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Pleistophora finisterrensis n. sp., a microsporidian parasite of blue whiting *Micromesistius poutassou*

J. Leiro[2], M. Ortega[2], R. Iglesias[2], J. Estévez[2] and M.L. Sanmartín[1]
[1]*Instituto de Investigación y Análisis Alimentarios, Laboratorio de Parasitología, Facultad de Farmacia, Universidad de Santiago de Compostela, 15706 Santiago de Compostela, Spain*
[2]*Departamento de Microbiología y Parasitología, Laboratorio de Parasitología, Facultad de Farmacia, Universidad de Santiago de Compostela, 15706 Santiago de Compostela, Spain*

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Abstract

Pleistophora finisterrensis n. sp. is a microsporidian parasite of the hypoaxial musculature of the blue whiting *Micromesistius poutassou* (Risso). Foci of infection are between 3 and 6 mm in length and have no evident effects on adjacent muscle fibres. We found only a single type of spore (uninucleate, with mean dimensions of 4 × 2 μm in fresh preparations), contained within sporophorous vesicles (mean diameter 19 μm in fresh preparations; 150–250 spores per vesicle). All of the development stages of this microsporidian are monokaryotic. The meronts are initially uninucleate and bounded by a plasmalemma. Towards the end of merogony, meronts are multinucleate plasmodia with a well-defined surface coat. Sporogony is polysporous, with multinucleate sporonts, which likewise have a well-defined surface coat (about 130 nm thick), dividing by plasmotomy to give rise to uninucleate sporoblasts. The polar tube is isofilar and consists of 8–9 turns in the posterior half of spore. The polaroplast is made up of an anterior lamellar part and a posterior vesicular part.

Introduction

The members of the phylum Microspora are strictly intracellular parasites infecting most animal groups and all vertebrate classes including bony fish (Canning & Lom, 1986). Some microsporidians are highly pathogenic, and infection may cause spectacular lesions (McVicar, 1975; Matthews & Matthews, 1980; Wolf, 1984; Estévez et al., 1992). In commercially important fish hosts, microsporidian infection often has negative effects on product salability (Grabda, 1978). In gadids, most microsporidian infections are due to species of *Pleistophora* Gurley, 1893, *Loma* Morrison & Sprague, 1981 or *Glugea* Thélohan, 1891 (Young, 1969; Morrison & Sprague, 1981a,b; Pulsford & Matthews, 1991). Several researchers have reported microsporidian infections of the hypoaxial musculature of the blue whiting *Micromesistius poutassou* (Risso, 1826) from the Atlantic (Grabda, 1978; MacKenzie, 1979). This microsporidian was initially placed in the "collective group" *Microsporidium* Balbiani, 1884 (Gaevskaya & Kovaleva, 1975) and later assigned to *Pleistophora* (see MacKenzie, 1979). To date, however, there have been no detailed studies of the development of this microsporidian, described below as *P. finisterrensis* n. sp., or of diagnostic ultrastructural characteristics. Here, we report the results of such a study.

Materials and methods

Fish

We examined 1,000 blue whiting (mean length 22 cm, range 19–25 cm) obtained during 1992 and 1993 from a local fish quay, immediately after unloading from trawlers which work the coast of northwest Spain.

Parasites

Infection foci were visible as small patches in the body wall musculature. Spores were extracted as described previously (Estévez et al., 1992).

Light and transmission electron microscopy
Samples of tissue from infected fish were removed and fixed overnight in 2.5% glutaraldehyde buffered to pH 7.2–7.3 with 0.1 M sodium cacodylate buffer. After rinsing in cacodylate buffer and post-fixation for 1 h in 1% osmium tetroxide, the tissue was dehydrated through a graded acetone series and embedded in Spurr's medium. Semithin (1 μm) sections were cut on an ultratome (Reichert-Jung, Ultracut E, Austria) and stained with 1% toluidine blue for light-microscopical examination. For transmission electron microscopy, ultrathin sections were stained in alcoholic uranyl acetate and lead citrate, and viewed under a Philips CM12 electron microscope at an accelerating voltage of 80 kV.

***Pleistophora finisterrensis* n. sp.** (Figures 1–8)

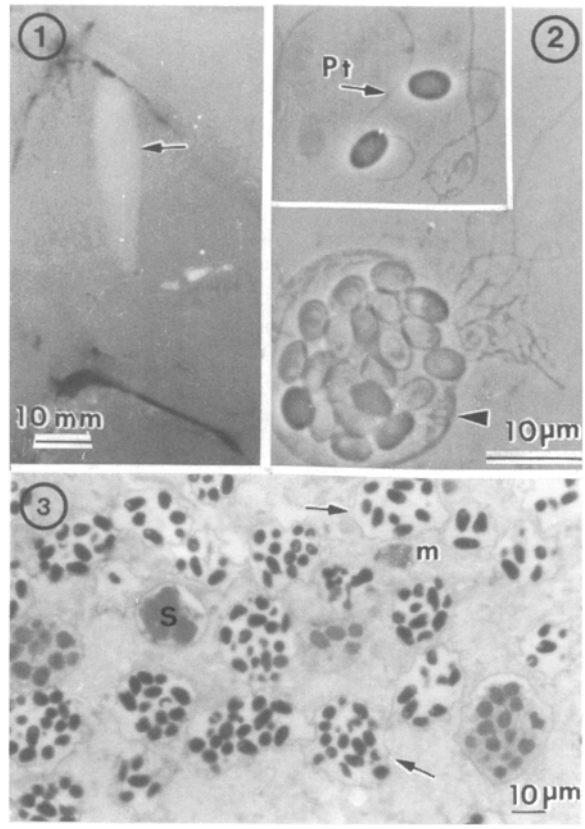
Occurrence
The prevalence of infection was 5%. Although the infection intensity was not quantified, most specimens had a few foci of infection. Only one of the 50 infected fish examined contained foci of infection in which all life-cycle stages of the parasite were observed; in all other infected fish only mature spores were present.

Location and structure
All foci were in the hypoaxial musculature and were yellowish white, fusiform and 3–6 mm long (Figure 1). Interestingly, the nodules were located in the right ventral muscle wall in sagittal sections of all specimens examined.

Developmental cycle and ultrastructure
Within a single focus of infection, various developmental stages of the parasite may be present simultaneously (Figure 3). The spatial distribution of the different types of sporophorous vesicle (SPV) appears random. In semithin sections stained with toluidine blue, meronts – and to a lesser extent sporonts – are less intensely stained than mature spores (Figure 3).

The presumed life-cycle stages occurring within the musculature of the fish host are represented diagrammatically in Figure 4.

Meronts and merogony
Since we did not have access to very recently killed fish, we were unable to obtain high-quality micrographs of the meront stage. Figure 4A–C, however, provides



Figures 1–3. 1. Foci of infection by *Pleistophora finisterrensis* n. sp. (arrow) in hypoaxial muscle of blue whiting. 2. Sporophorous vesicle (arrow head) and free spores showing extruded polar tube; isolated from muscle tissue of blue whiting infected by *P. finisterrensis* n. sp. (fresh preparation). 3. Semithin section of a focus of infection showing meronts and SPVs (arrows) containing either sporonts dividing by plasmotomy, sporoblasts or mature spores. *Abbreviations*: m, meront; Pt, polar tube; S, sporont; SPV, sporophorous vesicle.

some indications of meront morphology. In the material examined, meronts were visible as irregular cells in which the cytoplasm had similar electron density to the nucleus. The cytoplasm contained abundant ribosomes and was initially bounded by a thin plasmalemma (Figure 4A–B). Uninucleate meronts give rise, by repeated nuclear division, to multinucleate plasmodia (Figure 4C) which are surrounded by an amorphous coat lying external to the plasmalemma. On the basis of the material available, however, we are unable to determine the precise sequence of divisions undergone by meronts.

Sporonts and sporogony
Although we are not yet able to characterise the sequence of divisions undergone during merogony (and, more specifically, do not know how prolifera-

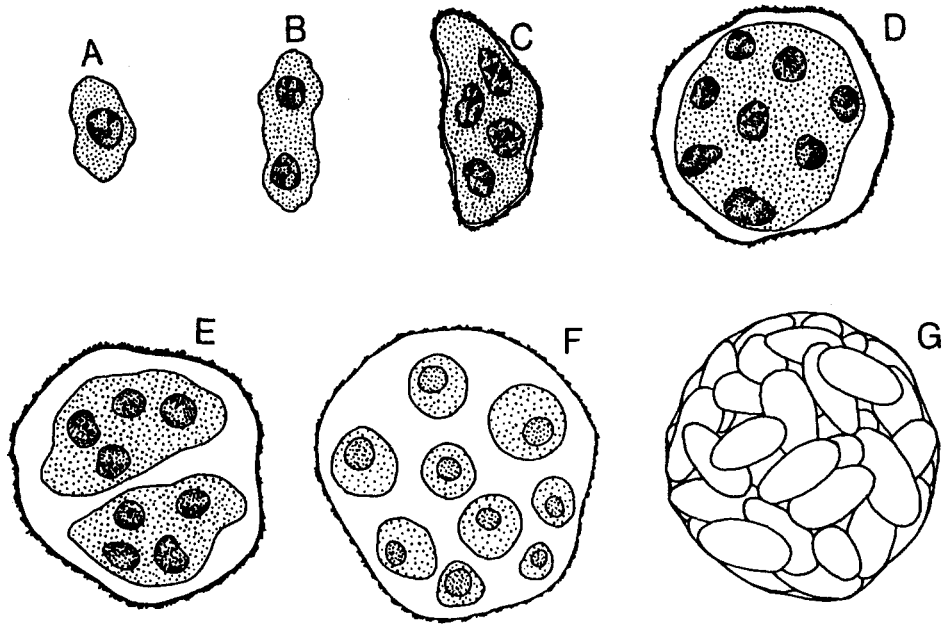


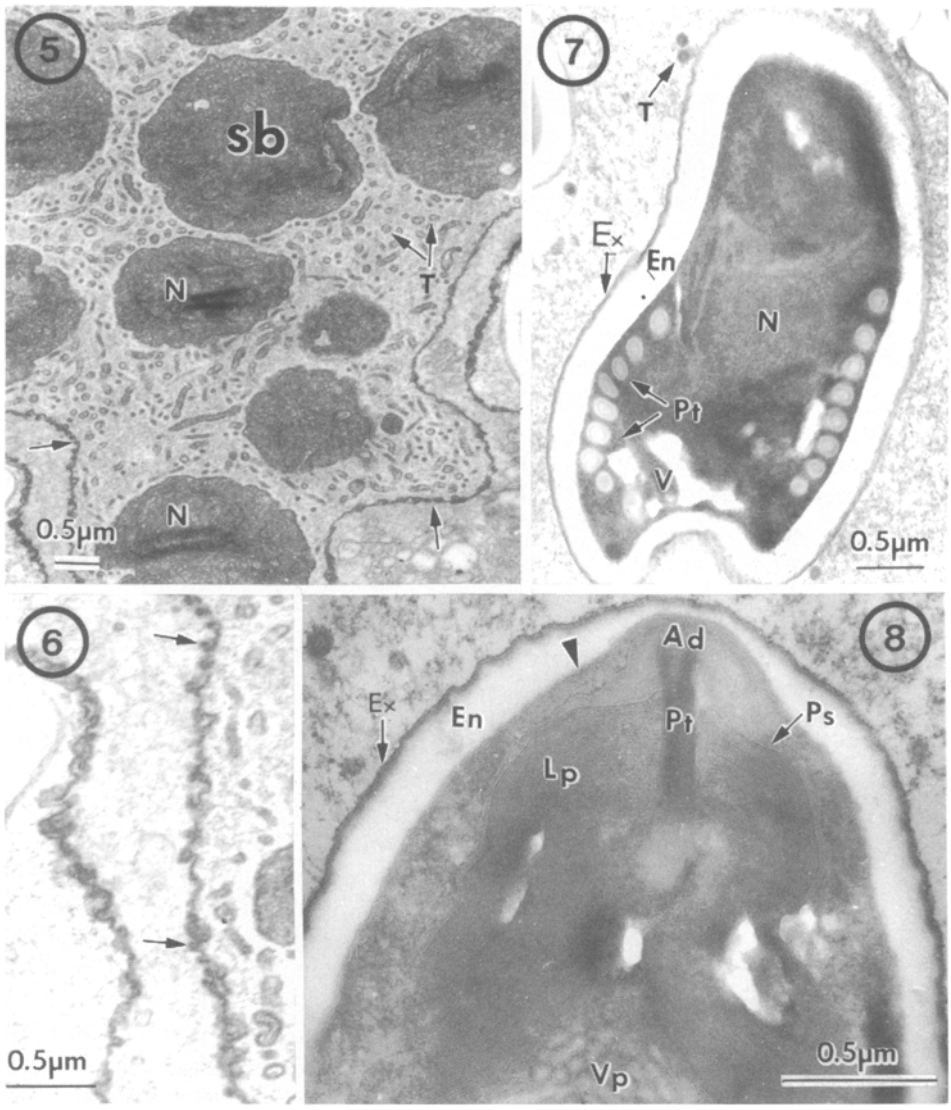
Figure 4. Diagrammatic representation of the presumed life-cycle stages of *Pleistophora finisterrensis* n. sp. occurring in hypoaxial muscle of blue whiting. A–C. meront growth – towards the end of merogony, meronts (C) are multinucleate and surrounded by a well-defined surface coat; D. plurinucleate sporont; E. division within the sporont gives rise to two multinucleate segments; F. continued division within the sporont eventually gives rise to uninucleate sporoblasts; G. sporoblasts give rise to spores within a sporophorous vesicle.

tion occurs), our results suggest that the final products of merogony (merogonic plasmodia) develop directly into sporogonic plasmodia (i.e. sporonts) (Figure 4D). Initially, sporonts appear to be surrounded by an amorphous surface coat similar to that of the merogonic plasmodia. Sporogonic plasmodia can be distinguished from merogonic plasmodia (a) by the space observed between the plasmalemma and the surface coat and (b) by the greater abundance of endoplasmic reticulum in the parasite cytoplasm. In addition, excreted material is occasionally visible between the plasmodium and the surface coat of the sporonts. The surface coat of the sporont is about 130 nm thick and is maintained throughout sporogony. Sporogony takes place within a SPV (Figure 5). The SPV envelope is very thin, although thickened externally by electron-dense spherical structures (Figure 6). Sporonts appear to divide by plasmotomy (Figures 3,4E), eventually giving rise to uninucleate sporoblasts (Figure 5). Sporoblast nuclei appeared to contain parallel electron-dense structures. These might be interpreted as sectioning artefacts (since all are aligned in the same direction); however, they are not present in all sporoblasts, and might be depressions in the nucleus associated with chromatin masses (Figure 5). Throughout sporogony, tubular structures with a diameter of about 80 nm are present at high density in the episporontal space (Figure 5). These tubules mainly disappear as the sporoblast forms and matures (Figure 7). More mature sporoblasts have a more electron-dense cytoplasm.

Spores

All spores found were of a single type: ovoid or slightly pear-shaped, uninucleate and with mean dimensions of 4.0×2.0 μm (range $3.5–4.5 \times 1.5–2.5$ μm; n = 100) when fresh. Spores contained a vacuole (mean diameter 1.5 μm) in their posterior region. The spores were contained within SPVs (Figures 2, 3), these having a mean diameter of 18.8 ± 1.0 μm (range 15.5–24.5 μm) when fresh and 17.6 ± 1.1 μm (range 13.0–24.0 μm) when fixed and stained. The mean length of the polar tube is 35 μm (Figure 2). On the basis of the average dimensions of spores and of SPVs, each SPV can be estimated to contain 150–250 spores.

The spores are of uniform size, with a large posterior vacuole, a distinct electron-dense exospore (visible as a double membrane overlaid by electon-dense material) and an electron-lucent endospore (Figures 7,8). Macrospores were not observed. Spores contain a single nucleus located close to the centre of the cell. The



Figures 5–9. Electron micrographs of *P. finisterrensis* n. sp. in blue whiting. 5. Several uninucleate sporoblasts bounded by a thick surface coat (arrows) observed at the end of sporogony. Numerous tubular structures are visible in the episporontal space. 6. Detail of the surface coat, showing electron-dense sperical structures (arrows). 7. Mature spores contain a single nucleus, a posterior vacuole and a polar tube coiled 8–9 times. 8. Ultrastructure of mature spore showing details of the anchoring disc and of the polaroplast. The plasmalemma is clearly visible inside the endospore (arrowhead). *Abbreviations*: Ad, anchoring disc; En, endospore; Ex, exospore; Lp, lamellar polaroplast; N, nucleus; Ps, polar sac; Pt, polar tube; sb, sporoblasts; T, tubules; V, posterior vacuole; Vp, vesicular polaroplast.

coil of the isofilar polar tube (diameter 110 nm) has 8–9 turns in a single row in the posterior half of the spore (Figure 9).

The extrusion apparatus comprises the polar tube, the anchoring disc, the polar sac and the complex membrane stack of the polaroplast (Figure 8). The anterior region of the anchoring disc is 450 nm in diameter and mushroom-shaped. The manubroid region of the polar tube runs obliquely across the polaroplast, then enters the polar sac where it joins the anchoring disc. The plasmalemma is clearly visible at the inner boundary of the endospore (Figure 8). The polaroplast has 2 distinct regions: a lamellar region located immediately within the lateral arms of the polar sac, and a vesicular region located posterior to the lamellae (Figure 8).

Diagnosis

Host and site of infection: Micromesistius poutassou (Risso), hypoaxial musculature.

Geographical distribution: Coastal waters of Galicia (northwest Spain) in the eastern Atlantic.

Lesion: Yellowish white fusiform masses of 3–6 mm in length.

Structure and life-cycle: Nuclei unpaired at all stages of merogony and sporogony.

Merogony. Meronts with irregular outline, containing one or several nuclei, initially bounded by plasmalemma. By end of merogony, meront has developed into multinucleate plasmodium and secretes amorphous electron-dense surface coat. We have not observed division by plasmotomy during merogony.

Sporogony. Merogonic plasmodia develop directly into sporogonic plasmodia without intermediate uninucleate stage. Sporulation polysporous, taking place within sporophorous vesicle with mean diameter of 19 μm (range 16–25 μm) and eventually containing numerous (150–250) spores. Sporonts multinucleate, rounded, bounded by amorphous surface coat of c. 130 nm thickness, dividing by plasmotomy to give rise to uninucleate sporoblasts.

Spores: Of single morphological type, uninucleate, oval, medium-sized (on average 4 μm long×2 μm wide in fresh preparations; range 3.5–4.5 × 1.5–2.5 μm), containing isofilar polar tube (diameter 110 nm) whose coil has 8–9 turns in a single row; length of polar tube 35 μm.

Type-material: Syntypes deposited in the Museo Nacional de Ciencias Naturales, Madrid (MNCN no. 36.02/1).

Discussion

The mean diameter of the SPVs observed in the present study was 19 μm (fresh preparations), and each SPV contained about 150–250 spores. In *P. typicalis* Gurley, 1893, the type-species of the genus *Pleistophora*, the mean diameter of SPVs in fresh preparations is 23 μm and each SPV contains at least 200 microspores (Canning et al., 1980).

In the *Pleistophora* species studied by us, we only detected a single type of spore, ovoid and with average dimensions of 4 × 2 μm. Canning & Hazard (1982) stated that spore dimorphism, as found in genera such as *Amblyospora* Hazard & Oldacre, 1975 which have complex life cycle (Sweeney et al., 1985), does not occur in *P. typicalis*, although they reported the occasional occurrence of an atypical sporulation sequence giving rise to eight macrospores (which resemble microspores except in size and the number of turns of the polar tube). Another species of this genus, *P. hyphessobryconis* Schäperclaus, 1941, has been reported to produce only a single type of spore (Lom & Corliss, 1967).

In *Pleistophora* spp., according to Canning et al. (1980), the meront is surrounded by a thick amorphous coat that lies external to the cytoplasm and is traversed by channels. This coat divides during plasmotomy and persists throughout sporulation, without dividing further, to become the major component of the surface coat of the sporophorous vesicle. The daughter products of schizonts contain two or more nuclei (Canning & Nicholas, 1980). These authors repeatedly draw attention to the juxtaposition of this coat and host muscle cells. However, the presence of such a coat during merogony does not appear to be a characteristic shared by all *Pleistophora* spp. The meronts of *P. hyphessobryconis* are bounded only by a simple plasmalemma (Lom & Corliss, 1967) and a surface coat develops only during sporogony. In the species studied by us, the amorphous coat appears to be completely formed by the end of merogony. It is probably of parasite rather than host origin, due to deposition of amorphous material external to the plasmalemma (as has been reported for *P. typicalis* by Canning & Hazard, 1982). Since external secretion appears to take place during merogony, SPVs can be considered to be "merontogenic" *sensu* Canning & Hazard (1982). Sprague et al. (1992), however, have rejected this term as ambiguous, because they consider it to imply production of something by the meront rather than presence of something within the meront.

In the *Pleistophora* species studied by us, nuclei were unpaired throughout merogony and sporogony. The meronts of *P. typicalis* divide by plasmotomy, with simultaneous division of the surface coat (Canning et al., 1980). In our material, we have observed uni-, bi- and multinucleate meronts, but have not been able to determine the precise sequence of divisions occurring between infection and sporogony. The production of new meronts (which must occur over this period, to account for spread of the infection) might occur either by plasmotomy or by multiple fission. Multinucleate meronts have similarly been reported to enter direct-

ly into sporogony in the microsporidian *Microgemma* Ralph & Matthews, 1986 (Ralph & Matthews, 1986).

While merogony in the species studied by us appears to differ in some respects from that reported for *P. typicalis*, sporogony follows the typical pattern for the genus (Canning et al., 1980; Canning & Hazard, 1982). The sporulation sequence is polysporous and the multinucleate sporont undergoes repeated segmentation, eventually giving rise to the uninucleate sporoblasts. In the early stages of sporogony, the plasmalemma is covered by a thick, amorphous coat, which appears to correspond to the future surface coat of the SPV. In *P. typicalis* the surface coat comprises three distinct layers of different electron-density; in the species described here, however, the surface coat is very thin, though thickened externally by electron-dense sperical structures. During the sporogony, a mass of tubular structures can be observed in the episporontal space. The presence of these structures may be related to the meront-to-sporont transition. Similar structures have also been reported from the sporonts of other microsporidia such as *Loma dimorpha* Loubès et al., 1984 (Loubès et al., 1984).

The new species described in the present report can be distinguished from other *Pleistophora* spp. infecting marine fish (*P. typicalis, P. littoralis* Canning & Nicholas, 1980, *P. destruens* Delphy, 1916, *P. duodecimae* Lom et al., 1980, *P. gadi* Polyanski, 1955, *P. hippoglossoideos* Bosanquet, 1910 and *P. macrozoarcidis* Nigrelli, 1946) as follows (Table I). In *P. typicalis* (see Canning & Nicholas, 1980; type-host *Myoxocephalus scorpius*), the amorphous coat of the sporont is thicker (0.5 μm versus 0.13 μm in *P. finisterrensis* n. sp.), macrospores are present (unlike *P. finisterrensis*) and microspore morphology is different (in *P. typicalis*, the polar tube coil has 10–22 turns in one to three rows, while in *P. finisterrensis* it is has 8–9 turns in a single row); in addition, the merogonic stage of *P. typicalis*, also appears to differ, although this needs to be confirmed, since our meront preparations were of poor quality. In *P. littoralis* (see Canning & Nicholas, 1980), which infects *Blennius pholis*, the SPVs are slightly larger (average diameter 28.3 μm, versus 17.6 μm in the new species); in addition, like *P. typicalis*, *P. littoralis* has macrospores (with up to 39 coils of the polar tube), while the polar tube coil of microspores has up to 17 turns. In *P. destruens* (see Delphy, 1916), which infects *Mugil auratus*, spores are smaller than in *P. finisterrensis*. In *P. duodecimae* (see Lom et al., 1980), which infects *Coryphaenoides nasatus*, macrospores are present and the SPVs contain only 50–100 spores.

Table I. Key differences between *Pleistophora finisterrensis* n. sp. and other *Pleistophora* spp. which infect marine teleosts.

Species	Type-host	SPV diameter (μm)	Spore size (μm)	Sporogonial plasmodium diameter	Spores per SPV	Number of coil turns	References
P. typicalis	*Myoxocephalus scorpius*	A) 23 [28*]	A) 2.3 × 4.4	20–40	A) 50–200	A) 10–22	Thélohan, 1891; Gurley, 1893;
		B) – [13*]	B) 3.0 × 7.5		B) 8	B) 33	Shulman, 1962; Canning et al., 1980
P. destruens	*Mugil auratus*	A) –	A) 1.5–2.5 × 2.5–3.5	–	A) –	A) –	Delphy, 1916
			B) none				
P. duodecimae	*Coryphaenoides nasatus*	A) –	A) 2.7 × 4.3	18–30	A) 50–100	A) –	Lom et al., 1980
		B) –	B) 3.3 × 6.2	B) –	B) –		
P. gadi	*Gadus morhua morhua*	A) – [18–23*]	A) 3.1 × 6.8	18–23	A) 100	A) –	Polyansky, 1955, 1963; Young, 1969
			B) none				
P. hippoglossoideos	*Drepranopsetta hippoglossoides*	A) 21–25	A) 2.0 × 3.5	–	A) –	A) –	Bosanquet, 1910
			B) none				
P. littoralis	*Blennius pholis*	A) – [20–40*]	A) 2.5 × 4.6	–	A) 200	A) 10–17	Thélohan, 1891, 1895;
		B) – [4-15*]	B) 3.8 × 7.7		B) 8	B) 33–39	Canning et al., 1979, 1980
P. macrozoarcidis	*Macrozoarces americanus*	A) 5–30	A) 3.5 × 5.5	–	A) –	A) –	Fischthal, 1944; Sandholzer et al., 1945;
		B) –	B) 2–4 × 4–7		B) –	B) –	Nigrelli, 1946
P. finisterrensis	*Micromesistius poutassou*	A) 18.8 [17.6*]	A) 2.0 × 4.0	40	A) 150–250	A) 8–9	This paper
			B) none				

A) Microspores, B) Macrospores. [*] Measurements obtained from fixed and stained material. – No data available.

In *P. gadi* (see Polyansky, 1955), which infects *Gadus morhua*, spores are considerably larger (2.7–3.6 × 5.4–7.2 μm) than in *P. finisterrensis*. In *P. hippoglossoideos* (see Morrison et al., 1984; type-host *Hippoglossoides platessoides*), muscle nodule morphology is different and the spores are somewhat larger (mean 2.7 × 4.7 μm) than in *P. finisterrensis*. In *P. macrozoarcidis* (see Nigrelli, 1946; type-host *Macrozoarces americanus*), both spore and SPV size differ considerably from those of *P. finisterrensis*; in addition, *P. macrozoarcidis* infection has characteristic histopathological effects, causing the development of tumour-like masses which may be up to 8 cm in diameter.

For the reasons outlined above, we consider the microsporidian studied by us to constitute a new species, which we describe above in the diagnosis and which we name *Pleistophora finisterrensis* n. sp. in reference to the region where the host specimens were caught.

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