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The Ultrastructure of Spores (Protozoa: Microsporida) from *Lophius americanus*, the Angler Fish[1]

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ABSTRACT. Spinal and cranial ganglia of American angler fish, *Lophius americanus*, are often infected with microsporidia. This protozoon elicits the formation of large, spore-filled, hypertrophied host cells, cysts. Previous reports of microsporidia in European lophiids identify the parasite as *Spraguea lophii*, a genus which has recently been shown to be dimorphic. The spores from *L. americanus* are monomorphic (2.8 × 1.5 μm) and uninucleate. Each spore contains a polar tube that forms six to nine coils. *Spraguea lophii* differs from the microsporidium described in *L. americanus* in several ways. *Spraguea lophii* has two spore types: a large spore (4.0 × 1.25 μm) containing a diplokaryon and three to four polar tube coils and a smaller uninucleate spore (3.5 × 1.5 μm) with five to six polar tube coils. Because of these major differences, the microsporidium from *L. americanus* is removed from the genus *Spraguea* and returned to its original genus, *Glugea*, as a new species, *G. americanus* n. sp. Other ultrastructural characteristics of *G. americanus* are included: the posterior vacuole encloses two distinct membranous structures; one is tubular and resembles a "glomerular tuft" and the second is lamellar and composed of concentric membrane whorls, additionally, the straight or manubroid portion of the polar tube proceeds beyond the posterior vacuole before it turns anteriorly and begins to coil.

NERVE cells from the spinal and cranial ganglia of European lophiid (angler) fishes, *Lophius budegassa* and *L. piscatorius*, are often infected with microsporidia that produce cell hypertrophy cysts (24). Because of the similarity of these cysts with those produced by Microsporida in the genus *Glugea*, the parasite was originally identified as *Glugea lophii* Döflein, 1898. This organism was subsequently transferred into the genus *Nosema* (23) where it remained until 1976, when a new genus, *Spraguea*, was established for it (24). A dimorphic developmental cycle for *S. lophii* in *L. budegassa* and *L. piscatorius* was recently demonstrated and its ultrastructure described in detail (5).

Microsporidian infections similar to those found in the European lophiids have also been identified in the American lophiid, *L. americanus* (3). The only morphological information presently available for the microsporidium in *L. americanus* is the gross description of cysts (3) and sporoplasm extrusion studies (12, 19, 20). The purpose of the present report is to describe the ultrastructure of the microsporidian spores from the American lophiid and compare them to spores of *S. lophii*.

MATERIALS AND METHODS

Angler fish, *Lophius americanus*, were collected during the spring and fall from various sites along the northeast Atlantic coastal region. The fish were anesthetized with MS-222 and dissected; their cranial and spinal ganglia were examined for the presence of cysts. Nerve tissue containing cysts was excised and placed in a chilled petri dish. A few cysts were placed on slides, crushed, and examined for the presence of spores by phase contrast microscopy. The remaining tissue was flooded with cold (4°C) 2.5% (v/v) glutaraldehyde buffered with 0.1 M sodium cacodylate (pH 7.2) and cut into 1-mm pieces. The fixed tissues were rinsed in buffer, post-fixed in buffered 1% (w/v) OsO_4, dehydrated in ethanol, and embedded in Araldite 502. Thin sections (silver-gray) were stained with uranyl acetate and lead citrate, then examined with a Philips 200 electron microscope operated at 60 kV.

RESULTS

Four of the examined *Lophius americanus* specimens contained cream white spherical cysts on their nerve tracts. Two of the fish had cysts on both the optic chiasma and the trigeminal nerves; the other two had numerous cysts on their spinal nerves near the kidneys. The cysts ranged in size from 1–6 mm in diameter. Unfixed, crushed cysts, examined by phase contrast microscopy, contained thousands of elongated oval spores which were uniform in size. The average dimension of 50 spores was 2.8 × 1.5 μm (Fig. 1).

The spore coat consists of a 12.5-nm-thick, uniformly staining, electron-dense exospore wall (averaged from several spores). The "corrugated" outer surface of the exospore wall is ornamented with numerous pyramidal ridges that are variable in length. These ridges are uniformly distributed over the spore wall and arranged in clusters of parallel arrays. The distance between the ridge peaks is approximately 40 nm (Figs. 2, 3). Underlying the exospore wall is a 70-nm electron-lucent endospore layer, which narrows to 24–28 nm at the polar tube attachment site in the anterior end of the spore (Figs. 4, 5). Adjacent to the endospore is a well defined membrane, the plasmalemma, which encloses the spore contents (Fig. 5).

Immediately distal to the anterior-most portion of the plasmalemma are the membranes of the anchoring disc of the polar tube (Figs. 4, 5). Abutted to the anchoring disc is the lamellar polaroplast, which is composed of a series of approximately 14-nm-wide pleated lamellae. They are arranged in parallel arrays and occupy approximately 20–40% of the total spore volume (Figs. 2, 4, 5).

The posterior laminations of the polaroplast are continuous with "tubular" structures that are approximately 28 nm in diameter (Fig. 6). These wider "tubules" attach to the polar tube shaft just below the polaroplast and continue along the shaft an additional 10–20% of the spore length. Electron micrographs of this portion of the polar tube illustrate the "tubules" radiating from the shaft into the sporoplasm (Figs. 2, 4, 6).

The polar tube is divided into two parts: the "straight" region (manubroid portion) which traverses the entire length of the spore (Figs. 2, 7) and the coiled region (Figs. 4, 8, 9). The manubroid portion of the polar tube is attached to the anchoring disc (Figs. 4, 5), and it is slightly larger in diameter than the rest of the polar tube shaft, which averages 95 nm. A few sections near the surface of the spore (outside the polar tube coil) demonstrate that the straight portion of the polar tube traverses the

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entire length of the spore from the anterior attachment disk to beyond the posterior vacuole (Figs. 2, 7). In the coiled region of the polar tube, the typical number of tube cross sections observed in longitudinal section of the spore is six to eight (Figs. 4, 5), and sometimes nine (Figs. 8, 9). The polar tube has a diameter that ranges from 95 to 110 nm, possibly a variation due to the angle of section. The interior of the polar tube, the core, is filled with very fine particulate material which stains medium electron-dense (Figs. 4, 10).

Beginning with the manubroid portion, at the termination of the tubular attachments and continuing along the remaining straight and coiled portion of the tube, the surface is covered with dense particles (Figs. 2, 4, 7, 10). These particles appear to be ribosomes.

The spore cytoplasm is characterized by the presence of a single, large (0.8 μm), centrally located nucleus and massive numbers of ribosomes distributed throughout the cytoplasm. The nucleoplasm contains euchromatin which stains slightly less electron-dense than the surrounding cytoplasm. There was no discernable heterochromatin present (Figs. 4, 10).

The posterior "vacuole" (Figs. 5, 8, 11–13), located in the posterior portion of the spore, is a large 0.9–1.0-μm membrane-limited structure. Its morphology varied among the spores examined. Two general types of structures were observed: tubular and lamellar. The former contained an aggregate of tubular structures (approx. 0.5–0.6 μm in diameter) which resembled a "glomerular tuft" surrounded by medium electron-dense flocculant material (Figs. 11, 12). The lamellar structures which were observed most frequently, consisted of concentric membrane whorls that form a lamellar body (approx. 0.4 μm in diameter) surrounded by fine particulate material of low electron-density (Fig. 13). The posterior-most coils of the polar tube were often in close proximity to the membrane of the posterior vacuole and on occasion appeared to abut it (Figs. 5, 11, 12).

DISCUSSION

Ultrastructural examination of the spores from *Lophius americanus* revealed the presence of a corrugated spore surface. Spore ornamentation of aquatic species of Microsporida appear to be common and may be necessary for transport or flotation (18). It has generally been accepted that the manubroid portion of the polar tube extends only to the beginning of the coiling region which begins somewhere in the medial portion of the spore near the nucleus (as illustrated, diagrammatically, in Fig. 28 of Vavra's classic ultrastructural description of the spore [18]). In a diagram of this same parasite from *L. americanus*, Weidner (19) depicted the polar tube in the classically accepted arrangement. The length of the straight region can easily be misinterpreted as traversing only ½ the length of the spore before beginning to coil if one observes only sections such as Fig. 4; however, the polar tube shaft traversed the entire length of the spore, from the anterior anchoring disc to just posterior of the posterior vacuole as illustrated by Figs. 2 and 7. This manubroid portion of the polar tube then proceeds to turn around the posterior vacuole before coiling. Although we were unable to determine the point at which the coiling begins or ends, we have shown it to be after the straight portion of the tube passes the posterior vacuole and then proceeds anteriorly.

Previously published micrographs of the microsporidia from *L. americanus* showed six to seven polar tube coils (19, 20). Our spores usually contained six to eight coils and on occasion nine, demonstrating relatively consistent observations.

The anterior portion of the spore is filled with several membranous structures, the laminar polaroplast, and the thickened tubular polaroplast. The tubular structures appear to be similar to vesicular polaroplast membranes (6, 18). Both the lamellar and vesicular polaroplast membranes radiate from the manubroid polar tube shaft towards the periphery of the spore.

Weidner (19) described the posterior vacuole of the spores from *L. americanus* as containing flocculant material. In addition to flocculant material, our spores contain two distinct morphological structures enclosed within the membrane-limited posterior vacuole, one tubular, surrounded by medium-dense flocculant material (Figs. 8, 11, 12) and similar to posterior vacuole structures previously discussed in the literature, e.g. vesicular structures in *Encephalitozoon cuniculi* (11), ovoid body in *Pleistophora schubergi* (13), tubular structures in *Nosema* sp. (14), and a reticulated body in *Loma morhua* (8). The

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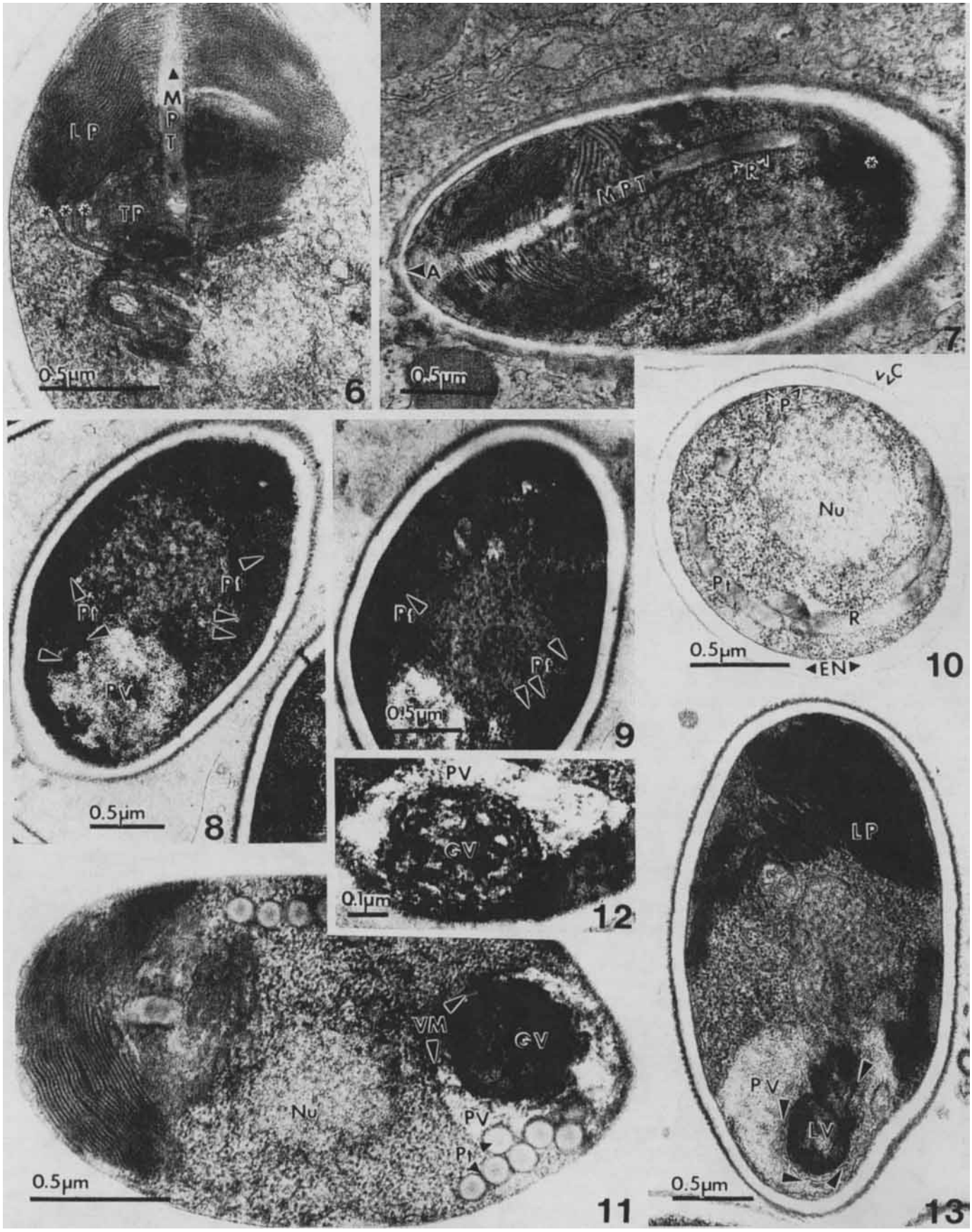
Fig. 1. Phase contrast micrograph of spores obtained from xenomas removed from the ganglia of *Lophius americanus*.

Figs. 2–5. Electron micrographs of spores from *L. americanus* cysts. 2. Oblique section of a spore. The manubroid portion of the polar tube (MPT) extends from the anterior polar aperture (open arrows) to the posterior end of the spore (*). The lamellar polaroplast (LP) and tubular polaroplast (TP) membranes radiate from the polar tube shaft into the sporoplasm. The electron-lucent endospore coat (EN) narrows at the polar aperture. The exospore wall (E) is ornamented with corrugations (C). 3. Spore surface ornamentation is composed of clusters of corrugations (C) in parallel arrays (arrows). 4. Oblique section of a spore depicting the "classical" arrangement of the manubroid portion of the polar tube (MPT). It appears to emanate from the anchoring disc (A) in the anterior-most portion of the spore (open arrow) and terminate at the medial portion of the spore, where the polar tube coils (*) are observed. Ribosomes (R) are associated with the coils of the polar tube (Pt). A single large nucleus (Nu) is centrally located in the sporoplasm. A limiting membrane, the plasmalemma (P), encloses the sporoplasm, and an electron-dense exospore wall (E) covers the electron-lucent endospore (EN). 5. Longitudinal section of a spore. The anchoring disc membranes (A) are attached to the polar tube shaft in the anterior-most portion of the spore. The spore contents are enclosed by a membrane, the plasmalemma (P). The single nucleus (Nu) is located in the medial portion of the spore. The posterior vacuole (PV) is closely associated with the polar tube coils (Pt).

Figs. 6–13. Electron micrographs of spores from *L. americanus* cysts. 6. Anterior portion of the polar tube (MPT) with lamellar polaroplast membranes radiating from the tube shaft into the sporoplasm. Note the transition (*) from lamellar membranes (LP) to tubular structures (TP). 7. Oblique section of a spore. The manubroid portion of the polar tube (MPT) extends from the anterior anchoring disc (A) to the posterior end of the spore where it begins to coil (*). The polar tube shaft is studded with ribosomes (R). 8, 9. Spores containing 8 and 9 cross sections of the polar tube (Pt), respectively. Note the particulate material (*) in the posterior vacuole (PV). 10. Cross section through the medial portion of a spore. The sporoplasm limiting membrane (P) is covered by a uniform thick electron-lucent endospore coat (EN). This coat is covered by the corrugated (C) electron-dense exospore. The single nucleus (Nu) is surrounded by the polar tube coils (Pt), whose core is composed of medium electron-dense material. Sheets of ribosomes (R) are abundant throughout the spore. 11. A uninucleate (Nu) spore containing a membrane-limited (VM) posterior vacuole (PV). A "glomerular" vesicle (GV) composed of tubular material is inside the posterior vacuole. Note the proximity of the polar tube coils (Pt) to the posterior vacuole (PV). 12. High magnification of the glomerular vesicle (GV) inside a posterior vacuole. Note the tubular nature of this structure. 13. Oblique section of a spore. The anterior portion of the spore is filled with lamellar polaroplast membranes (LP). The large posterior vacuole (PV) contains a vesicle composed of concentric laminations (LV and arrowheads).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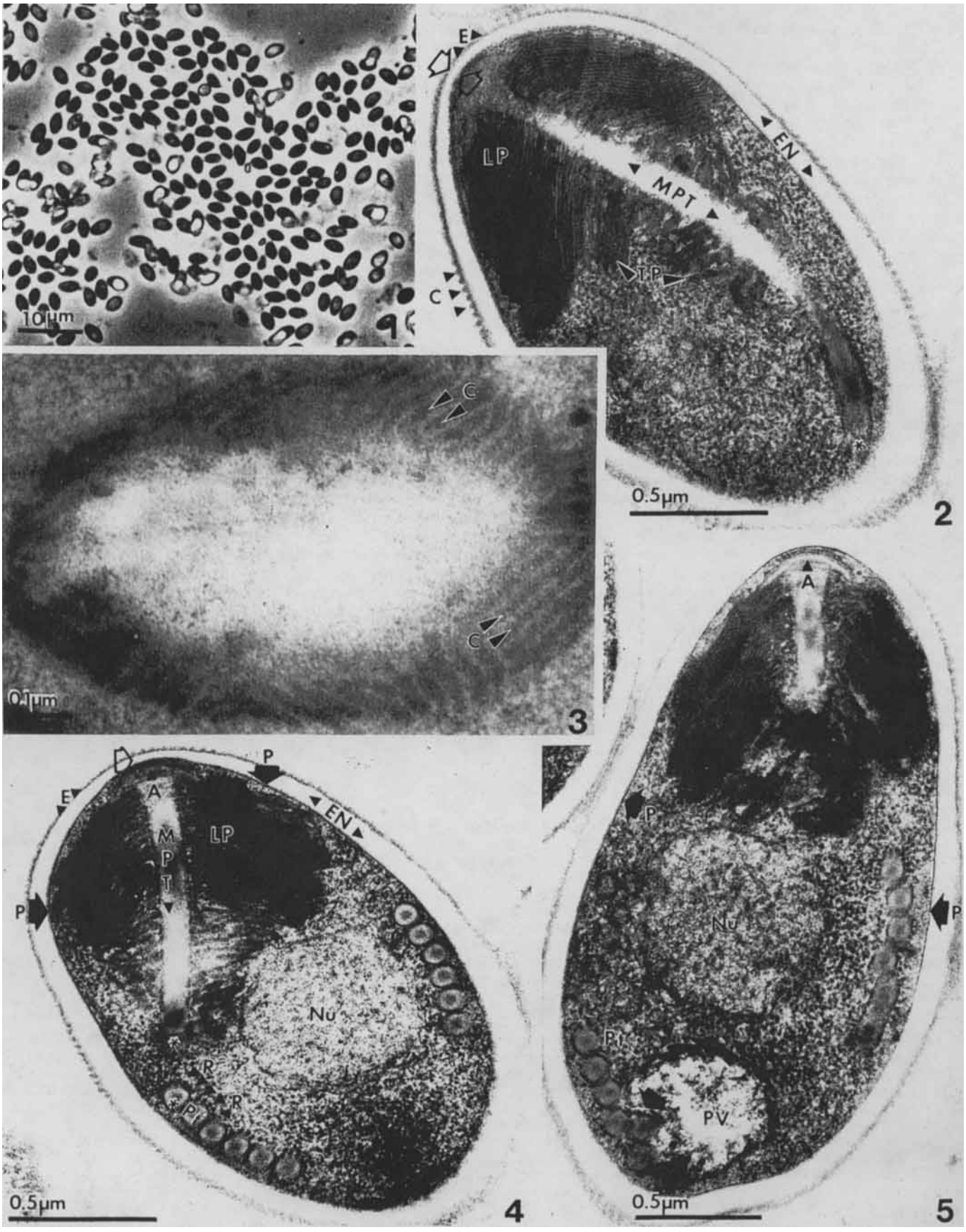
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TABLE I. *Comparison of spore characteristics between* Glugea americanus *n. sp. and* Spraguea lophii *(Döflein, 1898).*

	Glugea americanus[a]	*Spraguea lophii*[b]	
Host	*Lophius americanus*	*L. piscatorius* and *L. budegassa*	
Development	Monomorphic	Dimorphic	
Developmental form	"Glugeidae"	"*Nosema*"	"Nosemoides"
Nuclear arrangement	Uninucleate	Binucleate (diplokaryon)	Uninucleate
Spore dimension	2.8 × 1.5 μm	4 × 1.25 μm	3.5 × 1.5 μm
Spore ornamentation	Present	Absent	Present
Number of polar tube coils	6–9	3–4	5–6

[a] This paper.
[b] After Loubès et al., 1979 (7).

tubular structure may be the remnant of the Golgi-like structure that is associated with polar tube formation (18). The second structure observed inside the posterior vacuole is a lamellar body surrounded by fine particulate material (Fig. 13), resembling the concentric laminated membranes described in *L. morhua* (7).

Although we did not observe the tubular and lamellar structures in the same posterior vacuole, they are probably present concurrently. Electron micrographs of some *L. morhua* spores contain both of these structures in the same posterior vacuole simultaneously (7). These membranous structures may be the structural component of the dense "posterior body" or "inclusion body" previously described in other microsporidian spores (17, 18). Additionally, we have observed a close relationship between the most posterior coil(s) of the polar tube and the posterior vacuole membrane. The presence of these tubular and lamellar structures in the posterior vacuole suggests that they may be involved with the posterior terminus of the polar tube or its attachment to the posterior vacuole.

Our spores contained numerous polysomal aggregates in the cytoplasm and ribosomes on the polar tube surface. The presence of numerous ribosomal aggregates (Figs. 2, 4, 5, 7, 10) have been documented in several microsporidian species (1, 10, 18, 19).

During our study, we noted that the spores appeared uniform in size and contained a single large nucleus. No other published descriptions of the microsporidium from *L. americanus* have indicated a dimorphic or variable size, nor have they demonstrated paired abutted nuclei (12, 19, 20), as is the case with the microsporidium in the European lophiids (5).

We wish to eliminate any confusion which might be caused by assuming characteristics of the microsporidium from *L. budegassa* and *L. piscatorious* to be the same as those from *L. americanus*. To properly identify this microsporidium, we must review its taxonomic history as well as morphology.

Taxonomy. In the microsporidium in *Lophius piscatorius* and *L. budegassa,* nerve cells from the spinal and cranial ganglia of the European lophiids, *L. budegassa* and *L. piscatorius,* are often infected with Microsporida that produce cell hypertrophy cysts (4). Since these cysts and those produced by the genus *Glugea* are similar, the parasite obtained from *L. piscatorius* was originally identified as *Glugea lophii* by Döflein in 1898 and was called *Glugea* by several authors (2, 9, 21, 22). In 1911, this organism was transferred into the genus *Nosema* based on the belief that a sporont stage did not form during the parasite's developmental cycle (23). In 1976 a new genus, *Spraguea,* was established for this parasite (24). This monotypic genus included characteristics relating to distribution of the parasite within the host cell. The first description of dimorphism for *Spraguea lophii* in *L. budegassa* and *L. piscatorius* was demonstrated and described by Loubès et al. in 1979 (5).

The first identification of the microsporidium in *L. americanus* was in an abstract by Jakowska & Nigrelli from the Meeting of the Society of Protozoologists in 1958; they described it as "... *Glugea*-cysts, resembling *Glugea lophii* ...." Subsequent abstracts and reports of the microsporidium from *L. americanus* describe the parasite as "Nosematiasis ... a microsporidian" (abstract of Jakowska & Nigrelli at the 1959 Meeting of the Society of Protozoologists), "*Glugea* or *Nosema*" (3), and "*Nosema lophii*" (19).

The microsporidium from *L. americanus* was included in Weissenberg's 1976 review of *N. lophii,* but he commented to the effect that the parasite from *L. americanus* should be studied and compared to the microsporidium in European lophiids. In the editors' addendum to Weissenberg's review, the parasite (*N. lophii*) was transferred into a new genus, *Spraguea,* with *S. lophii* as the type species (24).

In 1977, Sprague included Jakowska & Nigrelli's 1959 description of the "Microsporidian" from *L. americanus* in *Spraguea lophii* in his annotated list of the Microsporida (15), thus considering the microsporidium from *L. americanus* to be the same as the one from the European lophiids. In our preliminary observations (abstract from a presentation at the 1983 Society of Protozoologists Meeting), we identified the organism in *L. americanus* as *S. lophii* because our material appeared similar to the uninucleate form described in the European lophiids (5).

Morphology. A study of the ultrastructure of *S. lophii* from its European fish hosts describes a dimorphic life cycle in which two different types of spores are produced: one, the "*Nosema* form," results in smooth-walled elongated spores (4 × 1.25 μm) containing a polar tube which forms three to four coils. Each spore contains a pair of abutted nuclei similar to those of the genus *Nosema.* The other spore type is ornamented, oval (3.5 × 1.5 μm), uninucleate, and contains five to six coils of the polar tube (5).

A comparison of the microsporidian spores from several specimens of *L. americanus* collected from different geographic locations and during different seasons failed to reveal any binucleate spores. The uninucleate spores differ in several ways (spore size and number of polar tube coils) from those observed in the European lophiids (Table I), which are the type host for *S. lophii.* Additionally, a comparison with the microsporidium observed in *L. americanus* by other researchers only demonstrated the presence of uninucleate spores (12, 19, 20).

When the spore differences and the lack of a dimorphic life cycle are considered, it is apparent that the microsporidium from *L. americanus* is not the same parasite as that from *L. budegassa* and *L. piscatorius.* Since the American microsporidi-

um is not dimorphic, it must be removed from the dimorphic genus *Spraguea.*

The presence of uninucleate spores developing in cell hypertrophy cysts in a fish host are characteristics of the genus *Glugea,* the genus in which the *Lophius* parasite was originally placed (2). Although we do not know if it will remain in the genus *Glugea,* we are going to revert to this genus until such time as characteristics may be demonstrated that would place it in another genus. Therefore, at present we believe the microsporidium in *Lophius americanus* should be considered as separate from those identified in European lophiids and should be given a new species name within the genus *Glugea.* Since this parasite was found in *L. americanus,* we propose the name *Glugea americanus* n. sp.

Glugea americanus n. sp.

Host species. Lophius americanus (Pisces: Lophiidae).

Type locality. Atlantic Ocean (east coast USA).

Host site. Nerve cells, ganglia.

Pathology. Host cells are enlarged in the form of macroscopic spherical cysts (xenomas).

Early proliferative forms. Not observed.

Sporogony. Uninucleate sporoblasts.

Spore. Uninucleate, uniform size, oval in shape, 2.8 μm by 1.5 μm. Spore surface is ornamented with corrugated ridges.

Polar tube. Manubroid portion extends length of spore, coils variable, six to nine.

Type material. Slides will be sent to the International Protozoan Type Slide Collection, Division of Echinoderms and Lower Invertebrates, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Other slides. Zoology and Physiology Department, Rutgers University, Newark, New Jersey 07102.

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