

# Ultrastructure and development of *Pleistophora senegalensis* sp. nov. (Protozoa, Microspora) from the gilt-head sea bream, *Sparus aurata* L. (Teleost, Sparidae) from the coast of Senegal

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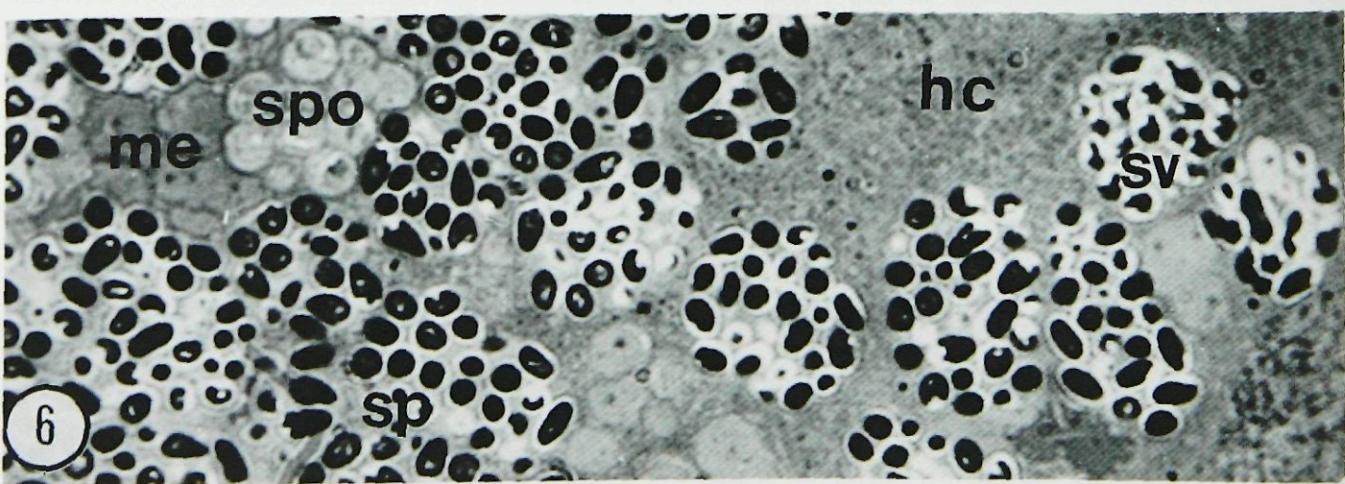
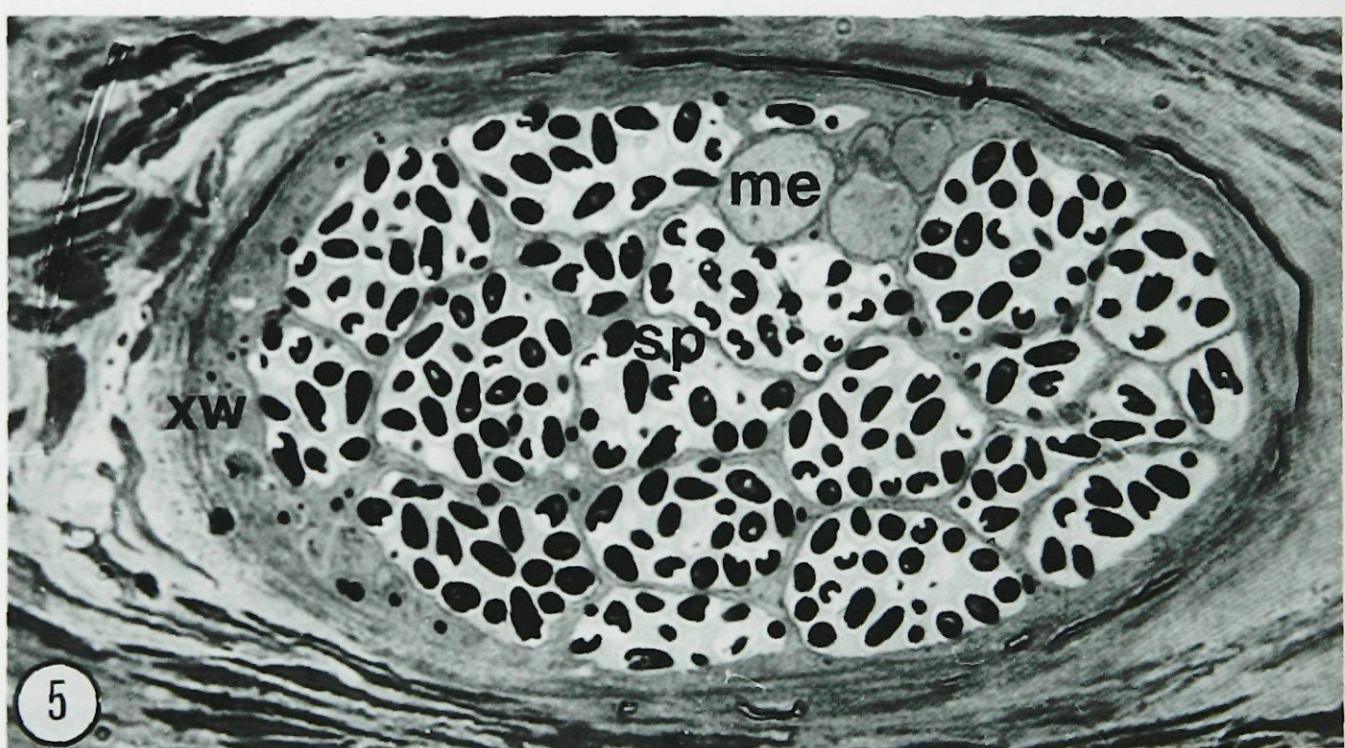
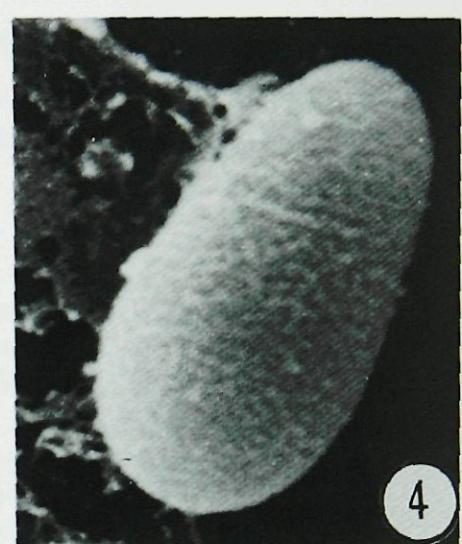
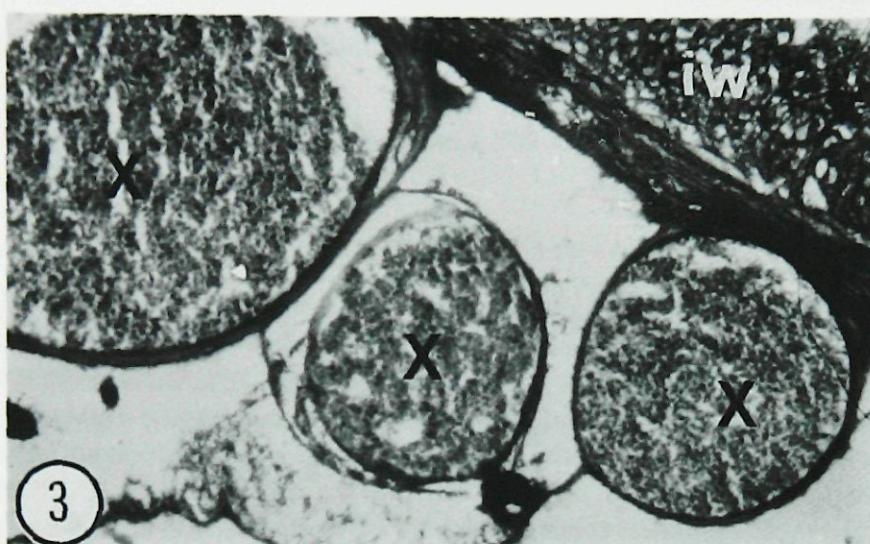
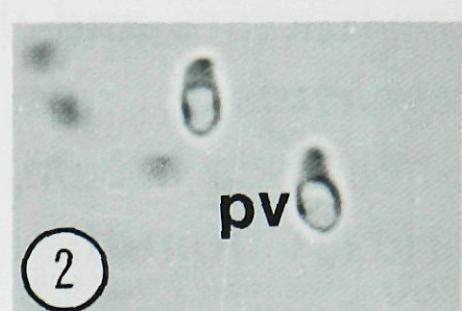
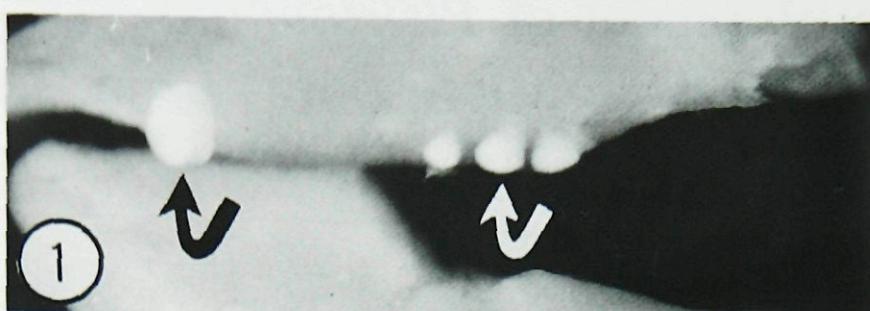
**Abstract.** The microsporidian *Pleistophora senegalensis* sp. nov. parasitizes the gilt-head sea bream, *Sparus aurata* L. The parasite is found in the intestinal wall where it forms small xenomas in the muscularis. The development cycle of this species is described by light and electron microscopy. Meronts are rounded plasmodia dividing by plasmotomy and bounded by an amorphous and very regular wall. At the onset of sporogony, sporophorous vesicles are formed by separation of the plasma membrane from the external wall which then becomes a characteristic mesh. Mature spores ( $4.45 \times 2.37 \mu\text{m}$ ) are ovoid and slightly pyriform with a large posterior vacuole.

## Introduction

Among the numerous microsporidia described in fish, the genus *Pleistophora* is certainly one of the best represented (Sprague 1977; Canning & Lom 1986). Since the first species *Pleistophora typicalis* was described by Gurley (1893) in *Myoxocephalus scorpius* L. (Cottidae), over 30 species of *Pleistophora* have been recorded in fish. Unfortunately, most of them have been very inadequately described and certain specific determinations are incorrect or questionable. The development cycles and ultrastructure of only four species have been analysed using electron microscopy: *P. hyphessobryconis* Schäperclaus, 1941 by Lom & Corliss (1967); *P. littoralis* Canning & Nicholas, 1980 by Canning, Hazard & Nicholas (1979); *P. typicalis* Gurley (1893) by Canning & Nicholas (1980); and *P. hippoglossoideos* Bosanquet, 1910 by Morrison, Marryatt & Gray (1984).

It is known today that the genera of microsporidia can only be defined accurately using ultrastructural characters. Thus, it is not surprising that a doubtful status should be assigned to numerous species, particularly in the light of the difficulties in distinguishing between certain genera close to *Pleistophora*. In addition, there may remain unsolved or recently solved problems of synonymy. *Pleistophora typicalis* and *P. littoralis* (Canning & Nicholas 1980) are two different species, whereas *P. ehrenbaumi*, *P. macrozoarcidis* and *P. duodecimae* (Canning & Lom 1986) may be synonymous, as may *P. mirandellae*, *P. elegans*, *P. longifilis* and *P. oolytica* (Maurand, Loubes, Gasc, Pelletier & Barral 1988).

Several microsporidia were found in various fish during several months of surveying along the coast of Senegal. In this paper, the authors describe the structure and ultrastructure of



*Pleistophora senegalensis* sp. nov., which forms small xenomas (Fig. 1) in the intestinal wall of *Sparus aurata* L. (Teleost, Sparidae), a particularly sought-after fish sold on markets in Senegal. *Pleistophora senegalensis* is compared with the four species previously studied using the same techniques.

## Materials and methods

The sea bream were from the beaches of Hann and Soumbedioune (Dakar, Senegal). Two out of 15 fish examined were parasitized (prevalence 13.3%).

### Light microscopy

Smears of infected intestines were examined fresh by phase contrast microscopy for spore measurement or stained using the May-Grunwald-Giemsa method. Material for histology was fixed in Carnoy's fluid and sections were stained with Heidenhain's Azan and Masson's trichrome.

### Transmission electron microscopy

Fragments of tissue were fixed for 1 h with 2.5% glutaraldehyde in sodium cacodylate buffer, 0.1 M, pH 7.2, and then for 1 h with 2% osmium tetroxide in the same buffer. After dehydration with ethanol and propylene oxide, they were embedded in Spurr's resin, sectioned with a Reichert 0M U2 microtome, stained with uranyl acetate and lead citrate and finally observed using Jeol 100B and 200CX microscopes (Central Electron Microscopy Laboratory, USTL, Montpellier, France).

### Scanning electron microscopy

Several spores of *P. senegalensis* were observed using scanning electron microscopy. The material was prepared using the CO<sub>2</sub> critical point method, coated with gold-palladium and observed with a Jeol JSM 35 microscope (Department of Biology, University C.A. Diop, Dakar, Senegal).

**Figure 1.** Xenomas (arrows) on the intestinal wall of *Sparus aurata* ( $\times 6$ ).

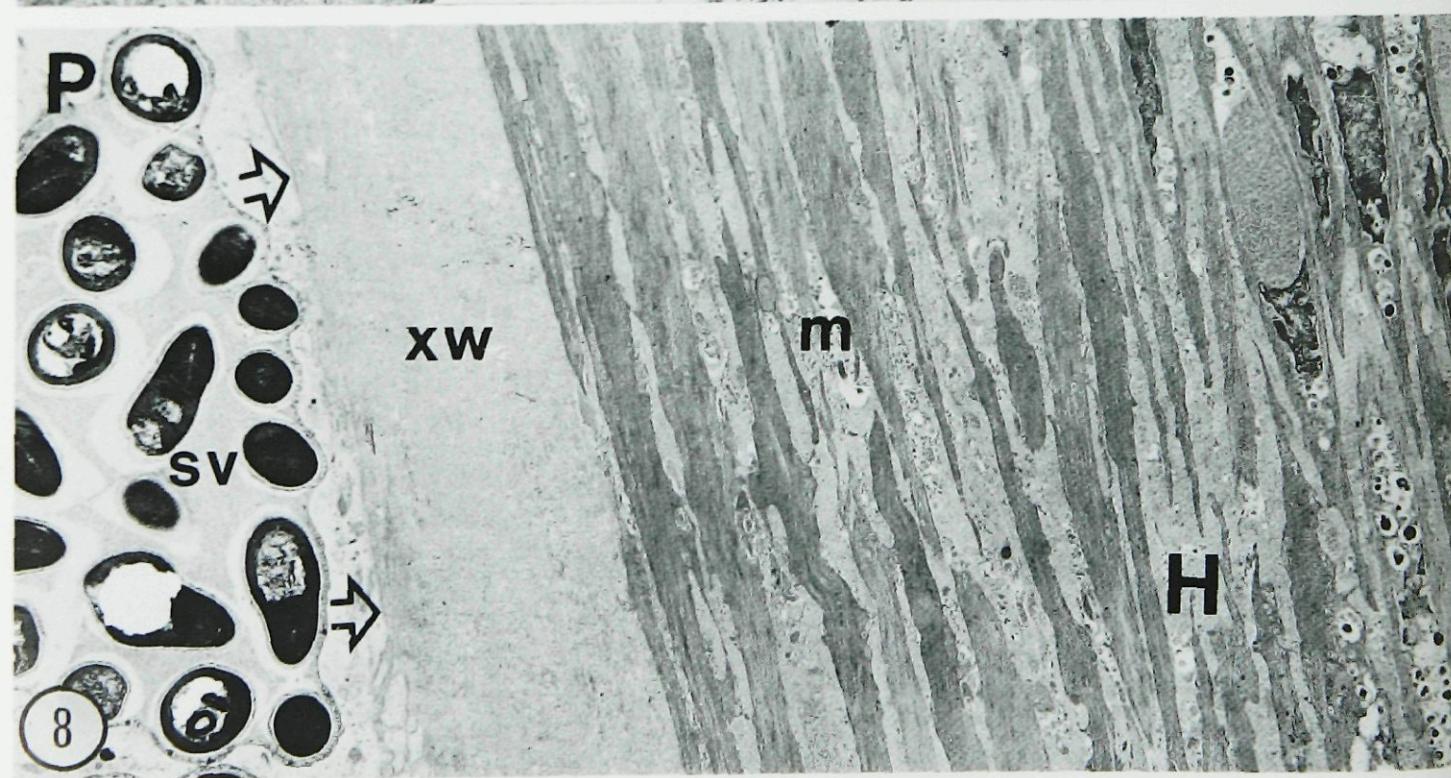
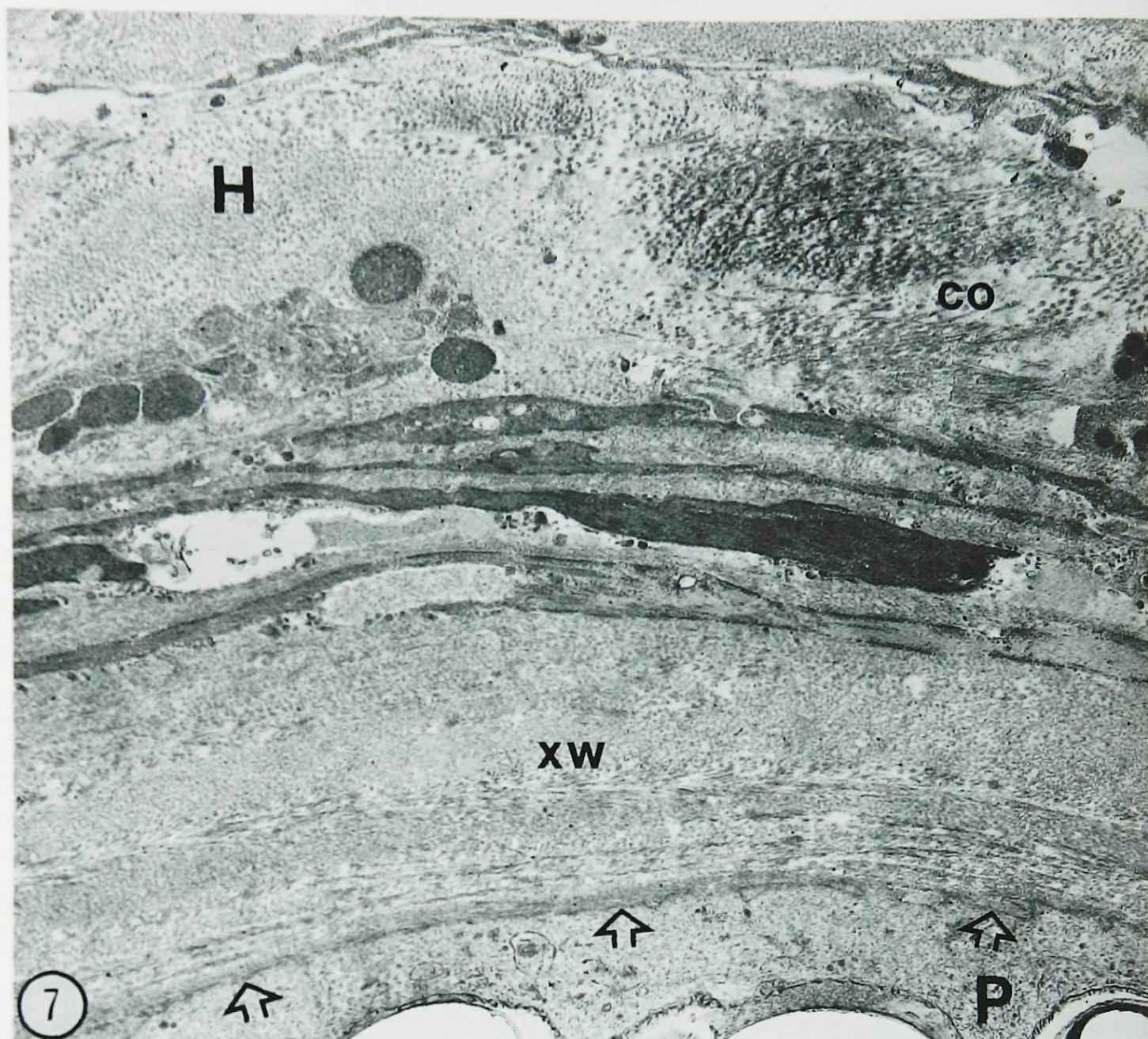
**Figure 2.** Two spores; the large posterior vacuole (pv) reaches the mid-line of the spore ( $\times 2350$ ).

**Figure 3.** Three xenomas (x) in the muscularis of the intestinal wall (iw) ( $\times 100$ ).

**Figure 4.** Spore: note slight folds on the spore wall ( $\times 13500$ ).

**Figure 5.** Tangential semi-thin resin section of a xenoma; numerous sporophorous vesicles can be seen containing spores (sp); merogonic stages (me) are also present. Xenoma is limited by the xenoma wall (xw) ( $\times 1350$ ).

**Figure 6.** Semi-thin resin section in central part of a xenoma; here the host-cell cytoplasm (hc) is abundant and sporophorous vesicles (sv) are separated: me, merogonic stages; spo, sporoblasts; sp, spores ( $\times 1350$ ).



**Figures 7 & 8.** Periphery of xenomas showing the relation between the host (H) and the parasite (P) and the organization of the xenoma wall (xw). Note the position of the host-cell plasma membrane (arrows): co, collagenous fibres; sv, sporophorous vesicle; m, muscularis (Fig. 7,  $\times 5100$ ; Fig. 8,  $\times 3600$ ).

## Results

### *Organisation of xenomas*

*Pleistophora senegalensis* formed small, whitish xenomas in the gut wall; they were oval and less than a millimetre long (300–800 µm). They were located in the muscular layer and caused bulges on the outer surface which made detection easier (Figs 1 & 3).

The various developmental stages were easy to identify in each cyst in semi-thin sections (Fig. 5): meronts, sporonts and sporophorous vesicles, sporoblasts and spores (several tens in each vacuole). Host cytoplasm was always present between parasite elements, especially in a granular central zone where sporophorous vesicles were very widely spaced (Fig. 6).

The spores were the easiest elements to examine *in vivo*. They were oval or pyriform and measured 4·45 (2·50–5·40) × 2·37 (1·60–2·80) µm. The posterior vacuole was very well developed, occupying over half the spore volume (Fig. 2). The surface displayed slight wrinkling (Fig. 4).

By electron microscopy, the xenoma wall measuring 7–8 µm in thickness appeared to be bounded by layers of collagen fibres whose periodicity was clearly visible in places (Figs 7 & 8). These fibres frequently lay in different planes. Passing inwards towards the parasite, the wall was continued by host cell elements in a concentric arrangement: fibroblasts (at the origin of the fibres), then muscle cells which did not appear to have deteriorated in spite of the presence of the parasites (Fig. 8). Finally, a single host-cell plasma membrane separated the wall from the contents of the xenoma. The cytoplasm displayed mitochondria, ribosomes and probably several nuclei. There was no ectoplasmic differentiation; the outermost sporophorous vesicles were in contact with the cell membrane itself.

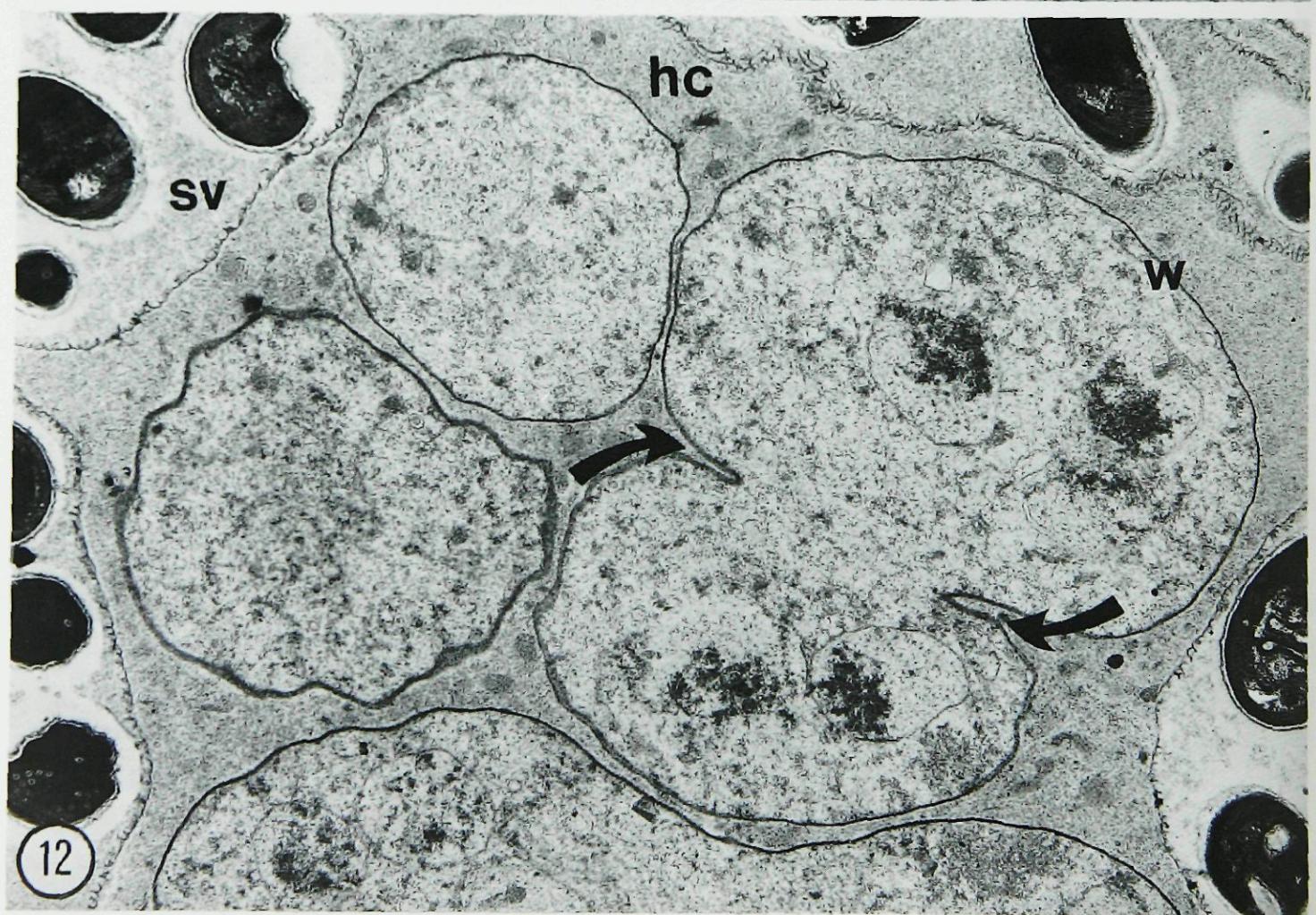
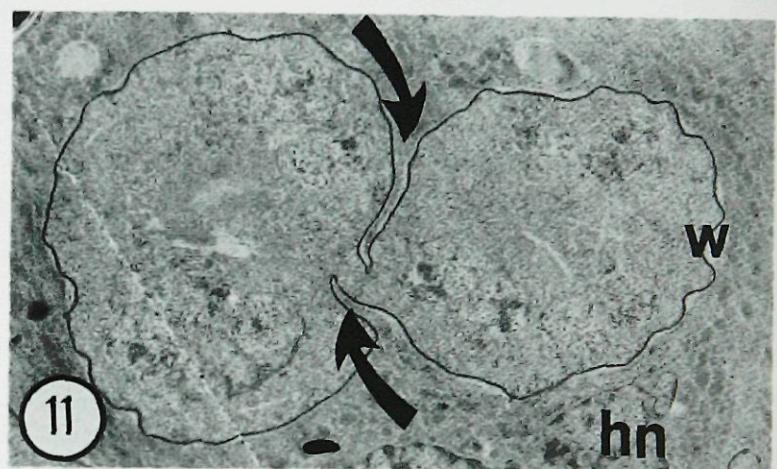
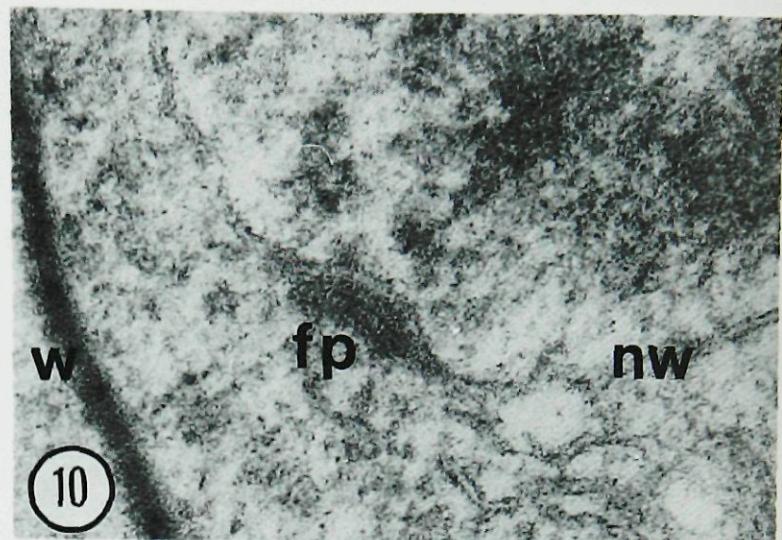
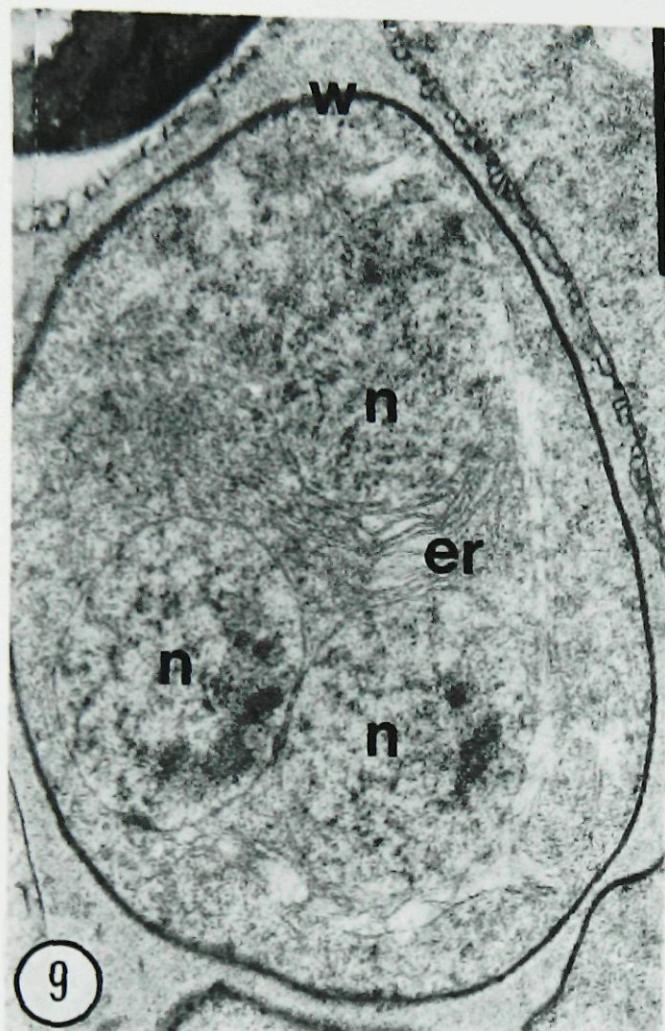
### *Development cycle*

The different stages of development occupied the xenoma without any particular stratification.

*Meronts and merogony* (Figs 9–12). Merogonic stages were in direct contact with the host cytoplasm which was rich in mitochondria close to the parasites. There were multinucleate merogonic plasmodia with an average size of 5–15 µm which contained only a few isolated nuclei, numbering about 10 in the biggest plasmodia (Figs 9 & 12). Growth and multiplication of vegetative stages was by nuclear division, as indicated by commonly-occurring spindle plaques (Fig. 10), followed by plasmotomy (Figs 11 & 12). The resulting plasmodia always contained more than two nuclei.

The organelles in the meront cytoplasm were abundant ribosomes sometimes grouped as polyribosomes, an important system of saccules and vesicles, smooth endoplasmic reticulum and, in more rare cases, vesicles assembled as Golgi apparatus. However, the most characteristic structure was the wall (Figs 9, 10 & 12) consisting of an electron-dense, amorphous wall of very even thickness (approximately 500 nm) formed external to the bounding plasma membrane. It was difficult to affirm the presence of communicating canaliculi between parasite and host as observed in *P. typicalis* by Canning & Nicholas (1980).

*Formation of sporophorous vesicle and sporonts* (Figs 13–18). Considerable change occurred in the plasmodia wall at the end of merogony. This took the form of vacuolisation (Fig. 15) of the dense, amorphous zone which appeared to be caused by the parasite component (Fig. 13). At the same time the plasma membrane retracted and became more clearly visible (Fig. 14).



The space thus formed enlarged progressively and the sporophorous vesicle containing the sporogonial plasmodium was formed (Figs 16 & 17). Various formations produced by the sporogonial plasmodium accumulated in the vacuole. There were tubules and vesicles; the latter appeared to be produced from the former by fragmentation and came to lie close to the wall (Figs 16, 17 & 22). They were mixed with a homogeneous granular matrix between the sporoblasts (Figs 22 & 23) which persisted until the end of sporogenesis. The wall thus acquired a latticed network structure which is distinct in tangential sections (Fig. 19). This is the final appearance of the sporophorous vacuole wall, possibly with very slight disorganization at the end of the cycle (Fig. 18). At the same time, the plasma membrane thickened in patches (Figs 16 & 17) and then all around its periphery, as is typical. The cytoplasm displayed the usual organelles: ribosomes and endoplasmic reticulum, but these were less abundant than during merogony. The nuclei in the sporogonial plasmodia continued to divide (polysporous sporogony).

*Sporoblasts* (Figs 20–23). At the end of sporogony, uninucleate sporoblasts became formed by successive fragmentation of the plasmodium into elements with a decreasing number of nuclei (Figs 20 & 21). Several tens of sporoblasts were produced in the sporophorous vesicles. The cytoplasm was less dense and organelles less frequent than in the preceding stages. Smooth endoplasmic reticulum was piled in more or less regular sheets (Figs 22 & 23). The start of sporogenesis was marked by a lengthening of sporoblasts and polarisation of the nucleus. The number of tubules increased markedly in the sporophorous vesicle and the granular matrix became denser (Fig. 22).

*Spores* (Figs 24–27). Uninucleate spores measured  $4.45 \times 2.37 \mu\text{m}$  on average (Fig. 24). Thickness of the endospore was 55–60 nm and that of the regularly, lightly corrugated exospore was 25–30 nm (Fig. 26). The diameter of the polar filament was uniform (approximately 130 nm) and displayed 19 to 25 spiral turns (Figs 25 & 27). The highly-developed posterior vacuole displayed thick entangled filaments that can be considered as the remains of the Golgi apparatus. The two usual parts of the polaroplast were distinct (Fig. 26), i.e. a lamellar anterior polaroplast and posterior vesicular polaroplast with enlarged lamellae.

## Discussion

This, the first microsporidian described off the coast of Senegal in gilthead sea bream, undoubtedly belongs to the genus *Pleistophora* Gurley, 1893, amend. Canning & Nicholas, 1980, as recently defined (Canning & Nicholas 1980; Canning & Hazard 1982; Canning & Lom 1986; Larsson 1986, 1988). The following characteristics supported this generic identification:

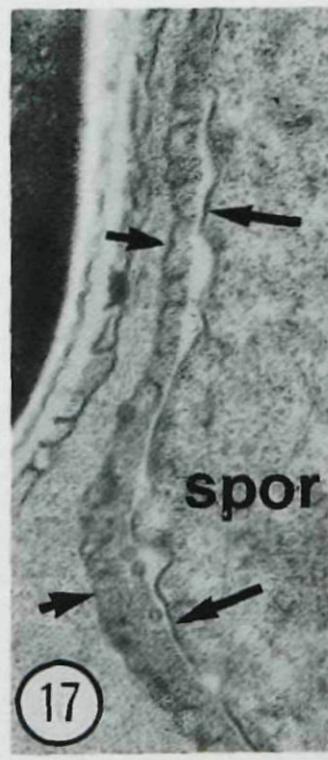
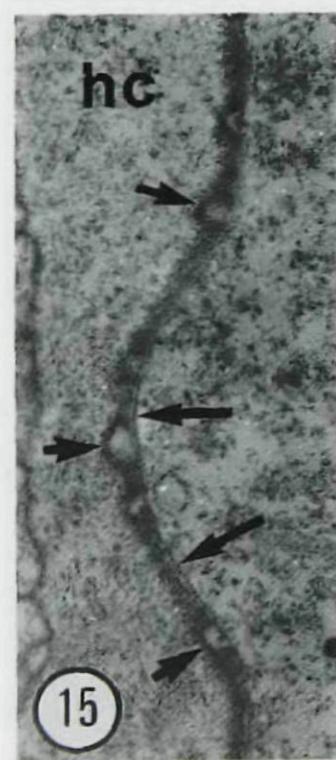
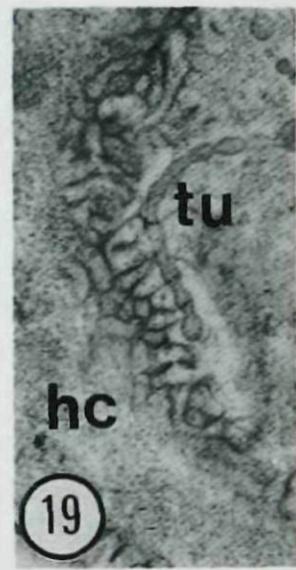
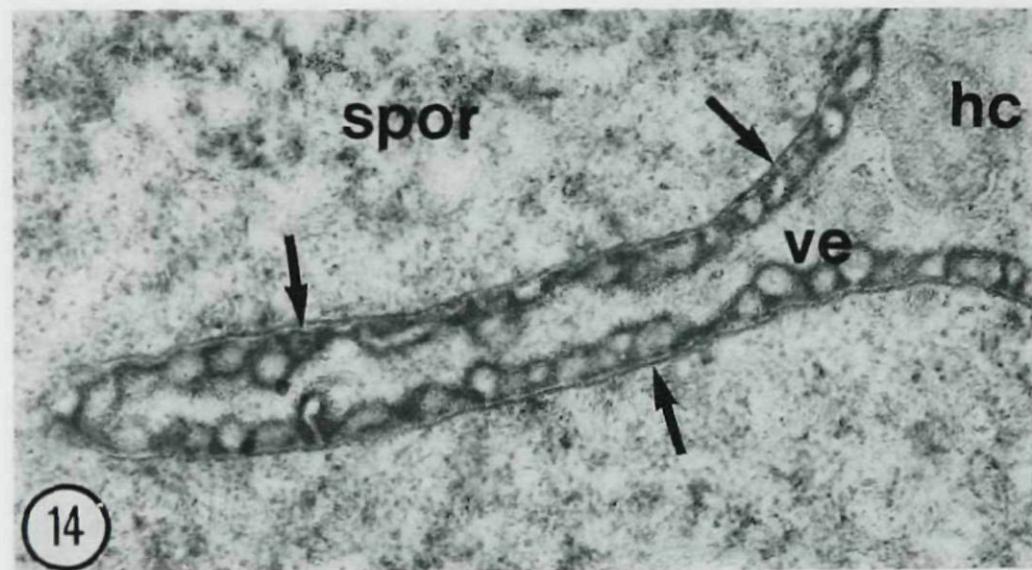
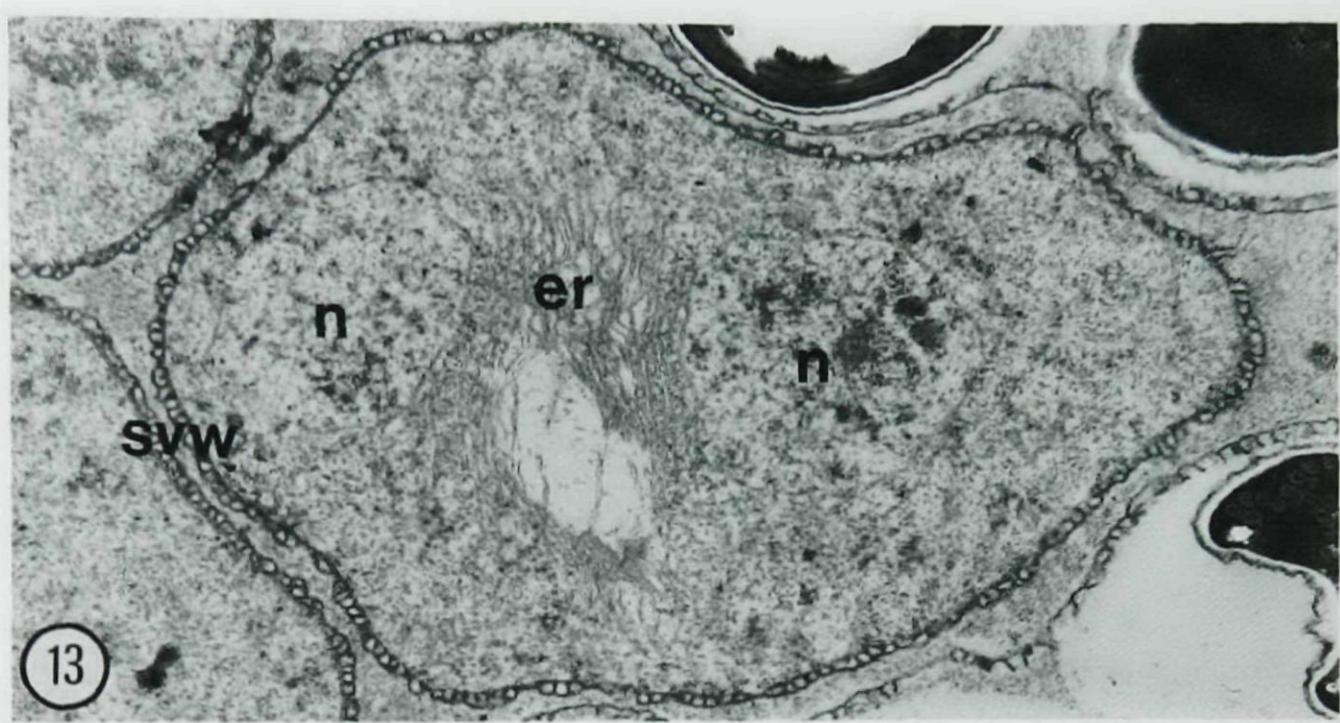
- (1) nuclei were isolated at all stages of development;

**Figure 9.** Merogonic plasmodium with three nuclei (n) and surrounded by an amorphous wall (w): er, endoplasmic reticulum ( $\times 16000$ ).

**Figure 10.** Details of a spindle plaque (fp) during merogony: nw, nuclear envelope; w, amorphous wall of the plasmodium ( $\times 70000$ ).

**Figure 11.** Plasmotomy (shown by two arrows): w, amorphous wall; hn, host nucleus ( $\times 4700$ ).

**Figure 12.** Group of meronts each limited by an amorphous wall (w) and surrounded by host-cell cytoplasm (hc); one meront is dividing by plasmotomy (arrows): sv, sporophorous vesicle ( $\times 7800$ ).



- (2) merogony stages were bounded by a dense, amorphous wall and multiplied by plasmotomy;
- (3) the amorphous wall became detached from the plasma membrane at the beginning of sporogony and remained as a thick, persistent sheath forming the sporophorous vesicle wall;
- (4) the sporogonial plasmodium possessed a plasma membrane thickened by the deposit of dense material;
- (5) sporogony was polysporous by successive divisions of plasmodium until the formation of uninucleate sporoblasts;
- (6) there were numerous spores in the sporophorous vesicle; they were ovoid and uninucleate with a strongly developed posterior vacuole and the polaroplast divided into two parts.

The double sporogonic sequence leading to two types of spore (macrospores and microspores) was not observed in *P. senegalensis* although it has been described in *P. typicalis* (Canning & Nicholas 1980), *P. littoralis* (Canning *et al.* 1979) and also in *P. mirandellae* (Maurand *et al.* 1988), *P. duodecimae* (Lom, Gaievskaya & Dykova 1980) and *P. priacanthus* (He Xiaojie 1982; Hua & Dong 1983). Three types of spore have in fact been described in the last species: macrospores, medium-sized spores and microspores, but recently only the first two were retained in *P. priacanthus*, as the microspores were considered to belong to a distinct species, *Microsporidium zhanjiangensis* (Hua & Zhang 1988). Spore polymorphism has not been encountered in either *P. hyphessobryconis* (Lom & Corliss 1967) or in *P. hippoglossoideos* (Morrison *et al.* 1984) and may not be a diagnostic character of *Pleistophora*.

Likewise, it must be accepted that *Pleistophora* can develop in their hosts either in diffuse infections or with the formation of xenomas within modified host-cell walls as in *Sparus aurata*. Morrison *et al.* (1984) described a very different xenoma in *P. hippoglossoideos*. The thick wall consisted of connective tissue and the whole of the peripheral area was occupied by host cells. It was not specified whether the xenoma was uni- or pluricellar. The xenoma wall in the sea bream species displayed certain similarities with *Glugea atherinae* (Berrebi 1979) and *Loma* (Bekhti & Bouix 1985) xenomas.

It is difficult to compare the parasite of sea bream with all the *Pleistophora* currently

**Figure 13.** A young sporont with two nuclei (n) and well-developed endoplasmic reticulum (er), surrounded by the sporophorous vesicle wall (svw), before the retraction of the plasma membrane ( $\times 15\,000$ ).

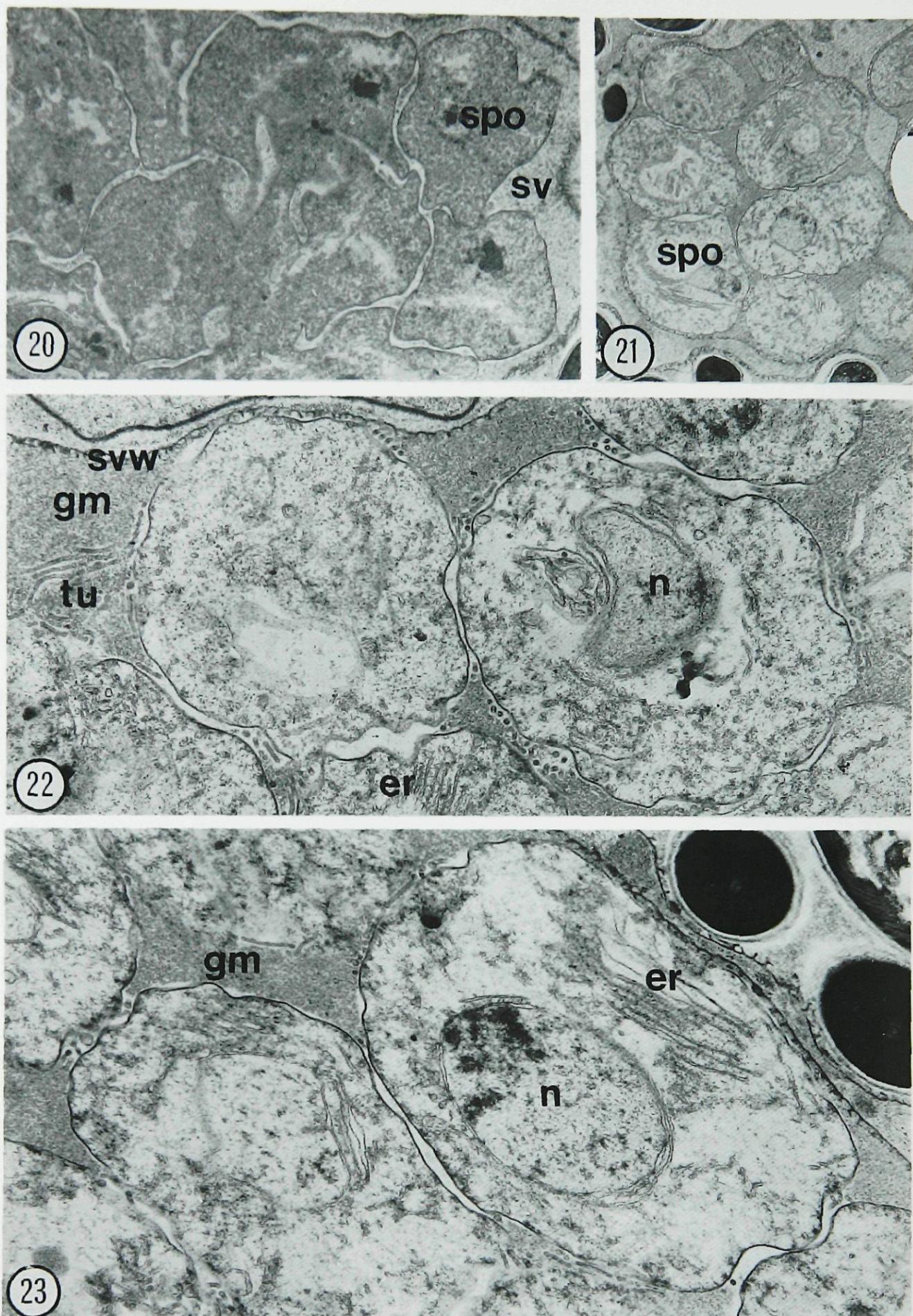
**Figure 14.** Higher magnification of sporophorous vesicle wall at the same stage; the plasma membrane (arrows) of the sporont (spor) is obvious and the amorphous wall is now expanded into numerous small vesicles (ve): hc, host-cell cytoplasm ( $\times 40\,000$ ).

**Figure 15.** First stage in sporophorous vesicle formation when few vesicles (short arrows) are visible in the wall; long arrows indicate the plasma membrane: hc, host-cell cytoplasm ( $\times 40\,000$ ).

**Figures 16 & 17.** Intermediate stages when the outer wall (short arrows) takes on a meshwork structure and detaches from the plasma membrane (long arrows); in the resulting space bundles of tubules (tu) can be seen: me, meront; spor, sporont ( $\times 28\,000$ ).

**Figure 18.** Later stage when the sporophorous vesicle (sv) contains mature spores (sp): hc, host-cell cytoplasm ( $\times 40\,000$ ).

**Figure 19.** Tangential section of the wall at the same stage showing the meshwork; hc, host-cell cytoplasm; tu, tubules ( $\times 20\,000$ ).



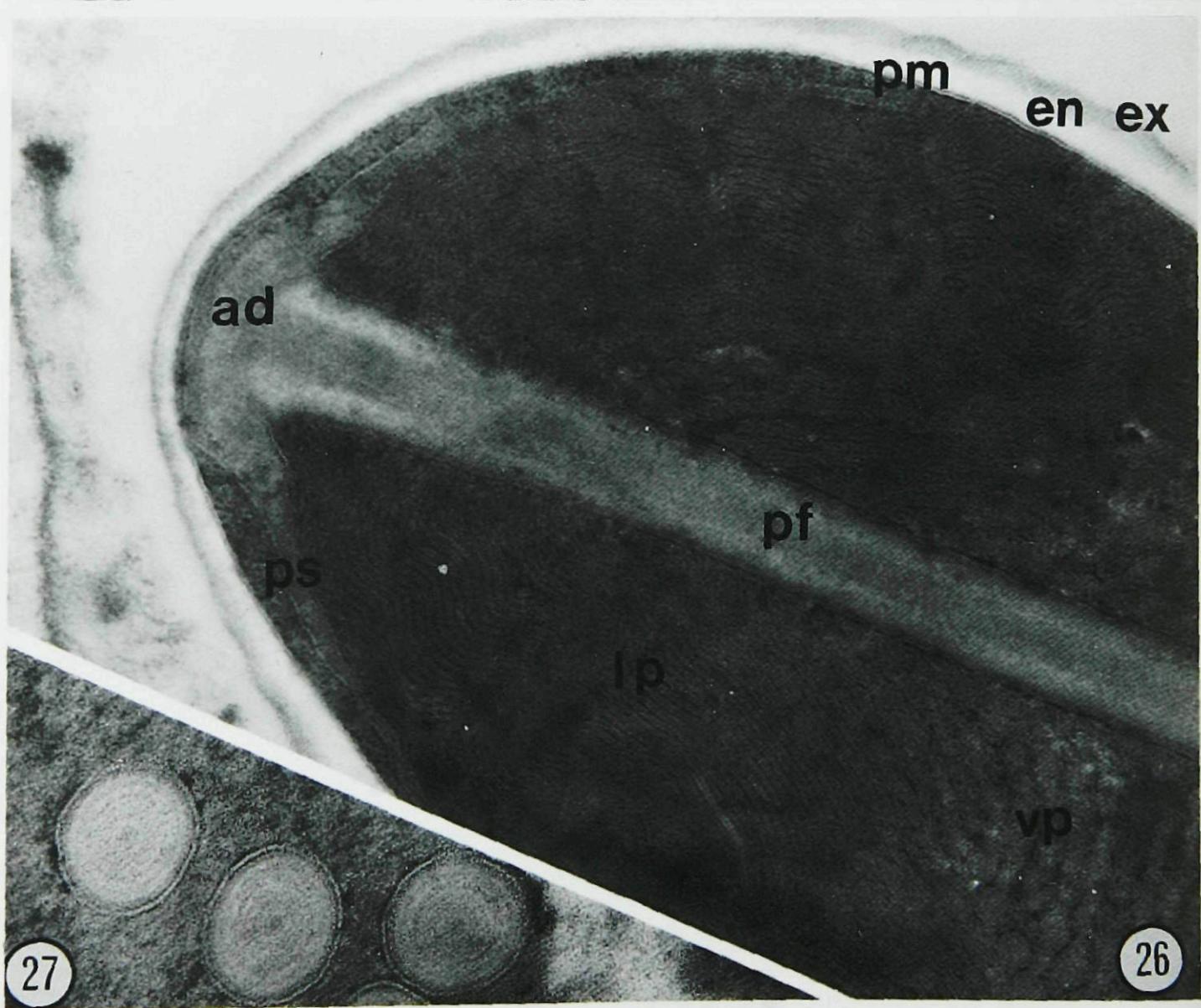
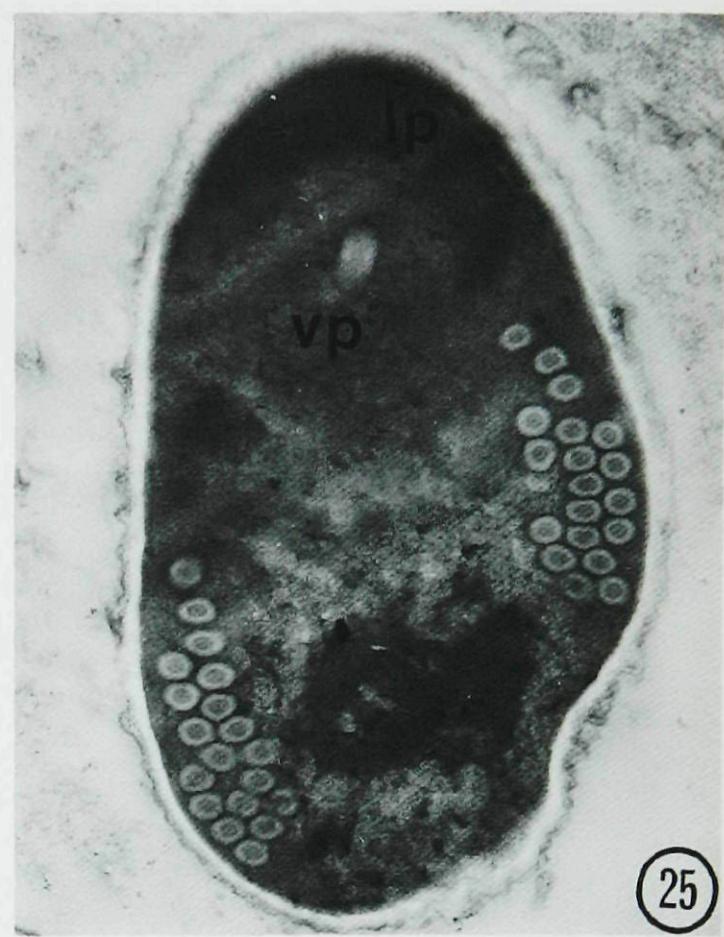
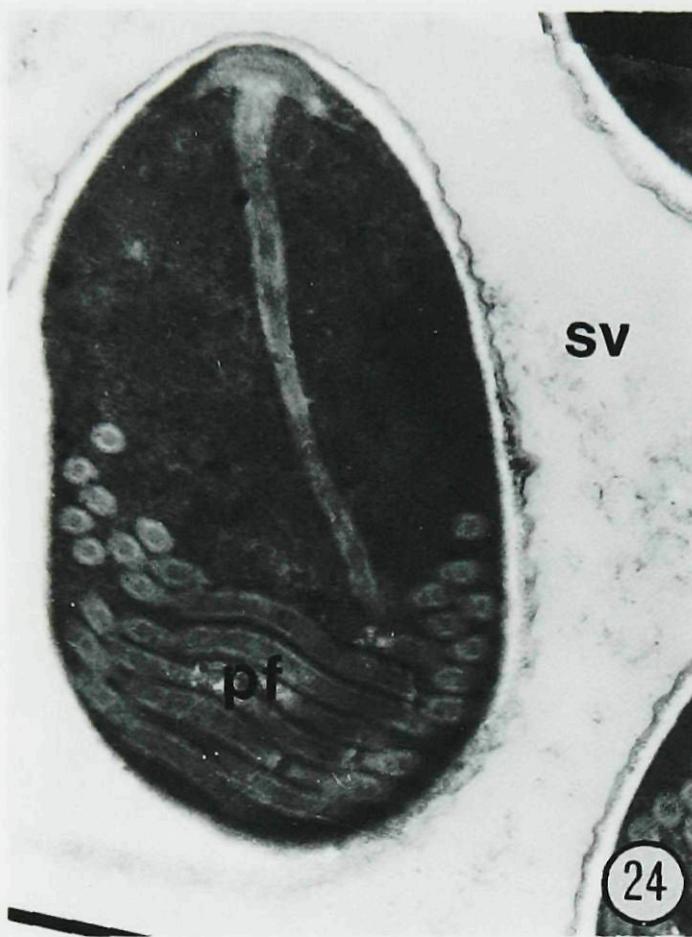
**Figure 20.** Division of the sporogonial plasmodium giving uninucleate sporoblasts (spo) inside the sporophorous vesicle (sv) ( $\times 8000$ ).

**Figure 21.** Sporoblasts (spo) in the sporophorous vesicle ( $\times 5000$ ).

**Figures 22 & 23.** Details of sporoblast structure (n, nucleus; er, endoplasmic reticulum); the sporophorous vesicle, surrounded by the wall (svw), is filled with a granular matrix (gm) containing bundles of tubules (tu) (Fig. 22,  $\times 15200$ ; Fig. 23,  $\times 15600$ ).

**Table 1.** Characteristics of *Pleistophora* of fish described by electron microscopy

Species	Authors	Hosts (family)	Site of infection	Xenoma	Measurements ( $\mu\text{m}$ )	Spores		
							Coils of polar filament	Posterior vacuole
<i>P. hyphessobryconis</i> Schäperclaus, 1941	Lom & Corliss (1967)	Characidae Cyprinidae Poeciliidae Pseudochromidae (fresh water)	Skeletal muscles	—	6 × 4	About 34	Very large	Lamellar and vesicular
<i>P. littoralis</i> Canning and Nicholas, 1980	Canning, Hazard & Nicholas (1979)	Blenniidae (sea water)	Skeletal muscles	—	Microspores 3.9 × 2.3	10–17	"	"
<i>P. typicalis</i> Gurley, 1893	Canning & Nicholas (1980)	Cottidae (sea water) Gasterosteidae (brackish water)	Skeletal muscles	—	Microspores 4.4 × 2.3 Macrospheres 7.5 × 3.0	Up to 33	33–39	"
<i>P. hippoglossoides</i> Bosanquet, 1910	Morrison, Marryatt & Gray (1984)	Pleuronectidae (sea water)	Skeletal muscles	+	3.7 × 2.2	7–8	Medium	"
<i>P. senegalensis</i> sp. nov.	Present work	Sparidae (sea water)	Intestinal wall	+	4.45 × 2.37	19–25	Very large	"



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described in fish. Comparison is only valid with species whose ultrastructure and full development cycle is known. Table 1 clearly shows that no comparison can be envisaged. There are, however, numerous discriminating characters for this species: host and environment, location in host, mode of infection, size and shape of spores. This is a new species and it is proposed that it should be named *P. senegalensis* after its country of origin.

### *Diagnosis*

*Pleistophora senegalensis* sp. nov.

Host: *Sparus aurata* L. (Sparidae).

Location: gut wall (muscularis).

Lesion: small, whitish, oval xenomas (0.30–0.80 mm).

Spores: oval to pyriform, slightly narrowed at the anterior pole; dimensions: 4.45 (2.50–5.40) × 2.37 (1.60–2.80) µm; uninucleate; relatively thick endospore; lamellar polaroplast and vesicular polaroplast; 19–25 spiral turns of polar filament; well-developed posterior vacuole.

Location: coast of Senegal (near Dakar).

The preparations (light and electron microscopy) of material are held at the Laboratoire de Parasitologie, Faculté des Sciences, Dakar, Senegal.

*Pleistophora senegalensis* is the fifth species of *Pleistophora* described by electron microscopy and it has been possible to describe the formation and nature of the sheath walls during merogony and sporogony. The first visible stages in merogony are plasmodia with a small number of nuclei whose bounding membrane is always covered by a dense, amorphous wall. This wall is remarkable for its opacity and very uniform thickness in *P. senegalensis*. It is paler and above all much broader in the other species (*P. typicalis*, *P. littoralis* and *P. hippoglossoideos*). In addition, the present authors were unable to detect canalicula connecting host and parasite components. This wall is certainly the site of important exchanges between the two as shown by the abundance of cytoplasmic organelles (mitochondria) near the parasite.

At the end of merogony or at the very beginning of sporogony, the plasma membrane moves away from the amorphous wall which then undergoes considerable changes of parasitic origin; these modifications begin by vacuolization. The space thus formed then becomes enlarged (sporophorous vesicle) and is filled with a persistent granular matrix, whose role is not known, and tubular structures running from the plasmodium membrane; these structures are also found in *P. hyphessobryconis* (Lom & Corliss 1967) and *P. littoralis* (Canning *et al.* 1979). In *P. senegalensis*, the tubules are much more numerous and regular; they break down into vesicles which become integrated in the wall, which then acquires its final latticed network structure which appears to be much more open than in *P. typicalis* and *P. littoralis*.

**Figures 24 & 25.** Longitudinal sections of mature spores: lp, lamellar polaroplast; pf, polar filament; sv, sporophorous vesicle; vp, vesicular polaroplast (Fig. 24,  $\times 30000$ ; Fig. 25,  $\times 25000$ ).

**Figure 26.** Anterior part of mature spore; note the anchoring disc (ad), the polar filament (pf), the polar sac (ps), the lamellar (lp) and vesicular polaroplast (vp), the wall with exospore (ex), endospore (en) and plasma membrane (pm) ( $\times 90000$ ).

**Figure 27.** Transverse sections of polar filament ( $\times 135000$ ).

In conclusion, the wall structure is noticeably different in *P. senegalensis* in comparison with the previously-described species *P. hyphessobryconis*, *P. typicalis*, *P. littoralis* and *P. hippoglossoideos*. However, it is surprising to find several common points with the wall described in *Glugea habrodesmi* (Loubes, Maurand, Gasc & Bouix 1976a, b).

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