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Vlaams Instituut voor de Zee  
Flanders Marine Institute

ON THE MORPHOLOGY AND LIFE-HISTORY  
OF *LEPIDAPEDON ELONGATUM*  
(LEBOUR, 1908) NICOLL, 1910  
(TREMATODA, LEPOCREADIIDAE)

Marianne Køie

Marine Biological Laboratory, Strandpromenaden 5, DK-3000 Helsingør, Denmark

ABSTRACT

The cercaria of *Lepidapedon elongatum* develops in rediae in *Onoba aculeus* (Gould) (Prosobranchia, Rissoidae). The cercaria differs from all known lepopocreadiid cercariae in being non-ocellate and in having a small, nearly spherical tail. The cercaria has penetration glands but no stylet. Encysted metacercariae of *L. elongatum* were found in polychaetes and molluscs from the northern Øresund, Denmark. Under experimental conditions cercariae encysted in brittle stars too. Metacercariae develop to infectivity during four weeks in polychaetes, whereas they never or rarely become infective in molluscs and echinoderms. The Atlantic cod *Gadus morhua* L. is the final host in Danish waters, in Greenland waters it also occurs in *G. ogac* Richardson.

Rediae, cercariae, metacercariae and adults of *L. elongatum* were examined by means of light microscopy and stereoscan electron microscopy. The tegument of undeveloped extrarredial cercariae is covered by short microvillus-like structures. The long microvilli which encircle the oral and ventral suckers of fully developed cercariae are lost a few days after encystment. The metacercariae do not grow, but the shape of the spines changes gradually from being pointed to being flattened and multi-pointed.

The larval stages and the life-cycle of *L. elongatum* are compared with those of other lepopocreadiids.

*L. microcotyleum* Odhner is regarded as a synonym of *L. elongatum*. *L. elongatum* has been recorded from several families of littoral and deep-water fishes from throughout the world, but more than one species are obviously involved.

INTRODUCTION

*Lepidapedon elongatum* (Lebour, 1908) Nicoll, 1910 (Trematoda, Lepocreadiidae) is the most abundant digenetic trematode in the Atlantic cod *Gadus morhua* L. from Danish and adjacent waters (Køie 1984). In Greenland waters it occurs in *G. ogac* Richardson as well.

This is the first known life-cycle of a species of *Lepidapedon*, a genus within which there is considerable taxonomic confusion, which is rich in species, and has a world-wide distribution. The life-cycle and larval stages are compared with those

of other lepopocreadiids. The different developmental stages are described using the stereoscan electron microscope.

Appreciation is due to Dr A. Warén, University of Göteborg, Sweden, for information on the geographical distribution of *Onoba aculeus*. The interference contrast microscope used in this study was financed by the Danish Natural Science Research Council.

## MATERIAL AND METHODS

The snail host *Onoba aculeus* (Gould) (Prosobranchia, Rissoiidae) was dredged in the northern Øresund, 18 m. Other invertebrates from the same dredge hauls were examined to detect naturally infested second intermediate hosts. The snails were crushed and various invertebrates were exposed to the freed cercariae. The material intended for examination in the stereoscan electron microscope was treated as described previously (e.g. Køie 1975).

## RESULTS

### *The snail host*

24% of 300 (Sep. 1984) and 20% of 140 (May 1985) *Onoba aculeus* (Gould) from the northern Øresund, 18 m, were infested with rediae and cercariae of *L. elongatum*. Infective cercariae were found in both September and May. Most infested snails harboured 10-20 rediae and approx. 10-100 extraredial cercariae at different developmental stages.

### *The redia*

The rediae occur in the tissue between the tubules of the digestive gland. Only one redial generation was found. The rather inactive, nearly cylindrical rediae are slightly pointed posteriorly. The terminal mouth is often surrounded by an annular thickening (Figs 1A, 2A). In infestations with extraredial cercariae also, the rediae measured (based on 20 randomly selected slightly flattened specimens) 480-1000  $\mu\text{m}$  (mean: 570  $\mu\text{m}$ ) in length and 150-300  $\mu\text{m}$  (mean: 200  $\mu\text{m}$ ) in width. The pharynx is 50-90  $\mu\text{m}$  (mean: 65  $\mu\text{m}$ ) in diameter. The redia has a short wide caecum. The birth pore is situated anteriorly in the brood chamber. The flame cell formula is 2(2+2).

The tegument covering the external surface is highly increased by closely arranged irregular inter-related ridges or folds. Irregular bodies are often found on the top of the folds (Fig. 1B). The tegument of the buccal cavity is provided with closely arranged short microvillus-like structures (Fig. 1D).

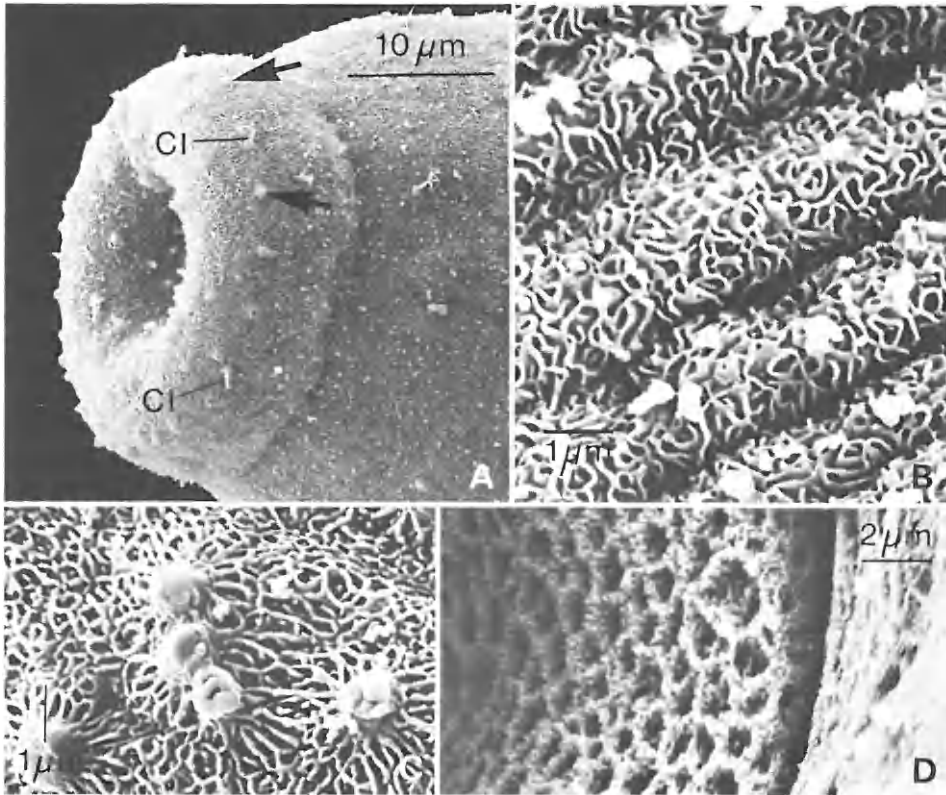


Fig. 1. Stereoscan micrographs of rediae of *Lepidapedon elongatum*. A, anterior end showing the mouth and unciliated sensory structures (CI) and non-ciliated, presumed sensory structures (arrows). B, the external surface. Irregular bodies occur on some of the folds. C, presumed sensory structures close to the mouth opening. D, detail of buccal cavity (left) with short microvilli.

Two types of presumed sensory structures surround the mouth. One type forms an irregular tegumental projection and has no protruding cilium (Fig. 1C). The other type is of the simple unciliate type (Fig. 1A).

#### *The cercaria*

The cercariae leave the rediae while still undeveloped and complete the development in the snail tissue. The most developed cercariae (Figs 2B, 5A) from crushed snails measured (based on 20 slightly flattened specimens) 180-240  $\mu\text{m}$  (mean: 210  $\mu\text{m}$ ) in length and 90-130  $\mu\text{m}$  (mean: 115  $\mu\text{m}$ ) in greatest width. The oral sucker is 44-52  $\mu\text{m}$  (mean: 50  $\mu\text{m}$ ) in diameter, and the ventral sucker, which occurs just posterior to the middle of the body, measures 44-50  $\mu\text{m}$  (mean: 46  $\mu\text{m}$ ) in diameter.

There is a long prepharynx. The pharynx, which is pyriform and widest posteriorly, is 18-24  $\mu\text{m}$  (mean: 20  $\mu\text{m}$ ) long and 15-20  $\mu\text{m}$  (mean: 18  $\mu\text{m}$ ) at the

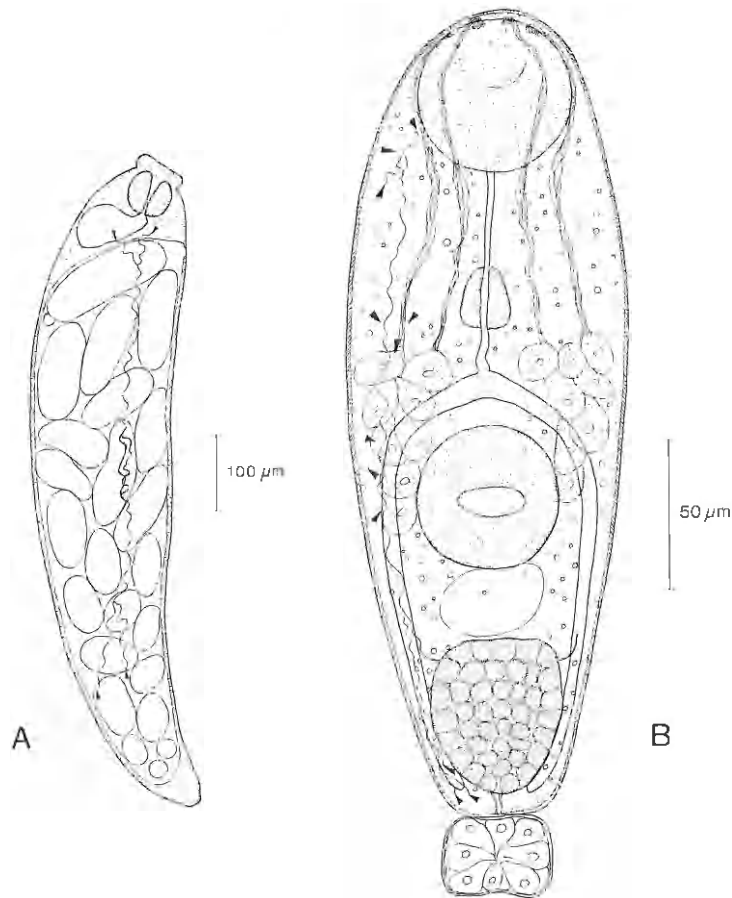


Fig. 2. The redia and cercaria of *Lepidapedon elongatum*. Drawn after living, slightly flattened specimens. A, a fully developed redia. B, ventral view of cercaria.

greatest width. The oesophagus divides into the caeca about halfway between the pharynx and the ventral sucker. The caeca end close to the posterior extremity.

Two groups of long gland ducts occur on each side of the cercarial body. The ducts open anteriorly to the oral sucker. Laterally there are five openings and more medially three openings. The gland cell bodies occupy the area from the posterior limit of the pharynx to the midacetabular level.

The wall of the spherical to pyriform excretory vesicle is composed of large cells. Numerous small spherical bodies, probably lipid droplets, occur throughout the body of fully developed cercariae. On each side the flame cells are apparently arranged in four groups each with three cells, but the unravelling of the flame cell formula is complicated because the ciliated ducts may be misinterpreted as flame cells.

The tail, which measured 25-30  $\mu\text{m}$  (mean: 28  $\mu\text{m}$ ) in length and 30-40  $\mu\text{m}$  (mean: 36  $\mu\text{m}$ ) in width, is filled with large, presumed glandular cells. The tail surface of extrarredial cercariae is covered with small microvillus-like projections (Fig. 3F).

The external surface of non-infective extrarredial cercariae is increased by numerous knobs or short microvillus-like projections (Figs 3C, 4A). They disappear

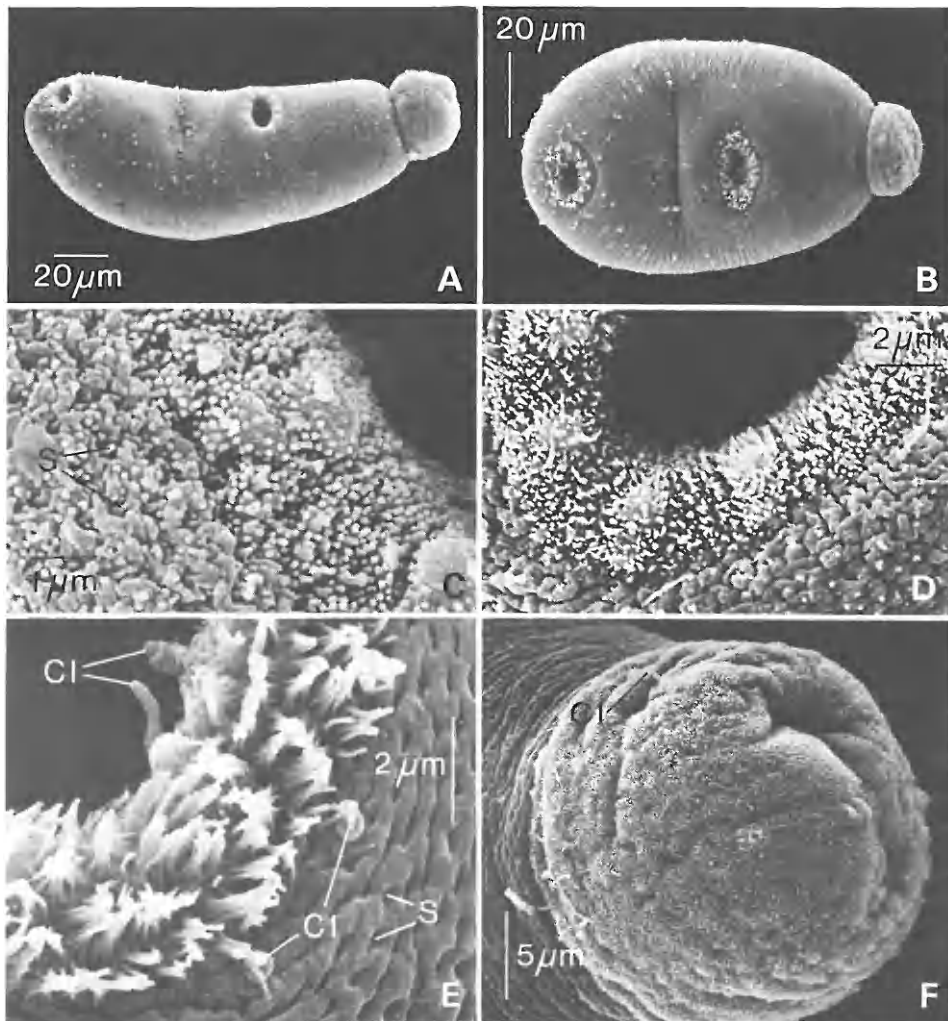


Fig. 3. Stereoscan micrographs of extrarredial cercariae of *Lepidapedon elongatum*. Anterior end of all specimens towards the left. A, an undeveloped cercaria. B, a fully developed infective cercaria. C, detail of external surface and ventral sucker of young cercaria showing short microvillus-like projections and spines (S). D, as C, but of older cercaria with short microvilli on the rim of the ventral sucker. E, detail of infective cercaria showing part of the ventral sucker whose rim carries long microvilli. Different kinds of unciliate sensory structures (CI) are seen. F, the tail of an infective cercaria.

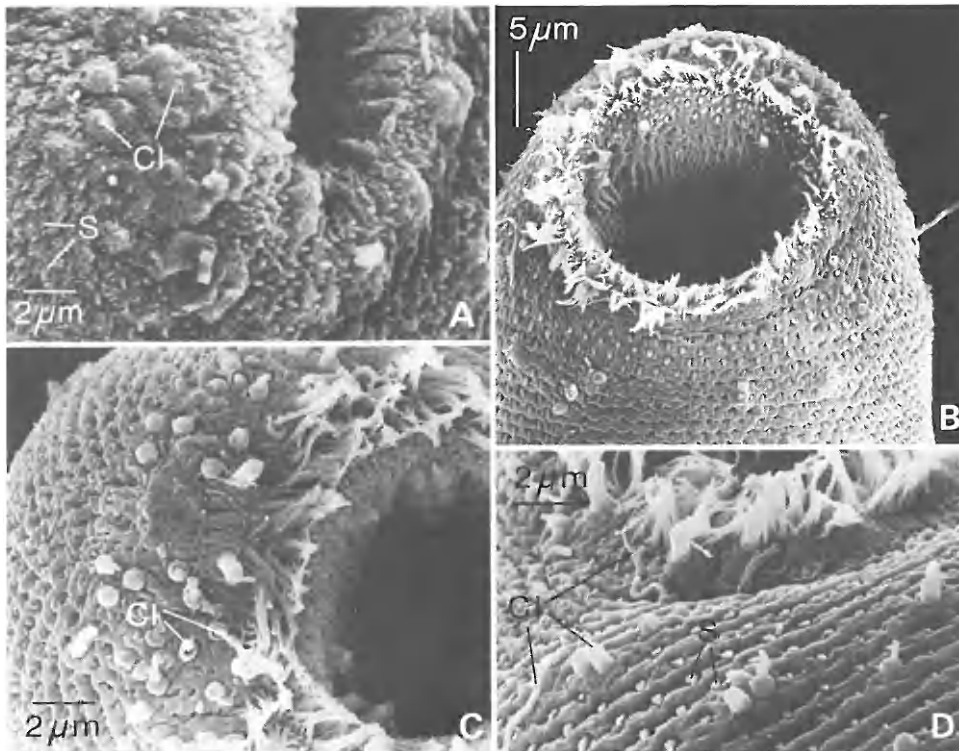


Fig. 4. Details of the anterior ends of extrarredial cercariae of *Lepidapedon elongatum*. A, the oral sucker of a non-infective cercaria showing different kinds of sensory structures (CI) and spines (S). The surface is covered by short microvilli. B, the anterior end of an infective cercaria. C, the extreme anterior end of an infective cercaria. D, area just posterior to oral sucker of an infective cercaria showing different kinds of unciliate sensory structures (CI) and spines (S).

before the cercariae are infective except those which occur on the rim of the suckers. The latter grow to a length of about  $4\ \mu\text{m}$  (Figs 3D, E, 4B-D).

Different types of unciliate sensory structures are common in association with the suckers, but are also found ventro-laterally on the forebody (Figs 3E, 4A-D) and on the tail (Fig. 3F). The base of some cilia are surrounded by an annular collar. The length of these cilia ranges from less than  $0.5\ \mu\text{m}$  to about  $10\ \mu\text{m}$ . In other cases the cilia, apart from the apical ends, are surrounded by an about  $1\ \mu\text{m}$  long tube-like tegumental collar. Nine, slightly domed, large papillae without protruding cilia occur on the rim of the ventral sucker (Fig. 3A, C, D).

Small regularly arranged pointed spines, which are most numerous and longest anteriorly, protrude through the tegument throughout the body.

The cercaria has a superficial resemblance with cotylomicrocercous (opecoelid) cercariae, with a short tail specialized for adhesion, and they behave in the same

way (Køie 1981). They crawl, using the tail and the suckers, especially the anterior one, and attached by the tail they stretch out the body and swing from side to side in search of a suitable second intermediate host.

#### *The second intermediate hosts*

Various invertebrates from the same dredge hauls as the snail host were examined for metacercariae of *L. elongatum*. Metacercariae were found in the foot and mantle of small specimens of the bivalve *Astarte* sp., in the snails *Onoba aculeus* and *Odostomia* sp., but only about 1% of these molluscs were infested and no infested molluscs contained more than one metacercaria.

The polychaetes *Lumbrineris fragilis* (Müller), *Anobothrus gracilis* (Malmgren) and members of Polynoidae, Hesionidae and Phyllodocidae were found infested. Only about 20 metacercariae were found in the most heavily infested polychaete (*L. fragilis*). Metacercariae were found in the head region only, and especially in the muscular pharynx. No metacercariae of *L. elongatum* were found in brittle stars or other members of the invertebrate groups examined.

In some of the bivalves, polychaetes and brittle stars examined, the encysted metacercariae of *Zoogonoides viviparus* (Olsson, 1868) were found, which dif-

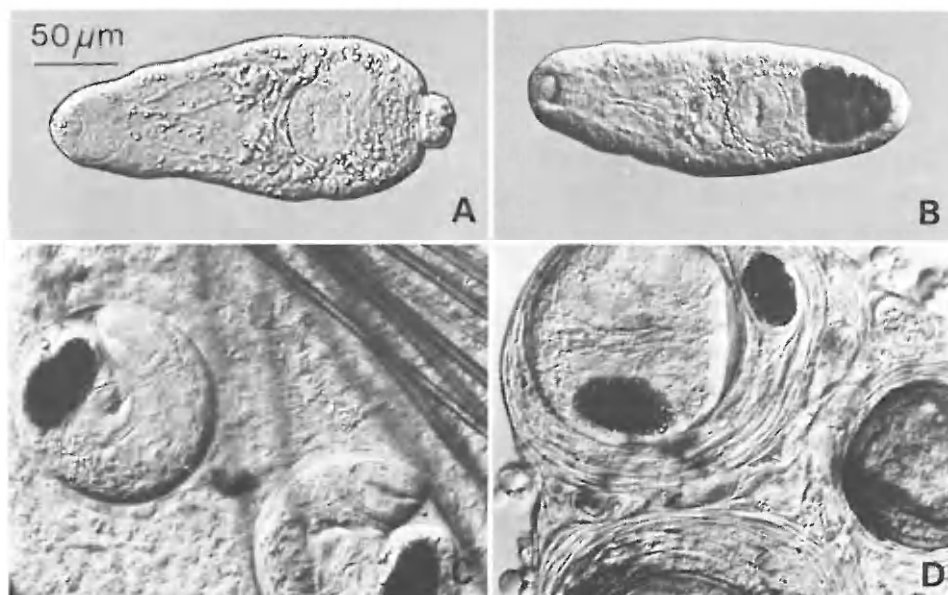


Fig. 5. Cercaria and metacercariae of *Lepidapedon elongatum* from experimentally infected *Nereis diversicolor*. Interference contrast. All to the same scale. A, an infective cercaria. B, an excysted two-week old metacercaria. C, two four-week old metacercariae in parapodium. D, part of two living (left) and one dead eight-week old metacercariae. The small dark body probably represents the remains of a dead metacercaria.

ferred from those of *L. elongatum* by being larger, and by having the ventral sucker larger than the oral one (Køie 1976).

Various invertebrates belonging to different phyla were exposed in small glass containers without sediment to hundreds of cercariae from crushed snails for 24 to 48 h (10°C). Encysted metacercariae were found in the foot or mantle of all the exposed bivalves, e.g. *Spisula subtruncata* (da Costa), *Cardium* spp., *Astarte* spp. and *Abra* spp. The cercariae also encysted in the brittle star *Ophiura albida* Forbes. Both bivalves and brittle stars are apparently unsuitable hosts as all the metacercariae died within two weeks. A few host cells adhered to the cyst wall, but the host tissue response was so weak that it may not have caused the death of the metacercariae.

To avoid a possible natural infestation *Nereis diversicolor* Müller, *Nephtys* sp. and *Pectinaria* sp. from shallow sandy bottoms, where the snail host does not occur, were used as experimental hosts. The cercariae encysted less than six hours after penetration. The encysted metacercariae were found in the muscles throughout the body including the parapodia (Fig. 5C), but most were found in the head region especially the pharynx. In *N. diversicolor* about one third died within eight weeks, and both living and dead metacercariae were surrounded by several layers of host cells (Fig. 5D). A similar host reaction was not found in naturally infested polychaetes, which indicates that *N. diversicolor* is a more susceptible host than the remaining polychaetes examined.

#### *The metacercaria*

The following descriptions are based on metacercariae from experimentally infected *Pectinaria* sp., *Nephtys* sp. and *N. diversicolor*. The diameter of slightly flattened recently encysted metacercariae is 110-140  $\mu\text{m}$  (mean: 120  $\mu\text{m}$ ). No growth takes place during the metacercarial stage.

Small refractive globules appear in the excretory vesicle a few days after encystment. The excretory vesicle of two-week old metacercariae is filled with these refractive globules (Fig. 5B). Most of the contents of the penetration glands disappear after penetration and encystment, but traces of the ducts and cell bodies were still visible in two-week old metacercariae. Most of the presumed lipid droplets in the body had disappeared or decreased in size. At this age small unicellular glands appear under the tegument of the forebody. The number of these glands had increased and the excretory globules had slightly increased in size in 4- and 8-week old metacercariae. The flame cell formula is the same as that of the cercaria. No development of the reproductive system had apparently taken place.

The longest cilia of the unciliated sensory structures and most of those surrounded by a tube-like collar had disappeared less than three days after penetration (Fig. 6A, B). Only unciliated structures with a short cilium remained in four-week old metacercariae (Fig. 6E). The microvilli which encircle the suckers of the



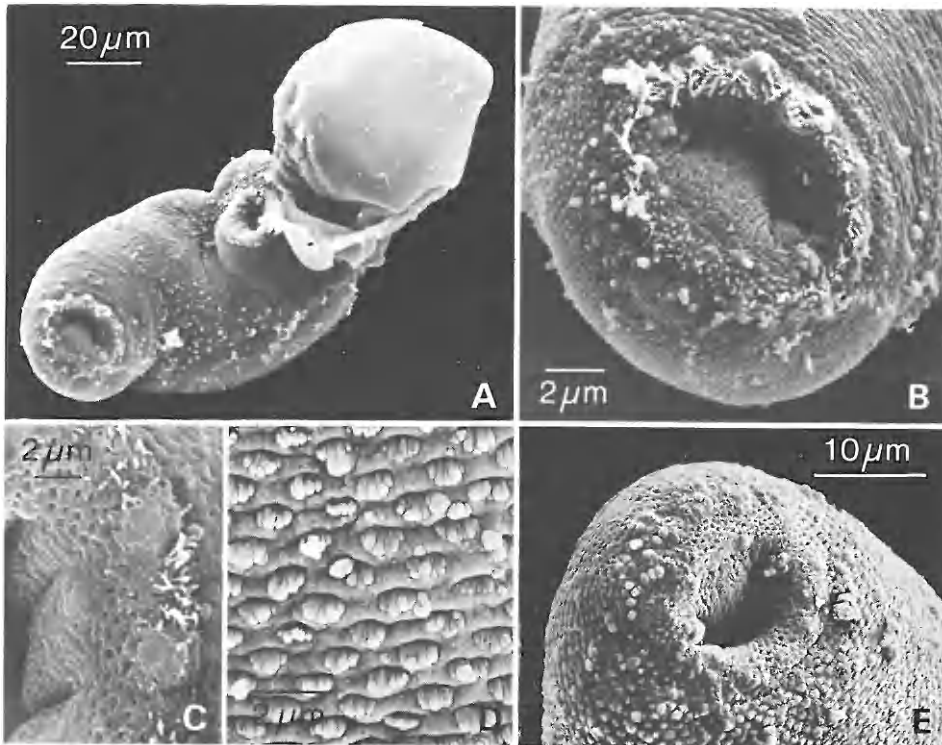


Fig. 6. Metacercariae of *Lepidapedon elongatum* from experimentally infected *Nereis diversicolor*. A-C, three-day old specimens. D & E, four-week old metacercariae. A, partly excysted metacercaria. B, the oral sucker of A. C, part of the ventral sucker of another metacercaria. D, spines on the anterior end. E, the anterior end showing the flattened serrated spines.

cercaria are lost a few days after encystment (Fig. 6A-C). The spines gradually change from being single pointed to being multipointed and flattened (Fig. 6).

The metacercariae found in naturally infested polychaetes all fall within the range of the above description.

#### *The final hosts*

*L. elongatum* is the most abundant adult digenean in the cod from Danish and adjacent waters (Køie 1984). In Greenland waters it occurs in *G. ogac* as well (unpubl. obs., July 1978, September 1984). *G. ogac* is a new host for *L. elongatum*.

Even though several hundred specimens of *L. elongatum* occurred in the pyloric caeca of a cod, most often no host tissue reaction was observed. However, in some cases, the apical ends of the pyloric caeca were red due to haemorrhage caused by the parasites. The haemorrhage was apparently not directly dependent on the number of parasites as caeca, each with less than 10 adult *L. elongatum*, were occasionally red, whereas sometimes up to about 30 adult specimens in a caecum did not cause any haemorrhage.

The cod used for experimental infections had been kept in tanks for 12 months and fed on frozen food only. Individual cod were given pieces of *N. diversicolor* harbouring one-week, four-week and eight-week old metacercariae of *L. elongatum*. Only the four-week and eight-week old metacercariae were infective. The two experimentally infected cod, which were examined 6 and 40 days after infection, harboured between 50 and 100 immature *L. elongatum*.

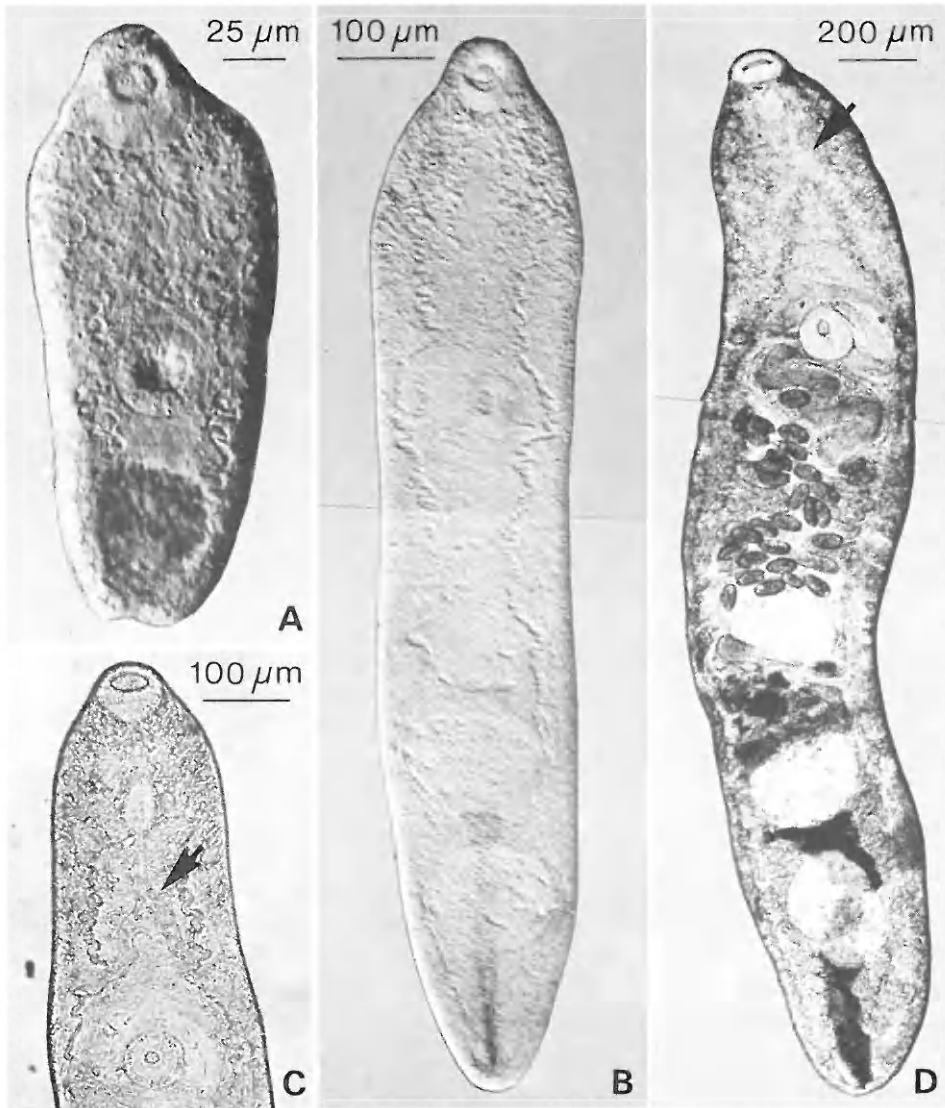


Fig. 7. Adult *Lepidapedon elongatum*. A & B, living flattened worms from experimentally infected cod. Interference contrast. C & D, living flattened specimens from natural infestations. Arrows indicate the intestinal bifurcation. A, six-day old worm. B, 40-day old worm. C, anterior end of immature specimen. D, mature worm.

*The adult*

The specimens found in the pyloric caeca of cod six days after ingestion of the metacercariae did not differ from excysted four- or eight-week old metacercariae, apart from that most of the refractive globules in the excretory vesicle had disappeared, and the number of unicellular glands of the forebody had increased (Fig. 7A).

The 40-day old specimens (Fig. 7B) measured (based on 20 living slightly flattened specimens) 600-1100  $\mu\text{m}$  (mean: 800  $\mu\text{m}$ ) in length and 200-300  $\mu\text{m}$  (mean: 250  $\mu\text{m}$ ) at the greatest width. The diameter of the oral sucker was 76-82  $\mu\text{m}$  (mean: 80  $\mu\text{m}$ ), and that of the ventral sucker 65-72  $\mu\text{m}$  (mean: 70  $\mu\text{m}$ ). The sucker ratio was 1:0.81-0.95 (mean: 1:0.88). The number of unicellular glands had increased. These glands are especially common in the anterior part of the forebody, and most open ventrally and laterally. The testes and ovary were distinct, but eggs had not developed.

Mature specimens from naturally infested cod have a similar sucker ratio, and in no case was the ventral sucker larger than the oral one. The intestinal bifurcation is about midway between the suckers (Fig. 7). The length of the pharynx is identical

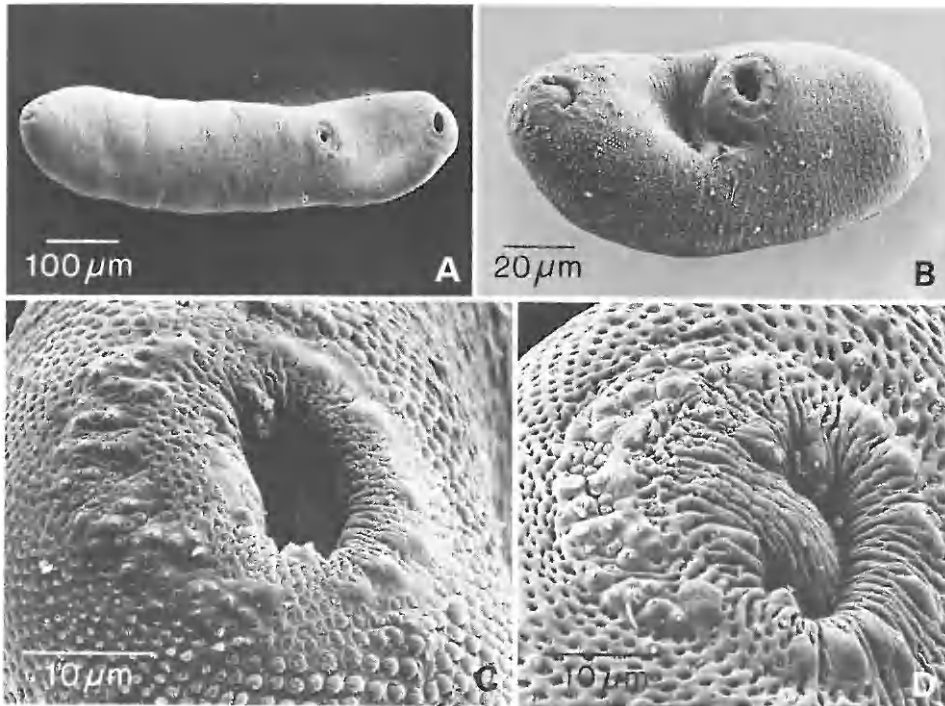


Fig. 8. Adult *Lepidapedon elongatum*. A, C & D, mature specimens from naturally infested cod. A, whole specimen. B, six-day old worm from experimentally infected cod. C, anterior end with extended spines. Different kinds of sensory structures are seen. D, as C, but with retracted spines.

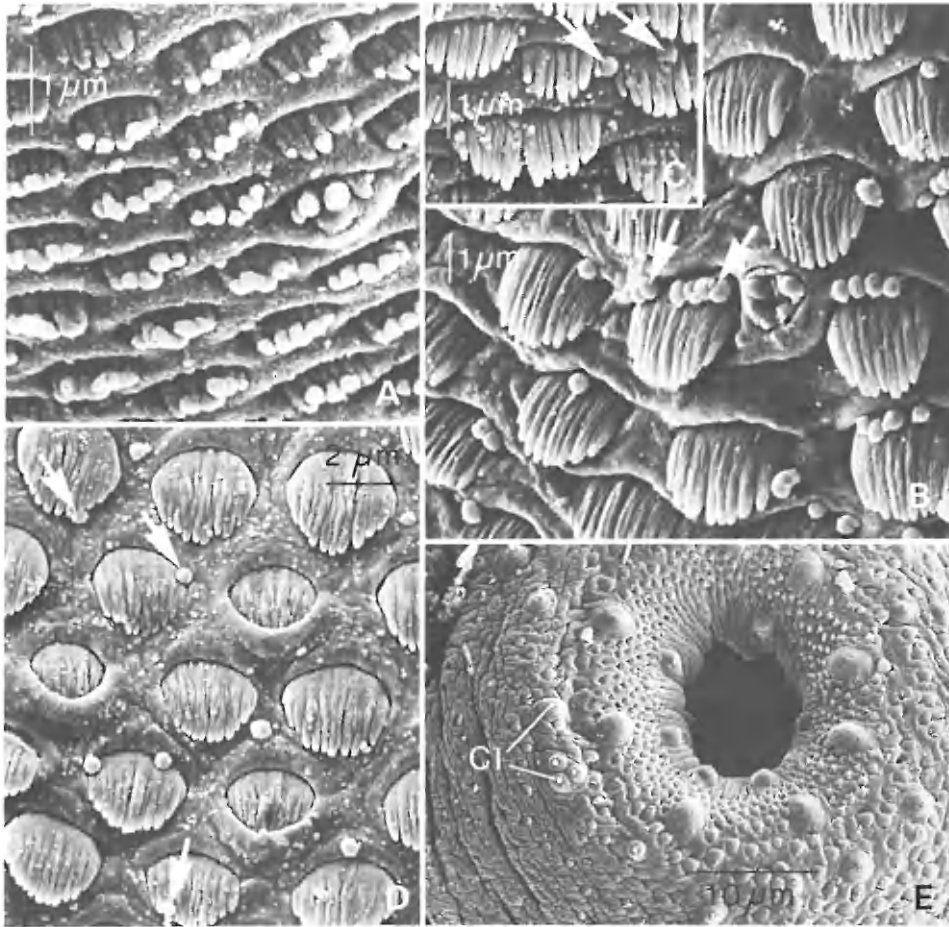


Fig. 9. Details of six-day old (A) and mature *Lepidapedon elongatum* (B-F). A, detail of anterior end with spherical bodies on the flattened serrated spines. B, spines with detached bodies (arrows) and presumed opening of unicellular gland. C, spine during division and spherical bodies (arrows). D, spines, some of which have the tips retracted into the tegument and spherical bodies (arrows). E, ventral sucker showing spines, cilia (Cl) of sensory structures and large domed papillae on rim of the sucker. Genital opening in upper left corner.

to, or slightly smaller than, the diameter of the ventral sucker. The testes of mature worms occur in the posterior half of the hindbody (Fig. 7D).

The sensory structures appear as those of infective metacercariae. All specimens in the final host have multipointed flattened spines anteriorly (Fig. 9). The spines become more scattered and have fewer points towards the posterior end (Fig. 8B). The number of spines increases with increasing size of the worm (Fig. 9C). The tips of the serrated spines may be completely withdrawn into the tegument (Figs 8D, 9D). Small spherical bodies are apparently released from the tips of the spines, especially of young specimens (Fig. 9A, D). Similar bodies are common on the

general surface or occur in rows just anterior to the spines of mature worms (Fig. 9B-D). The function of these bodies is unknown. Openings in the tegument between the spines may be the apertures of the unicellular glands (Fig. 9B).

## DISCUSSION

Zelikman (1966) found a cercaria twice, which he suggested belonged to Zoogonidae, among an unmentioned number of *Onoba aculeus* from the littoral White Sea. Although the description and figures are inadequate, the measurements, the position of the suckers, the shape of the cercarial tail, and the morphology of the redia (described as a sporocyst) indicate that these larval stages probably belonged to *L. elongatum*.

*L. elongatum* has been found in cod living in Lake Mogilnoe on the Kildin Island (Dogiel 1936). Lake Mogilnoe has been separated from the Barents Sea for at least five hundred years. Some marine animals have survived in the lake, but compared with the fauna of the surrounding Barents Sea the marine invertebrate fauna in the lake is poor. Only four prosobranchs have been found: *Margarites helycinus* (Fabricius), *Littorina littorea* (L.), *O. aculeus* and *Skeneopsis planorbis* (Fabricius). *O. aculeus* may thus also there act as first intermediate host of *L. elongatum*.

However, nearly 1400 *O. aculeus* from the littoral and upper sublittoral zone of the Barents Sea have been examined by Chubrik (1966) and Podlipaev (1979), but only well known cercariae were found.

*Cercaria bistilosa* Chubrik, 1966, which is extremely common in the Barents Sea littoral trochid snails (Chubrik 1966) is, apart from the two stylets (?), very similar to the cercaria of *L. elongatum*. However, the more detailed redescription of *C. bistilosa* by Marasaev (1984) shows that this cercaria is not identical with the cercaria of *L. elongatum*. It is unlikely that *C. bistilosa* belongs to another species of *Lepidapedon*. Apart from *L. rachion* (Cobbold, 1858), which is rare in the Barents Sea, the remaining *Lepidapedon* species in the Barents and White Seas are alternately mentioned as *L. elongatum* and *L. gadi* (Yamaguti, 1934) (see Køie 1984, and Timofeeva & Marasaeva 1984). The descriptions and figures of these specimens do not justify a separation into two species. *L. gadi*, which is described from *Gadus macrocephalus* Tilesius from the Sea of Japan (Yamaguti 1934), is considered a synonym of *L. elongatum* by Hanson (1950).

Amosova (1955) found up to more than one thousand metacercariae of *L. gadi* in individual *Nereis pelagica* L. from the Barents Sea. 88% of the littoral *N. pelagica* were infested, whereas all sublittoral worms were uninfested. The metacercariae occurred in the body wall, especially at the basis of the parapodia, but most were found in the first segments. The morphology of the metacercaria is identical with that of the metacercaria of *L. elongatum*.

*O. aculeus*, which is the only arctic Atlantic species of the genus (Warén 1974), is common in Danish waters (Warén, pers. comm., see Køie 1984). It is found on

the Norwegian west coast, the Kola Peninsula, Svalbard, Iceland, East Greenland from Frans Joseph Fjord and southward, the west coast of Greenland from Godhavn and southward, the east coast of Canada and the Maine and Massachusetts coasts of the north-east United States (Warén 1974). It is a shallow-water species living at depths of 0-20 m (Warén, pers. comm.), probably deeper in the Baltic Sea. In British waters, it has not been found south of the Northumberland coast in north-east England (Seaward 1982), which is the type-locality of *L. elongatum*. It is unknown whether *O. aculeus* occurs in the Pacific Ocean (Warén, pers. comm.).

In the Atlantic Ocean and adjacent seas the geographical distribution of *L. elongatum* in the type-host *G. morhua* apparently coincides with that of *O. aculeus*. This species is common in the littoral Barents Sea, but it is unknown why it has not been found infested there, especially since *N. pelagica* from this area is highly infested with metacercariae of *L. gadi* (a supposed synonym of *L. elongatum*).

The distribution of *L. elongatum* is difficult to define as several other species apparently have been wrongly assigned to this species. The question of distribution is additionally complicated by the description of apparently identical species under other names, e.g. *L. microcotyleum* (Odhner), *L. gadi*, and others (see e.g. Bray 1973, 1979).

The specimens found in *G. morhua* and *G. ogac* from the North Sea, the Øresund, and Greenland waters mostly agree with *L. elongatum* as described by Lebour (1908), Dogiel (1936) and Linton (1940) from the type-host *G. morhua*. The specimen illustrated by Lebour (1908) differs by its lack of intergenital and post-testicular vitellaria. However, the distribution of the vitellaria is variable and not a good feature to use for differentiating species in this group. The unicellular glands of the forebody have been overlooked by all authors except Linton (1940), although they, especially in living specimens, are very conspicuous.

Apart from *L. elongatum*, only *L. microcotyleum* (and *L. racion* which may not be confused with *L. elongatum*) has been described from Danish and adjacent waters. Odhner (1905) mentioned the findings of a new species of *Lepodora* in the pyloric caeca and anterior part of the intestine of *G. morhua* from Kristineberg, western Sweden. The specimens were not described. Odhner's slides, some of which were labelled *Lepodora microcotylea* were studied by Dollfus (1953), who described *Lepidapedon microcotyleum* based on Odhner's specimens and own material from *G. morhua* from the Faroes and Iceland. *L. microcotyleum* differs according to Dollfus (1953) from *L. elongatum* in the greater separation of the ovary and testes by invasion of vitellaria between them and across the preovarian area, and in having fewer and larger eggs. Dollfus (1953) also considered that *L. elongatum* of Linton (1940) from *G. morhua* and other hosts from Woods Hole, USA, and of Dogiel (1936) from the cod from the Barents Sea, belonged to *L. microcotyleum*. Polyanski (1955) suggested that the latter belonged to *L. gadi*. However, the specimens assigned to *L. microcotyleum* by Dollfus (1953) show great morphological variation, apparently mostly due to various methods of treatment and fixa-

tion, and there is no justification to describe them as a separate species. I conclude, that *L. microcotyleum* is not a valid species but a synonym of *L. elongatum*, in accordance with the opinion of Thulin (1971).

There is considerable taxonomic confusion within the genus *Lepidapedon*, and Hanson (1950), Skrjabin & Koval (1960), Srivastava (1966), and McCauley (1968) have all prepared keys to the species of this genus. Hanson (1950) did not include *L. microcotyleum* in her key. As mentioned above she regards *L. gadi* as a synonym of *L. elongatum*. Srivastava (1966) considered *L. microcotyleum* as a synonym of *L. gadi*, which was regarded as a valid species. Skrjabin & Koval (1960), McCauley (1968) and Yamaguti (1971) considered *L. elongatum*, *L. gadi* and *L. microcotyleum* as all being valid species.

In Danish and adjacent waters, including the Faroese waters, *L. elongatum* was most common at stations at depths of 40 m or less (Køie 1984). In other areas *L. elongatum* has been found at depths between 300 and 650 m (Manter 1934, Bray 1973, 1979). However, these deep-water lepopocreadiids probably belong to other species. Manter (1954) regarded, in accordance with Dollfus (1953), his previous description of *L. elongatum* from the Florida coast (Manter 1934) not to belong to this species as the bifurcation of the intestine was too near the acetabulum. Bray (1973, 1979) found *L. elongatum* in *Lepidion eques* (Günther) from the Bay of Biscay and Canadian Atlantic waters. The specimens (1973) differ from *L. elongatum* from the type-host *G. morhua*, in that the diameter of the pharynx is of similar size, or larger than the ventral sucker, and that the testes occur close together in the middle of the hindbody. *L. elongatum* from Canadian waters (Bray 1979) has an oral sucker which is much smaller than the ventral sucker, and the bifurcation of the intestine is too close to the ventral sucker.

The family Lepocreadiidae comprises an enormous number of species, which occur nearly exclusively in the digestive tract of marine fishes. *L. elongatum*, *L. rachion* and *Opechona bacillaris* (Molin, 1859) are common in Danish gadoid fishes (Køie 1984). The known life-cycles of lepopocreadiid trematodes have been reviewed by e.g., Yamaguti (1975), Køie (1975) and Stunkard (1979), and lepopocreadiid life-cycles have later been described by Stunkard (1980a, b) and Watson (1984). Unencysted metacercariae of *Neopechona pyriforme* (Linton, 1900), *N. cablei* Stunkard, 1980, *Lepocreadium areolatum* (Linton, 1900), and *O. bacillaris* occur in medusae and ctenophores. The genus *Lepocreadium* harbour in addition apparently one metacercaria which encysts and one which occurs unencysted in molluscs (see Yamaguti 1975). The metacercaria of *Lepidauchen stenostoma* Nicoll, 1913 occurs unencysted in prosobranchs (Prévôt 1968), that of *Holorchis pycnopus* Stossich, 1901 encysts in bivalves (Bartoli & Prévôt 1978), and encysted metacercariae of *Paralepidapedon hoplognathi* (Yamaguti, 1938) have been found in sea urchins. The cercaria of the latter is unknown (Shimazu & Shimura 1984). The above-mentioned lepopocreadiids, which together with the genus *Lepidapedon* are placed by most authors in Lepocreadiinae, harbour thus both unen-

cysted and encysted metacercariae. Three species belonging to Sphincterostominae encyst in freshwater fishes (Yamaguti 1975, Watson 1984). All previously described lepopcreadiid cercariae are ophthalmotrichocercous.

The cercaria of *L. elongatum* differs from all known lepopcreadiid cercariae by the absence of eyespots and by the shape of the tail. *L. elongatum* is the only species with known life-cycle within the large genus *Lepidapedon*, which has a world-wide distribution. The cercaria of *L. elongatum* and that of *H. pycnoporos* develop in snails belonging to Rissoacea, whereas the remaining known lepopcreadiid cercariae develop in snails belonging to Buccinacea, and most have members of the genus *Nassarius* as first intermediate host (see also K ie 1975). One lepopcreadiid cercaria with unknown adult stage develops in a snail belonging to Conacea (see Bartoli 1984).

The tegument of the redia of *L. elongatum* is very similar to that of *Cryptocotyle lingua* (Creplin, 1825) (Irwin *et al.* 1978). The redial structure presumed to be a sensory organ which forms an irregular projection and is without a cilium, is most similar to a spiral-shaped projection described by Bennett (1975). The uniciliate sensory structure without a tube-like collar is extremely common in all developmental stages of digeneans and has previously been described from other redial species examined by means of the stereoscan or transmission electron microscopes (K ie 1971a, K ie *et al.* 1977, Hoskin 1975, Irwin *et al.* 1978, Page *et al.* 1980, and Rees 1980, 1981). Sensory cilia surrounded by a tube-like tegumental collar have previously been found in an opacoelid cercaria (K ie 1981). The large, slightly domed papillae on the rim of the ventral suckers of the cercaria, and on both suckers of later developmental stages are apparently similar to the contact receptors described by Bennett (1975) and the button papillae described by Hoole & Mitchell (1981).

The change from simple pointed spines in cercariae to scale-like multipointed spines in later developmental stages has been found in several families. The single pointed spines are found in migratory developmental stages and the scale-like serrated spines in more stationary stages where they may have an abrasive effect on the host tissue for feeding purposes, and help in anchoring the parasite to the host tissue (K ie 1977, Davies 1979, see also Shoop & Corkum 1984). The spherical bodies which apparently are expelled from the tips of the spines have not been observed previously, and neither has the phenomenon that the tips of the spines may be withdrawn into the tegument.

The unicellular glands which are most frequent anteriorly and laterally in infective metacercariae and adult *L. elongatum* may be comparable with the unicellular glands of *M. similis* (see Davies 1979). In both parasites the glands occur in the forebody only, and the openings of the glands were found between the scale-like serrated spines. Davies (1979) found that the glands secrete cholinesterase, which may serve to compensate for the irritating effect of the toothed spines by neutralizing host acetylcholine and so reducing the movement of the villi in the



immediate vicinity of the fluke thereby reducing the likelihood of dislodgement and expulsion. As the chemical nature of the secretion of the glands of *L. elongatum* is not known, it is also unknown whether they may have a similar function in this species.

The possible functions of the microvilli which encircle one or both suckers of some cercariae were discussed by Køie (1981). Higo & Ishii (1983) observed microvilli around the mouth opening of cercariae of *Paragonimus*. These and the present observations show that the microvilli occur in several digenean families whose cercariae encyst in a second intermediate host.

The short microvillus-like structures found on the surface of undeveloped extra-renal cercariae may increase the absorptive surface of the growing cercariae, which at this developmental stage probably only absorb nutrients through the external surface. The microvilli found throughout the body surface of undeveloped intrasporocyst cercariae of *Zoogonoides viviparus* (Olsson, 1868) were suggested to have a similar function (Køie 1971b).

#### REFERENCES

- Amosova, I. S., 1955. On the occurrence of trematode metacercariae in some polychaetes of the Barents Sea. — Zool. Zh. 34: 286-290. (In Russian.)
- Bartoli, P., 1984. Redescription de *Cercaria setifera* F.S. Monticelli, 1914 (nec. J. Müller) (Trematoda) parasite de *Conus ventricosus* Hwass; comparaison avec quelques cercaires optalmotrichocercques de Méditerranée occidentale. — Anns Parasit. hum. comp. 59: 161-176.
- Bartoli, P. & G. Prévôt, 1978. Le cycle biologique de *Holorechis pycnopus* M. Stossich, 1901 (Trematoda, Lepocreadiidae). — Z. ParasitKde 58: 73-90.
- Bennett, C. E., 1975. Surface features, sensory structures, and movement of the newly excysted juvenile *Fasciola hepatica* L. — J. Parasit. 61: 886-891.
- Bray, R. A., 1973. Some digenetic trematodes in fishes from the Bay of Biscay and nearby waters. — Bull. Br. Mus. nat. Hist. (Zool.) 26: 151-183.
- Bray, R. A., 1979. Digenea in marine fishes from the eastern seaboard of Canada. — J. nat. Hist. 13: 399-431.
- Chubrik, G. K., 1966. Fauna and ecology of trematode larvae from molluscs in the Barents and White Seas. — Trudy murmansk. biol. Inst. 10(14): 78-166. (In Russian.)
- Davies, C., 1979. The forebody glands and surface features of the metacercariae and adults of *Microphallus similis*. — Intern. J. Parasit. 9: 553-564.
- Dogiel, V., 1936. Parasites of cod from Lake Mogilnoe. — Uchen. Zap. leningr. gos. Univ. 7. Ser. Biol. 3: 123-133. (In Russian.)
- Dollfus, R. P., 1953. Parasites Animaux de la Morue Atlanto-Arctique. — Encycl. biol. 43: 1-423.
- Hanson, M. L., 1950. Some digenetic trematodes of marine fishes of Bermuda. — Proc. helminth. Soc. Wash. 17: 74-89.
- Higo, H. & Y. Ishii, 1983. Comparative studies on surface ultrastructure of *Paragonimus* cercariae. — Jap. J. Parasit. 32: 251-259. (In Japanese, Eng. sum.)
- Hoole, D. & J. B. Mitchell, 1981. Ultrastructural observations on the sensory papillae of juvenile and adult *Gorgoderina vitelliloba* (Trematoda: Gorgoderidae). — Intern. J. Parasit. 11: 411-417.
- Hoskin, G. P., 1975. Light and electron microscopy of the host-parasite interface and histopathology of *Nassarius obsoletus* infected with rediae of *Himasthla quissetensis*. — Ann. N. Y. Acad. Sci. 266: 497-512.

- Irwin, S.W.B., L.T. Threadgold & N.M. Howard, 1978. *Cryptocotyle lingua* (Creplin) (Digenea: Heterophyidae): observations on the morphology of the redia, with special reference to the birth papilla and release of cercariae. – *Parasitology* 76: 193-199.
- Køie, M., 1971a. On the histochemistry and ultrastructure of the redia of *Neophasis lageniformis* (Lebour, 1910) (Trematoda, Acanthocolpidae). – *Ophelia* 9: 113-143.
- Køie, M., 1971b. On the histochemistry and ultrastructure of the tegument and associated structures of the cercaria of *Zoogonoides viviparus* in the first intermediate host. – *Ophelia* 9: 165-206.
- Køie, M., 1975. On the morphology and life-history of *Opechona bacillaris* (Molin, 1859) Looss, 1907 (Trematoda, Lepocreadiidae). – *Ophelia* 13: 63-86.
- Køie, M., 1976. On the morphology and life-history of *Zoogonoides viviparus* (Olsson, 1868) Odhner, 1902 (Trematoda, Zoogonidae). – *Ophelia* 15: 1-14.
- Køie, M., 1977. Stereoscan studies of cercariae, metacercariae and adults of *Cryptocotyle lingua* (Creplin, 1825) Fischöeder, 1903 (Trematoda, Heterophyidae). – *J. Parasit.* 63: 835-839.
- Køie, M., 1981. On the morphology and life-history of *Podocotyle reflexa* (Creplin, 1825) Odhner, 1905, and a comparison of its developmental stages with those of *P. atomon* (Rudolphi, 1802) Odhner, 1905 (Trematoda, Opcoelidae). – *Ophelia* 20: 17-43.
- Køie, M., 1984. Digenetic trematodes from *Gadus morhua* L. (Osteichthyes, Gadidae) from Danish and adjacent waters, with special reference to their life-histories. – *Ophelia* 23: 195-222.
- Køie, M., P. Nansen & N.Ø. Christensen, 1977. Stereoscan studies of rediae, cercariae, cysts, excysted metacercariae and migratory stages of *Fasciola hepatica*. – *Z. ParasitKde* 54: 289-297.
- Lebour, M., 1908. Fish trematodes of the Northumberland coast. – *Rep. scient. Invest. Northumb. Sea Fish. Comm.* (1907): 23-67.
- Linton, E., 1940. Trematodes from fishes mainly from the Woods Hole region, Massachusetts. – *Proc. U.S. natn. Mus.* 88: 1-172.
- Manter, H.W., 1934. Some digenetic trematodes from deep-water fish of Tortugas, Florida. – *Pap. Tortugas Lab.* 28: 257-345.
- Manter, H.W., 1954. Some digenetic trematodes from fishes of New Zealand. – *Trans. R. Soc. N.Z.* 82: 475-568.
- Marasaev, S.F., 1984. Three species of cercariae from benthic molluscs of the central and south-eastern parts of the Barents Sea. – *In Ecological-parasitological Investigations of Northern Seas*, pp. 51-59. Kola Branch Akad. Nauk USSR, Murmansk Mar. Biol. Inst., Apatity. (In Russian.)
- McCaughey, J.E., 1968. Six species of *Lepidapedon* Stafford, 1904 (Trematoda, Lepocreadiidae) from deep-sea fishes. – *J. Parasit.* 54: 496-505.
- Odhner, T., 1905. Die Trematoden des arktischen Gebietes. – *Fauna arct.* 4: 291-372.
- Page, M.R., M.J. Nadakavukaren & H.W. Huizinga, 1980. *Ribeiroia marini*: surface ultrastructure of redia, cercaria, and adult. – *Intern. J. Parasit.* 10: 5-12.
- Podlipaev, S.A., 1979. Parthenitae and larvae of trematodes in littoral molluscs from eastern Murman. – *In Ecological and experimental Parasitology* 2: 47-101. Leningr. Univ., USSR. (In Russian.)
- Polyanski, Y.I., 1955. Parasites of the fish of the Barents Sea. – *Trudy zool. Inst. Leningr.* 19: 5-170. (English translation: I.P.S.T. 1966, 158 pp.)
- Rees, F.G., 1980. Surface ultrastructure of the redia of *Parorchis acanthus* Nicoll (Digenea: Philophthalmidae). – *Z. ParasitKde* 63: 33-46.
- Rees, F.G., 1981. The ultrastructure of the epidermis of the redia of *Parorchis acanthus* Nicoll (Digenea: Philophthalmidae). – *Z. ParasitKde* 65: 19-30.
- Prévôt, G., 1968. Contribution à la connaissance du cycle de *Lepidauchen stenostoma* Nicoll, 1913 (Trematoda, Digenea, Lepocreadiidae Nicoll, 1935, Lepocreadiinae Odhner, 1905). – *Annl. Parasit. hum. comp.* 43: 321-332.
- Seaward, D.R., (ed.), 1982. *Sea Area Atlas of the marine Molluscs of Britain and Ireland*. – *Nature Conservancy Council*, Shrewsbury, UK, 243 pp.

- Shimazu, T. & S. Shimura*, 1984. *Paralepidapedon* g. n. (Trematoda: Lepocreadiidae), with descriptions of metacercariae of *Paralepidapedon hoplognathi* (Yamaguti, 1938) comb. n. and of two other species from sea urchins. – Zool. Sci. (Japan) 1: 809-817.
- Shoop, W.L. & K.C. Corkum*, 1984. Tegumental changes of *Alaria marcianae* (Trematoda) during migration in the domestic cat. – J. Parasit. 70: 244-252.
- Skrjabin, K.I. & V.P. Koval*, 1960. Suborder Allocreadiata Skrjabin, Petrov and Koval', 1958. – In K.I. Skrjabin: Trematodes of Animals and Man. Essentials of Trematodology 18: 9-272. Akad. Nauk SSSR, Moskva. (English translation: I.P.S.T. 1965, 532 pp.)
- Srivastava, L.P.*, 1966. The morphology of *Lepidapedon cambrensis* sp. nov. (Digenea: Lepocreadiidae) from the large intestine of *Onos mustelus* (L.), with a historical review of the genus. – Ann. Mag. nat. Hist. 13: 111-122.
- Stunkard, H.W.*, 1979. Observations on the life-history of lepecreadiid trematodes. – Revta ibér. Parasit. 39: 493-503.
- Stunkard, H.W.*, 1980a. The morphology, life-history, and taxonomic relations of *Lepocreadium areolatum* (Linton, 1900) Stunkard, 1969 (Trematoda: Digenea). – Biol. Bull. 158: 154-163.
- Stunkard, H.W.*, 1980b. Successive hosts and developmental stages in the life history of *Neopechona cablei* sp. n. (Trematoda: Lepocreadiidae). – J. Parasit. 66: 636-641.
- Thulin, J.*, 1971. Parasitic platyhelminths in cod (*Gadus callarias*). – Zool. Revy 33: 76-84.
- Timofeeva, S.V. & E.F. Marasaeva*, 1984. The parasitic fauna of two forms of cod from the Kandalaksha Bay of the White Sea. – In Ecological-parasitological Investigations of Northern Seas, pp. 62-76. Kola Branch Akad. Nauk USSR, Murmansk Mar. Biol. Inst., Apatity. (In Russian.)
- Yamaguti, S.*, 1934. Studies on the helminth fauna of Japan. Part 2. Trematodes of fishes, I. – Jap. J. Zool. 5: 249-541.
- Yamaguti, S.*, 1971. Synopsis of Digenetic Trematodes of Vertebrates. – Keigaku Publish. Co., Tokyo, Vol. I: 1074 pp.; Vol. II: 349 pls.
- Yamaguti, S.*, 1975. A synoptical review of Life Histories of Digenetic Trematodes of Vertebrates with special reference to their larval forms. – Keigaku Publish. Co., Tokyo, 590 pp., 219 pls.
- Warén, A.*, 1974. Revision of the Arctic-Atlantic Rissoidae (Gastropoda Prosobranchia). – Zool. Scripta 3: 121-135.
- Watson, R.A.*, 1984. The life cycle and morphology of *Tetracerasta blepta*, gen. et sp. nov., and *Stegodexamene callista*, sp. nov. (Trematoda: Lepocreadiidae) from the long-finned eel, *Anguilla reinhardtii* Steindachner. – Aust. J. Zool. 32: 177-204.
- Zelikman, E.A.*, 1966. Some ecological and parasitological interconnections in the littoral zone of the northern part of the Kandalaksha Gulf. – Trudy murmansk. biol. Inst. 10(14): 7-77. (In Russian.)

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