FOLIA PARASITOLOGICA (PRAHA) 31: 141—145, 1984.

SENSE ORGANS OF THE NEMATODES TRICHINELLA PSEUDOSPIRALIS GARKAVI, 1972 AN D T. NATIVA BRITOV ET BOEV, 1972

D. HULÍNSKÁ and B. SHAIKENOV

Institute of Parasitology, Czechoslovak Academy of Sciences, Prague,
and Institute of Zoology, Academy of Sciences of the Kazakh SSR, Alma-Ata

Abstract. The structure and distribution of the sense organs of the head and the tail of two day-old *Trichinella* species (females) have been determined by transmission (TEM) and scanning (SEM) electron microscopy. In both species occur 16 cephalic sense organs, which contain three modified dendritic processes, in addition to the amphids. The nerve cell bodies are situated in the area above the nerve ring. The amphid contains ten dendritic processes. The sense organs open to the external environment by pores through the cuticle. Above the bulbous tip, the dendritic processes are surrounded by hypodermal cells. They enter posteriorly the pseudocoelom and join in subventral, subdorsal and two sublateral nerves, with transparent nuclei, in the area above the nerve ring. The distribution of the sense organs of larvae from the muscles and from the uterus is similar to that of the adults. The dendritic processes are short, most of their distal chamber is compacted with a dense, filamentous material. The rectum in the tail end of the female is innervated from the dorsal gangliom composed by multipolar cells with numerous dendrites and a single axon. Close to the excretory pore occurs a hemizonid which consists of six to eight dendrites and is situated between the hypodermis and the muscles. This organ has not been found in the larva.

The structure and distribution of the sense organs are used as a diagnostic sign by which the individual nematode species can be distinguished. This accounts for the numerous studies on the anatomy of the sense organs. Recent studies on the fine structure of these organs (Wright 1974, McLaren 1976) suggested differences both in their morphology and their function among the individual species. Amphids are regarded as chemoreceptors, but several dendritic processes are similar to insect mechanoreceptors in their fine structure (Moran et al. 1971). There is less information available on nematodes of the superfamily Trichuroidea (Wright 1974) than on the larger nematode species, e. g. *Syngamus trachea* (Jones 1973), *Necator americanus* (McLaren 1974), *Meloidogyne incognita* (Wergin et Endo 1974), and on filariids (McLaren 1972, 1976).

One of the least-studied aspects of the biology of *Trichinella* has been the nervous system. In a recent electron microscopic study on the surface of *T. spiralis* (Kim et Ledbetter 1980), the authors found 16 openings of cephalic sense organs. Our present study has determined numbers and the structure of cephalic sense organs in two day-old females of *T. pseudospiralis* and *T. nativa* in addition to those in larvae from the uterus and the muscles in order to compare the individual sense units of these nematode species, and to confront our findings with literary data on *Capillaria hepatica*.

MATERIALS AND METHODS

The two day-old females of *T. nativa* and *T. pseudospiralis* examined in this study are the same as used in previously reported studies on the fine structure of the cuticle and the sexual organs (Hulínská et Shaikenov 1982, 1983). In addition, worms were taken from the intestine of experimentally

infected mice and fixed in a mixture of 2.5 % paraformaldehyde and 2.5 % glutaraldehyde in a 0.1 M cacodylate buffer in a vacuum, then postfixed in 1 % OsO_4 at 4 °C, pH 7.2, and embedded in Epon 812 or Vestopal. Series of sections from eight specimens were stained with uranyl acetate and lead citrate. Larvae from the uterus of females were recovered at day 7 of development in the intestine. Muscle larvae of *T. pseudospiralis* aged 40 days, from experimentally infected mice, were isolated with Berman's digestive method. Specimens to be examined with the SEM were dried with the critical point method CO_2, coated with Au/PD, and inspected with the scanning equipment of the JEOL 100 B electron microscope.

RESULTS

The diameter of the head of a two day-old female of *T. pseudospiralis* is about 16 μm, that of T. nativa about 18—19 μm. The buccal cavity of *T. pseudospiralis* contains a stylet (Plate I, Fig. 1) which is fixed to the thin cuticle lining the cavity by means of dense granules. The wall lining the buccal cavity forms lateral elevations (A) close to the mouth (Plate I, Fig. 1). Then follows a bulge (B) divided by dorsoventral wedges below which occur laterally two elevations (C). There are no sense organs either on bulge B or on bulge C. On bulge A, there are pores through which the two pairs of inner labial sense organs open to the surface (D) (Plate I, Fig. 4). According to their position, they are similar to type-I sense organs reported by Wright (1974) for *Capillaria hepatica*. Through these pores open three modified dendritic processes (two processes in *C. hepatica*). Bird (1971) uses the term "cilium" for such sensory processes on nerve fibres, we are using "dendritic processes" (Wright 1974).
The lateral sense organ (F) (Plate I, Fig. 5) occurs at the level of the amphid in direction to the mouth opening. Dorsolateral and ventrolateral of the amphid are four pairs of outer, cephalic sense organs (G) (Plate I, Fig. 4; Plate II, Fig. 1) of which one pair always (H) is at the level of the inner labial sense organs (D). There are a total of 16 sense organs, including two amphids, on the head of both *T. pseudospiralis* and *T. nativa* (Plate II, Fig. 1). The cephalic sense organs are innervated with dendrites arising from the area of the nerve ring (Plate II, Fig. 2). Modified dendritic processes contain longitudinally aligned microtubules (Plate I, Fig. 2), and are surrounded by a dense material. A thin membrane covers the surface of the processes. They are flat, disk-shaped, at the top (Plate I, Fig. 3; Plate IV, Fig. 2). The basal, attenuated portion of the dendritic process contains microtubules arranged in a circlet of nine doubled peripheral tubules and three separate inner tubules (Plate IV, Fig. 6). Then, the processes pass into the bulbous tip (Plate III, Fig. 1) occupied by dense vesicles and mitochondria (Plate IV, Fig. 1). Up to their entrance in the bulbous tip, the dendritic processes lie in a chamber which opens through a pore to the surface. The pore is lined by a cuticular fold. The chamber of the inner labial organ is the smallest in diameter, that of the amphids which contains 10 dendritic processes the largest. The remaining sense organs contain three dendritic processes each. In the dorsolateral sense organ (H) (Plate I, Fig. 2), two dendritic processes are of a common morphology, one forms an expansion which is filled with a dense, filamentous material.
The elongate part of the chamber is surrounded by hypodermal cells (Plate III, Fig. 1) which enclose the dendritic processes until they reach the bulbous tip, past it they lie freely in the pseudocoelom (Plate III, Figs. 1, 3). Farther on, they fuse in sublateral nerves (Plate III, Fig. 4; Plate IV, Figs. 1,2). Above the nerve ring occur two sublateral and subdorsal and subventral nerves, as in the adult (Plate IV, Fig. 3) and in the infective muscle larva (Plate IV, Fig. 1). The nerves contain dense vesicles and mitochondria, their nuclei situated above the nerve ring are electron lucid (Plate IV, Figs. 2,3).
The arrangement of the cephalic sense organs of a seven day-old larva from the uterus is similar to that of the adult. The amphidial chamber is elongate, compacted

with a dense material, and contains ten differently long dendritic processes (Plate IV, Fig. 4). The dendritic processes of the inner labial organs are extremely short. Their basal part contains nine doubled microtubules (Plate IV, Fig. 6). Six dendrites lying between the hypodermis and the muscle cells occur on the ventral side of the body of *T. pseudospiralis* close to the excretory pore (Plate IV, Fig. 5). They contain mitochondria and dense vesicles with granules. The formation resembles a hemizonid observed in other nematode species.
A nerve ganglion containing neurons with a transparent large nucleus occurs in the tail area of the female of *T. nativa*, at the level of the rectal region. The cell body varies in size from 8 μm to 12 μm and contains mitochondria and vesicles. Digital dendrites arise from between the muscle cells to above the rectal wall (Plate III, Fig. 2). Distally occur the dendritic processes of the rectal area between the elongate nuclei of the rectal wall.

DISCUSSION

The similarity of cephalic sense organs of females of *T. pseudospiralis* and *T. nativa* aged two days is evident. The stylet is present in the buccal cavity of the larval *T. nativa*, but is absent in the adult. By contrast, both the larva and the adult (two day-old females) of *T. pseudospiralis* have a stylet. It is joined by granules to the extensions of the buccal cavity, i. e., to the two sublaterals and the one dorsal of the triradial lumen. Chen et Wen (1971) reported a similar attachment of the stylet of *Paratylenchus penetrans*. Bird (1969) suggested that the granules near the stylet of *Meloidogyne incognita* originated from the dorsal esophageal gland. Since no glands occur in the esophagus of *Trichinella*, their function is taken on by the stichosome (Bird 1971).
Trichinella have a total of 16 cephalic sense organs including the amphids. The fine structure both of the amphids and the sense organs of trichinellids is similar to that of *Capillaria hepatica* (Wright 1974). On the inner labial elevation close to the mouth occur four pores of the inner lateral labial organs which contain three dendritic processes in contrast to two processes reported for *C. hepatica*. A pair of lateral sense organs is situated on the inner circlet of *C. hepatica*, i. e., on the inner oral elevation, while in *T. pseudospiralis*, this organ lies outsite the area of the inner elevation, near to the amphid. The structure of this organ (type-II sense organ; Wright 1974) suggests its mechanoreceptive function. In *Trichinella*, the greatly enlarged dendritic process which is packed with a dense filamentous material occurs at the level of the distal tips of the two normal processes. In *C. hepatica*, the modified dendritic process lies under the cuticle folding inward in the chamber. The bulbous dendritic process compacted with a dense material in which microtubules could not be detected, resembles the mechanoreceptive organs of arthropods (Moran et al. 1971). McLaren (1972) found eight mechanoreceptive papillae in the filarioid *Dipetalonema viteae*, and described glands and supporting cells associated with the sense organs. Similar structures have not been observed either in *C. hepatica* (Wright 1974) or in *Trichinella*. In its structure, the amphid of *Trichinella* resembles that of *C. hepatica*. The pore measuring 0.8 μm in diameter associates with a chamber (1.2 μm in diameter) in which occur ten equally long dendritic processes, both in the adult and the larva. In *C. hepatica*, these processes are differently long, the longest occurs on the periphery of the chamber. Hypodermal cells supporting the dendrites ensheath their attenuated part up to the base (Wright 1974). Then, the bulbously enlarged part of the dendrite lies freely in the pseudocoelom. In *Trichinella*, the dendrite in the amphid remains surrounded by hypodermal cells, the dendrites of the remaining sense

organs lie freely in the pseudocoelum. The cuticle lines the pores and partly the chambers of all sense organs, it expands farthest in the amphid. According to Dick et Wright (1973), the dense material between the microtubules of the dendritic processes has a stimulating function. The basal part of the processes consists of nine doubled- and three central microtubules. Wright (1974) found 9 + 0 tubules in *C. hepatica*. A hemizonid consisting of six dendrites situated between the hypodermis and the muscle cells occurs in adults of *T. pseudospiralis*. Bird (1968) suggests that the hemizonid of *Meloidogyne javanica* is a receptor organ which controls the synthesis of protein granules in the subventral esophageal gland. The enzyme in the granules enables the larvae to penetrate the egg shells. The neurosecretory activity of the hemizonid (Bird 1971) leads to the production of enzymes which support molting. The location of the hemizonid of *Trichinella* is similar to that of the remaining nematode species in its position close to the excretory pore (Rogers 1968, McLaren 1976).

The neuron of the dorsal rectal ganglion on the posterior end of *Trichinella* can readily be distinguished with the electron microscope by its low electron density. The neuron is a multipolar cell (containing mitochondria) with numerous dendrites and a single axon. Dendrites reach the space between the muscle layer and the basal lamella of the rectum wall.

СЕНСОРНЫЕ ОРГАНЫ НЕМАТОД *TRICHINELLA PSEUDOSPIRALIS* GARKAVI, 1972 И *T. NATIVA* BRITOV ET BOEV, 1972

Д. Гулинска и Б. Шайкенов

Резюме. При помощи трансмиссионной и сканирующей электронной микроскопии изучали распределение и структуру сенсорных органов головы и хвоста двухдневных самок рода *Trichinella* (*T. pseudospiralis* и *T. nativa*). У обоих видов имеется 16 головных сенсорных органов, содержащих, кроме амфид, 3 модифицированные реснички. Тела нервных клеток расположены перед нервным кольцом. Амфида содержит 10 ресничек. Сенсорные органы открываются на поверхность кутикулы через отверстия. Кутикула отграничает дистальную камеру. Процессы дендритов над их луковице-видным расширением окружены гиподермальными клетками. По направлению к задней части тела они проникают в псевдоцел и над нервным кольцом соединяются в субвентральный и субдорзальный и 2 сублатеральных нерва с прозрачными ядрами. Распределение сенсорных органов личинок из мышцев и маток не отличается от распределения в половозрелых нематодах. Процессы дендритов короткие и дистальные камеры большей частью выполнены плотным, фибриллярным веществом. Прямая кишка в хвостовом конце самок иннервирована из дорзального ганглия, состоящего из мультиполярных клеток с многими дендритами и 1 аксоном. В области расширенной части аксона находятся митохондрии и плотные везикулы. В области перед экскреторным отверстием между гиподермой и мышцами находится 6—8 аксонов, образующих гемизонид. Этот орган не встречается у личинок.

REFERENCES

BIRD A. F., Changes associated with parasitism in nematodes. III. Ultrastructure of the egg shell, larval cuticle and contents of the subventral oesophageal glands in *Meloidogyne javanica* with some observations on hatching. J. Parasitol. 54: 475—489, 1968.

—, Changes associated with parasitism in nematodes. V. Ultrastructure of the stylet exudation and dorsal oesophageal gland contents of female *Meloidogyne javanica*. J. Parasitol. 55: 337—345, 1969.

—, The structure of nematodes. Academic Press, Inc., New York and London, 272 pp. 1971.

DICK T. A., WRIGHT K. A., The ultrastructure of the cuticle of the nematode *Syphacia obvelata* (Rudolphi, 1802). II. Modifications of the cuticle in the head end. Can. J. Zool. 51: 187—202, 1973.

HULÍNSKÁ D., SHAIKENOV B., The ultrastructure of the reproductive system, and the oogenesis of two day-old fertilized females of *Trichinella spiralis* and *T. nativa*. Folia parasit. (Praha) 29: 39—44, 1982.

CHEN T. A., WEN G. Y., Ultrastructure of the feeding apparatus of *Pratylenchus penetrans*. J. Nematol. 4: 155—159, 1971.

JONES G. M., Ultrastructure of the amphids and amphidial glands of *Syngamus trachea*. Parasitology 67, Abstr. 32: 1973.

KIM C. W., LEDBETTER M. C., Surface morphology of *Trichinella spiralis* by scanning electron microscopy. J. Parasitol. 66: 75—81, 1980.

McLAREN D. J., Ultrastructural and cytochemical studies on the sensory organelles and nervous system of *Dipetalonema viteae* (Nematoda: Filarioidea). Parasitology 65: 507—524, 1972.

—, The anterior glands of adult *Necator americanus* (Nematoda: Strongyloidea): I. Ultrastructural studies. Int. J. Parasitol. 4: 25—37, 1974.

—, Nematode sense organs. Advances in Parasitology. B. Dawes (Ed.), Acad. Press Inc., London 14: 195—265, 1976.

MORAN D. T., CHAPMAN K. M., ELLIS R. A., The fine structure of cockroach campaniform sensilla. J. Cell. Biol. 48: 155—173, 1971.

ROGERS W. P., Neurosecretory granules in the infective stage of *Haemonchus contortus*. Parasitology 58: 657—662, 1968.

WERGIN W. P., ENDO B. Y., Ultrastructure of the cephalic sensory organs in the southern root-knot nematode *Meloidogyne incognita*. Proc. 3rd Int. Congr. Parasit. 1: 444—446, 1974.

WRIGHT K. A., Cephalic sense organs of the parasitic nematode *Capillaria hepatica* (Bancroft, 1893). Can. J. Zool. 52: 1207—1213, 1974.

Received 29 August 1983.
Translated by: E. Kalinová

D. H., Parasitologický ústav ČSAV,
Flemingovo n. 2, 166 32 Praha 6,
ČSSR

EXPLANATIONS

A — lateral mouth elevations, B — bulge, C — lower lateral elevations, D — inner labial sense organs, E — amphid, F — lateral sense organ, G — dorsolateral and ventrolateral sense organs, H — sense organ at the level of the inner labial organ, bb — basal bodies, c — cuticle, d — dendrits, dp — dendritic process, dv — dentritic vesicles, dn — dorsal nerve, fm — filamentous material, he — hemizonid, m — mitochondria, mc — musculatur, n — nucleus, ln — lateral nerv, lr — lumen of the rectum, p — pseudocelom, rc — rectum cell, rn — rectum neuron, sdn — subdorsal nerves, sln — sublateral nerves, st — stylet

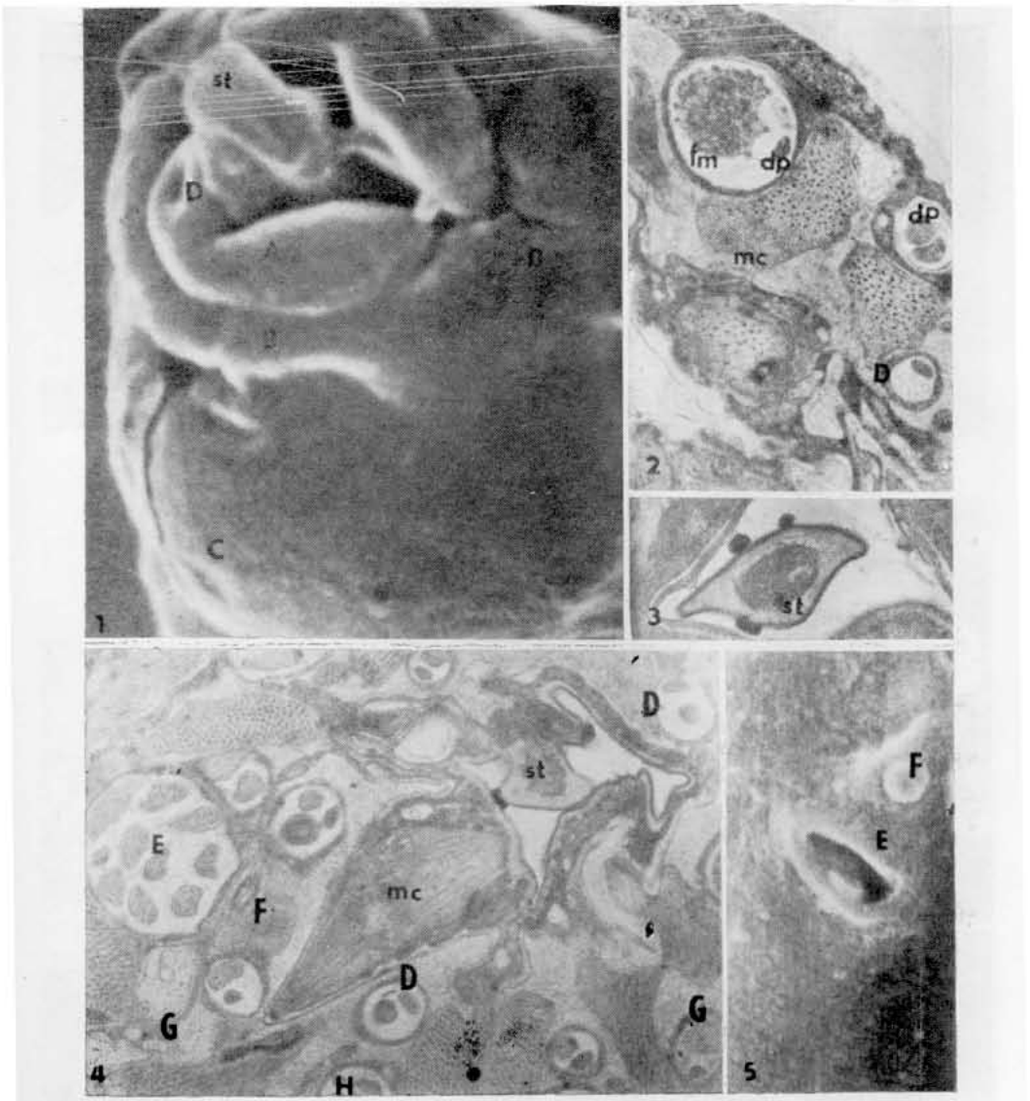

Fig. 1. The buccal cavity of the female of *T. pseudospiralis* has a stylet and is surrounded by two lateral inner elevations (A) followed by a bulge (B) below which occur laterally two elevations (C) (×26 000). **Fig. 2.** showing the inner lateral and subdorsal sense organs of *T. nativa*. In the opening of the chamber are the distal tips of two longer dendritic processes. A dense material occurs in the opening of the amphid to the surface (×23 100). **Fig. 3.** The stylet in the buccal cavity of *T. pseudospiralis*. Granules on the surface of the stylet stick to the outer cortical membrane of the cuticle linnig the oral cavity (×34 300). **Fig. 4.** Oblique section through cephalic sense organs of *T. pseudospiralis*. An amphid with ten dendritic processes, below it a section through the basal body of the organ (F) (×21 500). **Fig. 5.** An amphid of *T. nativa* lying freely below the lateral elevation. It is surrounded by a smooth cuticular rim (×20 000).

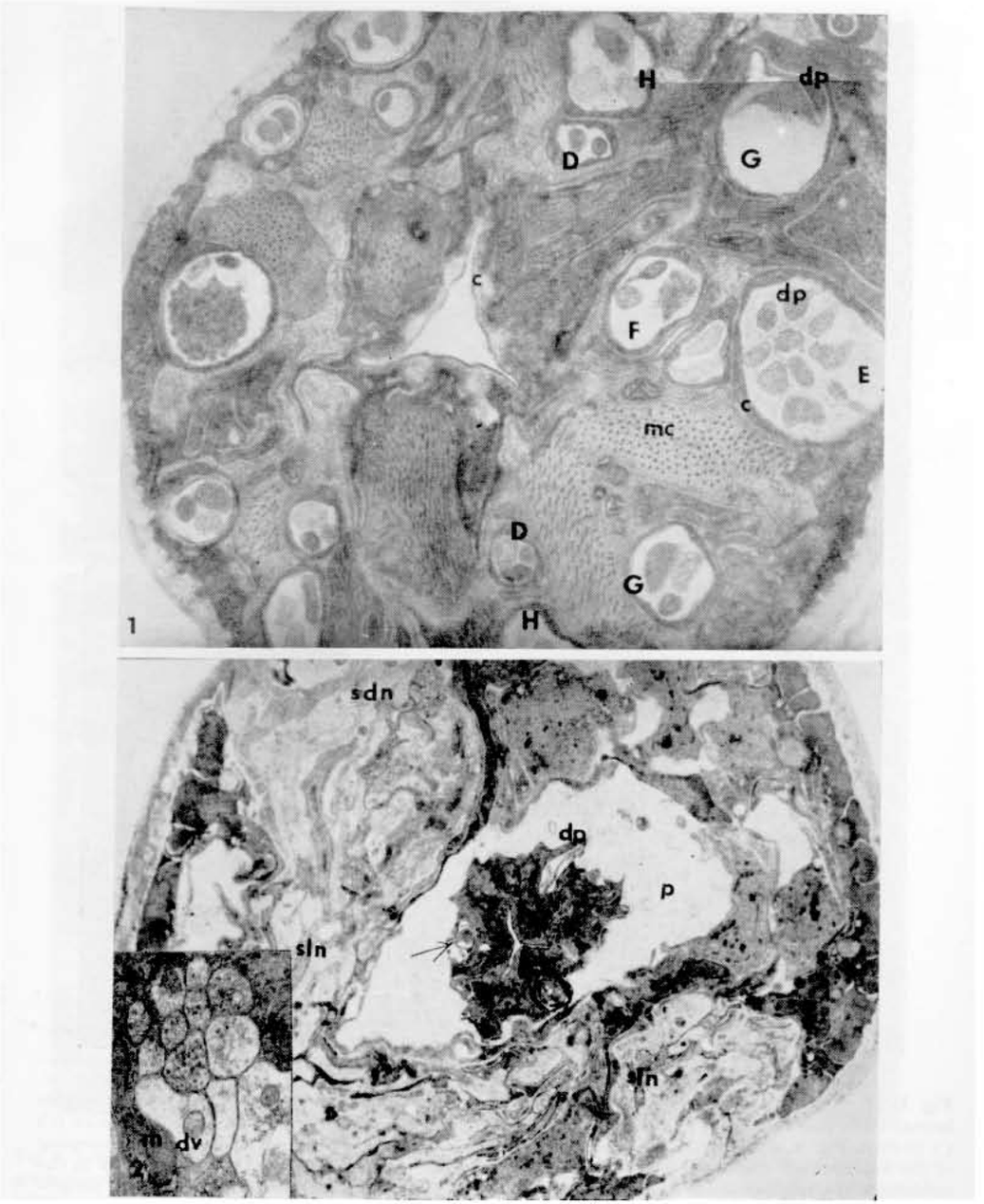

Fig. 1. Transverse section through the cephalic sense organs of *T. nativa* showing 16 pores through which the cephalic sense organs including the amphids open to the external environment (×21 000.) **Fig. 2.** The fusion of dendrites before entering the nerve ring of *T. pseudospiralis*. The widely enlarged part of the dendrite contains dense vesicles and synaptic vesicles. Groups of dendrites forming the subdorsal nerves (sdn) and the sublateral nerves (sln) occur in the pseudocoelom in the area between the esophagus and the muscle cells (mc). In the esophagus are the openings of two sublateral nerves and one subdorsal nerve in a chamber which contains dendritic processes (×12 000).

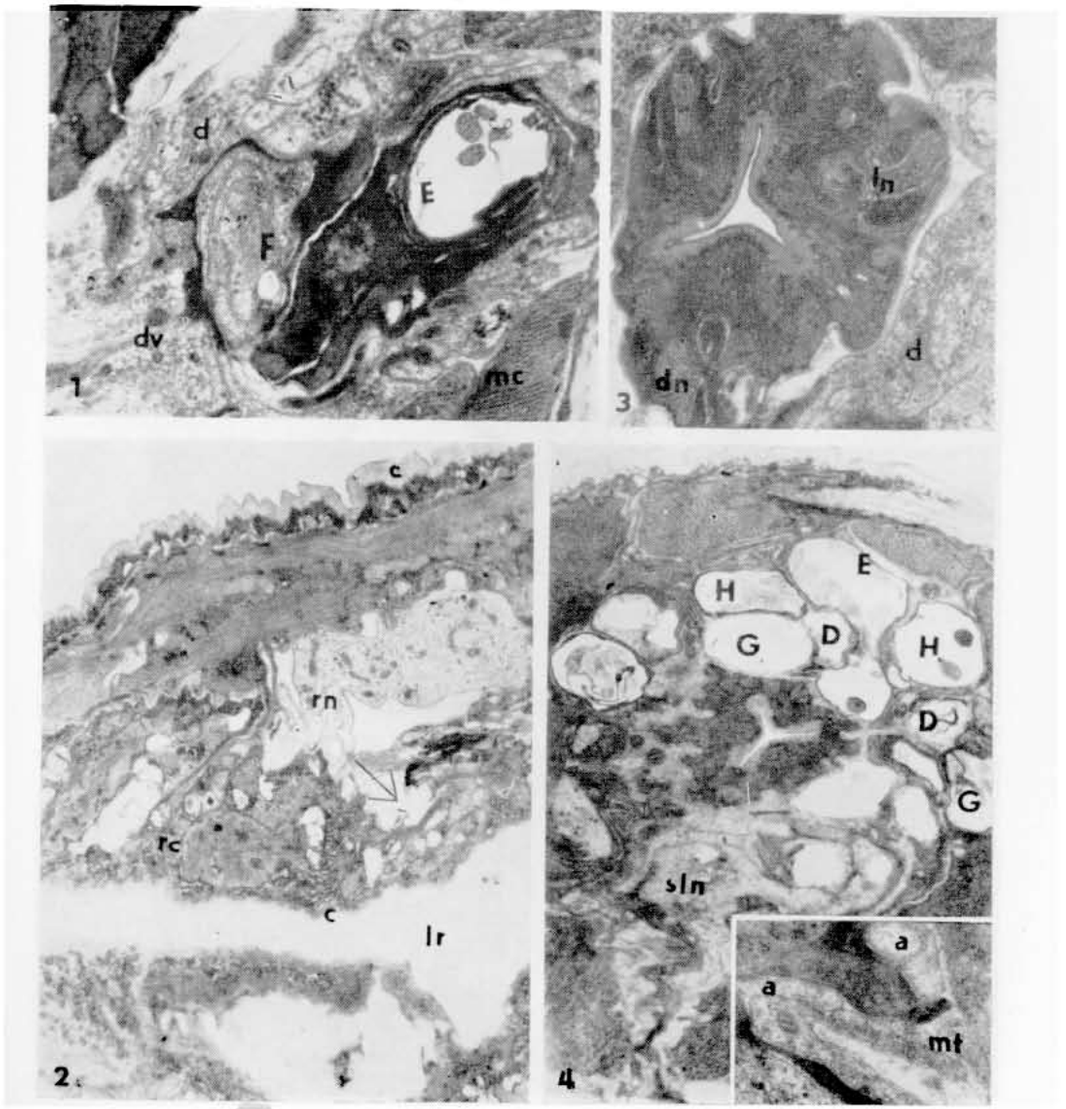

Fig. 1. The lateral sense organ and the amphid (transverse section through the chamber) are surrounded by hypodermal cells. The widely enlarged dendrites of the remaining sense organs lie freely in the pseudocoelom (×12 000). **Fig. 2.** Dendritic processes project to below the muscles of the rectal wall composed of cells with elongate transparent nuclei. The rectal cuticle is less thick than the body cuticle (×10 000). **Fig. 3.** In the esophagus of *T. pseudospiralis* is a dorsal nerve and two sublateral nerves containing transparent vesicles. Desmosomes fix the muscles to the cuticle. The enlarged parts of dendrites lie freely in the pseudocoelom surrounding the esophagus (×15 000). **Fig. 4.** Oblique section through the head of *T. pseudospiralis*. The cuticle of the head folds deeply before passing into the annulate body cuticle. Near the esophagus are sections through dendrites. The amphid contains ten dendritic processes, in the subdorsal chamber are sections through the basal part of dendritic processes. Dendrites of the sensory organs (D + F + G) join in the sublateral nerve (×10 500).

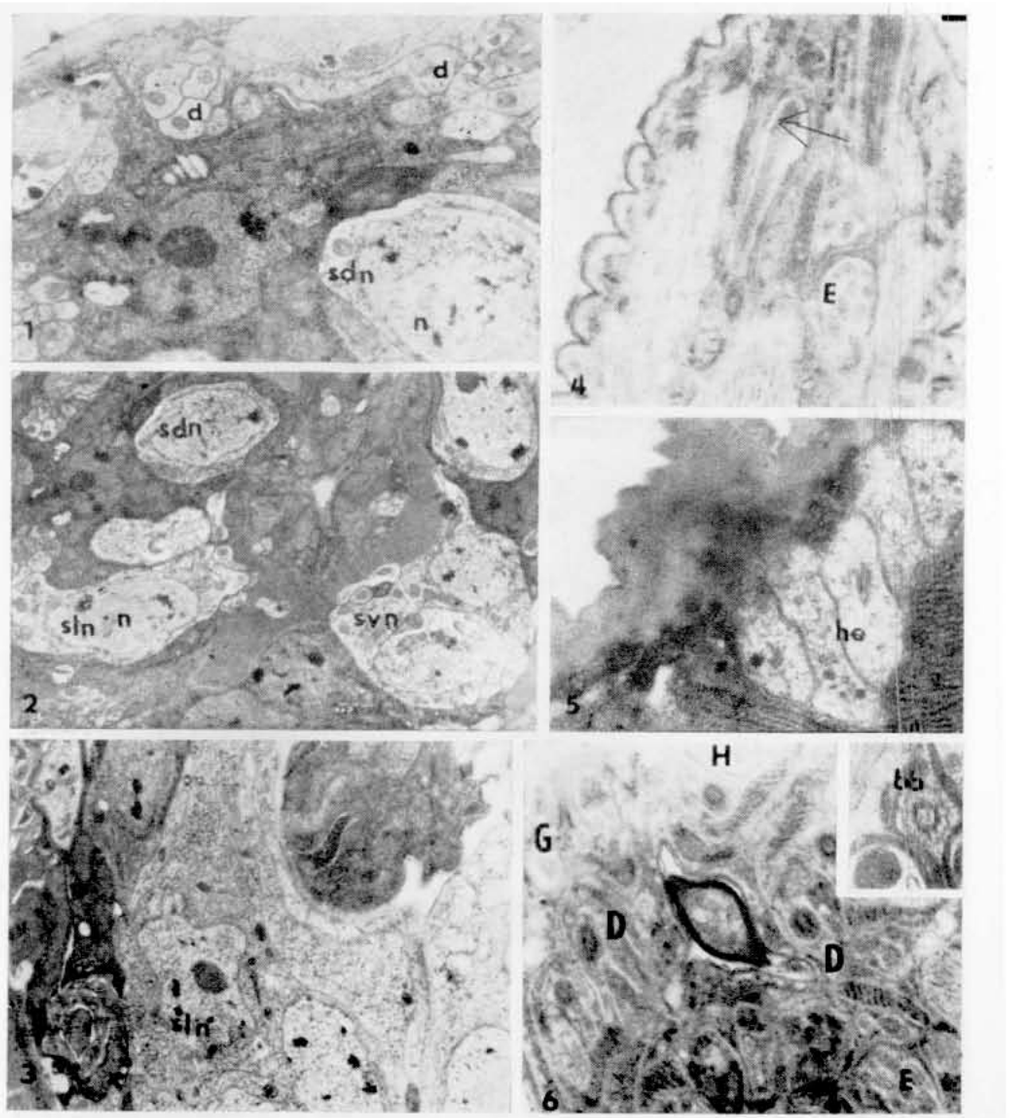

Fig. 1. Dendrites of the sublateral nerve lying among the muscle cells of a larva of *T. pseudospiralis* (from the muscles). The dendrites contain dense vesicles. The nucleus of the subdorsal nerve (×13 400). **Fig. 2.** Subventral, subdorsal and two sublateral nerves of the larva of *T. pseudospiralis* with a transparent nucleus. The esophagus is surrounded by a wide, membrane-bound strip of homogeneous material (×9 100). **Fig. 3.** The sublateral nerve of an adult *T. pseudospiralis* with a nucleus, dense vesicles, granules and transparent mitochondria (×10 000). **Fig. 4.** Longitudinal section through the head of a seven day-old larva of *T. pseudospiralis* recovered from the uterus. The chambers of the amphids (arrow) are filled with a dense filamentous material. Sections through ten dendritic processes in the attenuated part of the chamber. Below the muscles are sections through the basal part of the dendrites (×13 400). **Fig. 5.** The hemizonid of an adult female of *T. pseudospiralis:* It consists of six dendrites which contain dense granules (×18 800). **Fig. 6.** Transverse section through the head of an infective larva of *T. pseudospiralis* (from the muscles): The stylet fills the buccal cavity. Sense organs occur on an outer and inner circlet. Sections through inner sense organs at the level of the basal part of dendritic processes (×13 400).