

The genera of the phylum Orthonectida.

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Résumé : Sept espèces d'orthonectides ont été étudiées par techniques d'imprégnation argentique, qui montrent avec précision l'arrangement des cellules épidermiques et leurs cils. Ces caractéristiques, et la disposition des spermatozoïdes et des ovocytes, sont à la base des distinctions entre les quatre genres, dont les espèces types sont *Rhopalura ophiocomae*, *Intoshia linei*, *Ciliocincta sabellariae*, et *Stocharthrum giardi*. Également, *Rhopalura granosa*, *Intoshia leptoplanae*, et *Ciliocincta julini* sont classées définitivement, et quelques autres, parmi les 18 espèces décrites depuis 1877, peuvent être classées provisoirement. Une liste des hôtes d'orthonectides ni décrits ni identifiés est assemblée.

Abstract : Seven species of orthonectids have been studied with the aid of techniques of silver impregnation, which demonstrate the arrangement of epidermal cells and the pattern of ciliation. The four recognized genera, whose type species are *Rhopalura ophiocomae*, *Intoshia linei*, *Ciliocincta sabellariae*, and *Stocharthrum giardi*, are distinguished on the basis of these features and the disposition of sperm and oocytes. *Rhopalura granosa*, *Intoshia leptoplanae*, and *Ciliocincta julini* are also assigned definitively to genus. A few other species, among the 18 that have been named since 1877, are classified tentatively. Hosts for orthonectids that have not been described or identified are listed.

INTRODUCTION

The first orthonectid to be given a name was *Rhopalura ophiocomae* Giard (1877), a parasite of the ophiuroid *Amphipholis squamata* (= *Ophiocoma neglecta*) at Wimereux, France. In the same paper, Giard proposed names for two other species. One of them, *Intoshia linei*, was found at Wimereux in nemerteans identified as *Lineus* "gesserensis" and *Lineus sanguineus*. This organism had been mentioned, but neither named nor classified, by McIntosh (1874), in the second installment of his monograph on British nemerteans. The other species, *I. leptoplanae*, had not been seen by Giard, but he recognized its similarity to *I. linei* from an illustration in the work of Keferstein (1869) on polyclad turbellarians at Saint-Malo.

There are, at the present time, eighteen named species of orthonectids. The ones that were described in sufficient detail, or that I have personally observed, belong to four genera : *Rhopalura*, *Intoshia*, *Ciliocincta*, and *Stocharthrum*. The purpose of this paper is to define the genera on the basis of the morphology of the type species and other species I have studied. Emphasis will be given to the arrangement and characteristics of epidermal cells, patterns of ciliation, location of genital pores, and disposition of oocytes and sperm-features that are easily demonstrated with light microscopy and therefore more useful in systematic work than the arrangement of muscles and certain other internal structures. Of the described species that I have not seen, several can be assigned with reasonable certainty

to genus. The ones whose systematic position is still in doubt will be mentioned, however, and I will also cite published reports of undescribed or unidentified orthonectids that have been found in various hosts.

My descriptions of species and diagnoses of genera are based entirely on sexually mature individuals, although most preparations of parasitized tissue show many stages in development. With respect to the "plasmodium", within which germinal cells develop into adult orthonectids, I will simply state that my studies with transmission electron microscopy, not yet published, have convinced me that this semifluid mass consists of host tissue that has been destroyed. In other words, although multiplication of germinal cells and development of adults take place within it, the "plasmodium" itself is not a stage in the life cycle.

The genus *Pelmatosphaera* is excluded from this account, because its placement in the Orthonectida is probably not justified. The only known species, *P. polycirri*, was discovered by Caullery and Mesnil (1904) in the terebellid polychaete *Polycirrus haematodes* at l'Anse Saint-Martin, Cap de la Hague. Caullery (1961) created the family Pelmatosphaeridae for it, to set it apart from true orthonectids, which he placed in Rhopaluridae. Earlier, Hartmann (1925) also divided the Orthonectida into two families, Orthonectidae and Heteronectidae, the latter having *Pelmatosphaera* as its sole representative. We may hope that the morphology and systematic status of this interesting organism will soon be investigated thoroughly.

METHODS

The seven species of orthonectids available to me were studied intensively while alive, with both bright-field and phase-contrast microscopy, as well as in permanent preparations. All procedures of staining or impregnation were carried out with smears of parasitized tissue prepared on coverglasses. Impregnation with silver nitrate was used for demonstrating the arrangement of epidermal cells. Smears dropped face down on a 2 % solution were usually left in this for about an hour, then placed in sunlight or bright north light, either while still in the silver nitrate or after being transferred to distilled water. Sometimes, however, they were exposed to light directly after being dropped on the silver nitrate solution. The Protargol method was valuable for showing patterns of ciliation, the distribution of nuclei of epidermal cells, and the arrangement of oocytes and sperm. Prior to being placed in activated Protargol, smears were fixed in Bouin's fluid or Champy's fluid. After the fixative had been washed out and the smears had been hardened in 70 % alcohol, they were treated for five minutes in 0.25 % potassium permanganate, washed, left for five minutes in 2 % oxalic acid, then washed again. Bouin's fluid was used for fixation of material that was to be stained with iron hematoxylin. My work on *Rhopalura ophiocomae* (Kozloff, 1969) provides information on some other techniques that I have used in studying entire orthonectids with light microscopy, but these are mostly concerned with demonstrating glycogen, lipids, and nuclear DNA.

SYSTEMATICS

Genus *Rhopalura* Giard, 1877

The genus *Rhopalura* is characterized by conspicuous sexual dimorphism, the demarcation of the body into regions being much sharper in males than in females. In both sexes, some rings of epidermal cells are completely ciliated, whereas others lack cilia. In males, however, certain of the rings of one division in the anterior half of the body have a single transverse row of cilia near their anterior or posterior borders. Males are also characterized by the presence of conspicuous crystalline inclusions or large refractile granules in some epidermal cells. In females, the numerous oocytes form a compact mass that occupies most of the body ; in males, the sperm mass is located in the middle third of the body.

Type species : *Rhopalura ophiocomae* Giard, 1877 (Figs. 1-8)

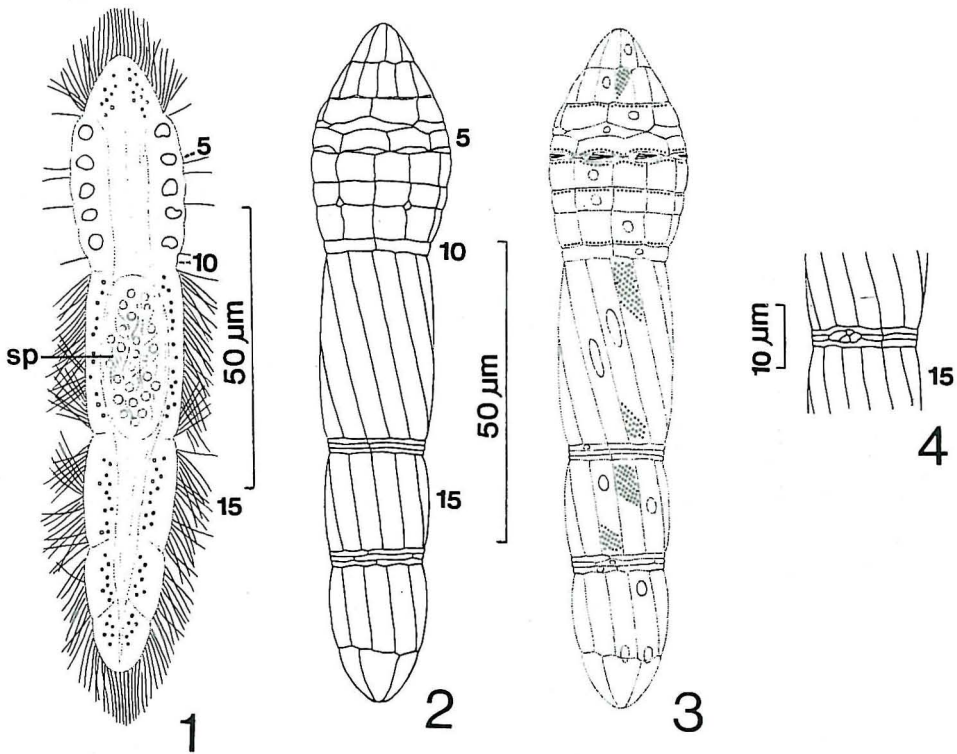
Rhopalura ophiocomae has been reported from many localities. In its usual host, *Amphipholis squamata*, it is known to occur in France at Wimereux, Roscoff, Dinard, and Sète (Cette) ; in Great Britain at Holy Island (Northumberland), Wembury (Devonshire), and the Isle of Man ; in Italy at Napoli and La Spezia ; in the United States on San Juan Island (Washington) and Point Pinos (California). What is perhaps the same species has been found in *Ophiothrix fragilis* at Holy Island (Fontaine, 1968) and in Norway at Strømme (Bender, 1972). Bender also reported the parasite in *Ophiura albida* at Hillersholmene. Shtein (1954) erroneously credited Atkins (1933) with finding *R. ophiocomae* in *O. fragilis* ; what Atkins had said, in fact, was that she had not found it in this ophiuroid.

The general morphology and ultrastructure have been described in considerable detail in an earlier paper (Kozloff, 1969). Only a summary of the characteristics of both sexes needs to be provided here.

Male

Mature males (Figs 1-3) from *Amphipholis squamata* range from about 90 μm long by 20 μm wide to about 130 μm long by 25 μm wide. The first division of the body is a conical cap consisting of two rings of cells that are completely ciliated (except for a small area on the anteriormost portion of the first ring). In the second division, where the body is widest, the cells of rings 3, 5 and 7-9 have a single transverse row of cilia near their anterior or posterior borders, and contain conspicuous crystalline inclusions. The cells of rings 4 and 10 are without cilia ; those of ring 6 also lack cilia, but have what may be kinetosomes and rootlets. The cells of rings 11, 15, and 19-20, which form the other three prominent divisions of the body, are comparatively large and ciliated, whereas the cells of rings 12-14 and 16-18 are small and lack cilia.

The genital pore (Fig. 4), in the midst of rings 12-14, is surrounded by four cells, these being without cilia. The sperm mass (Fig. 1) is within the area enclosed by ring 11 (the

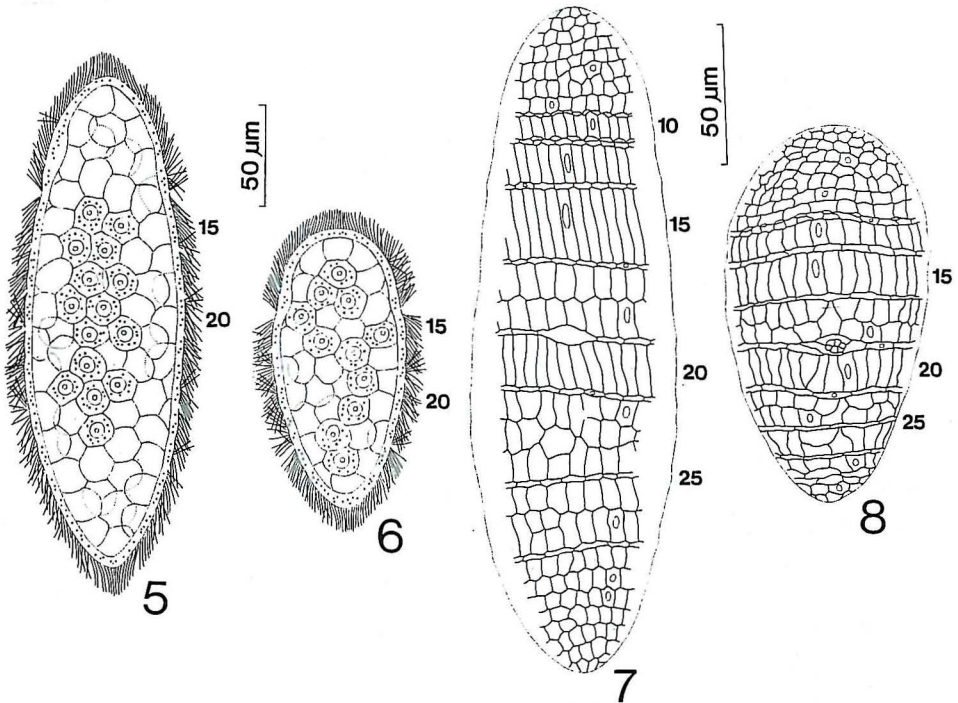


Figs. 1-4: *Rhopalura ophiocornae*, male. 1. Live specimen, optical section, showing distribution of cilia, crystalline inclusions in cells of rings 3, 5, and 7-9, sperm mass, and small lipid droplets in some epidermal cells; sp, sperm. 2. Boundaries of epidermal cells; silver nitrate impregnation. 3. Composite drawing, based on specimens impregnated with silver nitrate to show boundaries of epidermal cells, and with Protargol to show arrangement of kinetosomes of cilia. 4. Small cells surrounding genital pore.

third superficial division of the body) and is surrounded by a sheath of contractile cells. Eight other contractile cells--in one pair and two trios--run almost the entire length of the body. Beginning at about the mid-level of the sperm mass, and reaching nearly to the posterior end of the body, are four cells containing fibers that may consist of paramyosin.

Female

There are two types of females. One type (Figs. 5, 7) consists of elongated individuals 235 to 260 μm long and 65 to 80 μm wide; the other (Figs. 6, 8) consists of ovoid individuals about 125 to 140 μm long and 65 to 70 μm wide. There are fewer rings of epidermal cells in the ovoid females than in elongated females, but to facilitate comparison of the two types, the numbers assigned to certain rings in my figure of the ovoid female (Fig. 8) correspond to apparently homologous rings in the elongated type. In both types, most rings of epidermal cells are completely ciliated; the rest--rings 9, 11, 12, 14, 16, 19, 21, 25, 28 in



Figs. 5-8 : *Rhopalura ophiocomae*, female. 5. Live specimen of elongated type, optical section. 6. Live specimen of ovoid type. 7. Boundaries of epidermal cells of elongated type ; silver nitrate impregnation. (The small cells surrounding the genital pore, in ring 19, are not shown). 8. Boundaries of epidermal cells of ovoid type ; silver nitrate impregnation.

the elongated type, and similar rings of small cells in the ovoid type--are nonciliated. None of the rings has just one row of cilia, as is the case in the male. While some of the rings of ciliated cells are very uniform, others are irregular. A particular ring of cells, for instance, may rather abruptly become two rings, or two rings may be replaced by three. Such deviations from perfectly regular arrangements of cells are more commonly noted in females of the ovoid type than in those of the elongated type.

The genital pore (Fig. 8), in ring 19, is surrounded by several small cells, and the whole complex lies within a ring of nonciliated cells. The many oocytes fill up most of the body. Beneath the epidermis, there are numerous longitudinally oriented contractile cells similar to the eight that run much of the length of the body of the male, and there are also contractile cells that follow a circular or slightly oblique course.

I have never observed both types of females in the same host, nor females that were intergrades between one type and the other. It is possible that we are dealing with two species, in which the females are decidedly different, but in which the males are so nearly similar that distinctions between them have escaped notice.

Other species of *Rhopalura*
Rhopalura granosa Atkins, 1933 (Figs. 9-11)

This species was found by Atkins in the small bivalve *Pododesmus squamula* (*Heteranomia squamula*) (Anomiidae), at Plymouth, England. It was present in only three of 444 *P. squamula* I removed from carapaces of the crab *Maia squinado* at Plymouth during March, 1965. None of the 70 specimens taken from colonies of the bryozoan *Pentapora foliacea* (*Lepralia foliacea*) and shells of the gastropod *Buccinum undatum* was parasitized. My best sources of *R. granosa* at Plymouth were specimens of *P. squamula* attached to small rocks that had been collected at low tide on the breakwater, and that were already in display tanks when I arrived at the laboratory. Of 168 of these bivalves, 23 had *R. granosa*. At Roscoff, between April and August, 1965, I examined 258 *A. squamula* taken from *Maia squinado* on sale in fish markets, and found two of these to be parasitized.

Atkins' illustrations of live specimens are good, and I can add little to her descriptions. I had relatively little material to work with, and my Protargol and silver nitrate preparations, especially of males, do not show details comparable to those I have seen in *R. ophiocoma* and in other orthonectids.

Male

Atkins' measurements gave the length as 87 to 95 μm and the width as 20 μm . The relatively few mature specimens I observed while they were alive fell into the range for length, but were slightly broader--24 to 26 μm . It should be noted, however, that Atkins was able to study males that had been released naturally from *P. squamula*. If these were the ones she measured, they may have been more slender than those I obtained by opening parasitized hosts. The body, as in *R. ophiocoma*, appears superficially to consist of five divisions (six, according to Atkins, but the last two, taken together, correspond to the fifth division in *R. ophiocoma*). Most of the epidermal cells of the first division contain large refractile granules. Some similar granules are found in the anterior part of the second division, where the body is widest. The granules seem not to be comparable to the ones that characterize cells of the second division of *R. ophiocoma*, for they are not crystalline. Furthermore, they take up neutral red applied *in vivo*, and they persist through conventional procedures of fixation, staining, and transfer through ethyl alcohol and toluene. As Atkins noted, the cilia on the second division of the body appear to be more widely spaced than those in the first and third to fifth divisions. Because my Protargol and silver nitrate impregnations are not satisfactory, I have been unable to establish the pattern of ciliation in this region. I suspect, however, that the wider spacing of cilia is due to their being concentrated in a few transverse rows (as they are in the second division of *R. ophiocoma*) instead of being distributed all over the cells.

I have not seen the genital pore. The sperm mass, as Atkins showed, occupies much of the third superficial division of the body, and is clearly evident in some Protargol preparations (Fig. 10).

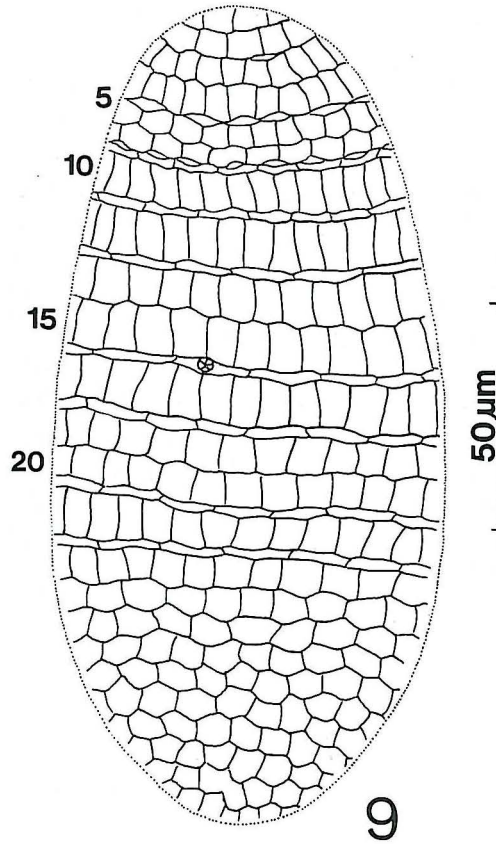
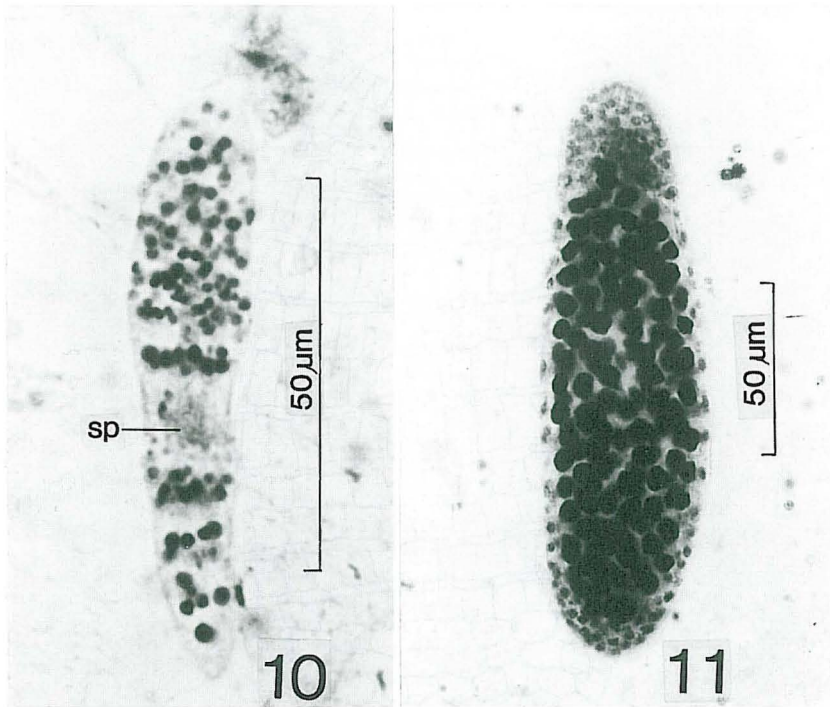


Fig. 9 : *Rhopalura granosa*, female ; silver nitrate impregnation.

Female

The specimens I measured fell into the ranges given by Atkins for individuals that were typical : length 190 to 210 μm , width 60 to 75 μm . She observed some specimens that were proportionately more slender (230 by 55 μm), but I did not encounter any of this type. The arrangement of epidermal cells, shown in Fig. 9, is similar to that of elongated females of *R. ophiocoma*. Behind the first four rings of ciliated cells, there is a ring of small nonciliated cells. This is succeeded by two rings of ciliated cells, and then by two rings of small nonciliated cells, those of the first ring being smaller than those of the second. (This pair of rings [8, 9] is comparable to a similar pair [11, 12] in females of *R. ophiocoma*). Rings 10, 12, 14-15, 17, 19-20, 22, 24, and the remaining rings (usually nine or ten) are completely ciliated, whereas rings 11, 13, 16, 18, 21, and 23 consist of small nonciliated cells. Not all of the rings of ciliated cells are perfectly regular ; sometimes, for instance, a pair of conse-



Figs. 10, 11 : *Rhopalura granosa* ; photomicrographs of specimens fixed in Bouin's fluid and impregnated by the Protargol method. 9. Male ; sp, sperm. 10. Female.

cutive rings will be interrupted by a single large cell. The several (usually eight or nine) slightly bulging superficial divisions of the body correspond to the locations of ciliated cells.

The genital pore, surrounded by several small nonciliated cells, is in ring 16. The oocytes (Fig. 11) occupy nearly all of the space beneath the epidermis, and their arrangement is similar to that in *R. ophiocomae*. I have not been able to study the arrangement of muscles, for these are not distinct in my Protargol preparations.

Rhopalura philinae Lang, 1954.

Lang obtained his material from the opisthobranch gastropod *Philine scabra* (Philinidae), collected near Kristineberg, Sweden. Most of the mature individuals he saw were females, and these fit clearly into *Rhopalura*. Lang studied only two males, however. They had the conspicuous epidermal inclusions characteristic of males of *R. ophiocomae* and *R. granosa*, but according to Lang they were larger (540 and 700 μm long) than the females (223 to 314 μm long).

Probable species of *Rhopalura* (none adequately described)

Rhopalura elongata Shtein, 1953.

This orthonectid was found in the bivalve *Astarte crenata* (Astartidae) at Murmansk, Russia ; only females were seen.

Rhopalura murmanica Shtein, 1953

This species was reported from the gastropod *Admete viridula* (Cancellariidae) at Murmansk ; both males and females were observed.

Rhopalura litoralis Shtein, 1953

The gastropods *Rissoa aculeus* (Rissoidae) and *Columbella rosacea* (Columbellidae) were reported to be hosts for this species at Murmansk ; both males and females were studied. The possibility that two species of orthonectids are involved must be considered, for the hosts are not closely related.

Rhopalura major Shtein, 1953

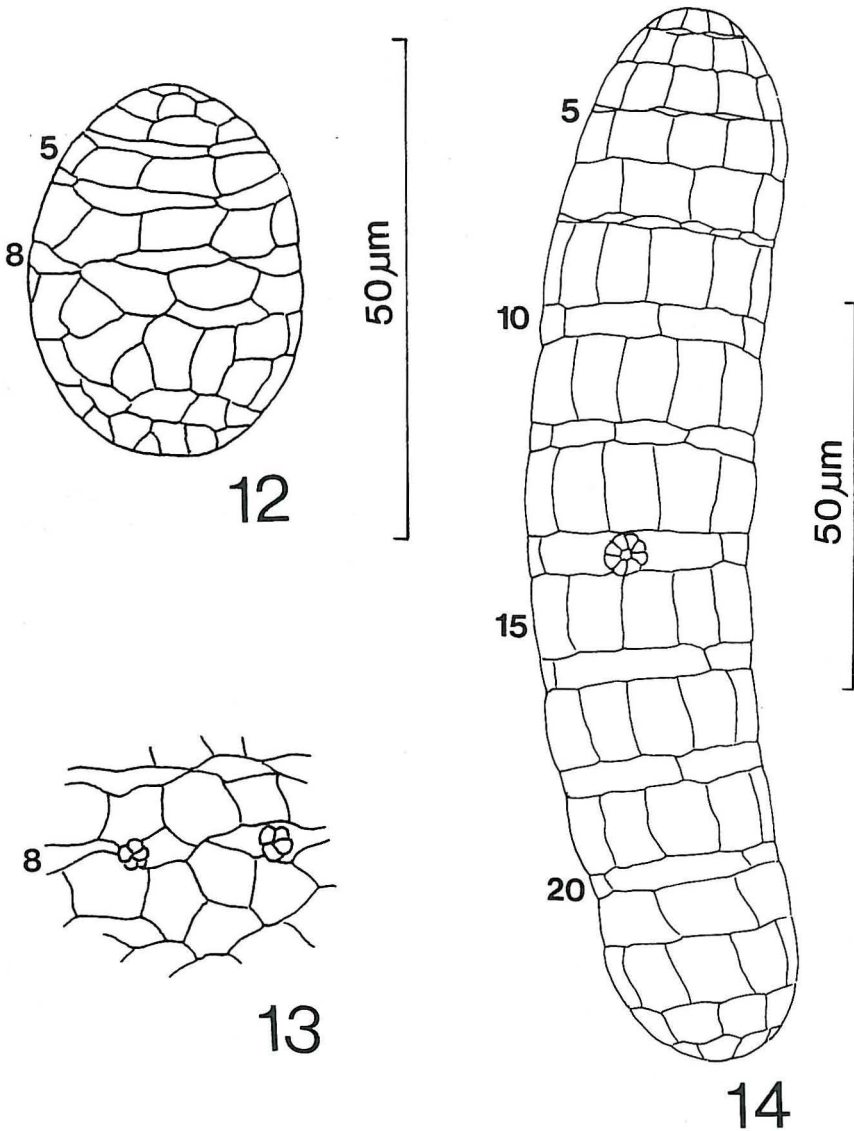
This species was found in the gastropods *Lepeta caeca (coeca)* (Lepetidae), *Natica clausa* (Naticidae), and *Solariella* sp. (Trochidae) at Murmansk ; both males and females were observed in the first two hosts, females only in *Solariella*. Because the hosts belong to three very different families, it is possible that each one harbors a separate species.

Genus *Intoshia* Giard, 1877

In species of *Intoshia*, more than half of the rings of epidermal cells are completely ciliated ; the rest lack cilia. There are no rings that have a single transverse row of cilia near their anterior or posterior margins, or both. Sexual dimorphism is pronounced in the type species, *I. linei*, and also in *I. metchnikovi*, in which males are much smaller than females, are ovoid rather than elongated, and have two genital pores instead of one. It is much less marked in *I. leptoplanae*, in which males are merely slightly smaller and more slender than females. In females of all described species that can be assigned to this genus, the oocytes fill most of the axial mass, and are packed together in such a way that they may seem to form two or three rows.

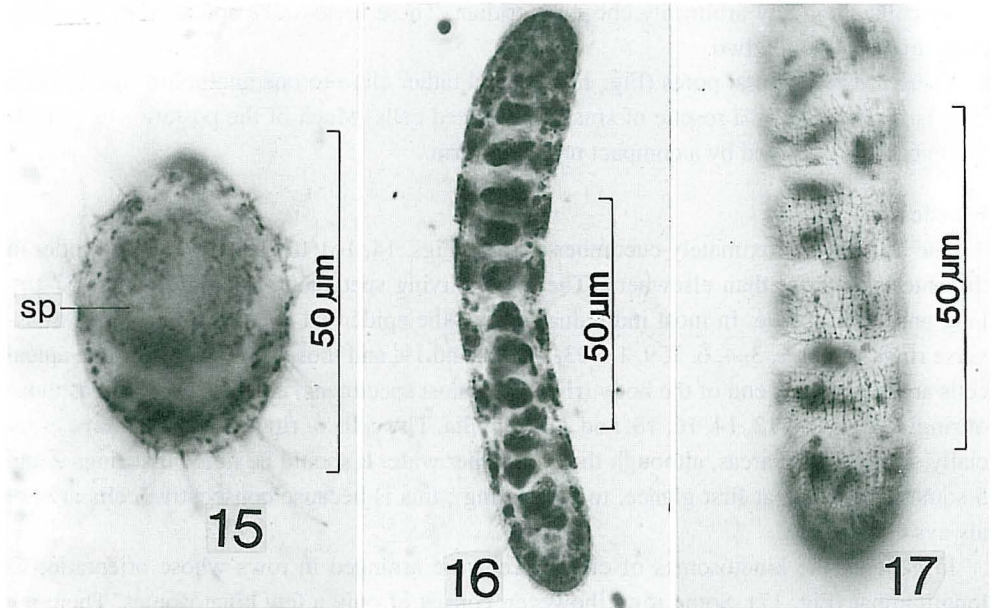
Type species : *Intoshia linei* Giard, 1877 (Figs. 12-17)

Intoshia linei is designated as the type species because it was the first of two orthonectids to which Giard applied the genus name, the other being *I. leptoplanae*. Although the males of *I. linei* and *I. leptoplanae* are decidedly different, the females are so similar that it seems best to keep both species in the same genus.



Figs. 12-14: *Intoshia linei*; silver nitrate impregnations. 12. Male. 13. Portion of male, showing small cells surrounding genital pores. 14. Female.

Intoshia linei was first seen by McIntosh (1874) in the nemertean he called *Lineus* "gesserensis". Giard's material was obtained from *L. "gesserensis"* and *L. sanguineus* at Wimereux. The name *gesserensis* is no longer in general use; greenish or olive worms formerly assigned to this species are now referred to *L. viridis*, whereas reddish or reddish brown specimens are placed in *L. ruber*. Nouvel (1935 a) reported the occurrence of *I. linei*



Figs. 15-17 : *Intoshia linei* ; photomicrographs of specimens fixed in Bouin's fluid and impregnated by the Protargol method. 15. Male ; sp, sperm. 16. Female. 17. Posterior portion of female, showing arrangement of kinetosomes of cilia.

in *L. viridis* (that is, in greenish *L. "gesserensis"*) at Roscoff, and in later papers (1935 b, 1939) he carefully described the arrangement of cells of the epidermis. I also found this species in *L. viridis* at Roscoff. *Intoshia linei* from *L. ruber*, which seems to be less commonly parasitized than *L. viridis*, has been the subject of recent papers by Langlet and Bierne (1989), Vernet (1990), Vernet and Fargette (1990), and Haloti, Vernet, and Bierne (1992). An orthonectid from an unidentified species of *Lineus* (close to those of the *L. viridis-ruber* complex) collected intertidally in the Barents Sea was the subject of a detailed study by Aleksandrov (1989). His recognition of the parasite as *I. linei* (*Rhopalura linei*) is, I feel, absolutely correct.

Male

The body is approximately egg-shaped (Figs. 12, 15), the anterior half being more obviously tapered than the posterior half. Of the specimens I measured while they were alive, the largest were 41 µm long by 25 µm wide. In the anterior half of the body, most of the epidermal cells fit into rather distinct transverse rings. Rings 1-3, 5, and 7 consist of ciliated cells ; rings 4, 6, and 8 consist of cells that lack cilia and that are much broader and shorter than most of the ciliated cells. Behind ring 8, all epidermal cells are ciliated, but they are not so regularly arranged as those in the anterior half, and there is considerable variation from specimen to specimen. In most individuals, behind ring 8, there will be five

or six cells along any arbitrarily chosen meridian. These include the apical cells, of which there are usually only two.

There are two genital pores (Fig. 13), located rather close to one another in ring 8. Each pore is surrounded by a rosette of small nonciliated cells. Much of the posterior two-thirds of the body is occupied by a compact mass of sperm.

Female

The body is approximately cucumber-shaped (Figs. 14, 16), but usually slightly wider in the anterior quarter than elsewhere. The largest living specimen I measured was 157 μm long and 34 μm wide. In most individuals, all of the epidermal cells fit into distinct transverse rings. Rings 1, 3, 4, 6, 7, 9, 11, 13, 15, 17, and 19, and those from ring 21 to the apical cells at the posterior end of the body (ring 24 in most specimens) are ciliated, whereas those of rings 2, 5, 8, 10, 12, 14, 16, 18, and 20 lack cilia. The cells of rings 2, 5, and 8 have especially small surface areas, although they are rather wide. It should be noted that rings 2 and 5 sometimes seem, at first glance, to be missing; this is because consecutive cells are not always contiguous.

In general, the kinetosomes of ciliated cells are arranged in rows whose orientation is longitudinal (Fig. 17). Some rows, however, consist of only a few kinetosomes. There are also rows that have a slightly oblique orientation.

The genital pore (Fig. 14), within a rosette of extremely small cells that lack cilia, is located in ring 12. The axial mass consists almost entirely of oocytes (Fig. 16). There are from 11 to 20 of these, packed tightly together in such a way that they may seem to form two rows.

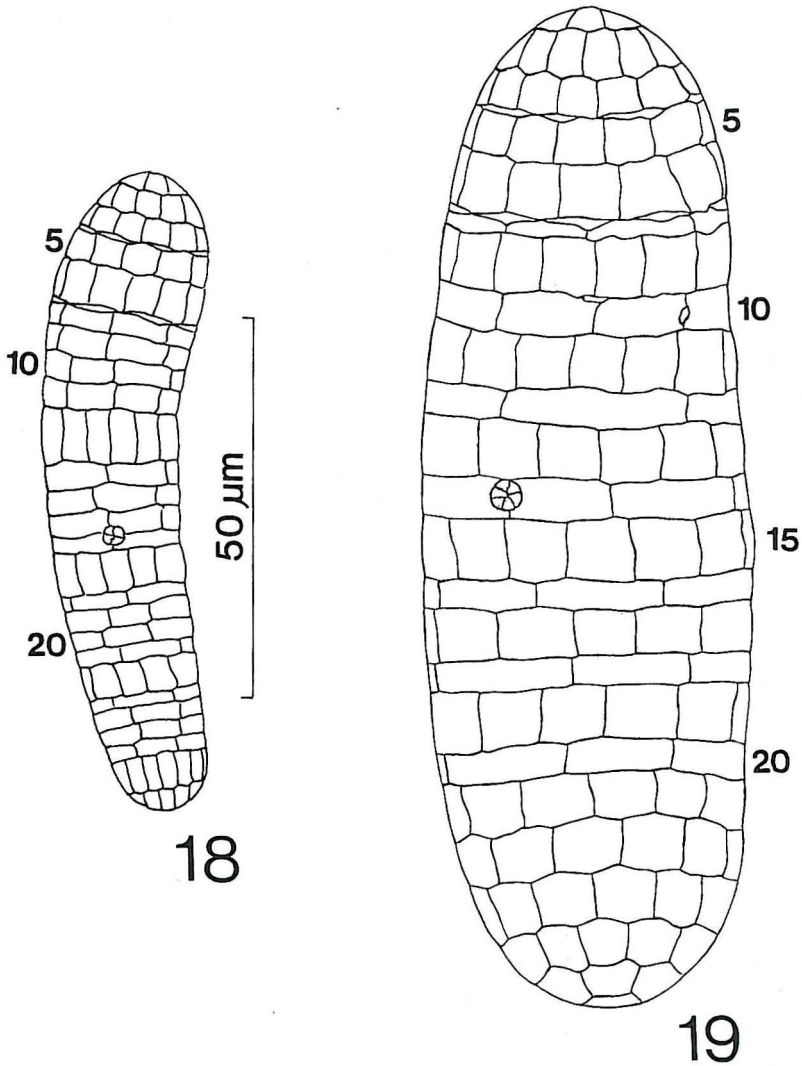
Other species of *Intoshia*

Intoshia leptoplanae Giard, 1877 (Figs. 18-23)

Keferstein (1869) found this species in the polyclad turbellarian *Leptoplana tremellaris* at Saint-Malo. His single illustration and explanatory legend constitute, in fact, the first published reference to an organism that can be recognized as an orthonectid. McIntosh (1874) commented on its similarity to the parasite that he observed in the nemertean *Lineus "gesserensis"*, and that soon afterward was named *I. linei* by Giard (1877).

Jourdain (1880) described what was certainly the same species living in *L. tremellaris* at Saint-Vaast-la-Hougue. Thinking that it had a complete digestive tract, Jourdain could not accept the idea that it should be placed in Giard's new class Orthonectida. Moreover, he was not sure that the parasite he found was the same as the one seen by Keferstein and named by Giard, so he proposed that it provisionally be called *Prothelminthus hessi*.

Besides Saint-Malo, Saint-Vaast-la-Hougue, and the unspecified locality where McIntosh found *I. linei*, there are records for l'Anse Saint-Martin (Caullery & Mesnil, 1901) and Roscoff (Nouvel, 1935 a, 1939). Caullery and Mesnil did not have an opportunity to study *I. leptoplanae* until after their monograph had gone to press. They found a subs-



Figs. 18, 19 : *Intoshia leptoplanae* ; silver nitrate impregnations. 18. Male. 19. Female.

tantial percentage of *L. tremellaris* at l'Anse Saint-Martin to be parasitized. They described the adults and "plasmodial masses" in a footnote, and illustrated the species in a supplementary plate.

Nouvel (1935 *a*) stated that of the hundreds of *L. tremellaris* collected between the laboratory and the port at Roscoff, at about the level reached by high water of neap tides, only one was parasitized by *I. leptoplanae*. In his paper of 1939, in which the arrangement of epidermal cells was described precisely, Nouvel reported that parasitized worms were rela-

tively abundant near the lowermost limits of the *Fucus*-zone ; about one in five specimens at this level were parasitized. My experience with respect to the vertical distribution of parasitized hosts at Roscoff was similar to Nouvel's.

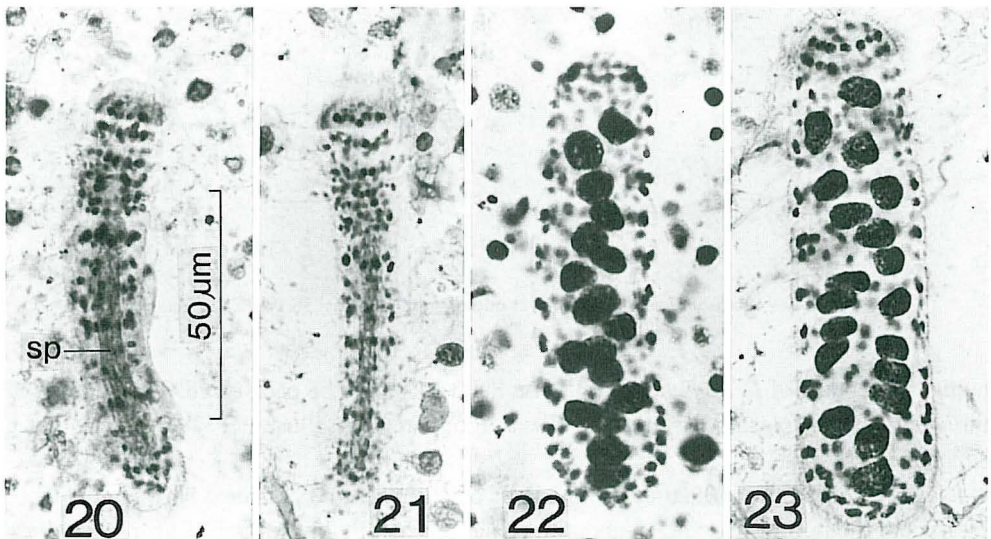
Male

The length of most individuals is about 100 μm , the width about 16 μm . In the epidermis (Fig. 18), the cells of rings 1-3 are ciliated. Ring 4 consists of cells that have a small surface area and lack cilia. The cells of rings 5 and 6 are completely ciliated. Ring 7 is much like ring 4. The cells of rings 8-10, 14-15, 19-20, and 24-25 are broader than long and ciliated ; rings 12, 17, 22, and 27-28, also ciliated, are longer than broad. Rings 11, 13, 16, 18, 21, 23 and 26 are broader than long and lack cilia.

The genital pore (Fig. 18), surrounded by four small nonciliated cells, is located in ring 16, or on the boundary between rings 15 and 16. The compact mass of sperm occupies much of the posterior two-thirds of the body (Figs. 20, 21).

Female

The body reaches a length of about 130 μm and a width of about 39 μm , and the shape (Figs. 19, 22, 23) is similar to that of the female of *I. linei*. As in the male, the cells of epidermal rings 1-3 are ciliated, and those of ring 4 are small and nonciliated. Rings 5 and 6, consisting of ciliated cells, are succeeded by two rings of cells that have a small surface area and that lack cilia. Rings 9, 11, 13, 15, 17, 19, and 21-23, and the cells farther posteriorly, which do not form distinct rings, are all much alike, being ciliated and having expo-



Figs. 20-23 : *Intoshia leptoplanae* ; photomicrographs of specimens fixed in Bouin's fluid and impregnated by the Protargol method. 20, 21. Males ; sp, sperm. 22, 23. Females.

sed surfaces that are nearly square or slightly broader than long. Rings 10, 12, 14, 16, 18 and 20, on the other hand, consist of cells that are considerably broader than long and that lack cilia.

The genital pore (Fig. 19), within a rosette of small cells, is within ring 14. The number of oocytes ranges from 14 to 20 ; as in *I. linei*, they occupy nearly all of the axial mass (Figs. 22, 23) and are packed together in such a way that they may seem to form two or three rows.

Intoshia metchnikovi Caullery and Mesnil, 1899

This species was originally found by Caullery and Mesnil (1899 a) in the spionid polychaete *Spio martinensis* at l'Anse de Vauville, Cap de la Hague, France. Subsequently, Caullery and Mesnil (1901) reported its occurrence in a nemertean that they called *Tetrastemma flavidum* variety *lactaeum*. The nemertean lives in the same habitat as *S. martinensis* ; the incidence of parasitism, in the experience of Caullery and Mesnil, was higher in the nemertean host than in the polychaete.

Intoshia metchnikovi exhibits the same sort of sexual dimorphism as is characteristic of *I. linei*. Caullery and Mesnil considered the possibility that it is indeed *I. linei*, and Caullery (1961) mentioned this again after Nouvel (1935 b, 1939) reported on the morphology of this species. To determine if it is conspecific with *I. linei* will require study of specimens from *S. martinensis*, which is the host from which material for the original description was obtained.

The identity of the nemerteans to which Caullery and Mesnil applied the name *T. flavidum* variety *lactaeum* is also in doubt. The worms were either uniformly white or white tinged with pink, so the varietal name was proposed to distinguish them from more typically colored *T. flavidum*, which is decidedly pink, reddish, or yellowish. The name *lactaeum* is, in any case, a *nomen nudum*, and we cannot be sure that the worms to which the varietal name was given fit *T. flavidum* in other respects.

Intoshia paraphanostomae (Westblad, 1942) comb. nov.

This species, described as *Rhopalura paraphanostomae*, was found by Westblad (1942) in the acoel turbellarians *Paraphanostoma macroposthium* and *P. brachyposthium*. Westblad stated that the parasite was widespread in these acoels in Scandinavian waters, but added that *P. macroposthium* appeared to be more commonly parasitized than *P. brachyposthium*. Although the orthonectids occurring in these two closely related turbellarians may belong to a single species, it is also possible that they are different. A more recent report of an orthonectid in *P. brachyposthium* was published by Dörjes (1979).

Unfortunately, Westblad's account is not sufficiently detailed to enable me to state unequivocally that the orthonectid he observed belongs in the genus *Intoshia*. His figure 18, B, however, represents a mature or nearly mature female that resembles females of *I. leptoplanae* and *I. linei*. The arrangement of oocytes is especially similar to that in *I. leptoplanae*.

Figures 18, C and D also seem to show portions of females, although Westblad thought that D might represent a male. He may have mistaken the deeply stained granules within the oocytes for stages in spermatogenesis. Lang (1954) restudied Westblad's sections and did not recognize any males. On the basis of the four sketches provided by Westblad, I conclude that this species fits best under *Intoshia*. It certainly cannot be assigned to any other described genus.

Genus *Ciliocincta* Kozloff, 1965

The genus *Ciliocincta* is characterized by slight sexual dimorphism. Males are smaller than females, but the arrangement of epidermal cells and the pattern of ciliation are similar in both sexes. Of the cells that are ciliated, only those of a few rings close to the anterior end have more than one transverse row of cilia at a particular locus. Most have a single row close to either their anterior or posterior borders, or both. In the male, there are no crystalline inclusions comparable to those in certain epidermal cells of males of *Rhopalura*. In the female, the oocytes are in a single series.

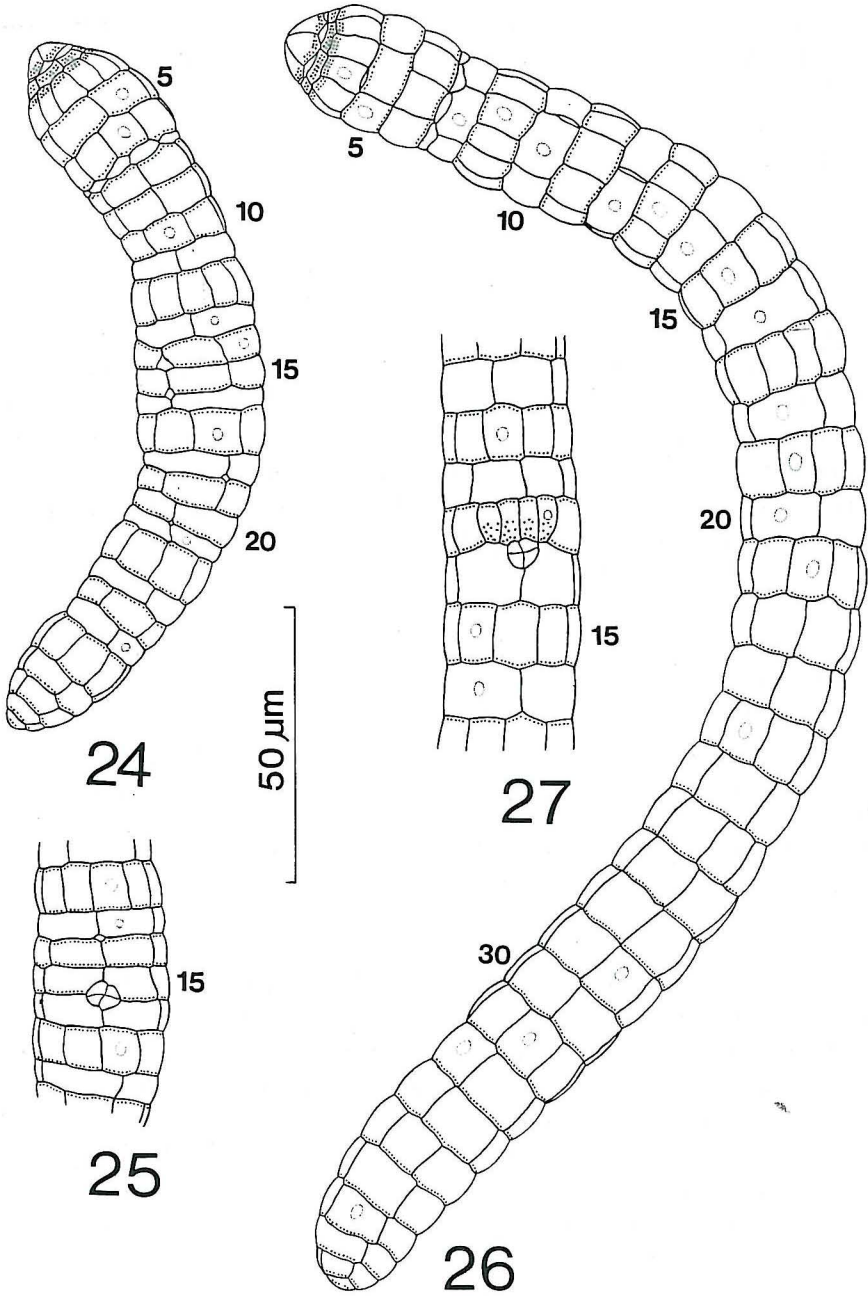
Type species : *Ciliocincta sabellariae* Kozloff, 1965 (Figs. 24-30)

Ciliocincta sabellariae is a parasite of the sabellariid polychaete *Sabellaria cementarium*. The type material was collected at a depth of about 12 meters off Dot Rock, close to Decatur Island, in the San Juan Archipelago, Washington. I have found the orthonectid in worms dredged at this locality at various times over a period of several years, but never in specimens collected elsewhere. It was the subject of a detailed morphological and ultrastructural study (Kozloff, 1971) ; the account below is reduced to features useful in systematics.

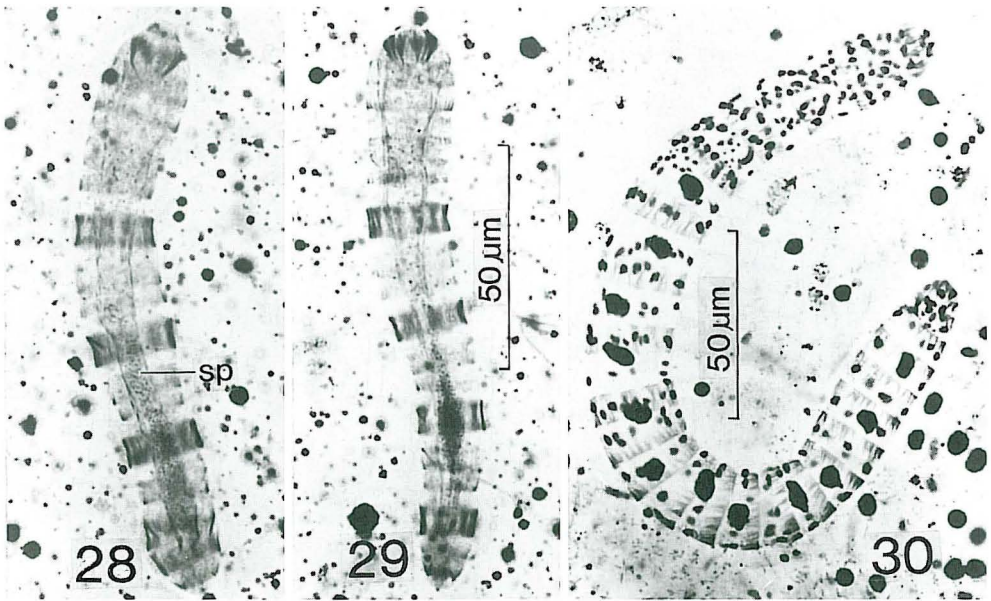
Male

Mature individuals (Fig. 24, 28, 29) range in size from 125 μm by 20 μm to 135 μm by 21 μm . There are usually 30 rings of epidermal cells. The cells of ring 1 have two transverse rows of cilia near their posterior margins ; those of ring 2, which have a very small surface area, are nonciliated. There are two rows of cilia on the slightly larger cells of ring 3, and two rows near the anterior margins of the cells of ring 4. The cells of rings 5, 10, 12, 14, 17, 19, 22, 24 and 26 have a transverse row near both the anterior and posterior margins ; rings 6, 15, 20 and 27-30 have a row near their posterior margins. Rings 8 and 9 have cilia only near their anterior margins. Rings 7, 11, 13, 16, 18, 21, 23 and 25 lack cilia.

The genital pore (Fig. 25), surrounded by four nonciliated cells, is at the level of the boundary between rings 15 and 16. The mass of sperm, about half the length of the body, begins at the level of ring 17. Peripheral to the sperm mass are some large secretory cells, and anterior to it there is an assemblage of contractile cells whose primary orientation is circular or circular-oblique. These cells, like the sperm mass, are internal to the four pairs of contractile cells that lie just beneath the epidermis.



Figs. 24-27 : *Ciliocincta sabellariae* ; composite drawings, based on specimens impregnated with silver nitrate to show boundaries of epithelial cells, and by the Protargol method to show the arrangement of kinetosomes. 24. Male. 25. Portion of male, showing small cells surrounding genital pore. 26. Female. 27. Portion of female, showing small cells surrounding genital pore and four specialized cells anterior to these.



Figs. 28-30 : *Ciliocincta sabellariae* ; photomicrographs of specimens fixed in Bouin's fluid and impregnated by the Protargol method. 28, 29. Males ; sp, sperm. 30. Female.

Female

Mature individuals (Figs. 26, 30) range in length from 250 to 265 μm , and in width from 22 to 24 μm . There are usually 38 or 39 rings of epidermal cells. The arrangement and pattern of ciliation of rings 1-7 is the same as in the male. Ring 8, however, lacks cilia. Rings 9, 11, 13, 15, 17, 19 and 21 have a transverse row of cilia near their anterior and posterior borders ; rings 22-30 have a transverse row only near their posterior borders. Rings 10, 12, 14, 16, 18 and 20 are nonciliated.

The genital pore (Fig. 27), surrounded by four small nonciliated cells, is located in ring 14. Four cells of ring 13, two of which are contiguous with two of those around the genital pore, are unlike the others of this ring in having cilia scattered over the posterior halves of their surfaces. The oocytes, whose number ranges from 9 to 12, are in a single series ; the anteriormost one is just behind the level of the genital pore. As in the male, there are four pairs of longitudinal contractile cells just beneath the epidermis.

Other species of *Ciliocincta*

Ciliocincta julini (Caullery and Mesnil, 1899) comb. nov. (Figs. 31-36)

The host of *C. julini* is the spionid polychaete *Scololepis fuliginosa*. The parasite was found by Caullery and Mesnil (1899 a) at l'Anse Saint-Martin, Cap de la Hague, France.

I have found it in the same host polychaete at Point Perharidic (Perharidy), near Roscoff. Of 153 worms examined at various times from May to mid-July, 16 were parasitized. None of 55 worms taken from the same locality in mid-August had the orthonectid.

Male

Mature specimens (Figs 31, 33, 34) measure about 92 μm by 25 μm . They are somewhat bottle-shaped, being widest near the middle, and rather obviously narrower in the anterior two-fifths. The apical cells of ring 1 bear two transverse rows of cilia near their posterior margins. The small cells of ring 2, which lack cilia, are succeeded by some appreciably larger cells that have two transverse rows of cilia. The more elongated cells of ring 4 have two rows of cilia near their anterior margins. Ring 5 consists of cells that are broader than those of ring 4, and that have a transverse row of cilia near their anterior and posterior margins. Ring 6 consists of similar cells that have a transverse row of cilia only near their posterior margins.

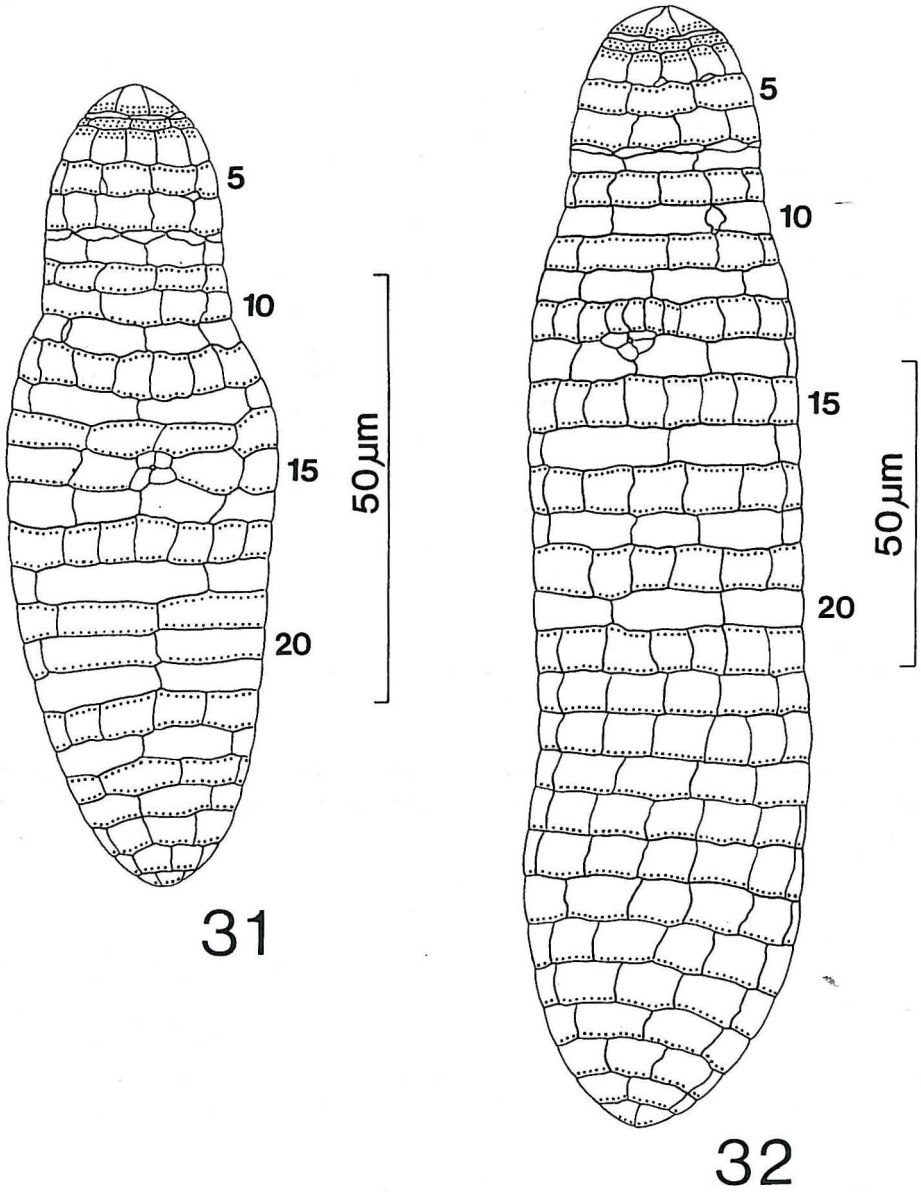
Rings 7 and 8, which consist of cells of decidedly different sizes, lack cilia. The cells of ring 9 are ciliated near both their anterior and posterior margins, but those of ring 10 are ciliated only next to their posterior margins. Rings 11 and 13 lack cilia, but the cells of ring 12 have a transverse row of cilia near their anterior and posterior margins. Rings 14, 17, 19, 22 and 24 are ciliated near both their anterior and posterior margins, but rings 15 and 20 are ciliated only near their posterior margins. Rings 16, 18, 21, and 23 lack cilia. From ring 25 to the end of the body, the cells are ciliated only near their posterior margins. There are usually 28 rings, sometimes 27 or 29.

The genital pore (Fig. 31) and the four unciliated cells that surround it are located within ring 15. The sperm mass extends through the posterior half of the body (Figs. 33, 34).

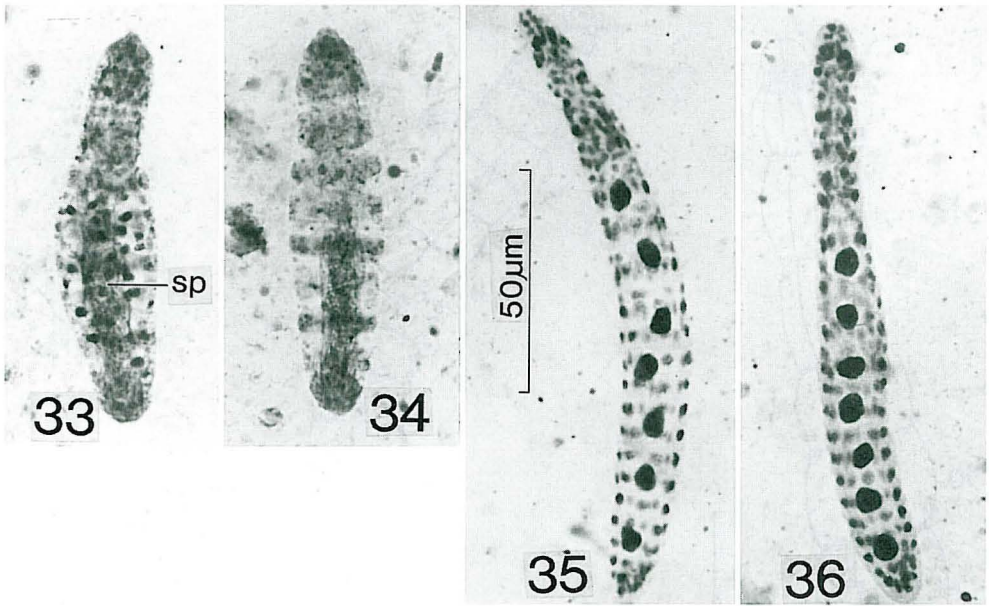
Female

Mature individuals (Figs. 32, 35, 36) reach a maximum size of about 205 μm by 29 μm . As in the male, the greatest width is near the middle, and the anterior two-fifths are somewhat narrower. The arrangement of rings 1-7, and the pattern of ciliation down to this level, are as they are in the male. Ring 8, however, is not ciliated. Rings 9, 11, 13, 15, 17, 19 and 21 are ciliated near both their anterior and posterior borders, but the rings that alternate with them (10, 12, 14, 16, 18 and 20) are not ciliated. Beginning with ring 22, the epidermal cells bear cilia only near their posterior margins. There are usually 33 rings, but a few specimens have 32 or 34.

The genital pore (Fig. 32) is located in ring 14. There are four small, nonciliated cells surrounding it, and two of these are contiguous with some of the cells of ring 13. These cells, whose number ranges from four to six, are appreciably smaller than the other cells of ring 13, but they differ from comparable cells of *C. sabellariae* in that they seem not to have cilia except for those near their posterior borders. In some individuals, the genital pore is not centered behind them, so that one of the cells surrounding the pore touches a larger cell. In my specimens, there are six to eight oocytes. Caullery and Mesnil (1899 a, 1901) gave the number as eight to ten, although the only pertinent figure in their 1901 paper shows seven.



Figs. 31, 32 : *Ciliocincta julini* ; composite drawings based on specimens impregnated with silver nitrate to show cell boundaries, and by the Protargol method to show arrangement of kinetosomes. 31. Male. 32. Female.



Figs. 33-36 : *Ciliocincta julini* ; photomicrographs of specimens fixed in Bouin's fluid and impregnated by the Protargol method. 33, 34. Males ; sp, sperm. 35, 36. Females.

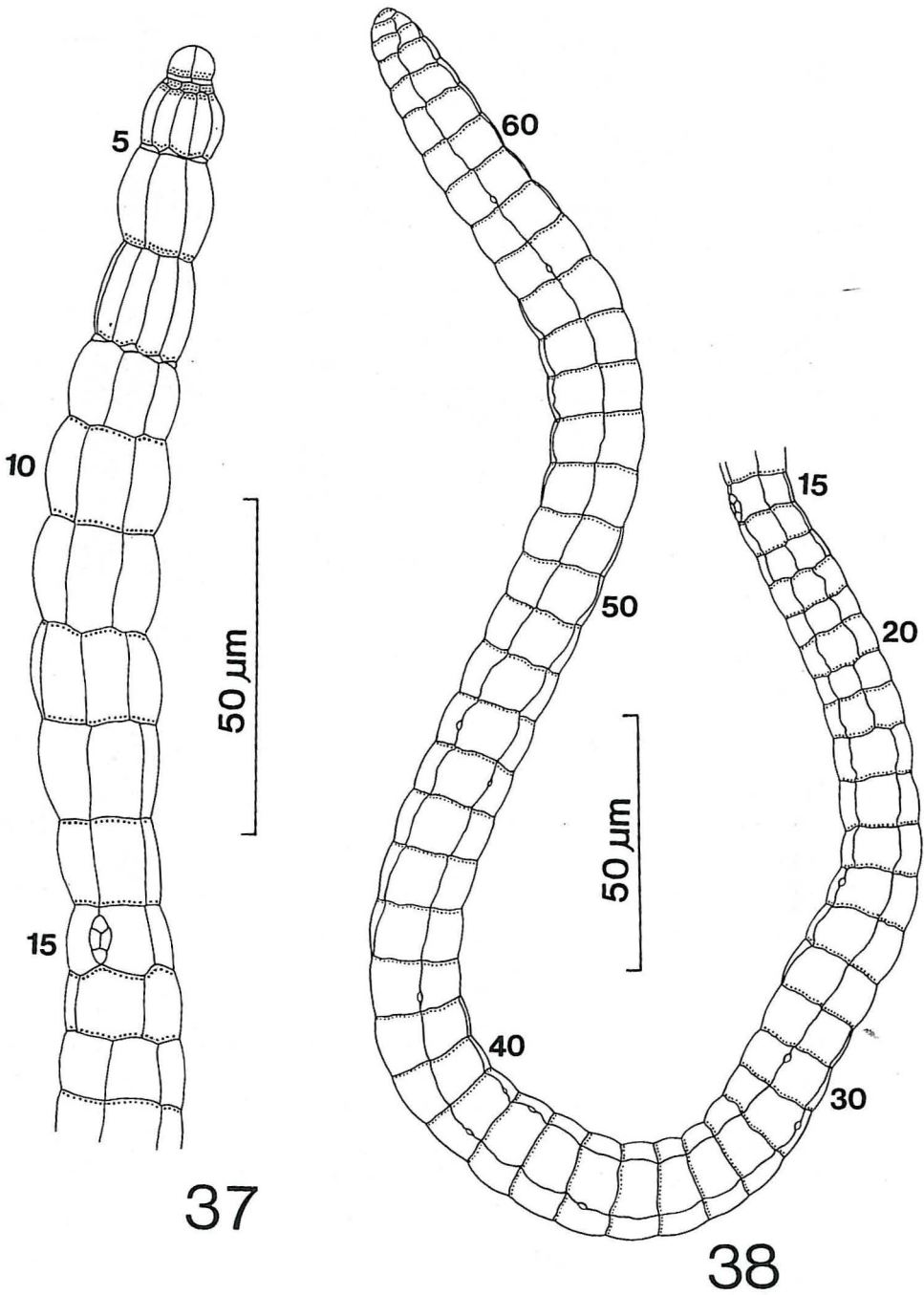
Caullery and Mesnil (1899 a, 1901) believed that some crowded small cells anterior to the first oocyte formed a rudimentary testis. In *C. julini*, as in *C. sabellariae*, the part of the axial mass anterior to the oocytes does contain numerous small cells, but at least some of these are probably portions of the long muscle strands that lie beneath the epidermis. I have never seen a cluster of nuclei that resemble those of spermatogonial masses in other orthonectids.

Ciliocincta akkeshiensis Tajika, 1979

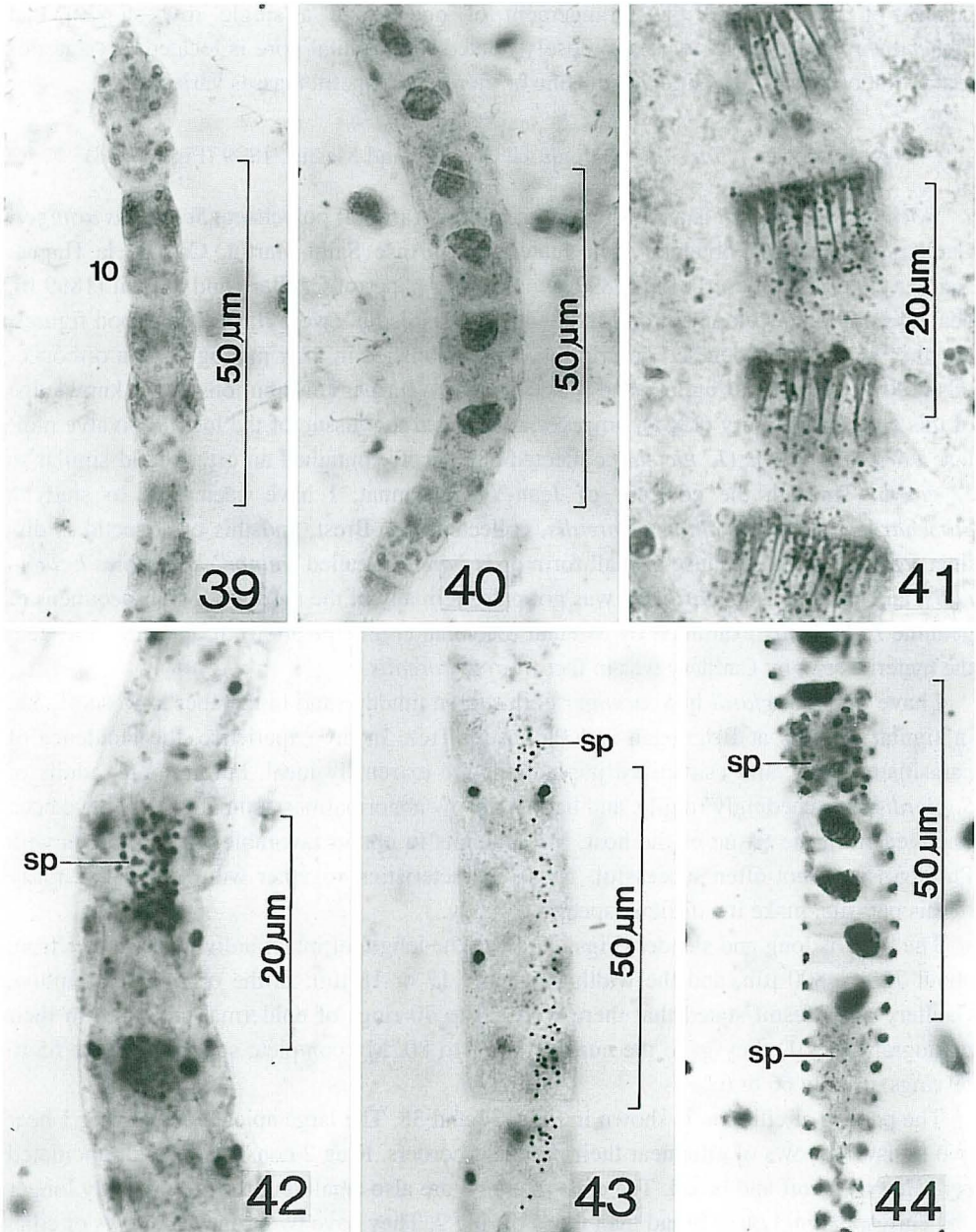
This species was found in an unidentified turbellarian of the family Coelogynoporidae (order Proseriata). The type locality is Akkeshi, Hokkaido, Japan. Little material was available to Tajika, but he worked diligently with what he had. On the basis of his photomicrographs of living females, and his drawing that shows the pattern of ciliation in a female, it appears probable that placement of this orthonectid in the genus *Ciliocincta* is correct.

Genus *Stoecharthrum* Caullery and Mesnil, 1899

The genus *Stoecharthrum* is characterized by a greatly elongated body, with many more rings of epidermal cells than are found in other orthonectids, and by hermaphroditism. The



Figs. 37-38: *Stoecharthrum giardi*; composite drawings based on specimens impregnated with silver nitrate to show boundaries of epidermal cells, and by the Protargol method to show arrangement of kinetosomes. 37. Anterior portion, up to ring 18. 38. Rings 14 to the posterior end of the body.



Figs. 39-44 : *Stoecharthrum giardi* ; photomicrographs of specimens fixed in Bouin's fluid and, except for Fig. 42, impregnated by the Protargol method ; sp, sperm. 39. Anterior portion. 40. Posterior portion. 41. Ciliary rootlets near middle of body. (Posterior side at top). 42. Mass of sperm (or precursors of sperm) anterior to first oocyte ; iron hematoxylin. 43. Sperm mass between epidermis and several oocytes, near middle of body. (The nuclei of the oocytes are not distinct.) 44. Sperm mass behind last oocyte of an immature specimen, and precursors of sperm interrupting the row of oocytes at a slightly more anterior level.

pattern of ciliation and the arrangement of oocytes in a single row suggest that *Stoecharthrum* and *Ciliocincta* are closely related. The genital pore is located just anterior to the first oocyte. The position of the one or more small sperm masses varies.

Types species : *Stoecharthrum giardi* Caullery and Mesnil, 1899 (Figs 37-44)

Stoecharthrum giardi is a parasite of the orbiniid (ariciid) polychaete *Scoloplos armiger*. Caullery and Mesnil obtained their material at l'Anse Saint-Martin, Cap de la Hague. Neither the original description (1899 a) nor a later paper of Caullery and Mesnil (1899 b), dealing with the development of adults within "plasmodia", were illustrated. Good figures, together with a more detailed description, were published in their monograph on orthonectids (1901). Evidently, Caullery and Mesnil made no further contributions to our knowledge of this species. Caullery (1961), however, mentioned that tissue of the lucinid bivalve mollusc *Loripes lucinalis* (*L. lacteus*) collected at Roscoff contained an orthonectid similar to *S. giardi*. Through the courtesy of Jean-Yves Monnat, I have been able to study a *Stoecharthrum* from *Lucinoma borealis*, collected near Brest, and this orthonectid is distinct from *S. giardi*. Because a small form of *L. borealis*, called "minor", resembles *L. lucinalis*, and because *Stoecharthrum* was not present in any of the more than 400 specimens of genuine *L. lucinalis* examined by Monnat (personal communication), it appears likely that the material seen by Caullery was in fact from *L. borealis*.

I have found *S. giardi* in *S. armiger* collected in muddy sand in the aber at Roscoff, and in similar habitats at Brignogan and Plounéour-Trez. In my experience, the incidence of parasitism is low, and parasitized populations are extremely local. Furthermore, adults of *S. giardi* are exceedingly fragile, and begin to show abnormalities soon after they have been liberated from the tissue of the host. My attempts to obtain favorable impregnations with Protargol were not often successful. These characteristics, together with the relative rarity of this parasite, make it a difficult species to study.

The body is long and slender (Figs. 37, 38). The length of intact individuals ranges from about 720 to 800 μm , and the width is usually 17 or 18 μm . In the original description, Caullery and Mesnil stated that there were 60 to 70 rings of epidermal cells, but in their monograph (1901) they gave the number as 70 to 80. My complete specimens have 65 to 69 rings, usually 66 or 67.

The pattern of ciliation is shown in Figs. 37 and 38. The large apical cells of ring 1 bear two transverse rows of cilia near their posterior borders. Ring 2 consists of small unciliated cells that are short and broad. The cells of ring 3 are also small, but they are slightly longer and correspondingly less broad than those of ring 2. They have two transverse rows of cilia. Ring 4 consists of elongated cells that bear two rows of cilia near their anterior margins and one row near their posterior margins. Ring 5 consists of small unciliated cells that do not always contact one another. Rings 6 and 7 are similar to ring 4, but their cells are usually larger; the cells of ring 6 bear two rows of cilia near their posterior margins, whereas those of ring 7 have only a single row of cilia in this position. The small cells of ring 8 are like

those of ring 5. Rings 9, 11, 13, 15, 17, 19 and 21 consist of cells of moderate to large size, and are not ciliated, but the cells of rings 10, 12, 14, 16, 18, 20 and 22 have cilia near both their anterior and posterior margins. From ring 23 to the end of the body, the cells are ciliated only near their posterior margins. There are usually just two apical cells at the posterior end, and sometimes apparently only one.

The ciliary rootlets of *S. giardi*, like those of *Ciliocincta sabellariae* and *C. julini*, are conspicuous in most Protargol preparations (Fig. 41).

Each epidermal cell of rings 9-12 contains several spherical, ovoid, or elliptical granules. These granules, well described and illustrated by Caullery and Mesnil, are greenish and refractile in transmitted light. Like the larger, glassy inclusions that occur singly in cells of certain rings of the second superficial division of the body of *Rhopalura ophiocomae*, they are dissolved by acid fixatives. The cells that contain the granules are nevertheless distinct in stained and Protargol-impregnated specimens (Fig. 39).

The genital pore (Figs. 37, 38) and the four small cells that surround it are invariably located between two of the moderately large cells of ring 15. The oocytes (Figs. 40, 44), in a single row, extend from the level of the genital pore nearly to the posterior tip of the body. In the complete specimens in which I could count the oocytes, there were from 36 to 42. The number and location of sperm masses, or precursors of sperm, is not constant. When there is only one, it is sometimes just in front of the first oocyte (Fig. 42), sometimes at a more posterior level, in which case it may lie between the epidermis and a series of oocytes (Fig. 43), interrupt the series of oocytes (Fig. 44), or be behind the last oocyte (Fig. 44). Specimens with two sperm masses are rather common in my material, and a few individuals have three, as Caullery and Mesnil reported. Although sperm masses, or clusters of cells in the process of becoming sperm, are often obvious in *S. giardi* that are not quite mature, many fully mature specimens seem to have no sperm at all. Perhaps this may be interpreted to mean that sperm produced by some immature individuals scatter and enter oocytes before maturity is reached.

Species that cannot be assigned with reasonable
certainty to any of the four genera
Rhopalura intoshi Metschnikoff, 1881

This orthonectid was found in the nemertean *Lineus lacteus* (*Nemertes lacteus*) at Messina, Italy. Metschnikoff described it rather well, considering the fact that he worked on it before good methods had been developed. The general appearance of the female, and the arrangement of oocytes in a compact mass (instead of in one or more linear series), are reminiscent of a *Rhopalura*. Although the male is also something like that of a *Rhopalura*, it is almost uniformly ciliated, there being no region that is comparable to the second superficial division of the body in *R. ophiocomae*, in which ciliation is restricted to transverse rows on certain rings of epidermal cells.

Rhopalura pterocirri Saint-Joseph, 1896

This orthonectid was found in *Eulalia macroceros* (*Pterocirrus macroceros*), obtained by dredging in Baie de la Forêt, near Concarneau, on the Atlantic coast of France. There have been no other reports of its occurrence. The description given by Saint-Joseph is of little help in assigning this species to genus. The illustration of the female shows that the cilia, except those at the anterior and posterior ends of the body, are restricted to three very narrow divisions that separate larger, unciliated divisions. Partly because this orthonectid occurs in a polychaete annelid, and partly because I can appreciate that cilia arranged in transverse rows close to the margins of the larger cells might appear to originate from the narrow unciliated rings, I suspect that this species will eventually be shown to belong to *Ciliocincta*, or to a closely related genus that has the same general pattern of ciliation. Saint-Joseph did not illustrate the arrangement of what he believed to be ova; he only said that they were round or polyhedral. He also did not describe any males, but his drawing of a small ciliated individual thought to be an embryo almost certainly represents a male. As Caullery and Mesnil (1901) pointed out in their discussion of *R. pterocirri*, embryos of orthonectids do not become ciliated until they have reached adult size.

Rhopalura pelseneeri Caullery and Mesnil, 1901

This orthonectid was found by Caullery and Mesnil at l'Anse de Vauville, Cap de la Hague, in the nemertean that they considered to be a variety (*lactaeum*) of *Tetrastemma flavidum*. The varietal name, as was pointed out in the discussion of *Intoshia metchnikovi*, is a *nomen nudum*; moreover, the worm they were dealing with could have belonged to a different species of *Tetrastemma*.

Rhopalura pelseneeri is unusual in that it is represented by some individuals that are female, some that are like *Stocharthrum giardi* in being hermaphroditic. Caullery and Mesnil, having found orthonectids of four different types in *T. flavidum* (i. e., male and female *Intoshia metchnikovi*, and female and hermaphroditic *R. pelseneeri*), considered the situation carefully with a view to recognizing ontogenetic relationships that might exist between them. They observed that although *I. metchnikovi* and hermaphroditic individuals of *R. pelseneeri* sometimes occurred in the same host, they were always in separate "plasmodia"; purely female *R. pelseneeri* were never found in association with hermaphroditic individuals. Caullery and Mesnil therefore decided that *I. metchnikovi* (if it is distinct from *I. linei*) and *R. pelseneeri* are unrelated. Because specimens of *R. pelseneeri* that lacked a sperm mass had embryos instead of oocytes, they also concluded, with some reservations, that females of *R. pelseneeri* were derived by transformation of hermaphroditic individuals.

Neither *R. pelseneeri* nor its "variety" *vermiculicola* (see below) has been studied since Caullery and Mesnil reported the latter in 1914. Although I cannot conscientiously assign it to any of the genera I recognize, I suspect that it belongs in *Intoshia*. The hermaphroditic individuals, as observed by Caullery and Mesnil, certainly resemble females of *I. leptopla-nae* and *I. linei*.

Rhopalura pelseneeri variety *vermiculicola* Caullery, 1914

This orthonectid was found only once in the nemertean *Tetrastemma vermiculus* ; the host was collected at Roches-Bernard, in the port of Boulogne, France. All of the individuals that Caullery observed were females containing developing embryos. The absence of males led him to believe that this species was like *R. pelseneeri*, from "*T. flavidum* variety *lactaeum*" in being hermaphroditic. Caullery considered the possibility that orthonectids from *T. vermiculus* and *T. flavidum lactaeum* were identical, but several differences persuaded him to give the parasite of *T. vermiculus* a varietal name. It is smaller than *R. pelseneeri* (105 by 25 μm instead of 120 to 150 by 30 μm ; it has about 13 instead of 10 "bands" containing granules of a refractile whitish pigment ; the ciliated larvae, when ready to leave the parent, are slightly smaller than those of typical *R. pelseneeri*).

It appears best to regard *vermiculicola* provisionally as a separate species. If Caullery's counts of the bands containing pigment are reliable, there should be a rather significant difference in the number of rings of ciliated cells in the epidermis.

Reports of undescribed or unidentified orthonectids

The presence of undescribed or unidentified orthonectids in various invertebrates has been mentioned in several papers. In some cases, the parasites were referred to as "mesozoans" ; from a sketch published in one account, it is obvious that the organism labelled "dicyemid" is an orthonectid. I am indebted to Tor G. Karling and Kirill Aleksandrov for a few records that have not been published.

Platyhelminthes : Turbellaria

Acoela (all cases recorded by Dörjes, 1979)

Haplogonaria syltensis

Haplogonaria viridis

Paraphanostoma brachyposthium

Paraphanostoma gracilis

Philachoerus johanni

Philactinoposthia viridorhabdites

Neorhabdoceola : Kalyptorhynchia

Amphirhynchus caudatus (Schilke, 1970 b)

Cheliplana boadeni (Schilke, 1970 a, 1970 b)

Cicerina brevicirrus (Schilke, 1970 a)

Cicerina sp. (Fize, 1974 [sketch, without mention in text])

Ethmorhynchus anophthalmus (Karling, personal communication)

Macrorhynchus crocea (Aleksandrov, personal communication)

Mesorhynchus terminostylus (Karling, personal communication)

Proschizorhynchus gullmarensis (Schilke, 1970 a)

Schizochilus choriurus (Schilke, 1970 a)

unidentified sp. (Dörjes, 1979)

Proseriata

Archilopsis unipunctata (Sopott, 1972)

Archimonocelis coronata (Karling, personal communication)

Coelogynopora axi (Sopott, 1972)

Nematoplana coelogynoporoides (Sopott, 1972)

Nemertea

Amphiporus ochraceus (Meinkoth, 1956)

Annelida

Polychaeta

Ampharete grubei (Fauvel, 1897)

Harmothoe sp. (Shtein, 1954)

Nicomache lumbricalis (Arwidsson, 1903)

Mollusca

Gastropoda (all cases recorded by Shtein, 1954)

Littorina saxatilis

Lora pyramidalis

Velutina undata

Bivalvia

Nucula tenuis (Shtein, 1954)

Mytilus edulis (Foster, 1982)

To the various reports given above, I can offer two additional unpublished records. One is for an orthonectid parasitizing *Ascidia callosa* (Urochordata : Ascidiacea) ; the other is for a species that occurs in the lucinid bivalve *Lucinoma borealis* (Monnat, personal communication). The latter was mentioned in connection with my account of *Stoelocharthurum giardi*.

Of the organisms found by Porchet-Hennere and M'Berri (1987) in the coelom of the polychaete *Nereis diversicolor*, one was presumed to be an orthonectid. On the basis of the little information they presented concerning the parasite, I can state emphatically that it is not an orthonectid.

ACKNOWLEDGEMENTS

I express my warmest appreciation to the directors and staffs of Station Biologique de Roscoff and the Plymouth Laboratory for providing excellent facilities. Especially helpful at Roscoff were Gilbert Deroux and Claude Chassé, who directed me to localities and habitats where I could find invertebrates known to be hosts for described species of orthonectids. Jean Dragesco very kindly provided transportation for several field trips. Support of much of this study by National Science Foundation Research Grant GB-3199 is also gratefully acknowledged.

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