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HOFERELLUS GILSONI (DEBAISIEUX, 1925) COMB. N. (MYXOZOA, MYXOSPOREA) : REDESCRIPTION AND MODE OF ATTACHMENT TO THE EPITHELIUM OF THE URINARY BLADDER OF ITS HOST, THE EUROPEAN EEL

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SUMMARY

Sinuolinea gilsoni DEBAISIEUX, 1925, a myxosporean infecting the lower urinary tract of European eels *(Anguilla anguilla)* is redescribed using light and electron microscopy. Its proper classification is *Hoferellus gilsoni* (DEBAISIEUX, 1925) comb. nov. Subspherical, posteriorly slightly flattened and longitudinally striated spores are produced in pansporoblasts in which they form pairs adhering by their posterior parts with caudal bristles. Formation of pansporoblasts may be an additional character separating the genus *Hoferellus* from its close kin, the genus *Sphaerospora.* The widened basal parts of the trophozoites are attached to the surface of epithelial cells of the urinary bladder by specialized, desmosome-like zones of the plasmalemma. In these zones, the latter is subtended by an electron dense layer and the narrow gap separating it from the host cell membrane is spanned by fibrillar connections. Between the attachment zones, small surface evaginations of the host cell are drawn into corresponding invaginations of the trophozoite membrane. The available electron micrographs indicate that these evaginations are later pinched off the host cells while the invaginations become digestive vacuoles. This process may serve for nutrition of the parasite, rather unique among coelozoic myxosporeans.

Key words : Myxosporea, Taxonomy, Ultrastructure, Attachment, *Hoferellus gilsoni, Anguilla anguilla,* Urinary bladder.

RÉSUMÉ

Sinuolinea gilsoni DEBAISIEUX, 1925, Myxosporidie localisée à la partie distale des voies urinaires de l'anguille européenne *(Anguilla anguilla)* est redécrite en microscopies photonique et électronique. Sa nomenclature correcte est *Hoferellus gilsoni* (DEBAISIEUX, 1925) *comb. nov.* Les spores sont subsphériques, aplaties postérieurement et leur surface apparaît striée longitudinalement. Formées par paires dans un pansporoblaste, elles sont unies l'une à l'autre par leur partie postérieure pourvue de soies rigides.

La présence de pansporoblastes chez *Hoferellus* accentue sa séparation d'avec le genre *Sphaerospora.*

Le plasmalemme de la partie basale, élargie des trophozoïtes, est modifié au niveau de leurs zones d'adhérence aux cellules épithéliales de la vessie urinaire. La couche dense qui renforce ce plasmalemme et la présence de trabécules fibrillaires dans l'espace compris entre lui et la cellule épithéliale suggèrent une jonction cellulaire de type desmosomal. De part et d'autre de ces zones de contact, la surface des cellules épithéliales se soulève en évaginations qui s'enfoncent dans des invaginations correspondantes de la surface des trophozoïtes. Ces évaginations semblent se détacher ultérieurement des cellules épithéliales et s'incorporer dans les vacuoles digestives dans les invaginations des trophozoïtes myxosporidiens. Il pourrait s'agir d'un processus nutritif tout à fait original chez les Myxosporidies coelozoïques.

Mots-clés : Myxosporea, Taxonomie, Ultrastructure, fixation, *Hoferellus gilsoni, Anguilla anguilla,* Vessie urinaire.

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INTRODUCTION

Elvers collected at three fish farms in Hungary were found to be infected with several species of protistan parasites : *Epieimeria anguillae* (Léger and Hollande), *Dermocystidium anguillae* Spangenberg, *Myxidium giardi* Cépède, *Myxobolus kotláni* Molnár, Lom and Malik, and, finally, with a myxosporean which could be identified with *Sinuolinea gilsoni* Debaisieux, 1925. Only the original, sketchy description exists of this species. This paper presents its redescription, its proper taxonomic assignement to the genus *Hoferellus* and ultrastructural observations on its sporogenesis and mode of attachment to the surface of epithelial cells in the host urinary bladder.

MATERIAL AND METHODS

Elvers about 8-15 cm in length and young pigmented eels 15-30 cm in length were obtained from three fish farms in Hungary raising eels in intensive cultures. These elvers had been caught at the West European shores. In the Fisheries Research Institute at Szarvas elver stocks were reared in concrete basins with moderate flow of water. The bottom of these basins was covered with mud. In the other two fish farms eels were raised in regularly cleaned plastic tanks and concrete basins with an intensive flow of water. In the years 1983 and 1985 elvers from the Szarvas station were collected regularly at one-month intervals, and occasionally pigmented eels were also examined. Elvers and eels from the two collecting places were examined at irregular intervals. Fishes in all three fish farms were fed special elver food. The parasites were studied in fresh state, samples of infected bladders were fixed in 10 % formalin or Bouin's solution, for light microscope investigation. For ultrastructural studies they were fixed in 2 % osmic acid in 0.1 M cacodylate buffer, embedded in Epon-Araldite mixture (MOLLENHAUER, 1964). Ultrathin sections were produced with the LKB IV ultramicrotome, double stained with uranyl acetate and lead citrate and observed with JEM 100 B electron microscope operated at 80 kV.

RESULTS

The extensity of infection of elvers with *Hoferellus* in the Szarvas Research Institute was nearly 90 %, and in the majority of cases heavy infection of the urinary bladder and the lower parts of the ureter by 30-200 *Hoferellus* plasmodia was recorded. An intensive infection with a mass of elongated trophozoites firmly attached to the wall of the urinary blader was easily recognizable with the unaided eye because of the whitish colour of the bladder. There were no significant differences in the seasonal incidence of the infection, and developing and spore-containing plasmodia were equally found in different seasons of the year. Among pigmented eels both the extensity and intensity of infection were lower. In one of the two other fish farms we found only one infected fish among the 45 specimens examined, while in the biggest eel-farm of the country about 78 % of the elvers and 24 % of the pigmented eels showed infection after examining 100 and 30 fish, respectively.

In heavy infections, the mass of trophozoites covering the epithelium of the urinary bladder formed an almost continuous layer reminiscent of cylindrical epithelium (Figs. 2, 3). Elongated trophozoites were up to 55 × 20 µm

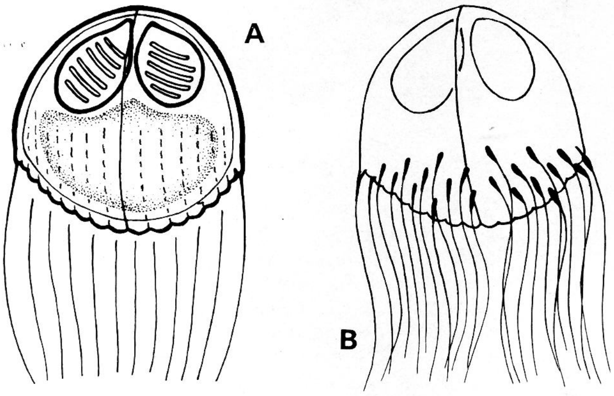
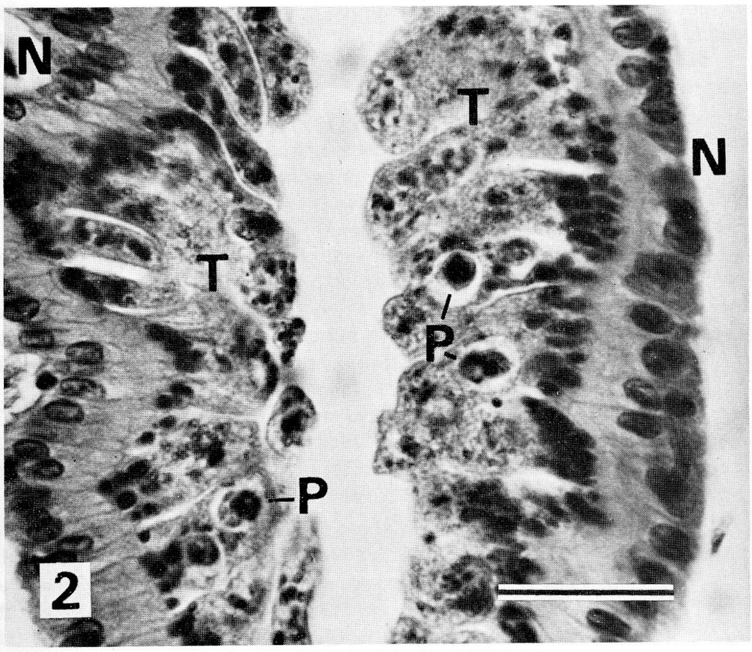


FIG. 1. — Diagrammatic drawing of spores of *Hoferellus gilsoni*. A : general structure of the spore. B : insertion of caudal bristles at the posterior pole of the spore. Bar = 5 µm.

FIG. 2. — Longitudinal section through part of the urinary bladder with trophozoites of *H. gilsoni*. T : trophozoites. P : pansporoblasts with spores. N : nuclei of the epithelial cells. Arrows point at the agglomerations of generative nuclei close to the adhesive sole of the plasmodium. Bar = 30 µm.

FIG. 3. — Tranverse section through the urinary bladder the epithelium of which is completely covered with trophozoites. Bar = 62 µm. Figs. 2 and 3 : Hematoxylin-eosin.

FIGS. 4 to 8. — Fresh spores of *H. gilsoni*. 4 : two spores within a pansporoblat, clinging together with their posterior parts. 5 : spore pair released from the pansporoblast envelope. 6 : two spores, the upper one in sutural view, the bottom one in apical view revealing the surface ridges. 7 : spore in sutural view with focus on the surface striation. 8 : groups of spores at low magnification revealing the caudal bristles. Bar = 5 µm applies to Figs. 4 and 7; Figs. 5 and 8 are reproduced at a smaller magnification, the bar being also 5 µm.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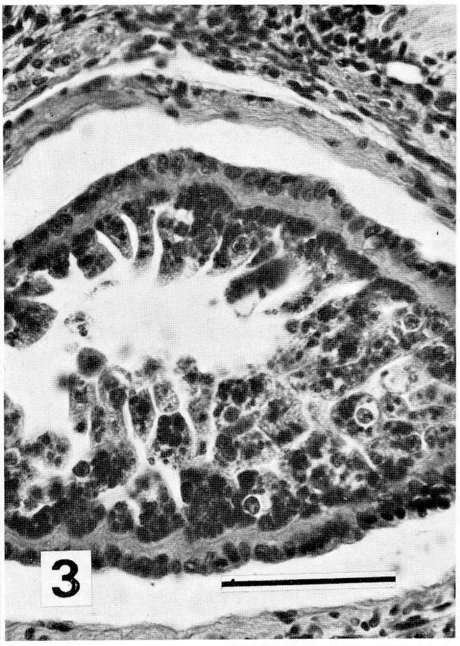
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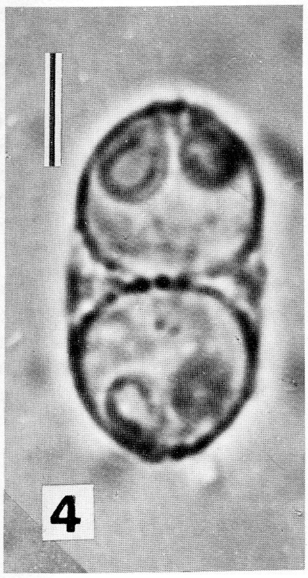
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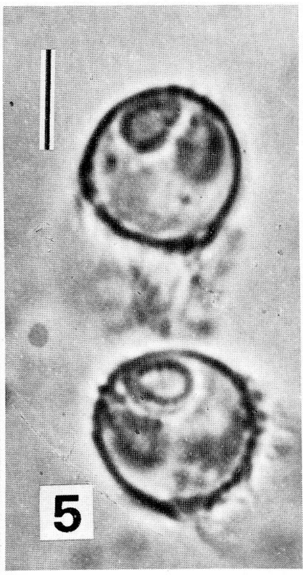
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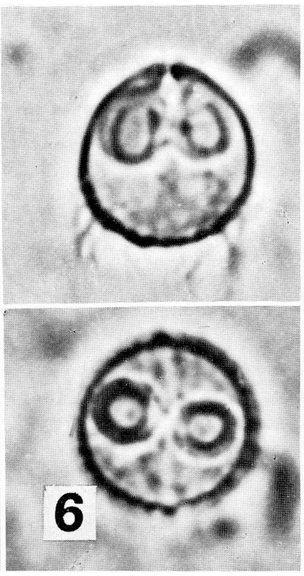
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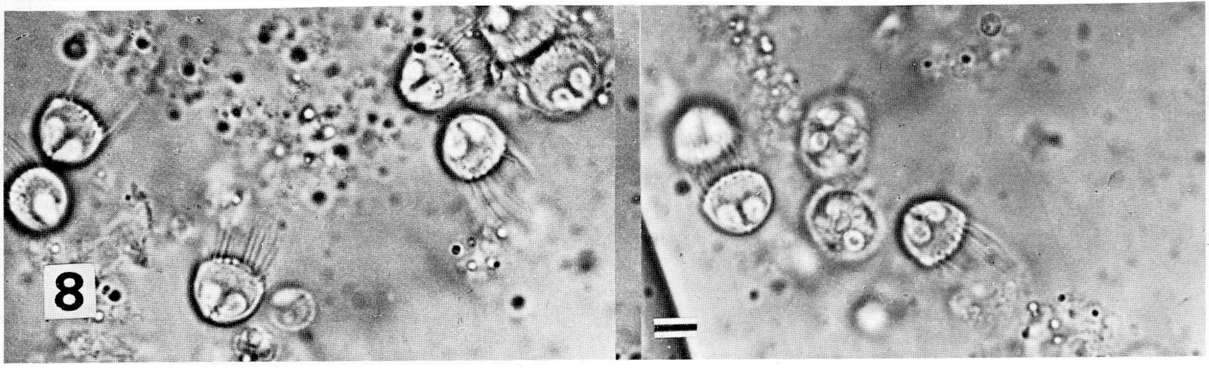
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in size sometimes even 200 μm in length and had a broad, sole-like basal surface closely adhering to the surface of the host epithelial cells. In the trophozoites the vegetative nuclei and generative cells were more abundant at the basal, attached end. When observed fresh, the trophozoites appeared dark due to the presence of numerous light breaking granules in their cytoplasm. At the time of our observation, in April 1984, only a minority of the trophozoites harboured sporoblasts and mature spores. One, two or more pansporoblasts with two spores each were observed in one trophozoite.

Spores (Fig. 1) were released in pairs, sticking closely together by their posterior parts within the remnants of the pansporoblast envelope cell (Fig. 4). This union soon breaks down and the posterior bristles straighten up and can be seen in their full length. In apical view, the outline of the spores is regularly circular with the suture slightly visible (Fig. 6). In sutural view, the spores are subspherical, slightly flattened posteriorly (Figs. 1, 5, 8). Length is 7.8 (7.2-8.7), width 7.6 (6.7-8.7) μm. The surface is longitudinally striated, each shell valve bearing about 13-14 fine ridges (Fig. 7). At the posterior flattened half of the spore, stiff bristles extend from the ridges, about 30 to 40 in number, reaching about 5 μm beyond the posterior end of the spore. Polar capsules are of equal size, measuring 3.5, (2.9-4.3) × 2.6 (1.9-3.1) μm, oval, anteriorly pointed with 5 to 6 tightly coiled threads of polar filament situated at an angle of 45° or almost perpendicularly to the longitudinal axis of the capsule.

ELECTRON MICROSCOPY

Trophozoites

The cytoplasm abounds in mitochondria conspicuous by their densely staining matrix contrasting with the lucent space within the cristae, reminiscent in this way of mitochondria in e.g., *Myxidium lieberkühni.* There is a variety of vesicles of various sorts, atypically shaped Golgi bodies, vegetative nuclei and generative cells in various degree of development. There is a large amount of free ribosomes but there are no conspicuous fibrillar structures in the cytoplasm. The cytoplasm of generative cells is densely packed with free ribosomes so that they have an electron opaque appearance. The plasmalemma of the trophozoites is smooth, without villosities or apparent pinocytotic activity. In trophozoites already producing spores the cytoplasm may harbour various dense inclusions.

The contact zone between the trophozoite and epithelial cells of the host's urinary bladder appears on thin sections as a very sinuous line. These sinuosities represent in fact evaginations of the host cell membrane drawn into corresponding invaginations in the parasite surface. It seems that under normal conditions the cell membranes of the host and parasite cells adhere closely together (Fig. 9, 10) leaving between them a narrow space of 9.6 to 13 μm across. The contact zone is thus reminiscent of a gap junction of metazoan tissue cells. In areas between the invaginations, the plasmalemma of the trophozoite is modified to form a desmosome-like complex (Fig. 11, 13). It is subtended by a thick, single or double electron dense layer up to 23 μm across. From this layer, microfibrils may emanate into the trophozoite's cytoplasm.

In these areas, the gap between the cell membranes of the host cell and the trophozoite is spanned by fibrillar connections spaced at about 17 μm (Fig. 12). The space between the cell membranes of the host cell and the trophozoite, at points where projections of epithelial cells reach into the invaginations in the trophozoite surface, may be considerably widened. An excessive enlargement is probably due to fixation artifacts. The sections examined make the impression that the tiny projections are finally pinched off the host cell and enclosed into the invaginations in the trophozoite surface as if in small vacuoles (Fig. 1, arrows) which then proceed into the trophozoite's interior and become small phagosomes. In the long run, such continuing damage to the host cells might impair the integrity of the epithelium.

The neighbouring trophozoites adhering to the host epithelium may be so closely joining each other that their cell membranes run jointly together in a way reminiscent of membranes of cells in metazoan tissues (Fig. 16). Distinct cell junctions between trophozoites, however, could not be observed.

Sporogenesis

Due to rather scarce spore formation in the trophozoites observed, we could not establish a full series of the

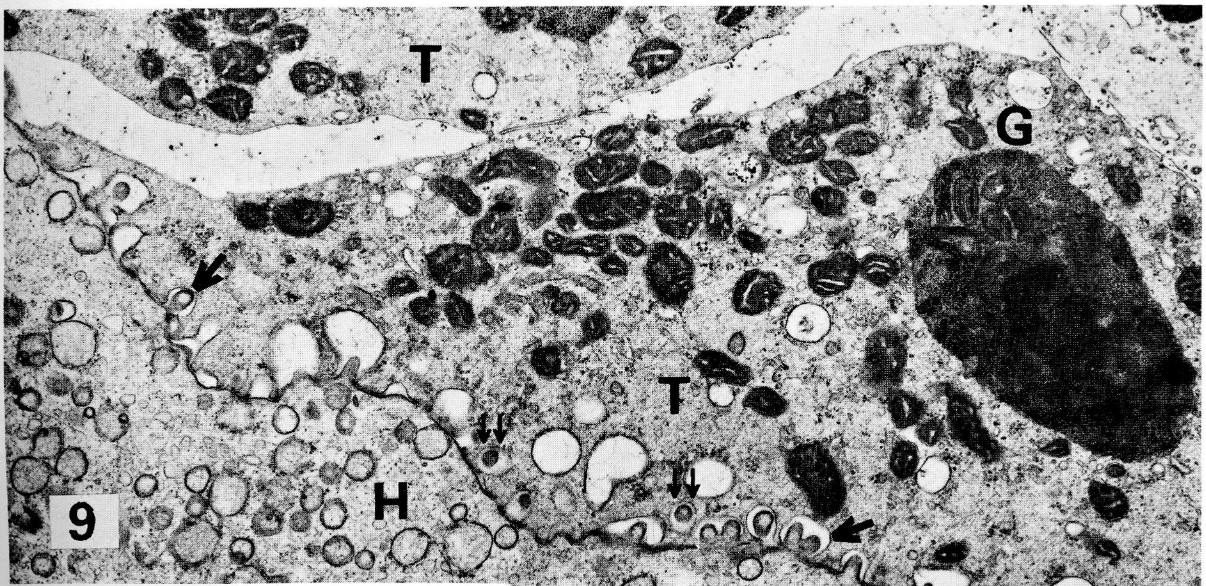
FIG. 9. — Electron micrograph of a section through the part of a trophozoite closely adhering to the host epithelial cell (H). Arrows point at invaginations of the parasite's plasmalemma encircling projections of the host cell; some of these invaginations appear to have become phagosomes containing cytoplasmic parts detached from the hosts cell (double arrows). G — generative cell with a centrally located nucleus and cytoplasm of a high density due to large amount of free ribosomes. Bar = 2 μm.

FIG. 10. — A trophozoite (T) deeply embedded between the epithelial cells (H). Notice the evaginations of the host cell surface interlocked with the invaginations in the plasmalemma of the trophozoite. Bar = 2 μm.

FIG. 11. — Interface between the trophozoite (T) and host cell (H) showing the elaborate cell junction (arrow) between the host cell projections drawn into the invaginations of the trophozoite surface. Bar = 0.2 μm.

FIG. 12. — The cell junction between the trophozoite and host cell showing no periodical structure between the two membranes. D — dense substance subtending the trophozoite membrane. Bar = 0.1 μm.

FIG. 13. — Enlarged part of the host-parasite interface indicated in Fig. 11 by an arrow. Bar = 0.1 μm.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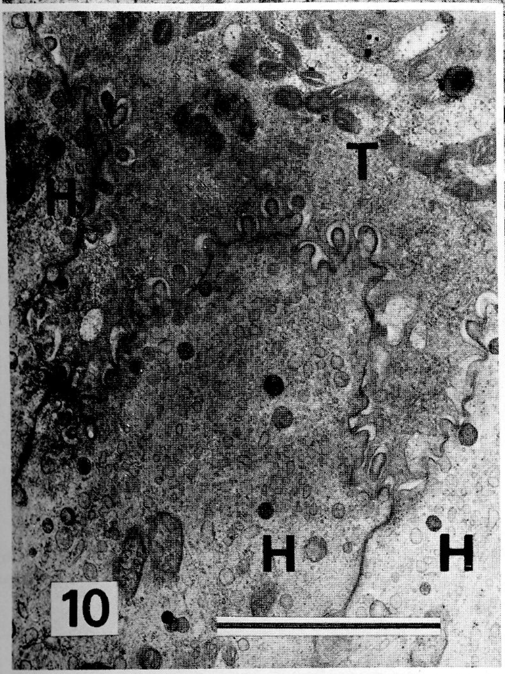
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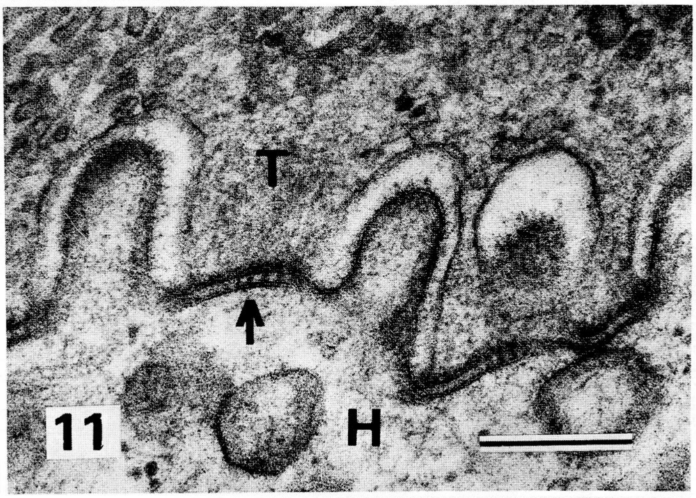
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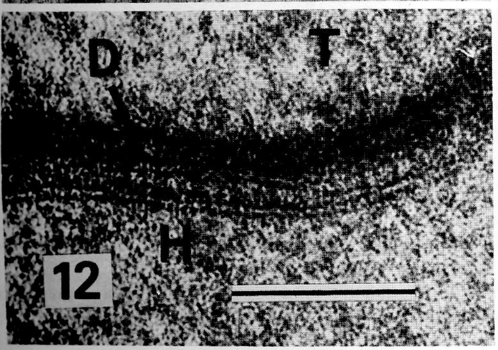
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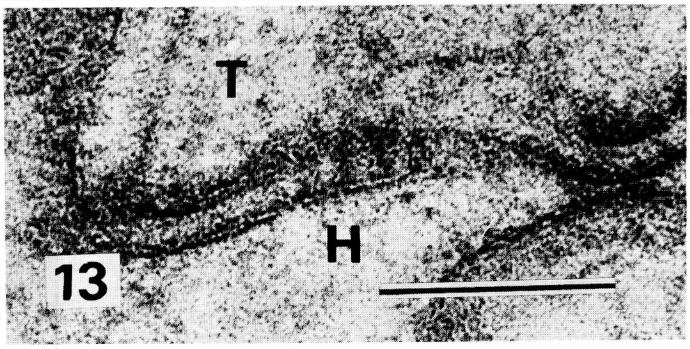
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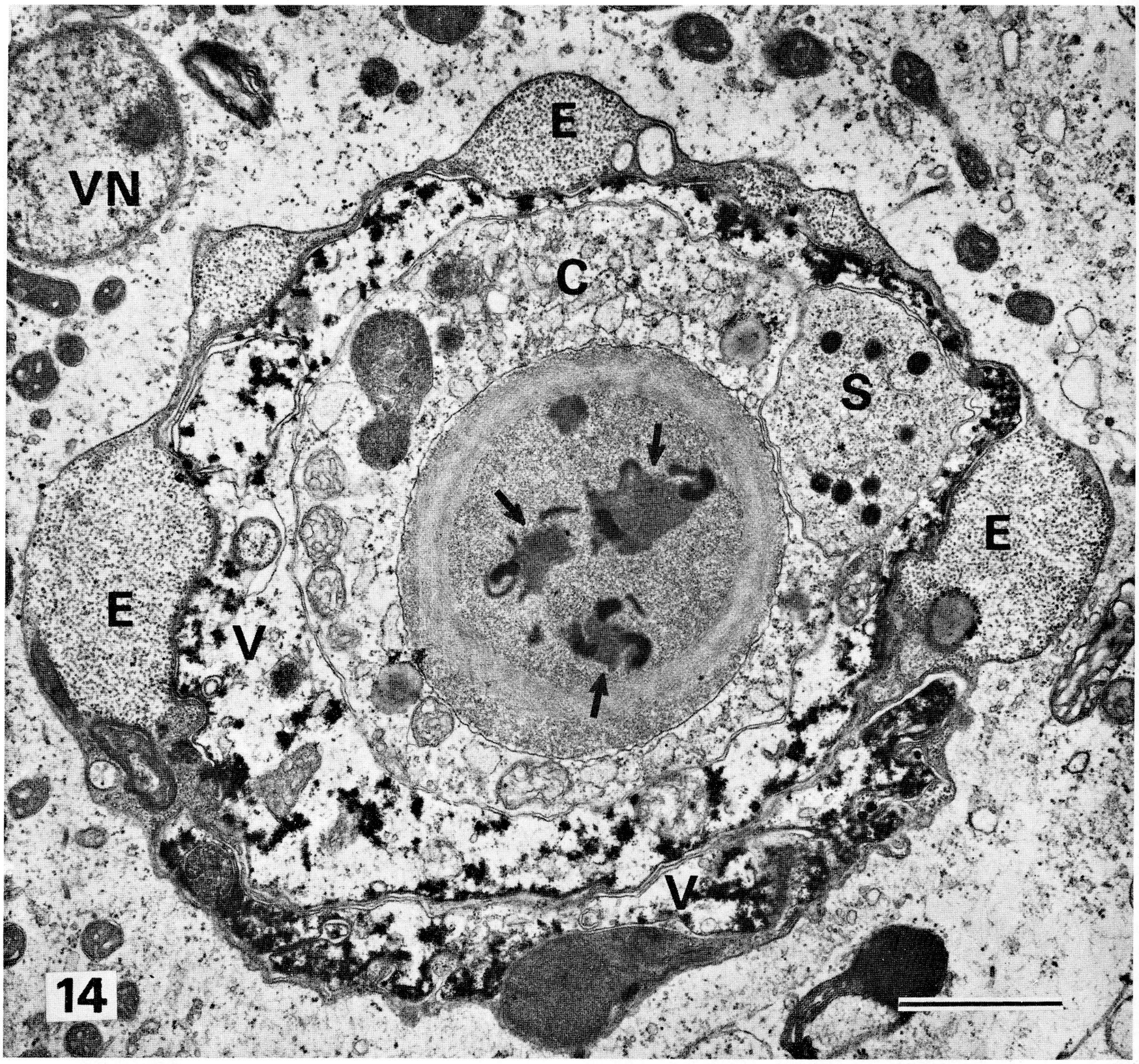
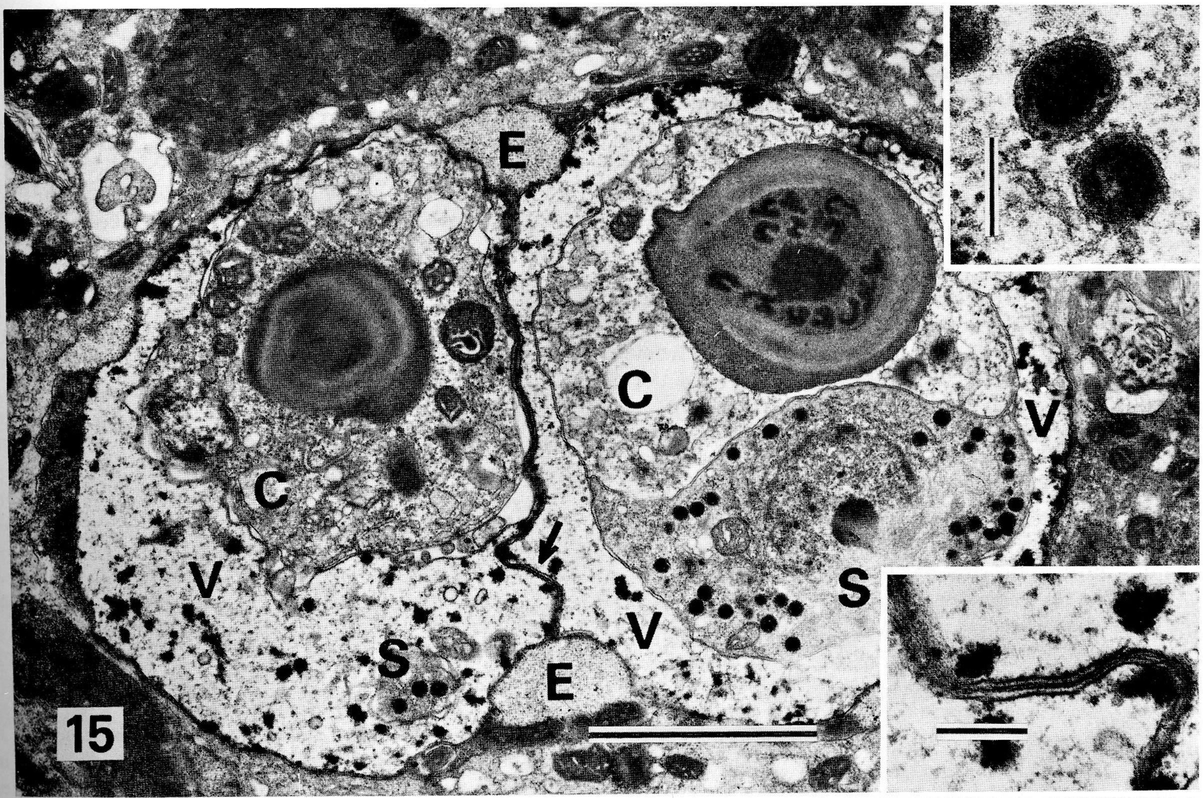


FIG. 14. — Transverse section through a pansporoblast showing cells of one sporoblast. E : remnants of the enveloping cell, pericyte. V : valvogenic cell. S : young sporoplasm with sporoplasmosomes. C : capsulogenic cell with the early stages of polar filament formation (arrows) within the capsular primordium. VN : vegetative nucleus of the trophozoite. Bar = 1 μm.

FIG. 15. — Longitudinal section of a more advanced pansporoblast showing the two sporoblasts. The remnants of the pericyte (E) have already grown thin and the septum it forms between the two sporoblasts is only represented by two cell membranes with almost no cytoplasm between them (arrow; this area is enlarged in the lower right inset, bar = 0.25 μm). V : valvogenic cell, S : sporoplasmic cell with the nucleus and sporoplasmosomes (enlarged in the upper right inset, bar = 0.2 μm) C : capsulogenic cells; in the capsular primordium of the right sporoblast is the filament in an advanced stage of formation. Bar = 2 μm.

FIG. 16. — Cell interface between the host cell (H) and two neighbouring trophozoites (T) the plasmalemmas of which are closely apposed. Somewhere, fine fibrils converge to certain areas at the membranes (arrow). Bar = 0.3 μm.

FIG. 17. — Posterior part of an almost mature spore showing crenated outline of the shell valve and cross sections through the caudal bristles (B) extending (arrow) from the valves. Note the dark appearance of the sporoplasm cytoplasm in which the sporoplasmosomes are no more clearly seen. Bar = 2 μm.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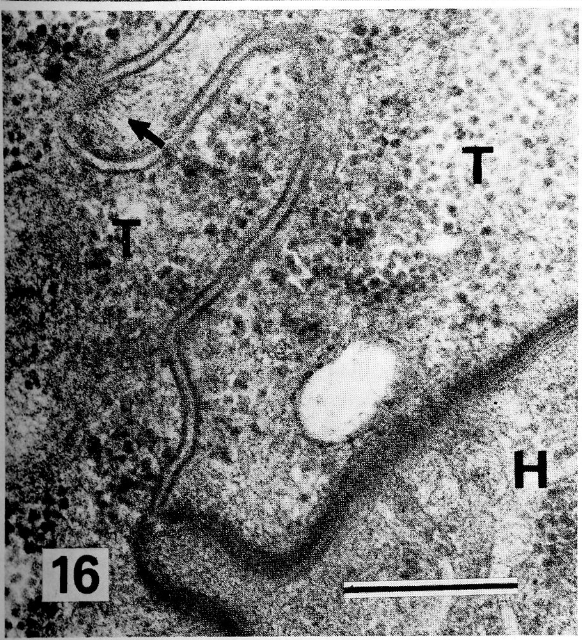
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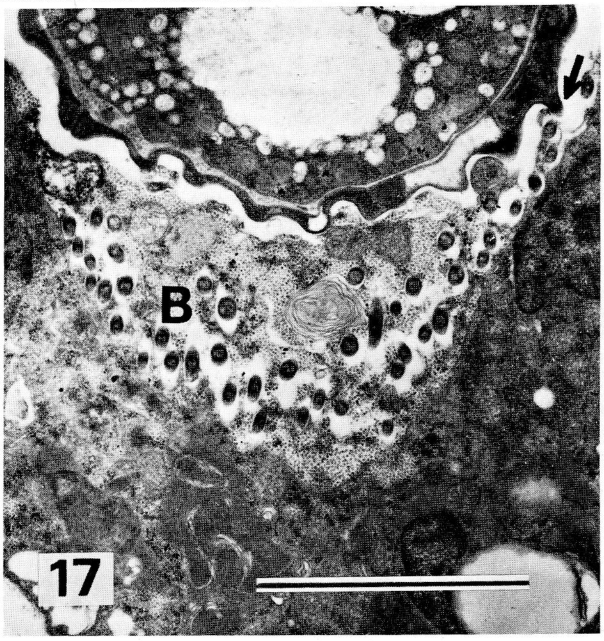
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event. We could, however, observe the existence of pansporoblasts encasing within the common pericyte envelope two sporoblasts. Within the pericyte envelope, the two sporoblasts are separated by a thin membrane-lined septum also formed by the pericyte, as it is the case in sporoblasts of other myxosporeans (Fig. 15).

Sectioned sporoblasts show gradual reduction in the size of the pericyte cell (Fig. 14 and 15). In the less advanced stage, the pericyte cell still represents a sizeably thick envelope and shows various structures in its degraded cytoplasm (Fig. 14). In a more advanced stage, the thickness of this envelope is greatly reduced to become a thin sheet holding together mature spores released from the plasmodium (Fig. 15). The mode of formation of the polar capsule follows the general pattern of myxosporea. In the developing sporoplasm there are conspicuous dense bodies about 0.145 µm in diameter with electron dense core and a thin lucent envelope about 16 µm thick. To a slight extent they remind of haplosporosomes. We propose to designate them sporoplasmosomes.

Sections through maturating spores (Fig. 17) reveal the caudal bristles in transverse section as solid rods with darker periphery. They are outgrowths of the shell valves composed of the same material as the shell itself.

In all other aspects, sporogenesis follows the pattern well established in other myxosporeans.

DISCUSSION

Debaisieux (1925) himself proposed two possible generic assignments for the myxosporean he described, *Sphaerospora* or *Sinuolinea*. Because of large plasmodia and having observed sometimes a sigmoid, wavy sutural line he allotted it in the genus *Sinuolinea*. Complying with the recently proposed solution of the taxonomic position of *Hoferellus* (Doflein, 1898), Berg, 1898 of which *Mitraspora* Fujita, 1912 is a junior synonym (Molnár *et al.*, 1986; Lom, 1986) we assign *Sinuolinea gilsoni* into the genus *Hoferellus*. This genus includes sphaerosporids with spores equipped with many filaments or fine bristles at the posterior spore end and polysporous trophozoites, at variance with sphaerosporas lacking these filaments and with mono- or disporous pseudoplasmodia.

The species seemingly representing transition between the two genera *(H. caspialosae* (Dogiel, 1939) and *H. donecae* (Gasimagomedov, 1970)) may not have been described thoroughly enough. *H. gilsoni* differs sufficiently enough from other hoferelli with spores oval in sutural view *(H. caudata* (Parisi, 1910), *H. dubinini* (Shulman, 1962) or *H. sinensis* (Lee and Nie, 1965) to consider it a well established species.

Wierzbicka (1986), completely ignoring the existence of the old paper by Debaisieux (1925), described *H. gilsoni* from eels in Poland as a new species, *Sphaerospora anguillae*. Her description leaves no doubt that *S. anguillae* is a synonym of *H. gilsoni*. *H. gilsoni* also is different from *Sphaerospora reichenowi* Jacob, 1953 infecting the intestine of *Anguilla anguilla*.

H. gilsoni seems to be widely distributed; in addition to France, Hungary, and Poland it also occurs in Portugal. Ventura and Paperna (1984) studying *Myxidium giardi* have also found *H. gilsoni*. They supplied excellent photographs of developing plasmodia in the urinary bladder mistaking them erroneously for presumed coelozoic forms of *M. giardi*.

The surface of the trophozoites of *Hoferellus gilsoni* is covered by a simple cell membrane much alike that in most other coelozoic myxosporeans (e.g., Lom and de Puytorac, 1965; Lom, 1969; Uspenskaya, 1984). The membrane lacks, however, microvillosities or pinocytotic activity known in most of such parasites. This is compensated by the extreme specialisation of the cell membrane adhering to the surface of epithelial cells of the urinary bladder of the host. It appears that there is an alternation of sites where both host and cell membranes are firmly bound together by a desmosome-like junction with areas without such a firm union. In the latter sites the invaginated cell membrane seems to serve as a port of entry for the particulate food derived from host cells. Such a mode of nutrition perhaps makes up for the apparent lack of pinocytosis in trophozoites. Phagocytosis is by no means exceptional in myxosporeans (see the review of Uspenskaya, 1984) but the mechanisms through which it is accomplished in *H. gilsoni* is rather unique. Although in the light microscope no evident damage to the bladder epithelium could be observed, one can presume that the prolonged action of the trophozoite may result in injury to the epithelium.

Modifications of trophozoite plasmalemma reminiscent to some extent of those found in desmosome-like sites at the cell surface of *H. gilsoni* have been recorded in sime histozoic myxosporeans in the form of a simple electron dense layer coating the plasmalemma (in *Henneguya adiposa* - Current, 1979; in *Myxobolus funduli* - Current *et al.*, 1979). There may also be what appears as a double plasmalemma linked by electron dense connections spaced at regular intervals *(Henneguya exilis* - Current and Janovy, 1978). The most elaborate surface modification was recorded in *Myxobolus disparoides* by Uspenskaya (1984). In this species, the plasmalemma is coated with a lucent layer containing pyramidal stacks of electron dense discs. None of these modifications, however, is in any relation to the adhesion of the trophozoite to the host cell membrane. In other coelozoic myxosporeans the structures at the point of adhesion of their cell membrane to the host cell surface are much more simple; e.g., a thin layer of opaque material subtending the plasmalemma of the trophozoite in *Sphaerospora renicola* (Lom *et al.*, 1982).

The formation of pansporoblasts within a large plasmodium in *H. gilsoni* clearly sets this species apart from those of the genus *Sphaerospora* which have thus far been studied ultrastructurally *(S. renicola* - Lom *et al.*, 1982; Desser *et al.*, 1983; *S. molnári* - Desser *et al.*, 1983; *S. tincae* and *S. galinae* - Lom *et al.*, 1986). In these sphaerosporas, sporogonic cells differentiate into one or two sporoblasts — depending on the species — directly within a small pseudoplasmodium which can thus be compared with "free" pansporoblast (LOM *et al.*, 1982; DESPORTES and THÉODORIDÈS, 1982). If these features are confirmed in other hoferelli and sphaerosporas they may constitute an important difference between the two genera.

Thus far, the occurrence of the two principal modes of sporoblast formation and hence their taxonomic significance are largely unknown. In large polysporic plasmodia of the genera *Chloromyxum, Henneguya, Myxobolus, Myxidium* and *Zschokkella* (see references in LOM *et al.*, 1982) the spores are formed within a pansporoblast originating from the union of the pericyte and sporogonic cell, while in small pseudoplasmodia of *Sphaerospora*, of *Ceratomyxa shasta* (YAMAMOTO and SANDERS, 1979), of large plasmodia of *Kudoa lunata* (LOM and DYKOYÁ, 1982) and of *Leptotheca elongata* (DESPORTES and THÉODORIDÈS, 1982) the sporogonic cells directly produce spores within the trophozoite which in fact substitutes the pericyte or enveloping cell. DESPORTES and THÉODORIDÈS (1982) described in *Leptotheca elongata* a frequent union of simple disporic pseudoplasmodia (or "free" pansporoblasts) into a large plasmodial entity. Whether this is a normal phenomenon and whether the union is permanent is not clear since these authors mention that such large plasmodia soon degenerate. More data are thus needed to elucidate the problem which could help to improve myxosporean taxonomy.

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