CHARACTERISTICS OF INTERSTITIAL SAND TURBELLARIA: THE SIGNIFICANCE OF BODY ELONGATION, MUSCULAR DEVELOPMENT, AND ADHESIVE ORGANS

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CHARACTERISTICS OF INTERSTITIAL SAND TURBELLARIA: THE SIGNIFICANCE OF BODY ELONGATION, MUSCULAR DEVELOPMENT, AND ADHESIVE ORGANS[1]

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ABSTRACT: The adaptations of sand dwelling Turbellaria may be correlated with the occurrence of the animals in particular parts of the interstitial sand habitat. Highly-elongated forms are characteristic of the intertidal subsurface sand and it is postulated that the elongation is an adaptation to the rise and fall of water in the interstitial spaces and to the presence of air bubbles during low tide. An elongated body would provide traction with the sand grains against the water currents and would also prevent the animals becoming entangled in the surface film of small air bubbles. In contrast to these subsurface sand animals, the otoplanids found in the swash zone are less elongated and are characterized by extreme development of the adhesive glands and by highly developed muscles which give the animal great rapidity of movement. Species found in the smaller-grained subtidal sands are smaller and less specialized. Finally, species found in a unique sand-flat environment near Dennis on Cape Cod are the least specialized of any studied. They live only in the upper few centimeters of the sand and it is suggested they may represent the beginnings of an evolution toward interstitial adaptations.

Ever since attention was first called to the interstitial habitat conspicuous anatomical features have been noted for its fauna. Remane (1933) described the sand microfauna as being distinguished by smallness of size, dependence largely on ciliary movement, and the presence of a large number of "adhering animals." G. B. Wilson (1935) described the copepods of the interstitial habitat as being restricted in size to 0.5–1.0 mm, elongated, flexible, with increased tactile equipment, with reduced or modified swimming legs, with flattened and closely appressed ovisacs. Meixner (1928, 1929) described species of Turbellaria (*Eukalyptorhynchia*) sent to him by Remane and listed their special features as follows: adhesive apparatus in addition to the caudal glands commonly present in members of this taxon, tail appendages, lack of eyes in some, lack of pigment, and in many cases unpaired gonads. More recently Ax (1963, 1966) has discussed these same characteristics, not only in interstitial turbellarians but also in members of other phyla as well. He adds the following as being also characteristic of many sand animals: a ventral creeping sole, cuticular mouth parts, lack of free swimming larvae, and chordoid skeletal tissue. Both Meixner and Ax confirm Wilson's emphasis on the elongated body form. Swedmark's (1964) review of the interstitial fauna of marine sands includes a similar list.

Studies of the exact location of the interstitial animals in particular beaches show that they are not evenly distributed in the sand (Schultz, 1937; Brunet, 1965; Bush, 1966; Feuchel & Jansson, 1966; Jansson, 1966) and a number of factors have been studied that might account for this. Wiesser (1959) stressed the effect of grain size and Feuchel & Jansson reported on temperature, salinity, oxygen, and the like in various parts of the beach. Remane (1933) described different types of sand habitats and other authors have added to the list. It is

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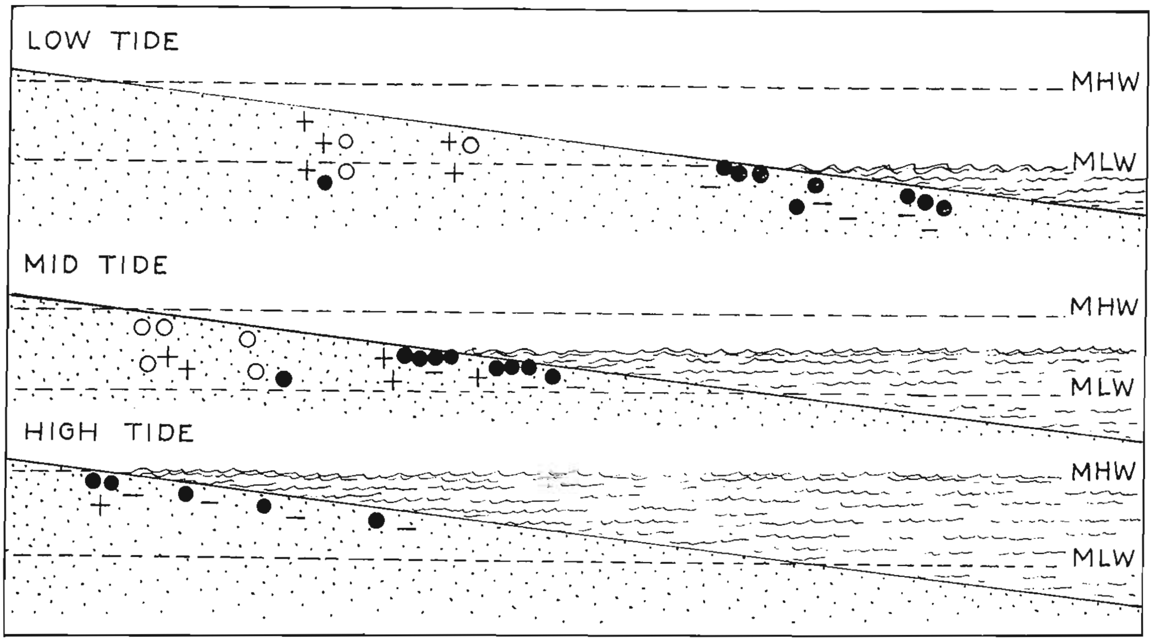
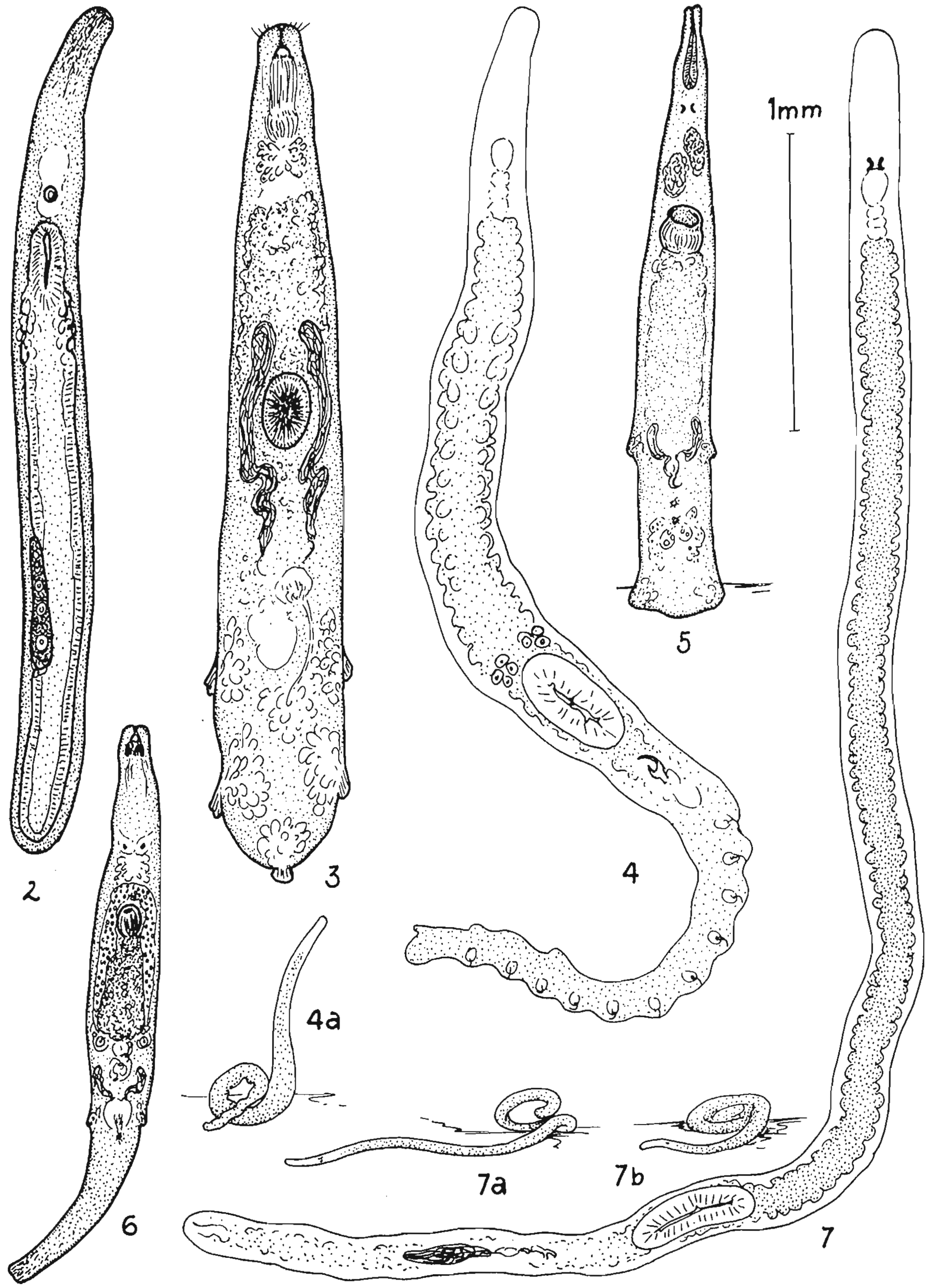


FIG. 1. Distribution of Turbellaria at high, medium, and low tide on the small beach in front of the Marine Biological Laboratory, Woods Hole, Massachusetts. + *Nematoplana* sp. present; – *Nematoplana* sp. absent; ● *Parotoplana*? sp. present; ○ *Parotoplana* sp. absent. Data combined from 28 samples taken 1, 5, 13, 30 July and 8, 9 Aug. 1966 and on 3, 9 Jan. 1967.

evident as a result of all these studies that the sand habitat, far from being uniform, is varied and complex and no one factor or set of factors will explain the distribution of all the animals in it. Rather we need to make careful analyses of the situation for each species. After this is done in a sufficient number of cases then we may be able to combine the results into a discernible pattern for the whole. This discussion is therefore limited to an attempt to explain the distribution of certain species of Turbellaria which have been collected on beaches of the Cape Cod region and intensively studied for the last four years.

Although, as noted, morphological adaptations to the interstitial habitat have been listed many times, the exact way in which certain of these are related to conditions in the habitat seems not to have been considered. An extreme elongation of the body is found in the most common turbellarians of the subsurface intertidal sand and an extreme muscular development and highly specialized adhesive organs occur in the turbellarian family Otoplanidae which inhabits the swash zone on the beach. A lesser development of these three features is found in related species which live in the subtidal sand, and finally, species that show none of these specializations occur in the interstitial habitat only near the surface in a few highly protected areas. The purpose of this paper is to point out that these three features play an important role in the adaptations of the animals to particular features of the habitat, that this adaptation is primarily to the amount and kind of movement in the substratum and that this relationship in turn determines the distribution of the animals.

Somewhat elongated bodies characterize all the turbellarians belonging to the suborder Proseriata but extreme elongation occurs in *Nematoplana* (Fig. 7). In the Cape Cod region *Nematoplana* sp. is collected only in the subsurface sand of the intertidal zone. Special studies made on the small beach in front of the Marine Biological Laboratory at Woods Hole illustrate this distribution (Fig. 1). A similar species of *Nematoplana* is collected in the same part of beaches in New

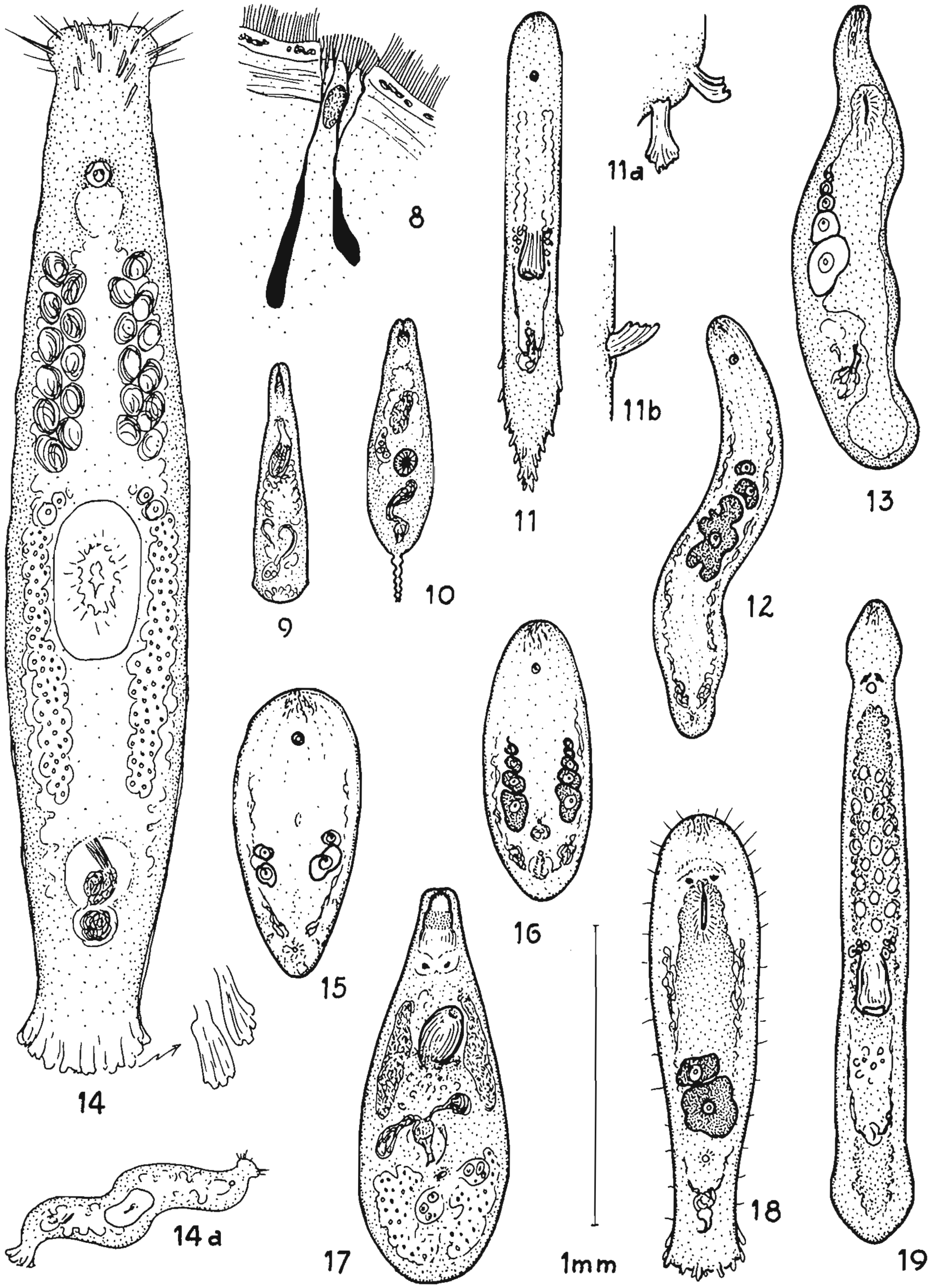


FIGS. 2–7. Turbellaria of the subsurface interstitial sand habitat. **2.** Macrostomidae sp. ? **3.** Kalyptorhynchidae sp. ? **4.** *Polystylophora* sp. **5.** *Proschizorhynchus* sp. **6.** *Cicerina* sp. **7.** *Nematoplana* sp.

Jersey and Florida and other somewhat elongated species of *Proseriata* (Fig. 4) are found in the same locations. Members of the orders Eukalyptorhynchia (Figs. 3, 5, 6) and Macrostomida (Fig. 2) collected in this part of the beach are also elongated more than related species from other habitats (Figs. 17, 18, 19). The conclusion may be made that an elongation of the body is associated with life in this particular part of the interstitial sand habitat.

A comparison of the elongated species with related forms from other habitats also shows that the elongation is not just the result of narrowing or stretching out the body while maintaining a certain volume or total size. This might be expected if the elongation were simply an adaptation enabling the animal to squeeze more readily between the sand grains. On the contrary, the bodies of these animals are just as wide as those of the unmodified species; the elongation has resulted actually in a larger animal and in a greater total volume for the body than is found in the species not so modified. Since the elongation has thus overridden another general tendency among interstitial animals, namely to decrease in size, it appears that this is a most important adaptation and leads to the conclusion that either the increased length or something associated with it is a specific adjustment to some special feature of the environment. The problem, then, is to account for the selective advantage in this particular habitat of an extremely long body.

One possible advantage of the elongation might be that, if food is only available intermittently, the increase in length of the gut that accompanies the elongation would provide for larger in-take and storage of nourishment. However, since the entire body is enlarged and the proportionate size of the gut appears to be about the same, this does not account for the condition. A consideration of the situation in the interstitial spaces, however, suggests an answer. As the tide rises, water flows into the spaces, forcing out air that often can be seen coming to the surface in bubbles; as the tide ebbs, the water recedes and air at least partially fills the spaces again. Emery (1945) discusses the entrapment of air in the interstitial spaces but he does not consider the effects on small animals of either the water currents or of the surface tension in the air-water interface of the bubbles. Both the water currents and the surface tension of the bubbles would be sizable forces for such small, soft-bodied animals as turbellarians. I suggest that the elongated bodies allow these animals to brace themselves against the flow of water by twisting about between several sand grains. Also, the greater length of body would prevent their becoming entangled in the surface films, since there would always be enough of the body away from the film of any one bubble to enable the animal to pull itself free. Thus the long body plus the moderate development of adhesive gland cells found in these species should enable them to move about in the interstitial spaces throughout most of the tidal cycle. Observations of their feeding habits (Bush, 1966, and unpublished data) show that they do indeed move considerable distances through the sand in order to feed on dead animals cast up on the beach. That the length of the body might be a disadvantage at time of storms when the sand of the beach is moved about is obvious, but this contingency may be met by the habit of coiling into a tight ball when forced into unnatural surroundings. *Nematoplana* does this when left in a finger bowl in the laboratory without sand in which to hide (Fig. 7a,b). At first they make a desperate effort to penetrate the substratum, then, after a time, they coil themselves up and appear to go into a state of quiescence which can only be broken by a considerable stimulus. In such a state they would be carried about by movements of the substratum but would certainly be less liable to injury by moving sand than if they remained stretched at length. Although other experiments have not yet been carried out to study the reactions of these animals, it may be hypothesized that their elongated bodies enable them to withstand



FIGS. 8–19. Interstitial sand Turbellaria. **8**. Adhesive gland and button of an otoplanid. **9**. *Cheliplanilla* sp. **10**. *Kalyptorhynchia* sp. ? **11**. *Monocoelus* sp. **12**. Acoela sp. ? **13**. Macrostomidae sp. ? **14**. *Parotoplana* sp. **15**. *Mecynostomum* sp. **16**. *Convoluta* sp. **17**. *Phonorhynchus* sp. **18**. *Macrostomum beaufortensis*? **19**. *Monocoeles* sp.

the forces of surface tension and water movement in this environment, and the coiling reaction protects against injury at times of great stress. Those species with elongated bodies are therefore the species found in the subsurface intertidal zone and for the Turbellaria this part of the sand is a distinctly different habitat from other sandy areas.

The swash zone on the beach is characterized by the presence of members of the turbellarian family Otoplanidae, a group showing very conspicuous adhesive organs and well-developed longitudinal muscles. Although species of Otoplanidae may be found in other parts of the sand, they are almost universally present in the strip where the waves are breaking and the sand is being actively moved about. Often they are the only animals present in this zone, a circumstance that suggests that they are peculiarly adapted to the rigorous conditions that prevail in a shifting substratum. These animals have large, flattened, and only slightly elongated bodies equipped with an array of adhesive organs and a thicker layer of longitudinal muscles than are present in any related group. The adhesive organs not only consist of gland cells as in other Turbellaria, but also have various sorts of protrusions associated with them (Figs. 8, 14) in such a way that the chances of effective attachment are greatly increased over that prevailing when the glands open only onto a flat surface. The arrangement of the organs is also significant; adhesive papillae are thick-set all over the posterior end of the animal (Fig. 14) and all along the lateral and dorsal sides adhesive buttons cover most of the surface (Fig. 8). Since the presence of adhesive organs precludes the presence of cilia in the same area, the cilia of these animals are confined largely to the ventral surface where they are well developed and form a creeping sole. Such an arrangement of adhesive structures insures that the animal can adhere to any convenient surface either above, below, or lateral to it, and the creeping sole and great development of muscle fibers gives this group a highly characteristic method of locomotion. When observed in a culture dish, they move more rapidly than any other turbellarian I have ever seen and may either glide about over the bottom or propel themselves erratically through the water by means of jerky contractions which flip the body back and forth into c-shapes or rippling curves. This rapid and varied movement, combined with the abundance of adhesive organs set on all sides of the body, is clearly adapted to a "catch as catch can" existence in a shifting substratum. Indeed it can be shown that at least a proportion of the individuals move or are moved up and down the beach with the moving line of surf and thus indicate a definite preference for this zone (Fig. 1). In this habitat, where the movement of the sand and water is a limiting factor for most other animals, the Otoplanidae thrive and have indeed given their name to the layer which is often known as the otoplanid zone. Here again, as in the subsurface sand, the water currents determine the types of Turbellaria inhabiting the area. The swash zone must be considered a distinct and different habitat from the rest of the beach.

In marked contrast to the above are two other insterstitial habitats that have been studied on Cape Cod, namely, the subtidal sands and one sandy flat area in a marsh near the Aquaculture Corporation at Dennis. The subtidal sands are composed of smaller grains than the beach sands and these become progressively finer and more mixed with mud as one works away from the shore. The Turbellaria in this habitat are smaller than those found in the beach (Figs. 9–11), an observation that correlates with the findings of Wieser (1959), who concluded that grain size was a limiting factor for interstitial animals. Jansson (1966) also observed that interstitial animals seemed to respond to certain grain sizes. Many more different species and families of Turbellaria are represented in the subtidal sands and, in general, they are much less specialized in body length, gland cell arrangement, or muscle development than the animals already discussed. Some are slightly elongated (Figs. 11, 12), however, and possess more adhesive glands than Turbellaria in general. Less forceful water currents and generally more uniform conditions in the subtidal area would not require the extreme adaptations necessary in the other two zones.

Even less specialized are the Turbellaria of the sand flat at Dennis (Figs. 15–19). This is an unusual situation in that the even flow of water from the salt marsh carries away the fine materials from an area along the stream without much disturbing the sand at the same time. The in-coming tide covers the sand slowly as the water backs up the shallow channel and the whole neighborhood is protected from all but the heaviest storms by a line of dunes. Since the sand lies at about midtide level, it is exposed to the air for only a short time or not at all as the water flows out of the marsh slowly and always at least fills the capillary spaces between the sand grains. In short, here is an interstitial habitat with very little disturbance of the substratum, an even flow of water, and little or no penetration of air into the spaces. As a result, in the summer a rich fauna and flora builds up on the surface and in the upper one-half inch of the sand. Below this layer the sand is black, odorous with H_2S, as is usual under anaerobic conditions, and contains almost no plant or animal life. Certain Turbellaria, particularly some species of acoels and macrostomids, which feed on the plentiful diatoms, occur in the surface layer in great numbers. None of these species are modified as to body length or adhesive gland cells, yet study of them in the laboratory shows that many of them do creep about between the sand grains. At the slightest disturbance of the dish in which they are kept, they tend to go down into the substratum whenever possible. It seems that such a tendency might in time evolve into the assumption of a true interstitial existence. Can it be that in such a protected area we see the first beginnings of the evolution toward an interstitial life? Regardless of whether the animals are evolving in this direction and should be considered with the interstitial fauna or not, this group does afford a significant contrast with the other three groups discussed here. Studying all four habitats we can see that the degree of lengthening of the body, development of adhesive organs, and complexity of muscle layers varies from the least modified form on the sand flat, through the small and slightly changed group in the intertidal zone, to the two highly specialized types, the one lengthened enormously to meet the conditions in the subtidal sand, the other with adhesive organs and muscles highly developed to meet the rigorous conditions of the swash zone.

Whether the animals are, in addition, distributed within the four habitats in correspondence with such factors as light, temperature, oxygen pressure, and pH has not been ascertained. Undoubtedly, these might be limiting factors for an entire habitat under certain extreme conditions. Collections made throughout the year on the sand flat at Dennis show that with the first heavy frost certain of the Turbellaria disappear from the area and all winter long are to be found only in the deeper parts of the nearby stream in the trash which collects there. In the subsurface beach sand, on the other hand, animals have been collected at about their usual depth in the sand in the middle of winter when a layer of ice was present on the surface. Possibly anaerobic conditions and certainly low temperatures prevailed in both cases (see Gordon, 1960, for a discussion of anaerobic conditions in beaches). The Turbellaria are evidently able to live under conditions with considerable variation in both temperature and oxygen level. Until more adequate instrumentation is available, especially for the measurement of oxygen tensions throughout the tidal cycle, it will not be possible to determine exactly the relationship of these factors with the position of the animals in any particular habitat.

In spite of the fact that the relation of some physical factors to the animal's position in the habitat is not understood, the correlation between the general adaptations discussed here and the subdivisions of the sandy areas is clear. The facts observed so far lead to the conclusion that the confinement of certain Turbellaria to certain zones or parts of the interstitial habitat is due to their morphological adaptations for meeting the problems of sand, water, and air movement through the spaces. This type of animal must be able to solve the problem of maintaining position and moving about in spite of air bubbles and water movement if it is to survive in these environments. For the Turbellaria of the Cape Cod region there are therefore at least four distinct subdivisions of the interstitial sand habitat.

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