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Modified Cilia in Sensory Organs of Juvenile Stages of a Parasitic Nematode

Abstract. *Electron microscopical studies revealed the presence of dendritic nerve processes in sensory organs of the third- and fourth-stage juveniles of* Haemonchus contortus, *which contained structures resembling modified cilia. With few exceptions, the outer circle of fibers consisted of ten doublets, and in place of typical cilia-like central fibers were small microtubules or vesicles varying in number from zero to five.*

Nematodes, especially the free-living forms, have sensory organs in the form of bristles and papillae, which are thought to be tactile. In parasitic nematodes these structures are either absent (although the terminal branches of papillary nerves are retained) or are present as small protuberances or pits connected to terminal branches of the papillary nerves. The amphids, well developed in free-living nematodes but greatly reduced in parasitic forms, are thought to act as chemoreceptors. In parasitic forms the amphids may also have a secretory function (*1*).

Very few details are available concerning the ultrastructure of these sensory organs. Hope (*2*) described sensory organs in *Thoracostoma californicus*, which contained structures that could be modified cilia, but he had no evidence for the presence of central fibers or basal bodies. Roggen *et al.* (*3*) described sensory organs in *Xiphenema index* as consisting, in part, of a dendritic nerve process having the structure of a cilium. The number of fibers in the cilia, however, varied (for example, 9 + 2, 9 + 4, 8 + 2, 8 + 4).

Third- and fourth-stage juveniles of *Haemonchus contortus*, after a 10- to 15-minute treatment at room temperature in $10^{-3}N$ iodine to straighten them, were fixed in Zetterqvist's fixative (*4*) for 3 hours at room temperature. It was necessary to cut each of the juveniles as short as possible to facilitate the entry of the fixative. After being washed and dehydrated each juvenile was embedded flat in Epon 812 (*5*). Each larva was then removed in a piece of Epon about 1.5 mm^3 and attached to a larger block for cutting. Sections were cut with glass knives on an LKB Ultratome, mounted on grids, and stained with Reynolds lead citrate (*6*). The sections were examined

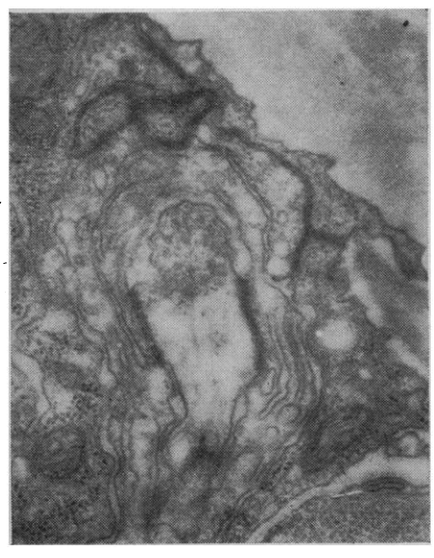

Fig. 1. Slightly oblique section of cervical papilla of third-stage juvenile showing cilia-like structure and fibers extending towards nerve axon at bottom of picture (× 31,680).

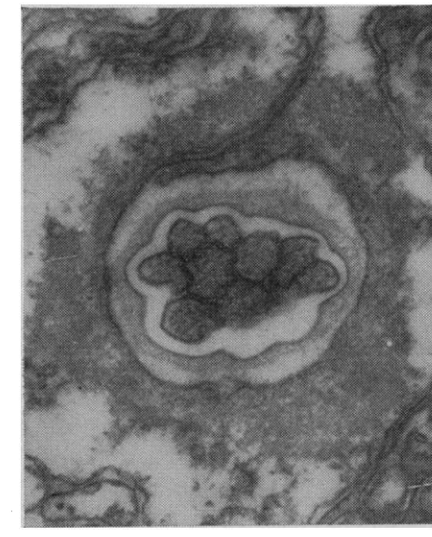

Fig. 2. Closely packed dendritic processes in the amphid near the aperture in third-stage juvenile (× 39,900).

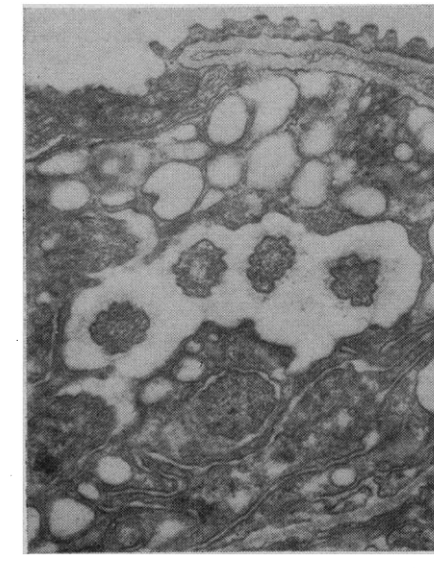

Fig. 3. Dendritic processes near the bottom of the amphid pouch showing cilia surrounded by highly vacuolated spaces. Doublet pattern clearly defined. Third-stage juvenile (× 26,040).

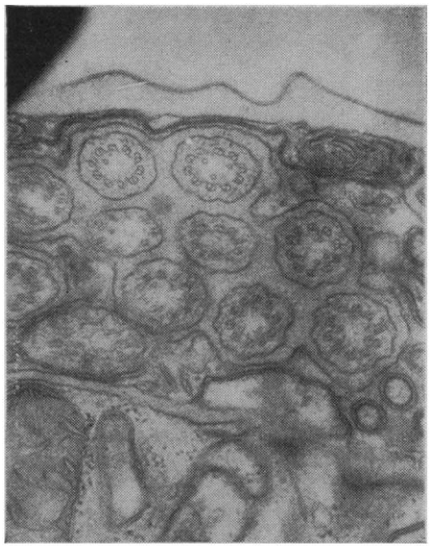

Fig. 4. Same location as in Fig. 3 but in fourth-stage juvenile. Note absence of vacuolated spaces and the closer packing of cilia-like structures (× 38,800).

with a Siemens Elmiskop I electron microscope at 60 kv.

The results showed that the labial, cephalic, and cervical papillae and the amphids all contain dendritic structures, part of which resemble a cilium. However, the number of fibers is not consistent with that of true cilia, and it is probable that the dendritic processes have been greatly modified. Each labial papilla consists of a single dendritic structure having ten outer doublets with zero to four microtubules or vesicles in the center. Further evidence is needed to determine the exact structure of these central fibers. The four cephalic papillae have a pair of these structures surrounded by an electron-opaque layer of tissue. The structure at the base of all the papillae is difficult to determine in the third-stage juvenile. However, in the fourth stage several unmyelinated axons can be seen extending posteriorly towards the nerve ring. The cervical papillae are not noticeable in the third-stage juveniles, as they are folded under the external cuticle. The papillae contain a single "cilium" that has ten doublets and zero to four central fibers and in which the fibers extend inwards until they merge with lateral nerve axons (Fig. 1). It is difficult to determine the exact position of the "cilium" in relation to the papilla, and it will be necessary to look at later parasitic stages to obtain this information.

The amphids in the third-stage juveniles consist of a cuticular pit ending in a pouch-shaped structure with a total length of 18 μ. The dendritic processes extending forward from the nerve endings at the bottom of the pouch become very closely packed (Fig. 2) and end just before the amphid aperture, the internal structure being difficult to interpret. Toward the bottom of the pit the dendrites become more clearly defined as they spread apart, and ten outer doublets with zero to four inner microtubules or vesicles become evident (Fig. 3).

There is a striking resemblance between the structure of the amphids in the third-stage juveniles and the structure of some types of insect sensory organs (*7*). Roggen *et al.* (*3*) also commented on this. This resemblance is lost when the juvenile reaches the fourth stage. The dendrites become more closely packed, and the vacuoles and villi-like structures disappear as the buccal capsule enlarges (Fig. 4).

Further studies in earlier and later stages could yield clues to the specific functions of these organs during the growth of the parasite from the free-living stage to the parasitic adult.

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Planktonic Foraminifera: Field Experiment on Production Rate

Abstract. *In a study of the rate of production of four species of planktonic Foraminifera in the region of the California Current it was found that their life spans are of the order of 1 month. Reproduction seems to take place mainly in the upper hundred meters. Results are in contrast to previous evidence presented in favor of yearly life cycles and maturing at great depth in other species of planktonic Foraminifera.*

Planktonic Foraminifera are of interest and value in studies of marine zoogeography and paleoecology. Little is known, however, about their life cycles and productivity. The hypothesis that reproduction of some planktonic Foraminifera takes place at great depth, expressed by Walther in 1893 (*1*), has recently been considered proven (*2*) based on the occurrence of heavily encrusted living foraminifera at depths of more than 500 m in the Atlantic. It has been suggested that in the North Atlantic *Globorotalia truncatulinoides* reproduces below a depth of 500 m during November, which implies a yearly cycle of submergence and reproduction for this species (*3*).

However, if one assumes an annual overturn for planktonic foraminifera, their production of empty shells was found to be inadequate by a factor of 10, when the budget for river influx and ocean sedimentation of calcium carbonate on a worldwide basis was examined (*4*). It therefore seemed problematic whether annual submergence and reproduction could be extrapolated to all or even most species.

We attempted to obtain evidence bearing directly on this problem by simultaneously ascertaining both the concentration of planktonic foraminifera in the water column by net hauls and the output of this population by collecting falling tests in a sediment trap. At the same time the physical characteristics of the water column were measured from the surface to the bottom (Fig. 1). The location of the experiment was in the center of the Santa Barbara Basin off Southern California. Here the bottom is shallow, and therefore the vertical distance traveled by the shells, as well as their lateral displacement during sedimentation, is minimized. The surface cir-