H. 1966. Lebenslauf und Lebensweise von *Hypsibius* (*H.*) *oberhaeuseri* Doyère (Tardigrada). Veröff. Uberseemus. Bremen, 3: 245-258.

Boaden, P. J. S. 1963. The interstitial fauna of some north Wales beaches. J. mar. biol. Ass. U. K., 43: 79-96.

Boaden, P. J. S. 1966. Interstitial fauna from Northern Ireland. Veröffentlich. Inst. Meeresforsch. Bremerh., Sonderbd. II: 125-130.

Bois-Reymond Marcus, E. du. 1952. On South American Malacopoda. Bol. Fac. Fil. Ciênc. Letr. Sao Paulo, Zool., 17: 189-209.

Brafield, A. E. 1964. The oxygen content of interstitial water in sandy shores. J. Anim. Ecol., 33: 97-116.

Brafield, A. E. 1965. Quelques facteurs affectant la teneur en oxygène des eaux interstitielles littorales. Vie et Milieu, 16: 889-897.

Brinck, P., Dahl, E. and W. Wieser. 1955. On the littoral subsoil fauna of the Simrishamn beach in eastern Scania. K. Fysiogr. Sällsk. Lund Förh., 25: 1-21.

Bruce, J. R. 1928a. Physical factors on the sandy beach. Part I. Tidal, Climatic and Edaphic. J. mar. biol. Ass. U. K., 15: 535-552.

Bruce, J. R. 1928b. Physical factors on the sandy beach. Part II. Chemical changes. J. mar. biol. Ass. U. K.,15: 553-565.

Callame, B. 1963. Le milieu interstitiel dans les sédiments sableaux intercôtideaux. Bull. Inst. oceanogr. Monaco, 60: 1-32.

Cobb, N. A. 1917. Nematode population of sandy beach. Notes on Nemas, 3: 124-125.

Dahl, E. 1953. Some aspects of the ecology and zonation of the fauna of sandy beaches. Oikos, 4: 1-27.

Delamare Deboutteville, C. 1960. Biologie des eaux souterraines littorales et continentales. Suppl. Vie et Milieu, 9: 1-740.

Delamare Deboutteville, C. and J. Renaud-Mornant. 1965. Un remarquable genre de Tardigrades des sables coralliens de Nouvelle-Calédonie. Compt. Rend. Acad. Sci. (Paris), 260: 2581-2583.

DeZio, S. 1962. Descrizione di Batillipes annulatus n. sp. e note su Batillipes pennaki Marcus, nuovo rinvenimento nel Mediterraneo (Heterotardigrada). Ann. Ist. Mus. Zool. Univ. Napoli, 14: 1-7.

DeZio, S. 1964. Distribuzione dei Tardigradi in spiagge pugliesi. Ann. Ist. Mus. Zool. Univ. Napoli, 16: 1-8.

DeZio, S. 1965. Distribuzione del mesopsammon in rapporto alla distanza della linea di riva e distanza da un corso di acqua salmastra. Boll. Zool., 32: 525-537.

DeZio, S. and P. Grimaldi. 1964a. Analisi comparativa del mesopsammon di due spiagge Pugliesi in rapporto ad alcuni fatteri ecologici. Arch. Bot. Biogeogr. Ital., 40: 357-367.

DeZio. S. and P. Grimaldi. 1964b. Ricerche sulla distribuzione ed ecologia de Batillipes pennaki Marcus in una spiaggia pugliese (Heterotardigrada). Cah. Biol. mar., 5: 271-285.

DeZio, S. and P. Grimaldi. 1966. Ecological aspects of Tardigrada distribution in S. Adriatic beaches. Ve-öff. Inst. Meeresforsch. Bremerh., Sonderbd. II: 87-94.

Emery, K. O. and J. F. Foster. 1948. Water tables in marine beaches. J. Mar. Res., 7: 644-654.

Enckell, P. H. 1968. Oxygen availability and microdistribution of interstitial mesofauna in Swedish fresh-water sandy beaches. Oikos, 19: 271-291.

Fenchel, T. and B.-O. Jansson. 1966. On the vertical distribution of the microfauna in the sediments of a brackish-water beach. Ophelia, 3: 161-177.

Fenchel, T., B.-O. Jansson, and W. v. Thun. 1967. Vertical and horizontal distribution of the metazoan microfauna and of some physical factors in a sandy beach in the northern part of the Øresund. Ophelia, 4: 227-243.

Fize, A. 1957. Description d'une espèce nouvelle de Tardigrade, Batillipes carnonensis, n. sp. Bull. Soc. Zool. France, 82: 430-433.

Franceschi, T., M. L. Lio, and R. Pierantoni. 1962-63. Risultati di una prima indagine ecologica condotta su popolazioni di Tardigradi. Bol. Mus. Ist. biol. Univ. Genova, 32: 69-93.

Franceschi Crippa, T. and A. Lattes. 1967. Analisi della variazione della lunghezza degli esemplari di una popolazione di Macrobiotus hufelandii Schultze in rapporto con l'esistenza di mute. Bol. Mus. Ist. biol. Univ. Genova, 35: 45-54.

Fraser, H. J. 1935. Experimental study of the porosity and permeability of clastic sediments. J. Geol., 43: 910-1010.

Ganapati, P. N. and G. Chandrasekhara Rao. 1962. Ecology of the interstitial fauna inhabiting the sandy beaches of Waltair coast. J. mar. biol. Ass. India, 4: 44-57.

Gerlach, S. A. 1954. Das Supralitoral der sandigen Meereskūsten als Lebensraum einer Mikrofauna. Kieler Meeresforsch., 10: 121-129.

Giard, A. 1904. Sur une faunule caractéristique des sables à Diatomées d'Ambleteuse. Compt. Rend. Soc. Biol. Paris, 56: 295-298.

Gordon, M. S. 1960. Anaerobiosis in marine sandy beaches. Science, 132: 616-617.

Govindankutty, A. G. and N. Balakrishnan Nair. 1966. Preliminary observations on the interstitial fauna of the southwest coast of India. Hydrobiol., 28: 101-122.

Graton, L. C. and H. J. Fraser. 1935. Systematic packing of spheres, with particular relation to porosity and permeability. J. Geol., 43: 785-909.

Green, R. H. 1966. Measurement of non-randomness in spatial distributions. Res. on Pop. Exol., 8: 1-7.

Guérin, M. 1960. Observations écologiques sur Convoluta roscoffensis Graf. Cah. Biol. mar., 1: 205-220.

Hay, W. P. 1917. A new species of bear-animalcule from the coast of North Carolina. Proc. U. S. nat. Mus., 53: 251-254.

Higgins, R. P. 1959. Life history of Macrobiotus islandicus Richters with notes on other Tardigrades from Colorado. Trans. Amer. Microsc. Soc., 78: 137-154.

Hyman, L. H. 1951. The Invertebrates. Vol. III. Acanthocephala, Aschelminthes, and Entoprocta. McGraw-Hill Book Co., Inc., New York, pp. 1-572.

Inman, D. L. 1952. Measures for describing the size distribution of sediments. J. Sediment. Petrol., 22: 125-145.

Jagersten, G. 1952. Studies on the morphology, larval development and biology of Protodrilus. Zool. bidrag Uppsala, 29: 425-512.

Jansson, B.-O. 1966. On the ecology of Derocheilocaris remanei Delamare & Chappuis (Crustacea, Mystacocarida). Vie et Milieu, 17: 143-186.

Jansson, B.-O. 1967a. The importance of tolerance and preference experiments for the interpretation of mesopsammon field distributions. Helgoländer wiss. Meeresunters.,15: 41-58.

Jansson, B.-O. 1967b. The significance of grain size and pore water content for the interstitial fauna of sandy beaches. Oikos, 18: 311-322.

Jansson, B.-O. 1967c. Diurnal and annual variations of temperature and salinity of interstitial water in sandy beaches. Ophelia, 4: 173-201.

Jansson, B.-O. 1968a. The availability of oxygen for the interstitial fauna of sandy beaches. J. exp. mar. Biol., 1: 123-143.

Jansson, B.-O. 1968b. Quantitative and experimental studies of the interstitial fauna in four Swedish sandy beaches. Ophelia, 5: 1-72.

Jansson, B.-O. 1968c. Studies on the ecology of the interstitial fauna of marine sandy beaches. Thesis presented to Department of Zoology, University of Stockholm: 1-16.

Johnson, R. G. 1967. Salinity of interstitial water in a sandy beach. Limnol. Oceanogr., 12: 1-7.

Karling, T. G. 1955. Über einige Kleintiere des Meeressandes des Nordsee- Ostsee-Gebietes. Ark. Zool., 7: 241-249.

King, C. E. 1962. The occurrence of Batillipes mirus Richters (Tardigrada) in the Gulf of Mexico. Bull. Mar. Sci. Gulf & Carib., 12: 201-203.

Kowalevsky, A. 1901a. Études anatomique sur le genre Pseudovermis. Mém. Acad. Sci. St. Petersb., 12 (4): 1-28.

Kowalevsky, A. 1901b. Les Hedylidés, étude anatomique. Mém. Acad. Sci. St. Petersb., 12 (6): 1-32.

Kramer, P. J. 1949. Plant and Soil Water Relationships. New York, McGraw-Hill Book Co., Inc., pp. 1-347.

Kuhl, H. and H. Mann. 1966. Änderungen im Chemismus des Interstitialwassers am Strand von Cuxhaven während einer Tide. Helgoländer wiss. Meeresunters., 13: 238-245.

Marcus, E. 1927. Zur Anatomie und Ökologie mariner Tardigraden. Zool. Jahrb., 53: 487-588.

Marcus, E. 1929. Tardigrada. In: Bronns, H. G. ed., Klassen und Ordnungen des Tierreichs, Band 5, Abt. IV, Buch 3, pp. 1-608.

Marcus, E. 1934. Tardigrada. In: Dorschelt, E. et al eds., Handwörterbuch der Naturwissenschaften, Band 9: 859.

Marcus, E. 1936. Tardigrada. Das Tierreich., 66: 1-340.

Marcus, E. 1946. Batillipes pennaki, a new marine Tardigrade from the north and south American Atlantic coast. Comun. Zool. Mus. Hist. Natur. Montevideo, 2: 1-3.

May, R. M. 1948. La vie des Tardigrades. Gallimard Hist. Nat., 8: 1-133.

McGinty, M. M. and R. P. Higgins. 1968. Ontogenetic variation of taxonomic characters of two marine tardigrades with the description of Batillipes bullacaudatus n. sp. Trans. Amer. Microsc. Soc., 87: 252-262.

McIntyre, A. D. 1969. Ecology of marine meiobenthos. Biol. Rev., 44: 245-290.

Murray, J. 1910. Tardigrada. Rep. Sci. Invest. Brit. Antarctic Exped., 1907-1909, 1 (5): 81-85.

Odén, S. 1962. Principiella problem rörande syrediffusionselektroder och deras utformning. Grundförbättring, 3: 150-178 (not seen in original).

Papi, F. 1952. Su alcuni Tardigradi raccolti nell'Italia centrale. Atti. Soc. Tosc. Sci. Natur., 59: 116-118.

Pennak, R. W. 1939. The microscopic fauna of the sandy beaches. Problems of LakeBiology (Amer. Assoc. Adv. Sci. Publ.), 10: 94-106.

Pennak, R. W. 1940. Ecology of microscopic Metazoa inhabiting sandy beaches of some Wisconsin lakes. Ecol.Monogr., 12: 537-615.

Pennak, R. W. 1942. Ecology of some copepods inhabiting intertidal beaches near Woods Hole, Massachusetts. Ecology, 23: 446-456.

Pennak, R. W. 1951. Comparative ecology of the interstitial fauna of fresh-water and marine beaches. Ann. Biol., 27: 449-479.

Pennak, R. W. 1953. Fresh-Water Invertebrates of the United States. The Ronald Press Co., New York. Chap. 11. Tardigrada: 240-255.

Perkins, E. J. 1958. The food relationships of the microbenthos, with particular reference to that found at Whitstable, Kent. Ann. Mag. natur. Hist., 13: 64-77.

Plesa, C. 1963. Étude sur la faune interstitielle littorale de la Mer Noire III. Vie et Milieu, 14: 775-813.

Purasjoki, K. 1953. Zwei verbesserte Apparate zum Auffangen von Kleintieren des See- und Meeres-bodens. Arch. Soc. Zool. Bot. Fen. Vanamo, 8: 110-114.

Rahm, G. B. 1931. Tardigrada of the south of America (Esp. Chile). Rev. Chilena, 35: 118-141.

Rahm, G. B. 1937. Eine neue Tardigraden Ordnung aus den heissen Quellen von Unzen, Insel Kyushu, Japan. Zool. Anz., 120: 65-71.

Ramazzotti, G. 1962. Il Phylum Tardigrada. Mem. Ist. Ital. Idrobiol., 14: 1-595.

Ramazzotti, G. 1964. Tardigradi del Cile. III. Con descrizione delle nuove specie <u>Oreella minor</u> e <u>Pseudechiniscus lateromamillatus</u>. Atti Soc. Ital. Sci. Natur., 103: 347-351.

Ramazzotti, G. 1965. Il Phylum Tardigrada (I^{o} Supplemento). Mem. Ist. Ital. Idrobiol., 19: 101-212.

Rao, G. Chandrasekhara and P. N. Ganapati. 1968. The interstitial fauna inhabiting the beach sands of Waltair coast. Proc. Nat. Inst. Sci. India, 34: 82-125.

Reid, D. M. 1930. Salinity interchange between seawater in sand and overflowing fresh-water at low tide. J. mar. biol. Ass. U. K., 26: 604-614.

Remane, A. 1952. Die Besiedlung des Sandbodens im Meere und die Bedeutung der Lebensformtypen fur die Ökologie. Verh. dtsch. zool. Ges., Wilhelmshaven, 1951: 327-339.

Renaud-Debyser, J. 1956. Répartition de deux tardigrades _Batillipes_ _mirus_ Richters et _Stygarctus_ _bradipus_ Schulz dans un segment de plage du bassin d'Arcachon. Compt. Rend. Acad. Sci. (Paris), 243: 1365-1367.

Renaud-Debyser, J. 1959a. Sur quelques Tardigrades du Bassin d'Arcachon. Vie et Milieu, 10: 135-146.

Renaud-Debyser, J. 1959b. Études sur la faune interstitielle des îles Bahamas III. Tardigrades. Vie et Milieu, 10: 296-302.

Renaud-Debyser, J. 1963. Recherches écologiques sur la faune interstitielle des sables (Bassin d'Arcachon, île de Bimini, Bahamas). Supple. Vie et Milieu, 15: 1-157.

Renaud-Debyser, J. 1965a. _Parastygarctus_ _higginsi_ n. g., n. sp. Tardigrade marin interstitiel de Madagascar. Compt. Rend. Acad. Sci. (Paris), 260: 955-957.

Renaud-Debyser, J. 1965b. Etude sur un Stygarctidé (Tardigrada) nouveau de Madagascar. Bull. Soc. Zool. France, 90: 31-38.

Renaud-Debyser, J. and B. Salvat. 1963. Elements de prospérité des biotopes des sédiments meubles intertidaux et écologie de leurs populations en microfaune et macrofaune. Vie et Milieu, 14: 463-550.

Renaud-Mornant, J. 1967a. _Parastygarctus_ _higginsi_ Renaud-Debyser, 1965, sur la côte orientale de Malaisie. Description de la femelle (Tardigrada). Bull. Mus. nat. d'Hist. natur., 39: 205-208.

Renaud-Mornant, J. 1967b. Tardigrades de la Baie Saint-

Vincent Nouvelle-Calédonie. Éditions de la Fondat. Singer-Polignac, Paris: 103-119.

Renaud-Mornant, J. and C. Jouin. 1965. Note sur la microfaune du fond à Amphioxus de Graveyren et d'autres stations. Trav. Inst. Biol. Mar. Univ. Bordeaux, 102: 1-7.

Renaud-Mornant, J. and L. W. Pollock. 1970. Systematics and ecology of marine Tardigrada. Proc. Ist. Internat. Meiofauna Confer., Tunis: in press.

Renaud-Mornant, J. and P. Serène. 1967. Note sur la microfaune de la côte orientale de la Malaisie. Cah. Pacif., 11: 51-73.

Richters, F. 1908. Marine Tardigraden. Zool. Anz., 33: 77-85.

Richters, F. 1909. Tardigraden-Studien. Ber. Senckenberg. Nature. Ges., Frankfurt, 1-2: 28-45.

Riemann, F. 1966. Die Verbreitung der interstitiellen Fauna im Elbe-Astuar. Veröff. Inst. Meeresforsch. Bremerh., Sonderbd. II: 117-123.

Riggin, G. T. 1962. Tardigrada of Southwest Virginia: with the addition of a description of a new marine species from Florida. Va. Agri. Exp. Sta., Tech. Bull., 152: 1-145.

Rudescu, L. 1964. Tardigrada. In: Fauna Republicii Populare Romîne, Arthropoda, Vol. IV, Fasc. 7: 1-400.

Rullier, F. 1957. Teneur en air et en eau interstitiel des sables marins et son influence sur les conditions d'habitat. Compt. Rend. Acad. Sci. (Paris), 245: 936-938.

Ruttner-Kolisko, A. 1956. Der Lebensraum des Limnopsammals. Verh. dtsch. zool. Ges., Hamburg, 1956: 421-427.

Ruttner-Kolisko, A. 1961. Biotop und Biozönose des Sandufers einiger österreichischer Flüsse. Verh. Internat. Verein. Limnol., 14: 362-368.

Ruttner-Kolisko, A. 1962. Porenraum und kapillare Wasserströmung im Limnopsammal, ein Beispiel für die Bedeutung verlangsamter Strömung. Schweiz, Z. Hydrol., 24: 444-458.

Salvat, B. 1964. Les conditions hydrodynamiques interstitielles des sédiments meubles intertidaux et la répartition verticale de la faune endogée. Compt. Rend. Acad. Sci. (Paris), 259: 1576-1579.

Salvat, B. 1967. La macrofaune carcinologique endogée des sédiments meubles intertidaux (Tanaidacés, Isopodes et Amphipodes), éthologie, bionomie et cycle biologique. Mem. Mus. nat. d'Hist. natur., 45: 1-275.

Schultze, M. 1867. Echiniscus Sigismundi, ein Arctiscoide der Nordsee. Ark. mikrosc. Anat., 1: 428-436.

Schulz, E. 1950. Psammohydra nana, ein neues solitares Hydrozoon in der westlichen Beltsee. Kieler Meeresforsch., 7: 122-137.

Schulz, E. 1951. Über Stygarctus bradypus n. g. n. sp., einen Tardigraden aus dem Küstengrundwasser, und seine phylogenetische Bedeutung. Kieler Meeresforsch., 8: 86-97.

Schulz, E. 1953. Eine neue Tardigraden-Gattung von der pazifischen Küste. Zool. Anz., 151: 306-310.

Schulz, E. 1955. Studien an marinen Tardigraden. Kieler Meeresforsch., 11: 73-79.

Schulz, E. 1963. Über die Tardigraden. Zool. Anz., 171: 3-12.

Swedmark, B. 1951. Contribution à l'étude de la microfaune des sables de Roscoff. Arch. Zool. Exp. Gén., 87: 22-24.

Swedmark, B. 1955. Gastrotriches marins de la region de Roscoff. Arch. Zool. Exp. Gén., 93: 10-19.

Swedmark, B. 1956a. Etude de la microfaune des sables marins de la region de Marseille. Arch. Zool. Exp. Gén., 93: 70-95.

Swedmark, B. 1956b. Nouveaux gastrotriches Macrodasyoides de la region de Roscoff. Arch. Zool. Exp. Gén., 94: 43-57.

Swedmark, B. 1959. On the biology of sexual reproduction of the interstitial fauna of marine sands. Proc. 15th internat. Congr. Zool. London, 327-329.

Swedmark, B. 1964. The interstitial fauna of marine sand. Biol.Rev., 39: 1-42.

Tambs-Lyche, H. 1939-40. Marine Tardigraden bei Bergen. Bergens Mus. Arbok, 1939-40: 1-5.

Thulin, G. 1928. Über die Phylogenie und das System der Tardigraden. Hereditas, 11: 207-266.

Thulin, G. 1942. Ein neuer mariner Tardigrad. Meddel. Göteborgs Mus. Zool., 99: 1-10.

Uhlig, G. 1964. Eine einfache Methode zur Extraktion der vagilen, mesopsammalen Mikrofauna. Helgoländer wiss. Meeresunters., 11: 178-185.