TEGUMENTAL ULTRASTRUCTURE OF RAILLIETINA CESTICILLUS DURING THE LARVAL-ADULT TRANSFORMATION, WITH EMPHASIS ON THE ROSTELLUM

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Abstract
BLITZ N. M. and SMYTH J. D. 1973. Tegumental ultrastructure of Raillietina cesticillus during the larval-adult transformation, with emphasis on the rostellum. International Journal for Parasitology 3: 561-570. No major ultrastructural reorganisation was observed in the tegument of Raillietina cesticillus during the larval-adult transformation. The rostellar tegument is very thin and densely vesiculated. In the freshly evaginated larva these vesicles are small and appear empty, whereas in the developing parasite they are more numerous, larger and have a flocculant content; they occasionally appear to fuse with giant vesicles in the perinuclear cytoplasm. The rostellar microtriches, in contrast to those on the strobila, lack a distal spike, a feature which may be associated with an absorptive function. There are numerous sensory endings on the rostellum which are characterised by a single cilium with a 9 + 6 + 1 substructure. The rostellum has well developed musculature with abundant intramuscular mitochondria.

The rostellar tegument thickens significantly during development, and other (minor) differences in ultrastructure were noted as the parasite developed. No mitochondria were observed in the distal cytoplasm of the strobilar tegument. The sensory endings in this region lacked a cilium, and often terminated within the distal cytoplasm.

INDEX KEY WORDS: Raillietina cesticillus; cestode; ultrastructure; scolex; rostellum; tegument; sensory endings; mitochondria; larval-adult transformation.

INTRODUCTION
THE ULTRASTRUCTURE of the cestode tegument has been the subject of numerous investigations since Read (1955) and Kent (1957) first described it. However, the majority of these studies have been concerned with the strobilar tegument of mature parasites, with relatively little attention being paid to the scolex, or to developmental aspects of tegument ultrastructure during the larval-adult transformation. It might be expected that this dynamic process would involve a switch in metabolism and major ultrastructural reorganisation associated with the change in environment from a cold-blooded to a warm-blooded host. This lack of interest in the scolex might be due to the long established belief that it was little more than an organ of attachment. There is increasing evidence, however, that the rostellum is an area of great physiological activity, and that it may be involved in the secretion of absorption of materials (Smyth et al., 1967; Smyth, 1969). This view is supported by the unique nature of the rostellar tegument, as demonstrated in the few studies on cestode ultrastructure in which it has been examined, (Rothman, 1963; Jha & Smyth, 1971; Smyth, 1972; Featherstoen, 1972). Associated with this, however, are formidable difficulties in fixation, which have been apparent in these studies on rostellar ultrastructure, and which also appeared in the present investigation.

This report deals with the rostellar ultrastructure of Raillietina cesticillus during the larval-adult transformation on passage from the poikilothermic intermediate host (the flour
beetle *Tribolium*) to the homiothermic definitive host (the fowl), and serves as a basis for further cytochemical studies on the role of the rostellum in the parasite’s physiology. The fine structure of the developing strobilar tegument is also examined, and some points raised by the early studies of Read (1955) and Kent (1957) on *R. cesticillus* are clarified in the light of the improved techniques now available.

**MATERIALS AND METHODS**

*R. cesticillus* is conveniently maintained in the laboratory in beetles of the genus *Tribolium*, and in chicks. Development of the larval stages of the parasite in the beetles is completed in approximately two weeks at 26°C, and the prepatent period in the chick is of similar duration (Dutt *et al.*, 1961).

Specimens for electron microscopy were obtained from cysts freshly dissected from beetles in full insect Ringers, (Landureau, 1966). Some larvae evaginated spontaneously under these conditions, whilst others were forced out of the cysts with fine needles. Developing parasites were obtained from young chicks after 1, 2, 4, 6, 8, 12 and 14 days post-infection. They were dissected out of the chicks’ intestines in Hanks saline at 39°C. The reagents used for the fixations, and the schedule followed, were as described by Lumsden (1970), except that the specimens were embedded in TAAB resin (TAAB Labs., Reading). Thin sections were cut on a Huxley Mark 2 ultramicrotome, mounted on uncoated copper grids, and stained with saturated uranyl acetate in 50% ETOH, followed by lead citrate (Venable & Coggeshall, 1965). They were examined with a Phillips EM 300 microscope at 60-80 kV.

**OBSERVATIONS**

The account below is based on freshly evaginated larvae from beetles, and on developing larvae and mature worms recovered from chicks. Attention is drawn to differences in these stages where they occur.

1. **Morphology of the scolex, and general structure of the rostellum**

   The basic structure of the scolex is shown in Fig. 1. At the base of the rostellum is a ring of numerous small hooks and a lip, bearing spines, encircles the hooks and the rostellum. There are four unarmed suckers on the scolex.

   Figure 2 diagramatically illustrates the general ultrastructure of the rostellum. A thin layer of densely vesiculated distal cytoplasm, 0.5-1.0 μm thick, and bearing microtriches, overlies a basal plasma membrane, invaginations of which commonly penetrate into the

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**Fig. 1. Diagram of the scolex of Raillietina cesticillus.**
distal cytoplasm. Below the basal plasma membrane is a basal lamina and a layer of small, superficial, transverse muscles followed by what is presumed to be the perinuclear cytoplasm (= subtegumental cells) (Fig. 4). A prominent basal lamina and a plasma membrane lacking invaginations, underlies the perinuclear cytoplasm, and below it is a layer of large, transverse muscles (Fig. 3). From parts of this muscle layer, thick bundles of longitudinal muscles run down to the base of the rostellum, where they join a layer of deep transverse muscles. The areas between these longitudinal muscles are packed with mitochondria (Fig. 3), as well as endoplasmic reticulum and occasional nuclei. Elsewhere, areas of the
subtegumental tissues are devoid of the longitudinal muscles but contain numerous nuclei, associated with a group of cells which may represent a rostellar gland.

2. Ultrastructure of the rostellar tegument

The rostellar microtriches are fairly uniform in structure; most are single, but occasional branched microtriches were observed. They are approximately 1·0 \( \mu \)m long and 0·1 \( \mu \)m in diameter (Fig. 4). The dense distal caps, so typical of cestode microtriches, are absent or greatly reduced, and fine filaments frequently extend from their tips. In transverse section (Fig. 9), the microtriches are seen to have a limiting plasma membrane and glycocalyx, and an electron lucid core that contains electron dense structures, possibly filaments.

The distal cytoplasm is profusely vesiculated. In the freshly evaginated cysticercoid, the vesicles are fewer, smaller (\( \sim 0·1 \mu \)m dia.), and appear empty (Fig. 4) in contrast to the situation in developing and mature parasites recovered from the chick, where the distal cytoplasm often appears to consist of nothing but vesicles, which are larger (0·3-0·5 \( \mu \)m dia.) and contain a flocculant material (Fig. 5). Only rarely were these vesicles observed opening to the exterior. Small, flattened, membrane-bound organelles occur in the distal cytoplasm between these fluffy vesicles (Fig. 5); they have electron-lucid contents and occasionally a small electron-dense particle. Mitochondria were not observed in the distal cytoplasm of freshly evaginated larvae, but were sometimes seen in developing worms recovered from chicks (Fig. 7). They often had unusual profiles.

Sensory endings were frequently observed in the rostellar tegument, and in one instance, five of them were counted within 5 \( \mu \)m of a single section. However, they are not evenly distributed over the surface of the rostellum, most being laterally placed, with relatively few on the apex. They are of uniform structure (Figs. 4 & 6), consisting of a sensory sac attached to the surface plasma membrane by a prominent septate desmosome, and usually containing a single mitochondrion and one or more microvesicles, as well as the basal body and inconspicuous rootlets of a single cilium. The cilium is of similar length to the microtriches, (approximately 1 \( \mu \)m) but is considerably thicker (roughly 0·15 \( \mu \)m dia.), and has an interesting distal substructure of 9 + 6 + 1 (Fig. 9) which is apparently reduced to 9 + 1 and then 9 + 0 basally. In all cases the nine outer microtubules have the typical doublet structure of cilia. Fibres appear to radiate from the junction between the a and b subfibres, of the 9 peripheral doublets, to the plasma membrane around the cilium.

The perinuclear cytoplasm generally resembles that described in other studies on cestode ultrastructure. Of interest, however, is the scarcity of nuclei in this layer and the large mito-

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**Figs. 3-15.**

**Abbreviations used in the Figures**

- *BL*-basal lamina
- *CB*-cytoplasmic bridge
- *CM*-circular muscle
- *DC*-distal cytoplasm
- *FL*-fibrous layer
- *GV*-giant vesicle
- *HD*-hemi desmosome
- *LM*-longitudinal muscle
- *M*-microthrix
- *Mc*-mitochondrion
- *MvB*-multivesicular body
- *PC*-perinuclear cytoplasm
- *Rt*-rootlets
- *SC*-sensory cilium
- *SD*-septate desmosome
- *Sp*-spine
- *TM*-superficial transverse muscle
- *TM*-intermediate transverse muscle
- *TW*-terminal web
- *V*-vesicle
Fig. 3. Low power micrograph of longitudinal section through the apex of the rostellum showing the musculature. Mature worm. × 10,700.
Fig. 4. Rostellar tegument of freshly evaginated larva. Note the small empty vesicles in the distal cytoplasm, and the sensory organelle. Also the large mitochondria with longitudinal cristae (arrows) in the perinuclear cytoplasm. $\times 37,600$. 
Fig. 5. Giant vesicle in the rostellar perinuclear cytoplasm. Note the apparent fusion with smaller vesicles from the distal cytoplasm (arrows), and their flocculent contents. Mature worm. ×28,600.

Fig. 6. Sensory organelle in the rostellar tegument of a freshly evaginated larva. ×75,000.

Fig. 7. Distal cytoplasm of rostellar tegument showing mitochondria with irregular profiles. Mature worm. ×32,600.

Fig. 8. Mitochondrion in the rostellar subtegumentary tissue. Mature worm. ×30,100.

Fig. 9. Transverse section of the distal end of a sensory cilium and rostellar microtriches. Note the 9 + 6 + 1 substructure of the cilium. ×180,000.
Fig. 10. Longitudinal section through the spiny lip encircling the rostellum. Note the normal (white arrow) and irregular (black arrows) mitochondria in the perinuclear cytoplasm. Freshly evaginated larva. × 25,500.

Fig. 11. Distal cytoplasm of the scolex posterior to the suckers. The large multivesicular body is assumed to be a lateral section through a sensory ending. Freshly evaginated larva. × 47,900.
FIG. 12. Distal cytoplasm of strobilar region of freshly evaginated larva. Note the terminal web below the microthrix border, the hair-like filaments (arrows), and the many round vesicles packing the distal cytoplasm and extending into the microtriches. Note also the absence of mitochondria.  x 41,000.

FIG. 13. Distal cytoplasm of strobilar region of 48 h old worm. Note the invaginations of the basement membrane (arrows), the shape and dense contents of the vesicles, and the absence of mitochondria.  x 34,900.
Fig. 14. Strobilar tegument of mature worm. Note the absence of mitochondria. × 10,100.

Fig. 15. Distal cytoplasm of mature parasite. Note the two double sensory endings (arrows) terminating in the distal cytoplasm and lacking a cilium. × 19,400.
chondria with longitudinal cristae, which were frequently observed (Fig. 4). Vesicles resembling those found in the distal cytoplasm are also found in this layer. In one mature worm a few ‘giant’ vesicles were located in the perinuclear cytoplasm (Fig. 5). They are 2–6 μm in diameter and of irregular shape. Fluffy vesicles identical to those in the distal cytoplasm, were observed adjacent to, and fusing with, these giant vesicles, and their contents are of a similar flocculant nature. Additionally, pieces of membrane were observed in the giant vesicles.

3. Ultrastructure of the (remaining) scolex tegument

As indicated in Fig. 1, a lip, bearing spines on its surface, encircles the rostellar and the ring of hooks. Under the electron microscope, these spines are seen to be modified microtriches of varying size and shape, but possessing the basic microthrix structure (Fig. 10). Similar microtriches were observed on the suckers. The distal cytoplasm of the spiny lip and the suckers somewhat resembles that of the rostellar, containing vesicles and, what appear to be, multivesicular bodies. The latter, however, are probably marginal sections through sensory endings, as typical sensory endings, of the type described earlier, were also observed on this lip. Below the basal lamina of the lip’s distal cytoplasm, are well developed muscle bundles which encircle the rostellar. The perinuclear cytoplasm, and possibly parenchymal cells, fill the interior of the lip. Some of the mitochondria in the perinuclear cytoplasm again show unusual profiles, with longitudinal and/or concentric cristae (Fig. 10).

The tegument covering the rest of the scolex (Fig. 11), appears generally similar in structure to the strobilar tegument. The microtriches are of the basic pattern, and the tegument is thicker and less vesiculated than on the rostellar.

4. Ultrastructure of the strobilar tegument

The strobilar tegument of *R. cesticillus* (Figs. 12–15) is comparable to that described in other studies on cestode ultrastructure. The microtriches have the characteristic pattern, with an electron dense terminal spike, and the distal cytoplasm, which is compact and studded with a variety of inclusions, overlies a basal plasma membrane with prominent invaginations (Fig. 13), some resembling the multitubular complex described in *Hymenolepis diminuta* (Threadgold & Read, 1970; Reissig, 1970). Sensory endings were also observed in the distal cytoplasm (Fig. 15), and tend to be concentrated in the interproglottidal region. Whilst possessing a similar basic structure to the sensory endings described in the scolex, they differ in a number of characteristic ways. Most important was the apparent absence of a distal ciliary process. One cannot rule out the possibility that the strobilar sensory endings were all sectioned lateral to the cilium, but this seems unlikely, as it was almost always seen in the rostellar endings, but never in those on the proglottids. Moreover, a number of these sensory endings appeared to terminate within the distal cytoplasm of the proglottids (Fig. 15), rather than on the surface, though here again the plane of sectioning might have been the cause of this observation. Finally, some of these organelles have double endings (Fig. 15), a condition that was never observed in the scolex.

A surprising feature of this species is the apparent absence of mitochondria in the distal cytoplasm of the strobilar tegument. Numerous specimens were examined at various stages of development, but in no case were mitochondria observed.

The freshly evaginated larvae (Fig. 12) has well developed microtriches and what appears to be a terminal web, just below the microthrix border. Round vesicles pack the distal cytoplasm and extend into the base of the microtriches. Many of these vesicles contain small,
electron-dense aggregates. Conspicuous, hair-like projections were also observed between the microtriches; these, as well as terminal web and the vesicles in the base of the microtriches, all disappear within the first two days of development in the chick, at which stage the vesicles take on a more flattened shape, and the aggregates of electron dense material in them appear larger (Fig. 13). After six days development, however, these aggregates were no longer observed. The distal cytoplasm thickens significantly during the 14 days development, from ~2 \( \mu \text{m} \) in the freshly evaginated larva to ~6 \( \mu \text{m} \) in the gravid proglottid. The musculature and perinuclear cytoplasm beneath the basement membrane of the distal cytoplasm fit the general cestode pattern, and warrant no further attention.

**DISCUSSION**

When fully evaginated, the dome-shaped rostellar of *R. cesticillus* presents a large surface area at the host–parasite interface, which is greatly increased by the microtriches covering its surface. However, this region of the parasite's surface also has the unique property of being fully retractable, which raises interesting questions regarding its function(s), and provides a possible explanation for the difference in gross structure between the rostellar and strobilar distal cytoplasm. The former is generally less than 1 \( \mu \text{m} \) thick and is, therefore, easily buckled on retraction, which would be difficult were it as thick as on the proglottids (6–7 \( \mu \text{m} \)). This difference was also noticed in *Echinococcus multilocularis* (Sakamoto & Sugimura, 1969), although the rostellar distal cytoplasm of *Taenia hydatigena* appears to be much thicker (Featherstone, 1972).

The longitudinal muscles, which presumably retract the rostellum, are well developed and are closely associated with numerous mitochondria, an arrangement which suggests considerable physical activity. Using an *in vitro* system, we have frequently observed 'probing' behaviour of the parasite and the presence of numerous sensory endings on the rostellum suggests that this activity might be important in site location. On the other hand, it is impossible to observe the action of the rostellum *in vivo*, and as the parasites are presumably attached most of the time, one questions the relevance of these observations. Nevertheless, the ability to retract its rostellum suggests that this is a vulnerable region of the parasite, possibly associated with specific sensory functions.

Two distinct types of sensory endings were observed in the tegument of *R. cesticillus*. One has a distal ciliary process and appears to be restricted to the surface of the scolex; the other apparently lacks the cilium and occurs on the surface or within the distal cytoplasm of the strobilar tegument. Featherstone (1972) also observed these two types of sensory endings in *T. hydatigena*, but in contrast to our findings he observed no sensory endings in the rostellum, and only found the ciliated endings in the more terminal proglottids of older worms. The other type were much more widely distributed over the surface of the tegument (Featherstone, pers. commun.). On the other hand, Jha & Smith (1971) have recorded similar sensory endings with a distal process in the rostellum of *E. granulosus*, as have Sakamoto & Sugimura (1969) in the rostellum and suckers of *E. multilocularis*. Morseth (1967b) has also reported them from unspecified areas of *E. granulosus*. There seems to be less information on the other type of sensory ending, but a number of earlier workers appear to have overlooked them in the strobilar tegument. Thus the 'evagination' in the strobilar tegument of *H. diminuta* described by Lumsden (1966; Fig. 9), is clearly one of these sensory endings and the 'subcuticular canals' of Yamane (1968, 1969) in *Diplogonoporus grandis* and *Diphylobothrium erinacei* are probably also sensory endings. The same can be said of the 'pore canals' described by Threadgold (1962) in *Dipylidium caninum*.
and by Morseth (1966) in *T. pisiformis*, as pointed out by Featherstone (1972). In none of these cases, however, is there any evidence of a distal ciliary process. Lyons (1969) and others, who have described similar sensory endings with a cilium in various trematodes, have tentatively ascribed a tangeoreceptor or rheoreceptor function to them. In the absence of any experimental evidence one could also speculate that they might as readily be chemoreceptors. Whatever their function, the ciliary substructure of 9 + 6 + 1 described here for *R. cesticillus* does not seem to have been reported before, and contrasts with the characteristic 9 + 2 substructure in the sensory cilium of *Gyrodactylus* and other monogeneans (Lyons, 1969). The substructure of the ciliary process in the sensory endings of other cestodes has not been elucidated. Morseth (1967b) has a micrograph showing a T.S. through the cilium within the sensory sac, in which one can see nine outer fibres, and possibly six inner ones, but no central (pair of) fibre(s) is visible.

Besides a sensory function, it is also possible to ascribe a 'placental' or absorptive role to the rostellar tegument, as suggested by Smyth *et al.* (1967) and Smyth (1969). This in itself is nothing new, as the tegument of cestodes has long been implicated in the uptake of nutrients, but most of the studies have been done on the strobilar tegument, the assumption being that the tapeworm scolex was simply an organ of attachment. The present investigation supports the findings of Jha & Smyth (1971), Featherstone (1972), Sakamoto & Sugimura (1969) and Rothman (1963) on *E. granulosus*, *T. hydatigena*, *E. multilocularis* and *H. diminuta* respectively that the rostellar microtriches differ significantly from those on the proglottids, being generally longer and thinner. Yet in all those reports it was the electron dense distal spike of the microthrix that was elongated, whereas in this study the electron dense cap was greatly reduced or absent. Sakamoto & Sugimura (1969) described similar microtriches, lacking a dense cap, on the brood capsule and germinal membrane of *E. multilocularis*. If, as Rothman (1963) and others have suggested, absorption is limited to the medullar base of the microthrix, with the spike acting mainly for locomotion and attachment, this would favour an absorptive function for the rostellar microtriches of *R. cesticillus*. Moreover, they certainly resemble epithelial microvilli more closely than most cestode microtriches described to date. There is, however, no experimental evidence for such diversity in microthrix function, and it is difficult to ascribe different roles to the rostellums of the few tapeworms investigated, as this would imply.

In a recent study of the host–parasite interface of three tetraphyllidean tapeworms, McVicar (1972) presented evidence which suggested that the scolex of *Acanthobothrium quadripartitum* and *Phyllobothrium piriei*, both of which lack a rostellum, had no nutritional function, with the bothria on them acting solely as holdfasts. The scolex of *Echeneibothrium*, however, has a protrusible extension, called a myzorhynchos, which, according to McVicar, is probably involved in the parasite’s nutrition. Thus, it seems possible that the myzorhynchos of this genus is functionally analogous to the rostellum of some cyclophyllidean cestodes.

Although it seems likely that the rostellar of *R. cesticillus* is involved in the uptake of nutrients, there was no evidence in this study of any secretions from the rostellar region, as has been reported in *E. granulosus* (Jha & Smyth, 1971). The contrast in matrix between the rostellar and strobilar distal cytoplasm has also been noted by other investigators (Rothman, 1963; Featherstone, 1972); the latter is always described as being compact or dense, with various small inclusions, whereas the former is highly vesiculated in *R. cesticillus*, as well as in *T. hydatigena* (Featherstone, 1972). The fluffy vesicles in the rostellar tegument could be pinocytotic vesicles, but there is, as yet, no direct evidence for this. Nevertheless, the fact that they were clearly seen to fuse with the 'giant' vesicles in the perinuclear cytoplasm could also be taken as support for their being (endo) pinocytotic, as the reverse process seems
rather unlikely. Although unsuccessful attempts have been made to demonstrate this phenomenon in cestodes (Lumsden et al., 1970), this does not invalidate the present suggestion, as previous investigations were limited to the strobilar tegument, whilst the so-called ‘fluffy’ vesicles and ‘giant’ vesicles observed in *R. cesticillus* were restricted to the rostellar tegument. Moreover, although vesicles were observed in the rostellar tegument of freshly evaginated larvae, they differed from the fluffy vesicles observed in worms recovered from the chicks, being both smaller and lacking the floculent contents. It is clear, however, that uptake studies, using tracers, will be necessary to resolve this question. Whatever their significance, it seems likely that the vesiculated nature of the rostellum is largely responsible for the difficulties it presents in fixation.

The apparent absence of mitochondria in the strobilar distal cytoplasm of *R. cesticillus* is surprising, particularly in view of earlier reports describing them in this species (Read, 1955; Kent, 1957). However, these were the first preliminary descriptions of the ultrastructure of cestode tegument, and close examination of the figures in them does not reveal any organelles that could be described as mitochondria with any confidence. Yet mitochondria can be observed in the micrographs of *H. diminuta* which appear in the same publications. Mitochondria have been observed in the distal cytoplasm of all the published accounts of cestode ultrastructure to date, although they are rare in *Calliobothrium verticillatum* (Lumsden, 1966), and Morseth (1966) quotes Rundell (1957) as having examined the body covering of six species of cestodes (unnamed), some of which had mitochondria, whilst others did not. The present results are in accord with those of Baron (1971) who was also unable to demonstrate mitochondria in the distal cytoplasm of the ‘scolex’ of *R. cesticillus* cysticercoids. The significance of this finding is difficult to assess, but clearly ultrastructural cytochemistry could yield some intriguing results.

Although mitochondria were not positively identified in the rostellar distal cytoplasm of freshly evaginated larvae, they were occasionally observed in worms of various stages recovered from chicks. These mitochondria frequently had unusual profiles, as did some of those in the perinuclear cytoplasm of the rostellum and the spiney lip, and in the deeper layers of the rostellum. They were larger than most of the other mitochondria, measuring up to $1.5 \times 0.5 \mu m$, and were packed with parallel arrays of longitudinal cristae. Nothing analogous was reported in Lumsden’s (1967) account of the mitochondria of *Lacistorhynchus tenuis*, but his observations were restricted to the strobila. It is interesting to record that the cristae in the strobilar mitochondria are generally short and sparse, a condition that is associated with the low oxygen tension of the tapeworm’s environment. Thus it seems possible that the unusual mitochondria observed in the rostellum of *R. cesticillus* are in some way related to the proximity of this organ to the host’s mucosa, which has a higher oxygen tension than the gut lumen in which the tapeworm’s strobila is located.

Comparison of the ‘strobilar’ tegument of the freshly evaginated larva (which does not, in fact, have a strobila per se, but has a posterior region which is structurally analogous to it) and mature or gravid proglottids, shows that remarkably little difference exists between them. Thus the tegument appears to be more or less fully formed in the infective larva. The significance of the vesicles and the ‘terminal web’ observed at the base of the microthrix border remains obscure, for although one can postulate that they are involved in the formation of the microtriches, these seem to be complete by this stage, unlike those in *E. granulosus* protoscoleces (Morseth, 1967a). The presence of dense inclusions within membranes in the strobilar distal cytoplasm, is a common characteristic of cestode teguments, and no definite role can be given to the electron dense granules observed within vesicles in the distal cytoplasm of the early developmental stages of this parasite.
Thus, although metabolic differences between the larval and adult stages might be predicted, no major ultrastructural reorganisation of the rostellar tegument appears to occur in *R. cesticillus*. There may, of course, be physiological differences due to changes in enzyme activity during the larval–adult transformation, but no cytochemical observations were made during this investigation to answer these questions. It is hoped to deal with these in a further study.

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