

SIPUNCULA OF THE WESTERN  
NORTH ATLANTIC

EDWARD BAYLER CUTLER

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## ABSTRACT

MORE THAN 8300 SIPUNCULANS from more than 500 stations off the east coast of the United States are identified and described. The area under investigation extends from Nova Scotia to Cape Kennedy, Florida, in depths from 10 to 5400 meters. Several abiotic factors of the environment (topography, currents, temperature, and sediments) are described. Each species is characterized morphologically and also in terms of depth, latitude, sediment, and temperature.

A key is given for the identification of all the 26 species collected. Distribution maps for the species are presented, as well as figures showing their morphology. In the description of each species, particular attention is paid to variation in morphology due to ontogeny. Several combinations of existing species names are suggested.

Based on abiotic niche features, the species are grouped into four major ecological units: southern, shallow, warm water; northern, shallow, cold water; slope; and abyssal. Competitive exclusion operates within each of these groups except the abyssal fauna; this group has more sympatric species than the shallower groups and their morphology is less distinctive.

One possible explanation is the limited magnitude of the significant environmental differences, which may be too small to be effective. Another is that the relatively low density greatly reduces the likelihood of two worms coming into contact and competing for given resources.

The continental slope may not be an ecotone, but ecotones may exist along its upper and lower boundaries. The existence of a shallow-water, zoogeographical barrier at Cape Hatteras is reaffirmed, but the role of currents on larval dispersal may be as important as temperature in maintaining this barrier. A barrier on the slope, maintained by the effect of the bottom currents on larval dispersion just south of Cape Hatteras (latitude  $34^{\circ}20' - 34^{\circ}30'N$ ), is proposed. Three of the four ecological groupings of species fit into pre-existing zoogeographical provinces (Carolinian, Nova Scotian, and Abyssal Atlantic subarea), but a new province (Atlantic Transitional) is proposed for the slope. Sipunculans in the Virginian Province are extremely rare. Two pieces of evidence support the concept that abyssal, cold-water fauna is ancestral to the warmer, shallow-water fauna.

## INTRODUCTION

THE PRESENT INVESTIGATION concerns 26 species of Sipuncula that have been collected off the east coast of North America between Nova Scotia and Cape Kennedy (in central Florida), from the subtidal region down to about 5000 meters. To introduce this analysis of the sipunculan fauna, I first present a generalized description of the topography, currents, sediments, and temperature of the study area.

I describe the species, taking into account their ontogenetic changes; I analyze their distribution according to latitude, depth, temperature, and sediment type, to facilitate grouping them into zoogeographical units. Many workers have subdivided the benthic marine environment and its inhabitants on the basis of depth, temperature, or sediment alone, but they have not combined these factors in a comprehensive manner. I also discuss certain ecological concepts, possible evolutionary patterns within the phylum, and the nature of the boundaries between the zoogeographical units in the Cape Hatteras region.

Most biologists agree that any given species has a particular niche (Hutchinson, 1957; MacArthur, 1957; Slobodkin, 1961; King, 1964). This niche is partially characterized by those abiotic factors unique to the particular place or places in which this species lives and reproduces. As Mayr (1965, p. 6) pointed out, "every species has an optimal environment, presumably somewhere near the center of its range, and definite limits of tolerance . . ." In other words, some of the parameters of this multidimensional hypervolume (Slobodkin, 1961) are physical and by describing them we are, to a certain extent, describing the niche of that species. A second basic assumption is that niches are unique and nonoverlapping (Gause, 1935; see Slobodkin, 1961). Slobodkin has pointed out cogently that a niche is to an ecologist what morphological characters are to a systematist. The present work is the first explicit attempt to combine the information on morphology and ecology and to characterize more effectively the sipunculans off the east coast of North America.

## EARLIER RESEARCH ON SIPUNCULA

The phylum Sipuncula is a group of marine worms which, with few exceptions, has been studied in a disorganized and superficial manner. One early consideration of the ecology of sipunculans was by Herubel (1907). Unfortunately, some of his conclusions are not valid because of nomenclatural problems and the paucity of his material.

The only extensive work on the east coast fauna was that of Gerould (1913). He identified the specimens collected by the United States Fish Commission ships during the 1870s and 1880s, together with other miscellaneous collections on deposit in the National Museum of Natural History, Smithsonian Institution. He previously had published on their embryology (1903, 1904, 1907) and had written a short note on the cephalic organs (1908). He published a final paper in 1938 on the sipunculan eyes and nervous system from material he had collected in 1902.

Most of the specimens to which Gerould had access were from northern waters; very few came from south of Cape Hatteras, and most of these were from southern Florida. The northern continental shelf was well sampled, but few specimens were from deeper waters. Of the 23 species belonging to seven genera that Gerould (1913) described, six were new. If one disregards the species found only off southern Florida, which are beyond the limits of my study, six genera and 16 species (four of questionable validity), remain in Gerould's work. Gerould's paper (1913) was limited to the morphology of the worms; little attention was paid to ecology or precise distribution. Moreover, the lack of keys decreased its usefulness to the nonspecialist.

The literature on sipunculans is scattered and often appears in obscure journals and technical reports. The point to emphasize is that almost all the early workers were schooled in the idea that species were immutable types and not biological populations of organisms containing a certain amount of morphological variation. The result of this typological philosophy and poor communication is a confused nomenclature burdened with synonymy, with incomplete or inadequate descriptions, a paucity of illustrations, and neither designation of type material nor indication of where the material is deposited.

Some species have been described on the basis of a single individual—and sometimes one

that was damaged or incomplete. Even though an awareness existed of the biological nature of a species in the 1940s and 1950s (Huxley, 1940; Mayr, Linsley, and Usinger, 1953) this concept did not have a very noticeable effect on the sipunculan literature. Mayr (1965, p. 5) commented: "for the typologist, the type (eidos) is real and the variation an illusion, while for the populationist the type (average) is an abstraction and only the variation is real. . . . The replacement of typological thinking by population thinking is perhaps the greatest conceptual revolution that has taken place in biology." I also discuss further problems caused by earlier typological practices.

## ORGANIZATION OF THE INVESTIGATION

The present investigation is composed of three parts: a description of the study area, descriptions of the sipunculans found there, and a discussion of the zoogeographical groupings of these animals. Included in the second part is a treatment of problems of sipunculan nomenclature. Several taxonomic revisions are suggested.

One outstanding problem for the taxonomist working with sipunculans is the great degree of variability of form they may exhibit and the lack of "hard parts" to count or measure. The indeterminate growth and the contractility of the whole worm increase the problems. Mayr (1965, p. 139) noted that "age variation is of considerable practical importance to the taxonomist, since age variants have often been described as separate species." With reference to sipunculans, Murina (1964a, p. 248) stated: ". . . various individuals of one species differ significantly from one another . . . of greatest importance for the systematics of sipunculids [*sic*] is the age variability of the main taxonomic characteristics . . . among adult individuals of various sizes (ages) of one species."

One outcome of continued research on sipunculans by various zoologists is a reduction in the number of constant characters. Several characters that past workers have considered highly stable within a given species have been shown to be subject to wide variations when a large series of individuals was studied (Théel, 1905; Murina, 1964a). It is difficult to make a comprehensive statement about the variation because any particular character that is not reliable in one taxon may be constant in several



others. At various points in the systematics section, I comment further on this subject.

The final part is based on information presented in the preceding sections. I construct several hypotheses, which may have broad implications for the entire infauna community. These hypotheses should be tested by similar studies on other groups of animals.

#### ACKNOWLEDGMENTS

Numerous individuals have assisted me in this investigation. In addition to supplying me with specimens, Dr. R. L. Wigley of the National Marine Fisheries Service, Woods Hole, Massachusetts, and Drs. H. Sanders and R. Hessler of the Woods Hole Oceanographic Institution, have discussed with me some of the problems encountered. Several members of the faculty of the Graduate School of Oceanography, University of Rhode Island, have guided my thoughts and provided me with information and suggestions, particularly, Drs. H. P. Jeffries, T. Napora, J. A. Knauss, R. L. McMasters, and A. N. Sastry. Many of my associates, especially J. C. Mallett and W. Cobb offered constructive criticism. Drs. I. E. Gray, L. McCloskey, and F. Grassle, formerly of Duke University, provided both specimens and comments. Officers and crew of the R/V *Eastward* and several student volunteers made possible the collection of material on three cruises. Dr. Mary Rice and the other members of the Division of Worms at the National Museum of Natural History, Smithsonian Institution also assisted me.

The late Dr. A. C. Stephen of Edinburgh, Dr. S. Edmonds, Adelaide, and particularly Dr. V. V. Murina, Sevastopol, USSR, aided me in problems of identification and nomenclature. Had it not been for a suggestion from Dr. Eve Southward, Plymouth, England, the present investigation never would have been undertaken.

Dr. D. J. Zinn, University of Rhode Island, was my principal adviser.

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temperature information from the National Oceanographic Data Center. The completion of this manuscript was aided by a grant from Utica College, Utica, New York.

Dr. W. K. Emerson and Dr. E. Kirsteuer, Department of Living Invertebrates, and the Graphic Arts Department of the American Museum of Natural History, assisted in the editing of the final draft of the manuscript and the preparation of the illustrations.

Finally, my wife, Norma, has assisted me in many ways in the collecting and processing of the material as well as in the preparation and typing of this manuscript.

#### METHODS AND MATERIALS

The material used for this investigation was accumulated from a variety of sources covering a broad area (tables 1 and 2). Most came from collections on the continental shelf and slope and were made by the United States Geological Survey and the National Marine Fisheries Service (formerly United States Bureau of Commercial Fisheries) and processed under the direction of Dr. R. L. Wigley of the Woods Hole, Massachusetts National Marine Fisheries Service. A second major contribution of specimens was made by H. Sanders and R. Hessler from their Gay Head-Bermuda benthic transect collections. Five projects at the Duke University Marine Laboratory, Beaufort, North Carolina, added to the material from the Cape Hatteras region. These collections were made by I. E. Gray, L. McCloskey, J. Day, Mary Potts, F. Grassle, and G. Rowe. The sipunculans from four museums were made available to me through the cooperation of the following zoologists: M. Rice, National Museum of Natural History, Smithsonian Institution; E. Kirsteuer, the American Museum of Natural History; E. L. Bousfield, Canadian Museum of Natural History; and W. H. Hartman, Yale Peabody Museum. Specimens were also obtained from a group at the Bedford Institute of Oceanography, Dartmouth, Nova Scotia, and from various members of the Systematics-Ecology Program at the Marine Biological Laboratory, Woods Hole, Massachusetts, as well as from M. L. Wass, Virginia Institute of Marine Science, Gloucester Point.

In addition, I have made three collecting trips in the Cape Hatteras region aboard the R/V *Eastward* to obtain sediment and biological

samples. One collecting trip in Narragansett Bay, Rhode Island, was made aboard the R/V *Billy II*. Figure 1 shows the positions of the recent samples in the Cape Hatteras area (see also Sanders, Hessler, and Hampson, 1965; and Emery, 1967). Because of the nature of these collections, the continental shelf and slope were more adequately sampled than either the very shallow (less than 10 meters) or the very deep waters (more than 1000 meters). I have not included the exact station data because they are rather lengthy; however, the data are available on microfilm from University Microfilms, Ann Arbor, Michigan, as Appendix D of dissertation no. 69-1030.

Various persons used different methods of

TABLE 1  
SOURCES OF RECENT SIPUNCULAN SPECIMENS USED IN  
PRESENT INVESTIGATION, EXCLUSIVE OF MUSEUM  
MATERIAL

Source	% of Total
R. L. Wigley	55.9
H. Sanders and R. Hessler	14.4
F. Grassle	11.5
J. Day and M. Potts	5.1
I. E. Gray	5.0
E. B. Cutler	4.8
G. Rowe	1.5
SEP-MBL	0.6
L. McCloskey	0.6
M. L. Wass	0.6
Bedford Institute	0.2
Totals	100.0

collecting. Most collections were made by a bottom grab or a dredge-trawl.

The methods used for washing and processing the samples were also varied. The collections that Sanders, Grassle, and I made were all treated similarly as follows: Any sediment remaining in the dredge or trawl (not having washed out on the way to the surface) was placed in a large garbage can which had a spout cut in it. Water from a firehose (high-volume, low-pressure) was applied to disperse the sediments and organisms. This dispersed material flowed onto a fine screen (1 mm. mesh or less). The material remaining on the screen was subsequently examined under a dissecting microscope in the laboratory. This procedure ensured the collection of smaller forms frequently lost by other methods and avoided damage to their soft parts. The collections were fixed with 5-10 percent Formalin in sea water on board ship, and subsequently transferred to 70 percent ethanol in the laboratory.

The methods used to collect and analyze sediment samples are discussed in the section on sediments. The analyses were made in the geological laboratories of the Graduate School of Oceanography of the University of Rhode Island. Data on sediment were also available from collecting stations of Sanders (1965) and F. Grassle (personal commun., 1966).

The available information on bottom temperature has varying degrees of reliability and significance. Some of the records are from reversing thermometers tripped "near the bottom," and others were obtained directly from the samples of mud. Both these techniques

TABLE 2  
NUMBER OF RECENT COLLECTIONS OF SIPUNCULANS USED IN PRESENT INVESTIGATION

Location	0-10	Depth (in Meters)			Total
		11-150	151-2000	2001-5000	
Cape Cod to Nova Scotia (42°-45°N)	0	40	29	0	69
Cape Hatteras to Cape Cod (35°-42°N)	1	104	83	34	222
Cape Kennedy to Cape Hatteras (28°-35°N)	8	133	75	9	225
Florida Keys to Cape Kennedy (24°-28°N)	2	16	9	0	27
Totals	11	293	196	43	543



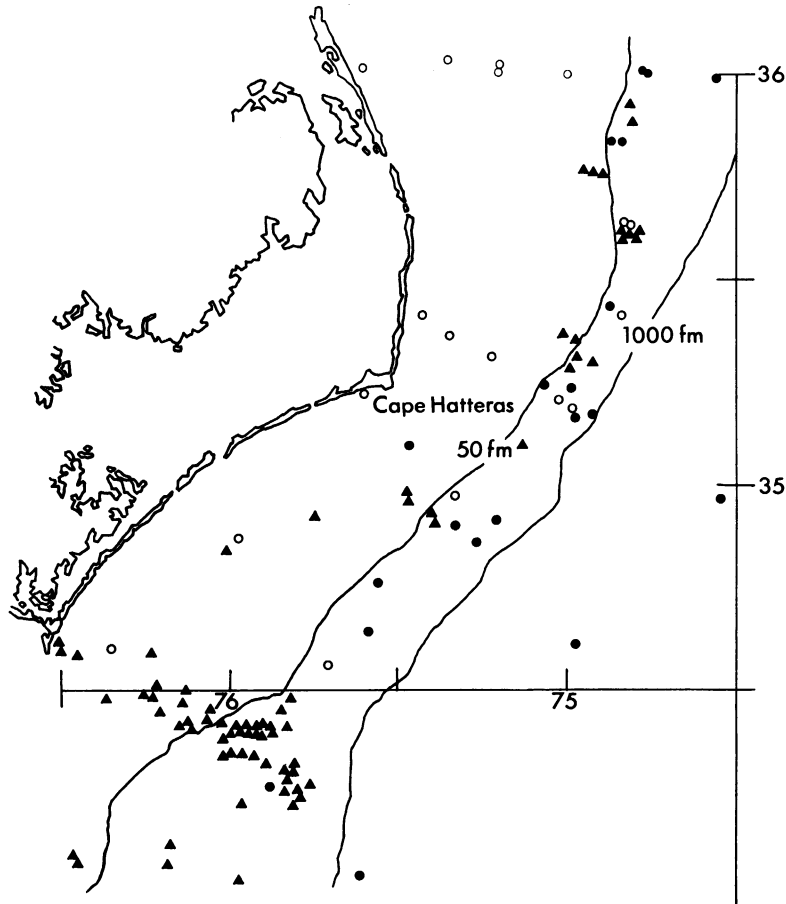


FIG. 1. Sampling stations for Cape Hatteras region.

Symbols: ○, ●, author's stations: ○, without sipunculans; ●, with sipunculans; ▲, collection stations of other investigators.

have room for error, as is explained in the section on temperature. I obtained most of the information from the literature, the National Oceanographic Data Center, Washington, D. C., and my own observations.

All the information connected with a given sample was coded and punched on a Hollerith card in a given format to facilitate data storage and retrieval. The format was modified from the invertebrate ecology data card used by the U. S. Bureau of Commercial Fisheries.

To identify the specimens I used a stereo-

dissecting microscope and, when necessary, a compound microscope. The specimens were first separated into genera, then subdivided further. This process was facilitated by the use of preliminary keys obtained from the late A. C. Stephen. These keys, which were prepared for inclusion in a monograph that he was writing at the time of his death, are here termed Stephen's unpublished keys. Appendix A gives the references to which I had access while identifying the various species.

## ENVIRONMENTAL FACTORS

### TOPOGRAPHY

THE AREA under consideration is divided into four major zones: the continental shelf, slope, rise, and the abyssal plain (fig. 2). The length of the shelf is about 2500 kilometers and its area about 420,000 kilometers<sup>2</sup>. The area of the slope is about 62,000 kilometers<sup>2</sup> including the Blake Escarpment. The total area of the zone between the shelf break and the 5000-meter contour is about 1,400,000 kilometers<sup>2</sup> (Emery, 1966a; Emery and Schlee, 1963).

The shelf is further subdivided into three

sections: southern (straits of Florida to Cape Hatteras); middle Atlantic (Cape Hatteras to Cape Cod); and northern (primarily the Gulf of Maine).

The general features of the southern and middle sections of the shelf are similar. They are both classed as wide, crescentric bights, the center portion of each section being much wider than the ends. At the southern end, the shelf is only 9 miles wide, increasing to about 75 miles off Georgia. It then decreases to about 19 miles off Cape Hatteras and increases again to about

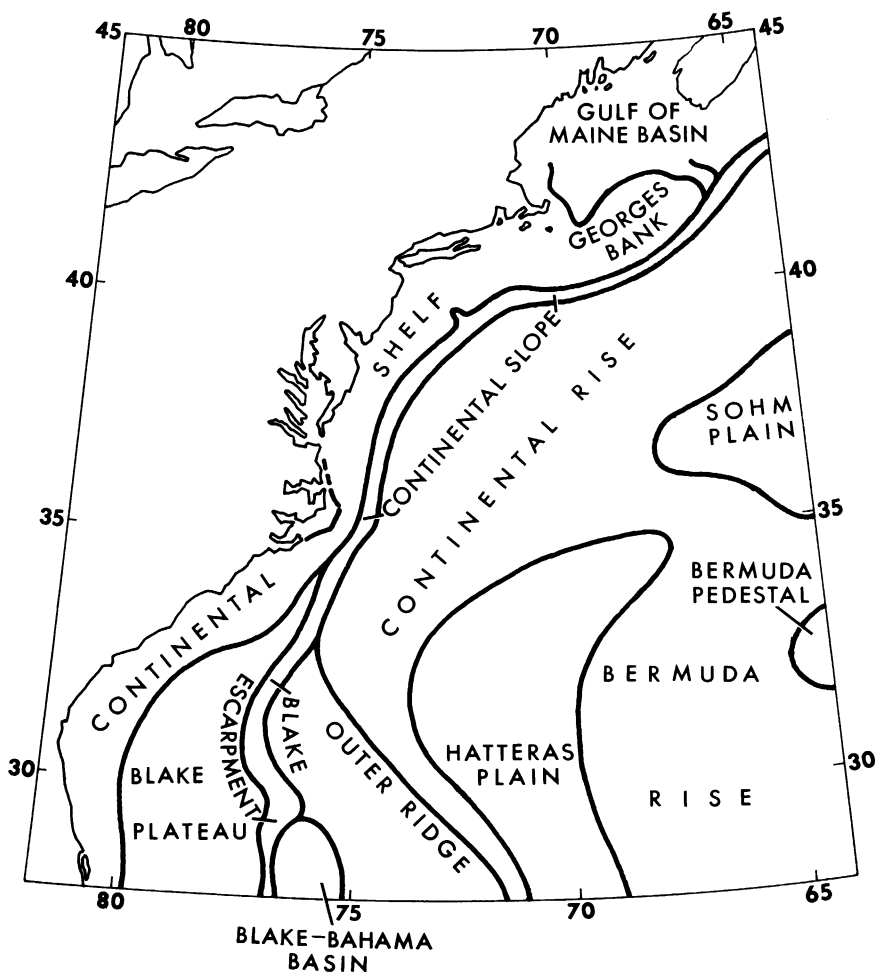


FIG. 2. Diagrammatic representation of major topographic features (adapted from Emery, 1966).



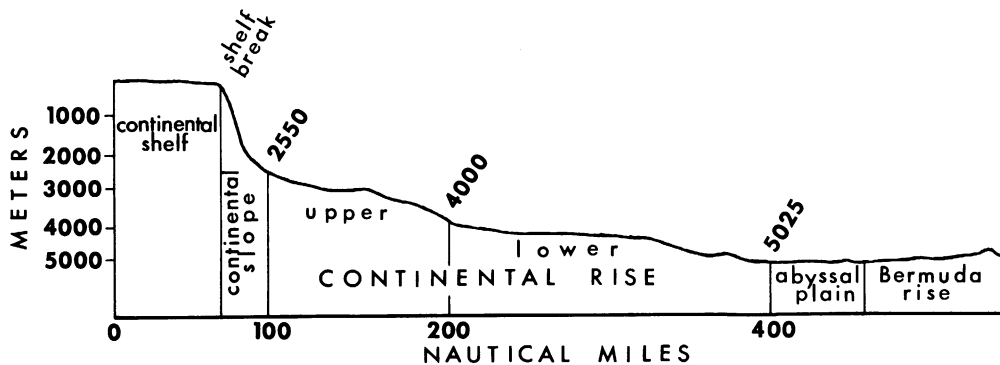


FIG. 3. Continental margin provinces type profile off northeastern United States (adapted from Heezen, Tharp, and Ewing, 1959).

90 miles off New Jersey. These regions also have a generally smooth, even bottom with a slow, gradual slope (less than one vertical unit per 1000 horizontal units) (see fig. 3).

The Cape Cod-Nantucket Shoals-Georges Bank boundary area is more complex topographically; Parr (1933) has offered a detailed description of it. North of this area the bottom is much less regular than to the south in the preceding sections. This irregularity results from the erosion and deposition of Pleistocene glaciers. A natural boundary around the 100-meter contour separates the peripheral shallows from a central bottlenecked basin that leads to the open sea via two channels. This irregular basin deepens to 275 or 300 meters in several places but commonly ranges from 210 to 240 meters. Numerous ledges, banks, swells, and knolls scattered throughout the area eliminate the possibility of broad generalizations about the depth.

The shelf break is between 100 and 200 meters, but usually found between 150 and 180 meters. At this point the gradient increases sharply from about 1:1000 to at least 1:40, and usually 1:8 to 1:15 (Heezen, Tharp, and Ewing, 1959). A minimum gradient of 1:40 defines the continental slope, which generally ranges from 150 meters down to about 2000 meters. The lower limit is shallower in the north (about 1400 meters) and deeper (2500) off Cape Hatteras. The uniformity of the slope off the mid-Atlantic states is broken by frequent submarine canyons, some of considerable dimensions.

South of Cape Hatteras, the slope is divided by the Blake Plateau, at a depth of 600–800

meters. This wedge-shaped “second shelf” has an area of about 128,000 kilometers<sup>2</sup> (Pratt and Heezen, 1964) and is bordered on the west by a uniform but abbreviated continental slope. The Blake Escarpment forms what might be considered the seaward, lower portion of the slope on the eastern side of the Blake Plateau. At about latitude 30°N is an eastward-projecting “nose” north of which this slope leads into the rise. South of this “nose” the slope is very steep (up to a gradient of 1:2) and goes down much deeper to about 4700 meters into the Blake-Bahama Basin. See Pratt and Heezen (1964) and Uchupi (1967) for detailed discussions of this area.

At the base of the slope the gradient decreases, generally to between 1:100 and 1:700. This region, the continental rise, extends down to depths of 4800 meters to 5000 meters with moderate to low local relief.

Flat abyssal plains and deep ocean floor with a gradient less than 1:1000 are represented in this area by the southwestern tip of the Sohm Abyssal Plain, the northern end of the Hatteras Abyssal Plain, and by a portion of the small Blake-Bahama Basin.

#### BOTTOM CURRENTS

The general movement of water over the bottom is southerly on the shelf and downward off the slope onto the rise, except in the area which lies underneath the Gulf Stream. Here the flow is north-northeast (Knauss, 1966). In the area of Cape Hatteras and the Gulf of Maine, eddies and countercurrents complicate the picture by introducing local variations.

## TEMPERATURE

The temperatures on the ocean floor of the study area are extremely varied, ranging from 0°C. or below in the Gulf of Maine to 28°C. off Florida. In addition to this trend from north to south, any given point in shallow water (less than 20 meters) may be subjected to annual fluctuations of 10–15°C.

The information presented in this section has been taken from a variety of sources. All the literature to which I had access on temperature concerns either surface temperatures or the temperatures of the entire water column; none of it deals exclusively with bottom temperatures. Three important papers (Bigelow, 1927, 1933; Parr, 1933) were written more than 35 years ago. Parr used surface temperatures from lightships and lighthouses and assumed they were valid down to about 20 meters depending on the location and season. Bigelow dealt with the general picture, the bottom temperature only incidentally, and to a certain degree extended these data from "near bottom" records. One of his papers (1927) was on the Gulf of Maine, the other (1933) considered waters off the mid-Atlantic states.

Anderson et al. (1961) and Wilcoxon (1964) used the data collected on the nine cruises of the M/V *T. N. Gill* during 1953 and 1954 in the

area between Cape Hatteras and Florida Straits for their temperature analysis. Again the bottom temperatures are estimated from the reversing thermometers nearest the bottom. Similarly, Sanders, Hessler, and Hampson (1965) constructed a benthic temperature profile from data gathered by several Atomic Energy Commission cruises between Woods Hole, Massachusetts, and Bermuda. A recent technical report by Stefansson and Atkinson (1967) provided information for the Cape Hatteras area down to 500 meters.

To supplement this material I have analyzed 256 sets of data from National Oceanographic Data Center for inadequately covered areas on the slope at depths between 150 meters and 2000 meters (fig. 4). They consisted of a series of temperatures from Nansen casts for which the deepest reading was between 70 and 100 percent of the distance to the bottom. Of the 256 sets only 226 were usable and 52 of these were from southern Florida. Of the 174 remaining sets less than 15 percent actually included bottom temperatures. Most of the sets I used had temperatures from at least 80 percent of the total depth. With these, I had to extrapolate and estimate the actual bottom temperature. This procedure is easier and relatively accurate at greater depths.

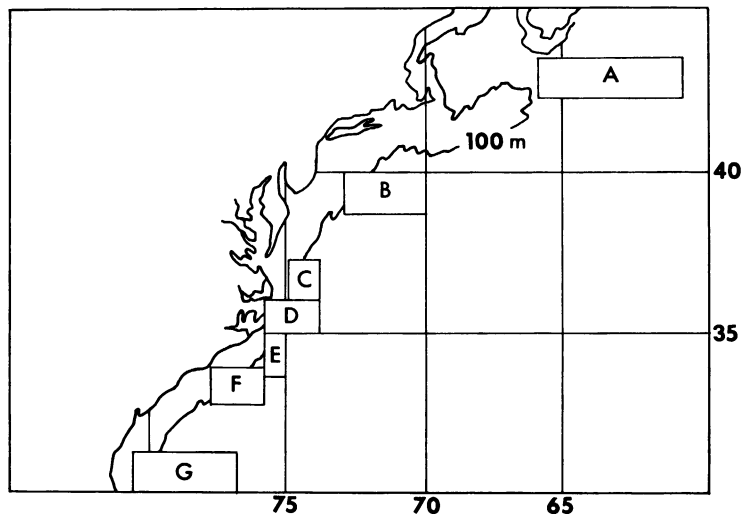


FIG. 4. Areas from which temperature information was obtained from National Oceanographic Data Center. Number of observations of bottom temperature at depths between 150 and 2000 meters: A, 39; B, 38; C, 13; D, 13; E, 6; F, 22; and G, 33.

TABLE 3  
GENERALIZED SUMMARY OF MAXIMUM AND MINIMUM BOTTOM SEA-FLOOR TEMPERATURE<sup>a</sup>

Depth (in Meters)	North	Central	South	Differential
0-10	-1-13° C.	3-23° C.	12-28° C.	14-20° C.
10-50	0-10	3-17	15-27	10-14
50-150	2-10	7-12 <sup>a</sup>	18-26	5-8
150-200	4-8	9-12	12-20	3-8
250-500	5-7	5-9	5-15	2-10
500-1000	4.0-5.5	4.0-5.5	4.0-5.5 <sup>b</sup>	1.5
1000-2000	3.2-4.0	3.2-4.0	3.2-4.0	0.8
2000-3000	2.5-3.4	2.5-3.4	2.5-3.4	0.9
3000-4000	2.3-3.0	2.3-3.0	2.3-3.0	0.7
4000-5000	2.2-2.4	2.2-2.4	2.2-2.4	0.2

<sup>a</sup>In the vicinity of Cape Hatteras, maximum in the central rises to 15° C.; minimum in south decreases to 15° C. for all shelf values.

<sup>b</sup>On the Blake Plateau, 700-850 meters, temperatures are between 8.5° C. and 10° C.; may go down to 6.5° C. or up to 13.5° C.

Information from all of these sources provides the following generalized description. One must accept this as a generalization, and look more closely at particular locations before drawing any conclusions, particularly in the regions of Cape Cod and Cape Hatteras where the topography and currents cause more erratic changes.

**DESCRIPTION:** As the depth increases, both the mean temperature and the temperature range decrease. At 1000 meters the temperature rarely exceeds 4° C., and below this point the temperature decreases by about 0.5° C. per 1000 meters to a low of 2.2° C. at 5000 meters. The variation at any given point is invariably less than 1° C. Between 500 meters and 1000 meters the temperature usually ranges from 4-5° C., rarely reaching 6° C. (table 3).

The Blake Plateau presents a unique situation because the Gulf Stream flowing over much of it affects the bottom temperature down to 750-850 meters. The temperature generally ranges from 8.5° C. to 10° C. but has extremes of 6.5° C. and 13.8° C. The fluctuations do not seem to be correlated with seasonal changes.

As the depth decreases beyond 500 meters the situation becomes more complex and the area must be subdivided into three broad regions as in the preceding section: northern (Nova Scotia to Cape Cod), central (Cape Cod to Cape Hatteras), and southern (Cape Hatteras to Cape Kennedy).

Although the 250- to 500-meter zone has a

low temperature limit at about 5° C. in all regions, the high temperature varies. In the north the high temperature rarely exceeds 7° C., but in the central region it may rise to 9 or 10° C. South of Cape Hatteras the meandering Gulf Stream may periodically bring water as warm as 15° C. in contact with this portion of the slope.

The first indications of seasonal variations occur along the shelf break (150-200 meters). In deep water, fluctuations are not associated directly with the changing surface climate. In the northern sector, the range is from 3 to 9° C. Centrally, a uniquely constant band lies along these depths up to about 125 meters. It usually stays between 10 and 12° C., sometimes it is a little cooler. South of Cape Hatteras, the temperature varies from 12 to 20° C.

On the outer part of the shelf (50-150 meters), south of Cape Hatteras, the temperature range is usually from about 18 to 26° C., occasionally colder at the northern end. The central region has a range of 7-12° C., and north of Cape Cod, the temperatures at similar depths (25-100 meters) range from a high of 10° C., to a low of about 2° C.

The bottom temperatures from 8 to 50 meters, which include most of the shelf area, are extremely variable. In the south, they fluctuate from about 15 to 27° C. (occasionally down to 12° C. around Cape Hatteras), centrally, the range is from 3 to 17° C. (3-15° C. off New



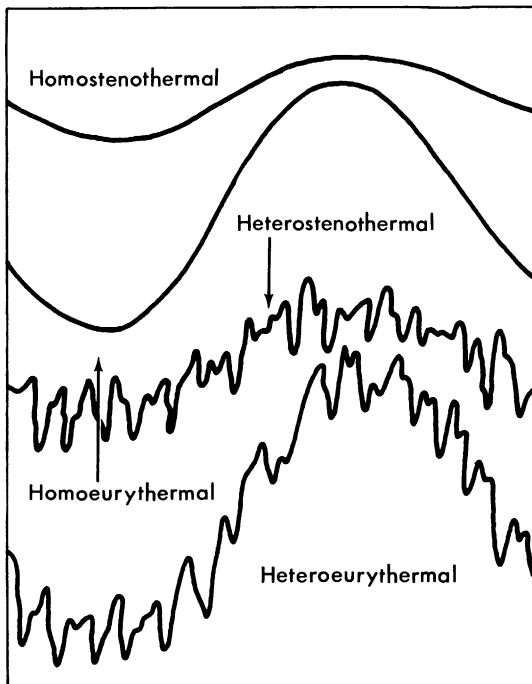


FIG. 5. Diagrammatic illustration of four main categories of temperature conditions (from Parr, 1933). Arrows indicate revisions suggested in this text. Abscissa is time, ordinate is temperature.

York; 5–17° C. off Virginia). In the northern sector the range is from 0 to 10° C.

In less than 10 meters of water the bottom temperature is essentially that of the surface. This shallow area has the widest extremes: –1 to 13° C. in the northern, 3–23° C. in the central, and 10–28° C. in the southern region.

Although the absolute temperatures undoubtedly play an important role in determining the distribution of most kinds of animals, the range of temperatures must not be overlooked. It is apparent that the greatest ranges occur in the shallowest water (0–25 meters—see table 3). Parr (1933) discussed temperature ranges at length and considered the rate of change. Figure 5 represents a restatement of his proposed nomenclature, which he pictorially summarized in his figure 27.

The conventional terms eurythermal and stenothermal are inadequate to describe the situation in these areas. For biological purposes it is necessary to consider not only the regular, periodic changes from season to season, but also the irregular fluctuations of short duration

around the seasonal trends. These two kinds of changes (sudden and gradual) may require a different type of response from an organism. A species having the ability to resist one type of variation is not necessarily able to resist both. These kinds of changes must be considered as two separate and independent factors in the environment. Therefore, Parr (1933) proposed a revised classification for geographical regions and for the organisms living therein.

1. Homostenothermal—most stable; short-term, seasonal fluctuations are slight.
2. Heterostenothermal—seasonal differences are great, but short-term, irregular fluctuations are slight.
3. Homoeurythermal—seasonal differences are slight, but irregular fluctuations are large.
4. Heteroeurythermal—least stable; both seasonal and irregular fluctuations are large.

Although not widely accepted, these terms have merit. It is unfortunate that Parr did not remain consistent in his use of eurythermal and stenothermal. He had previously used them in the conventional way, and the usage in conditions 1 and 4 of the preceding classification follows this pattern. His classes 2 and 3 should be reversed to preserve uniformity of usage. Therefore, I propose the following modifications:

2. Heterostenothermal—seasonal differences slight, but short-term fluctuations are great.
3. Homoeurythermal—seasonal differences great, but irregular fluctuations slight.

This scheme is used in subsequent discussions.

In summary, the environment is characterized as very stable and cold at depths greater than 500 meters. It is fairly stable and moderate between 125 and 500 meters north of Cape Hatteras (homostenothermal). South of Cape Hatteras it is more variable (heterostenothermal) because of the effect of the Gulf Stream. The situation is changeable in waters less than 100 meters. Parr (1933, p. 82) made the following summary: "In the shallow-water belt along the Eastern coast of the United States we have comparatively heterostenothermal conditions in the region of Cape Hatteras; more heteroeurythermal conditions in the region of Nantucket Shoals; homoeurythermal conditions in the Southern and Middle Atlantic bights; homostenothermal conditions in the Straits of Florida

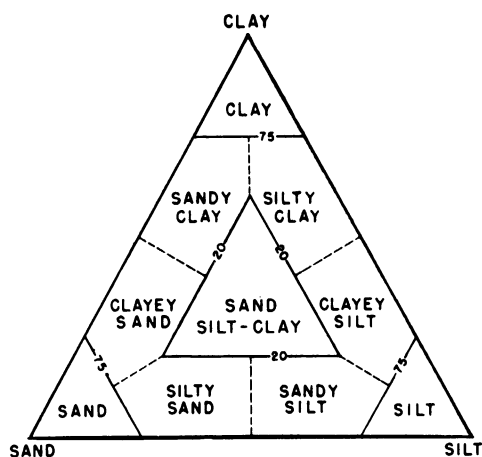


FIG. 6. Standard triangle diagram used to show the relationship between the three grades of sediment (Shepard, 1954).

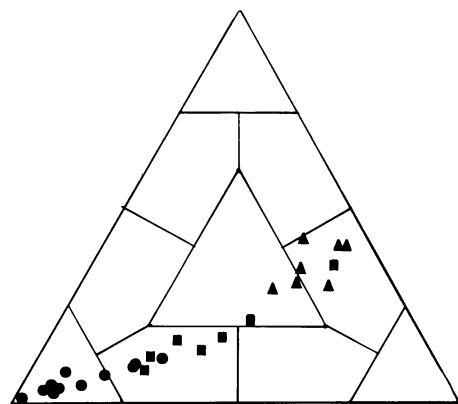


FIG. 7. Sediment triangle with points from author's Cape Hatteras stations.

Symbols: ●, 10–200 meters; ■, 400–600 meters; ▲, 1000–3000 meters.

and to a lesser degree towards the northern part of the Gulf of Maine.”

### SEDIMENTS

As most sipunculans included in this investigation live in the sediment (excluding those inhabiting cast mollusk shells, coral, rock, etc.), it seems appropriate to consider sediment as an important factor in determining the distribution of these species. Sediments can be analyzed in numerous ways, but my efforts have been directed solely toward the distribution of particle size. The mineral composition of the sediments

and the organic matter present may be important, but both are beyond the scope of my work. Accurate analyses of the amount of usable organic matter present are difficult and typically inconclusive (Sanders, Hessler, and Hampson, 1965; Southward, 1965).

The nomenclature used for describing sediments has had a rather turbulent history, but Shepard (1954) introduced some stability and his terms have been widely accepted. They are derived from the scheme shown in figure 6, which contains 10 classes based on the relative percentages of the three components (sand, silt, clay) in the sample. Table 4 lists the approximate limits of these classes (Shepard, 1954). Figure 7 shows the distribution of my Cape Hatteras samples according to Shepard's scheme. These descriptive terms facilitate comparison with other publications. The categorization is, in large measure, of restricted usefulness because each class has broad limits; e.g., sand may be coarse or very fine and thus suitable or unsuitable for a given species to inhabit. Although the scheme gives a true indication of the nature of the sediment, it is of limited precision. The description of the sediments is used in subsequent discussions on the distribution of the various species.

Because this study covers such a broad area, it would be unrealistic for me to attempt a detailed description of the entire region with all its peculiarities, assuming that the necessary information was available. Most previous investigations of marine sediments have been within rather limited geographical areas. In the near future the United States Geological Survey,

TABLE 4  
APPROXIMATE PERCENTAGE LIMITS OF THE THREE COMPONENTS OF EACH SEDIMENT CLASS

Class	Sand	Silt	Clay
Sand	75–100	—	—
Silty sand	45–75	20–45	—
Sandy silt	20–45	45–75	0–20
Silt	—	75–100	—
Clayey silt	0–20	45–75	20–45
Silty clay	0–20	20–45	45–75
Clay	—	—	75–100
Sandy clay	20–45	0–20	45–75
Clayey sand	45–75	0–20	20–45
Sand-silt-clay	20–60	20–60	20–60

Woods Hole, Massachusetts, should finish its analyses of the continental shelf and slope; our knowledge of this area then will be greatly expanded (Emery and Schlee, 1963). A preliminary report (Emery, 1966b) gave a brief general outline of the results.

**CONTINENTAL SHELF:** The sediments of the continental shelf, the most varied, do not lend themselves to sweeping generalizations because of the geological history of the region as well as the uneven topography, currents, and the influx of new materials from the major rivers. A number of papers were written between 1930 and 1960 on the sediments of this region, and these, together with earlier works, were reviewed in a paper by Uchupi (1963), which forms the basis for most of the following. Subsequent work (Pilkey, 1964; Sanders, Hessler, and Hampson, 1965; Garrison and McMaster, 1966; Menzies et al., 1966) have refined our knowledge about certain local aspects, but the general understanding remains little changed.

The Bay of Fundy, the most northerly portion of the shelf, is mostly sand with a shift toward sandy silt and silt in the upper bay. From the Bay of Fundy to Cape Cod are scattered rock outcrops with a thin layer of gravel and sand near the coast. The valleys have finer sediments. The extremely irregular topography of the offshore bottom causes the sediments to show a predominance of coarser materials on the hills with finer sands and silts in the intervening basins. The eastern and southern channels of the Gulf of Maine are covered with coarse sands and gravels. Georges Bank is predominantly sand with some gravel patches.

The shelf between Nantucket Island and Hudson Canyon changes with increasing depth from silty sand and sandy silt (some fine and medium sand) to coarse sand with patches of gravel between 25 and 59 meters back to silty sand, sandy silt, and silt toward the edge of the shelf.

From Hudson Canyon to Cape Hatteras are two zones: an inner one (to a depth of 40 meters) which has mixed medium to fine sand and patches of gravel, and an outer zone, which has finer and more uniform sand that again becomes somewhat coarser near the edge of the shelf.

South of Cape Hatteras, the inshore shelf (0–30 meters) is characterized by fine sand, silty sand, and sandy silt. Around 30–40 meters

shell fragments and other coarser materials become apparent. Farther out the sediment becomes sandy silt and silty sand with fragments of calcareous algae, ectoprocts, barnacles, and echinoids. This sediment may become coarse enough in places to be classed as medium sand. Some spots have shell hash, rock outcrops, or coral.

The condition of the area under study was summed up by Shepard (1963, p. 259) when he stated, "On the continental shelf the actual picture . . . is that of irregularly distributed sediment zones which show little relation either to depth of water or distance from the shore."

**CONTINENTAL SLOPE:** The continental slope has been studied less thoroughly than the shelf. From Uchupi (1963), Sanders, Hessler, and Hampson (1965), and Menzies et al. (1966), however, the following can be said: from Nova Scotia to Cape Hatteras the mean particle size of the sediments of the slope decreases with increasing depth and sediments are predominantly mixtures of silt and clay. The upper slope may have some fine sand, but below 1000 meters sand is not significant. Canyons have silt and clay on the sides and sands and gravel in the axes. From Cape Hatteras south the slope is covered by silty sand and sandy silt with planktonic foraminifera. Variation here is great. The Blake Plateau is predominantly *Globigerina* and pteropod ooze with some mineral nodules.

The steepness of the slope, the occurrence of slumps, and the presence of canyons cause marked deviations on the slope, resulting in a region of rapid transition in sediment types over a relatively short horizontal distance.

**CONTINENTAL RISE AND ABYSSAL PLAINS:** The continental rise and abyssal plains below 2500 meters are fairly uniform. As stated in Emery (1966b, p. A-10), "sediments on the continental rise and abyssal plains are clay interbedded with fine sands and coarse silts." Although detailed reports are scarce, no evidence exists of disagreement (Hedgpeth, 1957, p. 645; Shepard, 1963; Sanders, Hessler, and Hampson, 1965). The origin of the deposits may be either terrestrial or planktonic (calcareous or siliceous organisms), but the size of the particles is in the silt-clay segment of the "sediment spectrum." These sediments are frequently referred to as oozes if the major contribution is from pelagic animals. Deeper than 5000 meters the amount of silt and ooze becomes insignificant leaving



TABLE 5  
RELATIONSHIP BETWEEN DEPTH AND PERCENTAGE OF SEDIMENT TYPE ON A WORLDWIDE BASIS

Depth (in Meters)	Rock Gravel	Sand Silt	Reducing Clay	Oxidizing Clay	Siliceous Oozes	Calcareous Oozes
200	15	70	15	—	—	5
500	10	60	25	—	—	5
1000	10	45	35	—	—	10
2000	10	20	45	5	—	20
3000	5	10	30	15	—	40
4000	0	5	10	10	5	70
5000 <sup>a</sup>	0	5	0	60	25	10

<sup>a</sup>Below 5000 meters, the sediment is almost all oxidizing clay.

mostly clay. Table 5 is a generalized representation of the variation of sediment types with depth on a worldwide basis. It was derived from plate 3 in Bruun (1957). My own results agree in general with these figures.

ANALYSES IN THE CAPE HATTERAS REGION: I analyzed 33 samples from the shelf and slope in the Cape Hatteras region (fig. 8). The samples were obtained by using either a Pierce box (anchor) dredge, a Van Veen grab, or a Phleger corer. Subsamples were then sealed in plastic bags for transport to Rhode Island. The removal of the silt-clay fraction was accomplished in an inverter. The sand and coarser fractions were dried and the silt-clay portion placed in another sealed plastic bag for subsequent analysis. A 2-mm. sieve was used to separate the gravel (and shells) from the sands. The sand fraction was analyzed by means of the Emery Settling Tube (Emery, 1938; Poole, 1957) and the coarser material was sieved at 1/2-phi intervals (table 6). The silts and clays were analyzed by the hydrometer technique (Krumbein and Pettijohn, 1938). In a few samples the amount of fine material was insufficient to be completely analyzed and consequently the silts and clays are lumped. The calculations were made with the aid of the IBM 360 computer with programs written by T. Lachance. The apparent mode that frequently appears at 4.5 phi may be an artifact attributable to the overlap between the settling tube and hydrometer methods. Table 6 shows the millimeter equivalents of the phi scale. The results are summarized in table 7. A complete listing of the data necessary for drawing frequency distribution curves is available as appendix C,

dissertation no. 69-1030, University Microfilms, Ann Arbor, Michigan.

In general, the change of sediment with depth in this area is the same as elsewhere, i.e., the mean particle size tends to decrease with depth. Figure 9 shows this trend and the change in percentages of the three main components (sand, silt, clay). Figure 9 was based on the grouped data presented in table 7. The stations were grouped according to depth (0-75 meters, 150-200 meters, etc.) to illustrate the trends more clearly.

The characteristics of the sediments can be summarized as follows. Sorting: on the shelf, from 0 to 75 meters the sediments are mostly well sorted (with some exceptions); from 100 to 200 meters they are poorly sorted; and from 400 to 1000 meters they are very poorly sorted. The skewness never exceeds 1.0 in either direction. Negative values (skewness to the left, toward coarser particles) occur only on the

TABLE 6  
PHI SCALE AND PARTICLE SIZE (IN MILLIMETERS)

Phi Scale	Size	Wentworth Classes
-3	8.000	Pebble
-2	4.000	Granule
-1	2.000	Very coarse sand
0	1.000	Coarse sand
1	.500	Medium sand
2	.250	Fine sand
3	.125	Very fine sand
4	.062	Silt
8	.004	Clay

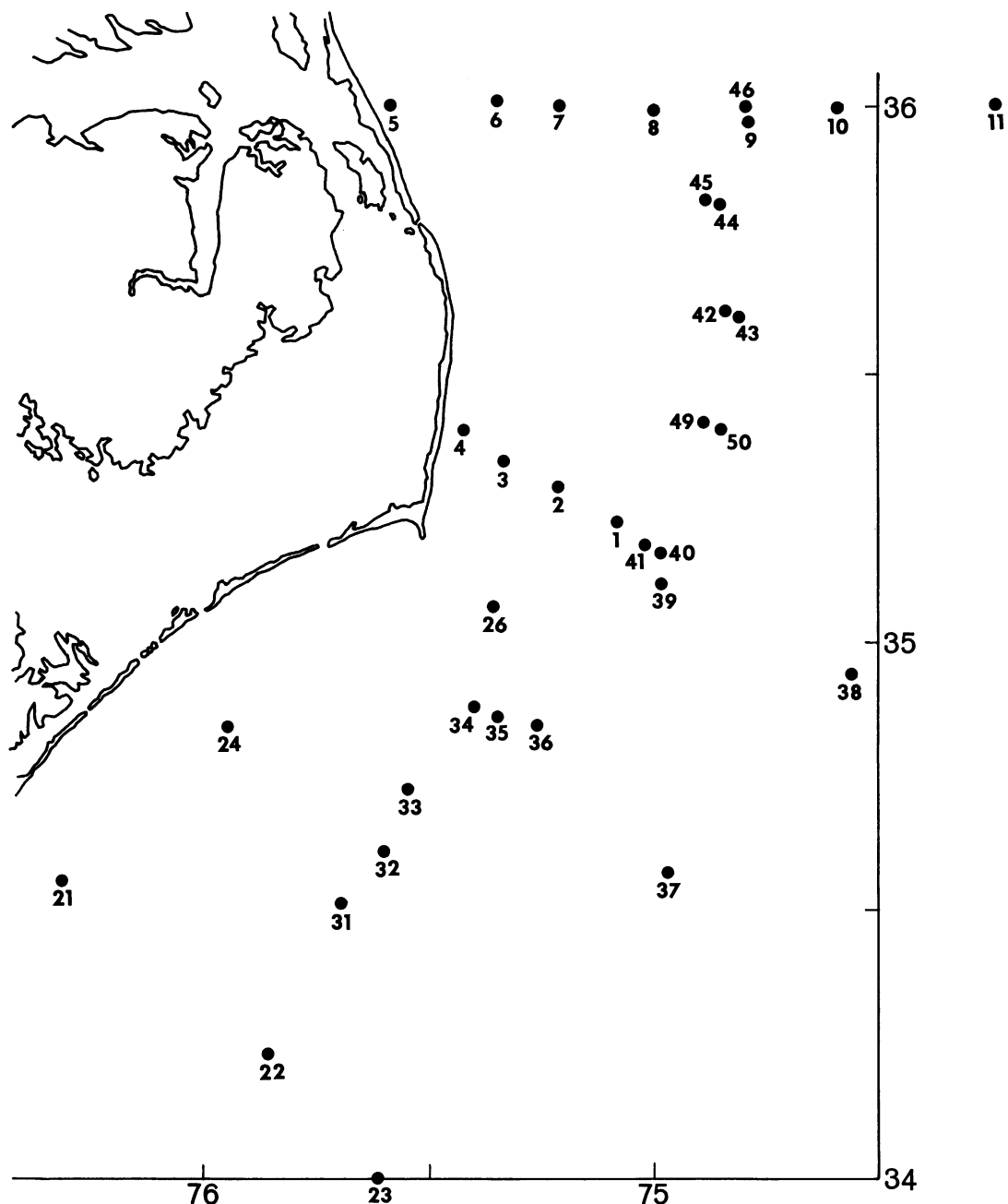


FIG. 8. Distribution of Cape Hatteras sediment samples. Numbers are author's station numbers.

shelf north of Cape Hatteras. The skewness values at the shelf break (150–200 meters) rarely exceed 0.4, indicating a relatively normal curve. Those farther down the slope (400–600 meters) range from 0.41 to 0.67, having a more uniform skewness toward finer particles. The

kurtosis values show a tendency to increase from inshore out toward the edge of the shelf, i.e., the distribution curves become more sharply peaked in the center. A value less than 1.0 at a few shelf stations indicates a deficiently peaked curve with more spread in the center than normal. I

TABLE 7  
SEDIMENT ANALYSIS OF CAPE HATTERAS STATIONS

	Depth Groupings (In Meters)				
	0-75	150-200	400-600	1000-1100	1800-3100
Number of samples	9	7	6	2	5
Textured class based on mean	Sand	Sand	Silty-Sand	Sand-Silt-Clay	Clayey-Silt
Median Phi					
Maximum	3.55	3.86	6.71	6.25	8.25
Minimum	1.24	2.11	2.96	5.76	5.48
Mean	1.90	2.70	4.20	6.50	6.60
% Gravel					
Maximum	9.97	3.98	1.75	0	0
Minimum	.06	0	0	0	0
Mean	2.30	1.40	.20	0	0
% Sand					
Maximum	99.90	91.43	75.29	27.74	21.04
Minimum	88.90	66.15	10.43	14.61	4.16
Mean	95.50	77.50	50.40	21.20	13.30
% Silt					
Maximum	10.44 <sup>a</sup>	22.81	52.73	43.38	54.55
Minimum	0 <sup>a</sup>	5.12	23.43	42.53	43.59
Mean	2.50 <sup>a</sup>	14.90	34.60	43.90	48.80
% Clay					
Maximum	<sup>a</sup>	9.77	36.83	41.96	52.25
Minimum	<sup>a</sup>	3.11	9.84	29.74	30.71
Mean	<sup>a</sup>	6.10	18.60	35.80	37.90
Sorting					
Maximum	1.949	2.579	3.174	—	—
Minimum	.333	.888	1.197	—	—
Mean	.634	1.269	1.948	—	—
Skewness					
Maximum	.172	.614	.671	—	—
Minimum	-.267	.010	.297	—	—
Mean	.064	.197	.548	—	—
Kurtosis					
Maximum	1.046 <sup>b</sup>	2.739	—	—	—
Minimum	.196 <sup>b</sup>	1.392	—	—	—
Mean	.695 <sup>b</sup>	2.210	—	—	—
Coarsest material present in sample	Very coarse sand and shell hash	Medium sand	Fine sand	Very fine sand	Very fine sand

<sup>a</sup>Clays and silts lumped.

<sup>b</sup>These figures are for sediments collected at depths of 0-40 meters.

*Symbols:* 0, no gravel at these depths; —, impossible to calculate values for these stations because of nature of sample.

used Inman's equations to calculate these values.

A series of eight pairs of stations was planned to elucidate the changes that occur at the upper part of the slope: one member of each pair was

at the shelf break (150-200 meters) and the other about 400 meters down the slope from the break at a depth of 500-600 meters. Several conclusions can be reached from the resulting sediment data. In every pair the percentage

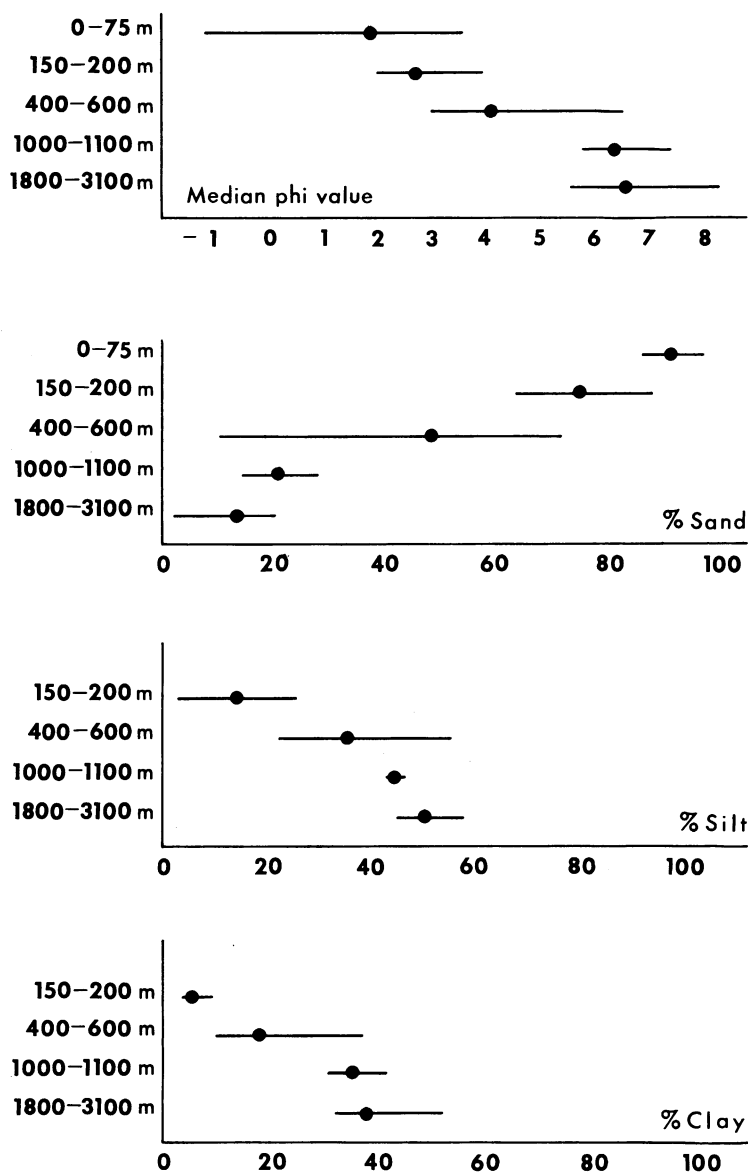


FIG. 9. Trends of characters exhibited by various sediments at different depths in the Cape Hatteras region.

sand and the median particle size decrease with depth; also, with only one exception, the sorting becomes poorer with increasing depth and the distribution curve is more skewed to the right. These factors considered as a whole show that in this region the physical nature of the sediment is consistently different at points relatively close together. This difference becomes important in discussions of species distribution and empha-

sizes the necessity of incorporating accurate locality information.

A few additional observations about the shelf stations should be included. Two stations were made south of the region immediately adjacent to Cape Hatteras, and at each of them the sediment was coarse. One station (no. 21) had much shell and shell hash. On the basis of information from others who have worked in this area, it is

apparent that local variation is considerable.

Immediately north and south of Cape Hatteras, the material becomes much finer (fine to very fine sand predominantly) with 10 percent silt and clay (the only place on the shelf where silts or clays were found). This condition is probably due to the existence of shoals and to the complex hydrography of this area. The mixed currents and the eddies here allow the deposition of finer particles.

At station 4, close inshore just north of the Cape, a large piece of Coquina rock (cemented shell hash) was obtained. Farther north of the Cape (along latitude 36°N) the principal component inshore was medium sand, which changed to fine sand in the middle of the shelf and back to medium sand toward the edge (all in less than 50 meters depth). The negative skew-

ness at all these stations indicated more than a normal share of coarser material.

One unusual feature of the results from the deep stations (2000–3000 meters) is the broad range in the amount of sand, 42–21 percent. None of this sand is larger than 100 microns (very fine sand), and to a great extent it is composed of foraminifera tests. In addition, the two deep stations (nos. 23 and 37) with less than 10 percent sand are south of Cape Hatteras, whereas the three (nos. 38, 10, and 11) with higher percentages are the northern ones.

The results of my investigations, although generally agreeing with statements of earlier workers, provide more specific data on the nature of the sediment from this much neglected and extremely interesting area.



## ECTOPARASITES AND COMMENSALS

ECTOPARASITES AND COMMENSALS were found primarily in or with sipunculans inhabiting discarded shells. Parasitic copepods were found on several *Phascolion strombi*. Commonly, there were two or three, rarely five or six, copepods per host. These parasites have been identified as a new species, *Heliogabalus phascolia* (Lützen, 1968).

The endoproct *Loxosoma* (cf. *minuta* Osburn,

1912) was found on several species, most commonly on *Phascolion strombi* but also on three shallow-water *Aspidosiphon* and on *Golfingia murinae murinae*.

A commensal syllid polychaete (cf. *Syllis cornuta*) was found inhabiting the shells along with the *Phascolion strombi* and *Aspidosiphon spinalis*.

## SYSTEMATICS AND DISTRIBUTION

IN THIS SECTION I present a generalized morphological description of the sipunculans, a key to the species reported herein, and a discussion of each species.

### GENERALIZED MORPHOLOGICAL DESCRIPTION

The phylum Sipuncula is composed of a group of marine, sedentary, vermiform coelomates which, although presumably related to the annelids, lack any trace of segmentation. They have been found in all oceans and live within the sediment or inside a protective shelter such as a discarded mollusk shell (pteropod, gastropod, or scaphopod), foraminifera test, polychaete tube, or crevice in rock or coral.

Sipunculans have two more or less distinct parts: the trunk (or body) and a retractable introvert (fig. 10). The mouth is at the tip of the introvert and is surrounded by tentacles of varying degrees of development and complexity. Behind the tentacular region is a zone which may bear chitinous, posteriorly directed hooks, arranged either in regular rings or scattered. The introvert may be less than half the trunk length in some species or many times its length in others. The demarcation between these two regions is usually well defined by the abrupt narrowing of the diameter where the introvert begins. This area generally coincides with the position of the anus, nephridiopores, or both.

The shape of the body may vary from almost spherical to cylindrical. In those forms inhabiting discarded gastropod shells, the living worm

retains the spiral shape of its habitation even after having been removed from the shell. There is a variety of epidermal structures such as papillae, holdfasts, shields, hooks, and spines. Generally pigmentation is scant but when present, is usually in shades of yellow or brown.

Internally these worms are relatively simple. The digestive tract has a straight esophagus and a double-coiled intestine extending back toward the posterior end of the body. The tract terminates in a rectum, which may bear a small caecum. The dorsal anus is at the anterior end of the trunk except in a few species where it is in the mid-region and in one genus (*Onchnesoma*) where it is on the introvert. The distal part of the rectum is anchored to the body wall by a sheet of muscle tissue referred to as the wing muscles. Near the anus a long strand of muscle tissue originates from the body wall and extends down the center of the gut coil, increasing its stability; this is the spindle muscle. It may terminate within the coil or extend beyond to the posterior end of the trunk. In addition, the worm may have fixing muscles, which are fine muscle strands anchoring the gut coils or esophagus to the body wall.

One or usually two simple, saclike nephridia (segmental organs) open on the ventral side at the anterior end of the trunk. The nephridia are invariably attached to the body wall at the nephridiopore and sometimes attached by more extensive mesentery along some portion of their length. The longitudinal and circular muscles of the body wall are frequently arranged in smooth, uniform layers but may be gathered

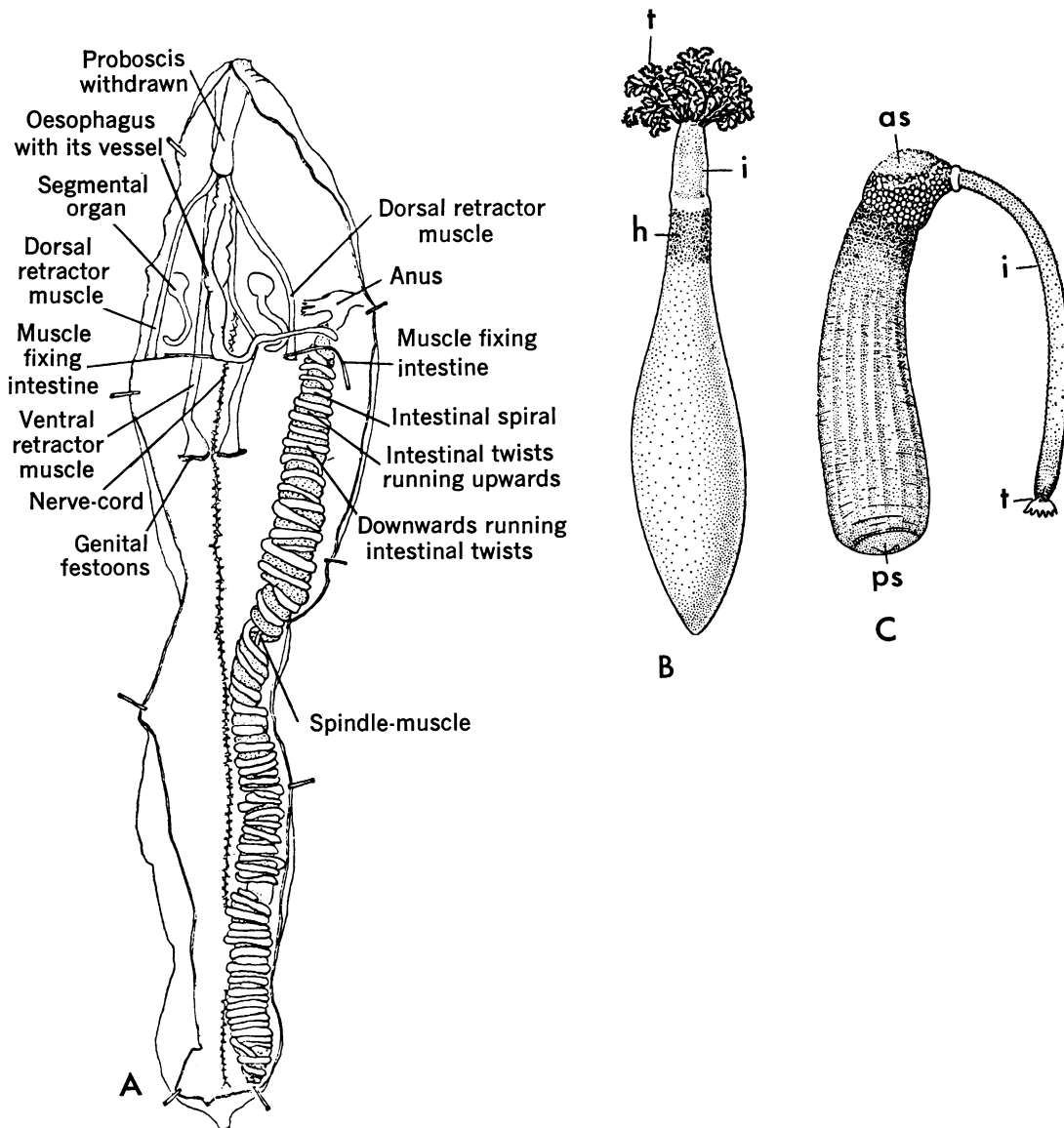


FIG. 10. General morphology of sipunculans (A from Stephen, 1960, after Théel, 1905; B after Fischer, 1922a; C after Selenka, deMan, and Bulow, 1883). A. Internal anatomy of *Golfingia margaritacea* (segmental organ equals nephridia, genital festoons, equals gonads, proboscis equals introvert). B, C. External form of two genera. B. *Themiste*. C. *Aspidosiphon*.

Abbreviations: as, anal shield; h, hooks; i, introvert; ps, posterior shield; t, tentacles.

into bundles. Two or four retractor muscles usually control the introvert. In some of the subsequent descriptions the discussion of the origins of these muscles includes a percentage range that represents a measurement of the distance from the anus to muscle origin as a percentage of the distance from the anus to the

posterior end of the trunk. These percentages are presented as an attempt to lessen the vagueness in previous descriptions of this character.

A ventral nerve cord with lateral nerves and a pair of cerebral ganglia is present. Two or sometimes four eyespots may be present on the "brain." Permanent gonads are uncommon.

The gametes are produced from a strip of tissue that develops near the base of the ventral retractors. The sexes are usually separate, and the nephridia serve as gonoducts. Hyman (1959) gave a general account of the biology of the sipunculans.

#### KEY TO THE EAST COAST SIPUNCULA

1. Anterior end of trunk with chitinous "shield". 2  
Anterior end of trunk without chitinous "shield" . . . . . 6
2. Longitudinal muscle layer generally smooth and continuous . . . *Aspidosiphon* (*Aspidosiphon*) 3  
Longitudinal muscle layer generally separated into separate bundles . . . . . 5  
. . . . . *Aspidosiphon* (*Paraspidosiphon*) 5
3. Anterior shield composed of coarse, dark brown units . . . . . *Aspidosiphon spinalis* (p. 175)  
Anterior shield composed of fine, small, pale units . . . . . 4
4. Posterior shield visible; found in less than 200 m. south of Cape Hatteras; adults longer than 5 mm. . . . . *Aspidosiphon albus* (p. 174)  
Posterior shield not apparent; found in more than 500 m.; adults less than 5 mm. long . . . . . *Aspidosiphon zinni* (p. 176)
5. Anterior shield with 10–12 longitudinal grooves; border of shield well defined . . . . .  
. . . . . *Aspidosiphon cumingii* (p. 179)  
Anterior shield generally without grooves; border poorly defined; gradual transition from pointed, conical papillae at border to blunt, normal papillae on trunk . . . . .  
. . . . . *Aspidosiphon parvulus* (p. 178)
6. Longitudinal muscles gathered into bands . . . 7  
Longitudinal muscles form continuous sheet . 10
7. Longitudinal muscle bands rarely anastomose; scalelike papillae on introvert . . . *Sipunculus* 8  
Longitudinal muscle bands frequently anastomose; scalelike papillae absent . . . . . 9
8. 28–33 longitudinal muscle bands; found in less than 500 m. south of Cape Hatteras . . . . .  
. . . . . *Sipunculus nudus* (p. 127)  
21–24 longitudinal muscle bands, found at depths greater than 500 m. . . . .  
. . . . . *Sipunculus norvegicus* (p. 128)
9. Skin smooth and undivided . . . . .  
. . . . . *Phascolopsis gouldi* (p. 131)  
Skin rough and subdivided into rectangles . . . . .  
. . . . . *Siphonomecus* sp. (p. 130)
10. One nephridium . . . . . 11  
Two nephridia . . . . . 14
11. Anus on introvert relatively near mouth; free living in sediment . . . . . *Onchnesoma* 12  
Anus on anterior of trunk; usually with chitinous holdfasts and living within some shelter . . . . . *Phascolion strombi* (p. 168)
12. Trunk covered with large squamiform papillae . . . . . *Onchnesoma squamatum* (p. 166)  
Trunk smooth, lacking large papillae . . . 13
13. Anus not immediately behind mouth; posterior of trunk with prominent ridges; found at depths greater than 3000 m. . . . .  
. . . . . *Onchnesoma magnibatha* (p. 167)  
Anus immediately behind mouth; posterior of trunk with rows of irregular scales; found in depths less than 800 m. . . . .  
. . . . . *Onchnesoma steenstrupi* (p. 164)
14. Tentacles branching in dendritic manner and well formed; contractile vessel with long, filiform, sometimes coiled tubules . . . . .  
. . . . . *Themiste alutacea* (p. 162)  
Tentacles simple, not dendritically branched, may be lacking; contractile vessel without tubules, but short villi present in one subgenus . . . . . *Golfingia* 15
15. Two retractors . . . . . 21  
Four retractors . . . . . 16
16. Spindle muscle, if present, unattached posteriorly . . . . . *Golfingia* (*Golfingia*) 17  
Spindle muscle attached posteriorly . . . . .  
. . . . . *Golfingia* (*Mitosiphon*) 19
17. Posterior end of trunk with caudal appendage and obvious posterior papillae . . . . .  
. . . . . *Golfingia muricaudata* (p. 133)  
Posterior end of trunk without caudal appendage. . . . . 18
18. Eyespots present; hooks generally present; less than 24 tentacles; body wall thin . . . . .  
. . . . . *Golfingia elongata* (p. 134)  
Eyespots and hooks absent; generally more than 24 complex tentacles; body wall generally thick and muscular . . . . .  
. . . . . *Golfingia margaritacea* (p. 136)
19. The four retractors of equal strength and at about equal distance from ventral nerve cord; two lobes of nephridia of equal length; introvert frequently more than 10 times body length . . . . . *Golfingia trichocephala* (p. 139)  
Ventral retractors twice as massive as dorsals; latter farther from ventral nerve cord; nephridia if bilobed with short, anterior lobe; introvert 4–6 times length of body . . . . .  
. . . . . *Golfingia murinae* 20
20. Single-lobed nephridia; found on slope and rise north of Cape Hatteras . . . . .  
. . . . . *Golfingia murinae murinae* (p. 145)  
Bilobed nephridia, but anterior lobe may be small (rarely absent); found on slope south of Cape Hatteras . . . . .  
. . . . . *Golfingia murinae bilobatae* (p. 145)
21. Contractile vessel with villi; found on outer shelf and upper slope . . . . .  
. . . . . *Golfingia* (*Thysanocardia*) *catharinae* (p. 146)  
Contractile vessel without villi . . . . .

- . . . . . *Golfingia* (*Phascoloides*) 22
22. Posterior of trunk with large, closely packed papillae and caudal appendage; found at depths greater than 1500 m. . . . .  
. . . . . *Golfingia flagrifera* (p. 153)
- Caudal appendage and large, closely packed papillae on posterior absent . . . . . 23
23. Body uniformly covered with prominent wart-like papillae; generally found on shelf south of Cape Hatteras . *Golfingia pellucida* (p. 159)
- Body without uniformly distributed, prominent papillae . . . . . 24
24. Anterior of trunk with necklike constriction; elongate trunk and short introvert . . . . .  
. . . . . *Golfingia constricticervix* (p. 153)
- Anterior of trunk without necklike constriction . . . . . 25
25. Trunk smooth; bulbous and stocky; normal tentacles . . . . . 26
- Trunk with papillae; small and slender; in some cases inhabiting foraminifera or hyalineous polychaete tubes; reduced tentacles . . . . . *Golfingia minuta* (p. 155)
26. Posterior of trunk narrowed and slender; spindle muscle present, but unattached posteriorly . . . . *Golfingia bulbosa* (p. 152)
- Entire trunk of equal diameter; spindle muscle absent . . . . . *Golfingia eremita* (p. 150)

#### GENUS *SIPUNCULUS* LINNÉ, 1766

**DIAGNOSIS:** Typically trunk smooth and cylindrical; short introvert covered with squamiform papillae. In large individuals trunk generally thick walled with longitudinal and circular muscle layers divided into regular bundles; unpigmented skin in some cases divided into rectangular areas by longitudinal and circular furrows; posterior end of body rounded or bluntly pointed, in some cases marked off from main trunk by limiting fold of skin; flat tentacular fold surrounds oral disk; from its margin tentacles of varying complexity develop. Introvert hooks and trunk papillae absent; four retractor muscles; intestine attached to body wall by numerous mesenteries.

#### *Sipunculus nudus* Linné, 1766

Figure 13

*Sipunculus nudus* has the distinction of being first described by Linné (1766–1768, vol. 12). It is a cosmopolitan species and has been reported from shallow, subtidal sand flats in the tropics or warm temperate localities by numerous workers. These specimens are generally large, commonly more than 100 mm. long, the

longest being 290 mm. The current study specimens, 10–60 mm., were taken in deeper waters; the shallowest example was from 12 meters. I. E. Gray (personal commun. 1966) found “large” specimens at spring low tide in the Cape Lookout, North Carolina, area. It is possible that some factor limits the development of large individuals in deeper water, but these data do not prove this view. They do suggest, however, that *S. nudus* found at greater depths are near the tolerable limit of some niche parameter. None of the specimens I examined had gametes or visible gonads.

**DESCRIPTION:** This material consisted of five specimens from five stations. The preserved material ranges from transparent and iridescent in the small ones to pinkish red in the larger forms. The surface of the skin in the larger animals is subdivided into small rectangular areas typical of this genus. The skin of the two smallest individuals (10 and 35 mm.) is smooth and lacks this feature, which is commonly used as a “key” character, however.

The trunk has no papillae, but the introvert is covered with triangular “scales” or large white papillae directed posteriorly. The specimens are not expanded sufficiently to show the tentacles, but others have described them as having four lobes—two dorsal and two ventral.

Internally, the longitudinal muscle bands number from 28 to 33, the latter number found only in the largest specimen (80 mm.). The appearance of these muscle bundles is highly variable. When the body muscles are contracted, the longitudinal bands appear as thick strong ridges, but if the animal is preserved in a relaxed state they appear as broad, flat, thin sheets. The four retractor muscles are separate and attach at the same level, each with a broad base extending over five to seven longitudinal muscle bands. The spindle muscle is attached just anterior to the anus. The gut is attached to the body wall by several fixing muscles or connective tissue strands throughout its length. The gut is very thin, transparent, and fragile. In the smaller animals the gut, which is easily damaged, contains coarse sand and shell fragments that produce peculiar bumps and irregularities. As a result, the rectal caecum is difficult to discern although I saw it in two individuals. The nephridia vary in length (1–15 mm.) and range from 10 to 20 percent of the trunk length. Most descriptions note that these

organs are attached to the body wall for 20–33 percent of their length; however, in the smallest animals I have, the nephridia are attached only at the anterior opening. The nephridiopores are anterior to the anus between the fourth and fifth longitudinal muscle bands. The ventral nerve cord is loosely attached anteriorly with numerous, large, lateral offshoots to the introvert.

**DISTRIBUTION:** In the area under investigation, *Sipunculus nudus* is distributed from just below mean low tide down to 35 meters. It does not extend north of Cape Hatteras, North Carolina; the northernmost record is latitude 34° 34' N at Cape Lookout, North Carolina. It is found southward into southern Florida (fig. 13). The sediments which this animal inhabits are coarse sand, and the temperature is generally warm, ranging from 15 to 26° C., possibly to 30° C., in the very shallow areas.

The distribution of *S. nudus* on a worldwide basis is as follows: In the western Atlantic it extends from Cape Hatteras southward through the Caribbean Sea to the coast of Brazil. In the eastern Atlantic it extends from the shallow waters of the North Sea and the British Isles to the coast of Senegal, Africa. *Sipunculus nudus* has been found in the western Mediterranean Sea, the Red Sea, and the Indian Ocean off India and Zanzibar. In the western Pacific, the range extends from the Islands of Japan as far south as Southern Australia. The distribution in the Eastern Pacific is from southern California to Panama.

*Sipunculus norvegicus* Koren and Danielssen, 1875  
Figures 11–13

Even though Gerould (1913) discussed and apparently agreed with Théel's (1905) and Roule's (1906) decisions that *Sipunculus priapuloides* is synonymous with *S. norvegicus*, he persisted in using the junior synonym, *S. priapuloides*, for this animal. There is no longer any reason to preserve this specific name. *Sipunculus priapuloides* was a description of a mature *S. norvegicus*, and as such, better fits most of the material. The latter name has priority however, and so has been retained, even though the original description is of a young, small stage and omits certain adult characters.

**DESCRIPTION:** The body size of the 27 specimens from 20 stations studied varied from 105 by 17 mm. down to 7 by 2 mm. Two specimens

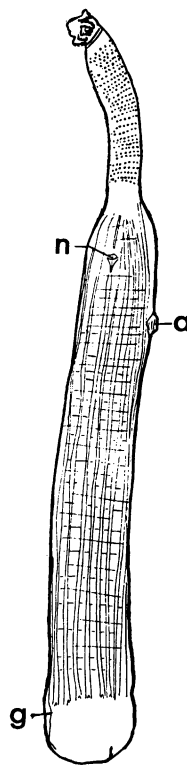


FIG. 11. *Sipunculus norvegicus*, external view (from Théel, 1905).

Abbreviations: a, anus; g, glans; n, nephridiopore.

measuring 5 by 1 mm., in which the longitudinal muscle bands were so thin and transparent they could not be counted accurately, were tentatively identified as *S. norvegicus*.

In the literature this species is variously described as transparent, grayish white, blue, yellowish gray, and pink. My preserved material varies from an iridescent transparent to a dirty grayish pink. All the specimens are at least partially retracted so I cannot comment on the nature of the tentacular arrangement which Théel (1905) described as "... a membranous disk, which protudes about twelve main lobes, each divided into two lobules, which in their turn, also may be bipartite." The introvert is covered with the typical, large, trianguloid papillae.

The form of the posterior "glans" region of the trunk has been the subject of much discussion. My specimens show three types. Some are the classical smooth, rounded form, but others are noticeably ridged, furrowed, and pointed,



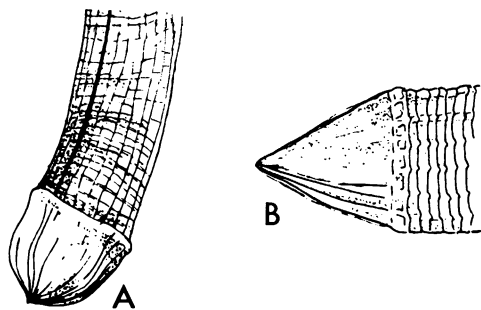


FIG. 12. *Sipunculus norvegicus*. A. Rounded posterior glans region. B. Posterior end showing pointed glans region.

coming to an obtuse tip (fig. 12). Sluiter (1900) offered the possible explanation (his figs. 6 and 7) that this folding is probably an artifact due to preservation. A third form is expressed by the small animals (less than 15 mm. long) in which the division is very poorly defined, and the longitudinal muscle bands extend almost to the posterior tip. In these small individuals, as well as in some of the larger forms, the posterior end has a puckered invagination of unknown function.

The annular ridge or fold separating this posterior region from the rest of the body is variable in expression as noted by Théel (1905) and Southern (1912). The ventral interruption in this ridge is also not consistently present. Southern and Théel both observed that in small animals this ridge is absent. Gerould (1913) concurred and concluded that "hence it is evidently not a characteristic of any morphological systematic importance." Stephen (1960), however, while describing this region remarked that "a circular fold of skin, broken ventrally and this also is a distinguishing feature." In the two 5-mm. specimens I have, in addition to the lack of a ridge, there is no differentiation of any sort and therefore no "glans" are discernible.

The number of longitudinal muscle bands varies from 21 to 24, but most frequently is between 22 and 23. The number of bands seems to be independent of the size and age of the animal. These muscle bands are seen externally as longitudinal furrows in the body wall. When the circular muscles contract, the body surface may be divided into squares or rectangles, but in my material this marking is the exception, not the rule.

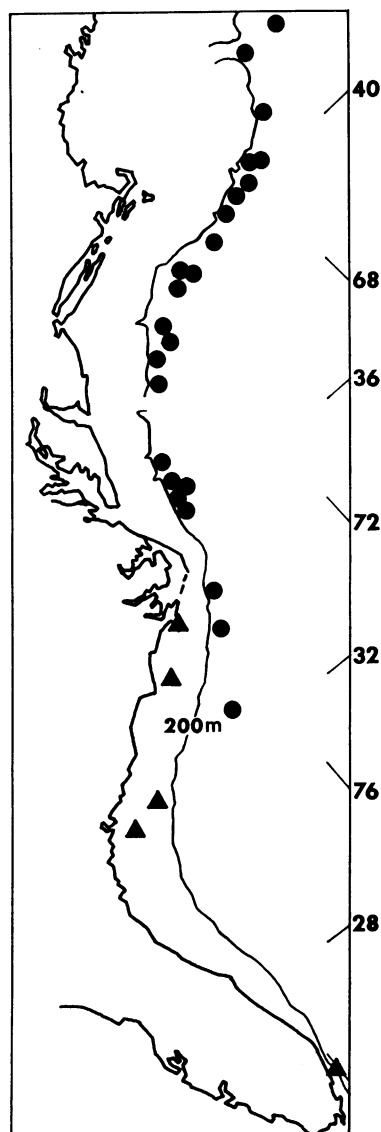


FIG. 13. Distribution of *Sipunculus nudus* (▲) and *S. norvegicus* (●).

The four retractor muscles are separate and large. Generally, they originate from only two longitudinal bands, not three to four as is sometimes reported. The spindle muscle is attached anterior to the anus, and the gut is attached to the body wall by numerous strands of tissue along its entire length. The gut is filled with fine, greenish gray silt and clay. A small caecum as well as a unique pair of racemose glands is present on the rectum. The nephridia are variable in size and pigmen-

tion, are entirely free, and open anterior to the prominent anus. They are generally of moderate length and are tan in the larger specimens and white in the smaller ones. The ventral nerve cord is prominent, and as in *Sipunculus nudus*, is loosely attached in the introvert with a large number of lateral branches, forming as Théel (1905) stated, "the most beautiful plexus." Gametes were found in the three largest specimens (85–105 mm), all collected in August.

**DISTRIBUTION:** Except for one individual identified by Gerould (1913) from latitude 32°39'N, all the records of this species from the western North Atlantic occur between latitude 34°30' and 41°N (fig. 13). The vertical distribution of this form is on the lower continental slope between 900 and 1800 meters. The sediments in this area are predominantly silts and clays with some very fine sand. Temperatures are between 3 and 4° C.

Outside this study area this species extends across to the eastern North Atlantic around the Scandinavian countries and the British Isles.

#### GENUS *SIPHONOMECUS* FISHER, 1947

**DIAGNOSIS:** Longitudinal muscle layer divided into freely anastomosing, stout bands. Between strong circular muscle bands, discontinuous transverse, coelomic lacunae connecting with subcutaneous pockets, longitudinally oriented, one for each rectangle of skin. Two retractor muscles; anus short distance behind nephridiopores; nephridia slender, free; spindle muscle strong, firmly anchored at posterior end of body.

*Siphonomecus* cf. *multicinctus* (Fisher, 1947)

**DESCRIPTION:** This single specimen is badly damaged and most of the internal organs are in a state which precludes specific identification. It definitely belongs in this genus, however, and possibly to this species. It is included here to show that this genus, whose type (and up to now only) locality was Key West, Florida (no depth reported), does extend northward into moderately deep water.

**DISTRIBUTION:** This specimen was found at latitude 27°02'N, longitude 77°40'W, in 545 meters of water. The sediments are silty sand and the temperature is probably 8–10° C. most of the time.

#### GENUS *PHASCOLOPSIS* FISHER, 1950

**DIAGNOSIS:** Adults commonly longer than 3

cm.; slender, smooth, elongate body; numerous tentacles surrounding mouth; longitudinal muscle layer divided into more than 25 anastomosing bands; hooks absent; spindle muscle not attached to posterior end of body; no villi or dorsal contractile vessel; four retractor muscles; two nephridia.

**DISCUSSION:** This genus contains only one species, *P. gouldi*. In the past this species name has been assigned to the genera *Sipunculus*, *Phascolosoma*, and *Golfingia*. The original describer of this species (Pourtalés, 1851) placed it in the genus *Sipunculus* at a time when the present-day *Siphonosoma* was also included in that genus. The genus *Siphonosoma* was not erected until 1912. Diesing (1859) removed *P. gouldi* to his genus *Phascolosoma* (later changed to *Golfingia*). In 1865 Keferstein placed the entity, which now serves as the type species for *Siphonosoma* (*S. australe*), in this *Phascolosoma* [*sic*] genus. In 1833 Selenka, de Man, and Bulow put *S. australe* and other modern *Siphonosoma*, as well as *P. gouldi*, back in to *Sipunculus*. The most thorough anatomical study on *P. gouldi* was done by Andrews (1890) who retained the name *Sipunculus*. In other words, the workers in the late 1800s thought that *P. gouldi* was closely related to the *Sipunculus*-*Siphonosoma* complex.

Gerould (1907) in his embryological paper maintained that *P. gouldi* strikingly resembled *Phascolosoma* [*sic*] *vulgare* and differed widely from *Sipunculus nudus*, so despite the musculature differences and largely on embryological similarities he put *gouldi* back into *Phascolosoma* (now *Golfingia*). However, he left behind others (such as *S. australe*) which may well be the same embryologically (none yet studied) and are more similar morphologically. Fisher (1950), in a review of the *Phascolosoma*-*Golfingia* situation, erected the name *Phascolopsis* as a subgenus of *Golfingia* but Stephen (1964) was of the opinion that the difference (presence of longitudinal muscle bands) indicated generic rank, so he elevated it to separate generic status without evidence of having considered other existing genera.

Although somewhat concerned over the lack of nomenclatural stability, I concur with Stephen's removal of this species from *Golfingia*. It seems more logical, however (on the basis of morphology and ecology), to place this species in a separate subgenus, within the genus *Sipho-*

*nosoma*. One of the outstanding features of *P. gouldi* is its unusual eurythermal and euryhaline capabilities, which are also characteristic of *Siphonosoma* (Cutler, 1965). In his key to the genera of Sipuncula, Stephen (1964) has *Phascolopsis* and *Siphonosoma* adjacent to one another thus:

Contractile vessel without villi, 30–40 longitudinal muscle-bands, much anastomosed . . .	<i>Phascolopsis</i>
Contractile vessel with villi, fewer than 30 longitudinal muscle-bands, little or no anastomosing . . . . .	<i>Siphonosoma</i>

The villi are used only at the subgeneric level in *Golfingia*; the number of longitudinal muscle bands and the frequency of anastomosing are not exact or precise differences, particularly in small individuals.

The questions of spindle muscle attachment and extensions of the coelom into the integument still remain. In *Golfingia* the spindle muscle attachment is used to differentiate on the subgeneric level and I think it should be used at that level here too. Although coelomic pouches were used by Spengel in his original description of the genus *Siphonosoma*, some species without them are already in the genus and I personally cannot put a great deal of weight on this character.

I strongly suspect that no other sipunculan biologist has had the opportunity to collect both *gouldi* and *Siphonosoma*, to compare their habitats, behavior, and morphology and to consciously raise this question as I have done. Therefore, on the basis of body form and niche, I conclude that *gouldi* does not warrant a monotypic genus and should be placed in the genus *Siphonosoma*. *Phascolopsis* would become one of four subgenera in this genus.

After conferring with several colleagues, however, I have decided not to make this change at this time. Hopefully, the necessary embryological studies on *Siphonosoma* will be done so that this issue can be resolved. For the present I am retaining the name *Phascolopsis* with serious reservations.

*Phascolopsis gouldi* (Pourtalés, 1851)

Figures 14, 15

DESCRIPTION: I have 62 specimens from 24 stations. The trunk length varies from 50–150 mm. Andrews (1890) recorded a length of

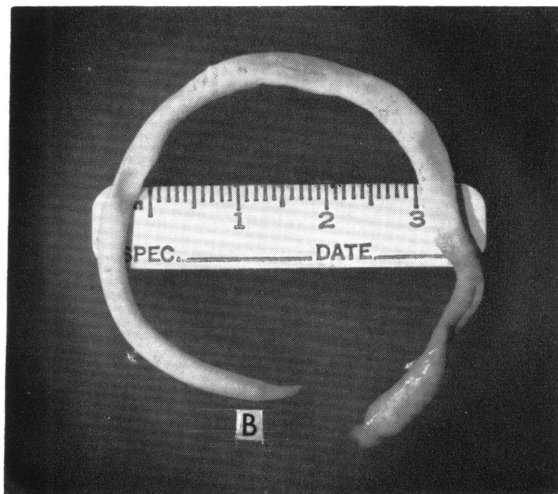
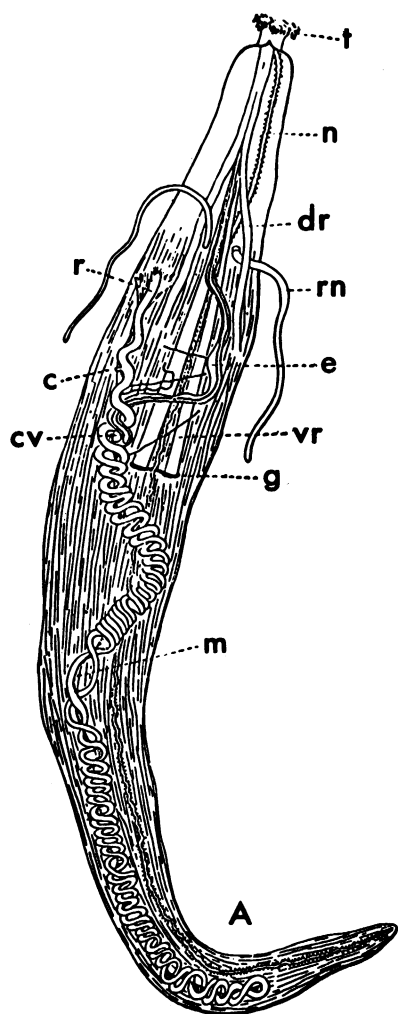
280 mm. and Verrill (1873) said that they measure a foot or more, or more than 300 mm. The diameter of the observed material rarely exceeds 5 mm., which gives this species a more typical "vermiform" appearance than most of the others. The introvert is about one-third as long as the trunk. The posterior end frequently tapers to a conical point. The larger animals are opaque and whitish gray, yellow, or pink but those under 10–20 mm. are transparent and whitish or pink. One gray individual from the Cape Hatteras area had a rusty red tinge on the introvert and anterior end of the trunk.

The tentacles are numerous and give the anterior tip of the animal a furry or fuzzy appearance. Andrews (1890) gave a detailed account of their arrangement and said the number may vary from 24 to around 200. The introvert is not distinctly set off from the trunk, but the anus is commonly distinct and provides a convenient reference point for measurements. The smooth skin has epidermal organs but they do not protrude above the general surface.

In the smaller individuals the longitudinal muscle bands can be seen through the body wall. Most have 30–40 of these bundles but in small individuals the number may be 26 or 27. Due to the frequent anastomoses, this number is only a relative measure and broadly fluctuates at different points within one individual.

There are four retractor muscles: the smaller dorsal pair originates just behind the anus and the larger ventral pair originates farther posteriorly but still in the anterior half of the trunk. The intestine is long and attached by four fixing muscles to the ventral body wall and by wing muscles on the rectum. The two free nephridia may be long and are brown or yellowish. The nephridiopores are anterior to the anus.

DISTRIBUTION: *Phascolopsis gouldi* is endemic to the east coast of the United States north of Florida. It was first reported from three localities near Cape Cod and subsequently collected in many localities off southern New England. Gerould (1913) gave its distribution as Casco Bay, Maine, to Long Island, New York. He also said it is a littoral species but that some were collected in Vineyard Sound "at a probably though unrecorded depth of several fathoms." In the American Museum of Natural History one specimen collected in 1936 from Cape Hatteras is identified by Van Name. Two specimens were collected on Virginia Beach



(Cape Henry) after a tidal storm in March, 1962. This is the only record from the area and it is impossible to determine the original locality for these worms. These recent collections expand its known range (fig. 15.) Table 8 shows some characteristics of three apparent subpopulations.

The latitudinal range included in this work is from latitude  $30^{\circ}10'$  to  $41^{\circ}31'N$ , but this northern limit would be near  $43^{\circ}45'N$ , if the earlier records are included. These data suggest a southerly extension of this species. As yet no sexually mature forms have been collected south of the Cape Hatteras area.

#### GENUS *GOLFINGIA* LANKESTER, 1885

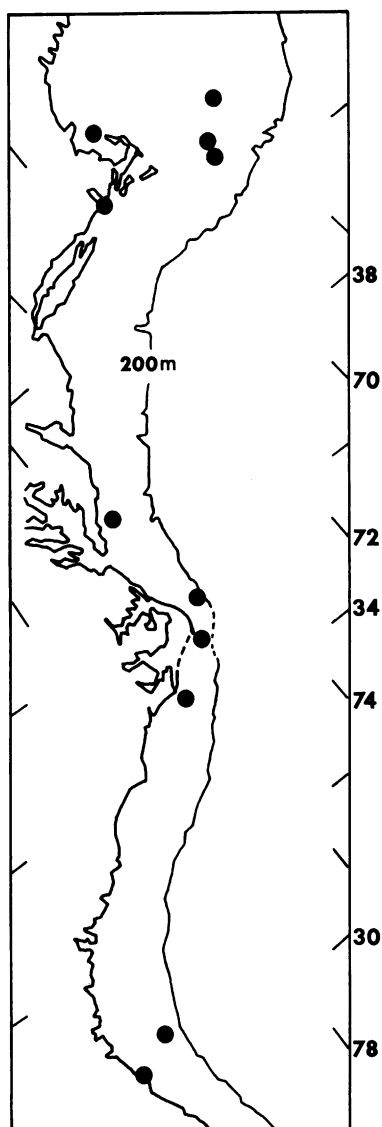
**DIAGNOSIS:** Generally small or moderate-sized, rather slender sipunculans with continuous longitudinal muscle layer. Distinct finger-shaped, leaf-shaped, or filiform tentacles surrounding mouth in one or more rows or in series of longitudinal double rows, interrupted in median dorsal line by ciliated nuchal organ; in a few species tentacles reduced to circumoral fold. Introvert with hooks present or absent; four or only two (ventral) retractor muscles of introvert; dorsal contractile vessel generally simple, but in subgenus *Thysanocardia* covered with villous outpouchings—in some cases rudimentary in species with few tentacles. Intestine forming double spiral coil of several to many whorls around axial spindle muscle originating near rectum, and in some cases anchoring spiral to posterior end of trunk; pair of nephridia generally hanging free.

#### SUBGENUS *GOLFINGIA* FISHER, 1950

**DIAGNOSIS:** Four retractors; contractile vessel without villi; spindle muscle not attached to posterior end of body.

FIG. 14. *Phascolopsis gouldi*. A. Internal view (from Andrews, 1890). B. External view.

**Abbreviations:** c, caecum; cv, contractile vessel; e, esophagus; g, gonad; m, mesentery; n, nerve cord; r, rectum; rd, dorsal retractor muscle; rn, right nephridium; t, tentacles; vr, ventral retractor muscle.

FIG. 15. Distribution of *Phascolopsis gouldi*.*Golfingia muricaudata* (Southern, 1912)

Figures 16, 19

*Phascolosoma muricaudatum* SOUTHERN, 1912, p. 21.*Phascolosoma hudsonianum* CHAMBERLIN, 1920a, p. 3.*Golfingia hudsoniana*: FISHER, 1950, p. 550.*Golfingia muricaudata*: FISHER, 1952, p. 390.

DISCUSSION: In 1912 Southern described this species on the basis of 56 examples from five stations off the coast of Ireland in depths of about 600–1000 meters. Eight years later, Chamberlin (1920a) described *Golfingia hudsoniana* from one example collected in Hudson Bay, the depth unreported. He did not compare this new species with any existing forms nor was there any list of references, so it is not known whether he was aware of Southern's species; they are strikingly similar.

After contrasting the two descriptions, it is apparent that the differences are few. The only outstanding one is that *G. hudsoniana* is said to lack hooks (*G. muricaudata* may have them). Two factors need be considered: 1) Chamberlin's specimen was not fully extended making it difficult to see the hooks, assuming he dissected the withdrawn introvert in the appropriate place; 2) this specimen was also more than twice the size of Southern's (trunk 70 mm. compared with 13–32 mm.). As Southern (1912, p. 22) pointed out: "in small and immature specimens the proboscis just behind the tentacles is dotted with powerful hooks, not arranged in any definite order. In several fully grown animals, the hooks are quite absent, thus adding another instance to prove the unreliability of this character as a specific criterion." It has been shown elsewhere that the number of hooks tends to decrease, even to the zero point, as the animal becomes larger. This decrease may well have taken place in Chamberlin's animal.

TABLE 8  
CHARACTERISTICS OF THREE SUBPOPULATIONS OF *Phascolopsis gouldi*

	Northern	Cape Hatteras	Northern Florida
Number of individuals	Many	5	3
Maximum length (in mm.)	150	100	20
Gametes	present	present	absent
Depth Range (in meters)	0–92	10–165	12–37
Temperature Range (in C.)	1–17	12–25	15–27
Sediment type	Sand	Silty sand	Sand

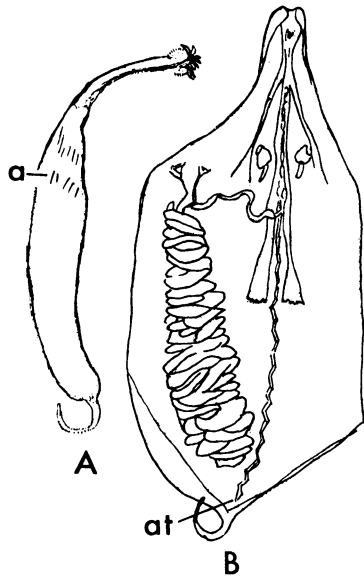


FIG. 16. *Golffingia muricaudata* (from Southern, 1912), A. External view. B. Internal view.

Abbreviations: a, anus; at, termination of nerve cord.

Fisher (1952, p. 390) stated in a footnote that *G. hudsoniana* is probably a form of *G. margaritacea*. V. V. Murina (personal commun.) agreed with Fisher but after I obtained Chamberlin's type specimen and compared it with Murina's and my material, I do not concur. For the above reasons, I suggest that *G. hudsoniana* be submerged as a junior synonym of *G. muricaudata*.

**DESCRIPTION:** The material is five specimens from five stations. The trunk length ranges from 4 to 10 mm., the introvert is about half the length of the trunk, and the caudal appendage (tail) is 1–2 mm. long. Specimens may be semi-transparent or cream color, becoming light brown toward the posterior end.

The body is covered with small papillae except at the posterior end where they are larger. With transmitted light, the papillae appear as clear spots against a darker background. The tail has fine papillae and is grayish white. The introvert is not fully extended in any of the specimens, but tentacles are present. Southern (1912) counted from 12 to 25 or 30 slender, well-formed tentacles. Scattered hooks are present in Southern's individuals.

Internally are four retractor muscles; the

stronger ventral pair originates from the middle of the trunk. The weaker dorsal pair originates more anteriorly near the level of the anus. The intestinal coil has one anterior fixing muscle; the spindle muscle is unattached posteriorly. No caecum is present. Delicate wing muscles anchor the rectum. The nephridia are single, unattached, and about one-fourth the length of the trunk. No gametes were found. The nerve cord terminates before the beginning of the tail.

**DISTRIBUTION:** Four of these five worms came from 2200 to 3000 meters; the fifth was collected in 650 meters just south of Cape Hatteras at latitude 34°15'N (fig. 19). The most northerly one was at latitude 39°25'N. In this area, the temperature ranges from 3 to 5° C. The sediments are predominantly silts and clays containing only small amounts of fine sand.

This species has been found in Hudson Bay, Ireland (latitude 50°N), the Atlantic coast of South America, and at 3000 meters off East Africa.

#### *Golffingia elongata* (Keferstein, 1862)

Figures 17, 19

*Phascolosoma elongatum* KEFERSTEIN, 1862, p. 39.

SELENKA, DEMAN, AND BULOW, 1883, p. 23.

THÉEL, 1905, p. 62. SOUTHERN, 1912, p. 16.

*Phascolosoma cylindratum* KEFERSTEIN, 1865, p. 200.

SELENKA, DEMAN, AND BULOW, 1883, p. 25.

GEROULD, 1913, p. 382–383.

*Phascolosoma forbesi* BAIRD, 1868, p. 83.

*Phascolosoma oxyurum* BAIRD, 1868, p. 83.

*Phascolosoma pellucidum*: SHIPLEY, 1900, p. 29.

*Phascolosoma teres* HUTTON, 1903, p. 29.

*Golffingia cylindrata*: FISHER, 1950, p. 550.

*Golffingia elongata*: FISHER, 1950, p. 550.

*Golffingia elongatum*: STEPHEN, 1960, p. 15.

**DISCUSSION:** Three years after he had first described *Golffingia elongata*, Keferstein (1865) described *G. cylindrata* but without making comparisons with closely related species. In Selenka's key (1883, p. 9) to the genus, these two species appeared next to one another. The separating character was the size and shape of the hooks: in *G. elongata* they were slender and 0.1 mm. long; in *G. cylindrata*, they were obtuse or blunt, 0.032–0.052 mm. long. Selenka also noted that *G. elongata* was from the west coast of Europe and the Mediterranean, whereas *G. cylindrata* was from Bermuda. Table 9 compares the size of the hooks with the trunk length from



TABLE 9

HOOK HEIGHT AND TRUNK LENGTH (IN MILLIMETERS) OF *Golfingia elongata* AND *Golfingia cylindrata* FROM THE LITERATURE AND PRESENT MATERIAL

Hook Height	Trunk Length	Source
0.032–0.052	20	Keferstein's <i>G. cylindrata</i>
0.056	15	Gerould's <i>G. cylindrata</i> from Key West
0.045–0.060	19	Present material
0.062	27	Fisher's <i>G. cylindrata</i> from Bermuda
0.080	48	Keferstein's <i>G. elongata</i>
0.100	90	Selenka's <i>G. elongata</i>

several sources. I suggest that a direct relationship may exist between the size of the animal and the size of their hooks, and that this character is not species specific. Théel (1905) added several records of *G. elongata* from the west coast of Sweden. He commented on the probability that the number of rings of hooks at first increased and then decreased, but he did not give measurements of hook size. The shape of the hook in figure 10 more or less agrees with Keferstein's (1865) figure 31. Southern (1912) recorded some examples of *G. elongata* from the British Isles but did not mention the hooks.

Gerould (1913) recorded three specimens of *G. cylindrata* from Key West, Florida. He mentioned slender, curved yellow-brown hooks but gave no measurements. The value presented in table 9 was based on his specimens in the National Museum of Natural History, Smithsonian Institution, as measured by me. Otherwise, his description could well fit *G. elongata*. This one record is the only other I have found of this name in the literature.

Stephen (1960) redescribed *G. elongata* from the earlier literature and mentioned that the hooks are thin and slightly bent but gave no measurements or figures. In his unpublished key the two above-mentioned species are next to one another, but he separated them thus:

Segmental organ small and short—*G. cylindrata*  
Segmental organ long and slim—*G. elongata*

Neither Keferstein (1865), nor Gerould (1913) mentioned the length of this structure in *G. cylindrata*. Keferstein's figure 30 of *G. elongata* and figure 40 of *G. cylindrata* illustrate the internal anatomy of these two forms. As measured in the respective drawings, the nephridia are not short in one species and long in the other, but equal about 29 percent of the trunk length in both.

Unless further evidence is found, I suggest that *G. cylindrata* be submerged as a junior synonym of *G. elongata*.

**DESCRIPTION:** The five specimens are from five stations. The length range of these specimens is 6–19 mm., and they are semitransparent or white and opaque. They are cylindrical with a rounded posterior end. The body surface is generally smooth but has some rounded epidermal protuberances toward the posterior end.

Normal tentacles (16–24) are in a single row around the mouth. The dark hooks are arranged in 15–25 regular rings. Larger specimens may have as few as 5–7 rings (Théel, 1905). From a 19-mm. worm I measured hooks 0.045 to 0.060 mm. high (table 9). The introvert is invariably shorter than the trunk.

Internally the four retractors have the typical arrangement: the larger ventral pair originate in the middle of the trunk and the smaller dorsal pair in the vicinity of the anus. The intestine has numerous coils. A spindle muscle unattached posteriorly and a small rectal caecum were observed in one specimen. One or two fixing muscles can be found near the front of the coil. The nephridia are free and brown or pale tan. The three southern, shallow-water forms had two prominent eyespots.

**DISTRIBUTION:** A statement on distribution of this form at first presents a problem, both from the standpoint of the suggested merger of *G. cylindrata* and *G. elongata* and from current collections (fig. 19). The recent material from shallow water south of Cape Hatteras contains three worms from latitude 27°50'N to 33°40'N in 10–14 meters of water. The sediment is sandy and the water warm (15–27° C.). To combine these occurrences (together with those of "*G. cylindrata*" from Bermuda and Key West) with records from the west and south coasts of

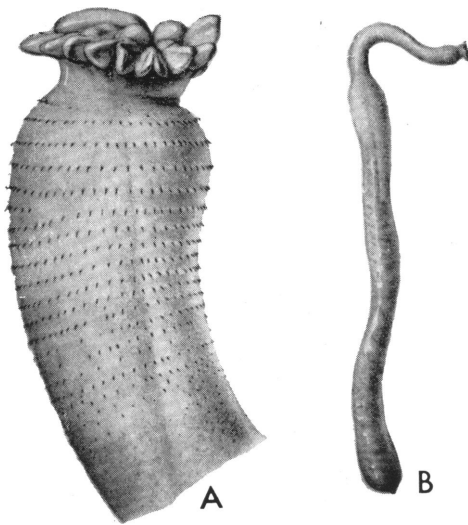


FIG. 17. *Golfigia elongata*. A. Distal end of introvert (from Théel, 1905). B. External view (from Théel, 1905). C. Internal view (from Keferstein, 1865).

Abbreviations: a, anus; c, dorsal blood vessel; g, ventral retractor muscle; n, nerve cord; r, dorsal retractor muscle; s, nephridia.

Europe of *G. elongata* would not give a unique distribution record for a sipunculan species. *Sipunculus nudus* is also found in shallow water in both areas.

Two animals are from 79 meters and 97 meters at latitude 40°20'N south of Cape Cod. The sediment is like that in the south, but the temperature is somewhat lower (7–12° C.). Although both animals have minor morphological differences, I tentatively assign them to this taxon.

This species is found in the eastern Atlantic from Scandinavia south into the Mediterranean. In the western Atlantic there have been three records before my collections: Woods Hole, Massachusetts; Key West, Florida; and Cuba.

*Golfigia margaritacea* (Sars, 1851)

Figures 18, 19

DESCRIPTION: The 76 specimens came from 15 stations. The length of the trunk ranges from 8 to 180 mm. Some have a plump short form, but most are elongate and slender. Not one is completely extended. The color ranges from a translucent tan through opaque tan to dark reddish brown, very much like the coloration of *Golfigia eremita*.

The skin of this species is generally smooth with small, flat papillae visible under magnification. Hooks are absent, and the introvert is generally shorter than the trunk. According to Théel (1905), the number of tentacles may vary from 8 to 104.

Internally the four separate retractor muscles easily distinguish this species from the externally similar *G. eremita* which has only two. The dorsal pair originates anterior to the noticeably stronger ventral pair. In some smaller, partially extended individuals these dorsal muscles have dimensions somewhat like a spindle muscle. The strong ventral retractors lie close to the nerve cord and originate midway in the trunk. In the long, slender forms these muscle origins are shifted farther anteriorly. The esophagus is partially attached to the retractors by a connective tissue sheet, and two or three fixing muscles are present. The gut is not attached posteriorly, but the spindle muscle is present anteriorly, as is the typical wing muscle that anchors the short rectum. The nephridia are variable in color and size but may become as long as one-fourth the total trunk length. They open anterior to the anus.

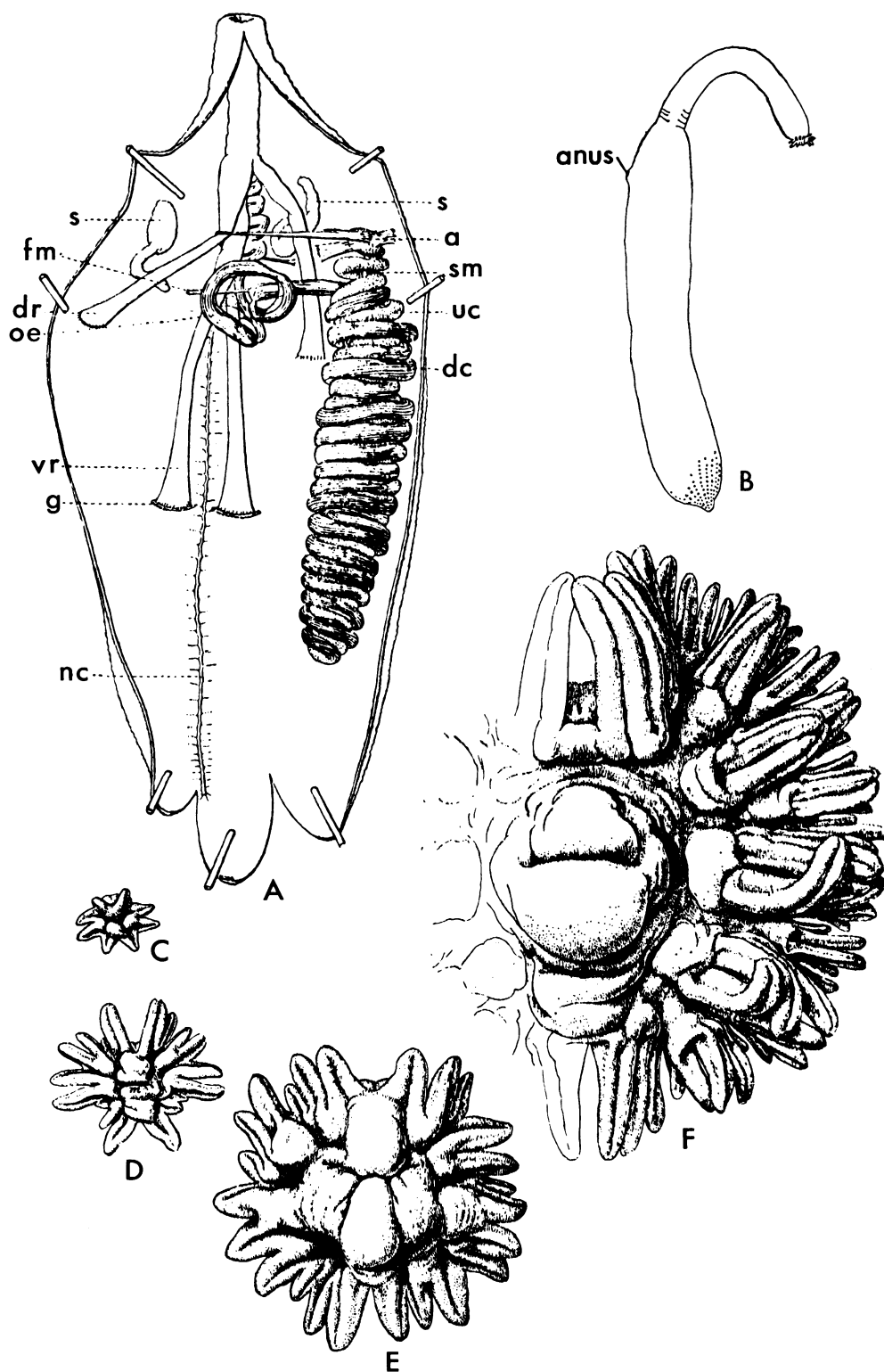


FIG. 18. *Golfinia margaritacea* (from Théel, 1905). A. Internal view. B. External view. C-F. Various stages of tentacular development.

Abbreviations: a, anus; dc, descending coil; dr, dorsal retractor muscle; fm, fixing muscle; g, gonads; nc, nerve cord; oe, esophagus; s, nephridium; sm, spindle muscle; uc, ascending coil; vr, ventral retractor muscle.

This species is easily identified because it is the only one in the study area that has a smooth skin, a continuous muscle layer, and four retractors originating in the anterior portion of the trunk, and lacks hooks.

**DISCUSSION:** The external appearance of this species is variable and as a result, has given rise to a number of varieties, forms, and subspecies. Following are some of the names which have been appended to this species, together with the characters which supposedly distinguish them from the main type.

*adelaidensis* Edmonds, 1956: a subspecies found off Southern Australia. Caecum absent or rudimentary; greater number of tentacles than in typical form; no reticular pigmentation in trunk.

*californiansis* Fisher, 1952: a subspecies found off California. Nuchal organ with three parts rather than two; tentacles short; body wall opaque; caecum rudimentary.

*capsiformis* Edmonds, 1965: a subspecies with stout, thick body wall; difference in number and arrangement of fixing muscles.

*finmarchica* Théel, 1905: a form, with body wall more thick; reticular structure more conspicuous.

*hansonii* Stephen, 1941: a variety found off Chile; thick opaque skin; posteriorly corky; longitudinal and transverse furrows on body wall.

*meridionales* Gerould, 1913: a variety having extremely elongated shape (common in this study).

*siberica* Théel, 1905: a form, with thin, transparent body wall; reticulation highly discernible.

*trybomi* Stephen, 1941: a variety found off Chile, the Falklands, Arctic, and Antarctic; difference in position of retractors and condition of skin; more pearly interior; short ventral retractors.

The above variations should be taken to illustrate the plasticity of form possible in this species. Their morphological constancy and thus their nomenclatural value must be held questionable.

**DISTRIBUTION:** The distribution of this species off the east coast of North America is very similar to that of *G. erimeta* (fig. 19). It had previously been found throughout the Gulf of Maine and southward to latitude 39°42'N (Gerould, 1913). The present investigation extends the range as far south as Cape Hatteras (latitude 34°55'N). The vertical range is generally from 100 to 325 meters (one station at 25 meters, one at 29 meters, and one at 1231 meters). When this species occurs south of latitude 40°N, it is generally found only on the upper slope. The two shallow-water stations

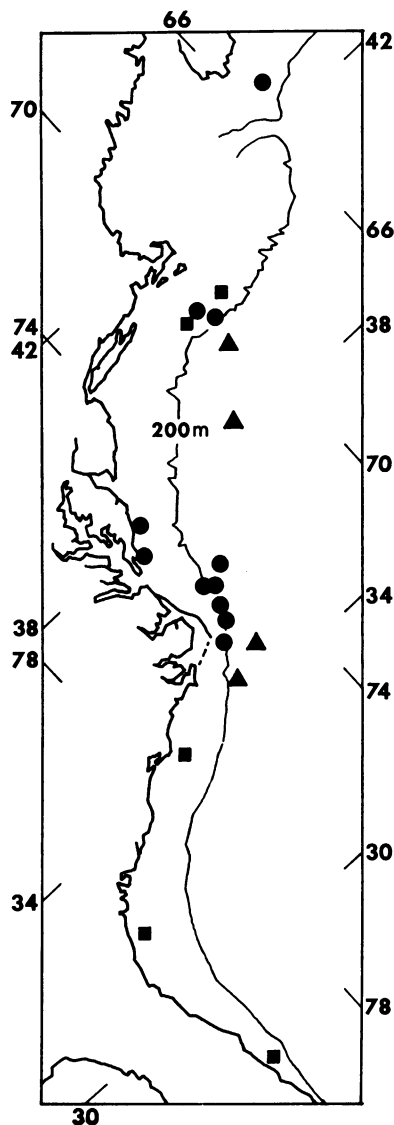


FIG. 19. Distribution of *Golfingia elongata* (■), *G. margaritacea* (●), and *G. muricaudata* (▲).

mentioned above, however, were off Virginia just north of Cape Charles. The temperature ranged from about 2° to 12° C. The sediments are mixed, but generally sandy.

This widely distributed species is found in all major oceans but most commonly in the North Atlantic. It has bipolar tendencies and apparently is absent from the equatorial regions.

SUBGENUS *MITOSIPHON* FISHER, 1952

DIAGNOSIS: Four retractors; nephridia either

bilobed or single-lobed; spindle muscle attached to posterior end of body; introvert hooks, if present, possibly with accessory comb of spinelets at base; tentacles possibly reduced; introvert longer than trunk.

*Golfingia trichocephala* (Sluiter, 1902)

Figures 20–22, 26

*Golfingia longirostris* WESENBERG-LUND, 1959, p. 186.

WESENBERG-LUND, 1963, p. 112.

*Golfingia tenuissima* WESENBERG-LUND, 1959, p. 183.

**DESCRIPTION:** The 206 specimens are from 18 stations. The trunk length varies from 2 to 8 mm. The introvert is many times longer than the trunk, frequently more than 10 times as long, but this character is extremely variable as it depends on the state of contraction of the animal. These worms are generally pointed at the posterior end, have a somewhat bulbous midsection to the trunk, then taper to the thin introvert. They are off-white or pink and semi-transparent unless the circular musculature is contracted making it more opaque. The contraction of these circular muscles may also produce the appearance of annular folds or ridges along the length of the trunk and out onto the introvert. The animals may or may not have complex glandular papillae even in a sample from the same place.

When present, the papillae are often oval and extended for some distance out on the introvert. Their length is 100–150  $\mu$  and their width 50–100  $\mu$ . I am not sure that any specimen I have is fully expanded and cannot comment on the nature of the hooks and tentacles (if present).

The body cavity in some worms is filled with the loosely coiled introvert, if it is withdrawn. The intestine is the typically double-coiled type with from 10 to 20 coils. It is fastened to the posterior end of the body by the spindle muscle. The esophagus is long; the rectum is short. The rectum exhibits the peculiar bend or "genuflection" because a small muscle attaches it to the dorsal body wall a short distance anterior to the anus. A caecum has not been observed.

The anus is rarely at the anterior end of the trunk and this fact can lead to confusion when measurements are made without dissecting the animal. No clear external demarcation exists, and unless a constant such as the position of the nephridiopore is used to mark the end of the

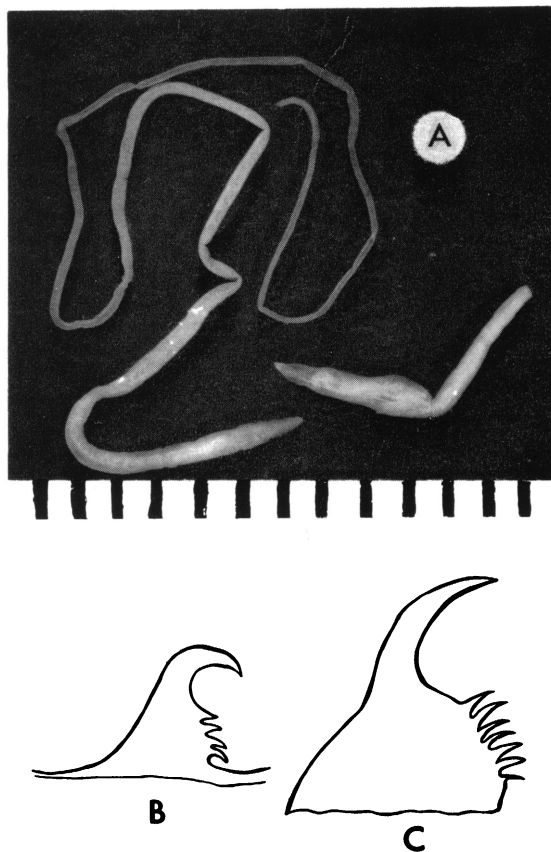


FIG. 20. *Golfingia* (*Mitosisiphon*). A. External view of *G. trichocephala* (scale in mm.). B. *G. misakiana* hook (from Ikeda, 1904). C. *G. hespera* hook (from Fisher, 1952).

trunk and the beginning of the introvert, the variation in measurements can be great.

The four retractor muscles are small and originate generally close to the ventral nerve cord. The terms ventral and dorsal, which are commonly applied to these two pairs of muscles, tend to lose their meaning as both are about equally distant from the ventral nerve cord. Wesenberg-Lund (1959) has commented that the two anterior muscles are more dorsal than the posterior pair, which is opposite from the usual condition, but even when present this difference is too slight to be emphasized.

The nephridia are bilobed, generally tubular, and free. The two lobes are generally of about equal length and somewhat coiled or curved. Both lobes may or may not be pointed in the same posterior direction. These organs are

yellow or orange and are very fragile. Even when no gametes are present, the two lobes are clearly visible.

The relative positions of the anus, nephridia, and the origin of the retractors are not constant. The nephridia invariably open anterior to the origin of the retractors, but the anus may be on a level with the origin of the anterior pair of retractors or at some distance posterior to both pairs of muscles. No clear pattern can be discerned.

The morphologically outstanding nature of this species makes it rather easy to identify. The bilobed nephridia, the four small retractors close to the ventral nerve cord, and the small pointed body with the extremely long, filamentous introvert are unique.

**DISTRIBUTION:** With one exception off New Jersey (latitude 39°20'N) in 178 meters, these specimens all came from the shelf south of Cape Hatteras (latitude 28°30'–35°20'N), from water 20–80 meters deep (fig. 26). The sediment is sandy and the temperature is fairly high but variable, 15–25° C.

This species has been reported from shallow water from Indonesia, South Africa, and West Africa.

**DISCUSSION:** The material I have on hand is without question *Golfingia trichocephala*. To clarify some nomenclatural confusion, however, it is essential to consider the work of seven authors pertaining to five names now in three subgenera of the genus *Golfingia*. The specific names are: *trichocephala*, *misakiana*, *hespera*, *tenuissima*, and *longirostris*. To supplement the descriptions in the literature I have: numerous specimens of *G. trichocephala* recently collected; Sluiter's type material of *G. trichocephala* from the Zoological Museum, Amsterdam; Chamberlin's holotype of *G. hespera* from the Museum of Comparative Zoology, Harvard; a *G. hespera* identified by Fisher from the American Museum of Natural History; and one specimen of *G. longirostris* and four contracted *G. tenuissima* from the Copenhagen Museum as identified by Wesenberg-Lund.

In 1902 Sluiter described a worm, *Apionsoma trichocephala*, that he thought was distinct enough to place in a new genus. He gave an exhaustive description that unfortunately was inaccurate in two important respects; the nephridia are bilobed, not single, and the spindle muscle attaches the intestinal coil to the posterior

end of the body rather than leaving the gut free. This species was subsequently placed in *Golfingia* and erroneously in the new subgenus *Golfingiella* by Stephen (unpublished keys). Fisher did not mention this species in his works.

In 1904, Ikeda described *G. misakiana* from Japan. It was the first sipunculan to be described as having bilobed nephridia. Sixteen years later Chamberlin (1920b) gave a brief and inaccurate description (without figures) of a "new species" from intertidal Californian waters, *G. hespera*. He did not mention Ikeda's species. In Fisher's 1952 paper, however, where he corrected Chamberlin's errors, he placed Ikeda's species in the same recently erected subgenus as *G. hespera*: *Mitosiphon* (Fisher, 1950).

Fisher's key to this subgenus separates *G. hespera* from *G. misakiana* on six features. *Golfingia hespera* has: 1) a longer introvert (six to eight times *vs.* four times trunk length); 2) more tentacles (12–20 *vs.* eight); 3) more denticles at base of hook (about seven *vs.* four to five); 4) caecum, present *vs.* absent; 5) no fixing muscle *vs.* one present; and 6) hooks moderately *vs.* abruptly curved at tip. Chamberlin's description (1920b) made no mention of the last five of these characters nor of the nephridia. In addition he claimed erroneously that there were only two retractor muscles. The holotype at the Museum of Comparative Zoology is badly macerated internally, but I could verify the presence of four retractors. The paratype had been lent to Fisher in 1948, but never returned.

From my studies of other forms, I can ascribe the first three "differences" of Fisher's to the larger size of his specimens. Ikeda's specimen is 50 mm. long overall, whereas Fisher described animals up to 140 mm. long. The caecum could have been easily overlooked by Ikeda. The amount of curvature at the tip of the hook is a subjective measure and perhaps a result of the artist's interpretation. Thus the sole surviving morphological character separating these two forms is the fine muscle that attaches the esophagus to the body wall. This character has been shown elsewhere (Murina, 1964a) to be of questionable systematic value.

Stephen's unpublished key separates these two species on the position of the retractor origins (*G. hespera*—"about the level of the anus" and *G. misakiana*—"in the middle of the trunk"). This feature is not helpful, as the anus is in the middle of the trunk in *G. misakiana*, i.e., in both



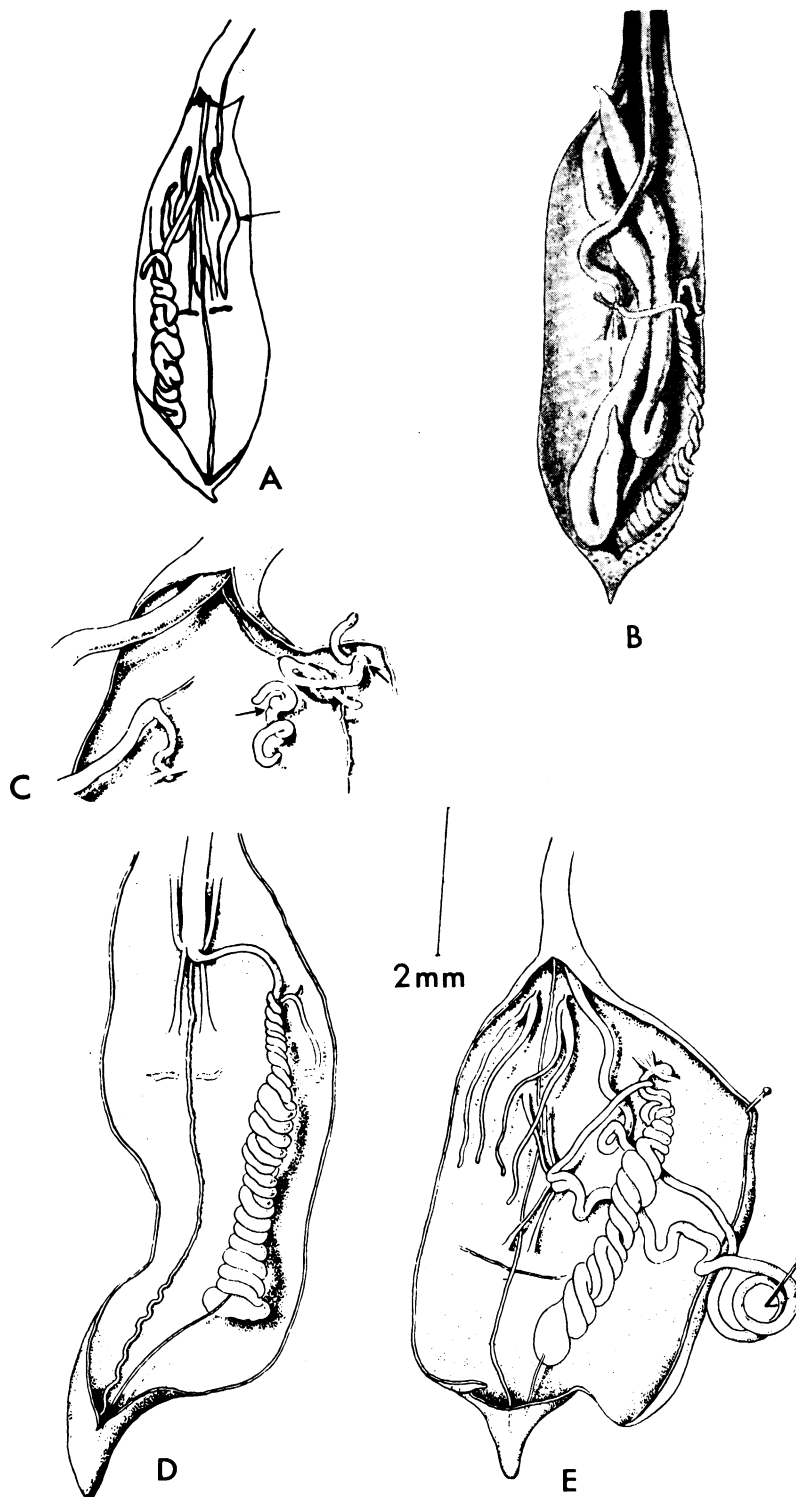


FIG. 21. *Golfigia* (*Mitosiphon*), comparative internal morphology. A. *G. misakiana* (from Ikeda, 1904). B. *G. hespera* (from Fisher, 1952). C, D. *G. tenuissima*. E. *G. longirostris* (C-E from Wesenberg-Lund, 1959). Arrows indicate the position of the nephridiopore.

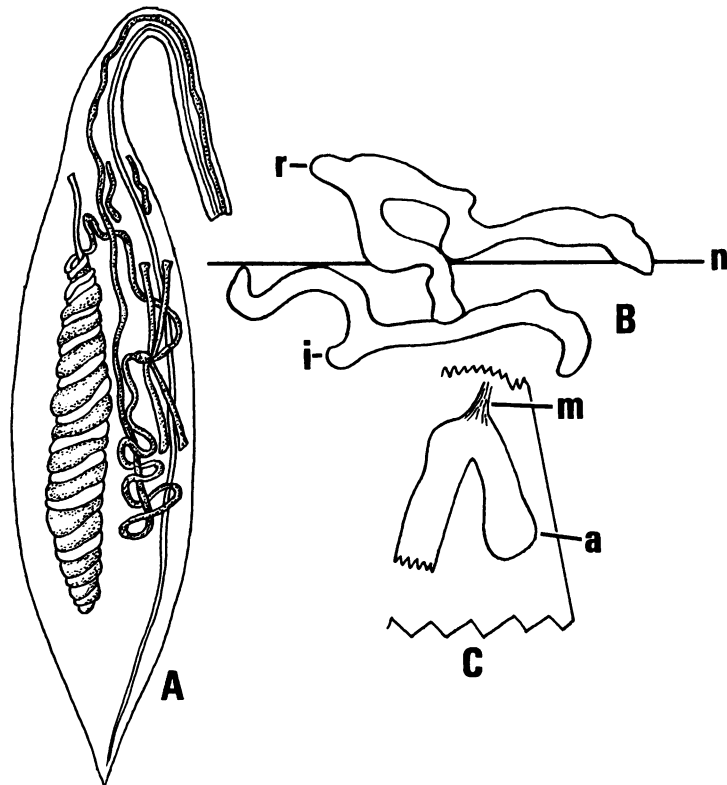


FIG. 22. *Golfingia trichocephala*. A. Internal view (as drawn by Sluiter, 1900). B. Bilobed nephridia (drawn from Sluiter's type material [length of lobes is 0.9 to 1.3 mm.]). C. Genuflected rectum (drawn from Sluiter's type material).

Abbreviations: a, anus; i, left nephridiopore; m, attaching muscle; in, nerve cord; r, right nephridiopore.

forms, the anus and retractor origins are found in the mid-region of the poorly delineated trunk.

There have been two recent records of *G. hespera* by Murina (1964a, 1964b), one from 3954 meters in the northwestern Pacific, the other from 173–1234 meters in the Mediterranean. Both of Murina's Pacific specimens were damaged—one severely, the other lacking only the tip of the introvert. Her description was based on the specimen with a 5-mm. trunk and a 78-mm. introvert. From the Mediterranean she had 13 specimens 1.3–75 mm. long, the largest having a 5 mm. trunk.

Murina's descriptions have a few noteworthy features. Most outstanding is the nature of the nephridia in her specimens. The Pacific specimen has single-lobed, urn- or flask-shaped nephridia (the free ends are slightly macerated). In her Mediterranean collection some nephridia

were single-lobed, others bilobed, and still others at various intermediate stages. Her contention was that this variability is merely a reflection of the sexual maturity of the animal i.e., as more gametes develop, the nephridia enlarge to form a second lobe of varying dimensions. In the Mediterranean material, a worm with a 2.2 mm. trunk had the beginnings of a second lobe, and 2 mm. and 5 mm. ones had two lobes, but the 5 mm. worm from the Pacific had only one lobe. This hypothesis is difficult for me to accept. My specimens had bilobed nephridia whether or not they contained gametes.

A second unique feature of Murina's description of *G. hespera* is the presence of one to three fixing muscles. She stated that the number of fixing muscles depends on the size of the animal but that this taxonomic character is unreliable because it is subject to individual

variation. A 5-mm. specimen from the Mediterranean had three fixing muscles but the 5-mm. Pacific animal had only one. Fisher (1952) noted that *G. hespera* had none, and this finding agrees with my observations on the California material. After extensive correspondence and exchange of materials with Murina, we agreed that her specimens are not *G. hespera* but rather *G. murinae*.

My involvement in this whole problem began when I attempted to identify the specimens I had from shallow water south of Cape Hatteras, which had four small retractors, bilobed nephridia, and unusually long introverts. Stephen's key led me into the subgenus *Phascolana* which Wesenberg-Lund erected in 1959 for the two species, *G. tenuissima* and *G. longirostris*, from West Africa. Stephen singled out the nature of the papillae to separate these two species. As many of my animals lack well-defined papillae, this key was not very helpful. Wesenberg-Lund used several criteria, but I thought it would be desirable to have some specimens as identified by her for comparative purposes, and for this reason obtained material from Copenhagen. This loan did not clear the confusion, however.

Wesenberg-Lund (1959a) differentiated these two species on the basis of whether: their papillae are crowded and prominent on the posterior end; their papillae have a few platelets or circular areas; the rectum is bent or straight, attached or not attached; the gonads are long or short; and on the shape and size of the nephridia. The gonads were not present in any of the Copenhagen material I have. The nephridia of the *G. longirostris* I received were nowhere near the length of those illustrated for this species but very similar to those shown for *G. tenuissima*—i.e., short and more or less coiled. The papillae are supposedly different but in the material that I have, the papillae are very indistinct in *G. longirostris* and almost impossible to see in *G. tenuissima*. With regard to the nature of the rectum, *G. tenuissima* has a bent or "genuflected" rectum attached by a small muscle anterior to the anus, whereas *G. longirostris* lacks this feature. In the *G. longirostris* I have from Copenhagen, the rectum is bent but not attached. The question arises whether this genuflection is a real difference or an accident because of carelessness in dissection (the attaching muscle is very fragile).

In other words, of the four criteria Wesenberg-

Lund used, I can dismiss the nature of the nephridia and gonads as being inconsistent within any one organism from one point in development to another. The nature of the rectum is possibly but not positively different in the two forms. The supposed differences in the papillae may be real or due to individual variation or to the preservative used, as these structures are glandular.

The only other report of a *Phascolana* was by Wesenberg-Lund in 1963 from South Africa. She said it was *Golfingia longirostris* and yet the viscera "were in very bad state; the intestine was totally 'gone to dust.'" The nephridia were present but neither gonads nor the rectum were present. She did not mention the papillae. Thus, of the four criteria she used for separating the two forms, only the one that concerns nephridia is usable. This evidence to me seems insufficient to make so positive an identification. I am not satisfied that these forms are, in fact, two different species.

The following five names have thus far been considered separately: *Golfingia* (*Golfingiella*) [*sic*] *trichocephala*, *G. (Mitosisiphon) misakiana*, *G. (Mitosisiphon) hespera*, *G. (Phascolana) tenuissima*, and *G. (Phascolana) longirostris*. In essence I have said that *G. misakiana* and *G. hespera* are synonyms, and that the same applies to *G. tenuissima* and *G. longirostris*.

When Wesenberg-Lund (1959a) described *G. longirostris* and *G. tenuissima*, she headed a section, "Remarks on the genus *Apionsoma* Sluiter, 1902," in which she wrote, among other things: "It is easily seen that in some respects Sluiter's species has many resemblances with the above discussed forms, but it is just as easily seen that it (*trichocephala*) cannot be identified either with Chamberlin's nor with Ikeda's nor with the present two species." Later she stated, "it is seen that this subgenus [*Apionsoma*] and the subgenus *Phascolana* only differ in the structure of the segmental organs and the features concerning the spindle muscle." This whole situation seemed to merit further study so I requested and received Sluiter's type material from Amsterdam. The vial contained many specimens, allowing a thorough study. It became evident that Sluiter gave an inaccurate description, as a posterior spindle muscle is indeed present and the nephridia are obviously bilobed. It is apparent that *Golfingia trichocephala* is identical with *G. longirostris* and *G. tenuissima*.

Furthermore, while looking at the specimens obtained from the American Museum of Natural History, I was startled by the similarity of *G. hespera* which had been identified by Fisher (1952) from our west coast, to the forms mentioned in the preceding paragraph. A long look at Fisher's descriptions and figures raised another question. As Wesenberg-Lund (1959a) said, the subgenus *Mitosiphon* (including *G. hespera* and *G. misakiana*) differs from *Phascolana* in that the latter, "totally lacks hooks and tentacles." Stephen's key does not mention the tentacles, leaving hooks as the only difference. This character has been criticized frequently by several authors during the past two centuries as being unreliable at the specific level, i.e., different individuals of one species may or may not have hooks (often present in young, absent in mature forms).

Fisher (1952) stated that the entire tentacular crown of *G. hespera* measures 0.25 mm. in diameter, and that on a specimen with an introvert of 115 mm. the zone of 20-50 rings of hooks, each measuring 0.02 mm., is only 3 mm. wide or 2.6 percent of the length of the introvert. In the specimen of *G. hespera* I have from the American Museum, I was unable to find hooks. However, this specimen was not fully expanded. It is entirely possible that hooks might have been overlooked inadvertently by Wesenberg-Lund because of their minute size. When she wrote (1959a, p. 189), "it is therefore considered justifiable to include *G. tenuissima* and *G. longirostris* in a new subgenus *Phascolana*," she was doing so on very little solid evidence.

In Stephen's (1964) key to the subgenera of *Golfingia*, he used the relative length of the introvert as well as "species fairly large" or "species small" to distinguish between *Mitosiphon* and *Phascolana*. Both characters are meaningless, as illustrated by the material in my possession. The introvert, in all individuals, is from four to nine times longer than the trunk, but whether this ratio represents a fully extended form is questionable.

In conclusion I suggest that, in view of the corrections made in the description of *Golfingia trichocephala*, *G. tenuissima* and *G. longirostris* be considered junior synonyms of this species. Secondly, unless further study proves otherwise, *G. hespera* is a junior synonym of *G. misakiana*. Whether these two forms (*G. trichocephala* and *G. misakiana*) should be considered the same is

still an open question. If hooks, tentacles, or both can be found in any specimens of *G. trichocephala*, the question should be taken up again.

I also suggest that the description of the subgenus *Mitosiphon* be modified to include the species which had been in the subgenus *Phascolana*. The diagnosis of the subgenus at the beginning of this section takes this change into account.

The environment of the *G. trichocephala* and *G. misakiana* group is shallow, warm water. This is also true of two other forms, which ought to be mentioned here even though they were not found in this study area: *Phascolosoma pectinata* and *Siphonides rickettsi*. The former was described by Keferstein in 1866, the latter by Fisher in 1952. Wesenberg-Lund (1959b) redescribed *P. pectinata* and made the following reference to the previously discussed species of *Golfingia*:

"*Ph. pectinatum* shows some anatomical features not common in Phascolosomatids and the allied genus *Golfingia*, viz. 1) the accessory combs of the hooks, 2) the bilobed nephridia, 3) the extremely long introvert, 4) the roots of the ventral retractors anterior to the dorsal ones. The comb at the bases of the hooks is found in two *Golfingia* species, viz. *G. hespera* (Chamberl.) and *G. misakiana* (Ikeda). The bilobed nephridia are found in the same two species and in *G. longirostris* E. W. -L. and *G. tenuissima* E. W. -L. (1959a). The extremely long introvert is found in all four species just mentioned. The reverse proportion regarding the situation of the roots of the dorsal and ventral retractors is to my knowledge unique among sipunculids. The four mentioned species have continuous, longitudinal muscles, and the tentacles surround the mouth; in the two species described by the present author they are reduced to an oral disc resembling the one in *G. minuta* (Kef.). In spite of many conformities, they are generically different from the here discussed species."

Despite these several unique similarities, in *Phascolosoma pectinata*, longitudinal muscle bands are present, a posterior spindle muscle is absent, the tentacles are dorsal to the mouth, and the rectum is straight and bears a caecum. These differences separate it from the aforementioned *Golfingia*.

Wesenberg-Lund (1959b) challenged the validity of Fisher's new genus and species, *Siphonides rickettsi* (Fisher, 1952). I wholeheartedly

agree with her on this point. Nevertheless, Stephen (1964) retained the genus in his brief revisionary paper, separating it from *Phascolosoma* in his key solely on the presence of the bilobed nephridia. By so doing he thereby excluded *P. pectinata* from *Phascolosoma*. He also misspelled it thus: *Siphonoides*. Murina (1968) erected a new subgenus of *Golfingia* called *Siphonoides* which may cause unfortunate confusion.

Fisher's diagnosis of his new genus is a classic collection of negative characters. The only positive features he mentioned are bilobed nephridia, numerous small tentacles, and minute complex hooks.

I repeat the suggestion of Wesenberg-Lund (1959b) that *Siphonoides rickettsi* is a junior synonym of *Phascolosoma pectinata* and that the monotypic genus *Siphonoides* is invalid.

*Golfingia murinae* Cutler, 1969

Figures 23–25

*Golfingia hespera*: MURINA, 1964a, p. 228; 1964b, p. 59; 1967, p. 1335; 1968, p. 197.

Murina (1964a, 1964b, 1967, 1968) has described several *Golfingia* which she placed in the species *G. hespera*. For reasons discussed in the preceding section (*G. trichocephala*), it is apparent that Murina's designation was incorrect and that her material represents a new species.

*Golfingia murinae murinae* Cutler, 1969

*Golfingia murinae unilobatae* CUTLER, 1969, p. 214.

The change in the subspecific name was necessary to comply with Article 47 of the International Code of Zoological Nomenclature.

The 201 specimens are from 35 stations. These worms have trunks from 1.5 to 13 mm. long. The introvert is at least four to six times the length of the body. They are semitransparent, tan, or brown, depending on their size and state of contraction; the larger ones are the darker and more rugose. The body is in many cases shaped like a plump spindle and has mammiform papillae on the posterior end. The anterior delineation of the trunk is not always clear as it may taper gradually into the long, delicate introvert. A few rows of transparent hooks, 25–40  $\mu$  long, are present. Some of the hooks have an accessory comb of spinelets or teeth at

their base. One specimen has short, stubby tentacles and their off-center orientation resembles the situation in *Phascolosoma*. The mouth could not be located. Most of the introvert has small papillae.

The body wall in some specimens is rather thick and may have loose-appearing epidermis with blister-like papillae. Smaller ones are thin-skinned and transparent. The papillae are discussed at length in Murina (1964b) and measurements are presented in her table 3. The most outstanding external feature of this species is the large posterior papillae.

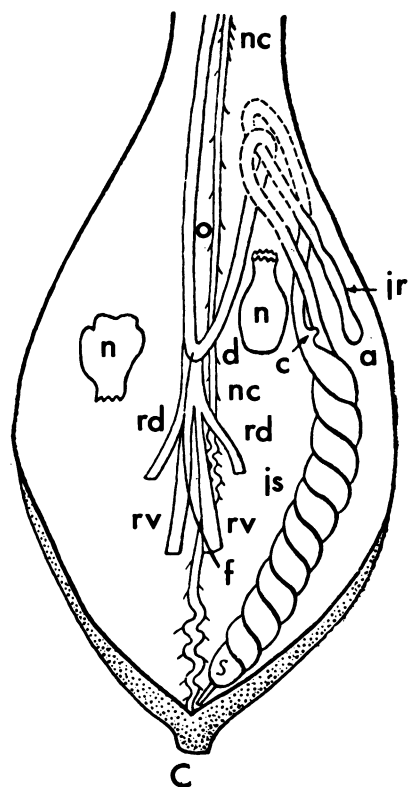
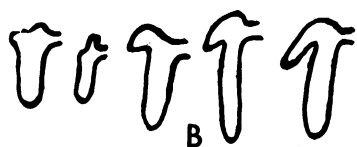
Internally the four retractors are more typically arranged than in the unique *G. trichocephala* complex, i.e., the ventral pair is about twice as massive as the dorsal pair, and both pairs are set off farther from the ventral nerve cord—the dorsals more so than the ventrals. The origin of the retractors generally lies in the posterior third of the body (65–85 percent) but may be found farther anteriad. The nephridia are free, sac-shaped, and open at the anterior of the trunk. The anus is invariably posterior to the nephridiopores, but the distance between them may vary. One and sometimes two fixing muscles were observed (Murina found up to three).

Included in this subspecies would be Murina's (1964a) Pacific specimens and her 1968 Atlantic Ocean example.

*Golfingia murinae bilobatae* Cutler, 1969

The 88 specimens are from 22 stations. Morphologically this subspecies is almost identical with *G. m. murinae*. The trunk lengths may be smaller (these were 2–7 mm. as compared with a maximum of 13 mm.), but this difference may be a result of inadequate sampling. It is generally the paler colored or transparent of the subspecies and has a thin body wall and is more tapered at the anterior end. As before, the striking feature is the presence of large mammiform papillae on the posterior end of the trunk. One internal difference is apparent, however, a small secondary anterior lobe on the nephridia (fig. 23). This lobe is infrequently lacking but if so the nephridium is long and slender, not short and plump as in *G. m. murinae*. This difference by itself may not be just cause for erecting a separate subspecies, if it were not for a distinctive distribution of this bilobed form.

Murina's Mediterranean and Gulf of Mexico



specimens are included in this subspecies.

**DISTRIBUTION:** The distribution of these two subspecies is spatially separate (fig. 25). *Golfingia murinae bilobatae* is found on the continental slope from the Florida Keys to Cape Lookout, North Carolina (latitude  $24^{\circ}10'$  to  $34^{\circ}16'N$ ), at depths of about 300–700 meters. The temperature here is generally  $6.5$ – $10^{\circ}C$ ., with an occasional influx of warmer water. The sediments are fine, silty sands and sandy silts with a high percentage of calcareous material. Some worms were removed from crevices in coral.

*Golfingia murinae murinae* is found from latitude  $32^{\circ}11'N$  to  $39^{\circ}59'N$ . The most southerly ones are all on the Bermuda slope between 1000 meters and 2000 meters. The rest are at depths between 2000 and 4800 meters on the continental rise between Cape Cod and Cape Hatteras. They are apparently absent from the intervening abyssal plain. The temperature off Bermuda is  $3.6$ – $7.4^{\circ}C$ . and that on the rise is  $2.3$ – $3.5^{\circ}C$ . The sediments in these areas are fine silts and clays, again with a high percentage of calcareous material.

In summary, this species prefers a relatively cold, stable, deep environment with fine sediments containing a significant amount of calcareous deposits. One subspecies is found in shallower, warmer areas with a slightly coarser substratum than the other (fig. 24).

#### SUBGENUS *THYSANOCARDIA* FISHER, 1950

**DIAGNOSIS:** Two retractors; contractile vessel with numerous simple or branched villi; hooks absent; nephridiopores invariably in front of anus.

#### *Golfingia catharinae* Müller, 1789

Figures 26, 27

*Phascolosoma catharinae* MÜLLER, 1789. GRUBE, 1867, p. 48. SELENKA, DEMAN, AND BULOW, 1883, p. 15. SELENKA, 1885, p. 13. TEN BROEKE, 1925, p. 83.

FIG. 23. *Golfingia murinae*. A. External view (scale in mm.). B. Several diagrammatic views of nephridia with small anterior lobes in *G. m. bilobatae* (from Cutler, 1969). C. Internal view of *G. m. murinae* (from Murina, 1964a).

**Abbreviations:** a, anus; c, caecum; f, fixing muscle; js, intestine; jr, rectum; n, nephridia; nc, nerve cord; o, esophagus; rd, dorsal retractor muscle; rv, ventral retractor muscle; s, spindle muscle.

*Phascolosoma procerum* MOBIUS, 1875, p. 157. SELENKA, DE MAN, AND BULOW, 1883, p. 39. THÉEL, 1905, p. 70. SOUTHERN, 1912, p. 24. GEROULD, 1913, p. 383. FISCHER, 1925, p. 20.

*Golfingia procera*: FISHER, 1950, p. 551; 1952, p. 402.

*Golfingia catherinae*: FISHER, 1950, p. 551. WESENBERG-LUND, 1963, p. 111.

*Golfingia procerum*: STEPHEN, 1960, p. 18.

**DESCRIPTION:** The 97 specimens are from 35 stations. The trunk length ranges from 1 to 60 mm. The animals are generally light gray but may be a creamy white or have patches where the epidermis has been rubbed off, allowing the internal organs to show through the semitransparent body wall. One feature often mentioned for this species is the fine wavy or zigzag

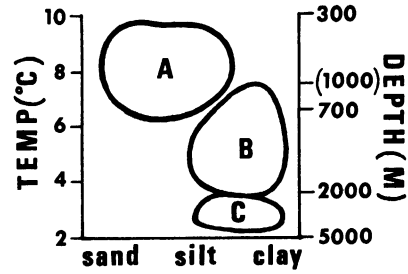


FIG. 24. Temperature, depth, and sediment relationships of the two subspecies of *Golfingia murinae*. A. *G. m. bilobatae*. B. *G. m. murinae*, Bermuda population. C. *G. m. murinae*, continental slope population. (The 1000-meter depth refers only to the Bermuda slope, where temperatures are warmer at greater depths than near the continental slope.)

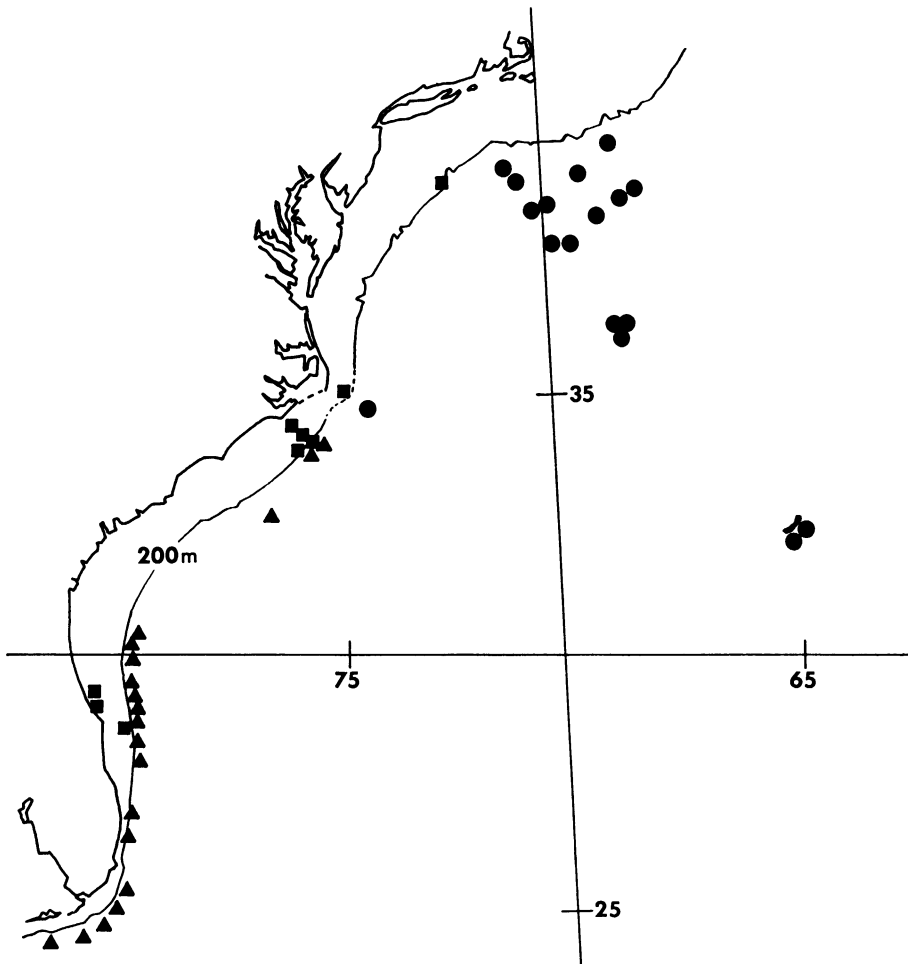


FIG. 25. Distribution of *Golfingia* (*Mitosiphon*): *G. trichocephala* (■), *G. murinae bilobatae* (▲), and *G. murinae murinae* (●).



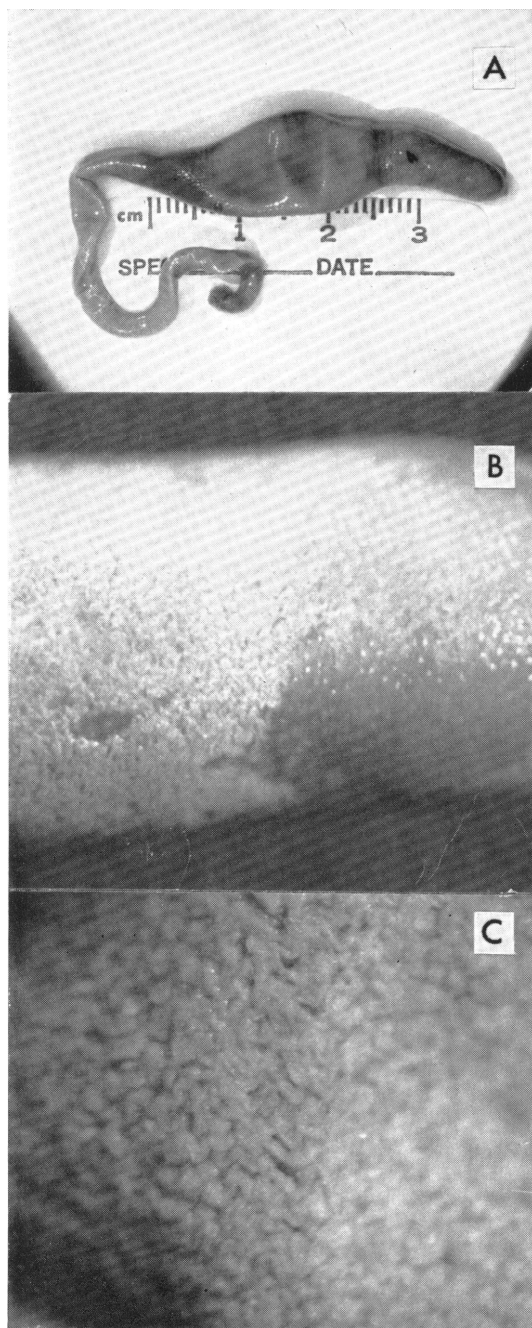


FIG. 26. *Golfingia catharinae*. A. External view. B. Area where gray calcareous coating is rubbed off. C. Magnified view of the epidermis showing indistinct zigzag lines.

lines, folds, or wrinkles on the body surface (fig. 26C). In my material these marks are generally present in the larger animals but seem to depend somewhat on the amount of contraction of the circular muscle layer. In animals less than 5 mm. long the lines are indistinct, and in the 1- and 2-mm. specimens they are not visible. The smaller animals have a general fuzzy appearance. The wrinkles seem to be accentuated if the body is covered with the typical gray substance which Théel (1905) demonstrated to be calcareous. This layer is probably calcareous ooze from the environment which adheres because of the secretion of mucus by the skin glands. It does not appear consistently in all specimens (fig. 26B).

The shape is cylindrical and the posterior end in many cases tapers to a very short "tail"; it may be rounded or occasionally invaginated. The anterior end of the trunk tapers gradually into the introvert which is about one-third to one-half the diameter of the trunk. The division between these two portions of the body is not distinct. This condition has led to some confusion with regard to the relative length of these parts. In most of my specimens the introvert is from one to two times the length of the trunk. Scattered over the body are small papillae, generally dark brown but in some cases pale honey-colored.

The introvert is smoother and more transparent than the trunk and is in some cases tinged with rusty red near the end. The tentacles are numerous and arranged in a series of paired rows surrounding the mouth; asymmetry is caused by the prominent nuchal organ on the dorsal side. The number of rows ranges from 8 to 14 but commonly is 10-12; the number of tentacles per double row is about 15-20. Therefore, the number of individual tentacles per animal may reach well over 100. The general appearance of this region is like that of a string mop.

Internally two strong retractor muscles originate near the posterior end of the body. The point of origin is generally 75-85 percent of the distance between the anus and the posterior end of the body, but may be anywhere between 70 and 95 percent of this distance. The esophagus runs between these two muscles for some distance before separating to go into the double coiled intestine. Along the esophagus lies a blood vessel with lateral villi coming off each

side. The size and complexity of these villi are extremely variable. In the smaller forms they are generally simple, undivided short tubes—a shape retained on the anterior portion of the vessel in some of the larger specimens. This simple tube bifurcates at the tip, and in larger animals (because of the subsequent dendritic branching) forms the tufts spoken of in the literature. In several specimens the shape changes from simple to tufted as one follows the vessel from anterior to posterior.

The esophagus has one strong fixing muscle which comes from the body wall on the same level as, but somewhat posterior to, the left nephridium. The intestine has from six to 25 double coils. In general, as the animal grows larger the number of gut coils increases. The rectum is short. A caecum was observed in one specimen. A strong wing muscle holds the distal end of the rectum to the body wall. The spindle muscle is attached anterior to the anus and runs through the coil but does not extend beyond it to the body wall.

The two nephridia are unattached to the body wall and in most animals open to the outside just anterior to the anus. In a 3-mm. specimen, the nephridiopores and anus are at the same level; in a 40-mm. animal the nephridia are 2 mm. anterior to the anus; and in a 60-mm. animal they are about 3 mm. anterior to the anus. One might conclude that as the animal grows longer the nephridia tend to move anterior from the anus. This generalization has exceptions however. The nephridia are about one-fourth to one-third the length of the trunk and are lightly pigmented in the larger animals but transparent in the smaller worms.

**DISCUSSION:** It is my opinion that *Golfingia procera* and possibly *G. semperi* are both junior synonyms for *G. catharinae*. I reached this conclusion after reviewing 12 articles by eight authors and studying the material I have on hand. When the different descriptions of these animals are compared, it is possible to find more variation within one species than between any two.

Two common variations concern the origin of the retractors and the position of the nephridiopore. As my study has shown, these characters can vary within one population. According to most descriptions, the retractor originates somewhere in the posterior third of the trunk, and the nephridia open somewhere anterior to the

anus. To illustrate my point, however, consider Wesenberg-Lund's (1955, 1959a, 1963) comments on one species, *G. catharinae*: In 1955, "nephridiopores in front of anus"; in 1959a, "instead of opening slightly in front of anus, here the segmental organs open slightly behind it"; and in 1963, "the anus is at the same level as the nephropores." With respect to the retractors she stated: in 1959a, "retractors, attached in the middle part of the body"; in 1963, "retractors, which is anchored at the anterior part of the hindmost third of the trunk." The fixing muscles also vary: in 1959, "there is only one fixing muscle . . ."; in 1963, "two fixing muscles were found (in accordance with Selenka and DeMan, 1883, whereas Sato, 1939, found only one)." Similar statements can be found elsewhere.

In the key of Selenka, deMan, and Bulow (1883) *G. semperi* and *G. procera* are separated from *G. catharinae* on the basis that the villi (Zotten) on the blood vessel were long in the first two and very short in the third. This character apparently is extremely variable and not species constant. Selenka subdivided *G. semperi* and *G. procera* on the basis of the size of the papillae and their type locality (one from the North Sea, the other from the Philippines). This distinction seems to me to be insufficient.

In summary, without having access to the type material, but on the basis of a comparison of the published descriptions, I am unable to find sufficient, consistent, morphological differences to justify the retention of these three different names. Further study might convince me otherwise, but at the moment I apply the most senior available name, which is *Golfingia catharinae* Müller, 1867. This subgenus has not been studied systematically and critically and other questions about it need answering.

The world distribution of these forms is somewhat distinct. *Golfingia procera* has been described from various parts of the North Atlantic at depths of 25–500 meters plus one Pacific Ocean report from Southern California. *Golfingia semperi* has been reported from off Brazil, the Philippines, Australia, and Zanzibar. *Golfingia catharinae* has been found in the tropical and southern Atlantic, extending around Africa to the southwestern Indian Ocean and one record exists from Korea in the western Pacific Ocean, from the intertidal zone to 3500 meters. It remains to be seen whether this difference in

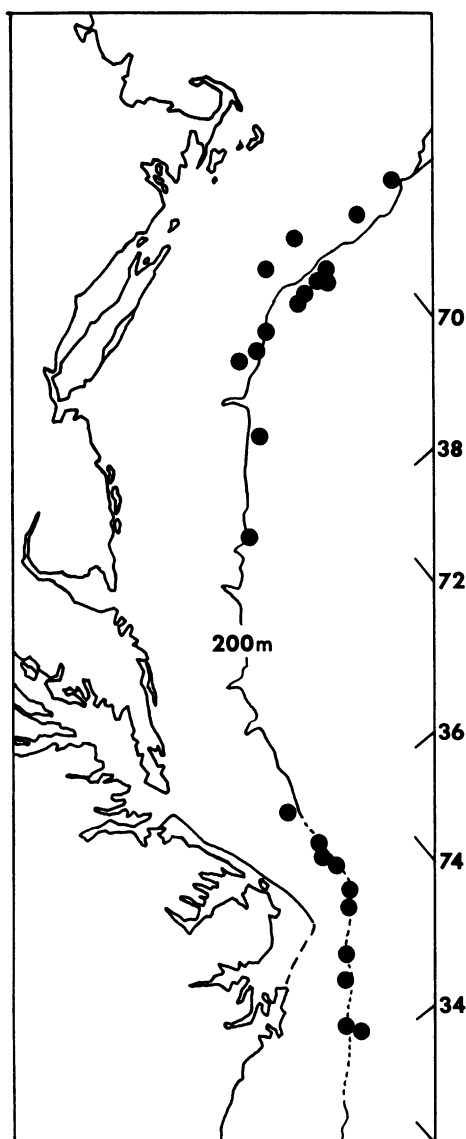


FIG. 27. Distribution of *Golfingia catharinae*.

distribution is real or an artifact of the tendency on the part of zoologists, when identifying an animal from a certain locality, to refer to earlier literature describing the fauna from only that same general area. This rationale, when working with poorly known groups of animals, may cause masking of a cosmopolitan species under several different names with different ranges—particularly when new species are described on the basis of a single specimen.

**DISTRIBUTION:** This species is restricted to a

narrow band along the outer edge of the shelf and the upper few hundred meters of the slope (fig. 27). The vertical distribution can be summarized:

11 stations 74–150 meters

23 stations 150–650 meters

The most southerly record is latitude  $34^{\circ}13'N$  and the most northerly is latitude  $40^{\circ}20'N$ .

The temperature in the range of this species is almost constant,  $5-10^{\circ}C$ . The sediments are within the limits of the fine sands to sandy silts, the median phi ranging from three to seven.

#### SUBGENUS *PHASCOLOIDES* FISHER, 1950

**DIAGNOSIS:** Two retractors; contractile vessel lacking villi; nephridia single-lobed; hooks, when present, simple (without accessory spines); spindle muscle not attached to posterior end of body.

#### *Golfingia eremita* (Sars, 1851)

Figures 28, 32

**DESCRIPTION:** The 64 specimens are from 22 stations. The size of the trunk ranges from 3 by 1 mm. to 25 by 5 mm.; most are 10–15 mm. long. The small forms are whitish or transparent, but the large individuals are pale creamy tan to dark reddish brown. Some individuals of the lighter variety have dark, scattered pigment spots. These two color forms have been noted by others. Gerould (1913) erected a new variety, *scabra*, which he characterized as having a “loose, thick, coffee-colored cuticle, which gives the surface the appearance of a rough woolen fabric.” Several specimens I looked at approached the above description, but whether this form deserves separation as a “variety” is debatable. Gerould’s “type” material consists of 18 individuals and the above-mentioned “cuticle” is transient and easily rubs off.

This species has the classical shape of a stocky, cylindrical trunk with an abrupt taper to the introvert. The skin appears to be very smooth although it is covered with very small, uniformly distributed papillae. Many individuals show transverse, parallel grooves of various sizes on the trunk wall, particularly on the posterior portion. The thickness of the body wall varies according to the amount of contraction, but the wall is commonly rather thick. None of my specimens is extended sufficiently for accurate

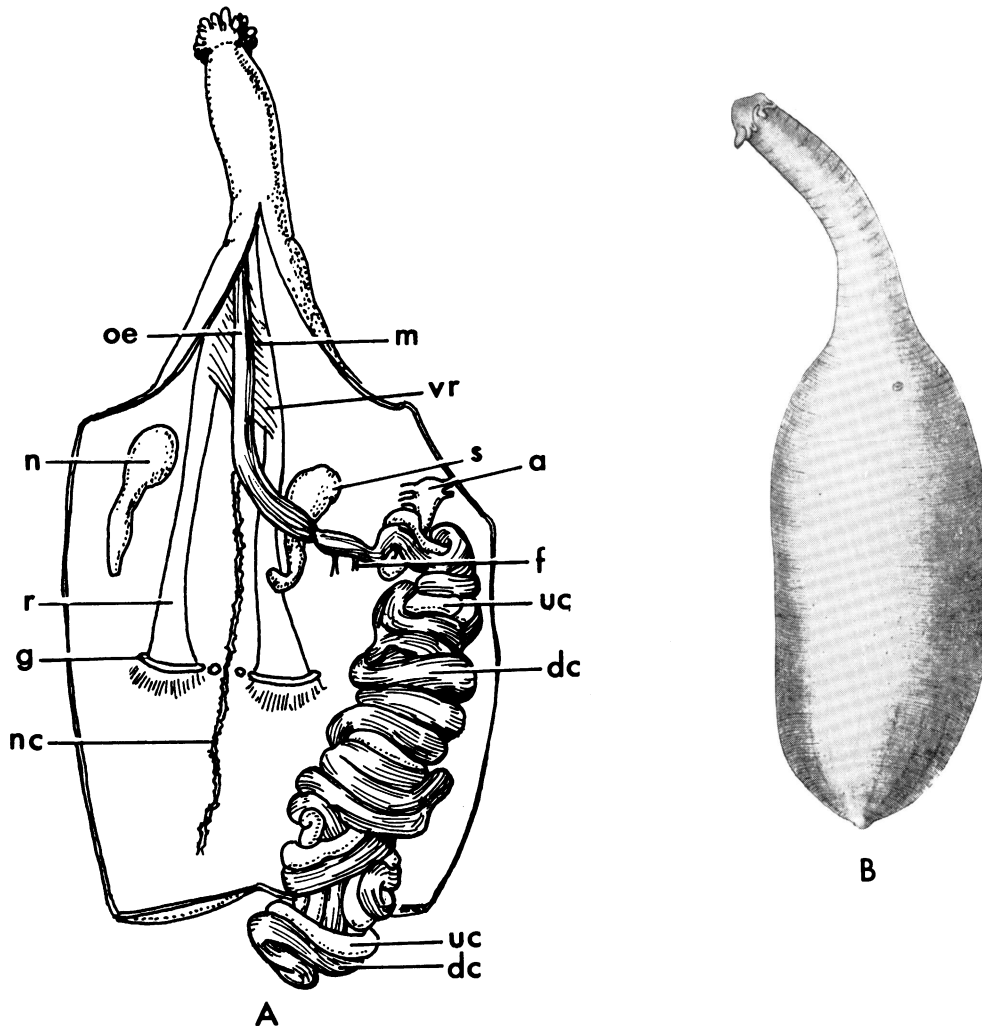


FIG. 28. *Golfingia eremita*. A. Internal view (from Théel, 1905). B. External view (from Gerould, 1913).

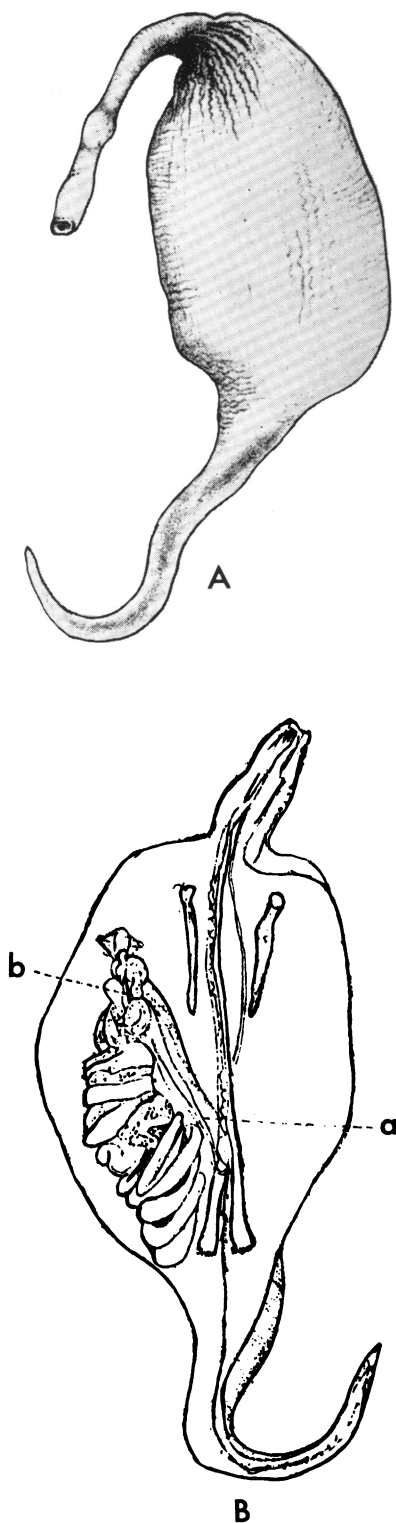
Abbreviations: a, anus; dc, descending coil; f, fixing muscle; g, gonad; m, mesentery; oe, esophagus; nc, nerve cord; n + s, nephridia; uc, ascending coil; r and vr, retractor muscles.

comment on either the length of the introvert or the number of tentacles. Gerould (1913) stated that the introvert is slightly shorter than the trunk. Théel (1905) showed that the number of tentacles in animals 17–37 mm. long may vary from 16–40. Hooks are absent.

Internally two well-developed retractor muscles originate from the mid-region of the body (fig. 28). They remain separate until inserting in the head region. The esophagus is attached to both retractors by sheets of connective tissue before it enters the intestinal coil. A fixing

muscle is attached to the esophagus, but no spindle muscle is present. The distal part of the short rectum is anchored by the wing muscle. The nephridia are about one-fifth to one-fourth the trunk length and are colorless in small animals to yellow-orange in the larger ones. They open at the level of the anus or slightly anterior to it.

DISTRIBUTION: This species is described as a typical Arctic form. Gerould (1913) said, "it is remarkable that this characteristically Arctic form extends southward along the American



coast in shallow waters as far as Massachusetts Bay, and in deeper waters as far south as about  $40^{\circ}$  N. latitude." The present report includes only 10 new records from recent collections, suggesting that it is not a common form along the Atlantic coast of the United States. When the 12 museum records are added to the 10 new records, certain facts appear. Of the total of 22 records, three are from Newfoundland, Greenland, 12 are from the Gulf of Maine, five from southern New England, one from about 20 meters off northern Virginia (latitude  $37^{\circ}43'N$ ), and one from just north of Cape Hatteras (latitude  $35^{\circ}37'N$ ) at 500 meters. The last of these is the most southerly record on this side of the Atlantic, but the Virginia record is from the warmest environment and therefore the most difficult to reconcile with the others. South of Cape Cod this species is generally not found on the shelf but is restricted to the slope, at depths of 229–2110 meters. It is apparent that this species prefers temperatures less than  $10^{\circ}$  C. The sediments in its range are variable and can cover a broad range of sand and silts.

This cold-water species is common on both sides of the North Atlantic up into the Arctic Ocean. One record is from the Pacific at 500 meters off California.

*Golfigingia bulbosa* (Southern, 1912)

Figures 29, 32

**DESCRIPTION:** The 13 specimens are from five stations. The size of the trunk ranges from 3 to 20 mm. They are grayish white or tan on the introvert and on the posterior end of the trunk; most of the rest of the body is transparent. The body is somewhat swollen anteriorly; the posterior third or quarter of it tapers into a narrower pointed region which might be interpreted as a tail—a different type of caudal extremity from that in *Golfigingia flagrifera* (fig. 29). Regions on some individuals exhibit fine zigzag lines similar to those on *G. catharinae*. Hooks are absent.

The two retractor muscles originate in the mid-region (40–75 percent) of the trunk. The spindle muscle is unattached posteriorly. The free nephridia open slightly anterior to the

FIG. 29. *Golfigingia bulbosa* (from Southern, 1912). A. External view. B. Internal view.

Abbreviations: a, fixing muscle; b, spindle muscle.

anus. The rectum is short and the intestine is rather loosely coiled.

**DISCUSSION:** This species was described in 1912 by Southern from the coasts of Ireland. It was based on eight specimens and apparently has not been reported since. The 13 specimens I am tentatively assigning to this category are not well defined but fit the essential criteria. There are many similarities between this form and *Golfingia novae-zealandiae* (see Edmonds, 1960).

Southern (1912) at one point said, "The peculiarity of shape from which it derives its specific name is common to all specimens." Later he added, "It is probable that the bulbous character of the anterior part of the trunk is not a specific character but is due to unequal expansion." With regard to the "tail" he wrote, "This latter portion, however, is really a slender portion of the trunk, not an appendage in the same sense as is the tail in *G. muricaudatum*." Later still he stated, "The filiform nature of the posterior portion of the trunk, is, however, characteristically shown by all specimens, and is probably the normal condition." How he can attribute one of these characters (bulbous anterior) to "unequal expansion" and the other (tail) as being "the normal condition" is difficult to understand.

**DISTRIBUTION:** The five stations are at 1102 meters, 1400 meters, 1500 meters, 1700 meters, and 2086 meters; three are on the lower slope south of Cape Cod, the other two are on the Bermuda slope (fig. 32). The temperatures range from 3.5 to 4.5° C. and the sediments are clayey silts. These data are very similar to those for Southern's material.

*Golfingia constricticervix* Cutler, 1969  
Figures 30, 32

**DESCRIPTION:** The 90 specimens are from 11 stations. These long, slender animals have a length about 15–20 times the diameter (15 by 0.67 mm., 5 by 0.33 mm.). They are generally transparent, becoming dark yellow toward the ends of the trunk. The introvert is about one-fifth the length of the trunk.

One of the unique features of this species is a constriction or neck at the base of the introvert. Because of this relatively weak connection, very few worms are whole. Those few that retain the introvert show the long hooks that cover its distal half. The hook size increases from 0.04 mm. to 0.28 mm. The hooks are single-pointed,

moderately curved, slender, and irregularly arranged. About 12–16 short, reduced tentacles are visible on one individual (fig. 30).

The anterior end of the trunk is generally swollen and the anus is on a small protuberance. Very small, slightly oval, clear, glandular papillae are visible at the anterior and posterior ends of the trunk, which is otherwise smooth and thin-walled.

Internally the two retractors originate from the body wall very close to the ventral nerve cord, about 15–25 percent of the distance to the posterior end of the trunk. These two muscles join before leaving the trunk to form one unit. The intestinal coil may be loose and the individual coils are in many cases relatively far apart from one another.

**DISTRIBUTION:** There are apparently two populations—one near Bermuda (latitude 32° 17'–33° 57' N) in depths of 1700–4800 meters and the other is on the continental rise and base of the slope (latitude 38° 16'–39° 47' N) at depths of 1500 to 3000 meters (fig. 32). The sediments are fine (mostly silts and clays), and the temperature is low and stable, 2.5–3.5° C.

**DISCUSSION:** This group of animals may contain two taxa. Complete worms with hooked introverts were found at only two stations near Bermuda. At some of the other stations, animals (similar in other respects) with longer, more slender, and apparently hookless introverts were observed.

*Golfingia flagrifera* (Selenka, 1885)  
Figures 31, 32

**DESCRIPTION:** The 24 specimens came from 17 stations. Trunk size ranges from 110 by 10 mm. (plus a 15-mm. tail) down to 2 by 0.33 mm. Most of the specimens are between 10 and 70 mm. long. The larger individuals are brownish gray (with some darker spots), and the smaller ones are milky white or semitransparent.

The entire body is covered with small papillae, but the posterior end, in the larger animals, has the large papillae characteristic of this species, i.e., these papillae have been described as wartlike (Gerould, 1913), as small scales directed anteriorly (Selenka, 1885), and as flat oval papillae projecting forward (Sluiter, 1900). These differences suggest that the form is variable, probably as a result of the amount of care used in the collecting and preserving. On a few animals in my collections, it is apparent

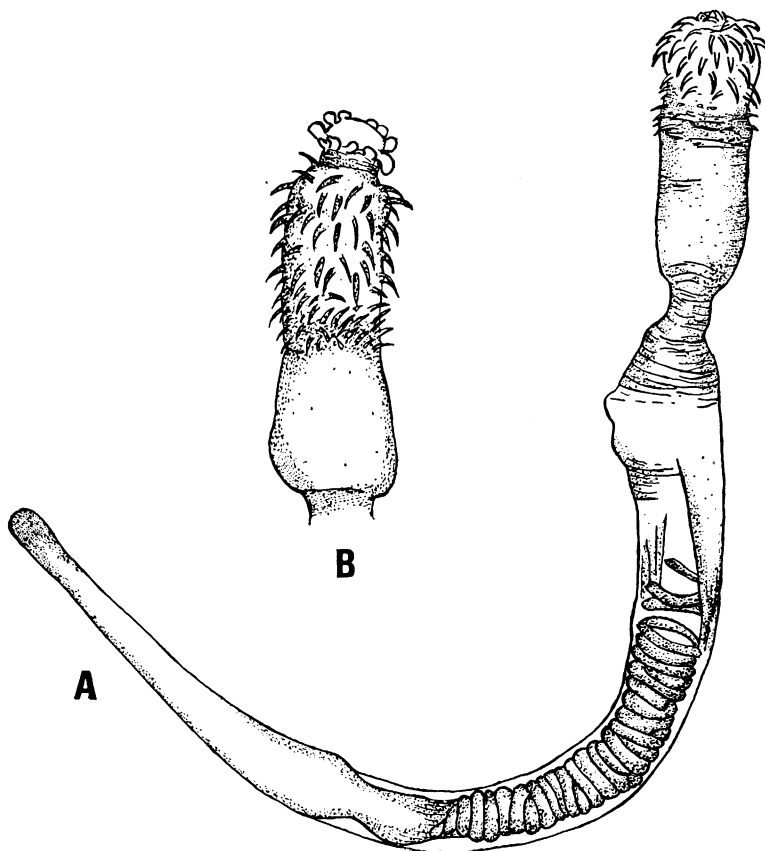


FIG. 30. *Golfingia constricticervix* (from Cutler, 1969). A. External view of entire worm showing coiled gut through transparent body wall. B. Fully extended introvert showing tentacles.

that these papillae are rather voluminous, hollow, subcylindrical, saclike structures which project outward and anteriorly. A few papillae exhibit two or three small, finger-like projections from the distal end. It is seen that, if allowed to become desiccated, the projections would appear as described by the above authors. According to my observations, however, they did not describe the morphology of these structures in nature.

The smallest worm observed by the previous authors was 60 mm., whereas in my material most animals were somewhat smaller than this. The question arises concerning differences in these papillae as the size of the animal changes. My observations showed that they are small on small worms, so that in a 5-mm. or 10-mm. worm they are not very prominent structures,

but rather average-looking, small papillae. I observed also that these papillae are not difficult to remove; the density of the papillae is somewhat lowered in a few individuals probably by abrasion from handling. In other words, these papillae, important in the characterization of this species, are extremely variable in size, shape, and density.

The caudal extremity ("whip-like appendage," "l'appendice en forme de fleau," "slender flagellum") which gives this species its name is likewise of variable size. It may be as long as 10 mm. or 15 mm. in the large animals, but it is reduced in smaller worms. It also is possible that this thin, fragile extension could be broken, either in part or entirely, during collecting or subsequent processing. Also, it is possible that at an early stage in ontogeny this structure



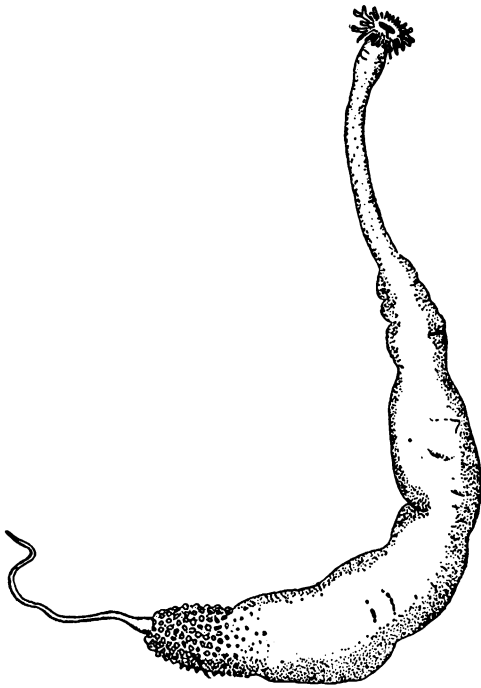


FIG. 31. *Golfigingia flagrifera* (from Selenka, 1885).

is not visible. A 5-mm. specimen had a suggestion of a tail, but the 2.5-mm. and 2-mm. specimens ended in a point and lacked a real tail. If this structure is lacking, does it automatically exclude that particular organism from being assigned to this species?

Although no individual in the current collections is entirely extended, the lack of hooks is verified. The length of the introvert is probably about equal to the trunk or slightly less. Tentacles are well-defined.

Internally the two retractor muscles have their origins in the anterior mid-region (30–50 percent) of the trunk. Two fixing muscles sometimes are visible at the anterior part of the intestine, but the intestine is not attached posteriorly. The strong spindle muscle is attached at some distance anterior to the anus (2 mm. in a 48-mm. animal; more than 5 mm. in a 90-mm. specimen). The rectum is short, and a small caecum can be observed in a few individuals. The nephridia are small, free, clear or yellow-orange, and open slightly anterior to the anus.

**DISCUSSION:** Previous reports of this species were based on very few specimens, all of which were large adults. The only characters that

distinguish this form from several others in this subgenus are the presence of the “tail” and the large posterior papillae. These features are certainly noteworthy and outstanding in intact, well-preserved, adult forms. If, however, a worm has been damaged during collecting or washing, if it has been poorly preserved, or if it is less than 5 or 10 mm. long, these structures may be missing or considerably modified, thereby making positive identification very difficult.

**DISTRIBUTION:** This species is found in depths ranging from 1500 meters (only two reports less than 2000 meters) to 5350 meters from a broad area between latitude 32°N and 40°N (fig. 32). The temperature here is uniformly low (2.2–3.7° C.), and the sediments are almost uniformly fine silts and clays. Worldwide there are a few scattered records from the Atlantic, Pacific, and Mediterranean—all at considerable depths.

*Golfigingia minuta* (Keferstein, 1865)

Figures 33–35

*Golfigingia cinctum* GEROULD, 1913, p. 398. FISHER, 1950, p. 551.

*Golfigingia improvisa*: MURINA, 1958, p. 1625.

*Golfigingia minuta*: MURINA, 1958, p. 1628.

**DISCUSSION:** This species has been the subject of much discussion and disagreement during the past hundred years. The most recent review was Murina's (1958) excellent and exhaustive article in which she added her own observations against the background of the earlier literature. At one time or another at least seven specific names and four generic names have been applied to this form. The two most commonly used are *Golfigingia minuta* and *G. improvisa* (see Murina, 1958, for synonymy). These animals are very small and have a rather variable form.

Sometimes, the presence or absence of hooks has been used to separate different forms within this complex, but it is generally agreed that this procedure is not reliable. An interesting example of a non-sequitur appears in Wesenberg-Lund (1955, p. 10–11) in this connection. It is an example of how the nomenclature of this species has become amazingly confused: “The character which originally was used as the most important separating character is the presence or absence of hooks, but there is no doubt that this is not a valid discrimination, since in old specimens the hooks have often fallen out or got

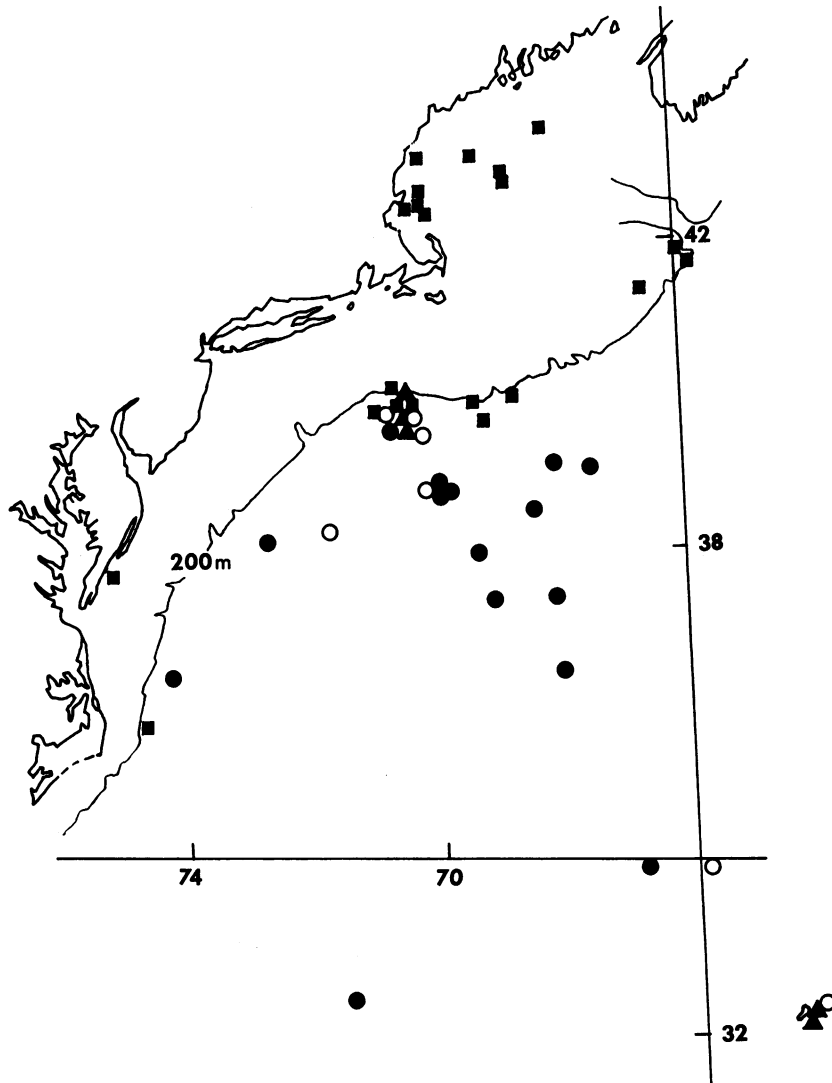


FIG. 32. Distribution of *Golfinigia bulbosa* (▲), *G. eremita* (■), *G. flagrifera* (●), and *G. constricticervix* (○).

worn; every graduation from a well developed girdle of hooks (in *sarsi* and *anceps*) to no hooks at all (*Ph. sabellaria*) may be found; therefore, the union of the species is undoubtedly justified . . . the specimens without hooks I refer to *G. minuta*, those with hooks to *G. improvisa*."

Before continuing it seems appropriate to review briefly the species *G. abyssorum* and Théel's "abyssorum section" as it applies to the species under consideration. The following excerpts are from Théel's "general remarks on the abyssorum section" (1905, p. 74-78):

"In this 'section' are comprehended all those northern forms of *Phascolosoma*, [*sic*] which are comprised under the names *Ph. abyssorum*; *Lilljeborgii*, *Sabellariae*, *improvisum*, *anceps*, *glaciale*, and *Sarsi*; . . . Any investigator who has had the opportunity of studying these forms, must perceive that the seven species in question really constitute one natural group of the *Phascolosoma*-genus. [Other authors have already synonymized *sabellariae*, *anceps*, *glaciale*, and *sarsi* under *minuta*.] They have all a narrow, cylindrical trunk with a lustrous, almost smooth surface

(except *P. improvisum*). In most cases their tentacles are reduced to an irregularly buckled or folded disk round the mouth. They are all in possession of two ventral retractors. . . .

"In consideration of the great conformity existing among several of the forms enumerated, there may arise the question as to whether they all are true separate species or not . . ."

After stating that to avoid confusion he prefers to keep them separate, Théel then proceeded to discuss, and discard, several morphological features as species specific, as follows:

"The proportions between the length of the proboscis and that of the remaining part of the body do not certainly give any true expression for the relationship of the species in question . . .

"... the shape of the tentacular crowns, two groups could be distinguished, one with tolerably well-developed tentacles, and the other with tentacles reduced to some minute, irregularly rounded protrusions of the oral disk.

"... However, my own inspection of *P. abyssorum* has given rise to the opinion in my mind, that its tentacles are in a low developmental state, presenting themselves as small, irregular knobs or elevations round the oral disk. . . . Thus, . . . the shape of the tentacular crown does not afford any true character distinguishing the two last mentioned species from each other, nor from the other *doubtful* species. It evidently presents a series of transitional stages, a thing of great scientific interest in itself, but *not exactly convenient for the systematist*." [Italics mine.]

Théel's figures 202, 197, and 206 provide an interesting series (fig. 33). If the animals were all the same size the differences might be more acceptable but in fact the first two were from animals with 10-mm. trunks and the third (*P. abyssora*) was drawn from a specimen with a 27-mm. trunk. The possibility again arises that this change is ontogenetic. The fact that the number of tentacles increases with size has been documented by several authors, including Théel (see his *G. margaritacea* figs. 195, 196, 194, and 192 reproduced here as fig. 18). Théel continued: "... it is evident that the length of the retractors, their attachment to the body-wall, and the degree of their coalescence are subject to rather considerable variations.

"It is a known fact that the presence or absence of hooks behind the tentacle does not

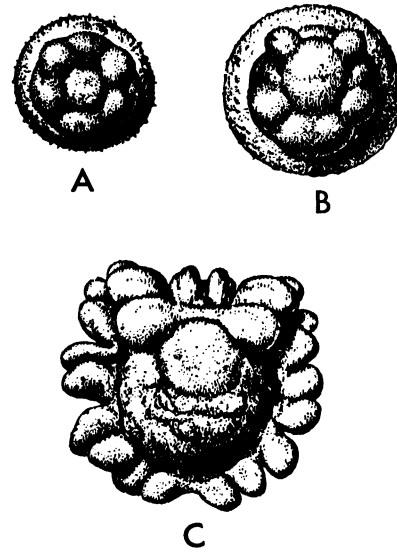


FIG. 33. Series of tentacles showing possible ontogenetic development (from Théel, 1905).

necessarily signify specific characters . . .

"What part do the papillae of the body-wall play in the system? . . . The presence or absence of them must, in several cases, be of questionable value for the systematist."

In summary then, Théel (1905) presented fairly conclusive evidence for disregarding the ratio of introvert to body length, shape of tentacular crown, length of retractors, presence of hooks, and presence of papillae as having any systematic value in this "section." The subsequent literature on these species, excluding *G. abyssorum*, contains a variety of opinions on whether there are one or two valid species (*G. minuta* and *G. improvisa*). Murina (1958) showed that some authors (Paul, 1909, Southern, 1912, Fischer, 1922a, and Lindroth, 1941) accepted the idea of a single species with a variable appearance, whereas others (Gerould, 1913, Fisher, 1950, Wesenberg-Lund, 1930, 1956) maintained there should be two species. Murina herself concurred with this latter group, but after carefully considering all the morphological and ecological evidence, her conclusion was based solely on the difference in the size of the papillae.

It seems possible that the larger papillae being more common in larger forms may represent merely an ontogenetic change, but this point remains to be demonstrated. It is true

that they are also present in small animals. Another suggestion is that these larger papillae may function more or less as holdfasts or anchoring mechanisms as this form is frequently found in hyalinaceous polychaete tubes and other similar dwelling places. The difficulty with this argument is that some *G. minuta* that live in tubes of various testaceous animals (foraminiferans, rhizopods) lack these structures. Because this species is generally very slender, it can readily inhabit tubes constructed by other animals. A 54-mm. animal was only 2 mm. in diameter.

This whole question seems to entail a subjective evaluation of what constitutes a significant difference. Careful study of material, with its gradations from one extreme to the other, makes it difficult for me to agree with Murina on this point. Until breeding experiments can be conducted, I concur with those authors who maintain that *G. minuta* and *G. improvisa* should be considered as one species: *G. minuta*.

On occasion these animals exhibit a "beaded" appearance, i.e., at intervals along the trunk, narrow bands of circular muscles have contracted so that the trunk resembles a kind of constricted balloon. Gerould (1913) erected a new species, *Phascolosoma* [*sic*] *cinctum*, based on two individuals. The main character which distinguished his species was, "coarse, isolated circular muscle fibers are prominent, especially in the introvert which is marked off obliquely and sharply from the trunk," and later, "the slender cylindrical introvert is united to the thicker trunk by an oblique line of junction . . ." His type material is in a poor state for study, but I believe he overemphasized this point. There is an indentation that is slightly oblique but not very sharp. This same constriction has been noted in the following description of *G. minuta*, and in all other morphological features Gerould's type is identical with larger individuals of *G. minuta*. At one of the two stations he also found *G. minuta*, and the second of his stations falls within the geographic range of this species.

Therefore, in view of the overwhelming similarity, I propose that *P. cinctum* is a junior synonym of *G. minuta*.

One final note on *Golfingia abyssora* is appropriate. It was originally described from Scandinavian waters in the same area as *G. minuta*. Since that time literally hundreds of individuals in this "abyssorum section" have been collected

by several workers, but only a handful of them have been identified as the species *G. abyssora*. When Théel (1905) did not find any, he used the type material for his discussion. Wesenberg-Lund (1930, p. 29) discussing her North Atlantic collections said, "The material in consideration contains a rather great quantity of small sipunculids belonging to this abyssorum section. . . . No specimen belonging to *abyssorum* is found in the material here dealt with." Southern (1912) noted, "A single specimen, which I refer with some hesitation to this species." Murina (1964a, p. 220) placed 36 examples from two stations in this species. In her earlier paper (1958), she placed 309 examples in *G. improvisa* and 52 in *G. minuta*. She also made no mention of *G. abyssora* and similarly in the 1964a paper there was the same omission of the disagreement on how *G. abyssora* differed from *G. minuta*. She did say *G. abyssora* had 8–10 tentacles (based on one specimen), but added that "a precise count was not taken, as the introvert was withdrawn." From my collections I was unable to find any specimen which I could ascribe to this species.

Because of the paucity of reports on *G. abyssora* and Théel's (1905) observations, I am inclined to believe that it is not a well-defined species and perhaps should be at least reduced to subspecific rank if not submerged entirely.

**DESCRIPTION:** The 826 specimens were collected at 80 stations. The length of the trunk ranges from 2 to 54 mm.; most are less than 10 mm. The animals are lustrous, semitransparent, with some yellow-white pigment. Several worms give a suggestion of darker squares on the skin. The form of the body is cylindrical, and the narrower introvert is invariably shorter than the trunk. At the base of the introvert there is sometimes a circular constriction, as if a sphincter muscle were being contracted. Murina (1958, p. 1628) also noted this ring-shaped groove, as did Wesenberg-Lund (1930, p. 31).

The tentacles are reduced to lobular projections—generally four to six. The area behind the tentacular lobes generally bears numerous hooks. Murina (1958) gave the height of hooks as 19–86  $\mu$ . Papillae, as in several other species, are more dense at the anterior and posterior ends of the trunk than in the middle (see Murina, 1958, for measurements). In most cases they are not pigmented and are small, but some worms have larger, brown papillae, particularly at the posterior end.

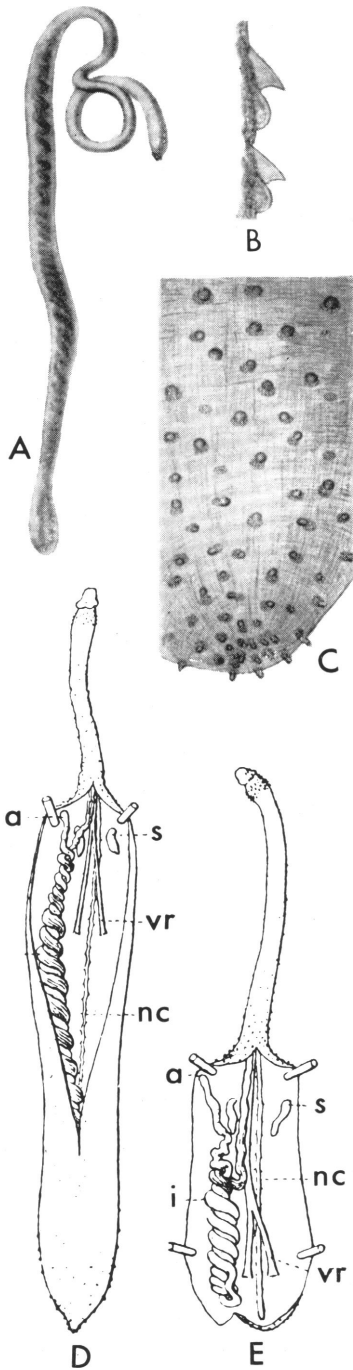


FIG. 34. *Golfigia minuta* (from Théel, 1905). A. External view. B. Hooks. C. Posterior with papillae. D, E. Two views to show extreme anterior (D) and posterior (E) origin of retractors.

Abbreviations: a, anus; i, intestine; nc, nerve cord; s, nephridia; vr, ventral retractor muscle.

Internally the two retractors may originate from a wide variety of locations. Théel (1905), who made an extensive number of measurements, showed that this point could range from 17–95 percent of the distance from the anus to the posterior end of the trunk; Murina (1958) found a range of 25–64 percent; and I found a range of approximately 15 to 80 percent. The intestine has numerous coils; the spindle muscle is unattached posteriorly. A small caecum can usually be found. The colorless or yellow nephridia are variable in shape, are free, and open a little behind the anus. Eggs and sperms were found in separate animals.

**DISTRIBUTION:** *Golfigia minuta* was collected at depths ranging from 1–3753 meters. Of the 817 individuals for which complete station data are available, only 34 were collected on the shelf (0–150 meters) north of Long Island. This number is about 4 percent of the total, whereas about 72 percent came from depths greater than 1000 meters. This species normally lives in a cold environment (less than 10° C.) that undergoes relatively little temperature change. It is taken as far south as latitude 33°N off Cape Fear, North Carolina, but well down the slope. The northernmost record in this investigation is in the Bay of Fundy (latitude 44°40'N). The sediment in these areas is predominantly mixtures of medium and fine sands and silts.

On a worldwide basis this species has a wide vertical (9–500 meters) and horizontal distribution. Most records are from the eastern North Atlantic, the northernmost being at latitude 70°N, but *G. minuta* is also recorded in the Mediterranean and off South Africa in the Atlantic. In the Pacific it is reported from latitude 32°S off Chile and a few records are from the Western Pacific. In the Indian Ocean the only record is from Durban Bay.

*Golfigia pellucida* (Keferstein, 1865)

Figures 36, 37

- Phascolosoma coriaceum* KEFERSTEIN, 1865, p. 432.  
 SELENKA, DEMAN, AND BULOW, 1883, p. 34.  
*Phascolosoma pellucidum* KEFERSTEIN, 1865, p. 204.  
 BAIRD, 1868, p. 86. SELENKA, DEMAN, AND BULOW, 1883, p. 32. LANCHESTER, 1905, p. 28. TEN BROEKE, 1925, p. 83.  
*Phascolosoma riisei* KEFERSTEIN, 1865, p. 206. BAIRD, 1868, p. 96. SELENKA, DEMAN, AND BULOW, 1883, p. 32.  
*Phascolosoma verrillii* GEROULD, 1908, p. 691; 1913, p. 388.

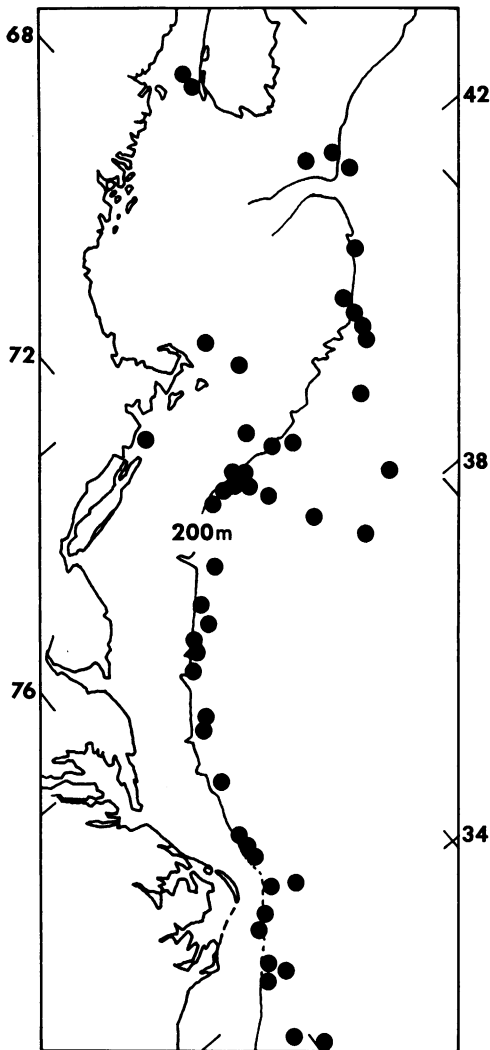


FIG. 35. Distribution of *Golfingia minuta*.

*Golfingia coriacea*: FISHER, 1950, p. 551; 1952, p. 396.

*Golfingia pellucida*: FISHER, 1950, p. 551; 1952, p. 396.

EDMONDS, 1956, p. 305.

*Golfingia verrillii*: FISHER, 1950, p. 551; 1952, p. 395.

DISCUSSION: In 1913, Gerould described *G. verrillii* from the east coast of North America. Earlier (1908) he briefly mentioned this worm but had not named it. No type was designated and the only two known examples of the material described in 1913 are now in the National Museum of Natural History. None is in the Yale Peabody Museum, the Museum of Comparative Zoology, or Dartmouth College (where he was working at the time). In his description he

stated it resembles *G. pellucida* (= *G. riisei*) in many ways except that, "the skin is not so thin and the papillae are perhaps not so slender and spine-like." He also noted that *G. pellucida* is twice the size of *G. verrillii*. These differences did not seem very significant; consequently I turned to Keferstein's original description (1865) of *G. pellucida*. He described both *G. pellucida* and *G. coriaceum* from 2 feet (0.6 meters) of water in coral off St. Thomas. *Golfingia coriaceum* was based on one specimen and *G. pellucida* on several.

In 1883, Selenka synonymized *G. pellucida* and *G. riisei* (Keferstein, 1865) and commented on the presence and absence of hooks in these species. His description of *G. coriaceum* is based on Keferstein rather than on his own observations. Southern (1912) said that the *G. pellucida* reported by Shipley (1900) is really *G. elongata*. The only other reference I have to *G. pellucida* is Edmonds (1956). I have no other reference to *G. coriaceum* except two worms from St. Thomas so identified by W. K. Fisher, in the National Museum of Natural History.

After I read the various descriptions, reviewed Selenka's and Stephen's keys, looked at many specimens from off Cape Hatteras, and examined a few *G. verrillii* identified by Gerould and *G. coriaceum* identified by Fisher, it became apparent to me that these may be all the same species.

*Golfingia coriaceum* was described by Keferstein (1865) from one specimen and in comparing his description of this species with that of *G. pellucida*, the following differences were noted: 1) both rectum and nephridia are long, whereas in *G. pellucida* they are short; 2) from Selenka's key, the body is described as not slender and the posterior papillae as not spine-like, whereas in *G. pellucida* they are slender and spinelike respectively. In addition, Keferstein (1865) stated and illustrated that *G. coriaceum* has "several long, cylindrical outpouchings from the contractile vessel." If it is assumed that these "Aussackungen" are anomalies (as they appear to be in Keferstein, 1865, fig. 23), rather than true villi, the four differences noted above are of questionable value in differentiating species. I can find in my material (all from one location south of Cape Hatteras), individuals with long and short rectums, with tall or short posterior papillae, and with slender or plump bodies.

Returning to Gerould's distinction between *G. verrillii* and *G. pellucida*, it does not seem reasonable to assume that the thickness of the skin is a species-specific character as he suggested. The variability of the papillae has been mentioned; generally the larger worms tend to have the larger, longer papillae. As most of Keferstein's specimens were about 40 mm. long and Gerould's about 20 mm., it is not surprising that they found differences in papillae size. Gerould's statement that *G. pellucida* is twice the size of *G. verrillii* overlooks the fact that his specimens may have been younger; if so, the apparent differences may be an artifact of sampling. There is one other report of *G. verrillii* (Murina, 1964a). The exact status of this specimen has not yet been resolved.

The presence or absence of hooks in this genus has been discussed by many authors. In my material most of the younger forms have many hooks, but in the larger individuals the hooks are fewer, more scattered, and harder to find, particularly if the introvert is withdrawn.

The question then is whether the following characters are sufficiently basic and constant to be utilized in separating these forms from one another: 1) presence of hooks, 2) length of rectum, 3) length of nephridia, 4) thickness of skin, 5) shape of papillae, and 6) body size. If these are not constant, then *G. coriaceum*, *G. verrillii*, and *G. pellucida* are all the same species.

**DESCRIPTION:** The specimens include 34 from 18 stations plus about 800 from L. McCloskey's two stations off Cape Lookout, North Carolina. The trunk size of the individuals ranges from about 3–25 mm. by 1–3 mm.; most are 6–10 mm. long. They are transparent, cream, tan, or brown the majority being a pale creamy tan. In a few males the mass of sperm gives a pink tinge to the animal.

The trunk is cylindrical with the posterior end generally rounded, but it may have an obtuse point or a small nipple-like protrusion or be almost flat across the posterior end. In the animals more than 5 mm. long, the body is covered with large, more or less uniformly distributed papillae which may be darker than the general body surface; they are not at all prominent in the smaller worms (3–4 mm.).

The introvert is shorter than the trunk (1/2 to 3/4) and tipped with a variable number of well-developed tentacles. The 3-mm. and 4-mm. animals have 12–16 tentacles; 10–12 mm. worms

have 20–30 tentacles. Behind the tentacles is usually a zone of hooks. These hooks seem to be more numerous in smaller forms; they are scattered or entirely absent in larger ones.

Internally the two strong retractors originate from the middle portion of the trunk (40–60 percent). The intestinal coil has the typical configuration; the spindle muscle extends through it but is unattached posteriorly. Larger worms have four or five fixing muscles in the anterior region of the gut; two to the left side, one or two going between the two retractors, and one going to the right side of the body. Smaller worms have only one or two. A small caecum lies on the long rectum, near the gut coil. Wing muscles are weakly developed. The two free nephridia open at the same general level as the anus. Frequently, these organs are bulbous near the orifice, attenuating to a digit-form appearance distally. Pigmented eyespots are present; in some cases two pairs (small black and larger brown) can be distinguished.

**DISTRIBUTION:** All the recently collected material came from shallow water south of Cape Hatteras (fig. 37). With the exception of three stations at 80, 94, and 128 meters, all were from less than 55 meters of water. The latitude ranged from 25°55'N to 34°58'N; one specimen was collected just north of Cape Hatteras close to shore at 35°24'N.

Gerould (1913) reported finding a few specimens from shallow water in Vineyard Sound and Buzzard's Bay, just south of Cape Cod, Massachusetts. These records are difficult to reconcile with the present distribution. If this species is in fact present in the Cape Cod area, its absence in collections made during the past 10 years is difficult to explain, especially in view of the intensive collecting being carried out by the Systematics-Ecology Program of the Marine Biological Laboratory and by others. Assuming Gerould's records to be valid, I suggest that some larvae were carried northward and managed to survive because of an apparently atypical set of conditions, but that the species was not able to maintain a permanent population because of the severity of climate or changing bottom conditions. As evidence of the scarcity of this worm during Gerould's time, the following quotation may be helpful, "I secured one specimen off West Falmouth in August, 1907, by dredging with the *Phalarope*, but several hauls made for this purpose in the same locality with

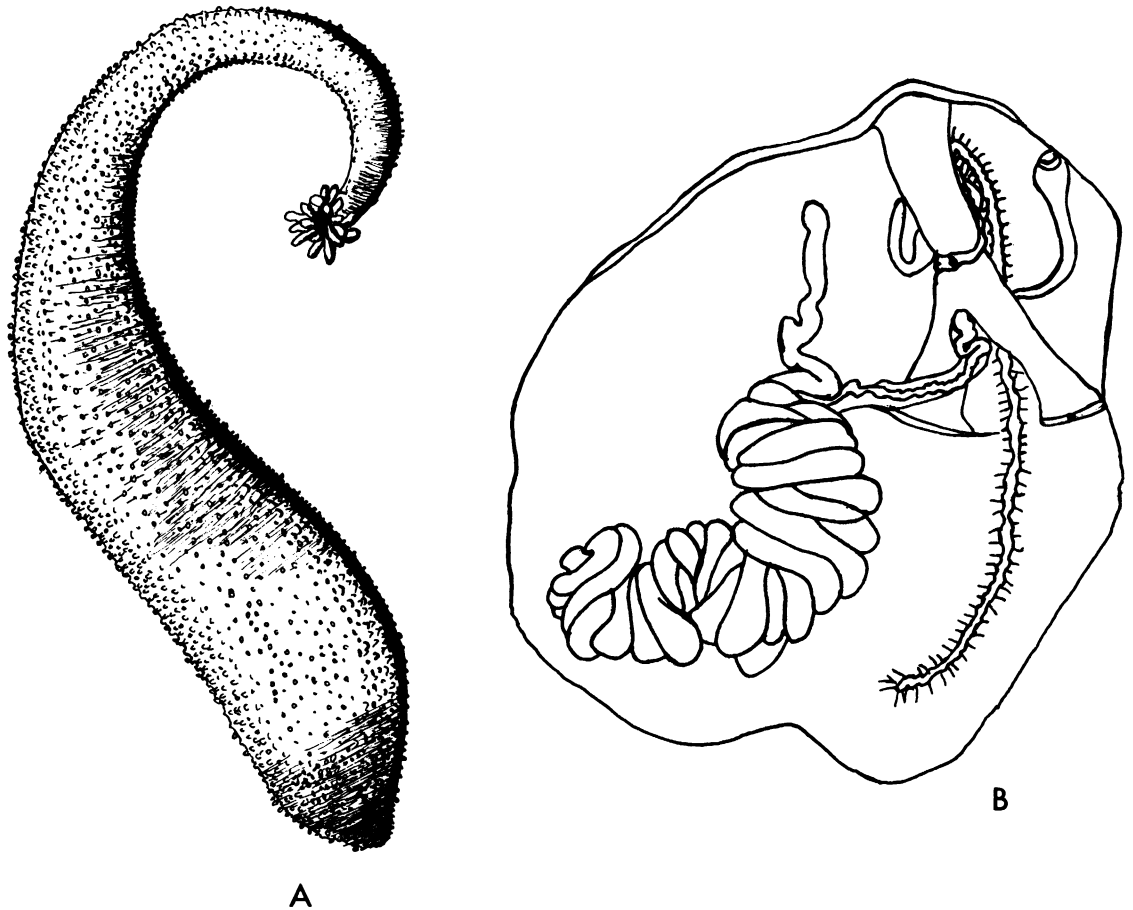


FIG. 36. A. *Golfingia pellucida*, external view. B. *G. verrillii* (= *G. pellucida*), internal view (from Gerould, 1913).

the larger apparatus of the *Fish Hawk* were unsuccessful" (Gerould, 1913, p. 388).

This species is very numerous in the heads of the coral *Oculina*. It was also in a mass of cemented shell hash (Coquina rock). Wells, Wells, and Gray (1964) reported finding the species living in calcareous polychaete tubes attached to the calico scallop (*Aequipecten*) off Cape Lookout, North Carolina, in 30–37 meters. Otherwise, it has been recovered in sand mixed with some coarser material. The temperature in its range varies from 12 to 28° C.

In addition the species has been recorded from shallow water off Western Australia, Philippines, and Singapore as well as in the Western Atlantic from Brazil through the Caribbean.

GENUS *THEMISTE* GRAY, 1828

DIAGNOSIS: Distinguished from other genera by

four to eight conspicuous tentacular stems branching palmately, dendritically, or pinnately. Longitudinal muscle layer continuous; two, rarely four, retractor muscles; spindle muscle attached anteriorly but not posteriorly; two free nephridia. Dorsal contractile vessel having several blind tubules (diverticula, caeca, Polian tubules).

DISCUSSION: The status of this generic name was recently a matter of discussion among sipunculan systematists. The junior synonym, *Dentrostomum* Diesing, 1859, has been used much more extensively in this century, but as Stephen (1964) pointed out, the name *Themiste* is based on good type material in the British Museum and does have priority.

*Themiste alutacea* (Grube, 1859)

Figures 38, 39

DESCRIPTION: I have 106 specimens from two



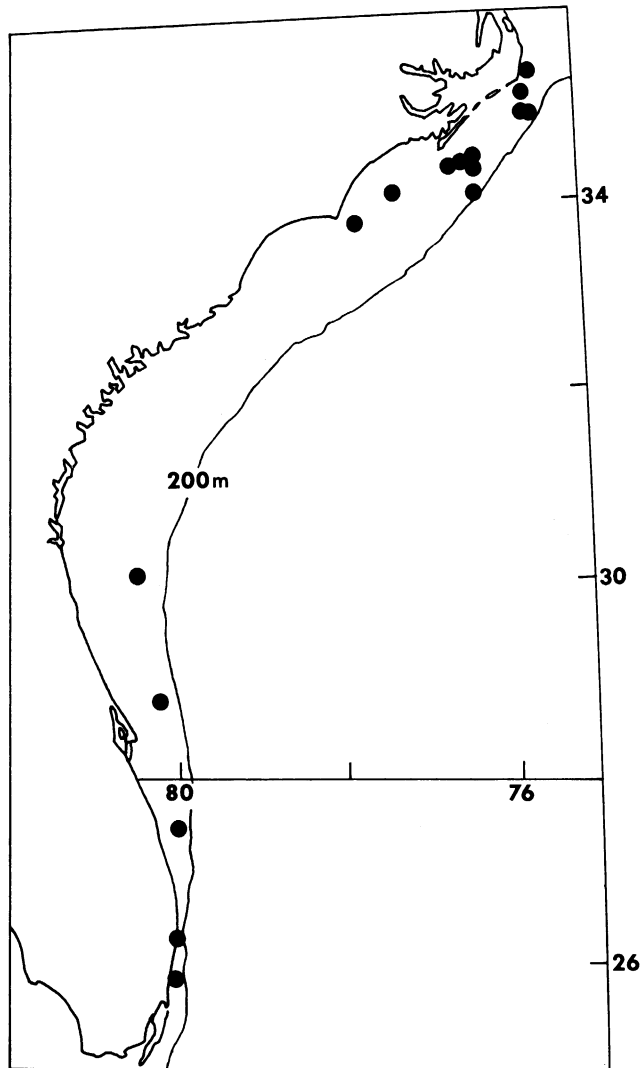


FIG. 37. Distribution of *Golfingia pellucida*.

stations. The trunks range from 3 to 15 mm. (generally 5–10 mm.) long and are cylindrical to pear-shaped. Most are pink or grayish but they may be brown, possibly as an artifact of preservation. The body wall is opaque or semi-transparent.

The numerous tentacles are derived from six main branches and are a pale tan with unique brown pigment spots scattered on their surface. The introvert is short and about equally divided between an anterior smooth region and a posterior region studded with large dark brown hooks. Gerould (1913) stated that the cuticle

at the base of the introvert is divided into rectangular blocks. This condition is rare in the current collections. The base of the introvert is rough but not noticeably blocked off as he figured. The body wall is generally smooth with some suggestion of annular grooves toward the posterior end in the larger examples.

Internally two large retractor muscles originate about three-quarters of the distance to the posterior end of the trunk (70–80 percent). The intestine is free posteriorly but anchored in the mid-region by one or two fixing muscles and anteriorly by the spindle muscle. The long, free

FIG. 38. *Themiste alutacea*, external view.

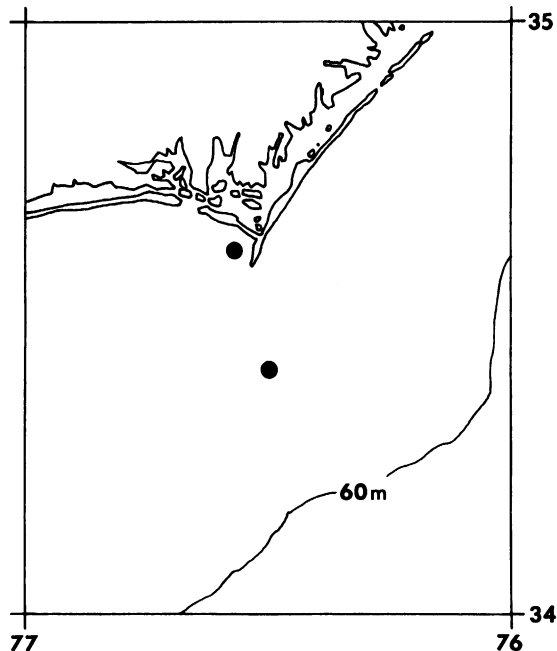
nephridia open near the level of the anus. Several long, white, thin, sometimes coiled, blind tubules (or diverticula) branch off the dorsal blood vessel and extend back toward the posterior end of the body. Two pale eyespots are generally visible.

**DISTRIBUTION:** These specimens were collected from L. McCloskey's two coral stations off Cape Lookout, North Carolina (fig. 39). Nine came from the shallow 6-meter station, and 98 from the deeper 24-meter station. They live in the spaces between the branches of the coral *Oculina* but not in well-defined burrows like the *Aspidosiphon*. The temperature at the shallow station ranges from about 9 to 26° C.; at the deeper one, which seems more favorable, the range is 14–24° C.

This species is found only in the western Atlantic from Cape Hatteras south to Brazil in shallow water.

GENUS *ONCHNESOMA*  
KOREN AND DANIELSSEN, 1875

**DIAGNOSIS:** Anus well out on introvert, some-

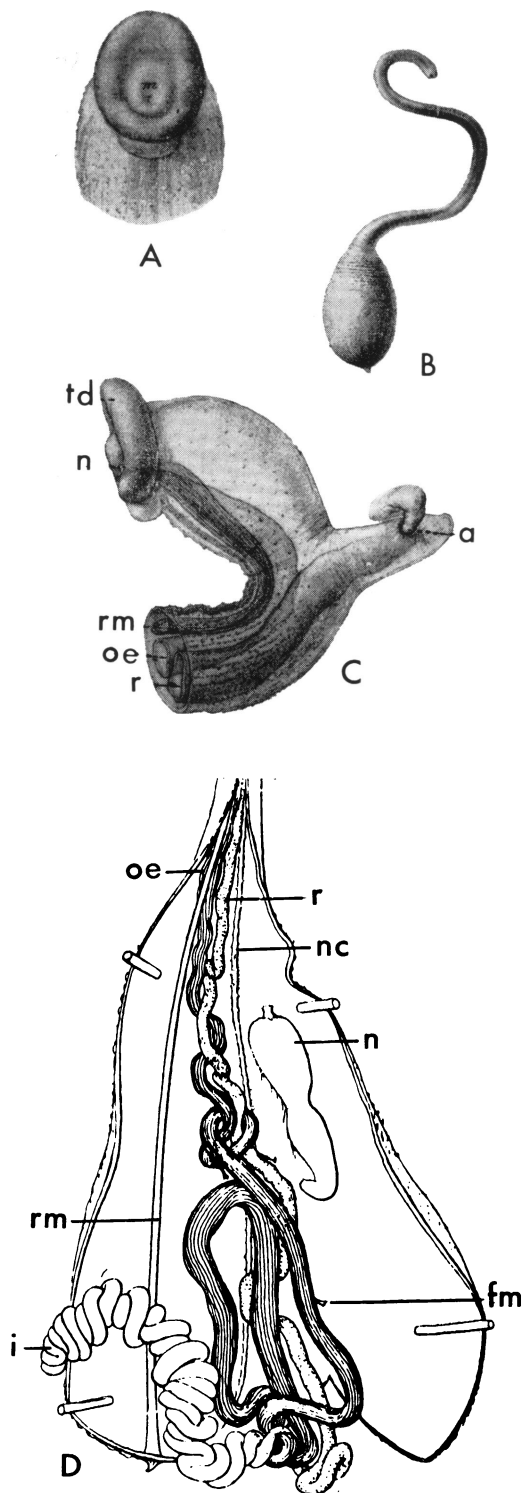
FIG. 39. Distribution of *Themiste alutacea*.

times just behind head region. One retractor, which may have two short roots, attached to posterior end of body; only one nephridium; tentacles few and small or reduced to oral lobes; trunk generally less than 8 mm.; introvert generally several times longer than trunk; longitudinal muscle layer continuous.

*Onchnesoma steenstrupi* Koren and Danielssen,  
1875

Figures 40, 43

**DESCRIPTION:** The 2009 specimens came from 49 stations (1470 from one station). The trunk size of most specimens ranges from 1 to 2.5 mm. (a few reached 4 mm.) by 0.8 to 1.3 mm. The shape varies from almost spherical through pear-shaped to club-shaped; most are pear-shaped; all have a pointed posterior tip. In many, the introvert is distinctly set off from the body proper and is invariably considerably narrower than the body. The worms have been referred to aptly as a "tiny football on a string." The introvert may be 5–10 times the length of the trunk. The body color is often a dusty rose-gray or pale creamy white; a few individuals have a rusty tinge. The skin is thin, tough, and semitransparent. The introvert is much more transparent and lacks coloration.



In expanded forms, the skin is smooth, but in a contracted state the anterior end of the trunk may have a series of transverse wrinkles or grooves. The posterior end appears to have a series of 20–30 longitudinal ridges or keels, merging at the apex; they are caused by a series of flat, chitinous scales of varying size. The size of the individual scales tends to increase toward the posterior end. Murina (1964b) gave measurements of these scales. The distance that they extend anteriorly varies from one-third to three-fourths of the total trunk length, the anterior ones becoming very small. In addition, this species has scattered, minute, true, multicellular epidermal glands with papillae. Tentacles, as such are absent, but an oral lobe or disk may have a food-gathering function.

Internally the one retractor is attached to the posterior end of the body. When the introvert is withdrawn it takes up much of the body cavity with its loose loops. The gut has a few loose coils before the posteriorly attached double helix begins. This attachment does not seem to be by a true spindle muscle; perhaps it could be more properly called a fixing muscle. The rectum is unusually long as it must lead to the anus which has a unique position only a short distance behind the mouth. The anus is frequently on a small, protruded dorsal papilla. The single nephridium is variously shaped but unattached by any connective tissue and lacks pigmentation. Gametes are seen frequently; the eggs are often well up into the introvert and have a diameter almost equal to that of the introvert.

**DISTRIBUTION:** This species has a depth range from 82 to 643 meters. This range can be subdivided thus:

DEPTH (METERS)	STATIONS
< 100	7
100–200	13
201–500	29
> 500	1

FIG. 40. *Onchnesoma steenstrupi* (from Théel, 1905). A. Distal end of introvert, front view. B. External view, with partially extended introvert. C. Distal end of introvert, side view. D. Internal view.

**Abbreviations:** a, anus, unusually protruded; oe, esophagus; fm, fixing muscle; i, intestine; m, mouth; n, nephridium; nc, nerve cord; r, rectum; rm, retractor muscle; td, tentacular disk.

It occurs in shallow water on the shelf in the northern part of its range off southern New England. South of Cape Hatteras, it is never found in depths of less than 200 meters.

The northernmost records (fig. 43) are from the large number of stations grouped around latitude 40°N (latitude 40°10'N, longitude 69°45'W). From here the species extends southward to latitude 30°23'N off central Florida. South of the Hatteras-Lookout region the six records represent only 11 worms of the total of 2009.

The sediments in the region off southern New England, where many individuals were collected, have been extensively studied by Garrison and McMasters (1966). From a study of their data plus additional unpublished material, it becomes evident that this species prefers a medium fine sand (median phi from 1.5 to 2.5). If the sand is still finer and includes significant percentages of silt, the sediment is poorly sorted and contains some medium sand (at least 15 percent). The temperature in this zone is not subject to much seasonal variation and generally ranges from 5 to 10° C. Worldwide the species is common in the North Atlantic, principally around the British Isles and Scandinavia. It is also in the Mediterranean and we have isolated reports from the southwestern coast of Africa.

DISCUSSION: Murina (1964b) has described a new species, *Phascolion dogieli*, which bears a striking resemblance to *O. steenstrupi*. After correspondence with her and an exchange of specimens, it became evident that *P. dogieli* does indeed belong to the genus *Onchnesoma* but is a distinct species.

*Onchnesoma squamatum* (Koren and Danielssen, 1875)  
(Figures 41, 43)

DESCRIPTION: My 81 specimens were collected at 25 stations. The length ranges from 1.5 to 8 mm.; most individuals are less than 6 mm. Those below 2.5 mm. are without gametes. The shape varies from almost spherical to pear-shaped to cylindrical. The posterior end is in many cases pointed. The dominant color is the gray of the large, somewhat overlapping scales of varying sizes; their free edges are directed backward. This particular structure, unique in sipunculans, facilitates the identification of this species. In the larger forms the scales

are in many cases underlain by a rusty orange skin. The introvert is practically transparent or pale yellow with minute papillae. It is from 1.5 to 2 times the length of the body. The tentacles, of normal shape, number eight as figured by Théel (1905). The rectum, visible through the introvert wall, terminates at the anus, which lies well out toward the mouth, but not so close to it as in *Onchnesoma steenstrupi*. In one specimen with a 6-mm. introvert, the anus is 1 mm. behind the mouth. Internally, the gut has the typical double helix and is fastened to the posterior end of the body. When the introvert is withdrawn, it occupies much of the body cavity. The retractor muscle has been a subject of some disagreement. The original describers (Koren and Danielssen, 1875) said it was a single retractor with four roots. Théel (1905) stated the retractor was single with two very short roots, and Fischer (1925) held the retractor had two very long roots. Wesenberg-Lund (1930) indicated, "single ventral retractor is well-developed, strong, and thick, inserted at hindmost end of body, the base is undivided." My observations show that the appearance of the retractor can vary greatly depending on the state of contraction of this muscle, i.e., whether the introvert is extended or withdrawn. In most animals, even in retracted specimens, the base of the retractor shows a slight notch (fig. 41). With the introvert extended, the muscle is not thick but is drawn out and thin.

Contrary to statements in much of the literature, the single nephridium is attached to the body wall by fine strands for one-half to three-fourths of its length. In most worms, this structure is on the right side of the body, but in one specimen it is on the left.

DISTRIBUTION: With the exception of three stations (253 meters, 370 meters, 400 meters) *O. steenstrupi* was taken at depths from 450 to 775 meters. It has not been collected north of Cape Hatteras and extends through southern Florida (i.e., fig. 43). The northern limit is latitude 34°20'N; the most southerly record is latitude 24°18'N. The sediment in this area is silty sand or sandy silt with some clay; the median phi ranges from 3 to 6.5. No particles are coarser than fine sand. The temperature varies little, ranging from 4 to 7° C.

Worldwide, this species is found in the eastern North Atlantic from Scandinavia to Spain, usually on the continental slope. One question-

able record exists for the eastern Mediterranean Sea.

*Onchnesoma magnibatha* Cutler, 1969  
Figures 42, 43

*Onchnesoma steenstrupi*: MURINA, 1968, p. 198.

**DESCRIPTION:** The 34 specimens came from 16 stations. The length of the trunk ranges from 2.5 to 6 mm., and the width from 1 to 2 mm. The shape varies from almost cylindrical to pear-shaped and the posterior end is bluntly pointed. The anterior one-fourth to one-half of the trunk is narrowed to a diameter equal to that of the introvert; only the posterior section is bulbous.

The skin of the central enlarged portion is very thin, fragile, and transparent, but that of the anterior narrowed part is opaque, somewhat rugose, and pale brown-tan. The posterior end has a series of longitudinal ridges merging at the apex and has a suggestion of the tan coloration. These ridges are more pronounced than in *O. steenstrupi* and more continuous, i.e., not composed of separate scales or plates.

The introvert has generally the same diameter as the anterior part of the trunk but is somewhat paler; it is smooth and transparent if extended. As none of my material is completely extended, I cannot comment on the tentacular arrangement. The introvert appears to be less than twice the length of the trunk and is often (measured on dissected, partially contracted specimens) only equal in length to the trunk.

Internally this species is much like the other *Onchnesoma*. The intestine has about 30 double coils; the esophagus and rectum are long; of the one or sometimes two fixing muscles, one attaches the esophagus near the posterior end of the body. The anus is about 75–80 percent of the distance toward the distal end of the introvert. The single nephridium is on the right side, unpigmented, and unattached to the body wall except at the nephridiopore. The retractor appears single in most contracted specimens, but had two distinct roots.

**DISCUSSION:** This species superficially resembles some members of the genus *Golfingia* more than the other *Onchnesoma*. The distribution is remarkably dissimilar also: the deepest *O. steenstrupi* in this area comes from about 500 meters, whereas the shallowest record of *O. magnibatha* is 3028 meters (33 of the 34 specimens were taken at depths greater than 3700

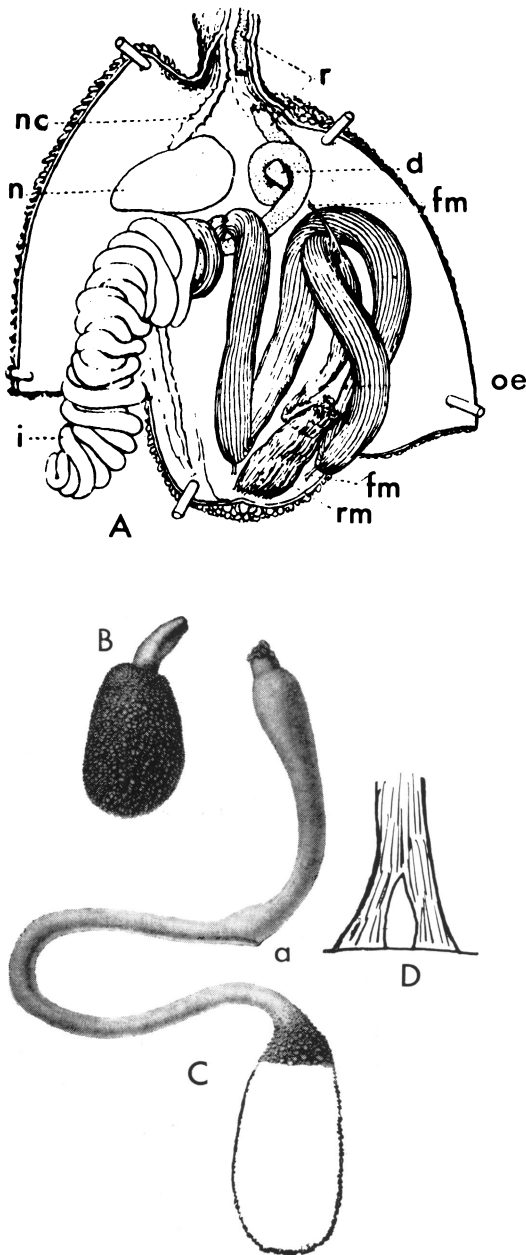


FIG. 41. *Onchnesoma squamatum* (all except D from Théel, 1905). A. Internal view. B. External view, with partially retracted introvert. C. External view, with extended introvert. D. View of retractor origins.

Abbreviations: a, anus; d, rectal caecum; fm, fixing muscle; i, intestine; oe, esophagus; n, nephridia; nc, nerve cord; r, rectum; rm, retractor muscle.

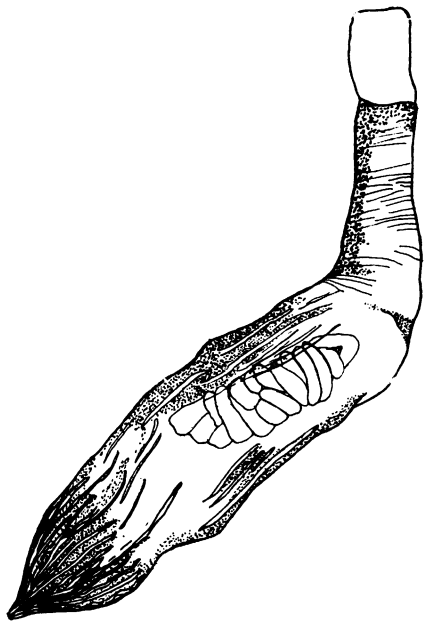


FIG. 42. *Onchnesoma magnibatha*, external view (from Cutler, 1969).

meters); the gap in the vertical distribution is about 3000 meters. Unquestionably this species belongs to the genus *Onchnesoma*; it has the single retractor, single nephridium, and anteriorly displaced anus. Murina (1968) identified two specimens from 3318 meters at approximately latitude 45°N, longitude 30°W as *O. steenstrupi*. Subsequent communication and exchange of material verified that they are *O. magnibatha*.

**DISTRIBUTION:** *Onchnesoma magnibatha* has a distribution which suggests the occupation of a unique niche (fig. 43). Vertically (with one exception at 3028 meters) it ranges from 3753 to 5021 meters. As a result, it is much farther offshore than the other two species occurring at least as far east as the Bermuda area. It does come closer inshore, however, as the station near Cape Hatteras indicates (latitude 35°52'N, longitude 74°29'W). Sampling at these depths has been so limited that these data should not be interpreted as complete.

The sediments are silty clay, clayey silt, or clay at these depths. The median phi ranges from 7 to 10, with less than 2 percent sand present. The temperature in this region is almost constant from 2.3 to 2.5° C.

#### GENUS *PHASCOLION* THÉEL, 1875

**DIAGNOSIS:** Longitudinal muscle layer continuous; one to three retractor muscles; intestine forming several loops rather than usual spiral. Only one nephridium; most species with holdfasts on trunk actually enlarged papillae with chitinous borders; single row of tentacles surrounding mouth with zone of recurved hooks behind.

#### *Phascolion strombi* (Montague, 1804)

Figures 44–46

*Phascolion strombi* is the most common and ubiquitous sipunculan in this study area—the Atlantic bounded by Nova Scotia, Bermuda, and Cape Canaveral. Unfortunately, it also has a very plastic external morphology, which has complicated the nomenclature with the introduction of several names of doubtful validity. Most of the confusion has been eliminated by earlier workers (Fischer, 1922a; Wesenberg-Lund, 1929), and agreement is general that the specific names *caementarium* and *tubicola* which have been applied to some of the *Phascolion* in this study area are junior synonyms of *P. strombi*.

Sluiter (1900) described *P. alberti* from this coast (Newfoundland, in 1267 meters) and A. C. Stephen (personal commun.) had put this name on several specimens (from Cape Hatteras and South Africa). Stephen's material did not seem to fit the original description so it seemed advisable to obtain some of Sluiter's material from the Musée de Monaco.

My interpretation of Sluiter's description agrees with Gerould's (1913, p. 416) summary. The supposed differences were all external. Internally *P. alberti* and *P. strombi* were the same, except that in *P. alberti* the ventral nerve cord extended slightly beyond the roots of the ventral retractor. My observations on Sluiter's material agree with this observation. The external differences (according to the description) amounted to the distribution of the chitinous holdfasts on the anterior and middle part of the trunk, but not posteriorly. The posterior region of the trunk was covered instead by oval papillae without the chitinous teeth and with small chitinous particles surrounding the central pore.

In the two specimens I obtained from Monaco, which had been identified as *P. alberti* by Sluiter, these attachment papillae were dis-

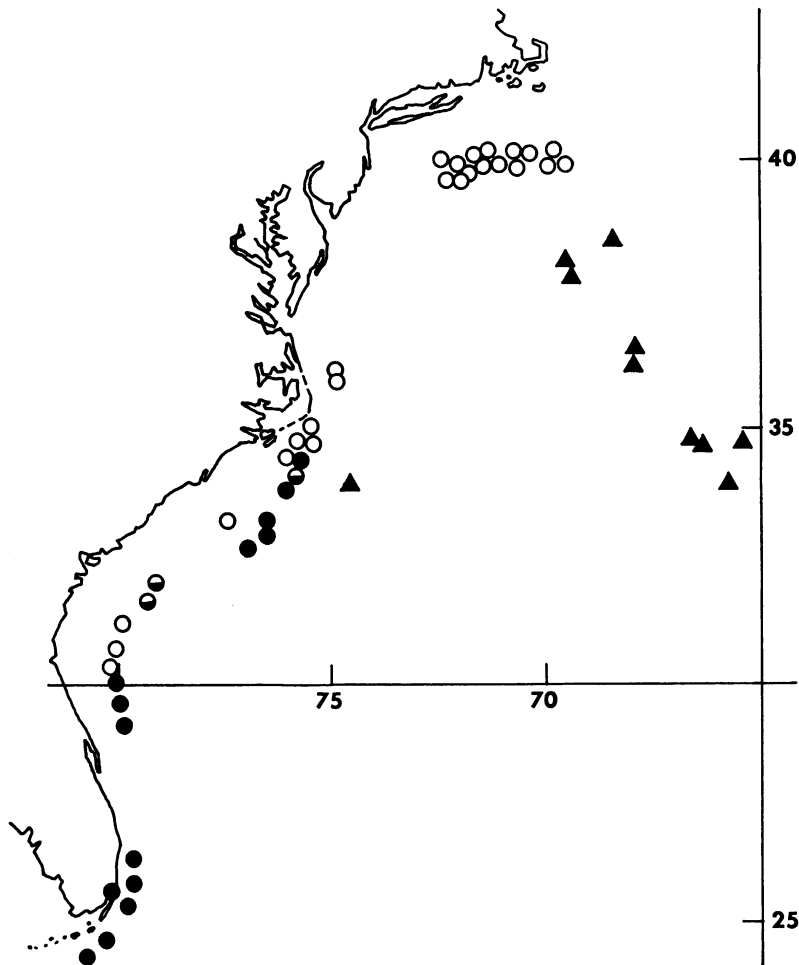


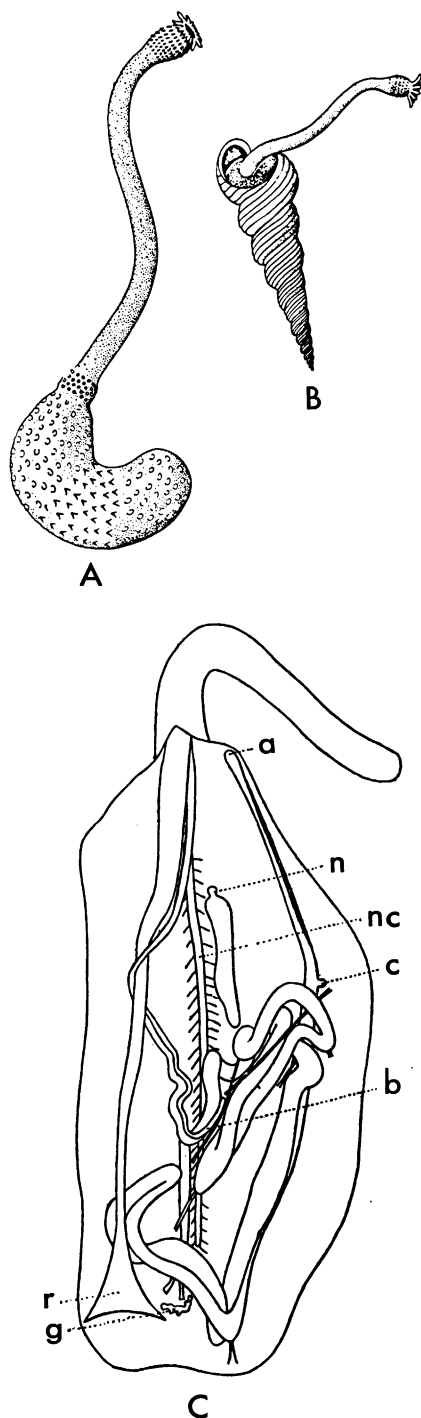
FIG. 43. Distribution of genus *Onchnesoma*: *O. steenstrupi* (○), *O. squamatum* (●), both the above (◐), and *O. magnibatha* (▲).

tributed sparsely over the entire body, not restricted to any particular area, i.e., Sluiter overlooked those in the posterior section. As noted in other species, the distribution of hold-fasts is too variable to be used as a specific character. With regard to the posterior oval papillae with chitinous particles, I did not see anything that resembled these structures in Sluiter's specimens. Moreover, Sluiter did not illustrate them and only referred to them once in the description. These specimens were not the type material, but were taken at the same station (161). Gerould (1913) pointed out that *P. alberti* has not been collected by any subsequent expedition to the region of the type locality, whereas numerous *P. strombi* have been obtained from that area.

Murina (1964b) identified two individuals from the Mediterranean Sea as belonging to *P. alberti*. She made no mention, however, of the peculiar posterior oval papillae. She mentioned a narrow zone on the anterior end of the trunk which has "flat oval bodies of rosy color . . . sharply outlined around edges which stand out against the light background." The attachment papillae with triangular chitinous points are distributed on the anterior-middle portion.

It is my conclusion, therefore, that *P. alberti* is not a distinct biological entity, but merely a form of *P. strombi*.

Gerould (1913) presented an extensive description of the morphological variation within *P. strombi*, but it is apparent from my observations that his varieties have little systematic



value. Wesenberg-Lund (1929) also made this point. In other words, we do not have seven constant combinations of characters; the characters may be found in numerous different combinations even from any one locality. Gerould (1913, p. 408) summarized the problem: "The most interesting fact in regards to this species is its extraordinary plasticity . . . How far this diversity in external features is due to the direct action of the environment . . . and how far it may be determined by heredity are questions which can be answered fully, of course, only by breeding and rearing the animals."

**DESCRIPTION:** My 2704 specimens came from 306 stations (plus several hundred museum records). These animals inhabit a variety of protective shelters. The most common are discarded gastropod shells, but they also occupy scaphopod shells, pteropod shells, calcareous polychaete tubes, hyalinaceous tubes, bits of old bone. The length of these worms is difficult to determine exactly as they retain the shape of their dwelling. Their form varies from straight and elongate to plump subspherical to coiled in a corkscrew manner. Their length commonly ranges from 5 to 15 mm., but some may be shorter or longer. The trunk may be transparent, white, pink, reddish gray-brown, tan-brown, yellowish gray, or various combinations of the above.

The introvert is invariably longer than the trunk and generally has a bulblike swollen region at the tip bearing numerous randomly arranged hooks. The 16 to 26 well-developed tentacles surround the mouth. At the base of the introvert on the anterior portion of the trunk are numerous, dense papillae of various dimensions and color. The shape may be tall and slender, subconical, dome-shaped, or flat and the color dark gray, red, pink, or white. The posterior end of the trunk may also have enlarged papillae, but these are rarely as dense or as large as those anterior. Most of the body surface bears only small, scattered papillae.

FIG. 44. *Phascolion strombi*. A. Stylized external morphology. B. Animal within gastropod shell (A and B from Tetry, 1959). C. Internal view (from Gerould, 1913).

**Abbreviations:** a, anus; b, contractile vessel; c, caecum; g, gonad; n, nephridiopore; nc, nerve cord; r, retractor.



The unique holdfasts (attachment papillae, Haftpapillen) also vary in size, shape, color, arrangement, and number. These large papillae with chitinous borders may be dispersed over 75 percent of the trunk; found only in the center, posterior, or anterior third; or may be restricted to a very narrow band. They may rise some distance above the body surface or closely adhere to it. The chitinous borders are generally dark brown but may be lighter and the form may vary from a sharp V-shape through U-shape to a circular form having several pointed projections. The holdfasts are generally directed forward but may have the apex pointing at varying degrees toward either side.

The internal morphology is less variable. The longitudinal musculature forms a continuous sheet and the two retractor muscles are unequal. The dorsal retractor is large and has a broad origin, which may appear to be split because of careless dissection near the posterior end of the body. The ventral retractor is much thinner and has two short roots which straddle the ventral nerve cord, or originate posterior to the termination of the nerve.

**DISCUSSION:** One interesting observation concerns an apparent shift in the distribution of *P. strombi* since 1880 in Narragansett Bay, Rhode Island. In 1880 the United States Fish Commission collected *Phascolion strombi* from several localities in the Bay as far up as Hope and Prudence islands (fig. 45). Stickney and Stringer (1957) did not report any from their studies in Greenwich Bay. During 1964 the United States Geological Survey made five stations in Narragansett Bay but failed to recover any *P. strombi* even though they were taken in Rhode Island Sound. In an attempt to document this situation more thoroughly, I made nine stations in approximately the same localities as the 1880 stations (fig. 45); they were made in May, 1967, from the R/V *Billy II* with a naturalist dredge borrowed from the Systematics-Ecology Program of the Marine Biological Laboratory, Woods Hole, Massachusetts. The results indicate the absence of this species (and all other sipunculans) from the Bay proper. It was found first southeast of Beavertail Point and then again off Brenton Reef.

The reasons for this shift may be manifold but two obvious possibilities present themselves.

One reason may be the increase of finer sediments in the Bay (McMaster, 1960). In other parts of its range, however, this species is found in fine sediment, and as it does not live within the substratum but on top of it in discarded shells, the make-up of the sediment does not seem to be critical.

A second suggestion is the effect of pollution. Since 1880 the countryside around Narragansett Bay has become much more industrialized and more densely populated. As a result the quality of the water in the Bay has changed. It is possible that this species was living near the edge of its physiological tolerance, e.g., temperature, which rises to 20 or 21° C., on the bottom during the summer (Hicks, 1959) and was only able to persist if all other factors were highly favorable. When the pollutants increased, however, the greater "physiological load" forced this species to move out to the mouth of the Bay where the temperature and concentration of pollutants were tolerable.

A group of about 200 specimens from several stations may be a new species but for the time being they are considered as a subgroup within *P. strombi*. This population was generally found in discarded pteropod shells. The trunk length ranges from 1 to 4 mm., and the shape is subspherical. The lack of holdfasts, the different type of papillae, unique dwelling place, and small size separate these animals from the rest of *P. strombi*. The presence of gametes in some individuals negates the possibility of their being juveniles.

Members of this subgroup have two retractors, of equal strength, each with a divided origin. Three fixing muscles are at the posterior end of the gut coil. A single nephridium is attached to the body wall along its entire length.

With the exception of one record at 1700 meters from the Bermuda slope, members of the subgroup are found on the upper continental slope from 215 to 1102 meters (fig. 46). The northernmost record is at latitude 39°57'N, and the southern is at latitude 34°39'N. The temperature in this area ranges from 4 to 9° C.<sup>1</sup>

**DISTRIBUTION:** *Phascolion strombi* has been taken from Nova Scotia to latitude 32°17'N off Cape Fear, North Carolina (fig. 46). The vertical range is from 14 to 3806 meters. An analysis

<sup>1</sup>Since submitting this manuscript, the above-mentioned subgroup has been described as *Phascolion microspheroidi* (see Cutler and Duffy, 1972).

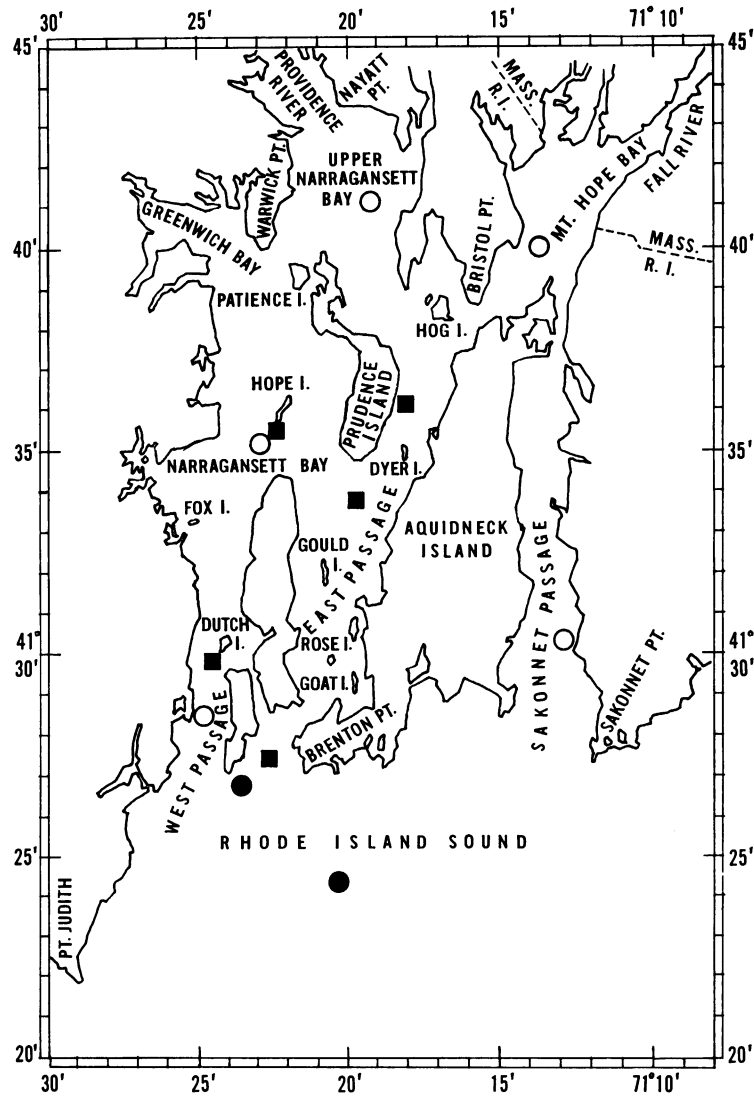


FIG. 45. Distribution of *Phascolion strombi* in Narragansett Bay, Rhode Island.

Symbols: ■, present in 1880, absent in 1967; ●, present in 1880 and in 1967; ○, absent in 1964.

of relative frequency of occurrence at different depths shows the following trend: it is common on the shelf as far south as Long Island, New York, with the exception of Georges Bank. Although Wigley (1961) reported its presence from Georges Bank, it is apparently rare. South of Long Island it moves out to the edge of the shelf and upper slope for the rest of the range. A notable exception is provided by the two records from Virginia at depths of 2 and 40 meters. One was a mature female with eggs. The eight

stations deeper than 1000 meters indicate the ability of the species to extend its range toward the depths. The National Museum of Natural History records also showed several recoveries from depths between 1000 and 2000 meters.

This species is generally exposed to temperatures between 2 and 20° C., although those few on the shelf south of Cape Hatteras may experience temperatures as high as 26° C., which makes this sipunculan very eurythermal. In general, specimens from deeper stations are

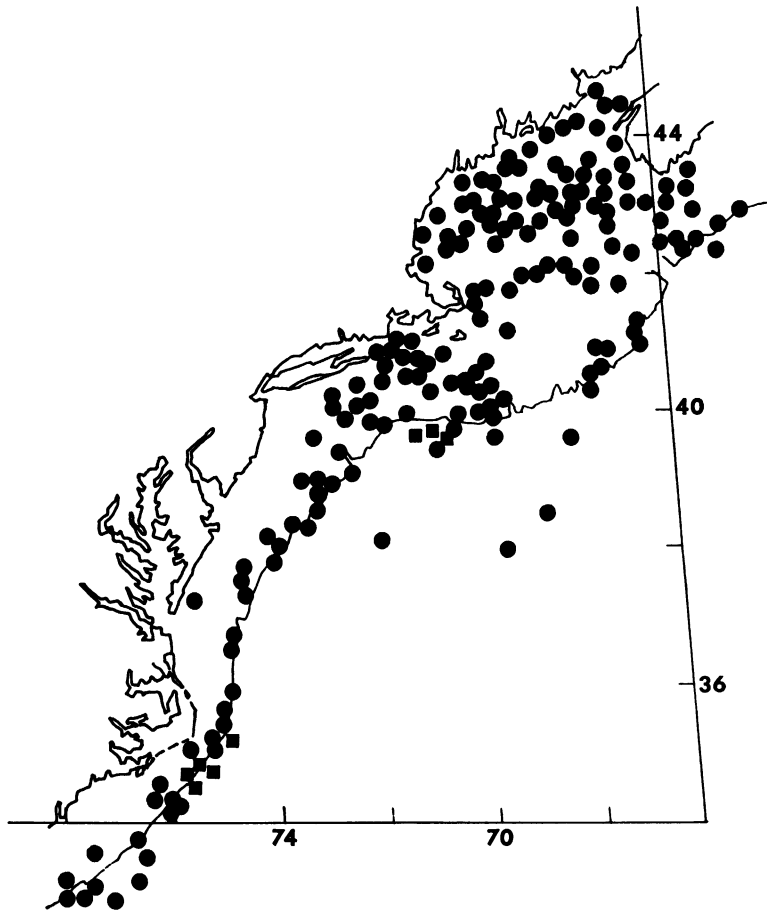


FIG. 46. Distribution of *Phascolion strombi*. Squares indicate a subpopulation from pteropod shells.

smaller than those on the shelf; the same relation holds for those south of Cape Hatteras. The northern population seems to be more robust, but occasionally large individuals are found elsewhere.

This species is common throughout the Atlantic from the Arctic to the Antarctic at a wide variety of depths. The only record from the Pacific is from off southern Chile.

#### GENUS *ASPIDOSIPHON* DIESING, 1851

**DISCUSSION:** Stephen (1964) divided the genus *Aspidosiphon* into two genera solely on the basis of their longitudinal body musculature. In *Aspidosiphon* it forms a continuous sheet, whereas in *Paraspidosiphon* it is divided into numerous bands or bundles. He believed this feature to be

constant and unequivocal. My observations (and those of others) do not support this contention, i.e., the nature of body musculature is not clear-cut. Some large individuals of *Aspidosiphon* species show a tendency for the layer to separate into more or less distinct units. This situation is frequent toward the anterior end of the trunk (*A. misakiensis* Ikeda; *A. venabulum* Selenka, deMan and Bulow, and elsewhere). In some small specimens of *Paraspidosiphon* species the longitudinal muscle bands are very difficult to distinguish. Stephen also believed this single feature was, by itself, a criterion significant enough to warrant generic rank. I remain unconvinced. My concept of a genus includes the idea of a complex of morphological and/or ecological differences. This

situation does not hold here. Therefore, I propose reducing *Paraspidosiphon* to subgeneric status.

DIAGNOSIS: A chitinous shieldlike structure invariably present at anterior and generally at posterior extremity of trunk; introvert arising from ventral side of anterior shield. Hooks with

one or two points in most cases present; longitudinal muscle layers continuous or in separate bands. Most forms having one pair of retractor muscles, more or less fused.

SUBGENUS *ASPIDOSIPHON* STEPHEN, 1964

DIAGNOSIS: *Aspidosiphon* with continuous longitudinal muscle layer.

*Aspidosiphon (Aspidosiphon) albus* Murina, 1967

Figures 47, 49

DISCUSSION: Murina (1967) described this species from one specimen taken in 14 meters of water off northwestern Cuba. In many ways it resembles *A. misakiensis* Ikeda, 1904. One difference is the absence of hooks in *A. albus*. I made several attempts to obtain Ikeda's material for comparison, but apparently his specimens have been lost or destroyed.

DESCRIPTION: The 74 specimens are from 43 stations. These worms are small and slender (trunk ranges from 2 by 0.3 mm. to 15 by 1 mm.; 95 percent under 10 mm.) with long introverts (about three to five times the trunk length). They are off-white or light tan with yellowish or light brown shields. The well-defined anal shield is round or oval and composed of unusually small platelets or granules that give it a fine-grained appearance. In most cases the edge is angled and the border shows short, radial furrows. The caudal shield is less well defined, but generally distinct except in the smallest animals. It is furrowed with about 20 grooves around the border and composed of fine granules. Although Murina described this species as having "some white tentacles" I was unable to observe any. Hooks are absent. Slender tubelike papillae arising from a broad, glandular base are arranged in annular rings along the introvert.

Internally the longitudinal muscle layer is continuous. In a few examples, however, I saw distinct bundles for a short distance behind the anterior shield. The two retractor muscles originate very near the posterior end of the trunk and join together for much of their length. Murina described it as one retractor with two roots. The intestine is anchored anteriorly and posteriorly by the spindle muscle and bears a small caecum on the rectum. The length of the rectum is variable; sometimes it is long and straight, but more often, it is convo-

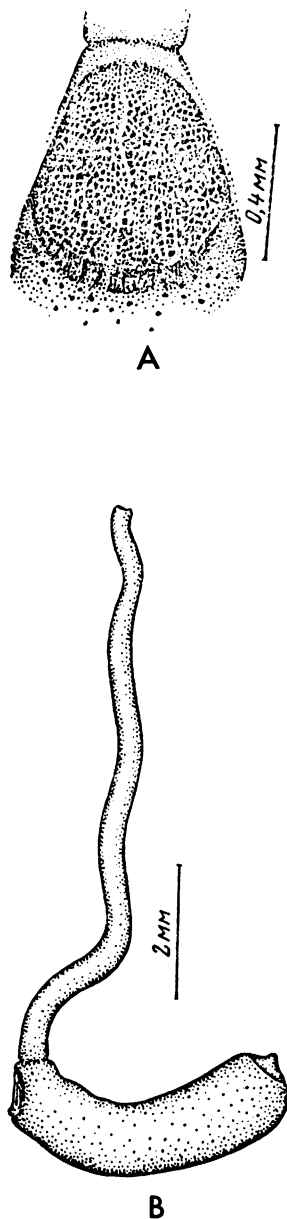


FIG. 47. *Aspidosiphon albus*. A. Anterior shield. B. External view, with introvert not completely extended (from Murina, 1967).

luted and twisted apparently involved in the intestinal coil. The caecum can be very difficult to find and should not be relied on to distinguish this species from its close relatives. The yellow or brown nephridia are slender and long (50–75 percent of the trunk length), attached for most of their length, and open at the level of the anus. A pigmented band of tissue, sometimes arranged as two distinct eyespots, is present on the brain.

**DISTRIBUTION:** This species was taken on the shelf southward from latitude 35°18'N (Cape Hatteras to southern Florida, fig. 49). Of the 43 stations, only one was deeper than 100 meters (123 meters) and six deeper than 50 meters. Eighty percent of the stations were between 10 and 35 meters. The temperature in this region varies from about 15 to 27° C.

Most of these worms were taken from discarded gastropod or scaphopod shells; a few came from calcareous polychaete tubes, and a few were apparently living in the substratum. Although the nature of the sediment is probably not overly important, the areas in which the animals were found were sand or shelly sand. The only other record of this species is from the coastal waters off Cuba.

*Aspidosiphon spinalis* Ikeda, 1904

Figures 48, 49

**DISCUSSION:** This identification is made with some reservations because no specimens of Ikeda's material are available for comparison and his illustrations are not very clear. The only previous records of this species are restricted to Japan which suggests a unique distribution if my identifications are correct.

**DESCRIPTION:** My 287 specimens were from 103 stations. As most of these worms are coiled, having been collected from gastropod shells, it is difficult to get accurate measurements. They are commonly from 5 to 15 mm. long but range from 2 to 22 mm. Their diameter is generally about 1 mm. The introvert is about two to three times the trunk length. The color is cream or pale tan with shields that vary from light to dark brown. In larger animals, the anterior third of the trunk appears brownish because of the development of darker cuticular plaques around the papillae. A few worms had commensal endoprocts, and three had commensal polychaetes living with them in the shells.

The diameter of the introvert decreases near

the end, just behind the tentacular crown which is composed of 8–10 small, finger-shaped tentacles. The many (25–60) regular rings of hooks gradually become scattered over most of the remainder of the introvert. The hooks near the end have secondary points and are called "double-pointed hooks"; those farther posterior are single-pointed. Ikeda (1904) called these single-pointed hooks "spines" but I fail to see any basic difference except that the latter are slightly less curved. The introvert also carries small papillae. The anal shield is composed of large, brown, polygonal, randomly arranged, chitinous papillae. In general, it has well-defined limits. The posterior shield composed of scattered chitinous papillae is generally paler and less well-defined. In some specimens these papillae give a suggestion of a radial arrangement.

Internally the body musculature is continuous except that a few large worms show a suggestion of separate bundles, particularly just behind the anal region. The two retractors



FIG. 48. *Aspidosiphon spinalis*, external view.

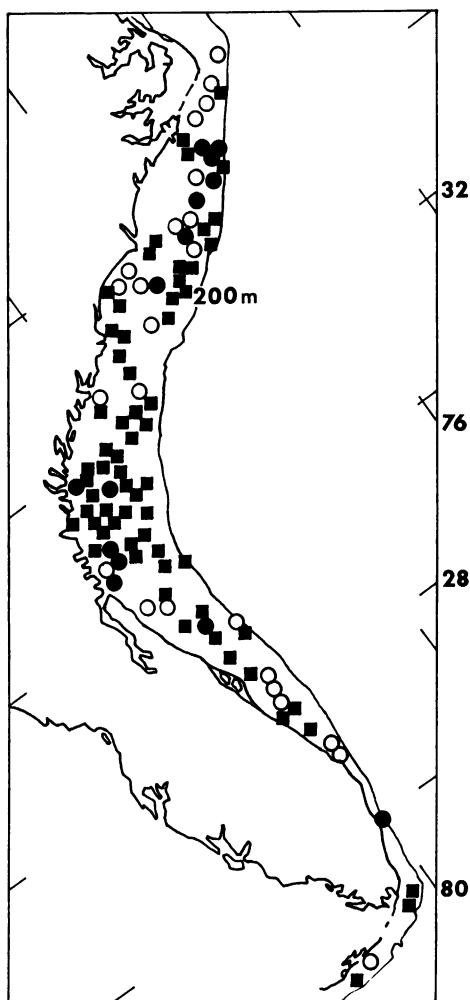


FIG. 49. Distribution of *Aspidosiphon albus* (○), *A. spinalis* (■), and stations where both species were collected (●).

originate from the posterior end of the body and merge to form one muscle, before inserting in the head region. The intestinal coil is anchored at both ends by the spindle muscle. The white or pale brown nephridia are about half the length of the body, and are fixed to the body wall for most of their length.

**DISTRIBUTION:** This species inhabits the shelf south of Cape Hatteras (fig. 49). The northernmost record is from latitude  $34^{\circ}50'N$ . Seventy-one percent of the records are from depths less than 35 meters, 17 percent between 35 and 85 meters, and 12 percent greater than 85 meters. The complete range is 7 to 185 meters. The

sediments are generally coarse, but most of these animals live in empty mollusc shells; sediment therefore, is probably not a critical factor. The temperatures range from 15 to  $28^{\circ}C$ .

*Aspidosiphon zinni* Cutler, 1969

Figures 50, 51

**DESCRIPTION:** The 347 specimens came from 21 stations. These worms are small (1–15 mm.) and fragile. Most are 2–3.5 mm. long by about 0.3 mm. in diameter. They are cylindrical and transparent except at the two ends that have some light brown pigmentation. The introvert is almost as long as the trunk and expands near its tip, giving it the appearance of a spiked club. Commonly these worms are in elongate, arenaceous foraminiferan tests.

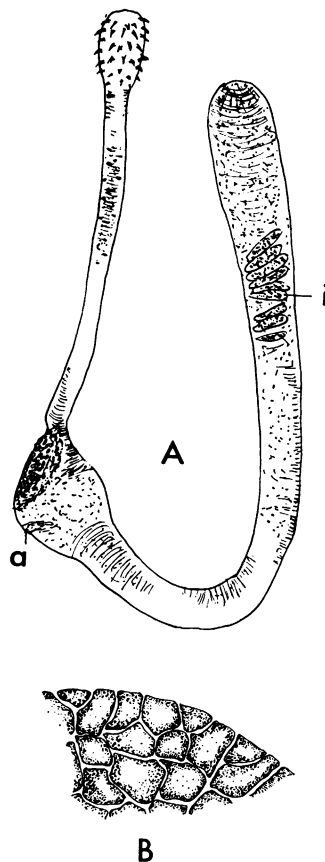


FIG. 50. *Aspidosiphon zinni*. A. External view. B. Enlargement of anal shield components.

Abbreviations: a, anus; i, intestine (from Cutler, 1969).

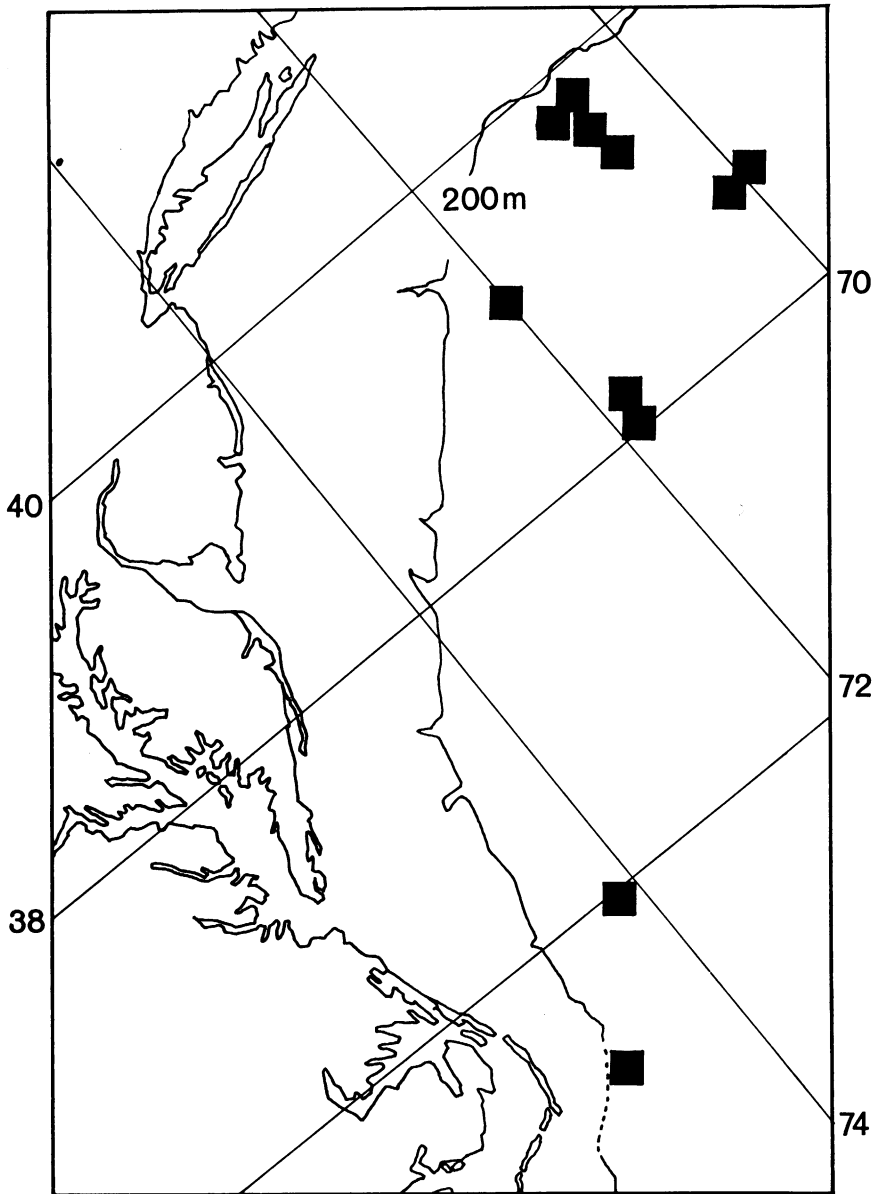


FIG. 51. Distribution of *Aspidosiphon zinni*.

The numerous irregularly arranged hooks are single-pointed and about  $15\text{--}20\ \mu$  from base to tip. No tentacles were observed. The anal shield is yellowish and composed of fine, closely grouped units that give it a granular look. This shield is flat and usually set off from the main axis of the trunk by 60 to 90 degrees. The posterior shield is almost lacking but annular wrinkles or folds are discernible at the posterior end of the trunk.

It is possible to see most of the internal structures through the body wall—a fortunate situation because all attempts at dissection thus far have been unsuccessful. The intestinal coil extends to the posterior end of the trunk and the anus is just behind the anterior shield. The two brown nephridia open at about the level of the anus and are usually less than 25 percent of the trunk length. The retractors originate near the ventral nerve cord about 65–80 percent of the

distance to the posterior end of the trunk.

**DISTRIBUTION:** This species is found on the base of the continental slope and upper continental rise and on the Bermuda rise (fig. 51). With the exception of four stations between 1100 and 1800 meters all the collections were from between 2000 and 3000 meters. The most southerly collection was made at latitude 32° 16' N off Bermuda and the northernmost at latitude 39° 49' N. The temperature in this area ranges from 2.5 to 4° C. The sediments are mostly silts and clays, but with sufficient fine sand to permit the construction of arenaceous foraminiferan tests which this species inhabits.

**SUBGENUS** *PARASPIDOSIPHON* STEPHEN, 1964

**DIAGNOSIS:** *Aspidosiphon* with longitudinal muscles gathered into several bands.

*Aspidosiphon* (*Paraspidosiphon*) *parvulus*

Gerould, 1913

Figures 52, 54

*A. spinoso-scutatus* FISCHER, 1922b.

**DISCUSSION:** In 1913 Gerould described a new species of *Aspidosiphon* from two small specimens (3 and 4 mm.) from 29 meters just south of Cape Hatteras. Along with these worms were found *Golfingia pellucida* (= *verillii*) and *Themiste alutacea*. Nine years later, Fischer (1922b) described a new species of this genus, on the basis of two specimens, the largest with a 20-mm. trunk, from shallow water off Barbados (St. Thomas Sound). *Golfingia pellucida* and *T. alutacea* have also been found in that general area. The collections of L. McCloskey (from the fauna associated with the coral *Oculina* off Cape Lookout, North Carolina), included three species of sipunculans: *G. pellucida*, *T. alutacea*, and an *Aspidosiphon*. These *Aspidosiphon* resemble Gerould's species (*A. parvulus*) except that *A. parvulus* was described as having a continuous longitudinal muscle layer; my specimens had distinct muscle bands. My attention then turned toward Fischer's species (*A. spinoso-scutatus*) and after a comparison of descriptions of the two species, the question arose concerning the existence of two separate species sharing so many ecological and morphological features.

The major differences in the descriptions are: 1) the variation in the longitudinal muscle layer (however, close inspection of Gerould's type material showed that longitudinal muscle bands are present, albeit very weakly developed);

2) the introvert is shorter than the trunk in *A. parvulus* and longer in *A. spinoso-scutatus* (i.e. the introvert was not fully extended in Gerould's two worms; thus his measurements are open to doubt); 3) Hooks are single-pointed in *A. parvulus* and double-pointed in *A. spinoso-scutatus* (the hooks in the current Cape Hatteras material are not all single-pointed, both conditions exist on a single worm), therefore, this is not a valid character; and 4) the center of the anterior (anal) shield has 10 furrows in *A. spinoso-scutatus*, but they are irregularly arranged in *A. parvulus* (this difference may be valid but, in studying the recent material I have found a wide degree of variation in the arrangement of these components; the previous distinction may be just a reflection of the small sample size).

All these characters, as well as additional lesser differences, possibly can be attributed (at least in part) to the differences in the sizes of the animals in each investigator's collections. Gerould's were very small, whereas Fischer's were five to six times larger (3–4 mm. vs. 20 mm.).

In view of the above, it seems advisable to move *A. parvulus* from the subgenus *Aspidosiphon* to *Paraspidosiphon* and to relegate *A. spinoso-scutatus* to the status of a junior synonym.

**DESCRIPTION:** I have 22 specimens from four stations, plus more than 1000 from L. McCloskey's coral collections. The length of the trunk ranges from 2 to 14 mm. The animals may be entirely brown or only at the ends, becoming pale creamy white over most of the trunk. In most worms, the longitudinal muscle bands can be seen through the body wall.

The introvert is longer than the trunk and bears numerous rings of hooks, each either with a single point or bearing a small secondary tooth. The double-pointed hooks are found more frequently at some distance behind the tentacles. In larger animals neither shield is sharply differentiated from the trunk because the epidermal papillae enlarge toward either end and tend to merge with the components of the shields. The anterior shield is commonly surrounded by a zone of tall, conically pointed papillae. Fischer (1922b) described them as a thick stand of spikelike papillae; Gerould (1913) called them sharply conical spines. The shield proper is composed of broad, flat, irregular units which may at times appear to be arranged in rows separated by grooves. The arrangement and pigmentation of these chitinous papillae



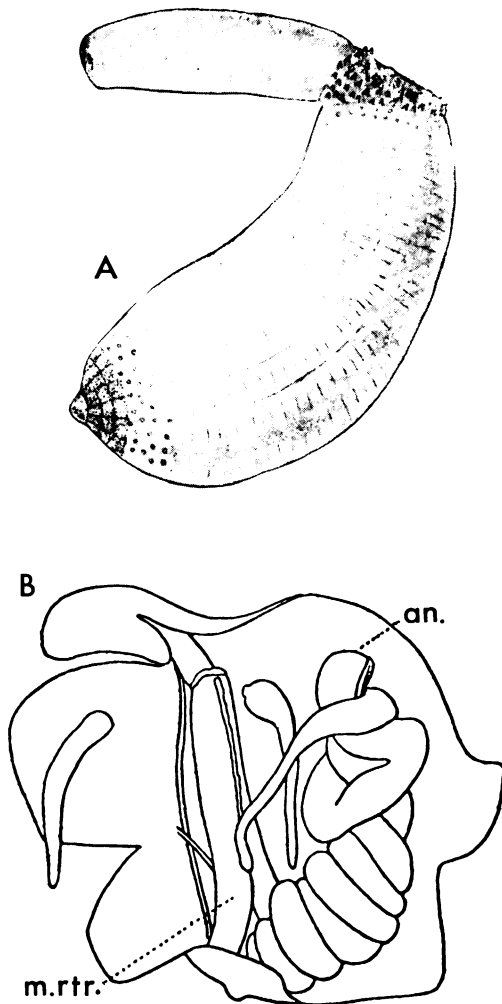


FIG. 52. *Aspidosiphon parvulus* (from Gerould, 1913).  
A. External view. B. Internal view.  
Abbreviations: an., anus; m.rtr., retractor muscle.

vary greatly. The posterior shield is more prominent in the smaller forms than in the larger because the neighboring papillae are not so well developed in this body region as in the larger worms. This dirty yellow shield has numerous radial grooves, most of which do not go all the way to the center.

Internally the two retractors merge well before inserting in the head region. Their origins are from the posterior end of the body. The longitudinal musculature is gathered into 22–26 bundles that anastomose frequently. The spindle muscle is attached both anteriorly and

posteriorly. There is no caecum; wing muscles are present; and the nephridia are colorless and long (about 60–75 percent of the body length). They are attached to the body wall for most of their length and open at the level of the anus or slightly posterior to it.

**DISTRIBUTION:** These specimens were taken from a restricted area between Cape Lookout and Cape Fear, North Carolina (latitude 33° 51'N to 34° 37'N), in shallow water (5–35 meters; fig. 54). A few were recovered from shelly sand, but they were found regularly in large numbers in the heads of the coral, *Oculina*. The temperature there ranges from about 15–27° C.

This species is found only in the Western Atlantic from Cape Hatteras to the Caribbean and in the Gulf of Mexico.

*Aspidosiphon* (*Paraspidosiphon*) *cumingii*  
Baird, 1868  
Figures 53, 54

**DESCRIPTION:** The one specimen has a trunk of 15 by 2 mm. The body wall is opaque with scattered transverse wrinkles and varies from light to medium brown. Both shields are distinctly set off from the rest of the body.

The introvert is partially withdrawn, but a zone of single-pointed hooks lies behind the tentacles. The introvert is about two-thirds to three-fourths the trunk length. Near the base of it are attached several commensal endoprocts (*Loxosoma*). The anal shield is oval, has 10–12

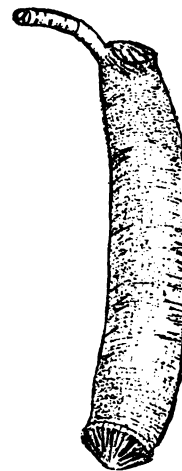


FIG. 53. *Aspidosiphon cumingii*, external view.

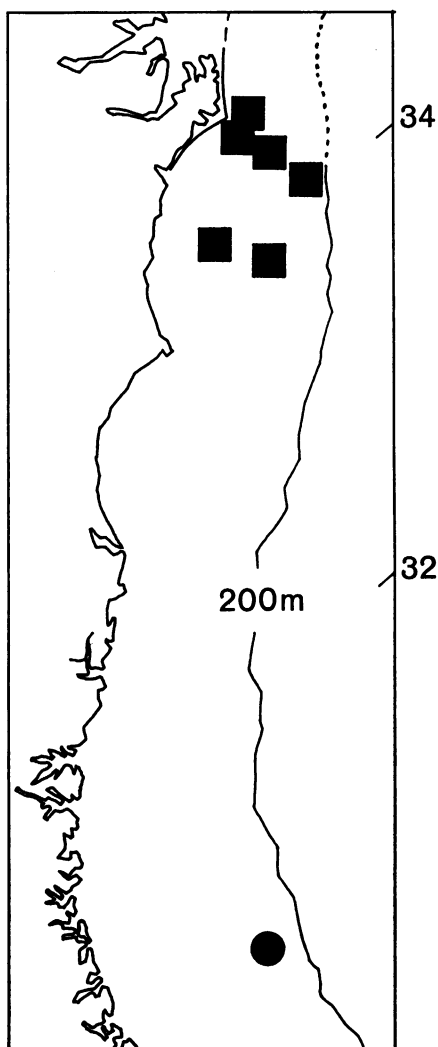


FIG. 54. Distribution of *Aspidosiphon parvulus* (■) and *A. cumingii* (●).

longitudinal grooves of various lengths, and a well-defined border. The posterior shield is strongly developed, and the constriction of the circular muscles at its anterior border distinctly sets it off. Approximately 24 grooves (some bifurcate) radiate outward from the center. The papillae are more noticeable at the ends of the body, diminishing toward the midportion.

Internally, one strong retractor muscle originates from a broad base about 75 percent of the distance to the posterior end of the body. The longitudinal muscles are divided into about 34–38 bundles which anastomose freely. The spindle muscle is attached at both ends of the trunk, firmly anchoring the gut coil. Selenka (1883) described the rectum as bearing villous outpouchings. Although the rectum in this specimen is peculiarly enlarged with extensive connective tissue and wing muscle, no villi were observed. The nephridia are brown, long, and partially attached to the body wall. They open slightly behind the anus.

**DISTRIBUTION:** This specimen came from 36 meters off Georgia at latitude  $30^{\circ}50'N$  (fig. 54). The sediment is sandy and the temperature varies from about  $16^{\circ}$  to  $27^{\circ}$  C. This is the first record of *P. cumingii* from this study area.

## BIOLOGICAL AND ECOLOGICAL CONSIDERATIONS

### ECOLOGICAL GROUPINGS

THE INFORMATION in the foregoing section on the distribution of the enumerated sipunculans makes possible an analysis of zoogeographical groupings from the standpoints of latitude, depth, temperature, and sediment. To visualize

the similarities and differences, the factors mentioned above were plotted for each species as shown in figures 55–58. The horizontal width of each column is an approximation of the relative frequency of occurrence. It has meaning only within a single column and no comparisons

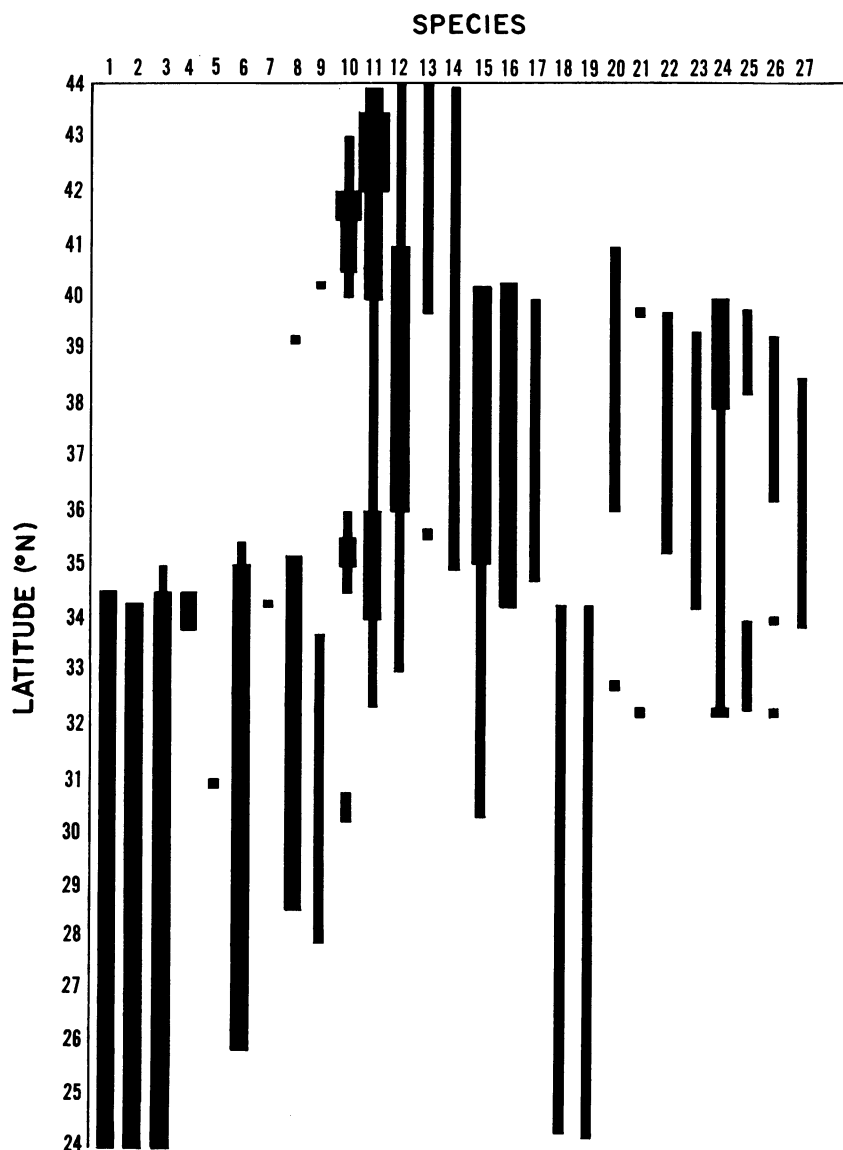


FIG. 55. Distribution of sipunculans according to latitude. (See text, p. 181, 182 for explanation of column widths and numbers.)

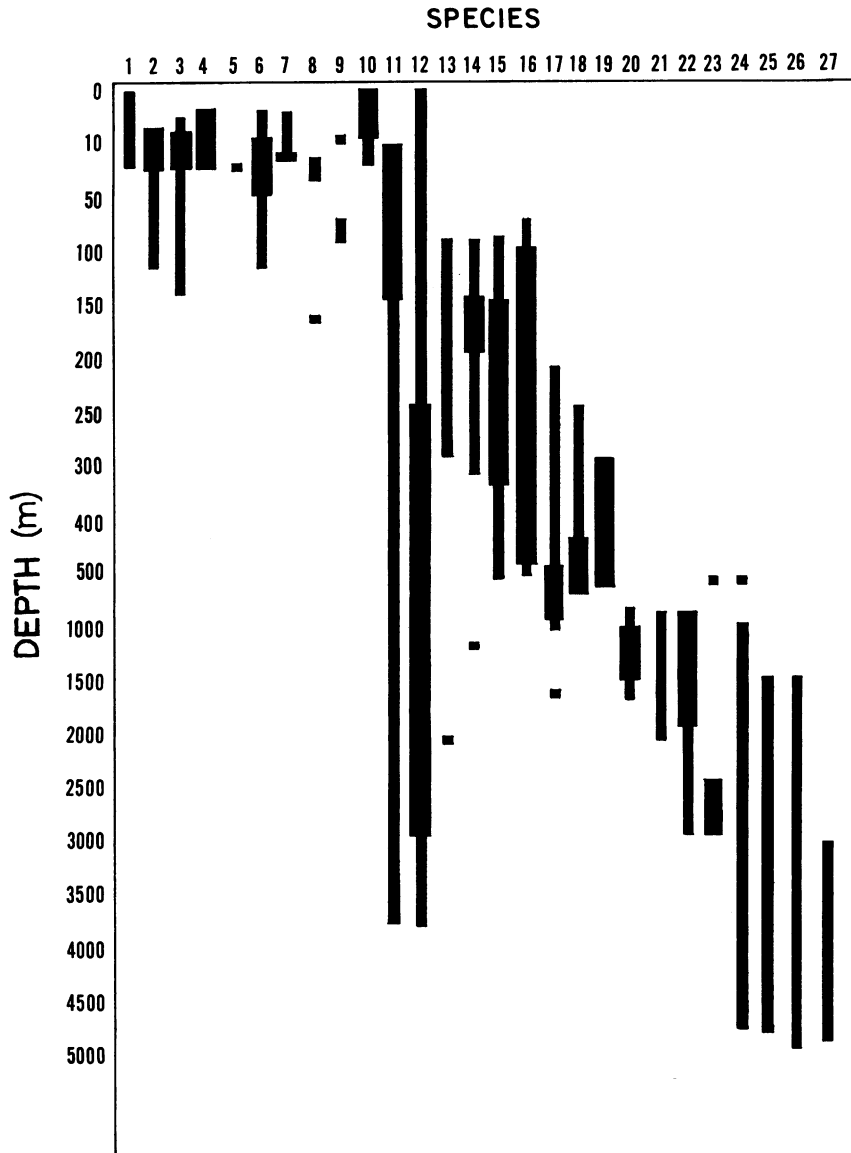


FIG. 56. Distribution of sipunculans according to depth. (See text, p. 181, 182 for explanation of column width and numbers.)

should be made between columns. The numbers at the heads of columns represent species as follows:

1—*Sipunculus nudus*, 2—*Aspidosiphon albus*, 3—*A. spinalis*, 4—*A. parvulus*, 5—*A. cumingii*, 6—*Golfingia pellucida*, 7—*Themiste alutacea*, 8—*G. trichocephala*, 9—*G. elongata*, 10—*Phascolopsis gouldi*, 11—*Phascolion strombi*, 12—*G. minuta*, 13—*G. eremita*, 14—*G. margaritacea*, 15—*Onchnesoma steenstrupi*, 16—*G. catharinae*, 17—*P. strombi* (pteropod population)

18—*O. squamatum*, 19—*G. murinae bilobatae*, 20—*S. norvegicus*, 21—*G. bulbosa*, 22—*A. zinni*, 23—*G. muricaudata*, 24—*G. murinae murinae*, 25—*G. constricticervix*, 26—*G. flagrifera*, and 27—*O. magnibatha*. As a result of this analysis four major groups have been established. Their major attributes and the included taxa follow.

GROUP 1A: South of Cape Hatteras on the continental shelf; in warm water; sand and coarser sediments; some living within a pro-

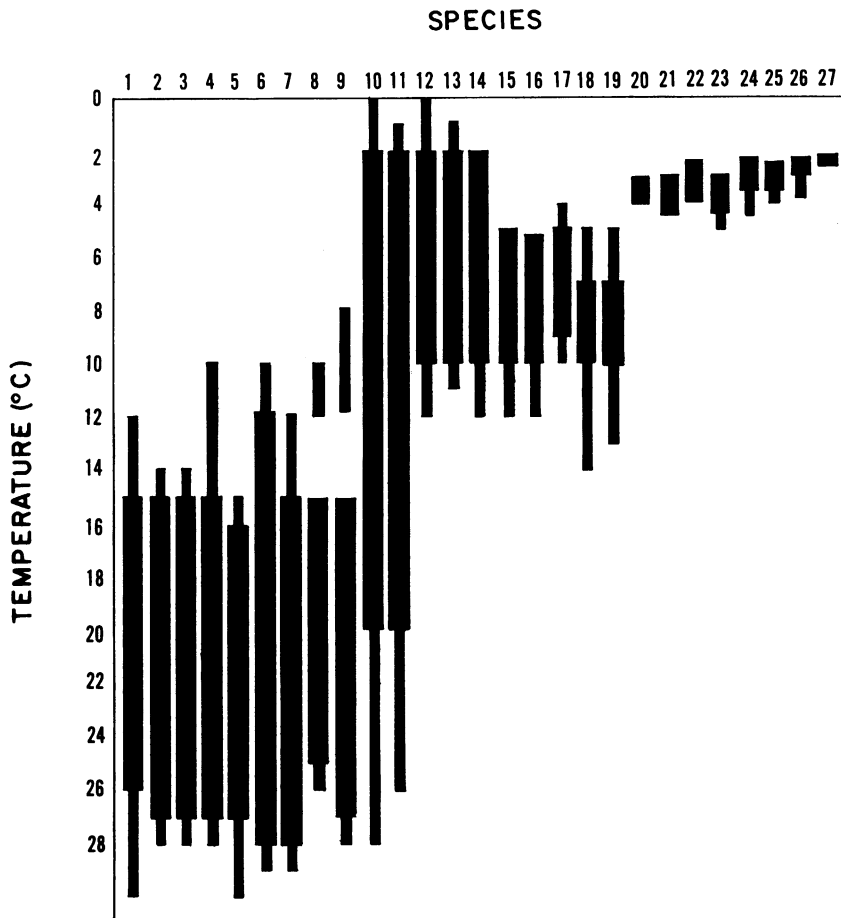


FIG. 57. Distribution of sipunculans according to temperature. (These values represent range of temperatures that any species may be exposed to throughout its range. See text, p. 181, 182, for explanation of column width and numbers.)

tective shelter (shell or coral); included are *Aspidosiphon spinalis*, *A. albus*, *A. parvulus*, *A. cumingii*, *Golfingia pellucida*, *Themiste alutacea*, and *Sipunculus nudus*.

GROUP IB: As above except that the member species occasionally are found farther north (latitude 39–40°N) on the shelf in colder water. These species are *Golfingia trichocephala* and *G. elongata*.

GROUP IIA: Predominantly northern forms with a broad vertical range; restricted to cold water; sandy and finer sediments; only rarely on shelf south of Long Island; included are *Golfingia eremita*, *G. minuta*, and *G. margaritacea*.

GROUP IIB: As above except that the member species are also found farther south in warmer

water. They are *Phascolopsis gouldi* and *Phascolion strombi*.

GROUP III: Moderate depths on the upper slope; low temperatures that are relatively stable; fine sands and silty sediments. One subgroup is found only south of Cape Hatteras and the other is predominantly north of Cape Hatteras. North: *Onchnesoma steenstrupi*, *Golfingia catharinae*, and *Phascolion strombi* (pteropod population). South: *Onchnesoma squamatum* and *Golfingia murinae bilobatae*.

GROUP IV: Found at depths greater than 1000 meters; fine sediments; low, almost constant temperatures. Three subgroups are:

a. Less than 3000 meters; including *Sipunculus norvegicus*, *Golfingia bulbosa*, *G. muricaudata*,

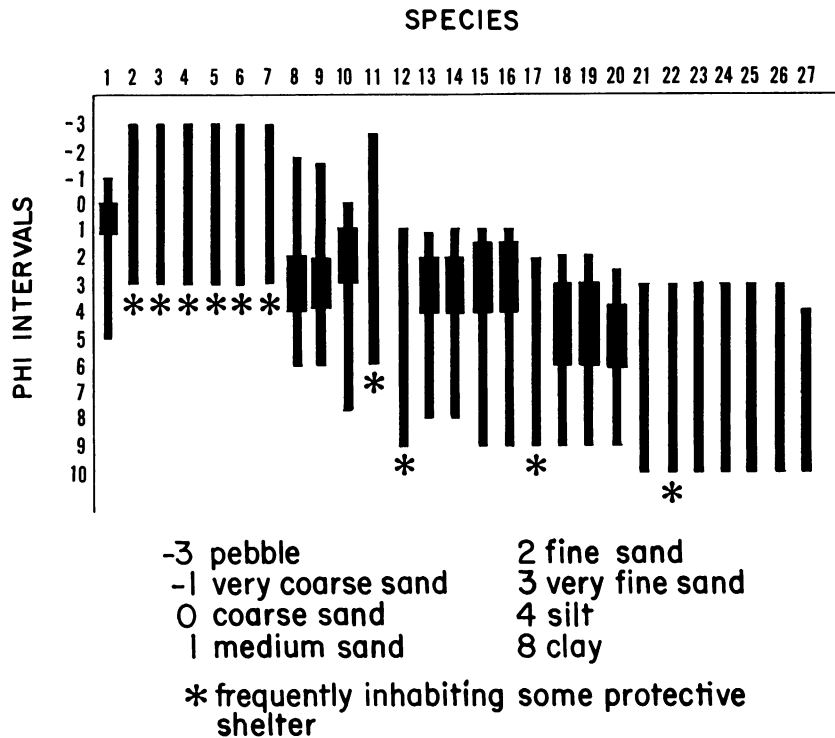


FIG. 58. Distribution of sipunculans according to sediments. (These values represent approximate limits of particle size present in significant percentages within the range of a species. For those species that commonly inhabit a shell or other protective shelter, the make-up of the sediment probably is not highly important. See text, p. 181, 182, for explanation of column width and numbers.)

and *Aspidosiphon zinni* (the first two less than 2000 meters).

- b. Greater than 3000 meters; including *Onchnesoma magnibatha*.
- c. Ranges above and below 3000 meters; including *Golfingia flagrifera*, *Golfingia constricticervix*, *G. murinae murinae*, *G. minuta*, and *Phascolion strombi*.

These features are summarized in table 10.

These four groups are based on rather broad criteria. As Valentine (1963, p. 462) pointed out, "Within the limits of its temperature tolerance a species will be found only where all other dimensions of its environmental requirements exist—In other words, where its fundamental niche is realized." The suggestion is that the various members of each group share a certain set of niche characteristics. I do not imply that their niches are the same. To illustrate how their niches differ (how they are unique and nonoverlapping), the following section compares and

contrasts the components of each group and subgroup, more closely looking for what Darwin (1859) referred to as "divergence of character." In addition, a more comprehensive description of the environmental criteria (limits of tolerance) used in separating the groups is presented.

#### GROUP IA

This group lives in shallow water south of Cape Hatteras. Most individuals are in less than 50 meters, but others extend out to the edge of the shelf. The most northerly records are commonly around latitude 35°N, but a few are at 35°20'N. The temperature generally fluctuates between 15 and 27° C., in some cases becoming higher or lower in the shallower depths (less than 10 meters) where it may range from 12 to 30° C. The temperature range for any one species within this area is greater than 10° C. Most of this region would be classed as homoeurythermal with a tendency toward a

TABLE 10  
COMMON RANGE OF GROUP ECOLOGICAL FACTORS  
(Total range in parentheses.)

Group	Depth in Meters	Temperature (in C.)	Sediments	Latitude Degrees North	Normal Temperature Range Tolerated by Any Member Species (in C.)
IA	10-50 (1-185)	15-27 (12-30)	Sandy or coarser	25-35 (35°24')	Greater than 10
IB	10-50 (10-178)	15-27 (7-27)	Sandy or coarser	28-35 (40)	Greater than 15
IIA	10-1000 (1-3750)	2-10 (0-15)	Sandy or finer	35-45 (33)	Less than 10
IIB	10-1000 (1-3806)	2-20 (2-26)	Sandy or finer	35-45 (30)	Greater than 20
III	150-700 (82-1100)	—	Very fine sand or finer	—	Less than 5
North	—	5-10 (4-12)	—	34-40 (30)	—
South	—	7-10 (5-15)	—	24-34	—
IV	1000-5000 (700-5350)	2.5-4.0 —	Silts and clays; very little sand	32-41	Less than 2
A.	1000-3000	—	—	—	—
B.	3000-5000	—	—	—	—
C.	1500-5000	—	—	—	—

heterostenothermal environment near Cape Hatteras. It coincides with the region commonly referred to as the Carolinian Province (Bumpus and Pierce, 1961, and others).

The sediments are generally sand plus some coarser material, but most of these species usually live within some type of protective shelter (coral, mollusc shell, etc.). In effect the sediments in these areas are probably not of primary importance for the sipunculan fauna in this group.

These seven species, although they live in generally the same environment, exhibit several interesting ecological differences. *Sipunculus nudus* is distinguished (in this group) by its large size and its habit of burrowing in coarse sand, frequently at very shallow depths. The other species live above the surface of the sediments in their protective shelters.

Two aspidosiphons (*A. spinalis* and *A. albus*) were most frequently found living a solitary

existence in mollusc shells, whereas the other three were commonly living together in the coral "community"; *Aspidosiphon parvulus* and *Golfingia pellucida* were occasionally found by themselves. The former aspidosiphons were taken from the same localities, and they show no significant difference in their vertical distribution. *Aspidosiphon albus* is a smaller, more delicate animal with a longer introvert than that in *A. spinalis*, which may cause a difference in feeding. The abiotic nature of their two niches is similar, however.

The three species found in the coral, *Oculina*, exhibit marked differences in density at the two localities. Table 11 is based on unpublished data provided by L. McCloskey. This table shows two trends: 1) the average density of sipunculans is greater in the deeper, more stable environment, and 2) the relative density of the three species shifts from a situation dominated by *Aspidosiphon parvulus*, with very few

TABLE 11  
DENSITY OF SIPUNCULANS IN THE CORAL *Oculina*

	Stations <sup>a</sup>			
	1	2	3	4
Number of worms per head of coral				
<i>Golfingia pellucida</i>	142	34	177	196
<i>Aspidosiphon parvulus</i>	389	188	60	58
<i>Themiste alutacea</i>	4	1	68	56
Weight of coral (in grams)	17,000	4,000	3,000	7,000
Number of sipunculans per 100 grams coral	3.1	5.6	11.6	7.7
Averages	4.4		9.7	

<sup>a</sup>1 and 2 represent subsamples (heads of coral) from a 6-meter station; 3 and 4 are subsamples from a 24-meter station.

*Themiste alutacea*, to one where *Golfingia pellucida* dominates and *A. parvulus* is numerically about equal to *T. alutacea*. The implications are that sipunculans generally prefer a stable environment, and secondly, that *A. parvulus* can tolerate a heteroeurythermal environment, whereas *T. alutacea* cannot; *G. pellucida* is intermediate between these two. It would be instructive to verify these observations in the laboratory.

The *A. parvulus* are separated from the other two species in that they live in their own self-made holes in the living portion of the coral. The other two species live in crevices and spaces toward the base and around the non-living areas of the coral head. The nature of the tentacular crown in *G. pellucida* and *T. alutacea* is distinct and strongly suggests utilization of a different type of food.

In summary, these six species can be ecologically separated into four groups on the basis of site selection; the two remaining pairs of species are probably separated by the type of food consumed.

#### GROUP IB

This subgroup is fundamentally like the preceding one. Its distinction is based on the presence of one or two records of each species from colder, deeper waters off New Jersey. Both species are usually found between latitude 28° and 35°N in 10–40 meters of water where the temperature ranges from 15–27° C. The isolated northern collections, however, were between latitude 39°20'N and 40°20'N in 80–180 meters where the temperature ranges from 7–12° C. This grouping is not very satisfactory as the number of individuals involved is small, and the atypical northern stations may

cause an unnatural bias toward this different environment. If this picture is accurate, however, then these species can tolerate temperature ranges of 15–20° C.

The existence of only one *Siphonomecus* of questionable specific affinity negates the desirability of discussing it in this context. It seems logical, however, to include the animal in this group as this current record (compared with the type locality) suggests the same kind of cold extension of a “naturally” warm-water form.

The five records of *Golfingia elongata* (three from the south and two from the north) are fewer than desirable for this discussion. *Golfingia trichocephala* is more common and shows the same anomalous northern extension by two individuals at one station as the preceding species. This situation is similar to that which apparently existed for *Golfingia pellucida* (= *verrilli*) in the early part of this century. As Mayr (1947, p. 275) pointed out: “There is a dispersal phase in the life cycle of every species during which many individuals are carried onto unsuitable locations and perish. Others may survive during favorable seasons and form the nucleus of a new population only to be wiped out again during the first adverse season.”

These species, with their population centers south of Cape Hatteras in shallow water, evidently can tolerate lower temperature and survive. Hutchins (1947) showed a similar situation for *Balanus*. Their ability to reproduce and establish a permanent extension of their range has yet to be demonstrated. This phenomenon may be associated with fluctuations of the marine environment that allow larvae to settle but do not permit successful reproduction. In other words, this fringe population (perma-



nent or temporary) may be entirely maintained by emigrants from the permanent range. Wells and Gray (1960) have shown a similar type of distribution in *Mytilus edulis*.

These species do not live in shells or coral, as do most of those in the preceding group. They are much smaller than *Sipunculus nudus* (the only species in Group IA that inhabits the sediment). *Golfingia trichocephala* is generally smaller than *G. elongata* and has an extremely long, thin introvert so the size of particles ingested is probably different.

#### GROUP IIA

This group is not usually found on the shelf south of latitude 40°N. Its latitudinal boundaries are from latitude 33°N to at least 45°N. The depth distribution varies with the latitude; the worms are common on the shelf and upper slope in the north and extend down to maxima of 1200, 2100, and 3800 meters for the three member species. The temperatures in these areas are usually between 2 and 10° C., but may range from 0–15° C. These species generally are homostenothermal with a tolerance range of less than 10° C. The sediments are predominantly sandy but may be finer.

In the past the members of this group have been referred to as typically Arctic forms. The restrictive geographical connotations of this term are unfortunate in view of the present evidence. *Golfingia minuta* is separated from the other two by its small size and habit of living within foraminiferan tests. It is also more common at greater depths. *Golfingia eremita* and *G. margaritacea* belong to different subgenera, but externally they are similar, except in the southern part of their range where *G. margaritacea* assumes the unique elongate, slender form which Gerould (1913) called a variety, *meridionalis*. In this southern zone (latitude 35–39°N), *G. margaritacea* is much more common than *G. eremita*; the reverse seems to be true in the north (latitude 39–44° N). This distribution might indicate an ecological separation. Their size and mode of life are very similar.

#### GROUP IIB

This group is similar to the preceding one in that most individuals of the two included species live in the same general environment. Significant numbers live in warmer, shallow water,

however, south of Cape Hatteras. This distribution makes this group the most eurythermal under consideration.

The temperature range is commonly 2–20° C. but may vary from 0–26° C., in the shallow or southern areas. The group spans latitudes from 30°10'N to at least 44°00'N. The depth of one species ranges from 1–27 meters, whereas the other lives in 14–3800 meters. This zone includes a wide variety of thermal conditions from heteroeurythermal to homostenothermal, and the temperature range for each species is about 20° C. or greater. These two species are both more common and generally more robust in the northern part of their range. This fact, together with the observation that these animals have been collected only recently south of Virginia, suggests a recent southerly extension of their ranges. They are able to produce gametes in the warmer waters to the south, but this ability may be an obverse situation of Group IB, that is the southern (deeper) populations may depend on the northern populations for immigrants to maintain their numbers.

The two species are ecologically distinct. *Phascolopsis gouldi* is free-living in shallow, sandy areas, and *Phascolion strombi* lives within some type of shelter on the surface of the sediments. Their size also differs significantly; *P. gouldi* grows much larger than *P. strombi*. *P. gouldi* has a much more complex tentacular apparatus than does *P. strombi*.

#### GROUP III

The five taxa within this group form a single unit except from the standpoint of latitude; three are generally northern (latitude 34°–40° 25'N), whereas the other two are southern (24°–34°N). All live on the upper slope (200–1100 meters) with some extension onto the outer shelf at the northern end of the range (up to 80 meters in one species). The temperature is generally 5–10° C., sometimes slightly higher in the shallower areas. This area is homostenothermal and the temperature range for any one species is less than 5° C. The sediments are predominantly fine sand and silt.

Within the northern subgroup including *Onchnesoma steenstrupi*, *Golfingia catharinae*, and *Phascolion strombi* (from pteropod shells), *O. steenstrupi* extends into the southern area but in relatively small numbers. These *P. strombi* are found only in pteropod shells, but the other two

species live within the sediments. *Golfingia catharinae* is found at the same stations with either *O. steenstrupi* or *P. strombi*, but never with both. *Onchnesoma steenstrupi* has not yet been collected together with *P. strombi*. These two are separated from *G. catharinae* primarily by size and by food selection. With its long introvert, *O. steenstrupi* lacks tentacles, whereas *G. catharinae* has a highly developed tentacular crown.

The second species pair is not as easily separated because they are of similar dimensions. *Onchnesoma squamatum* has small but well-defined tentacles, whereas tentacles have not yet been observed in *G. murinae bilobatae*. The peculiar large scalelike papillae on *O. squamatum* are probably biologically significant; their precise function has not yet been determined.

#### GROUP IV

These abyssal organisms live in the most nearly constant environment of the four groups. The temperature is invariably low (2.5–4.5° C.), and the sediments are mostly silts and clays together with some very fine sand. This group can be subdivided into three subgroups on the basis of depth.

*Onchnesoma magnibatha* has not been found in less than 3000 meters and is unique in this respect. *Sipunculus norvegicus* is restricted to depths between 900 and 1800 meters. *Golfingia bulbosa* has a similar distribution (1100–2100 meters) and occurs on the Bermuda slope as well as on the continental slope. The type locality of *G. bulbosa* is at depths of 1000–1100 meters off Ireland. If subsequent work confirms this unique distribution, it suggests bathypelagic larvae. *Golfingia muricaudata* and *Aspidosiphon zinni* have not been recorded below 3000 meters. These latter four species live only on the slope and never come in contact with *O. magnibatha*. As there are only four records of *G. muricaudata*, its apparent distribution may be deceptive. Murina (1964a) recorded it from depths as great as 6800 meters in the northwestern Pacific.

There remain *Golfingia flagrifera*, *G. murinae murinae*, and *G. constricticervix*. All three have a wide vertical distribution between 1500 to 5000 meters. *G. flagrifera* is the only sipunculan found deeper than 5000 meters in this investigation. This subgroup overlaps the other two but appears more commonly on the rise than on the slope. In addition, *G. minuta* is also found as

deep as 3750 meters and perhaps should have a double classification; it could be placed in this subgroup as well as in Group IIA.

To infer ecological separation on the basis of morphology becomes especially difficult in group IV. The ranges of the two species whose length may exceed 20 mm. (*Sipunculus norvegicus* and *Golfingia flagrifera*) overlap only at their fringes between 1500 and 1800 meters. Most of the other species are smaller, many lack tentacles, several have large hooks on the introvert, and two have the peculiar caudal appendage or tail. It has been suggested (Southern, 1912; Murina, 1964a) that these tails have a sensory or tactile function, but no experimental work has been attempted to test this possibility. Several have long introverts and three inhabit foraminiferan tests.

It is now evident that in the constant environment below 2000 meters, the diversity of species is great (Hessler and Sanders, 1967). Although this taxonomic diversity is not reflected in external, functional morphology, convergent evolution of these forms certainly is suggested. Murina (1964a) noted that "variability related to habitation at great depth bears an adaptive character. Sipunculids obtained from depths greater than 2000 meters, regardless of species, are characterized by a thin, transparent body wall, a poorly developed cutaneous muscular sack, uniform greyish and whitish coloring, a jelly-like tissue consistency, the presence in some species (*G. appendiculata*, *G. muricaudata*, *G. mawsoni*) of a shorter or longer caudal appendage, which clearly possesses a tactile function." In general, this characterization seems to hold also for my material. In conclusion, the distinctive niche characteristics are less obvious in this last group, perhaps as a result of the apparent uniformity of the environment. It may be that the subtleties of the significant abiotic differences in the deep-sea environment are not yet appreciated.

#### SYMPATRIC SPECIES AND COMPETITIVE EXCLUSION

In this discussion of the uniqueness or separation of niches (competitive exclusion principle), it is instructive first to consider the frequency of potential competition between species that are closely related on a systematic basis (congeneric). Table 12 summarizes the fre-

TABLE 12  
ANALYSIS OF SYMPATRY

Genus or Subgenus	Number of Included Taxa	Comments
<i>Sipunculus</i>	2	No overlap
<i>Aspidosiphon</i>		
<i>Paraspidosiphon</i>	2	No overlap
<i>Aspidosiphon</i>	3	Two species overlap; one separate
<i>Onchnesoma</i>	3	Two species with limited overlap; one separate
<i>Golfingia</i>		
<i>Golfingia</i>	3	No overlap
<i>Mitosiphon</i>	3	No overlap
<i>Phascoloides</i>	6	Four species with limited overlap at great depths; two distinct
<i>Thysanocardia</i>	1	—
<i>Themiste</i>	1	—
<i>Phascolion</i>	1	—
<i>Phascolopsis</i>	1	—
<i>Siphonomecus</i>	1	—

quency of overlapping ranges within genera or subgenera.

It is evident that sympatry between closely related species is less frequent than allopatry. The fact that sympatry occurs more frequently at great depths (over 2000 meters) than elsewhere is of interest in view of the preceding discussion of the morphological similarities of the sipunculan fauna at those depths. The implication is that the principle of competitive exclusion may not be functioning in these depths. If so, one reason might be as Mayr (1965 p. 80) suggested, "the density of a species may be fixed . . . at so low a level that its individuals are not in competition with a potential competitor whose population are equally widely spaced." Mayr also discussed several of the numerous studies of exclusion made on a wide variety of organisms and concluded, "the study of exclusion in the oceans is only beginning." Hessler (personal commun.) has suggested that it may be necessary to readjust our thinking that competition between closely related species is based primarily on food because a high percentage of the animals in the deep sea are utilizing the same source—detritus. Sokalova's (1959) data support this suggestion.

#### THE CONTINENTAL SLOPE—AN ECOTONE?

The apparent richness of the continental slope throughout most of this region poses an

interesting question: Could this area be considered as another example of the "edge effect" and should the slope be considered an ecotone? If one considers the shelf as one biotope and the rise and plain another, then the slope could be considered as a transition zone or borderland. Changes may be rapid within relatively short distances and a wide variety of niches are present. The other alternative is to give the slope the equal rank of a separate biotope with its own characteristic fauna.

A few shelf species are found on the upper slope and some abyssal species occur on the lower slope, but it also has several endemic species (Group III plus *Sipunculus norvegicus*). The evidence provided by sipunculan distribution does not fully support either contention but seems to favor giving the slope biotope rank with ecotones at the top and bottom.

#### CAPE HATTERAS BARRIER

This investigation has reinforced the concept that Cape Hatteras acts as a zoogeographical barrier for the shallow-water forms (fig. 59). This hypothesis has been recently augmented by Cerame-Vivas and Gray (1966) who presented an excellent review of the pertinent literature supporting both the hypothesis and the hydrographic bases for the barrier. The barrier is probably due to the inability of southern species to tolerate temperatures below 15° C. for an extended period of time or the necessity of

having water warmer than 20° C. for successful breeding (Hall, 1964; Hutchins, 1947). Many zoologists have said, in words similar to those of Wells (1963, p. 91), "It will at once be evident from the distribution map that a temperature gradient can be more effective as a barrier than any visible geographical feature." In addition to temperature, the fact that the larvae are subject to currents for dispersal may also explain absence of a species north of this point where the Gulf Stream turns eastward off the shelf.

A barrier does not seem to exist below 2000 meters (Group IV species). The factor that apparently imposes a shift in the distribution is that the Blake Plateau forces deep-water forms farther offshore to find their required depth. The plankton in the overlying water column is different in the Gulf Stream than north of it, and this also, as it contributes to the nutrients of the benthos, may be an effective barrier. The present investigation, however, uncovered no evidence to support this view. (see Be' and Hamlin, 1967). Very few stations have been made between 1000 and 2000 meters in this region. *Sipunculus norvegicus* is found commonly, however, at these depths north of Cape Hatteras; only one old record exists of its occurrence south of the Cape. The evidence implies that some kind of barrier is present at these depths, but it is probably a topographical one (the Blake Plateau).

Between 150 and 1000 meters evidence is sufficient to suggest a partial barrier which is effective for most species. The species found at these depths belong to Groups II and III (fig. 59). The only subgroup that does not extend north and south of the Cape is III south. The other three extend around the Cape, but in doing so are compressed into a very narrow band (about 2' longitude) so that in a large scale sampling program, without closely spaced stations, these species could easily be overlooked. Additional problems in locating these species are the difficulties in obtaining satisfactory bottom samples. The slope is very steep and irregular with as yet uncharted canyons. The swift current (about 2.5 knots on the surface) makes the maintenance of a station position difficult and the current on the bottom limits the effectiveness of the sampling gear.

The Group IIB species (eurythermal, eurybathic) are common on the shelf off Cape Lookout and as they are able to tolerate diverse

conditions, a study of their distribution will probably yield very little information for this analysis.

The Group IIA species (northern, cold-water) extend a short distance around the Cape near the shelf break (latitude 34°45'N), stopping short of the Cape Lookout latitude (fig. 59). One might postulate that these species could continue farther south by going to greater depths, but this movement does not seem to have occurred.

Group III north (5–10° C., upper slope and outer shelf) exhibits a distribution similar to Group IIA but at slightly greater depths. Two of its three taxa also disappear off Cape Lookout (latitude 34°13'N); the other (*Onchnesoma steenstrupi*) continues south in reduced numbers, to about latitude 30°N at slightly greater depths. The Cape Lookout area (latitude 34°16'–34°20'N) is the northern limit for the two species in Group III south (southern slope).

Evidence is good, therefore, that a partial barrier exists at depths between 150 and 700 meters. This barrier is displaced southward (latitude 34°20'–34°30'N) and not north of Cape Hatteras as might be suggested by the overlying Gulf Stream which does not turn eastward to leave the shelf until about latitude 35°30'N. Neither does it coincide with the limits of the Tropical (Caribbean) Province as shown by Cerrame-Vivas and Gray (1966). A barrier exists, but what kind of barrier is it?

The barrier is not depth or latitude alone. If it is sediment, it is very subtle as the particle size distribution is not very different, being only slightly finer and more calcareous in the south. The sediment differences may contribute to the southern boundary for the Group IIA species. Temperature is another factor to be considered. The normal range of temperature is the same north and south of this barrier, commonly a homostenothermal 5–10° C. The only apparent differences are the irregular influxes of warmer water (up to 15° C.) south of Cape Hatteras caused by the meandering of the Gulf Stream. This temperature factor may explain the southward limit of the Group IIA and the two Group III north species, that is, they are not heterostenothermal organisms and short-term, rapid temperature fluctuations above 10° C. may be fatal; this explanation seems unlikely, however. *Onchnesoma steenstrupi* (in Group III north), which extends southward, is also found on the

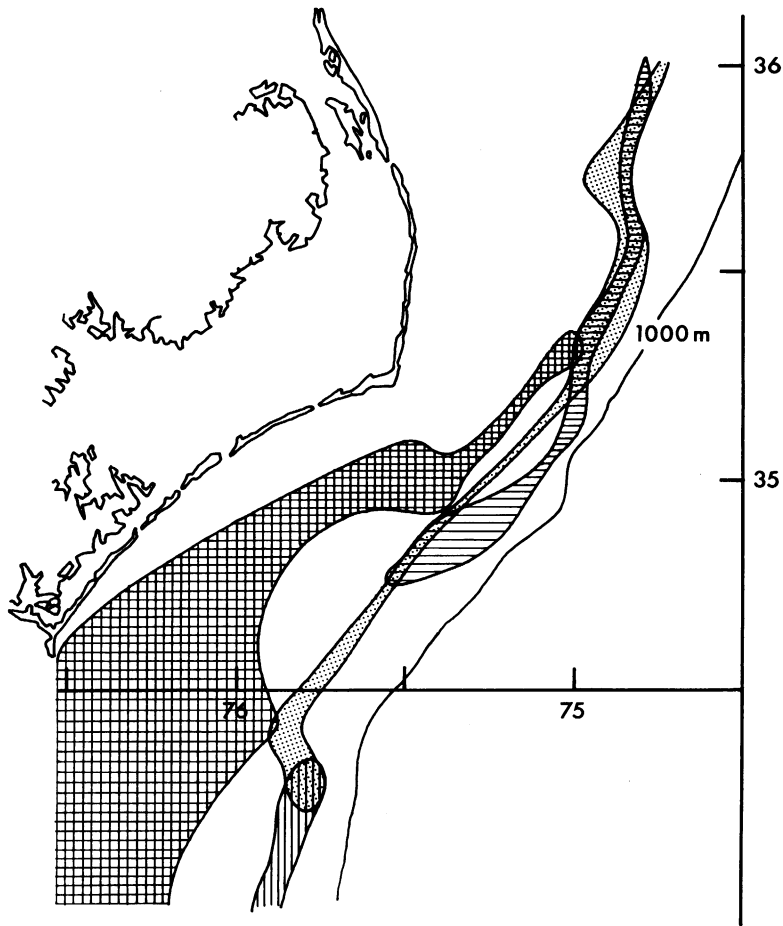


FIG. 59. Distribution of four groups of sipunculans in the Cape Hatteras region showing basis for suggesting existence of barrier on the continental slope between  $34^{\circ}20'N$  and  $34^{\circ}30'N$ .

*Symbols:* crosshatching, group IA; vertical lines, group III south; horizontal lines, group IIA; dots, group III north.

shelf off southern New England where the temperature may often be  $12^{\circ}C$ .

Temperature, however, does not explain the northern limit of the Group III south species, unless one assumes it is mandatory that they have a heterostenothermal environment. This explanation does not seem plausible. A sediment analysis that takes into account factors other than particle size might yield an explanation.

The bottom currents in this area are relatively complicated and are not well understood. It is here that the northward flowing Gulf Stream meets the southerly deep western boundary current. The water masses extend all the way to the bottom but exactly what happens where

they contact each other is not known. Although the temperatures of both water masses are similar, other chemical or biological factors may be different (L. Atkinson, personal commun.). This kind of difference can mean that certain physiological requirements are not met in one or the other area.

A further and possibly important effect of the currents is with regard to larval distribution. Larvae of these forms have short pelagic lives; nevertheless, they are dispersed by the bottom currents. Exact information on larval life is not available for many species, but collections of surface plankton in the Gulf Stream at various points across the Atlantic Ocean (Hall and

Scheltema, 1966) have yielded the young of several shallow-water, southern genera (Group IA). Neither *Golfingia* nor *Onchnesoma* has been taken in the surface plankton. Akesson (1958) pointed out that *G. minuta* has direct development and broods the young in the shelter (shell, crevice) used by the maternal worm. He also said with reference to *Phascolion strombi*, "the pelagic stage lasts from five to six days . . . Plankton samples have been taken . . . but no embryos have ever been found. . . . Embryos during the pelagic stage whirl around in the water layer just above the bottom. We can speak of a bottom-pelagic stage." The large size of the *Onchnesoma* egg suggests that it has direct development or a very short-lived pelagic stage (Rice, 1967). In general, a lecithotrophic larva with a shortened pelagic life is typical of cold-water forms (Brunn, 1957; Ockelmann, 1962).

The larvae of the southern slope group may be carried off the slope in a northeasterly direction, and similarly, the larvae of the northern forms also may be transported too far off-shore for favorable living conditions. If so, currents may be more important than previously suggested for the existence of both a shallow-water barrier and a slope barrier.

The important factors that have been ignored in this discussion are the various effects of other animals—the biotic factors. Attempts to define or explain phenomena such as barriers on abiotic bases alone, may fail because, as with other populations in different environments, the phenomena of competition, symbiosis, predation, and parasitism must have, in most situations, certain limiting effects. If "Occam's Razor" is applied to this problem, however, it could probably be almost entirely solved by referring to currents alone. Additional investigations are under way to elucidate this situation in greater detail.

#### ZOOGEOGRAPHICAL UNITS

Numerous authors, among them Hutchins (1947), Valentine (1963), and Hall (1964), have discussed the existence of zoogeographical units or provinces off the east coast of the United States. Unfortunately, in constructing their hypotheses, these authors have limited themselves to shallow-water forms, commonly intertidal fauna: molluscs, fish, crustaceans, or plankton. An example of oversimplification is found in Hutchins (1947, p. 334): "zonal boundaries of organisms are to be interpreted in

terms of summer and winter temperatures." He ignored the possibility that boundaries exist where temperature fluctuations are negligible. Another example of this narrow view is shown by one statement in Cereme-Vivas and Gray (1966, p. 262), "thus if biotic provinces do exist here, it is important to know the location of their North-South and East-West boundaries." Later (p. 268) they added, "it is also important to know distance from shore, depth, and the water masses involved."

Other authors (Vinogradova, 1959; Madsen, 1961) limited themselves to discussions of faunal zonation below 2000 meters. The lack of any consideration of the fauna between the shelf and the abyssal zone or any comprehensive attempt to consider the entire vertical range is puzzling. Perhaps it reflects the nature of past collections or simply that it was considered too overpowering a task to analyze such diverse areas altogether. Ekman's (1953) book indicates the monumental size of the task on a worldwide basis. Because of more adequate collections, however, it now seems possible to attempt this type of analysis in limited geographical areas. In Ekman's book only five of the 375 pages were devoted to the "archibenthic" (slope) fauna. He suggested a transitional zone from 200 to 600 meters and an abyssal zone extending from 600 to 6000 meters. In Hedgpeth's (1957) chapter, "Marine Biogeography," the word "slope" cannot be found, and only one paragraph is given to the deep-sea benthos.

One of the advantages of working with a small phylum such as Sipuncula is that without making any arbitrary, artificial limitations concerning which families or classes to consider, one can treat the whole group throughout its entire vertical range. Without being overwhelmed by a vast number of nomenclatural problems, it is possible to analyze their distribution critically and uncover inherent patterns.

Two factors that restrict one's extrapolation from a given set of distributional data are: 1) the confused state of nomenclature, resulting in a lack of certainty that any given name used by two different zoologists really applies to the same biological entity (and vice versa); and 2) the sparseness of adequate benthic sampling at great depths in many regions of the oceans. These limitations certainly hold for the sipunculans if not for many other groups of marine invertebrates. Nevertheless, Ekman (1953, p.

286) stated that, "Just as the archibenthal fauna occupies an intermediary position in the vertical distribution between the fauna of the shelf and the abyssal fauna, it also occupies such a position in the horizontal distribution, in that its species generally have a more extensive distribution than the shelf species, but less extensive than the abyssal species." This idea as it pertains to the abyssal fauna was modified somewhat by Vinogradova (1959, p. 205): "The species of deep-sea bottom invertebrates with a wide vertical range generally have an extensive horizontal range as well. Almost all cosmopolitan deep-sea forms are eurybathic. The stenobathic species, on the contrary, occur only in a restricted area." Murina (1964a) concurred with this generalization but acknowledged that her analysis of the zoogeography of the deep-water sipunculans was preliminary as many of them were known from only one to three locations. The factual basis behind Vinogradova's (1959) and Ekman's (1953) assumptions is the unfortunately inadequate sampling of abyssal benthic organisms. Hedgpeth (1957, p. 369) summarized the situation thus: "It is difficult to infer much about the zoogeography of the deep-sea benthos . . . Most of the species are still represented by single specimens or single collections, and such records are useless for zoogeographical purposes."

It is not surprising, therefore, that a species is listed as having a limited distribution if it has only been collected two or three times. A question that needs asking, however, is, do these records describe the actual situation or are they an artifact of sampling and nomenclatural problems? My evidence suggests the latter.

The three subdivisions Vinogradova (1959) proposed for the Atlantic Ocean are not supported by comparison of the results of this investigation with earlier records from the eastern and northern parts of the Atlantic Ocean. It appears now that most of the deep-water sipunculans are common to both sides of the Atlantic.

Of the four groupings of sipunculans proposed earlier in this section, Group I is part of the Carolinian (subtropical or outer tropical) Province fauna. Group II is generally within the Nova Scotia or cool temperate Province. Sipunculans are very rare within the Virginian Province (the shelf between Cape Hatteras and Long Island). Group IV species are in Vinogradova's (1959) Atlantic subarea of the abyssal

fauna. The Group III species are not in any established province. The temperature regime for this group corresponds to Vaughn's (1940) Subpolar Province, but this term is hardly apropos for species which occur off Miami, Florida. I propose the term Atlantic Transitional Province for this area.

This new province may be thought of as having two subprovinces in the study area (north and south) but probably it could be extended around the entire Atlantic Ocean. It is characterized by moderately cold ( $5-10^{\circ}$  C.), almost constant temperatures (no marked seasonal fluctuations), and by moderately fine sediments (at least 15-25 percent sand but no component coarser than medium sand, 1 phi). In other parts of the world, the depth range may differ; it is shallower off the Scandinavian countries and deeper in the Mediterranean, but in the northwestern Atlantic it is generally from 150 to 1800 meters.

#### EVOLUTIONARY CONSIDERATIONS

The evolution of benthic marine animals has been the subject of several speculative articles which tend to divide into two schools of thought. One claims that "without doubt the abyssal fauna stems from shallower depths" (Brunn and Wolff, 1961); the other maintains that the abyssal fauna is the more primitive (Zenkevich and Birstein, 1956; Zenkevich, 1961) and that evolution has been slower in the abyss than elsewhere (Carter, 1961). It is beyond the scope of this work to enter into the controversy but a few observations may be pertinent.

Although no taxa yet exists between genus and phylum, it is generally accepted (Selenka, de Man, and Bulow, 1883; Akesson, 1958) that the genus *Golfingia* is probably the most generalized (primitive) group and that *Aspidosiphon*, *Phascolosoma*, *Lithacrosiphon*, and *Cleosiphon* are among the more specialized genera. An analysis of distribution shows that the specialized genera typically dwell in tropical, shallow waters but the generalized group inhabits predominantly cold, deep waters. This same pattern holds for marine flatworms and for nemerteans (E. Kirsteuer, personal commun.).

Several reasons make it tempting to suggest an evolutionary sequence for the three species of *Onchnesoma*. Consider the length of the introvert, position of the anus, the tentacles, and the retractor muscles, which seem to show a trend

TABLE 13  
VARIABLE CHARACTERISTICS IN THE GENUS *Onchnesoma*

Species	Length of Introvert	Position of Anus <sup>a</sup>	Tentacles	Retractor Muscles
<i>magnibatha</i>	2 times trunk	70–80	?	2
<i>squamatum</i>	2–4 times trunk	70–80	Present	2
<i>steenstrupi</i>	at least 5 times trunk	95–98	Absent	1

<sup>a</sup>Percentage of distance between proximal and distal end of introvert.

in this genus. *Onchnesoma squamatum* and *O. magnibatha* still have two distinct retractors. Whether they are called two roots of one retractor or two retractors merged into one is a matter of semantics; in *O. steenstrupi* this fusion is complete. The tentacles in *O. squamatum* are small and relatively few; in *O. steenstrupi* they are absent. In *O. magnibatha* the introvert is invariably less than twice the length of the trunk; in *O. squamatum* it is at least twice the length, and in *O. steenstrupi* it is at least five times the length. The anus in *O. magnibatha* has shifted a long way from the normal position at the base of the introvert, about as close to the mouth as in *O. squamatum*; in *O. steenstrupi* it is almost at the end of the introvert.

If we construct a hypothetical, ancestral *Onchnesoma*, it would probably be closer to *O. magnibatha*; *O. squamatum* would be intermediate between it and *O. steenstrupi*. This relation is summarized in table 13.

I suggest that of the three species, *Onchnesoma steenstrupi* is the most specialized and the most modified because it has lost the tentacles, the retractors have been completely fused, the anus has shifted very close to the mouth, and the

introvert is the longest. There are also different vertical ranges for these species. The most generalized lives in the deepest water (3000–5000 meters), whereas the species suggested as being most specialized is in the shallowest (80–500 meters); *O. squamatum* is intermediate (300–700 meters). These relations support the earlier suggestion with regard to generic distributions and the Zenkevich-Carter school of thought concerning evolution in the sea.

The morphological and distributional information available in this group of worms has not yet been fully utilized to answer further questions of speciation and evolution. A more thorough analysis of morphological variation at different depths and latitudes is anticipated on the assumption that clues to the directions evolution is taking in this phylum may be found in an investigation similar to Mayr's (1954) work on the echinoids.

In concluding this section, it seems appropriate to quote Hutchinson (1957): "It is likely that something very important is involved here, but for the present what it may be is a mystery, a very good thing with which to end a discourse."



## SUMMARY

A STUDY of the sipunculans off the east coast of the United States was undertaken to elucidate their systematics, ecology, and distribution. It was designed as the first attempt to utilize morphological and ecological data from a large series of individuals to characterize this fauna more adequately. A general description of the bottom topography, currents, temperature regime, and sediments in the area bounded by Nova Scotia, Bermuda, and Cape Kennedy was presented, with special attention to the Cape Hatteras region.

The area under consideration, composed of the continental shelf, slope, rise, abyssal plain, and Bermuda pedestal, encompasses depths from 10 to 5400 meters. The two main currents are the Gulf Stream and the southerly flowing deep western boundary current. The temperatures which vary from almost 0° to 30° C., have characteristic patterns in different depths and latitudes. Marked seasonal fluctuations are apparent on most of the shelf (shallower than 100 meters) and conditions are very stable below about 500 meters. The particle size of the sediments generally decreases as depth increases. Most of the shelf is sandy with some shell hash or pebbles. The slope rarely contains material coarser than fine sand, and has significant amounts of silt and clay. Below 2000 meters the sediments are various combinations of silt and clay-sized particles with varying amounts of pelagic foraminiferan tests.

The general morphology of sipunculans was described and a key given to all the species found during this investigation. A brief account was given of the parasitic copepods, commensal endopods, and syllid polychaetes found on or with the sipunculans.

More than 8300 sipunculans from recent accumulations were identified in conjunction with a study of selected museum collections in this country and abroad. Descriptions of the morphological variability of each species were provided, with discussions of nomenclature, characterization of the abiotic environment, and distribution. For several species the reliability of various morphological characters was considered. It is evident that a good deal of morphological variation is possible in certain genera

primarily because of ontogenetic changes. Most descriptions in the past have been based on a few adult worms and are, therefore, inadequate for young, small individuals. Whenever possible, this shortcoming has been corrected.

The following species were found: *Sipunculus nudus*, *S. norvegicus* (= *priapuloides*), *Onchnesoma steenstrupi*, *O. squamatum*, *O. magnibatha*, *Golfingia margaritacea*, *G. muricaudata* (= *hudsoniana*), *G. elongata* (= *cylindrata*), *G. trichocephala* (= *tenuissima* plus *longirostris*), *G. murinae*, *G. eremita*, *G. flagrifera*, *G. bulbosa*, *G. pellucida* (= *verrilli*), *G. minuta* (= *improvisa* plus *cincta*), *G. catharinae* (= *procera*), *G. constricticervix*, *Phascolopsis gouldi*, *Themiste alutacea*, *Siphonomecus* sp., *Phascolion strombi*, *Aspidosiphon spinalis*, *A. albus*, *A. zinni*, *A. cumingii*, *A. parvulus* (= *spinoso-scutatus*).

These species were placed into four major ecological groups based on their abiotic niche parameters: 1) southern, shallow, warm water; 2) northern shelf or upper slope to Cape Hatteras, cold water; 3) Cape Cod and south on slope; and 4) deep water (below 2000 meters). The hypothesis that exclusion is operating within each group seemed to be generally acceptable for the shallow-water and slope forms; however, it could not be applied to the abyssal fauna. In this latter group the frequency of sympatry and the similarity of morphology in different genera were greater than in the others. It was proposed that the differences in this environment are too subtle to be appreciated and that perhaps the lower density of animals negates much of the competition prevalent in other biotopes.

It was suggested that the slope be considered ecologically as a biotope rather than an ecotone. The shallow-water barrier at Cape Hatteras was reaffirmed and an additional barrier on the slope was proposed near latitude 34°20'–34°30' N. The most likely cause for this barrier is the effect of the two opposing currents on larval distribution.

The pertinent zoogeographical literature was critically reviewed and the name Atlantic Transitional Province was proposed to encompass the slope fauna (150–2000 meters). This province is characterized by stable temperature (5–10° C.) and fine sediments containing at least 15 percent sand but none larger than 1 phi (medium sand).

The rarity of sipunculans in the Virginian province was noted.

Following a brief discussion of the literature on the evolution of marine fauna, two examples

from the Sipuncula are given which seem to support the concept that the deep-sea, cold-water fauna is older and more primitive than the shallow, warm-water fauna.

## APPENDIX A. REFERENCES USED IN THE IDENTIFICATION AND DESCRIPTION OF VARIOUS SPECIES

- Aspidosiphon*  
*albus* Murina, 1967.  
*cumingii* Baird, 1868; Edmonds, 1956; Keferstein, 1883; Sluiter, 1900.  
*parvulus* Fischer, 1922b; Gerould, 1913.  
*spinalis* Ikeda, 1904.
- Golfingia*  
*bulbosa* Southern, 1912.  
*catharinae* Broeke, 1925; Fisher, 1952; Lanchester, 1905; Selenka, 1885; Selenka, deMan, and Bulow, 1883; Southern, 1912; Stephen, 1960; Théel, 1905; Wesenberg-Lund, 1955, 1959, 1963.  
*elongata* Akesson, 1961; Gerould, 1913; Keferstein, 1865; Selenka, deMan, and Bulow, 1883; Southern, 1912; Stehle, 1953; Stephen, 1960; Théel, 1905.  
*eremita* Fisher, 1952; Gerould, 1913; Selenka, deMan, and Bulow, 1883; Théel, 1905; Wesenberg-Lund, 1930, 1959.  
*flagrifera* Gerould, 1913; Selenka, 1885; Sluiter, 1900.  
*margaritacea* Edmonds, 1956, 1965; Fisher, 1952; Gerould, 1913; Keferstein, 1865; Selenka, deMan, and Bulow, 1883; Stephen, 1941, 1948, 1960; Wesenberg-Lund, 1930, 1955.  
*minuta* Fischer, 1922a; Fisher, 1952; Gerould, 1913; Keferstein, 1865; Lindroth, 1941; Murina, 1958, 1959, 1964b; Paul, 1909; Selenka, de Man, and Bulow, 1883; Southern, 1912; Stephen, 1960; Wesenberg-Lund, 1930, 1955, 1963.  
*muricaudata* Chamberlin, 1920a; Southern, 1912.  
*murinae* Murina, 1964a, 1964b.  
*pellucida* Broeke, 1925; Gerould, 1908, 1913, 1938; Keferstein, 1865; Murina, 1964a; Selenka, deMan, and Bulow, 1883; Southern, 1912.  
*trichocephala* Chamberlin, 1920b; Fisher, 1948; Ikeda, 1904; Murina, 1964a, 1964b; Sluiter, 1902; Stephen, 1964; Wesenberg-Lund, 1959, 1963.
- Onchnesoma*  
*squamatum* Koren and Danielssen, 1875; Selenka, deMan, and Bulow, 1883; Stephen, 1960; Théel, 1905; Wesenberg-Lund, 1930.  
*steenstrupi* Koren and Danielssen, 1875; Murina, 1964b; Selenka, de Man and Bulow, 1883; Stephen, 1960; Théel, 1905; Wesenberg-Lund, 1930, 1959.
- Phascolion*  
*strombi* Fischer, 1922a; Gerould, 1913; Keferstein, 1865; Sato, 1937; Selenka, 1885; Selenka, deMan, and Bulow, 1883; Stephen, 1960; Théel, 1875, 1905; Verrill, 1873; Wesenberg-Lund, 1929, 1930, 1955.
- Phascolopsis*  
*gouldi* Andrews, 1890; Gerould, 1913; Pourtales, 1851; Selenka, deMan, and Bulow, 1883; Verrill, 1873.
- Siphonomecus*  
*Sipunculus*  
*norvegicus* Gerould, 1913; Roule, 1906; Selenka, deMan, and Bulow, 1883; Sluiter, 1900; Southern, 1912; Stephen, 1960; Théel, 1905; Wesenberg-Lund, 1930, 1959.  
*nudus* Broeke, 1925; Edmonds, 1962; Fisher, 1952; Gerould, 1913; Ikeda, 1904; Keferstein, 1865; Prashad, 1936; Sato, 1939; Stephen, 1941, 1958, 1960; Stephen and Robertson, 1952; Verrill, 1904.
- Themiste*  
*alutacea* Gerould, 1913; Grube, 1859; Selenka, deMan, and Bulow, 1883.

APPENDIX B: SEDIMENT ANALYSIS OF CAPE HATTERAS STATIONS  
(INMAN'S STATISTICS)

DEPTH	STATION	SORTING	SKEWNESS	KURTOSIS
14	26	0.398	— .078	0.701
22	21	1.949	.172	0.196
22	6	0.431	— .267	0.982
29	2	0.448	.065	0.792
29	3	0.367	.153	0.639
33	7	0.333	— .238	0.565
33	24	0.557	.068	0.636
40	8	0.747	— .095	1.046
75	1	0.499	.054	3.459
150	49	1.190	.614	1.885
160	45	1.161	— .346	2.349
170	46	.888	.129	2.739
185	41	1.659	.409	1.392
190	33	.896	.158	2.655
203	34	2.579	.410	—
375	9	1.824	.671	—
500	40	1.197	.590	—
520	35	2.982	.613	—
530	44	2.844	.413	—
600	50	2.635	.620	—
620	43	2.157	.631	—

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