learning therapy for other symptoms—for example, the rewarding of high-voltage electroencephalograms as a treatment for insomnia. While it is far too early to promise any cures, it certainly will be worth while to investigate thoroughly the therapeutic possibilities of improved instrumental training techniques.

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Gnathostomulida from America

This is the first record of the new phylum from North America.

R. J. Riedl

Members of the new animal phylum (*1*), Gnathostomulida, recently discovered in Europe, have now been found in unexpected abundance and diversity along the east coast of the United States.

Two million animal species have been described, but the rate at which new descriptions accumulate indicates that these two million are only about 50 percent of the extant species on earth. The increase in new species of birds (8600 known species) has sunk to less than 0.3 percent a year, but in many other classes (for example, Turbellaria with 2500 known species) the rate of increase indicates that undescribed species probably total more than 80 percent. Although only about half of the existing kinds of animals have been described, 80 percent of the families, 95 percent of the orders (*2*), and nearly all of the animal classes are presumably already known. Therefore a new phylum should be rare indeed.

About 24 phyla now divide the metazoa at the upper level of classification. A new phylum might give us a chance to increase our knowledge of principles of structural organization by 1/24. As a matter of fact, the second third of this century brought us many more new animal taxa of the higher categories than the systematics of the first third of the century allowed us to predict. This was based partly on more extensive collecting and more adequate methods and equipment, but also on the notable renaissance of interest in systematics (*3*).

The last phylum discovered prior to Gnathostomulida was Pogonophora. From the history of its discovery, given in Ivanov's voluminous monograph (*4*), we learn that at first there was a period of taxonomic uncertainty lasting one generation. This was followed by a progressive increase in numbers of discovered species, then of new genera, and finally of further new species (Fig. 1). The third stage was the initiation of studies of the embryology, ecology, ultrastructure, and physiology of the Pogonophora, encouraged naturally by the new organization and combination of principal structures characteristic of the new phylum.

The history of the gnathostomulids follows the same sequence of events as that of the Pogonophora. According to reports, the first representative gnathostomulid was seen by Remane in 1928 in the Bay of Kiel; but the first publication was by his collaborator, Ax, and appeared nearly a generation later in 1956 (*5*), with the addition of a second species and genus. The late '50's and the early '60's (Fig. 1) saw the first wave

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The author is Kenan professor of zoology and research professor of marine sciences, University of North Carolina, Chapel Hill.

of species discovery, an increase of about one new species per year by German, Russian, and Austrian authors (*6*), from Indian waters, the White Sea and the Caribbean Sea. With the mid-'60's, relatively earlier than in the case of the Pogonophora, there began a more rapid increase in newly discovered gnathostomulid genera, with new types from the Mediterranean, North, and Red seas (*7*). Most recently, the increment rate of new genera and new species, including those from the North American coast, is steeper than it ever was in the Pogonophora. At present, 43 species of gnathostomulids in ten genera are known to me (*8*). Already the third step of investigation is under way, the studies in embryology, ecology, physiology, and ultrastructure.

The late discovery of this group in spite of its predictably greater abundance than the Pogonophora, and even some of the old and well-known phyla, is due to a combination of four reasons. Gnathostomulida are small and delicate, often less than half a millimeter long, and are recognizable only when alive. They are also haptic (strongly sticking to the substratum) and need sophisticated extracting methods (*9*). They are unusually resistant to bad water conditions; in the past, stinking samples of substratum were usually discarded before the group started to emigrate and hence they were not detected. Finally, they are found in greatest diversity in an unexpected environment and were searched for in the wrong places.

General Features

The gnathostomulids belong to the general grouping of "lower worms." Their closest relationships are to Turbellaria but they also show some affinities to Gastrotricha and Rotatoria, and maybe to Archiannelida. They are similar to these four in being worm-shaped, cylindrical or slightly depressed, semitransparent, and in the higher genera having the external divisions of head and collar as well as tail. They also are like lower worms in their movement, which includes gliding, slow swimming in loops and spirals, caudal adherence to the substratum, quick body contractions, coiling, and nodding laterally with the head. But they have in addition many unique characteristics.

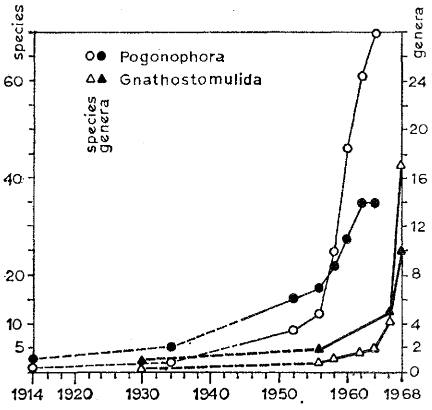

Fig. 1. Relation between time and increase of systematic knowledge in the last two new phyla, Pogonophora and Gnathostomulida.

The skin is a thin, one-layered epithelium that is completely "monociliated" (*10*); each of the polygonal epidermal cells bear only one cilium. Many parts of the skin are strongly adhesive without bearing distinct adhesive tubes. The basal membrane is thin, and there is no external skin cuticularization. Parenchyma often is poorly developed, and in such cases in large areas between gut and skin it is nearly lacking. Pseudocoelomic cavities do not exist. The nervous system is very simple. The peripheral system lies basiepithelially; a concentration of nervous tissue contains the anterior end. The sensory system (Fig. 2) shows stiff cilia, and in higher genera there is also a uniform anterior sensorium, which consists of a pair of stiff cilia on the anteriormost tip of the animal (apicalia). Four pairs of long, united (four to six) cilia (frontal, lateralia, dorsalia, and ventralia) surround the head, and a dense group of stiff, single cilia is located dorsally in a cushion of thicker skin and nervous tissue (*10*). I also observed statocysts in the foregut area.

Greater diversity (Fig. 3) exists in the foregut area. The mouth, which is located ventrally in the collar area, and in simpler groups far from the anterior end, is hardened by thin cuticularized basal plates, sometimes with a "jugum" in the upper lip, mostly with a "basal plate" in the lower lip area. The latter always bears lamellae, teeth, or a distinct tiny comb in its center. The large mouth cavity is surrounded by a complex muscle apparatus which becomes progressively more centralized and specialized from *Pterognathia* to *Gnathostomula* types. The same is true of a pair of lateral jaws in the mouth cavity, which vary from simple pincer and forceps types to complicated lamellar snap-jaws with three pairs of comblike rows bearing up to 60 teeth. The midgut is simple, consisting of large cells surrounding a gut cavity. There is no anus.

The reproductive system consists of a dorsal ovarium and in most cases two caudolateral groups of testes follicles in the same specimen. In higher genera in which the sperm cells are drastically reduced and immotile the male apparatus includes a simple tubular copulatory stylet, composed of muscles or a bunch of rods. They are slighty flexible, forming a tube and are always surrounded by accessory glands. The female apparatus in these genera includes a bursa for sperm storage, which has a lamellar wall on whose anterior extension a cuticularized opening, the "mouthpiece," is normally found. The complexity of the reproductive system is associated with the production of mucous "spermbearers" by accessory glands of the male system. Mucous layers come to surround sperm bunches during copulation, forming a prebursa in the fertilized female. I found that these "spermbearers" participate in prebursa building in the *Gnathostomula*—and possibly become spermatophores in the *Austrognathia* group (*10*). The latter also has a dorsal female genital pore in the same position as the point at which eggs are laid in *Gnathostomula*.

The North American Species

No gnathostomulids have been known previously from North American coasts. Four species were described from the Indo-Pacific (Red Sea, Indian Ocean, and the Sea of Japan) (*11*). I found *Gnathostomula* in 1956 in Puerto Rico. Kirsteuer described one from Venezuela and has descriptions of five species from Bimini in press (*12*). These had been the most recent findings to date, and they made worldwide distribution of the gnathostomulids obvious (*13*). I studied the fauna of the eastern coast of North America during 1967–68 and found 14 new species, in enormous quantities, including four new genera (*Semaeognathia, Labidognathia, Onychognathia,* and *Nanognathia*) (Fig. 2). Most were from collections along the North Carolina coast (Wrightsville, Morehead, Beaufort) but some were from Maine waters (Massachusetts Bay) (*14*).

New genus characters are mostly

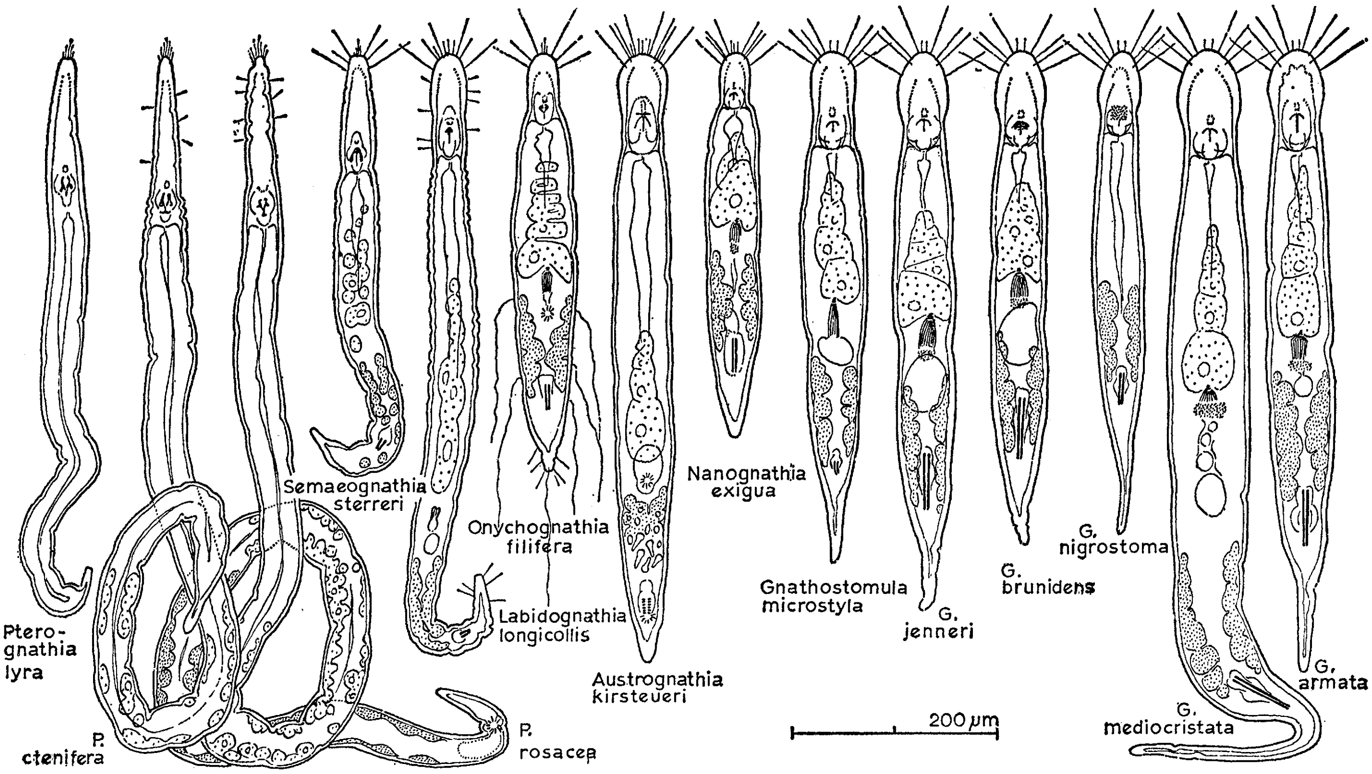

Fig. 2. New genera and species of Gnathostomulida from American shores. Parenchyma, pharynx, gut, and prebursa are in white; the bursa is striped; the ovarium is wide-dotted; the testis is tight-dotted; and the stylet is in black. Only sensory cilia are drawn. (*Pterognathia lyra* and *G. nigrostoma* are not fully developed.) Note the appearance of an anterior sensorium and the differentiation of a head stepwise from left to right.

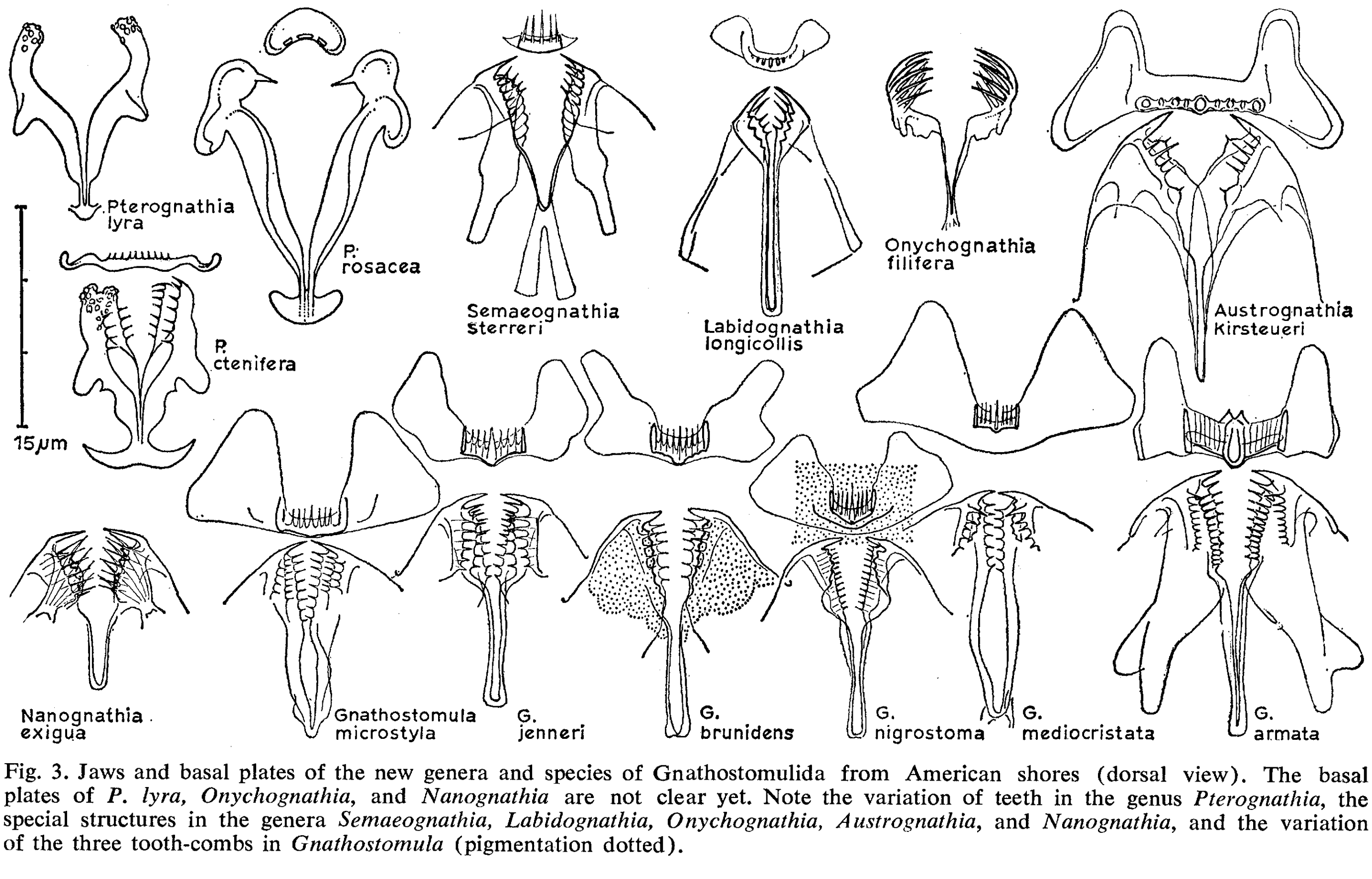

Fig. 3. Jaws and basal plates of the new genera and species of Gnathostomulida from American shores (dorsal view). The basal plates of *P. lyra, Onychognathia,* and *Nanognathia* are not clear yet. Note the variation of teeth in the genus *Pterognathia*, the special structures in the genera *Semaeognathia, Labidognathia, Onychognathia, Austrognathia,* and *Nanognathia*, and the variation of the three tooth-combs in *Gnathostomula* (pigmentation dotted).

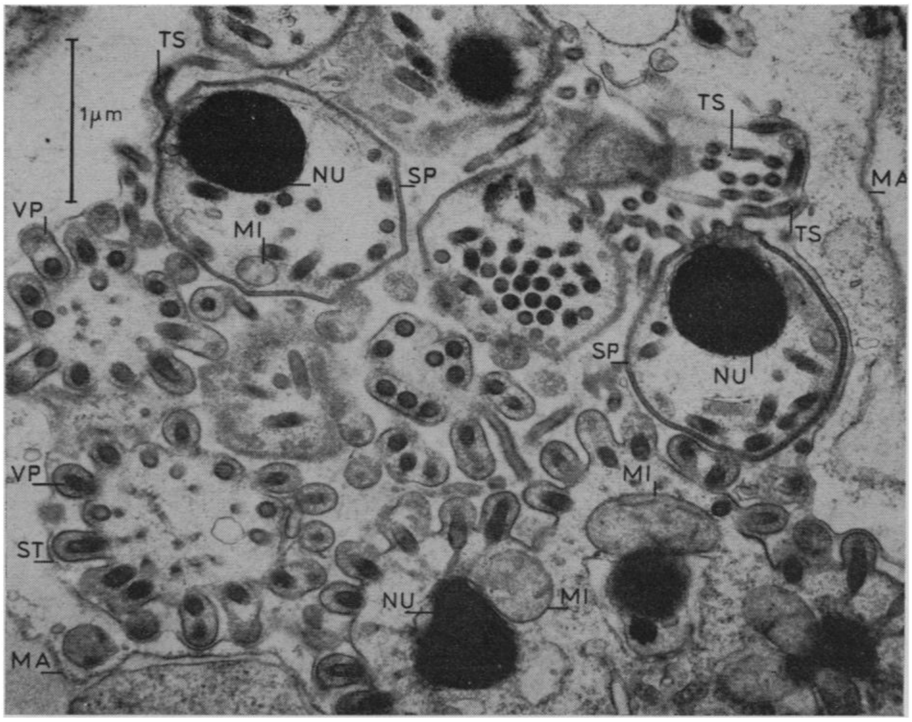

Fig. 4. Ultramicrograph of the testis region of *Gnathostomula jenneri.* Below spermatids; above sperm; (*MA*) matrix of testes follicle, (*MI*) mitochondrium, (*NU*) nucleus, (*SP*) spermium, (*ST*) spermatid, (*TS*) tail-like structure, and (*VP*) vesicular peduncle.

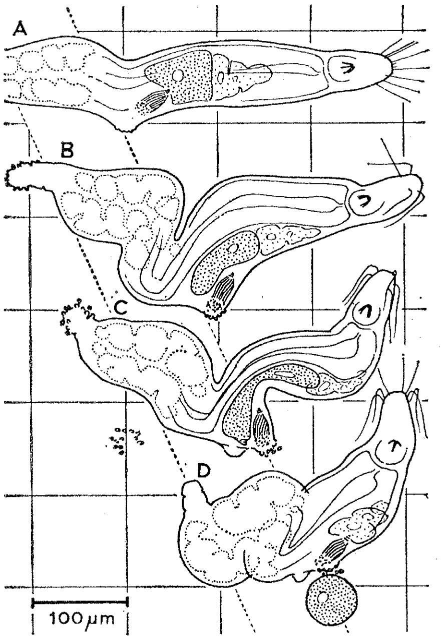

Fig. 5. Oviposition of *Gnathostomula jenneri.* (A) Start of adhering in nearly dorsal position, (B) contractions are beginning, (C) pressing action, (D) end of pressing action. Note position of bursa, sensory cilia, and gut. Time distance between positions is 15 minutes.

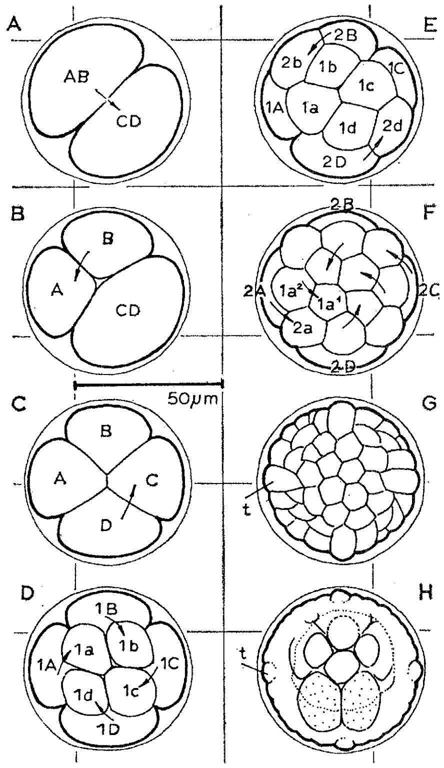

Fig. 6. Cleavage of *Gnathostomula jenneri.* (A to G) drawn from the animal, (H) from the vegetative side of the embryo. The "tip" cells of the micromere cross (*t*) appear in (G) and (H); in (H) the edge of epibolic gastrulation (broken line) and the two possible mesoblasts (dotted) are marked.

based on new pharynx types. The genus *Semaeognathia* is related to *Pterognathia.* The jaws however (Fig. 3) show long flaglike appendages from the tooth area and a central riffle-plain surrounded by two tooth-combs. In head and outline, semaeognathians are like pterognathians but they have rudiments of the anterior sensorium—three pairs of united flagella and a rudimentary dorsal sensory organ. It also has a small copulatory stylet. *Labidognathia* has similar development of sensorium and stylet but has head and collar differentiation and two-edged jaws with a horseshoe-like grouping of teeth on their peak. *Onychognathia* has jaws resembling bird claws, a bursa connected with a dorsal vagina, and some 70-μ long sensory flagella as further peculiarities. Only *Nanognathia* shows near relationship with the genus *Gnathostomula* but the three-edged jaws are particularly small, bearing in the margin long toothed combs in a fanlike arrangement (*15*).

New species characters were found within the genera *Pterognathia, Austrognathia,* and particularly the *Gnathostomula.* The relevant differences are extremely small; even bodily proportions and numbers and positions of teeth (Fig. 4) must be examined. Difficulties in determining differences arise from the fact that proportions vary with age, that jaws are only about 10 μ in size, that teeth combs are only 5 μ long, and that teeth are often less than 1 μ apart. Superior optics with phase or interference (anoptral) contrast are necessary in these studies. Electron-microscope resolution of ultrastructure is also required, as is the study of several stages of age. Some of the older descriptions of gnathostomulids, made without these techniques, may have to be altered.

Anatomical investigation of ultrastructure is indispensable in the study of Gnathostomulida. Four details obtained from electron micrographs of a series of cross sections of *Gnathostomula jenneri* are of particular interest. (i) The large mouth cavity is nearly completely filled with microvilli (*16*). These microvilli have the unusual length of 2 to 5 μ, are very closely and regularly arranged, and bear long series of presumably mucopolysaccharides in a uniform arrangement. The probable importance in digestion in the Gnathostomulida must await a future study. Shorter types of these villi surround the mouth opening and extend from there as a longitudinal and medioventral field almost to the anterior tip of the animal. Microvilli beds which may be analogous are found on the external surface of the tentacles of Pogonophora (*17*). Also the monocilia of the skin are, in a wide area, surrounded by shorter and less regularly shaped microvilli. (ii) Some of the cilia of the anterior sensorium are deeply sunken into the body; their bases are then surrounded by nervous tissue. (iii) The bursa is covered by several cell layers, each composed of three very flat cells, forming three bursa cristae at their edges. (iv) Finally the spermatocytes are covered with dozens of vesicles which later disappear; three to five tail-like structures (not longer than 1.5 μ) are then developed (Fig. 4).

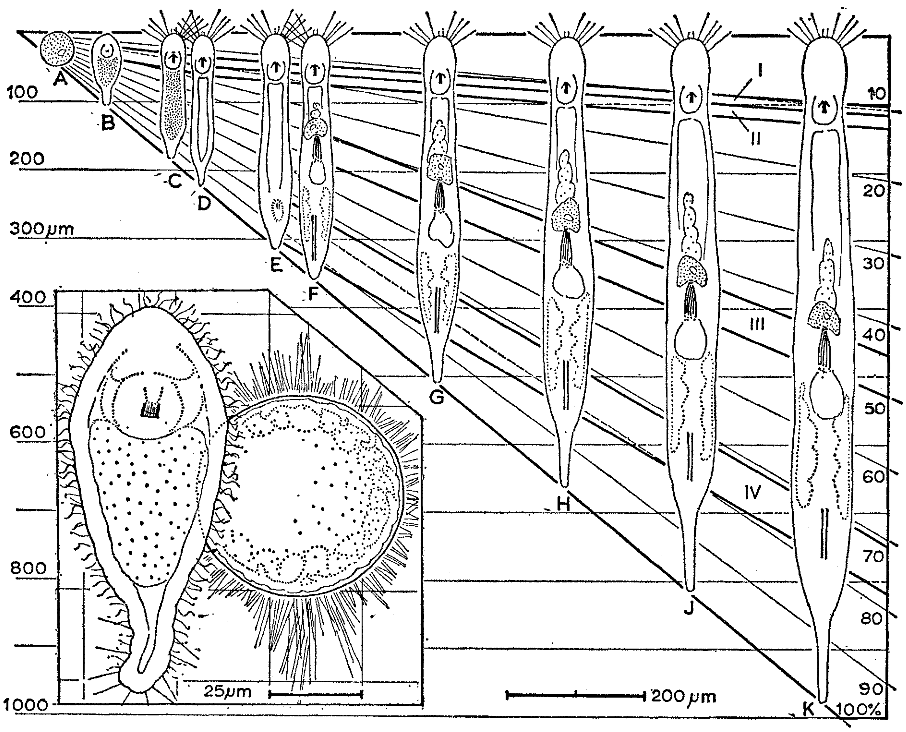

Fig. 7. Growth and proportions of *Gnathostomula jenneri*. Inset shows late embryo at right, and embryo after hatching at left. (A to K) Series of growth stages; formation of the pharynx (B), jaws (C), gut cavity (D), stylet (E), bursa and gonads (F), and largest specimen (K). Note proportions and displacement of jaws (*I*), pharynx (*II*), bursa (*III*), and stylet (*IV*).

Development

The culturing of hundreds of ripe specimens of the new species *Gnathostomula jenneri* (*18*) made possible a study of their embryonic development. In copulation the stylet of one worm injects dozens to hundreds of spherical sperm (each packet surrounded by a mucous ball 60 to 120 μ in diameter) into a region between the skin and gut of another worm posterior to the bursa. The mucous body then joins the proximal bursa margin as a "prebursa" and also extends a new mucous layer over the bursa wall as far as the bursa mouthpiece. At the same time the irregular, spindle-shaped sperm approach the bursa. During their period of accumulation in the soft caudal bursa region they become spherical again. In a few hours they take on a spindle form as they become tightly stored distally. The empty prebursa disintegrates and is resorbed. (Sometimes the prebursa is found in the gut cavity, and sometimes even when dorsal to the gut it contains food particles.) It is supposed that sperm migrate through the bursa mouthpiece and fertilize the most mature egg, which has become tightly pressed against the bursa peak.

Oviposition often takes over an hour. The specimen (Fig. 5) lies in a nearly inverted position, dorsal side down, tightly adhering at the caudal end and also just posterior to the bursa. Only the head is unattached. The egg, being very deformable, is pressed between gut and bursa caudally, penetrating the dorsal body wall right behind the bursa. Infrequently it breaks through into the gut cavity, where it bursts and is absorbed in a few days. During oviposition contractions run over the body, the head vibrates, the sensorium bends down, and the cilia produce a strong water current at the same time.

As soon as the egg appears, it becomes spherical (*19*). The diameter is about 55 μ. It sticks slightly to the substratum. The specimen moves away from the egg and regenerates in a few hours.

Cleavage begins a few hours after oviposition (temperature was maintained at 22°C). The first and second divisions are meridional (running from pole to pole), nearly equal, and holoblastic (cut completely through); the second division sometimes may be nonsynchronous with the C–D blastomere (cleavage cell) being delayed. Beginning with the third division, eggs exhibit a spiral plan with alternation between dexio- and leiotropic planes of cleavage. The first equatorial division is unequal, with dexiotropic or clockwise displacement of the first quartet of micromeres (Fig. 6). Further cleavages, after 20 hours, result in a mass of micromeres covering the animal hemisphere. On the 3rd day, "tip" cells of the micromere cross appear (similar to the annelid type of cleavage). On the 4th day, epibolic gastrulation is completed in accord with typical mesolecithal cleavage and without earlier formation of a blastocoel or blastopore. A pair of larger blastomeres, presumably $4d^1$ and $4d^2$, still remains visible for another day.

Postgastrula development is slow. Yolk resorption takes place, and a belt of long, unmovable fibers is formed on the outer surface of the egg capsule (Fig. 7).

The earliest free stage is 100 μ long,

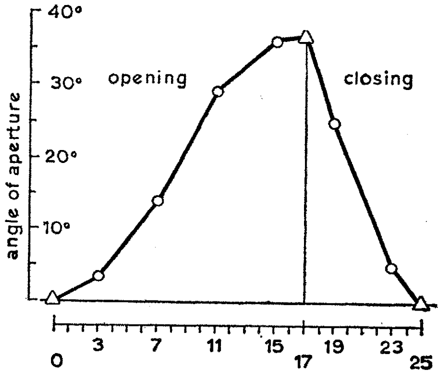

Fig. 8. Time course of snapping motion of the jaws of *Gnathostomula jenneri*, based on motion-picture analysis.

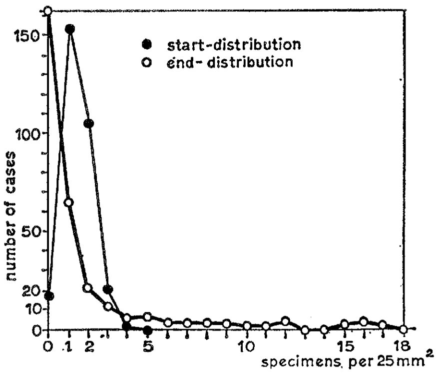

Fig. 9. Gregariousness of 400 specimens of *Gnathostomula jenneri*. In darkness and under equal temperature the random start-distribution turned into contagious end-distribution after 1 hour.

40 μ wide, and has about the volume of the egg. It is completely monociliated and bears a short tail with stiff sensory cilia. The anterior sensorium is missing as well as the jaws (Fig. 7). There is a rudiment of the pharynx. It separates a head and a trunk region and bears the comb part of the basal plate, but still has simpler teeth without the lateral wings of the plate of older specimens. The skin is relatively thick. The gut is well delimited, but no gut cavity is visible. Movement is by a slow swimming and gliding.

In the further postembryonic stages *Gnathostomula jenneri,* at least, continues to follow a direct type of development. When the juvenile is 200 μ long, the pharynx, head, and jaws are formed in nearly adult proportions (Fig. 7), and the anterior sensorium and gut cavity appear.

Life Stages

Observation of many specimens of *Gnathostomula jenneri* has shown an unexpected variety of sizes and body proportions; and there is evidence that the same is true in other species, at least for those of the "higher genera." These differences are related both to age and to sexual stage and, as mentioned, complicate the job of the systematist.

At hatching *G. jenneri* is 100 μ long. At a body length of 350 to 360 μ the rudiment of the copulatory stylet appears. At 360 μ the stylet is completed and the bursa appears. Many specimens reach 500 to 700 μ in length and some nearly 1 mm. During this time the head grows very slowly, the pharynx and jaws and bursa and stylet remain at their original size, and the trunk and tail are proportional to the increasing length (assuming that both bursa and stylet are present and that no large prebursa appears).

Species variability is particularly striking if the stylet is absent, or the prebursa is very large. Such animals, often with an expanded gut, have no tail at all. In addition, in animals without stylets, the bursa lies remarkably more posterior in position, and in prebursa specimens the stylet is often entirely displaced to the caudal end. In addition, the number of bursa cristae (shelf-like projections running the length of the bursa) varies at least from three to six, and pigmentation in the head may become remarkable. On the other hand, nearly no variation is observed in pharynges, jaws, and stylets.

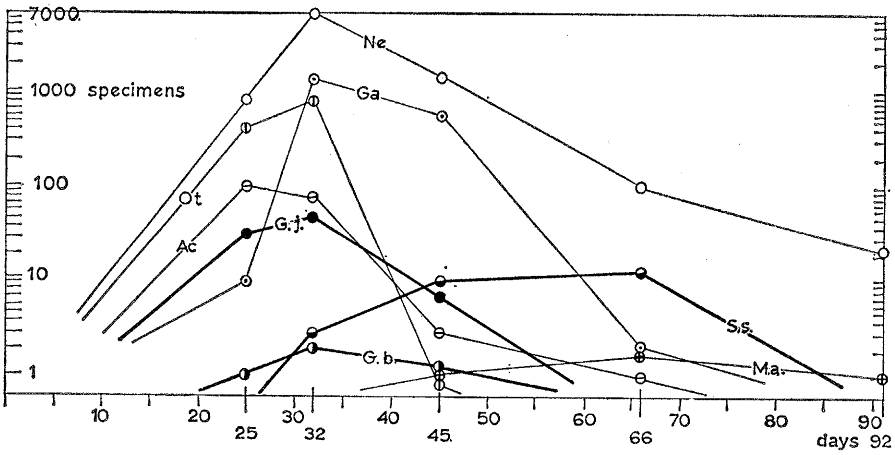

Fig. 10. Emigration of the sediment fauna during deterioration of the hydroclimatic parameters. Nematoda (*Ne*), Gastrotricha (*Ga*), and the turbellarian groups Acoela (*Ac*), Otoplanida (*Ot*), and Macrostomida (*Ma*) in relation to three gnathostomulids, *Gnathostomula jenneri* (*G.j.*), *Gnathostomula brunidens* (*G.b.*), and *Semaeognathia sterreri* (*S.s.*); in days and specimens per examination.

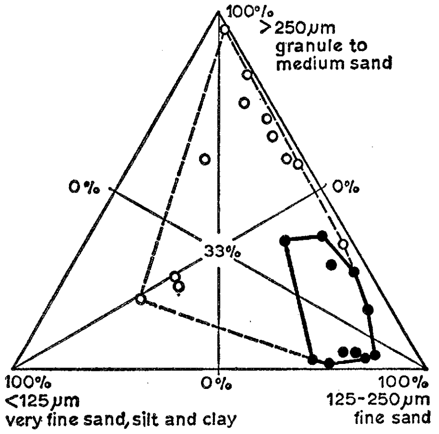

Fig. 11. Grain-size preference of American Gnathostomulida in coastal sediments. Coarse material in percentages toward the upper corner, fine sand to the right, and finest material to the left corner of the diagram. Negative samples, white circles; positive samples, black circles. Note preference for fine sand area.

Sexual stages observed in *Gnathostomula jenneri* include pure males, pure females, senile specimens, and many hermaphrodites. There is evidence that the bursa can disappear and be rebuilt again, and that the stylet can vanish.

Bursa rudiments always appear in association with a prebursa and presumably their formation is induced by the latter. With each further prebursa injection the bursa stores more sperm. The increase of bursa layers and bursa cristae seems also to result from prebursae additionally attached. The number of cristae therefore may be an indication of the number of copulations that occurred during one bursa stage. Bursae with about six cristae are often empty. They finally collapse and disappear, being later replaced by a new bursa rudiment at the next copulation.

The disappearance of the stylet, on the other hand, seems to be directly associated with one copulation at the end of the testis stage. Three facts make this interpretation likely: (i) the swelling of the stylet-rods during protraction, (ii) the presence of rod rudiments in an early prebursa, and (iii) stylet disappearance only in specimens with exhausted testes.

We might therefore adopt the theory that during the senile stage, which follows disappearance of the stylet and the multicristate bursa, these structures are regenerated. The senile stage with its swollen gut cavity represents, then, a feeding stage. A new stylet, new gonads, and a new bursa are regenerated after the next copulation. Finally the distribution of these stages over the size classes (from 380 to 930 μ in body length) makes it probable that this regenerative cycle happens more than once in a *Gnathostomula*'s lifetime.

Activity and Behavior

The vast amount of material available made it possible to take motion pictures and to make statistical studies upon activity and behavior (*20*).

Bacteria and fungal hyphae are to be observed in the gut cavity; furthermore tiny blue-green algae are found, but only in surface-living species. A cellulose test has shown that fungi are often preferred as food, especially Ascomycetes and Fungi Imperfecti. (But possibly they also sample free proteins which I would expect to be suspended in submicroscopical flakes on the vast "filtering surface" of the sediment layers.) The appearance in the gut of the microscopic food particles is restricted almost entirely to juveniles and to the intersexual life stage. Presumably feeding and sexual stages regularly alternate.

During food uptake, in *Gnathostomula,* the comb of the basal plate glides tightly against the substratum, and the jaws pass the scraped-off particles—sometimes hyphae longer than the specimen itself—into the midgut by rapid snapping movements. Motion-picture analysis has shown that the time taken to open the jaws (up to 36°) is 0.17 second, and to close them 0.08 second (Fig. 8). This snapping motion which includes a jaw retraction may also be followed by a quick pivoting of the jaw peaks about a ventrocaudal transverse axis of the pharynx.

Gregariousness was observed in nearly 400 grown specimens of *Gnathostomula jenneri,* which had been isolated in a petri dish of seawater. Under conditions of constant temperature and complete darkness, their random distribution after an hour became contagious (Fig. 9). Without recounting details I might mention that the distribution pattern ended with definite aggregations in which the distance between specimens just about corresponded to body length. In this respect the behavior of gnathostomulids lies between that of many gastrotrichs and that of turbellarians.

Climatic correlations can be predicted from observed behavior under various conditions. During deterioration of the hydroclimatical factors of stored sand–water samples different marine groups and species emigrate at different times to the sediment surface. Among the worms, the first to emigrate are the Otoplanida (Turbellaria), the most typical forms of the endopsammon (the environment between sand grains). Next come the emigration peaks of acoeles (Turbellaria), nematodes, gastrotrichs, and higher gnathostomulids meanwhile iron bacteria are growing rapidly. Very late (Fig. 10) appears the emigration peak of macrostomids (Turbellaria) and the simpler genera of gnathostomulids (*Semaeognathia*, for example). At that time even the nematodes are already drastically rdeuced, and gastrotrichs and the other turbellarian orders have started to disappear completely.

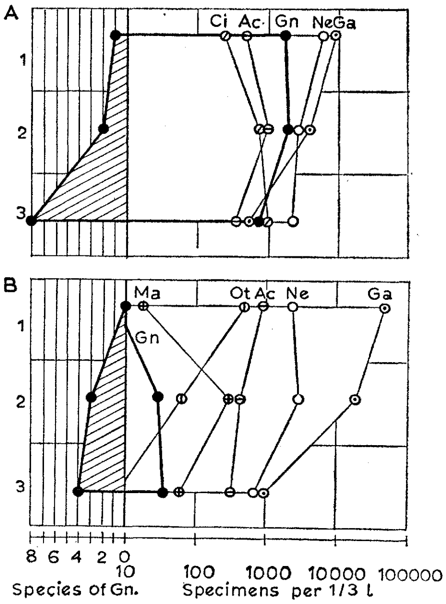

Fig. 12. Layering of the sediment fauna. (A) Pure fine sand; (B) fine and medium sand. 1, Surface layers; 2, deeper gray layer (oxygen disappeears); and 3, deep black layer (no oxygen). Left side indicates increase of gnathostomulid species and right side shows increase in specimen number of the most abundant groups; Acoela (*Ac*), Ciliata (*Ci*), Gastrotricha (*Ga*), Gnathostomulida (*Gn*), Macrostomida (*Ma*), Nematoda (*Ne*), and Otoplanida (*Ot*).

Microdistribution

The great abundance and diversity of the gnathostomulids is most clearly and strikingly shown during such emigrations. Ordinarily animal types which are late in being discovered show both a modest abundance and diversity (for example, Monoplacophora or Coelacanthida). The contradiction in the case of the gnathostomulids is due to their unusual environment (*21*).

Substrate preference and abundance of the gnathostomulids on the east coast of North America show the importance of fine sediments as environment, although I found some species on algae, eelgrass and marshgrass (*Zostera* and *Spartina*).

In the coastal sediments studied (Fig. 11), including all common compositions from sandy gravel to muddy sands, Gnathostomulida were found exclusively in fine sands. Apparently they require at least 50 percent and prefer 70 to 85 percent pure fine sand (grain size, 125 to 250 μ). Medium sand (250 to 500 μ) never reaches 40 percent in their habitats but finer fractions of very fine sand (< 125 μ), silt, and clay may compose up to 30 percent. The main biotope consists of 80 to 85 percent fine sand, about 12 percent very fine sand, and 3 percent medium silt to clay, containing about 0.1 percent organic matter (*22*). The mean grain size is about 150 μ. This is extremely small; the grain size usually considered minimum for the interstitial environment, at least for the common interstitial groups, is 200 μ (*23*). The minimum cross-sectional area of the free space between tightly packed spheres (simplified for sand grains) with a 150-μ diameter is about 900 μ^2. Since the cross section of many gnathostomulids is about 1900 μ^2, they must almost "flow" through the sediment pores. Gnathostomulids probably populate the minimum-sized interstitial environment occupied by Metazoa.

Fine sands with a modest amount of the finer fractions represent the most common sediment found from midtide level to some 30 feet (9.8 meters) in all the sounds which are distributed along the east coast of North America, from Maine to the Florida Keys. Gnathostomulids therefore must be enormously abundant throughout this region as well as on all other coasts of the world.

Although extracting methods are more successful now, we still should not trust the averages of quantitative investigations as presenting accurate estimates of gnathostomulid populations. From my quantitative investigations, I can be sure only that there were no fewer specimens per sample than those recorded. Even so, population density often exceeded 6000 specimens per liter of sediment; I have reliable evidence that in numbers this previously unknown group may, in their main environment, dominate all the other groups of the biotope, even the nematodes.

The main groups associated with gnathostomulids are nematodes, gastrotrichs, members of the Turbellaria (orders Acoela and Macrostomida), Ciliata (Holotricha and Hypotricha) and Foraminifera. Sometimes Rotatoria, Turbellaria-Kalyptorhynchia, Turbellaria-Otoplanida, and Tardigrada are also associated with gnathostomulids. The Crustacea and a great number of other typically endopsammal groups gradually disappear as interstitial spaces grow smaller.

Layering within the substratum shows another unexpected fact relating to diversity. With increasing depth in this muddy fine-sand sediment, with the change of redox potential from positive to negative, and with the color change of the sediment from brownish to gray to black, species diversity increases rapidly. In some beaches, the average diversity goes from one to two to eight species in going downward from the brown to the gray to the black layers (Fig. 12); and presumably the diversity is still higher in still deeper layers.

These deeper black, fine sediment layers with the smell of hydrogen sulfide produced by the great numbers of iron bacteria, and with presumably no oxygen at all are a very uncommon environment for interstitial organisms, but (as far as we know today) it is the main biotope of the Gnathostomulida.

Summary

The past few years have brought an unexpected increase in our knowledge of the most recently discovered Metazoan phylum, the Gnathostomulida. The facts now available allow us to predict worldwide distribution of a relatively large group with both ecological and evolutionary importance.

Recorded geographic distribution of species ranges from the tropics to the polar region (10° to 70°N) and in all oceans of the Northern Hemisphere. There is no doubt, therefore, that they are worldwide in their distribution, and that there is no coast where they are completely absent. The recent rate of species-increase has led me to predict a group of medium size, with up to 100 species per geographic region and several hundred species all together. I now distrust the assumption of wide geographic distribution of single species as was thought earlier. The estimation of numerous species is also based on the wide distribution of the environment in which they are found, and on its relative freedom so far from close examination.

Ecologically, gnathostomulids must play a very important role in their main environments where they are the dominant organisms and the most diverse. This is implied by the peculiarities of their food sources and of their biotope parameters, by their development and life stages, and by their mechanisms for digestion and energy storage under partially anaerobic conditions.

The phylogenetic relationships of the Gnathostomulida, although still doubtful in detail, seem closest to the "nonarticulated worms." Relationships will be clarified by a better knowledge of structures (especially ultrastructures) and processes, not only of the gnathostomulids but also of related groups. There is no doubt that the new characters of this phylum and some further new types of "lower worms" which have already begun to appear (*24*) will revise our understanding of the lower Bilateria (*25*).

References and Notes

1. Following the most accepted system of the animal kingdom used in English literature, as reported in E. Mayr, E. Linsley, R. Usinger, *Methods and Principles of Systematic Zoology* (McGraw-Hill, New York, 1953), pp. ix and 328, Gnathostomulida are to be considered as a new phylum; in other systems, dividing the "lower worms" into two phyla Platyhelminthes and Aschelminthes, as is often done in German literature, gnathostomulids appear as a new animal class.
2. The percentage of known taxa is estimated on the basis of the fauna of the Mediterranean. See R. Riedl, *Fauna und Flora der Adria* (Parey, Hamburg, 1963), pp. 640.
3. E. Mayr, *Science* **159**, 595 (1968).
4. A. Ivanov, *Pogonophora* (Consultants Bureau, New York, 1963), pp. xvi and 479.
5. P. Ax, *Akad d. Wiss. u. d. Lit. Mainz, Abhandl. d. math.-naturw. Kl. Jahrg. 1956* **8**, 1 (1956).
6. S. Gerlach, *Kieler Meeresforsch.* **14**, 175 (1958); Y. Mamkaev, *Dokl. Akad. Nauk SSSR* **141**, 1501 (1961); E. Kirsteuer, *Zool. Anz.* **172**, 436 (1964). Mamkaev's *Gnathostomula murmanica* was later considered to be identical with *G. paradoxa*—after my last experiences, I had better keep it as a separate species until we have more information on both organisms.
7. W. Sterrer, *Z. Morphol. Oekol. Tiere* **55**, 783 (1965); *Ark. Zool.* **18**, 405 (1966); *Veroeff. Inst. Meeresforsch. Bremerhaven* **2**, 201 (1966).
8. This is also based on reports of new discoveries by S. E. Kirsteuer and W. Sterrer, in press, as well as on my own observations presented in this article.
9. W. Sterrer, *Ark. Zool.*, in press.
10. The term "monociliated" is created by W. Sterrer; also the "sensorium," regularly composed of ten flagella groups, which he predicts is present in all "higher genera"; the "conuli" of the older literature are perhaps spermatophores, as also supposed (see *7*).
11. R. Riedl, *Zool. Jahrb. Syst.* **93**, 139 (1966); S. Gerlach and Y. Mamkaev (*6*).
12. Mentioned by R. Riedl (*11*), and E. Kirsteuer (*6*); E. Kirsteuer, *Proc. Annu. Conv. Assoc. Venez. Avan. Ciencia* **14**, 81 (1964); *Proc. Int. Symp. Coastal Lagoons*, Mexico City, 1967, in press; *Amer. Mus. Novit.*, in press.
13. To my knowledge, two persons have already found Gnathostomulida on the east coast of North America. G. Uhlig (Hamburg) mentioned briefly a *Gnathostomula* species, not identified from Woods Hole [G. Uhlig, *Amer. Zool.* **6**, 3 (1966)]; L. Bush (Madison) also saw specimens of this group, again perhaps from Woods Hole, but I do not have further information.
14. I thank the NSF for a 6-month visiting professorship; and the Department of Zoology, University of North Carolina, and the marine stations in Beaufort, Morehead, and Wilmington for space and facilities.
15. R. Riedl and W. Sterrer, *Breviora*, in press.
16. Corresponding observations are now being made on the European species, *Gnathostomula paradoxa* and *G. mediterranea* (I. Graebner, *Mikrosk. Zentralbl. Mikrosk. Forsch. Method.*, in press; *Verh. Deut. Zool. Ges., Zool. Anz. Suppl.*, in press; *Ark. Zool.*, in press). More details of *Gnathostomula jenneri* will also be given in these papers.
17. A. Nørrevang, *Sarsia* **21**, 37 (1965); B. Gupta, C. Little, A. Philip, *J. Mar. Biol. Ass. U.K.* **46**, 351 (1966).
18. I dedicate this species to C. E. Jenner whose help was as invaluable as his knowledge of the Carolinian fauna and their coastal environments.
19. First observation of oviposition was made by E. Kirsteuer on *Gnathostomula axi* (*6*).
20. I thank H. E. Lehman (Department of Zoology, University of North Carolina) for his help in taking motion pictures and J. Kohlmeyer (Institute of Marine Sciences, Morehead) for testing intestinal fungi of gnathostomulids.
21. For laboratory facilities, for literature, or for both I am grateful to A. Stiven (Department of Zoology, University of North Carolina), to R. Doyle (Department of Zoology, Duke University), and to R. Ingram (Department of Geology, University of North Carolina).
22. Geological terminology after R. Folk, *Petrology of Sedimentary Rocks* (Hemphill, Austin Texas, 1961), p. 154; determination of organic matter after micro-Kjeldahl, in W. Horwitz, *Methods of Analysis A.O.A.C.* (Assoc. Off. Agric. Chemists, Washington, D.C., 1965), pp. xx and 957; see furthermore A. Scheidegger, *The Physics of Flow through Porous Media* (Macmillan, New York, 1960), pp. xvi and 313; T. V. Brand, *Anaerobiosis in Invertebrates* (Biodynamica, Normandy, Mo., 1946), p. 328.
23. For "critical grain size" and its relation to drainage and animal distribution, see J. Webb, *Phil. Trans. Roy. Soc. London Ser. Biol. Sci.* **241**, 355 (1958); W. Wieser, *Limnol. Oceanogr.* **4**, 181 (1959); P. Boaden, *Cah. Biol. Mar.* **3**, 245 (1962); B. Jansson, *Oikes* **18**, 311 (1967).
24. Announced by A. Remane, in *The Lower Metazoa*, E. Dougherty, Ed. (Univ. of California Press, Berkeley, 1963), p. 247, and by R. Riedl (*11*); I also thank R. Higgins (Wake Forest University) for communication of recent observations.
25. I thank E. McMahan for revising my English text.