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M. K. S. Gustafsson: The histology of the neck region of plerocercoids
of *Trienophorus nodulosus* (Cestoda, Pseudophyllidea)

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THE HISTOLOGY OF THE NECK
REGION OF PLEROCERCOIDS OF
TRIAENOPHORUS NODULOSUS
(CESTODA, PSEUDOPHYLLIDEA)

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Abstract

GUSTAFSSON, M. K. S. (Inst. Biol., Åbo Akademi, Åbo, Finland): The histology of the neck region of plerocercoids of *Triaenophorus nodulosus* (Cestoda, Pseudophyllidea). — Acta Zool. Fennica 138:1—16. 1973.

The histology of the neck region of plerocercoids of *Triaenophorus nodulosus* (Pallas) was studied. The abundance of the various cell types was estimated and a map was drawn. Of the total cell population tegumental cells form 44 %, germinative cells 17 %, dorsoventral muscle cells 5 %, transverse muscle cells 3 %, longitudinal muscle cells 12 %, flame cells 2 %, calcareous corpuscle cells 1 %, cells surrounding the main nerve cords 5 %, cells surrounding the main excretory ducts 1 % and unidentified cells 10 %.

Some cell types were described in detail. The germinative cells are highly basophilic cells with large nuclei and nucleoli and a cytoplasm containing vacuoles. They proliferate actively. The dorsoventral and transverse muscle cells adhere to the muscle fibres and have a slightly vacuolated cytoplasm. The longitudinal muscle cells are large cells with processes extending towards the muscle fibres and into the outer parenchyma. The cells around the main nerve cords are small and form a protective layer. The unidentified cells are characterized by small nuclei surrounded by scanty cytoplasm. The nature of these cells is unknown.

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INTRODUCTION

The cytology of cestodes has attracted a great deal of interest ever since the end of the last century and in the beginning of this, when the histology of various cestodes was first studied (ZERNECKE, 1896; YOUNG, 1908; GOUGH, 1911; PRENANT, 1922; WISNIEWSKI, 1930; MICHAJLOW, 1932, 1933, 1934).

In the last decade interest has chiefly been focused on the tegument, the structure and absorptive function of which have been thoroughly investigated by several workers, including BARON (1968, 1971), BRÅTEN (1968 a, b) and LEE (1966). However, the histology and the different cell types involved have also been dealt with (REES & WILLIAMS, 1965; REES, 1966; LUMSDEN, 1966; COLLIN, 1969, 1970; BONSDORFF et al., 1971; WIKGREN & GUSTAFSSON, 1971).

In the article below, the histology and the different cell types present in the neck region of plerocercoids of *Triaenophorus nodulosus* are described. Regarding the tegumental cells, the flame cells, the calcareous corpuscle cells and the cells surrounding the main excretory ducts, only their distribution and the size of the cell populations will be dealt with.

The neck region is metabolically a very active region. According to BOLLA & ROBERTS (1971), the rest of the strobila in adults of *Hymenolepis diminuta* originates from the neck region, which they call the »germinative region». The importance of the neck region as a source zone for primary anlage formation in *Diphyllobothrium dendriticum* has been demonstrated by WIKGREN et al. (1971).

Knowledge of the size of the different subpopulations of cells in *T. nodulosus* is necessary as a basis for further studies on cell population kinetics and histogenesis in this tapeworm.

MATERIAL AND METHODS

Plerocercoids of *T. nodulosus* (Pallas, 1781) were obtained from cysts in the livers of burbot (*Lota lota*). The worms are very slender and difficult to measure in Hank's solution.

However, they were immediately fixed in a mixture of one part neutralized formalin and 10 parts 70 per cent alcohol, and in this condition they measure about 2—3 cm. The worms were embedded in paraffin wax and sectioned at 5—9 μ m.

The following staining methods were used: Brachet's methyl green-pyronine stain, Heidenhain's azan stain, Feulgen's basic fuchsin stain, Ehrlich's haematoxylin stain, Best's carmine stain and silver impregnation for nerve cells according to Golgi and Bubenaite and for connective tissue according to Bielschowski.

With Brachet's methyl green-pyronine staining method and Heidenhain's azan staining method very good results were obtained. In these sections most of the cell types could be identified. Best's carmine stain demonstrates the distribution of glycogen splendidly. The muscle cells, especially the muscle fibres, show up well with Bielschowski's staining method.

The different cell types were identified from sections stained with the various methods. The length and breadth of the cells in sections stained with Brachet's methyl green-pyronine were assessed by measuring 100—200 cells of each type with an ocular micrometer.

The light microscopic observations were made with a Leitz Ortholux microscope.

The terminology and definitions of the main layers in plerocercoids of *T. nodulosus* are the same as in *Diphyllobothrium dendriticum* dealt with by BONSDORFF et al. (1971).

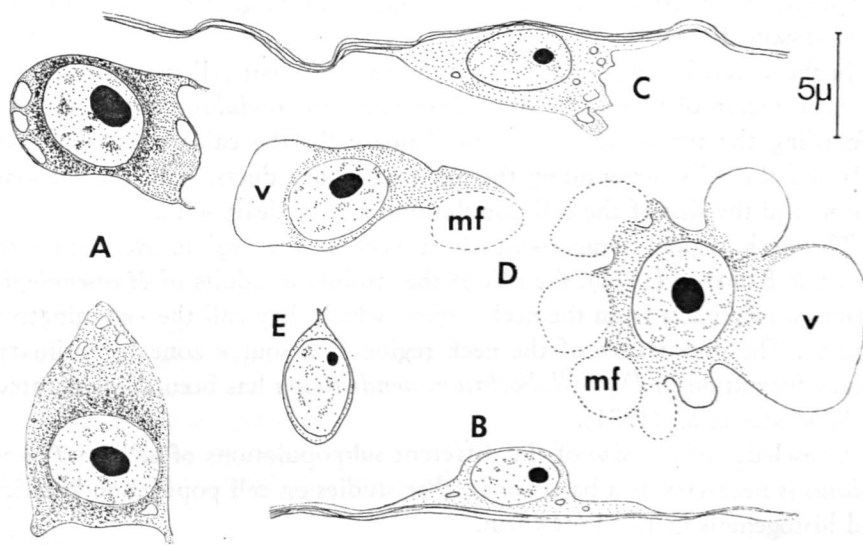


FIG. 1. Drawing showing cell types in the neck region of *T. nodulosus* plerocercoids. — A: highly basophilic germinative cells with large nuclei and conspicuous nucleoli. The cytoplasm contains vacuoles. — B: Dorsoventral muscle cell adhering to the muscle fibre. The nucleus is surrounded by slightly vacuolated cytoplasm. — C: transverse muscle cell and its undulating fibre. The cytoplasm follows the fibre and contains small vacuoles. — D: longitudinal muscle cells with large nuclei and nucleoli. The cytoplasm is drawn out into processes towards the muscle fibres (mf) and into the outer parenchyma, where they seem to surround large vacuoles (v). — E: binding cell with an oval nucleus and very scanty cytoplasm. This cell type forms a protective layer around the main nerve cord.

CELL TYPES

Germinative cells

Observations

The germinative cells are large cells with strong cytoplasmic basophilia, by which they can easily be distinguished in sections stained with pyronine and other basic stains.

The cells measure $10.6 \times 6.0 \mu\text{m}$ and are of very variable shape, but often elongated. The outline of the cell is distinct except at one end, where the cytoplasm is drawn out into thin processes, perhaps surrounding some nonbasophilic material. Small vacuoles are present in the cytoplasm (fig. 1 A).

The nucleus is large, mostly round or oval, and contains a very large and conspicuous nucleolus, measuring about $2 \mu\text{m}$ in diameter. The nucleoplasm is finely granular. The germinative cells are often seen in mitotic division.

The distribution of the germinative cells is very characteristic (fig. 2). Most of them occur in the inner parenchyma, where they are concentrated at the surface of and within the transverse muscle layer. In addition, scattered germinative cells occur in the rest of the inner parenchyma. In the longitudinal muscle layer they are fairly numerous, but the outer parenchyma contains only a few germinative cells, and there are none in the subtegumental cell layer.

Discussion

In his investigation of the cytology of the oncosphere and proceroid of *Triaenophorus nodulosus* and *T. crassus*, MICHAJLOW (1932, 1933, 1934) described germinative cells which closely resemble those of the plerocercoids I studied. According to him, the germinative cells measure $12.0 \times 6.4 \mu\text{m}$ and are very variable in shape. The cytoplasm is highly basophilic and the nucleus is large and round and contains a distinct nucleolus. These cells divide actively.

Not only in shape but also in distribution the germinative cells of *T. nodulosus* plerocercoids are very much like those of *Diphyllbothrium dendriticum* plerocercoids (BONSDORFF et al. 1971; WIKGREN & GUSTAFSSON, 1971). In both species they show very marked basophilia and are most abundant in the transverse muscle layer. The likeness between the two species is perhaps due to the fact that they both belong to the order Pseudophyllidea.

DOUGLAS (1961), in his study of *Baerietta diana*, described germinative cells located in a »germinal ring» along the transverse muscles. In *T. nodulosus* the aggregation of germinative cells is not so pronounced.

The problem of the number of cell types capable of division will be dealt with only briefly, because more information is needed. In the oncosphere and the proceroid of *T. nodulosus* and *T. crassus*, MICHAJLOW (1932, 1934) described two other dividing cell types besides the germinative cells, i.e. the germinative-somatic cells and the somatic cells. The presence of two kinds of dividing cells was noted by WISNIEWSKI (1930) in *Archigetes* and by DOUGLAS (1961) in *Baerietta diana*. In their study of cell proliferation and histogenesis in diphyllbothriid tapeworms, WIKGREN & GUSTAFSSON (1971) discuss the number of dividing cell types and conclude that in *Diphyllbothrium dendriticum* plerocercoids only one type of cell is capable of division. According to BOLLA & ROBERTS (1971), the germinative region in *Hymenolepis diminuta* contains germinative cells with the same characteristics as those of *T. nodulosus*. They, too, consider the germinative cells to be the only ones that divide and so act as stem cells for the development of the strobila of the mature worm. RYBICKA (1966) stated that from the oncosphere stage onwards growth is due to division of only one kind of cell. Despite a careful search I have not found any indication of division in other types of cells. I am therefore inclined to believe that the germinative cells constitute the main pool of dividing cells in plerocercoids of *T. nodulosus*. However, this point requires further investigation.

Summary

The germinative cells are highly basophilic cells with large nuclei and nucleoli and a cytoplasm containing vacuoles. They proliferate actively.

Dorsoventral muscle cells

Observations

The cell bodies of the dorsoventral muscles are situated in the inner parenchyma, especially between the two excretory ducts. These cell bodies adhere to fairly long muscle fibres which extend dorsoventrally through the transverse and longitudinal muscle layers to the outer parenchyma and are inserted between the subtegumental muscles. Before they reach the

tegumental cell layer they split into many fine branches. It is possible that some of the dorsoventral muscle fibres end in the longitudinal muscle layer.

The cell body is spindle-shaped and measures $9.5 \times 3.7 \mu\text{m}$. The weakly basophilic cytoplasm follows the muscle fibre for some distance and contains vacuoles (fig. 1 B).

The nucleus is oval and contains a small nucleolus (ca $1 \mu\text{m}$ in diameter). The nucleoplasm stains red-violet with Heidenhain's azan stain in contrast to that of the germinative cells, which stains red-orange. This may be due to the highly basophilic (orange) cytoplasm overlying the nucleus in the germinative cell.

Discussion

Long ago ZERNECKE (1896), in his admirable study of the cytology of cestodes, described spindle-shaped dorsoventral muscle cells with a finely granular cytoplasm and an oval nucleus. He pointed out that the muscle fibres split into fine branches in the middle of the outer parenchyma and then are inserted in the tegument. He considered the muscle fibres to consist of a central core of fine granular cytoplasm surrounded by a fibrillar cortex.

As to light microscopic observations the dorsoventral muscle cells in plerocercoids of *T. nodulosus* seem to be of the same types as those in the plerocercoids of *Diphyllobothrium dendriticum* (BONSDORFF et al., 1971).

Summary

The dorsoventral muscle cells are spindle-shaped and adhere to the muscle fibre. The cytoplasm contains vacuoles.

Transverse muscle cells

Observations

The transverse muscles form two weak layers at the inner border of the longitudinal muscles. In a section $5 \mu\text{m}$ thick each layer consists of about 8 fibres.

The long and slightly undulating fibres extend in a transverse direction along the longitudinal muscles and reach the subtegumental region, where they are inserted between the tegumental cells. The transverse muscle fibres send out thin processes to the longitudinal muscle fibres.

The cell bodies of the transverse muscles are of the same type as those of the dorsoventral muscles. They adhere to the fibres and measure $11.2 \times 4.3 \mu\text{m}$. The large elongated nucleus contains a distinct nucleolus (ca $1 \mu\text{m}$ in diameter) and is surrounded by a small amount of nonbasophilic, vacuolated cytoplasm (fig. 1 C).

Numerous germinative cells are interspersed in the transverse muscle layers, making detection of the muscle cells difficult.

Discussion

The transverse muscle layers in cestodes are not usually well developed (ZERNECKE, 1896; GOUGH, 1911; REES & WILLIAMS, 1965).

GOUGH (1911) held that the transverse muscle cells in *Avitellina centripunctata* are bipolar, with lateral fibres. He pointed out that the fibres split into fine branches before reaching the tegument.

In *Diphyllobothrium dendriticum* according to BONSDORFF et al. (1971) the transverse muscle cells are of the same type as the longitudinal muscle cells. However, the transverse muscle layer in this tapeworm is very compact and heavily loaded with germinative cells, which makes detection of the muscle cells difficult. It is thus possible that a mistake has been made concerning these cells.

Summary

The transverse muscle layers are weak. The spindle-shaped cell bodies adhere to the fibres and contain a slightly basophilic vacuolated cytoplasm.

Longitudinal muscle cells

Observations

The longitudinal muscles are well developed in the neck and anterior region of the worm but become sparser posteriorly.

The muscle cells are situated in the longitudinal muscle layer, especially at the border between this and the outer parenchyma. The cell body is very irregular in shape and is therefore difficult to measure. It is of roughly same size as the germinative cells.

The round or oval, rather large nucleus contains a large nucleolus and

is surrounded by basophilic cytoplasm, which is drawn out into blunt processes (fig. 1 D). In the middle of the muscle layer the cells send processes to many fibres. Those at the border send processes not only towards the muscle fibres but also into the outer parenchyma, where they seem to surround large vacuoles. The substance contained in these vacuoles is not known, but considering the large amounts of glycogen shown by Best's carmine stain to be present in the outer parenchyma, they may contain glycogen. The same staining shows that the muscle fibres are also surrounded by small glycogen sacs. Moreover, they seem to be hollow, containing a core of glycogen-rich sarcoplasm.

Discussion

Electron microscopic investigations have revealed that in cestodes the cell bodies of the muscle fibres are situated in an evaginated pocket of sarcoplasm at some distance from the fibre (LUMSDEN & BYRAM, 1967; COLLIN, 1969, 1970). This accounts for the fact that most of the longitudinal muscle cells in plerocercoids of *T. nodulosus* are found at the outer border of the muscle layers. In plerocercoids of *Diphyllobothrium dendriticum* the distribution is similar (BONSDORFF et al., 1971).

According to BONSDORFF et al. (1971), the longitudinal muscle cells are large and arachniform. Their cytoplasm is highly vacuolated and rich in glycogen. The muscle fibres are surrounded by small glycogen sacs and contain a core of glycogen-rich sarcoplasm.

LUMSDEN & BYRAM (1967) showed the presence of glycogen, especially in the β -form, in the sarcoplasm round the muscle fibres and in the perinuclear cytoplasm. This has also been demonstrated by COLLIN (1969, 1970) in the muscles of *Hymenolepis citelli* and by REISSIG & COLLUCCI (1968) in *H. diminuta*. This strengthens the assumption that the large vacuoles detected in the cytoplasm of the longitudinal muscle cells in *T. nodulosus* contain glycogen.

Marked reduction in the strength of the longitudinal muscle layers in the posterior part of the worm, comparable to that in *T. nodulosus*, was noted in *Acanthobothrium coronatum* by REES and WILLIAMS (1965).

Summary

The longitudinal muscle cells are large cells with processes extending towards the muscle fibres and into the outer parenchyma. They probably contain large amounts of glycogen.

Cells surrounding the nerve cords

Observations

The two main lateral nerve cords are partly surrounded by a group of small well-defined cells, »the binding cells». Most of these cells are located on the outer sides of the cords, where they form a layer two to three cells thick. The inner sides of the cords are often completely devoid of a binding cell layer.

The binding cells measure $5.8 \times 3.7 \mu\text{m}$. They are characterized by very scant, slightly basophilic cytoplasm, occasionally drawn out into thin processes. These processes may actually be cross-sections of thin sheaths surrounding the nerve cords. No processes are seen entering the nerve cords. Each cell has a large round or oval nucleus, containing a small nucleolus. The nucleoplasm is finely granular (fig. 1 E).

The cells are occasionally grouped beside the nerve cords as strands which can be followed through the inner parenchyma to the transverse muscle layer. The cells forming these strands do not differ morphologically from those investing the nerve cords but it is possible that they are components of a periphery nerve.

Discussion

ZERNECKE (1896) described the longitudinal nerves of *Ligula intestinalis* as surrounded by numerous parenchyma cells with long processes forming a »membrane» demarcating the nerves from the surrounding parenchyma. He found no branches entering the nerve cord and so suggested that the cells are modified parenchyma cells.

According to TOWER (1900), the binding cells surrounding the nerve cords of *Moniezia expansa* are elliptical, with a considerable number of branching processes running over the surface of the nerve. The function of these branching processes is to bind the nerve fibres into a compact bundle and separate them from the tissues in which they are embedded. He also found that, as in *T. nodulosus*, the arrangement of the binding cells is irregular.

In her study of the nerve cells in *Acanthobothrium coronatum*, REES (1966) described the binding cells around the lateral nerve cords. According to her, the cells measure about $6 \times 3 \mu\text{m}$ and are arranged singly or in groups of 2 or 3 on the outer side of the nerve cord. She points out that as the nerve cords grow the binding cells become more scattered and less abundant, presumably because their rate of division does not keep pace with the growth of the remainder of the strobila. Binding cells also occur

on other longitudinal nerves, on the ring commissures and around the intersections, or ganglia, between the nerves and the ring commissures.

The presence of binding cells on the longitudinal nerve cords suggests that the »sheath» which they form protects the nerves during contraction of the muscles.

Summary

The binding cells around the main nerve cords are small and form a protective layer.

ABUNDANCE AND DISTRIBUTION OF THE VARIOUS CELLS

Observations

Actual counts of the number and distribution of the various cell types in the neck region of plerocercoids of *T. nodulosus* would be a tedious task and only an estimate will be given here.

The difficulties inherent in making such an estimate have been discussed by BONSDORFF et al. (1971) with reference to the cellular composition of *Diphyllobothrium dendriticum* plerocercoids.

The over-all picture is based on a study of a great number of sections stained by various methods. Fig. 2 and table 1 show the result of a thorough investigation of one section from each of ten plerocercoids. These sections were stained with Brachet's methyl green-pyronine method and every cell was identified and located. Sections were stained with Heidenhain's azan stain for assessment of the number and distribution of flame cells. Unfortunately, the staining methods for nerve cells were unsuccessful and their number and distribution could not be confirmed.

According to fig. 2 and table 1, a certain number of cells could not be referred to any special cell type and have therefore been classed as »un-identified cells». These cells possess small nuclei surrounded by scanty cytoplasm. Some of these were probably nerve cells. However, the nature of the rest could not be assessed. More information is needed here.

Discussion

In general distribution of cells, plerocercoids of *T. nodulosus* closely resemble those of *Diphyllobothrium dendriticum* (BONSDORFF et al., 1971).

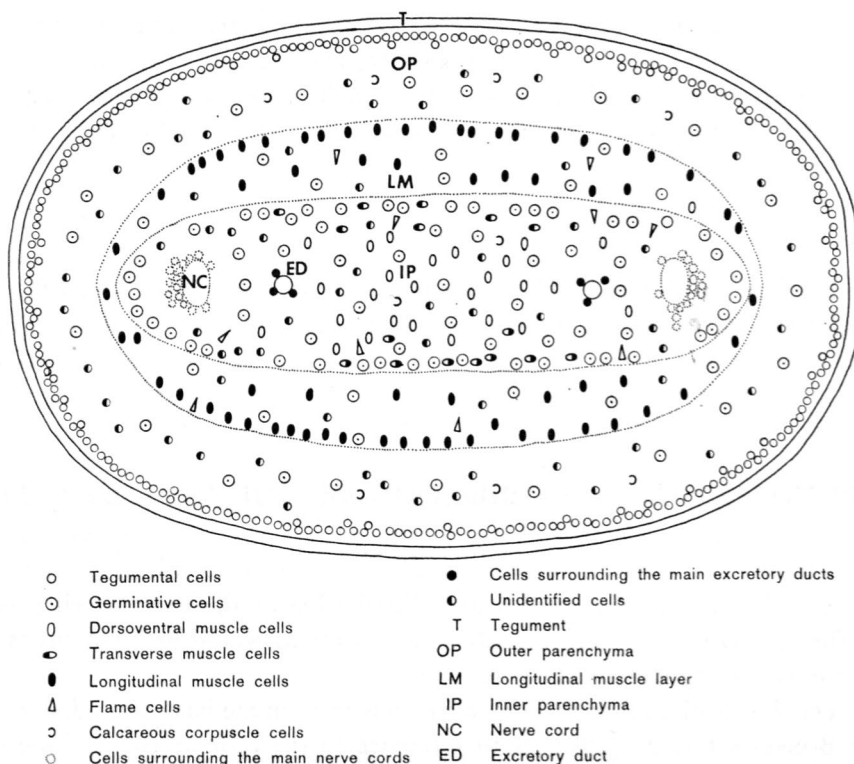


FIG. 2. Drawing showing the abundance and distribution of various cell types in a cross section of a *T. nodulosus* plerocercoid.

The likeness between the two species is understandable, because they both belong to the order Pseudophyllidea.

The total number of cells (595) in a section in *T. nodulosus* is much smaller than in *Diphyllobothrium dendriticum* (2087). A section of the latter worm appears quite packed with cells, but in *T. nodulosus* the cells are less dense which makes it much easier to study the cell types and their distribution.

The tegumental cell population in *T. nodulosus* is of the same order of magnitude (44 % of the total cell population) as in *Diphyllobothrium dendriticum* (41 %) (BONSDORFF et al., 1971). In both species it forms a metabolically very active layer of large and highly basophilic cells. For a discussion of the nature of this layer, see BARON (1968, 1971) and BRÅTEN (1968 a, b).

The proportion of germinative cells is much smaller in *T. nodulosus* (17 %) than in *Diphyllobothrium dendriticum* (32 %) (BONSDORFF et al.,

TABLE 1. The abundance of various cell types in the neck region of plerocercoids of *Trienophorus nodulosus*. The numbers are average for one cross section of medium sized plerocercoids.

Cell type	Subte- gument No	Inner paren- chyma		Longi- tudinal muscle layer		Outer paren- chyma		Total		Total less subte- gument %
		No	%	No	%	No	%	No	%	
Tegumental	260							260	44	
Germinative		66	37	15	16	22	34	103	17	30
Dorsoventral muscle		28	16					28	5	9
Transverse muscle		16	9					16	3	5
Longitudinal muscle				68	73			68	12	21
Flame		6	3	4	3			10	2	3
Calcareous corpuscle		2	1			7	12	9	1	3
Cells surrounding the nerve cords		32	19					32	5	9
Cells surrounding the excretory ducts		6	4					6	1	2
Unidentified cells		21	11	8	8	34	54	63	10	18
Total	260	177		95		63		595		

1971). Most of these cells are located in the inner parenchyma. This tissue is therefore characterized by active proliferation, which results in growth and anlage formation in the mature worm (WIKGREN et al., 1971). The longitudinal muscle layer contains a moderate number of germinative cells, which are presumably making their way to the outer parenchyma. According to WIKGREN & KNUTS (1970), in *Diphyllobothrium dendriticum* germinative cells migrate through the longitudinal muscle layer to the outer parenchyma, where they contribute to the growth of the tegumental cell layer. In *T. nodulosus* the outer parenchyma is composed of a relatively small number of cells, of which the germinative cells form a considerable proportion.

The dorsoventral and transverse muscle cells form a framework in which the rest of the cells are situated. I have referred the transverse muscle cells to the inner parenchyma because they form a very loose layer which extends inwards for a considerable distance.

In respect of the flame cells, the plerocercoids of *T. nodulosus* differ from those of *Diphyllobothrium dendriticum*. In *T. nodulosus* most of the flame cells are situated in the inner parenchyma and in the transverse and longitudinal muscle layers. Flame cells were only detected in the outer parenchyma on two occasions. In *Diphyllobothrium dendriticum* all but a few flame cells are situated in the outer parenchyma. In *Diphyllobothrium latum* and *Diphyllobothrium ditremum* there are flame cells in both the inner and outer parenchyma (BONSDORFF et al., 1971).

Most of the calcareous corpuscle cells occur in the outer parenchyma, where, because the total number of cells here is very small, they make up as much as 12 per cent.

The binding cells around the nerve cords form a considerable part (19 %) of the whole cell population in the inner parenchyma. The excretory ducts are surrounded by a few small cells.

The unidentified cells represent a so far unsolved problem. In the inner parenchyma and the longitudinal muscle layers they amount to less than 11 per cent, but in the outer parenchyma they form as much as 54 per cent of the total cell population. These are probably of some significance. Unfortunately, I am unable to offer any explanation.

In *Diphyllobothrium dendriticum* BONSDORFF et al. (1971) describe a cell type which they call »parenchyma cell». This undoubtedly very interesting cell type I have not been able to recognize in *T. nodulosus*. According to BONSDORFF et al. (1971), the parenchyma cells are specialized for carbohydrate storage and contain large amounts of glycogen. Large amounts of glycogen have also been detected in *T. nodulosus* by the

staining method of Best. Most of the glycogen occurs in the outer parenchyma in the form of large aggregates, of which some at least are in the longitudinal muscle cells. REISSIG & COLUCCI (1968), describing the distribution of glycogen in *Hymenolepis diminuta*, conclude that most of the glycogen is in the muscle cells. No indication was found of parenchyma cells specialized for glycogen storage.

General summary

The histology of the neck region of plerocercoids of *Triaenophorus nodulosus* was studied. The abundance of the various cell types was estimated and a map was drawn. Of the total cell population tegumental cells form 44 %, germinative cells 17 %, dorsoventral muscle cells 5 %, transverse muscle cells 3 %, longitudinal muscle cells 12 %, flame cells 2 %, calcareous corpuscle cells 1 %, cells surrounding the main nerve cords 5 %, cells surrounding the main excretory ducts 1 % and unidentified cells 10 %.

Some cell types were described in detail. The germinative cells are highly basophilic cells with large nuclei and nucleoli and a cytoplasm containing vacuoles. They proliferate actively.

The dorsoventral and transverse muscle cells adhere to the muscle fibres and have a slightly vacuolated cytoplasm.

The longitudinal muscle cells are large cells with processes extending towards the muscle fibres and into the outer parenchyma.

The cells around the main nerve cords are small and form a protective layer.

The unidentified cells are characterized by small nuclei surrounded by scanty cytoplasm. The nature of these cells is unknown.

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