

ROSTELLAR DEVELOPMENT IN THE LARVA OF MULTICEPS ENDOTHORACICUS (KIRSCHENBLAT, 1948)

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Abstract. The bladder of the larval *M. endothoracicus* bears several scolex anlagen which bulge in the shape of cellular buds in to the bladder cavity. A canal is differentiated from the thickened tegument which invaginates into these buds. The position of the tegument covering the bottom of the cellular anlage is more or less horizontal. The subtegumental layer is distinct. The rostellar cone differentiates from an increased number of cells situated below the tegument which covers the bottom of the canal. The tegument of the cone is covered with fine hooklets which break off gradually into the lumen of the canal. After the division of the cone into a bulb and praebulb we observed that the latter becomes overgrown by a lateral extension of the adjoining canal wall). Larger hooklets with a differently staining base were found in the thickened fold separating the praebulb from the bulb. The blade of the definitive hook differentiates from the modified tegument of this area, and from the larger hooklets after the formation of the hook organ. The lumen of the canal, and later also the spiral canal, harbour leukocytes from the tissue of the host; these attack the superficial microtrix border seen with the electron microscope. The tegument of the canal consists of a microtrix border (depth 6-7 μ m), of a thick zone of distal cytoplasm with oval and rod-shaped electron dense bodies. The cytoplasm traverses the basal fibrillar membrane between the subtegumental muscles and joins the subtegumental cells.

A description is given of the rostellar development in the cestode *Multiceps endothoracicus*. This larva is a special type of a polycephalic larva arranged generally to the coenurus type. Fig. 1 shows a mature larva of *M. endothoracicus*; its scoleces are attached to the reduced bladder by means of "attenuating stalks" (Plate I, Fig. 1). In its morphogenesis, this larva differs considerably from the coenurus (Šlais 1973, Hulínská 1975). Dollfus (1956) arranged a polycephalic larva from the thoracic cavity of *Apodemus sylvaticus*, named originally *Taenia rileyi* Lowen, 1929, to the cestode *Multiceps endothoracicus*. His decision was based on the number of hooks (54-64), and on the size of the large hooks (300-378 μ m) and the small hooks (201-226 μ m). The measurements given by Kirshenblat (1948) for the larva of *M. endothoracicus* were these: scoleces 0.830-0.840 mm in diameter, size of suckers 0.351×0.518 to 0.444×0.481 mm. Rostellum, 0.590-0.600 mm in diameter, surrounded by a double crown of hooks numbering 52-56. Length of large hooks 0.315-0.332 mm, of small hooks 0.203-0.218 mm. Large hooks with their moderately deflected shaft slightly shorter than blade, but considerably longer than basal extension. According to Agapova (1948), scoleces from the thoracic cavity of *Meriones tamariscinus* measured 2.5-2.6 mm in diameter, rostellum 0.660 mm, the surrounding large hooks 0.30-0.318 mm, the small hooks 0.209-0.22 mm, number

of hooks 56—64. Dollfus (1956) found 28 large hooks (0.340 mm) and 28 small hooks (0.221 mm) in the larva of *M. endothoracicus*. Dubnický (1952) gave these data for a maturing larva of *M. endothoracicus* from the intestine of *Vulpes vulpes*: scolex length 1.2—1.6 mm, rostellum armed with 52—60 hooks; measurements of large hooks 0.351—0.372 mm, of small hooks 0.224—0.241 mm. Gvozdev and Agapova (1963) counted 56—64 hooks on the rostellum of a larval *M. endothoracicus*: length of large hooks 0.290—0.297 mm, of small hooks 0.220 mm. In our larval material, we found 59 hooks arranged in two concentric circles on a completely differentiated rostellum. The large hooks measured 0.33—0.33 mm, the small hooks 0.22 mm (Plate I, Fig. 2).

MATERIALS AND METHODS

Differently old larvae of *Multiceps endothoracicus* were obtained from the thoracic cavity of *Rhombomys opimus*. The material was loaned from the collection of the Zoological Institute, Academy of Sciences, Kazakh S.S.R. by courtesy of Professor Gvozdev. Fresh material was obtained from experimental infection. The larvae were fixed in 4 % neutral formalin or in Baker's fixative, and embedded in paraffin with standard methods. Sections (5—7 μ m) were stained with Mallory's triple stain or picric acid (Lillie 1965), Goldner's blue trichrome, van Gieson's method, Gömöri's impregnation method, orange-eosin, toluidine blue in the method suggested by Dominici. Polysaccharides were demonstrated with Halle's method, with PAS in a modification by Mowry (Mowry 1963). The surface of the hooks was inspected with the scanning electron microscope JEOL 100 after dehydration in liquid nitrogen. The sample was fixed to the target with glue from Scotch tape. For electron microscopy the larvae were fixed for 4 hr in cool Millonig's phosphate buffered with 6 % glutaraldehyde, washed overnight in phosphate buffer and postfixed 1 hr in 1 % OsO_4 ; after dehydration embedded in Epon. Sections were cut on a Reichert microtome and stained with uranyl acetate-lead citrate.

RESULTS

In the bladder of the larva of *Multiceps endothoracicus*, several scolex anlagen originate by means of active cell proliferation. As the anlagen develop, the bladder tegument invaginates into them (Plate II, Fig. 1). The invaginating tegument is thicker than that of the bladder wall; its distinct homogeneous layer is lined with a low basophilic microtrich border. The cavity formed by the invaginating tegument harbours leukocytes from the tissue reaction of the host. The invaginating tegument deepens in a canal which enlarges horizontally at the bottom. The tegument of the canal bears a border of microtriches which attain a length of almost 1 μ m (Plate II, Fig. 2).

During the early stage of development of the scolex anlage, the cells of the germinal bud increase in number and push up the tegument covering the bottom of the canal so that it forms a hemispherical formation (Plate II, Fig. 3). This causes a thinning of the tegument on the peak of the formation. Continued cell proliferation is responsible for the differentiation of the hemispherical formation in a rostellar cone. As soon as the tegument started to invaginate, we observed a subtegumental muscle layer. This decreased in depth towards the bottom of the canal and disappeared completely under the tegument of the growing rostellar cone (Plate II, Fig. 4).

The tegument of the differentiating rostellar cone bears fine hooklets (length 10—15 μ m) which stain a different colour to that of the microtriches present on the tegument of the invaginated canal. The hooklets stain an orange colour with Mallory's PTAH, a blue colour with Masson's trichrome (Plate III, Fig. 1). The microtriches stain feebly blue with Halle's method and with the AB pH 2.6 method. Parts of the broken off hooklets were found also in the granular substance of the canal lumen above the rostellar cone. In more advanced stages the rostellar cone



is bigger, and it is divided by a membrane in a bulb and praebulb (Plate II, Fig. 2). The lateral wall of the invaginated canal bulges into the lumen and forms a crown around the praebulb. The tegument is thickened on the wall of these lateral extensions and in the fold separating the praebulb from the bulb; it bears more compact hooklets. With Masson's trichrome, the base of these hooklets stains blue, the distal peak orange. Inspection of a very slanted section in the electron microscope disclosed microtriches in the folded wall of the invaginated canal above its bottom. The microtrix base was less electron dense and in that similar to the oval bodies present in the distal cytoplasm (Plate II, Fig. 3).

As development proceeds, the bulb becomes overgrown by the praebulb. The bulb covered with a thin tegument, remains in connection with the cavity of the invaginated canal by means of a central slit. Suckers start to form in the lateral wall of the canal above the lateral extensions, and the invaginated canal differentiates in a spiral canal which proliferates from the suckers. At this stage, the tegument of the praebulbar base and that of the lateral extensions attains a thickness of up to 28 μm , and is finely granulated. The larger hooklets on the base of the praebulb stain differently on their base and surface (Plate II, Fig. 4). The blade of the definitive hook originates from these hooklets in that a substance is deposited on them from the modified tegument, which takes on the function of the hook organ as demonstrated by a number of authors for different cestode larvae. In a later stage of development of the rostellum, the bulb flattens out to form a rostellar pad and the thinned tegument on the peak of the rostellar pad changes into a membranous sheath. As the praebulbar tegument thickens and changes into a hook organ, the hooks assume a more vacuolate and striated appearance. The vacuoles contain granules which stain blue with Masson's trichrome, and are similar to those in the hook organ. This organ enlarges and also harbours large, orange-staining granules. The hook blade having completed its development separates from the hook organs and remains connected with it at the base only (Plate IV, Fig. 1). The hook organ extends in direction towards the wall of the lateral extensions. In the lateral wall, we observed the disappearance of the subtegumental muscle layer which had previously separated the tegument from the subtegumental cells. This enabled the contact of the hook organ with these cells. The rostellar pad becomes flattened into a transverse lens-shaped formation interwoven with numerous vertical and radial fibers (Plate IV, Fig. 2). The expansion of the rostellar pad continues below the fused praebulb.

The staining properties of the tegument covering the spiral canal differ from those of the tegument lining the original invaginated canal. With Giemsa and Mallory's method, the homogeneous layer of the tegument of the proliferating canal stains dark blue by contrast to the violet coloration of the same layer in the tegument of the invaginated canal. Electron microscopy disclosed a wide, distal cytoplasm containing rod-shaped bodies and dense membrane-bounded oval bodies in the tegument of the spiral canal (Lee 1966, Bråten 1968) (Plate V, Fig. 1). Also sensory endings tending to concentrate in the rostellar area of the spiral canal, were observed. Most important was the appearance of a distal ciliary process. Protoplasmic projections containing bodies and an occasional mitochondrion extend from the distal cytoplasm, traverse the basal membrane and join the subtegumental cells after passing a layer of subtegumental muscles (Plate V, Fig. 2). The superficial microtrix border is composed of microtriches measuring 6–7 μm in length. Their sharply pointed, electron dense distal half is slightly curved and lies at an oblique angle to the less electron dense basal region. The plasma membrane has a densification on its inner surface which continues into the basal part of the microtrix. The distal part of the microtrix is partly separated from the wider proximal part by a membranous cap

which is not continuous with the plasma membrane (Plate VI, Fig. 1). Threadgold (1965) obtained similar results. The lumen of the spiral canal, similar to that of the invaginated canal, harbours eosinophilic formations which, upon electron microscopic inspection, appear to be leukocytes (Plate VI, Fig. 2). Their visibly bisegmented nucleus and the plasma of the leukocyte contain mitochondria and cisternae of endoplasmic reticulum. Among the microtriches on the surface of the tegument we observed large, bulbous extrusion situated close to the leukocytes, with a lower electron density to that of the basal microtrich part. They extend from the distal cytoplasm and their plasma membrane carries the distal parts of the microtriches (Plate VI, Fig. 3). The plasma of the leukocytes contains vacuoles with phagocytized granules (Plate VI, Fig. 4). Plasmic processes extend from the leukocytes to the surface of the tegument (Plate VI, Fig. 5).

During the final stage of rostellar development, i.e., at the time of shaft formation, the hook organ folds to form pockets. These are arranged in concentric circles each enclosing the handle of the hook. Orange coloured granules stained with trichrome are no longer present in the hook organ which contains only feebly blue coloured granules. The rostellar pad is surrounded by a thick layer of fibers and cells which form the rostellar sac. Its shape is that of a biconvex lens, and it is traversed by a network of muscles. Hooks were observed on the mulberry-shaped, elongate praebulb the inside of which contained nuclei and several muscle fibers.

DISCUSSION

Various authors, e.g., Clapham (1942) distinguished larvae of the genus *Multiceps* by these diagnostic signs: mode of development, shape, number and size of hooks. Until the present, there has been little understanding of the histogenesis and morphogenesis of the larva of *Multiceps endothoracicus* and, consequently, of the development of its rostellum. Although considerable differences were found in the morphogenesis of the larva of *M. endothoracicus* and in that of larvae of *M. serialis*, *M. multiceps* and others (Hulínská 1975) the development of the rostellum and hooks is very similar in polyccephalic and other cestode larvae. The origin and development of rostellar hooks of *Cysticercus crassiceps* was described in detail by Bilquees and Freeman (1969) in their evaluation of the finding by Crusz (1948). Leuckart (1886) and Crusz (1948) suggested that the hook substance was deposited inside the hooks. Gläser (1909) believed that the substance was deposited on the surface, and that the blade was formed by the activity of the changed cuticle. Bilquees and Freeman (1969) demonstrated that the hook substance originated from the activity of the tegument. This has been confirmed by Race et al. (1965) in their electron microscopic study on *M. serialis*. The accelerated rate of cell production in association with the formation of the rostellar cone influences the division of the cone in a bulb and praebulb, and the disappearance of subtegumental muscle fibers which enables a communication between the tegument and the tegumental nuclei. A structure, the so-called hook organ, originates from the hypertrophied praebulbar tegument which extends to the wall of the lateral extensions of the invaginated canal. This part of the lateral wall bulges noticeably into the canal lumen and, apparently, shapes the blade. By contrast to other cysticerci, the lateral extensions of the larva of *M. endothoracicus* originate at the time of rostellar development. The tegument of the spiral canal of a larval *M. endothoracicus*, viewed in the electron microscope, is similar in appearance to that of the remaining cyclophyloidean cestodes. In the distal cytoplasm of the tegument of *M. endothoracicus* we observed "dense bodies" similar to those found by Lumsden (1966) in the tegument of *H. diminuta*, and

by Bråten (1968) in the plerocercoid of *Diphyllbothrium latum* (L.). The appearance of the distal cytoplasm of the tegument of *M. endothoracicus* is not vacuolated as that described by Race et al. (1965) for the tegument of *M. serialis*, and by Šlais et al. (1971) for the bladder tegument of *C. bovis*. It is delineated by a plasma membrane as this has been described by Lumsden (1966) for the tegument of *H. diminuta*. Sensory endings have been observed in the tegument of the spiral canal of *M. endothoracicus*. Jha and Smyth (1971) found similar sensory endings with a distal process in the rostellum of *E. granulosus* as have Sakamoto and Sugimura (1969) in the rostellum of *E. multilocularis*. Blitz and Smyth (1973) observed two types of sensory endings in the tegument of *Railletina cesticillus*. By contrast to Lumsden (1966) who described an evagination in the strobilar tegument, the extrusion between the microtriches of the tegument of the canal observed in our material has, evidently, nothing in common with sensory endings. Similar in type appears to be the extrusion caused most probably by leukocytes which bear on their surface remnants of microtriches. These extrusions are similar to bleb-like structures on the strobilar tegument of *Taenia hydatigena* described by Featherston (1971). They appeared to be exudates issuing from the distal cytoplasm.

РАЗВИТИЕ ХОБОТКА ЛИЧИНКИ *MULTICEPS ENDOTHORACICUS* (KIRSCHENBLAT, 1948)

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Резюме. В пузыре личинки *M. endothoracicus* закладывается несколько оснований сколекса, выпячивающихся в виде клеточных утолщений в полость пузыря. В эти утолщения инвагинируется утолщенный тегумент, дифференцирующийся в инвагинированный проход. Тегумент покрывающий дно клеточного основания более или менее горизонтальный. Субтегументальный слой заметен. Конус хоботка дифференцируется из увеличивающегося числа клеток под тегументом дна прохода. В тегументе конуса нежные крючки, которые постепенно отламываются в люмен прохода. Было обнаружено, что после дифференцировки конуса в бульбус и пребульбус, последний перерастает над бульбус. Прилегающая стена прохода вырастает в латеральный отросток и между ним и пребульбусом возникает складка. В утолщенном тегументе складки отделяющей пребульбус от латерального отростка растут новые крючки неправильной треугольной формы с изогнутым заостренным мягким лезвием. Из модифицированного гипертрофического тегумента латерального отростка и из тегумента пребульбуса укладывается субстанция в виде белковых гранул на поверхности мягкого лезвия крючков, которые увеличиваются. Лезвие больших крючков формируется согласно форме латерального отростка. В люмене прохода, который в следующей стадии развития формируется в спиральный проход, находятся лейкоциты из ткани хозяина, влияющие на поверхностный слой тегумента и между микротрихами возникают круглые эвагинации из дистальной цитоплазмы, как было показано в электронном микроскопе. Тегумент прохода состоит из края микротрихов (высотой 5—7 мк), толстой зоны дистальной цитоплазмы с овальными, палочковидными непроходимыми для электронов тельцами. Цитоплазма проникает через базальную фибриллярную мембрану между субтегументальной мускулатурой и соединяется с субтегументальными клетками.

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EXPLANATION OF FIGURES

B — modified bladder wall
BL — basal membrane
BE — bulboid extrusion
BU — bulb
CM — Circular muscle fibers
DC — distal cytoplasm
EL — leukocyte
F — attenuating stalk
H — hooks
HO — hook organ
IC — invagination cavity
LM — longitudinal muscle fibers
MC — membranous cap

Mi — microtriches
N — nucleus
OB — oval bodies
PB — praebulb
PH — hooklets
PM — plasma membrane
R — rostellum
RB — rod-shaped bodies
RC — rostellar cone
RS — rostellar sac
RP — rostellar pad
S — scolex bud
SP — sensory endings

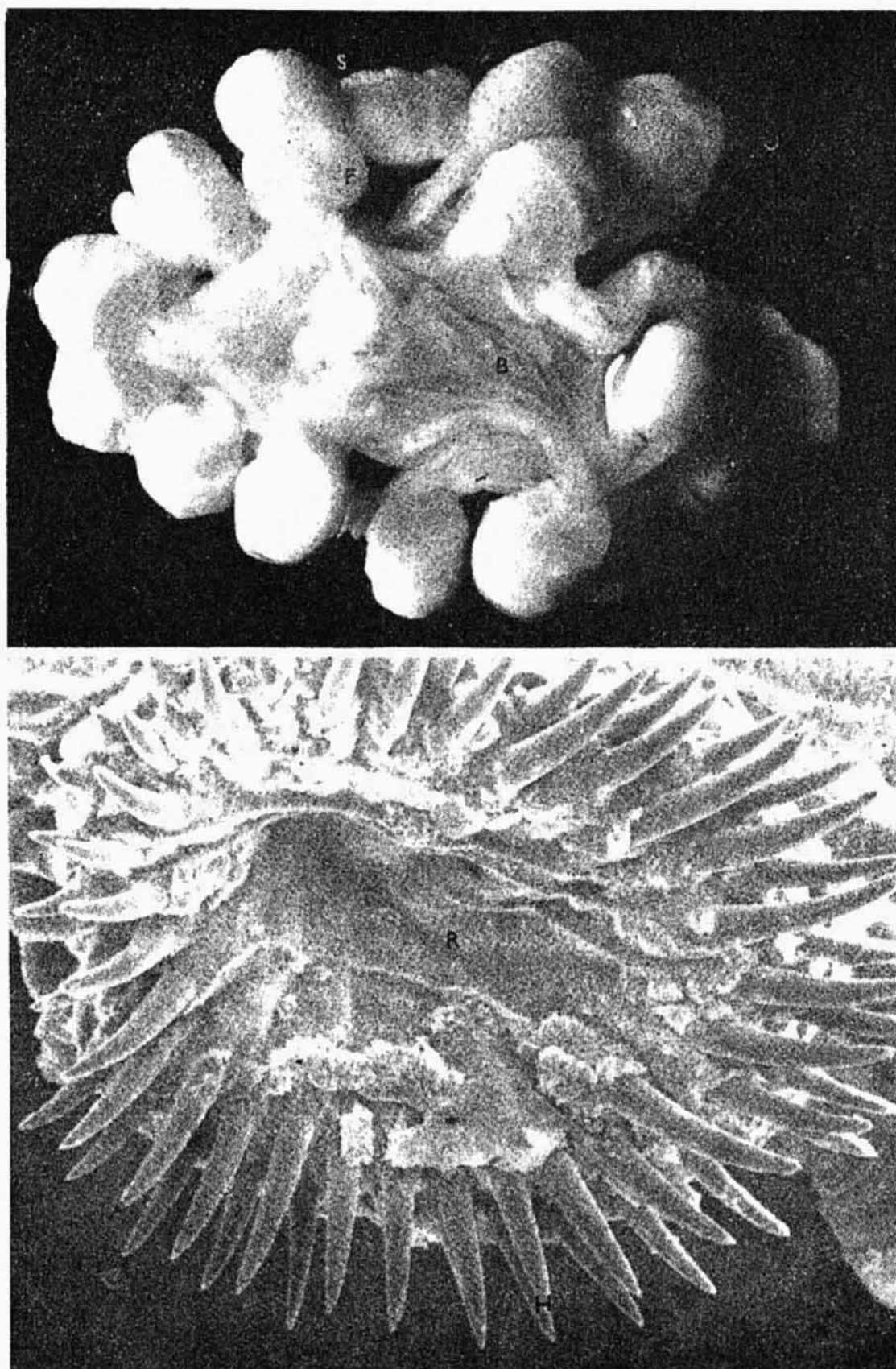


Fig. 1. Polyccephalic larva of *M. endothoracicus*. Spiral canal with scolex organs submerged completely in the rugate mount covered with a modified bladder wall (B). Communication of untrue outer scoleces with the reduced bladder by means of attenuating stalks (F) which are covered with the modified bladder wall and filled with connective tissue. (Fresh material, $\times 10.6$.)

Fig. 2. Rostellum (R) of a mature larva of *M. endothoracicus* with 59 hooks in two concentric circles. Scanning equipment of electron microscope JEOL 100 ($\times 20,000$).

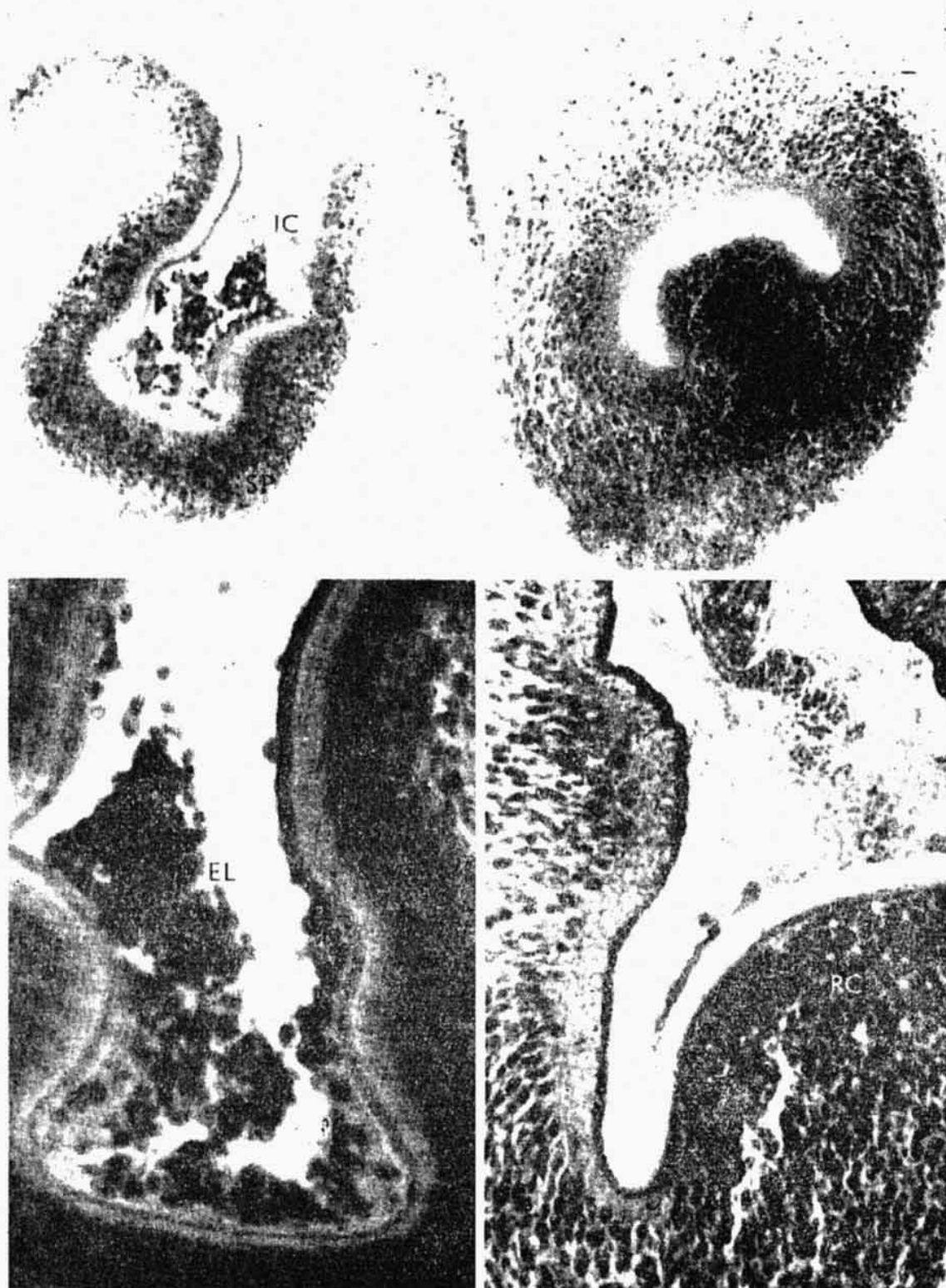


Fig. 1. Tangential section through the scolex primordium (SP) with invaginating bladder tegument. Leukocytes from the host's tissue in the cavity of the invagination (IC). (Haematoxylin eosin, $\times 29$).

Fig. 2. Tangential section through the canal cavity with a horizontally widened bottom filled with leukocytes (EL). Tegument covered with a low, basophilic microtrix border. (Trichrome blue, $\times 72$.)

Fig. 3. Bottom of the canal raised by amitotically dividing germinative cells to form a hemispherical formation. Transverse section. (Gallocyanine eosin, $\times 29$.)

Fig. 4. Tangential section through rostellar cone (RC). The thinned tegument on its surface covered with a microtrix border. Subtegumental muscle layer attenuating in direction of the cone. (Trichrome blue, $\times 72$.)

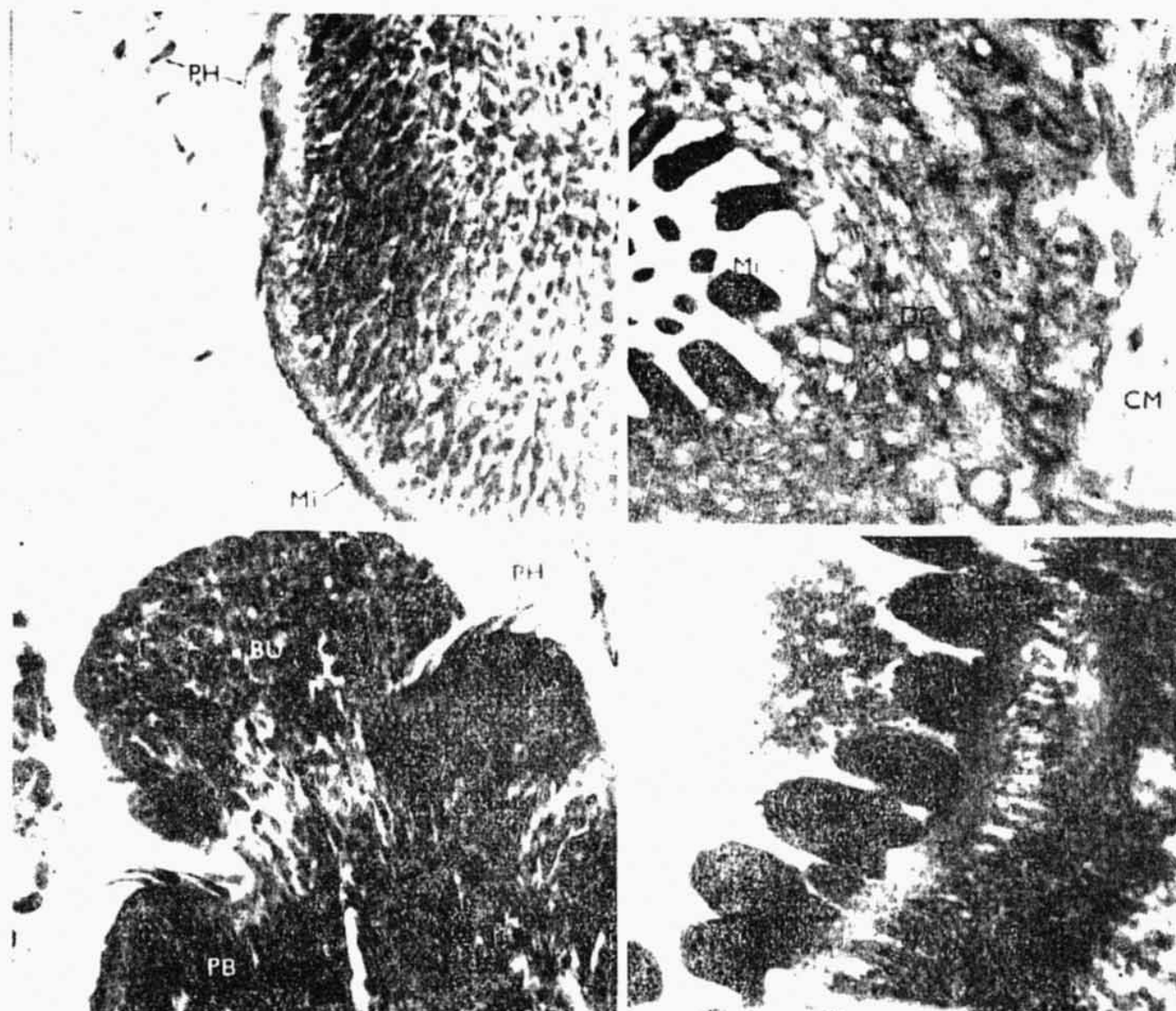


Fig. 1. Oblique section through rostellar cone (RC). In addition to microtriches (Mi), its tegument contains differently staining hooklets (PH); these break off into the canal lumen. (Mallory's PTAH, $\times 68$.)

Fig. 2. Tangential section through the cone divided into a bulb (BU) and praebulb (PB). The fold separating the praebulb contains larger hooklets (PH) with a differently staining base. (Masson's trichrome, $\times 68$.)

Fig. 3. Very slanted section through a fold in the tegument of the invaginated canal. The electron micrograph shows a microtrix border with electron dense distal peaks, and a narrow zone of vacuolated distal cytoplasm (DC). This is separated from the subtegumental muscle fibers (CM) by a thin basal membrane. (Uranyl acetate, $\times 10,262$.)

Fig. 4. Oblique section through the bases of larger hooklets in the fold of the tegument (T) separating the praebulb. (Goldner's trichrome, $\times 68$.)



Fig. 1. Tangential section through the bases of hooks (H) enclosed in the hook organ (HO). After staining with Goldner's trichrome, orange and blue coloured granules could be seen in this organ. ($\times 100$).

Fig. 2. Tangential section through the rostellar pad surrounded by a rostellar sac (RS). The elongate praebulb filled with nuclei and several muscle fibers. Note sections through hooks (H) in the hook organ. (Goldner's trichrome, $\times 25$.)

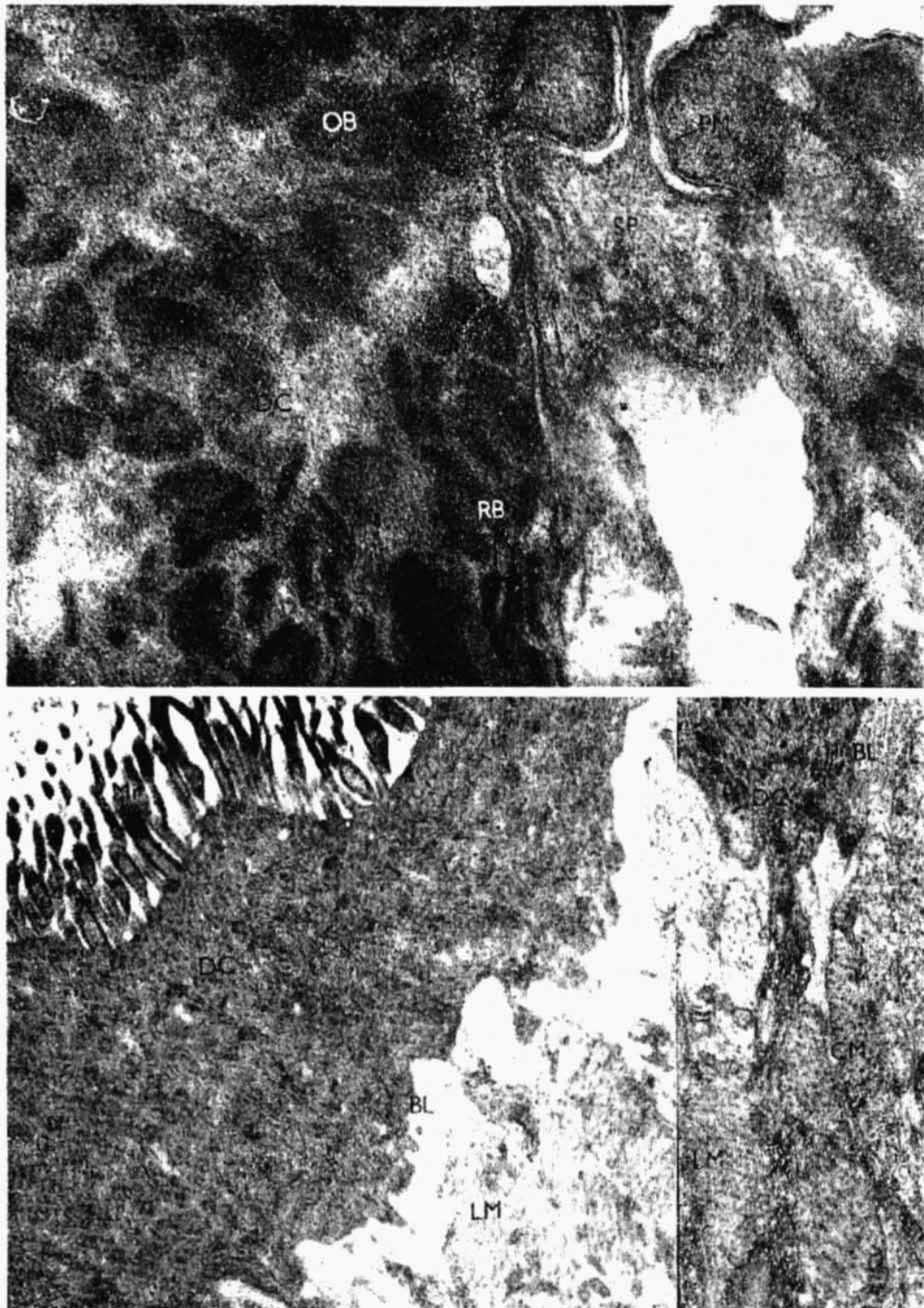


Fig. 1. The electron micrograph shows the upper section of the distal cytoplasm (DC) in the tegument of the spiral canal, with sensory endings (SP). The surface of the cytoplasm is delineated by a plasma membrane (PM) covering also the tips of the sensory endings. The cytoplasm contains rod-shaped bodies (RB) and dense, membrane-bounded oval bodies (OB). (Uranyl acetatelead citrate stain, $\times 50,980$.)

Fig. 2. Electron micrograph of the tegument of the spiral canal of *M. endothoracicus* showing the microtrix border (Mi) with electron dense distal peaks, the wide zone of distal cytoplasm (DC) and its processes traversing the basal membrane (BL) and proceeding between longitudinal (LM) and circular (CM) subtegumental muscle fibers. (Uranyl acetatelead citrate stain, $\times 10,060$.)

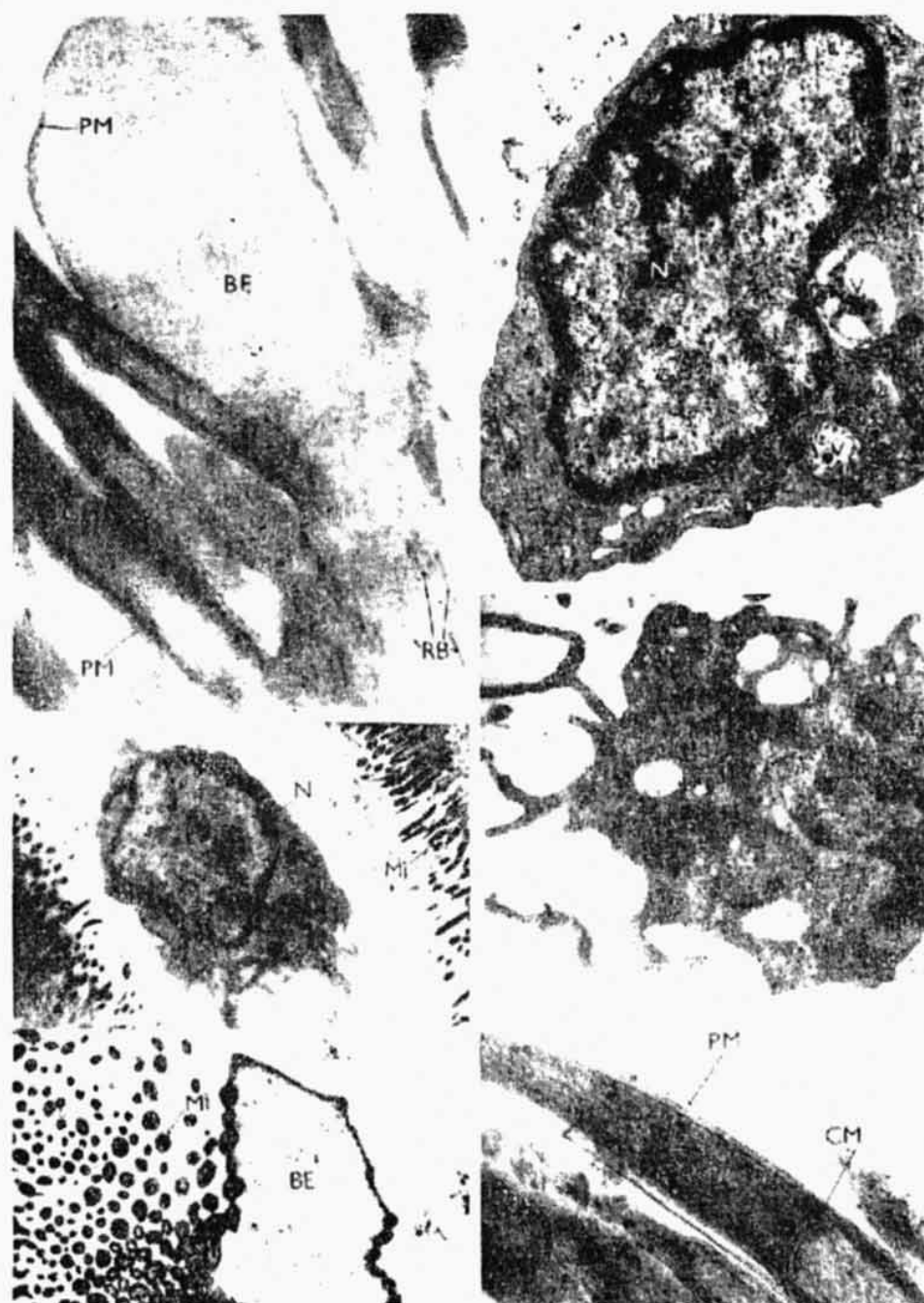


Fig. 1. Electron micrograph showing the superficial microtrix border. The distal half of the microtriches is electron dense, the basal region less electron dense. Densification on the surface of the plasma membrane (PM). The distal part of the microtriches is partly separated from the proximal part by a membranous cap. Among the microtriches is a bulboid extrusion (BE) filled with less electron dense material and bordered by a plasma membrane (PM). ($\times 15,190$.)

Fig. 2. Polymorphonucleate leukocyte in the lumen of the spiral canal. Note its bisegmented nucleus (N) and the granular substance in the vicinity of the tegumental microtriches (Mi). ($\times 3,375$.)

Fig. 3. Cytoplasmic extrusion in the microtrix border of the spiral canal in the vicinity of the leukocyte. The surface of the extrusion carries the distal parts of the microtriches. ($\times 4,890$.)

Fig. 4. Detailed view on part of the leukocyte with its nucleus (N). Vacuoles (V) with phagocytized remnants present in the plasma between the endoplasmic reticulum and the mitochondria (M). ($\times 16,875$.)

Fig. 5. Host cell in the lumen of the spiral canal between microtriches. Note part of the multi-segmented nucleus, vacuoles and numerous plasma processes extending towards the microtriches, in the host cell. A coralloid segmentation on the distal peak of a microtrix. ($\times 15,190$.)