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FURTHER NOTES ON A MARINE MEMBER OF THE SAPROLEGNIACEAE, *LEPTOLEGNIA MARINA* N.SP., INFECTING CERTAIN INVERTEBRATES

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(Text-figs. 1–5)

Twenty-five years ago I published a note (Atkins, 1929) on a then unnamed member of the Saprolegniaceae, a destructive fungal parasite of the pea-crab, *Pinnotheres*; the name *Leptolegnia marina* is now proposed for this fungus.

Sexual Reproduction

In the previous note what appeared to be young oogonia were figured (Atkins, 1929, fig. 5), but sexual organs were not then identified with certainty. In 1943, while preserved material of *Pinnotheres pisum* was being re-examined, the eggs beneath the abdomen of one female were seen to be crowded with round bodies, which proved to be the oogonia and oospores of a fungus (Fig. 1). Identification of these plants with the fungus previously described rests on the presence of that fungus in its asexual reproductive stage in the crab bearing the eggs, and in one of a cluster of sixty-eight eggs otherwise containing plants in the sexual stage. In some eggs containing few oospores the mycelium had in part been emptied, following the formation of zoospores, by short emission tubes resembling those of *Leptolegnia marina*, but definite proof that the oospores are the sexual organs of that species would need evidence from pure cultures. This was the only occurrence of the sexual stage of the fungus in more than 100 infected crabs.

The crab taken on 6 August 1928 from a *Mytilus edulis*, received 6 days earlier from the Camel Estuary, near St Issey Cliff, Padstow, north Cornwall, and which had been kept in a finger-bowl of sea water changed at intervals, was noticed to be moribund on 23 August. The cause of death was infection by *Leptolegnia marina*, the gills being crowded with hyphae. In one gill the mycelium was already empty except for a few cysts, in the others production of zoospores was proceeding; no oogonia were present. The crab was fully berried when taken from the mussel. The eggs, brown in colour, contained advanced embryos, most of which hatched before the death of the crab. The eggs remaining were dirty and degenerate, with a rich growth of bacterial filaments, while many bore clusters of vorticellids. Nearly all of them contained the oogonia and oospores of the infecting fungus, up to 200 in a single egg. Most plants with sexual organs had not previously produced zoospores; this was evident from the absence of projecting tubes on the surface of the *Pinnotheres* egg.

From 6 to 23 August 1928 the temperature of the laboratory sea water was about 16–17° C.

When the ovum of *Pinnotheres pisum*, which is only about 0·3 mm in diameter, is packed with a mass of tangled hyphae and with oogonia, it is exceedingly difficult to tease out the oogonia with mycelial connexions intact, so as to be able to discern the disposition of the sexual organs and especially the origin of the antheridia. That the fungus had attacked eggs containing pre-zoeae added to the difficulty, for the cuticle of these resembled the wall of empty hyphae. The hyphae tended to keep within the cuticle of the zoeae, even of the appendages.

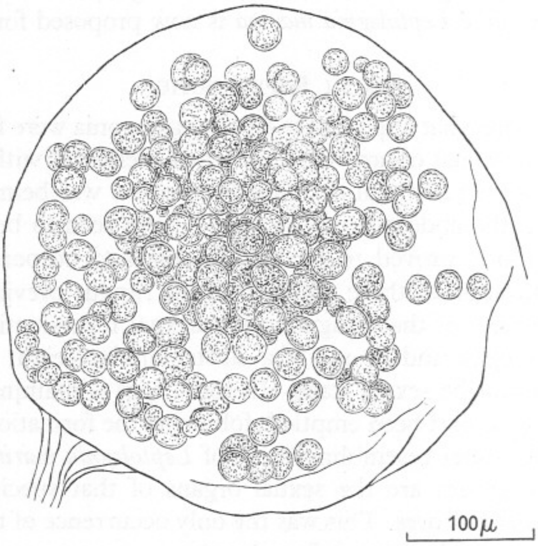

Fig. 1. *Leptolegnia marina*. Immature oospores, thin-walled and with food reserve in scattered drops or granules, within the egg of *Pinnotheres pisum*. Unstained, in 10% formalin.

In some *Pinnotheres* ova the mycelium was young and the oogonia immature (Fig. 2A–F). Other eggs contained plants with numerous oogonia in various stages of maturity. In these the mycelium was mainly empty, but where a few short lengths contained protoplasm these bore young oogonia. In yet others the mycelium was entirely empty and all oospores were ripe (Fig. 3). Septa were frequent.

Oogonia are borne on short side branches (Fig. 2B, E, F), sometimes sessile in diverticula of the hyphae (Figs. 2A; 3D, E), sometimes terminal (Fig. 2C). Fig. 3D is reminiscent of Butler's fig. 19 pl. V (1907) of the sexual apparatus, of *Pythium rostratum*. In *Leptolegnia marina* the frequently sessile position of the oogonium on the hypha may be due to the restricted condition of growth in the *Pinnotheres* ovum. The oogonia are smooth, thin-walled and spherical, although some tend to be pyriform or oval and an occasional one is irregular in shape. Very rarely there may be one or two papillae above the oogonium.

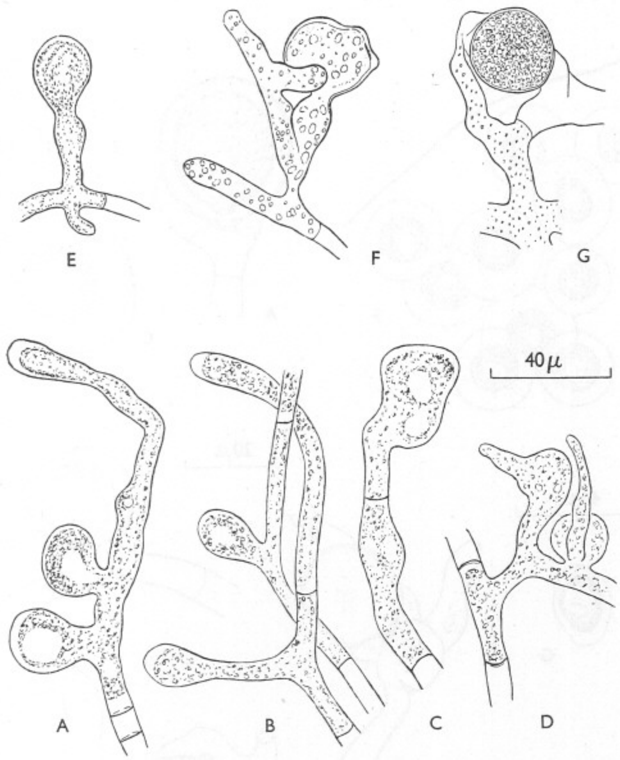

Fig. 2. *Leptolegnia marina*. Young oogonia and immature oospore. In E and F the swelling in the stalk below the oogonium is probably the initial of an hypogynous antheridium. Unstained, in 10% formalin.

Each oogonium contains a single oosphere which fills it completely, and measures 17·5–30μ and occasionally up to 37μ in diameter. The antheridia are hypogynous (Fig. 3A, D, E); those seen were mostly empty. The oogonium is produced into a slight beak where the hypogynous antheridium is applied, and such a structure has not been seen in any other position. It would appear that the antheridia are not always cut off by septa when the oogonium is sessile (see Fig. 3E). Diclinous antheridia have not been observed near young oogonia in the present material and I am not satisfied as to the interpretation of the portions of empty hyphae seen attached to the distal end of a number of oogonia containing ripe oospores, as, for instance, in Fig. 3E. They may be the remains of elongated protrusions similar to those described on the oogonia of *Leptolegnia subterranea* by Harvey (1925), or, more probably, merely a continuation of the growth of the hypha beyond the oogonium, the latter being intercalary; this is suggested by the formation of the oogonia in Fig. 2D. The oogonium depicted in Fig. 2G appears to have an androgynous antheridium,

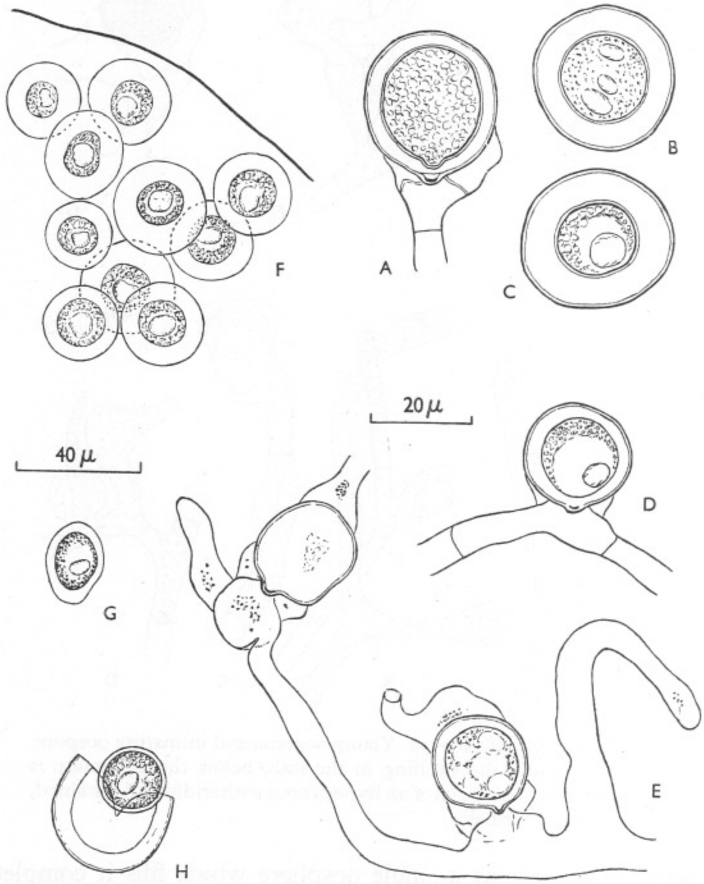

Fig. 3. *Leptolegnia marina.* A: oogonium with oospore and hypogynous antheridium: food reserve scattered. B and C: oospores containing three and one reserve food bodies respectively. D: sessile oogonium with mature oospore and hypogynous antheridium. E: two sessile oogonia on the same branch, both with hypogynous antheridia and both with a portion of hypha of problematical nature attached apically (see pp. 615–6). One oogonium is empty and the oospore in the other is highly vacuolated and perhaps abnormal. Small collections of shining residual granules are present in otherwise empty hyphae. F: fully mature oospores lying beneath membrane of *Pinnotheres* egg. G: pyriform oospore. H: oospore burst by pressure on cover-slip. Unstained, in 10% formalin. A–E to scale on right, F–H to scale on left.

but it may be merely a hyphal branch passing behind the oogonium, and certainly most of the oogonia seen had clearly hypogynous antheridia.

When the oospore is immature the wall is thin (Fig. 2G). As it matures the protoplasmic contents become reduced and the wall thickens greatly (Fig. 3); in fully ripe oospores it is about 7·5μ thick, and is two-layered. The extremely thick outer layer is smooth, colourless, transparent and very faintly stratified, too faintly to be shown in the figures. When oospores are burst by pressure on the cover-slip, sometimes the contents emerge entire, surrounded by a thin wall, the endospore (Fig. 3H). The thin oogonial wall is still distinguishable. In the immature oospore with thin wall, the fat or oily reserve is in scattered droplets (Figs. 2G; 3A); the mature oospore contains one to three reserve bodies, probably when fully mature there is but one, eccentric in position (Fig. 3C, D, F–H). In some oospores this has the appearance of a refringent body, in others of a large oil drop.

The specific characters of *L. marina* are given on p. 622.

Additional Records of Occurrence

In the Body, Eggs and Embryos of Pinnotheres pisum *and in the Body of one Individual of* Pinnotheres pinnotheres (=veterum)

In a previous paper (Atkins, 1929) this fungus was recorded as occurring in crabs taken from *Mytilus edulis* obtained from the Camel Estuary near St Issey Cliff, Padstow, north Cornwall, on 25 November 1927, 24 February, 25 April, 1 August and 14 September 1928. Crabs obtained from *Mytilus* from the same locality on 11 October 1928 were apparently free from infection. The disease was also recorded in crabs taken near the junctions of the Tamar and Tavy (Weir Point, on the Cornwall–Devon border) on 22 March, 10 and 20 April 1928; and from the Yealm Estuary, S. Devon, on 21 July 1928. Subsequently the fungus was again found in female *Pinnotheres pisum* from Padstow mussels received on 27 February, 6 June and 9 August 1929. These mussels were opened over a period of days: the crabs taken from them, and in particular the adult females, were mostly killed and examined the same day, or within a few days, of being found. This rapid examination no doubt explains the small number of crabs in which the fungus was found as compared with previous batches which had been kept together in bowls for several weeks and probably infected each other. In some crabs the fungus was only discovered when they were being searched for an entoniscid.

In June 1952 *Leptolegnia marina* developed in eggs of *Pinnotheres pisum*, ovigerous when obtained from Conway, North Wales; as the eggs were kept in filtered sea water, they probably brought the disease with them.

As stated previously (Atkins, 1929, p. 204), in some few instances it is certain that the crabs were already infected when taken from mussels on arrival from the beds. One instance may be given: among mussels received from Padstow at midday on 1 August 1928, one which was opened the same day contained an adult female carrying a few dead and degenerate eggs. By 2 August the crab was dead, the gills of the left side opaque and invaded by the fungus.

Information on the rate of development of the fungus and the length of time before death of the host ensues is lacking. The time varies no doubt with the disposition of the fungus in the body of the host: once it has invaded the gills then death is rapid. Death is probably more rapid under laboratory than under natural conditions.

A few crabs have shown the infection and have died within 8 days of reaching the laboratory, but more have died of the disease between the 15th and 57th days. In an exceptional instance one died after 78 days in the laboratory. For some time before death occurred this crab had been a milky orange colour, owing to the breaking down of the gonad among which hyphae were found; there were also patches of fungus in the abdomen, and hyphae were in the pleopods and the gills. Whether crabs could harbour the vegetative stage of the fungus for such a length of time before it became fatal seems doubtful, but they may have carried resting bodies caught in hairs, which germinated after the crabs reached the laboratory. On the other hand, it is possible, or probable, that the fungus is widespread and that some crabs became infected in the laboratory tanks. More females than males have been observed to be infected but more females than males have been examined, the proportion of female to male *P. pisum* in a total of 508 taken from mussels received on 27 February, 6 June and 9 August 1929 being approximately four to one.

Leptolegnia marina in vegetative and spore-producing stages has been found in crabs in the laboratory in all months of the year, except February and November, when its absence was probably due to chance. The temperature range of the laboratory sea water was between 8 and 17° C.

The only occurrence of infection of *Pinnotheres pinnotheres* was of a tiny female (2·1 mm carapace width) obtained on 15 March 1928 from Teignmouth and found dead on 4 May with the fungus visible in the walking legs. It most probably became infected in the laboratory.

In the previous paper, although attention was paid mostly to attacks on the crab itself, an infection was recorded in a few embryos which had hyphae radiating from them (Atkins, 1929). The formation of zoospores was not observed and the fungus was assumed to be that already known, as the crab carrying the embryos later developed the disease.

A few further instances of infection of the eggs of *P. pisum* by *Leptolegnia marina* have been observed, namely two egg-masses of 6 June 1929 and one of 1 September 1930. A number have probably been overlooked, for re-examination of preserved material in 1943 revealed the presence of the fungus in the egg-mass of two more crabs; in one the fungus had produced numerous oogonia, as already described.

The following observations were made in September 1930 on the living fungus in *Pinnotheres* eggs. The unbranched hyphae radiating from some of the eggs were up to 600μ long and 7·5–10μ broad, those within the egg were generally broader, 10–40μ. Spore formation was observed in fine external hyphae: the contents divided into a single row of more or less rectangular blocks, which gradually lost their angles and escaped from the small aperture at the tip of the hypha as pear-shaped, biflagellate zoospores. In the intra-matrical sporangia the spores were in more than one row. As in the fungus in the crab itself, sporangia were formed from unchanged hyphae.

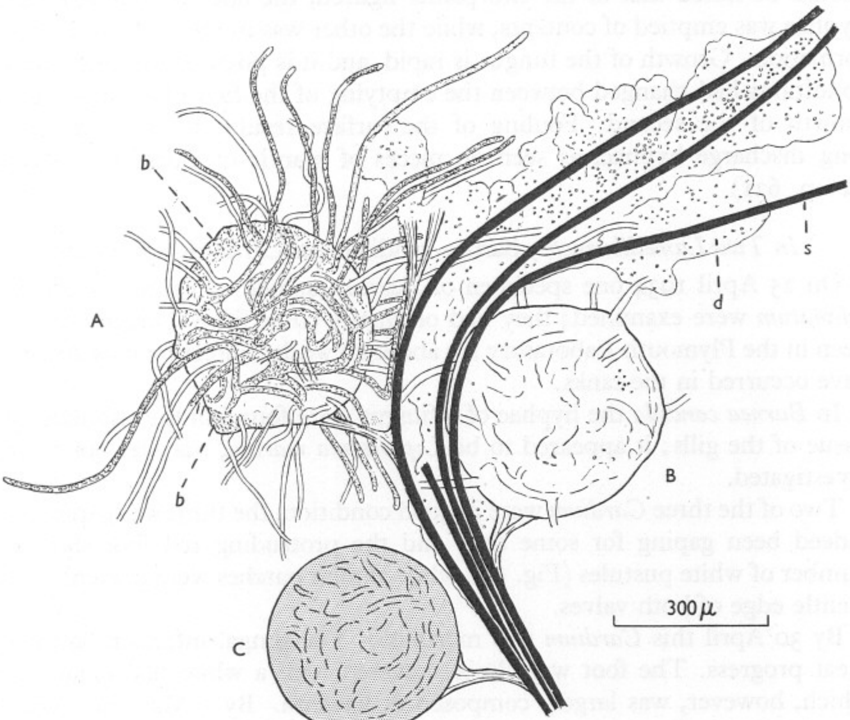

Fig. 4. *Leptolegnia marina*. Three ova of *Pinnotheres pisum* attached to the setae of a pleopod and all infected with the fungus. A: ovum with considerable extra-matrical growth of the fungus. The intra-matrical hyphae are clearly visible as the contents of the ovum have been mostly absorbed. Some hyphae contain zoospores, others are empty after their discharge. B: ovum with mycelium intra-matrical and entirely emptied by the formation of zoospores; the efferent hyphae are all short. C: ovum with mycelium entirely intra-matrical; no efferent hyphae yet formed: ovum opaque as indicated by stippling. *b*, bacteria; *d*, flocculent matter caught on setae (*s*), and in which are embedded numerous encysted spores of the fungus, some of which are indicated. Unstained, in 70% alcohol.

The formation of zoospores was very prolific, and collections of encysted spores on the crab eggs reached a size of 160 by 100μ. Spores also collected in piles on pleopod hairs; these reached a size of 700 by 300μ. It seems improbable that in the event of primary infection taking place soon after the extrusion of the crab eggs any would escape destruction.

There appeared to be a greater tendency to the formation of long discharge tubes when the egg was the substratum than when the crab itself was the host; many infected eggs, however, showed only short discharge tubes. Of plants in two adjacent eggs one may have all efferent hyphae short, while the other may have extra-matrical hyphae of considerable length (Fig. 4, p. 619), so that apparently external conditions are not responsible for the difference. But it should be noted that of the two plants figured, the one with short external hyphae was emptied of contents, while the other was in the midst of zoospore formation. Growth of the fungus is rapid, and it is possible that the external conditions had changed between the emptying of the first plant and external growth of the second. Fouling of the surface results in the formation of long discharge hyphae, as seen on pieces of mantle of *Cardium echinatum* (see p. 621).

In Two Lamellibranchs, Barnea candida *and* Cardium echinatum

On 25 April 1934 one specimen of *Barnea candida* and three of *Cardium echinatum* were examined; they had originally come from Torquay but had been in the Plymouth Laboratory for about 10 weeks; infection may therefore have occurred in the tanks.

In *Barnea candida* the hyphae of a fungus were found in the subfilamentar tissue of the gills; it appeared to be *Leptolegnia marina*, but was not further investigated.

Two of the three *Cardium* were in good condition, the third was gaping, had indeed been gaping for some days and the protruding red foot showed a number of white pustules (Fig. 5A), while similar patches were present on the mantle edge of both valves.

By 30 April this *Cardium* was moribund. The fungal infection had made great progress. The foot was almost covered with a white flocculent layer, which, however, was largely composed of bacteria. By 1 May the *Cardium* was dead. No fungus was found in the gills, although it was present round the point of their attachment to the siphons. In the mantle the tissue surrounding the pustules was invaded by a network of hyphae, but there was little extra-matrical growth. On the foot the extra-matrical hyphae reached a length of about 150μ only.

In the mantle edge broad vegetative hyphae were present, such as previously described and figured from the roof of the gill chamber of *Pinnotheres pisum* (Atkins, 1929, p. 206, fig. 2, p. 205). The hyphae farthest away from those discharging zoospores contained clear, transparent cytoplasm, with shining droplets, probably oil globules.

The fungus lived for about 12 days in mantle fragments placed on 1 May in dishes of sea water; by the end of the period the hyphae had become emptied of their contents by zoospore formation. By 5 May bacteria coated the fragments to some depth, and, apparently because of this fouling, the external hyphae were unusually long, up to about 400μ in length, allowing the zoospores to be liberated beyond the bacterial layer (see Fig. 5B). From

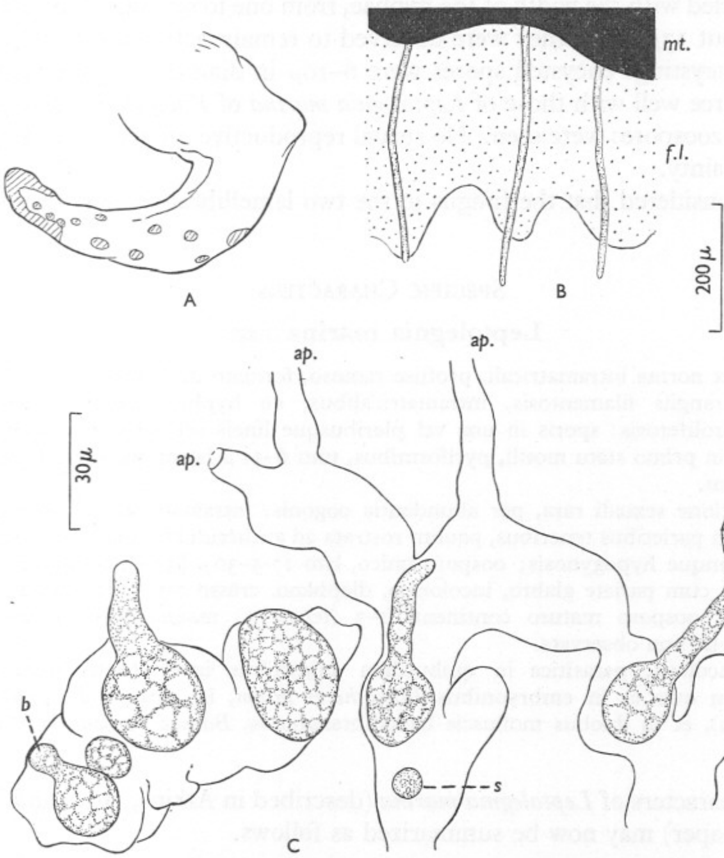

Fig. 5. *Leptolegnia marina* infecting *Cardium echinatum*. A: sketch of areas of infection on foot of the *Cardium*. B: efferent hyphae extending from the mantle (*mt.*) and passing through a flocculent layer (*f.l.*) composed of mucus, sloughed off cells, protozoa, bacteria, etc. C: unusually coarse hyphae (in mantle) most of the contents of which have been used up in zoospore formation, but with a number of rounded bodies of vacuolated protoplasm remaining. Several of the bodies have sent out hyphae; note bulge of tip (*b*) where pressed against wall. *ap.* aperture through which zoospores from old sporangium have been released; *s*, encysted spore. From living material.

7 May onward there was a great tendency for rounded masses and short lengths of protoplasm to remain when the rest of the hypha had emptied its contents in zoospore formation. Each of these bodies then sent out a hypha which eventually penetrated the wall of the old hypha; they were not thick-

walled, and possibly were vegetative portions reconstituting themselves for renewed growth (Fig. 5C).

The liberation of biflagellated pear-shaped zoospores was seen a number of times during the 12 days the fungus lived in the mantle fragments. The sporangia were formed from unchanged hyphae; the number of spores in a row varied with the width of the hyphae, from one to several. The zoospores were about 13μ long; they were observed to remain active for up to 30 min before encysting: encysted spores were 6–10μ in diameter. These measurements agree well with those of *Leptolegnia marina* of *Pinnotheres*, except that no small zoospores were seen. No sexual reproductive organs were identified with certainty.

It is considered that the fungus in the two lamellibranchs was *Leptolegnia marina*.

Specific Characters

Leptolegnia marina n.sp.

Mycelio ex norma intramatricali, profuse ramoso, formato de hyphis 7·5–20 μ [40 μ] latis; sporangiis filamentosis, intramatricalibus, de hyphis immutatis formatis, subinde proliferosis; sporis in una vel pleribusque lineis (de latitudine sporangii); zoosporis in primo statu motili, pyriformibus, tum 6–11 μ latitudine cum in capsulas inclusa sunt.

Generatione sexuali rara, per abundantia oogonia, intramatricalia, sphaeralia vel ovalia, cum parietibus teneribus, paulim rostrata ad antheridium adiunctum; antheridiis plerumque hypogynosis; oosporo unico, lato 17·5–30 μ [37 μ], complenti totum oogonium, cum pariete glabro, incolorato, diaphano, crasso 7·5 μ, de duobus stratis composito; oosporo maturo continenti 1–3 (ferme 1) magna corpora reservata; germinatione non observata.

Mari incolens; parasitica in quibusdam animalibus invertebratis marinis; in corpore, in ovis et in embryonibus *Pinnotheres pisum*, in corpore *P. pinnotheres* (=*veterum*), et in duobus molluscis lamellibranchiatis, *Barnea candida* et *Cardium echinatum*.

The characters of *Leptolegnia marina* (described in Atkins, 1929, and in the present paper) may now be summarized as follows.

Mycelium almost entirely intra-matrical and then freely branched. Hyphae 7·5–20 μ in diameter, sometimes up to 40 μ in diameter. Sporangia filamentous, formed from unchanged hyphae within the tissue of the host; occasionally proliferous: short branches for the discharge of zoospores lead to the exterior of the host. Number of rows of zoospores within the sporangium vary with its width, from one to several. When active within the sporangium the zoospores may be oval, pyriform or rod-shaped. First zoospores 8–14 μ in length, pyriform—when free swimming—biflagellate, swimming away upon emergence and encysting after an interval varying from a few to 50 min. Encysted spores 6–11 μ in diameter. Is probably diplanetic (Atkins, 1929, pp. 213–14). Sexual reproduction rare, then oogonia abundant. Oogonia formed within tissue of host: borne on short side branches, frequently sessile in diverticula of the hyphae, perhaps intercalary, generally spherical, sometimes pyriform or oval, rarely irregular in shape; thin-walled, smooth, very occasionally with one or two small papillae. A slight beak present where hypogynous antheridium attached. Antheridia generally hypogynous. Oospores single, completely filling oogonium, 17·5–30 μ in diameter, occasionally up to 37 μ in diameter. Wall smooth, colourless, transparent, exceedingly thick (up to 7·5 μ), two-layered, very faintly stratified and all surrounded by oogonial wall. Mature egg with 1 to 3, generally one, large eccentric oil or fat body. Germination not observed.

Habitat: marine, parasitic in certain marine invertebrates, being so far known from the body, eggs and embryos of *Pinnotheres pisum*, from the body of *P. pinnotheres* (= *veterum*), and from two lamellibranchs, *Barnea candida* and *Cardium echinatum*.

Affinities

The saprolegniacean fungus which attacks certain marine invertebrates, is considered to belong to the genus *Leptolegnia* with which it has the following characters in common: (i) sporangia filamentous, formed from unchanged hyphae; (ii) zoospores on emerging swim away; (iii) single oospore completely filling the oogonium, eccentric; (iv) ripe oospore wall exceedingly thick. (It differs from the genus *Saprolegnia* in characters i, iii and iv.)

Leptolegnia marina is distinguished from the three known species of the genus, *L. caudata* de Bary, *L. subterranea* Coker and Harvey and *L. eccentrica* Coker in its marine habitat, in which indeed it differs from all known members of the Saprolegniaceae,[1] although one member *Synchaetophagus balticus*, parasitic in the rotifer, *Synchaeta monopus*, has been recorded from brackish water, salinity 5·3–11‰, in the Baltic (Apstein, 1911). *Leptolegnia marina* is also peculiar in that the mycelium is almost entirely intra-matrical, although when *Pinnotheres* eggs are the substrata there is some tendency to extra-matrical growth, not exceeding 1·0 mm in length, the external hyphae being slender, 7·5–10μ thick, and rarely branched, with zoospores in a single row.

The mycelium of *Leptolegnia marina* is not only more freely branched than in the other three species, but is of somewhat coarser growth (7·5–20μ in diameter, sometimes up to 40μ), although Couch (1932, p. 584) records that strains of *L. caudata* vary considerably in their robustness, the hyphae from some often approximating a well-developed *Saprolegnia* in thickness and length. In *Leptolegnia caudata* the hyphae are about 10–18μ thick (Coker & Matthews, 1937, p. 29), in *L. subterranea* 9·4–11·8μ thick (Harvey, 1925, p. 158) and in *L. eccentrica* 4·8–7·2μ thick (Coker, 1927, p. 215).

L. marina differs from the other species in that the zoospores are formed typically in more than one row in the sporangium, the number varying with its width from one to several. In *L. caudata* and *L. subterranea* the zoospores are said to be typically in a single row (Coker & Matthews, 1937, pp. 29, 30), from which it would appear that they are not invariably so. The peculiar bending back or reshaping of the spores before swimming away, which

[1] Since this was written a second marine member of the Saprolegniaceae, *Plectospira dubia* n.sp., has been found (Atkins, 1954).

is characteristic of the other species (Petersen, 1910; Coker, 1923, 1927; Harvey, 1925; Mathews, 1932) was not observed in *L. marina*.

In *L. caudata* the antheridia are diclinous (Coker, 1923, p. 158; Couch, 1932, p. 596; Coker & Matthews, 1937, p. 30), in *L. eccentrica* closely androgynous (Coker, 1927) and in *L. subterranea* lacking (Harvey, 1925), while in *L. marina* they are generally hypogynous.

L. marina agrees with *L. caudata* in being a destructive parasite of an animal, but the latter species is also found saprophytic on animal and vegetable substrata (Couch, 1932, p. 584). It moreover agrees with *L. caudata* in the occasional renewal of the sporangium within an empty one (for *L. caudata* see Coker, 1923; Coker & Matthews, 1937; and for *L. marina* see Atkins, 1929); in the rarity of sexual reproduction (for *L. caudata* see Petersen, 1910; Coker 1923; Couch, 1932) and the formation of oogonia within the tissue of the animal host (for *L. caudata* see Petersen, 1910, p. 513).

In *L. marina* the greater part of the protoplasm of the mycelium may be absorbed in zoospore formation (Atkins, 1929, pp. 209–210), agreeing in this with *L. caudata* (Petersen, 1910) and *L. eccentrica* (Coker, 1927). As in *L. eccentrica* and *L. subterranea* so in *L. marina* spore discharge occurs commonly at night.

L. marina in the great thickness of the mature oospore wall (up to 7·5μ thick) resembles most nearly *L. eccentrica* (5μ or more, Coker, 1927) and *L. subterranea* (3·7–5·5μ, rarely 6·5μ, Harvey, 1925) but differs from them in that the wall is smooth. The oospore wall is stated by Couch (1932) to be very thick in *L. caudata*, but he gives no measurements: according to Coker (1927) it is only about one-third as thick as in the other two species.

In *L. marina* the food reserve in the fully mature oospore is in the form of a single large eccentric refringent body or oil drop, thus agreeing with *L. eccentrica* (Coker, 1927) and differing from *L. caudata* (Coker, 1923; Couch, 1932) and *L. subterranea* (Harvey, 1925) in both of which it takes the form of a lunate cap of small oil drops.

I gratefully acknowledge the kindness of the late Prof. J. H. Orton, F.R.S., Dr W. B. Turrill, Miss E. M. Wakefield and the late Miss M. A. Sexton in procuring for me excerpts from the *Journal of the Elisha Mitchell Scientific Society* which I was unable to obtain on loan. Mrs A. H. Beers of the Botany Department, University of North Carolina, kindly supplied me with references to descriptions of two species of *Leptolegnia*. I wish to record my appreciation of the great help the Surrey County Library—with its associated network of libraries—has been to me in supplying on loan many necessary publications.

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Type material has been deposited in the British Museum.

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