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MULTICILIATE SENSORY ENDINGS IN THE REDIA OF ECHINOSTOMA REVOLUTUM (TREMATODA, ECHINOSTOMATIDAE)

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Abstract. In addition to uniciliate sensory endings, three types of multiciliate sensory endings have been demonstrated on the anterior end of *Echinostoma revolutum* redia using transmission and scanning electron microscopy. This is the first finding of multiciliate sensory endings in the parthenogenetic generation of trematodes. In the first type, 12 cilia are situated in a pit communicating with the tegument surface. In the second and third types, there are two and four short cilia, respectively. They protrude from the nerve bulb above the surface of the tegument. The significance of multiciliate sensory endings in rediae and their similarity to multiciliate sensory endings in miracidia and cercariae is discussed.

The rediae and sporocysts of trematodes have been known to possess only uniciliate and nonciliate sensory endings (Rees 1966, 1980; Krupa et al. 1967, 1968; Bibbi and Rees 1971; Køie 1971a, b, 1985, 1987; Irwin et al. 1978; Page et al. 1980; Dobrovolskii et al. 1983). However, during a detailed study of serial sections of *E.revolutum* rediae in transmission electron microscope we have observed typical multiciliate receptors around the oral opening. Since from the phylogenetic point of view the parthenogenetic generation of trematodes is considered a reduced parasitic generation of adults (Žďárská 1986), the echinostome parthenitae, on the basis of demonstrated multiciliate receptors, would represent a group of parthenogenetic generation with best preserved receptors similar to free-living forms of flatworms. The receptors of *E.revolutum* redia resemble most of all the sensory endings of free-living Turbellaria, free-swimming larvae of Amphilinidea (Cestodaria), and free-swimming miracidia and cercariae of trematodes. The multiciliate sensory endings in the rediae seem to enable their orientation in the snail tissue during its mechanical damaging and, particularly, their predatory and cannibalistic activity.

MATERIALS AND METHODS

The rediae of *E. revolutum* were isolated from *Planorbarius corneus* (according to Kanev 1985 this trematode species develops only in snails of the family Lymnaeidae). They were fixed in 3% glutaraldehyde in 0.1 M cacodylate buffer, pH 7.2, at 4 °C for 2 h and postfixed in 1% OsO_4 for 2 h. Then they were dehydrated through an alcohol series and transferred through acetone to Durcupan. Ultrathin sections were cut by Reichert's OM-U2 ultramicrotome, contrasted by saturated water solution of uranyl-acetate and Reynolds' solution of lead citrate, and examined in JEM 100B and PHILIPS 300 electron microscopes. For scanning electron microscopy, the rediae were dehydrated through alcohol and acetone series, critical point dried, coated with gold and examined in TESLA BS-300 scanning electron microscope at 15 kV.

RESULTS

The described types of sensory endings were found in the tegument of anterior end of the redia body wall (Pl. I, Figs.1, 2; Pl. II, Fig.1; Pl. III, Fig.2; Pl. IV, Fig.1). The tegument of the whole body wall projects into short microvilli. The microvilli are preserved even on the tegument covering the pit in the first type of sensory endings and on the tegument close to the other two types of receptors. The second and third types of receptors are localized close to one another (Pl. III, Figs.1, 2), being separated only by a narrow stripe of tegument also provided with microvilli. The nerve fibres of the last two types of receptors penetrate through the layer of longitudinal and circular muscles and lamina basalis and form a bulb in the tegument. Only cilia, but no microvilli are protruding from the nerve fibre.

The multiciliate receptor of the first type (Pl. III, Fig.1; Pl. IV, Fig.2) has the shape of a pit with at least 12 short cilia directed toward its centre. The pit is covered with a fold of tegument, the plasma membrane of which is attached by a septate desmosome to the apical part of the disc- or cup-shaped nerve fibre containing a wide, electron-dense ring and electron-lucid vesicles. In the apical part of the nerve fibre, the basal bodies are anchored to it at the periphery. Short cilia project from the basal bodies toward the centre of the disc or cup (Pl. III, Fig.1; Pl. IV, Figs.1, 2). Between the cilia, short, fine microvilli project from the nerve fibres too.

The multiciliate receptor of the second type (Pl. III, Fig. 2) has two short cilia anchored in the nerve bulb by a basal body. No rootlet is developed. The nerve bulb terminates at the level of tegument surface, the basal body lies higher than the septate desmosome, which is situated at the level of two thin, electron-dense rings reinforcing the nerve bulb. The cilia are not surrounded by a tegument collar, not even by a nerve collar.

The multiciliate receptor of the third type (Pl. III, Fig.2; Pl. IV, Fig.1) has four short cilia, the basal bodies of which are situated in the apical part of the nerve bulb reaching up to the tegument surface. The nerve bulb contains neurotubules and mitochondria. The plasma membrane of the bulb is connected with the plasma membrane of the tegument by a septate desmosome. The bulb is reinforced by a thick, electron-dense ring at the level of the desmosome. There are no microvilli projecting between the cilia from the nerve fibre. The cilia are not surrounded by a collar of tegument or nerve collar.

DISCUSSION

The previous transmission electron microcsopic studies of rediae revealed only uniciliate sensory endings. Only a SEM photomicrograph published by Køie (1987) showed multiciliate-like receptors near the oral opening of *Mesorchis denticulatus* redia.

Considering the known potential antagonism of echinostome rediae to the sporocysts and rediae of other species in case of double infection (Lim and Heyneman 1972, Combes 1982) and their mechanical damaging of the host tissue, it can be supposed that they are provided not only with a well developed feeding apparatus, but also with well developed sensory endings, both chemo- and mechanoreceptors. It has been observed that echinostome rediae consume trematode larval stages not only in case of double infections, but also in single infections. Cannibalism has been recorded by Nasir (1962) in *Echinostoma nudicaudatum* rediae and by Køie (1987) in *Mesorchis denticulatus* rediae feeding on extraredial cercariae of their own species. In our opinion, the good orientation of echinostome rediae inside the host is enabled by special multiciliate receptors similar to the receptors of free-swimming miracidia (Wilson 1970, Chia-Tung 1980), larvae of Amphilinidea (Rohde and Garlick 1985, Rohde et al. 1986), cercariae (Matricon-Gondran 1972, Žďárská et al. 1987) and free-living Turbellaria (Bedini et al. 1975). In all of these worms various types of receptors serving as both mechanoreceptors and chemoreceptors are concentrated at the anterior end of the body.

The receptors observed by us in *E.revolutum* rediae are localized at the anterior end of the body around the oral opening. In all of the three types of receptors the modified and short cilia possess only a basal body, while the rootlet is lacking.

The receptor of the first type (pit with 12 radially arranged cilia) conforms in the shape and number of cilia with the multiciliate deep-pit nerve ending of miracidia of *Schistosoma mansoni* described by Chia-Tung (1980) and is very similar to the receptor of *Paryphostomum segregatum* and *Echinostoma paraensei* cercariae described by Matricon-Gondran (1971). The second and third types of sensory endings in *E. revolutum* redia are very similar to the third type of receptors in Turbellaria described by Bedini et al. (1975), in which the authors observed two and more modified cilia and microvilli and considered this type of receptor to be a chemoreceptor. The sensory ending of the third type resembles also the quadruciliate receptor of *Austramphilina elongata* larva (Rohde and Garlick 1985, Rohde et al. 1986). Since the function of individual types of receptors has not yet been experimentally demonstrated in the plathelminthes, it may be only hypothesized on the basis of their localization and structure whether they are sensitive to mechanical, thermic or chemical stimuli. The receptors communicating with the tegument surface, as is the case of the three types of multiciliate receptors demonstrated by us in *E. revolutum* redia, seem to be both chemo- and mechanoreceptors. Both types of receptors are necessary for the redia with regard to its way of feeding, be it the mechanical damage of the host tissues, predation or cannibalism. This first finding of multiciliate sensory endings in a parthenogenetic generation of trematodes is of phylogenetical and theoretical importance. It confirms the relation of the first parasitic generation of trematodes (parthenitae), to free-living Turbellaria and free-living stages of parasitic flatworms. In addition to the known facts it confirms that the lowest grade of receptor regression, as a result of the parasitic way of living, occurs in the parthenogenetic generation of echinostomes. It is possible that it will be demonstrated also in the parthenitae of other trematodes in the future.

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МНОГОРЕСНИЧНЫЕ СЕНСОРНЫЕ ОКОНЧАНИЯ У РЕДИИ *ECHINOSTOMA* ***REVOLUTUM*** (TREMATODA, ECHINOSTOMATIDAE)

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Резюме. Кроме одноресничных, три типа многоресничных сенсорных окончаний были обнаружены на переднем конце редии *Echinostoma revolutum* с помощью трансмиссионной и сканирующей электронной микроскопии. Это первая находка многоресничных сенсорных окончаний у партенит. У окончаний первого типа имеется 12 ресничек в ямке, соединенной с поверхностью тегумента. У сенсорных окончаний второго типа две реснички и у третьего типа четыре короткие реснички выступают из нервной луковицы над поверхность тегумента. Обсуждается значение многоресничных сенсорных окончаний у редий и их сходство с сенсорными окончаниями у мирацидий и церкарий.

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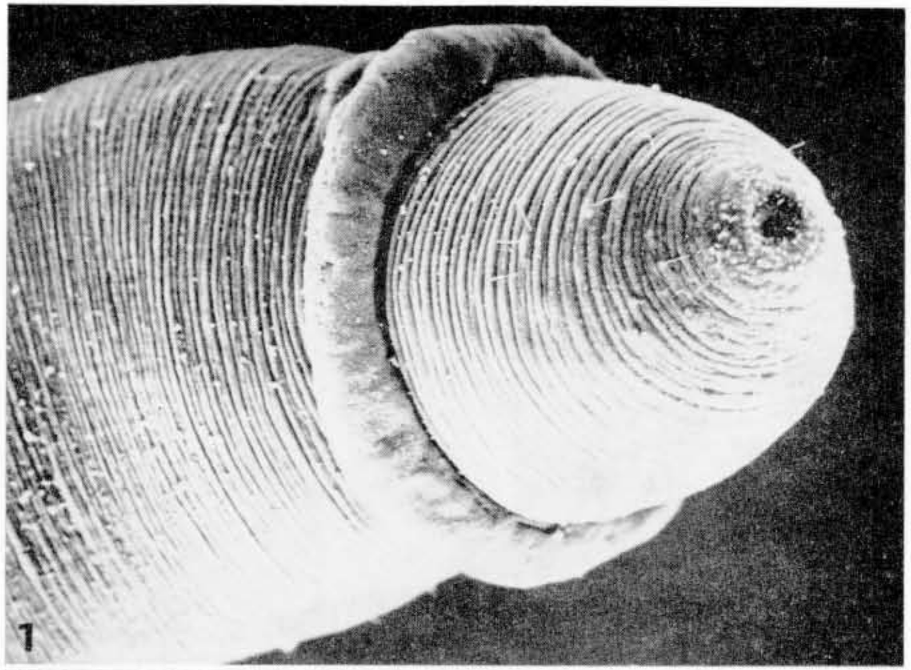


Fig. 1. Anterior end of body of *E. revolutum* redia with 3 types of sensory endings around the oral opening (× 770). **Fig. 2.** Uniciliate and multiciliate (arrows) sensory endings close to oral opening (× 1,350).

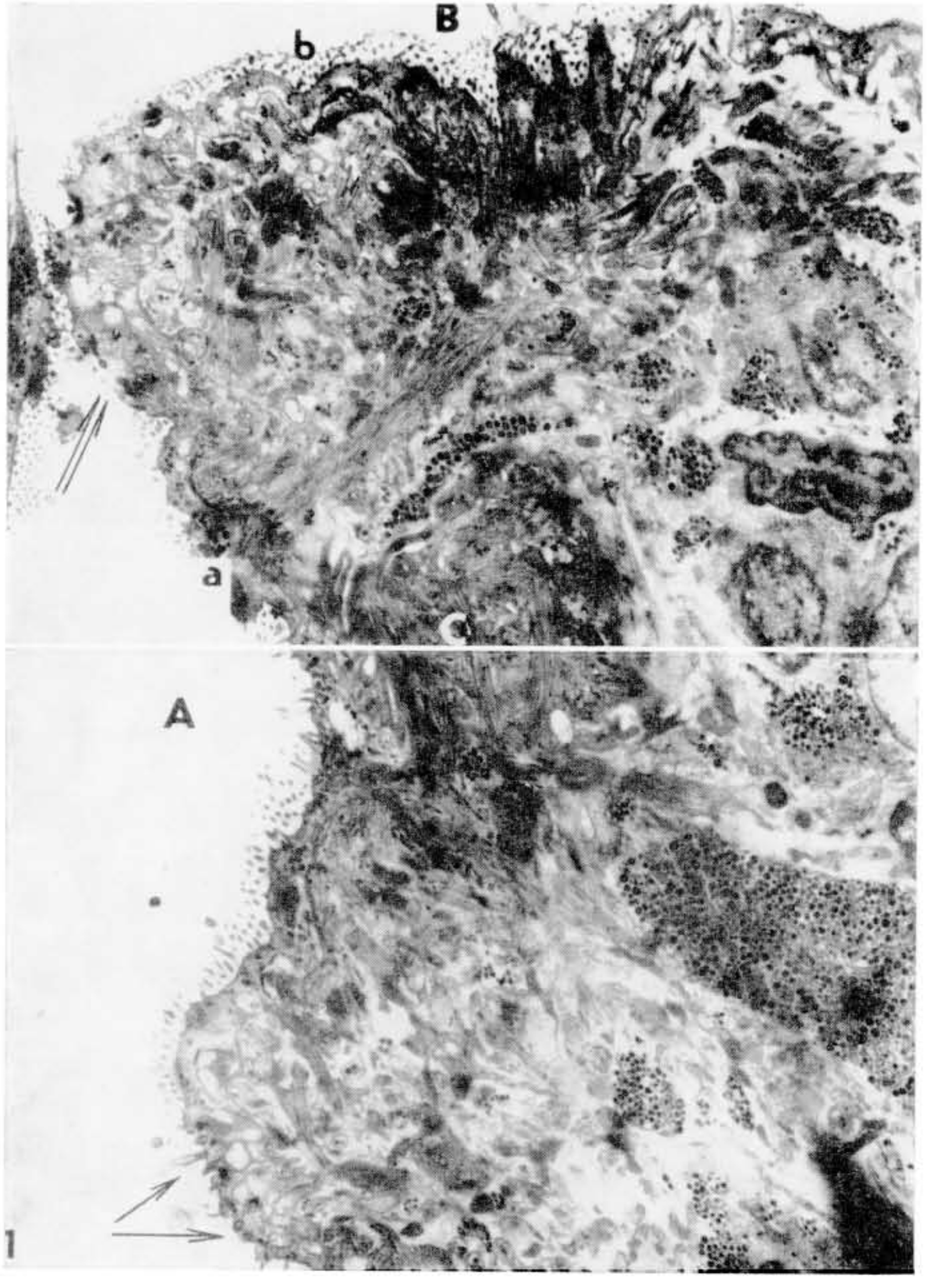
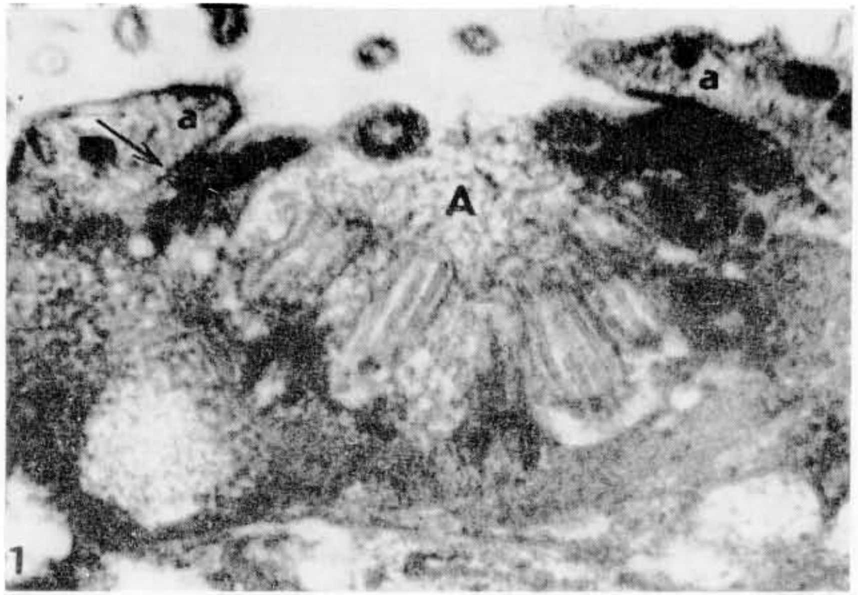


Fig. 1. Longitudinal section through anterior part of *E. revolutum* redia showing the localization of the first type (double arrow) and second and third types (arrows) of multiciliate sensory endings. A — anterior end of redia near the oral opening, B — lateral part of redia body, C — muscles of pharynx; microvillous zone of tegument of oral opening (a) and of lateral part of redia body (b) (G, Os, UAc, Pb) (× 4,500).



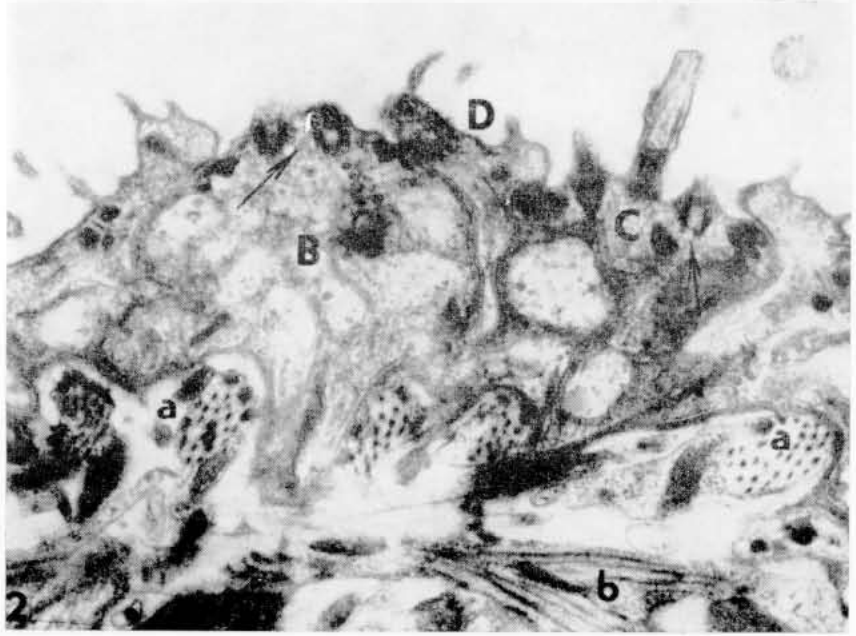


Fig. 1. Detail of the first type of multiciliate sensory ending (a) from Plate II, Fig. 1 (double arrow), which has the shape of a pit with radially arranged short cilia. a — tegument covering the pit, arrow — septate desmosome (G, Os, UAc, Pb) (× 36,980). **Fig. 2.** Second type (B) and third type (C) of receptors depicted in Plate II, Fig. 1 (arrows). The receptors are separated by a narrow stripe of tegument with microvilli (D). a — circular muscles, b — longitudinal muscles of redia body wall, arrows — basal bodies of cilia (G, Os, UAc, Pb) (× 20,880).

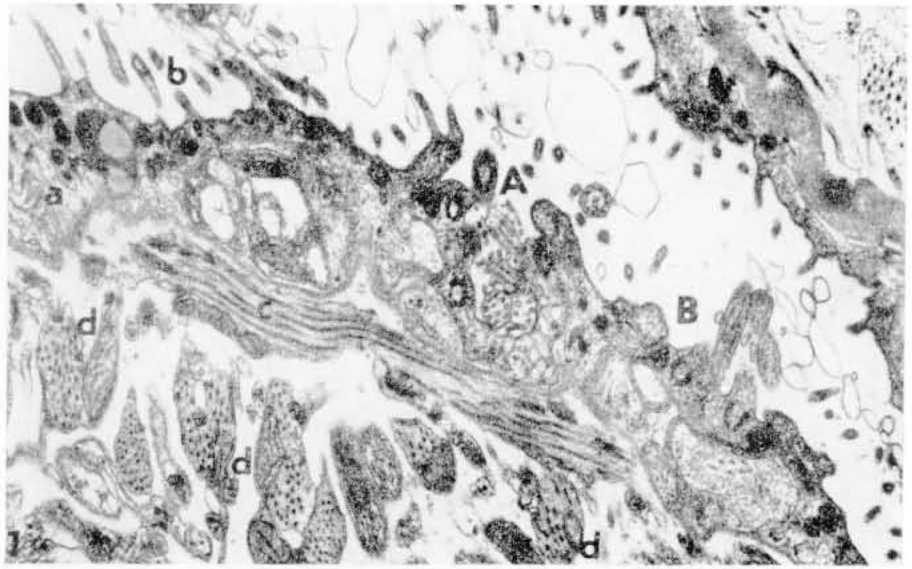


Fig. 1. Transverse section through the body of *E. revolutum* redia at the site of a sensory complex formed by multiciliate pit (A) and quadruciliate receptor (B). a — tegument, b — microvilli, c — circular muscles, d — longitudinal muscles (G, Os, UAc, Pb) (× 17,300). **Fig. 2.** Detail of multiciliate pit from Fig. 1. a — cilia, b — basal bodies, c — electron-dense ring, d — electron-lucid vesicles, arrows — microvilli projecting from the nerve fibre, double arrow — septate desmosome (G, Os, UAc, Pb) (× 40,800).