Scanning electron microscope study of dinospores of *Amyloodinium* cf. *ocellatum*, a pathogenic dinoflagellate parasite of marine fish, and comments on its relationship to the Peridiniales

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ABSTRACT: Trophonts of a parasitic dinoflagellate were obtained from the gills of feral and cultured red drum *Sciaenops ocellatus* and aquarium-housed sebae clownfish *Amphiprion clarkii*, imperator *Pomacanthus imperator*, mandarin goby *Pterosynchiropus splendidus* and flame angelfish *Centropyge loriculus*. After incubation of tomonts, dinospores were studied by scanning electron microscopy. Dinospores have a plate pattern and tabulation of Po, cp, x, 4', 1a, 7", 6 to 8?c, ?s, 5''', 2'''', which are similar to that of the free-living Peridiniales. The parasite is tentatively identified as *Amyloodinium* cf. *ocellatum*. Most descriptions of parasitic dinoflagellates rely only on the morphology of the trophont. However, despite the fact that some past studies have questioned the validity of using dinospores in making taxonomic classifications because of their plastic and unstable morphological characteristics, dinospore characterization is critical. Traditionally, dinospores of parasitic dinoflagellates have been described as unarmored (naked) and have been considered to have gymnodinioid, gyrodinioid or cochlodinioid forms. Ultrastructural fixation techniques used for *A.* cf. *ocellatum* revealed the presence of thin plates arranged in Kofoidian series. Such plates could be more prevalent in other dinoflagellate species than has been previously indicated, and existing taxonomic-classification schemes may need to be emended. Dinospores of other parasitic dinoflagellates should be reevaluated for the presence of similar diagnostic characteristics.

KEY WORDS: Parasite · Dinoflagellate · *Amyloodinium* · Fish · Peridiniales · Classification

INTRODUCTION

The Florida Department of Environmental Protection's (FDEP) Florida Marine Research Institute (FMRI) is conducting a long-term research program to determine the feasibility of increasing depleted feral stocks of red drum *Sciaenops ocellatus* (L.) by releasing cultured fish [raised at the Stock Enhancement Research Facility (SERF) at Palmetto, Florida, USA] into the wild. Since 1988, *Amyloodinium* sp. infestations have occurred in red drum broodstock and fingerlings in culture tanks. In closed-tank systems, infestation levels can build up rapidly and become lethal in a few days. Such infestations caused heavy mortalities initially, but because of successful management and treatment

strategies to prevent and control this parasite (Vermeer et al. unpubl.), extensive mortalities now rarely occur. We have also recently determined that fish mortality in a 500 l marine home aquarium was associated with *Amyloodinium* cf. *ocellatum* (Landsberg et al. in press). *A. ocellatum* is a nonspecific, marine fish ectoparasite (Brown 1934, Brown & Hovasse 1946). There are numerous reports of its incidence and pathogenicity in mariculture and aquarium systems (Lawler 1977a, b, 1979, 1980, Paperna & Baudin-Laurencin 1979, Ghittino et al. 1980, Paperna 1980, Baticados & Quinitio 1984, Barbaro & Francescon 1985, Aiello & D'Alba 1986). The life cycle, development and morphology of *A. ocellatum* have been described (Brown 1931, 1934, Nigrelli 1936, Brown & Hovasse 1946, Cheung et al.

1981). The life cycle consists of 3 stages: a trophont that feeds while attached to skin and gill surfaces, an encysted tomont that develops after the trophont detaches from the fish, and motile dinospores that are released after the tomont divides. Each tomont can produce up to 256 dinospores, each of which has the potential to infect a new host and develop into a trophont (Brown & Hovasse 1946). Dinospore production and infectivity occur over a broad range of temperatures (16 to 30 °C) and salinities (10 to 60 ppt) (Paperna 1984).

Typically, trophonts are found on fish after heavy mortalities in culture (Paperna 1980, Noga et al. 1991) or in the wild (Lawler 1980, Alvarez-Pellitero et al. 1993, Overstreet 1993) and are usually reported as *Amyloodinium ocellatum*. Some recent studies have suggested that there may be more than 1 species or strain of *Amyloodinium* (Lom & Lawler 1973, Lawler 1980, Noga et al. 1991), yet few attempts have been made to differentiate between forms by studying the surface structure of the dinospore using scanning electron microscopy (SEM) (Cheung et al. 1978, Cheung et al. 1981). SEM evaluation of the surface structure of the theca of flagellated (motile) stages, including plates if present, is a normal procedure in the systematic study of free-living or symbiotic dinoflagellates (Dodge & Steidinger 1979, Dodge 1987). Until recently, however, the ultrastructure of the trophont (dominant vegetative stage) has been emphasized in the classification of parasitic dinoflagellates (Lom & Lawler 1973, Lom 1981, Lom & Schubert 1983, McLean & Nielsen 1989, McLean & Galt 1990, Mills & McLean 1991, Lom et al. 1993). Landsberg et al. (in press) presented a preliminary description of the thecal plate pattern and tabulation of the dinospore of *A.* cf. *ocellatum* isolated from parasitized fish in a marine home aquarium. The present communication further describes the dinospore morphology of *A.* cf. *ocellatum*, confirms its natural occurrence in red drum, questions its relationship to the form described as *A. ocellatum* (Brown & Hovasse 1946), and comments on its relationship with the Peridiniales. We also emphasize that SEM analysis of motile stages should be used in classifying parasitic dinoflagellates.

MATERIALS AND METHODS

Red drum juveniles raised in culture at SERF were obtained in February and March 1993. Juvenile feral red drum were obtained from Bishop's Harbor, in Manatee County, Florida, in January and June 1993 and monthly from Murray Creek, in Volusia County, Florida, from March through June 1993. Fish obtained on several occasions from a marine home aquarium (St. Petersburg, Florida) from April through June 1993

included clownfish *Amphiprion ocellaris*, sebae clownfish *Amphiprion clarkii*, mandarin goby *Pterosynchiropus splendidus*, imperator *Pomacanthus imperator*, flame angelfish *Centropyge loriculus*, Pacific blue tang *Paracanthurus hepatus*, achilles tang *Acanthurus achilles*, cleaner wrasse *Labroides dimidiatus*, half black angel *Centropyge vroliki* and blue damsels *Chrysiptera* sp. The fish were examined for parasites, and viable trophonts were obtained from red drum, mandarin goby, imperator, sebae clownfish and flame angelfish. Tomonts were cultured according to methods previously described (Landsberg et al. in press) and were checked daily for division until dinospores emerged. Dinospores from individual tomonts were chemically fixed by different methods so that we could determine the most appropriate technique for analyzing thecal plate pattern and tabulation. The fixation methods tested included combinations of either 1 % or 2 % osmium tetroxide buffered in 0.1 or 0.2 M sodium cacodylate. The initial pH of the sea water was 7.9 to 8.3. We also tested a cold (4 °C) combination fixative composed of 9.4 % glutaraldehyde (GTA) and 2 % osmium tetroxide buffered with sodium cacodylate (pH 7.3) [modified from Steidinger et al. (1989)]. The osmolality (isotonic to hyperosmotic, $\Delta 62$ Mosm) and length of fixation time (15 to 60 min) of this latter fixative were varied. Fixed specimens were critical-point dried, sputter-coated with gold-palladium, and examined on a Cambridge Instruments/Leica Stereoscan 240 Scanning Electron Microscope.

RESULTS

All fish species examined were infested with trophonts of *Amyloodinium* sp. Mean standard lengths and size ranges of fish parasitized by *A.* cf. *ocellatum* (confirmed by SEM study of dinospores) are given in Table 1. Incu-

Table 1 Mean standard lengths and size ranges of fish parasitized by *Amyloodinium* cf. *ocellatum*. SERF: Stock Enhancement Research Facility (Palmetto, FL, USA); BH: Bishop's Harbor (FL, USA); VC: Volusia County (FL, USA)

Species	Mean standard length (cm)	Range (cm)	n
Red drum			
SERF (Feb)	5.4	4.5 – 6.7	30
SERF (Mar)	10.6	8.7 – 12.3	8
BH	9.1	5.6 – 12.7	9
VC	8.3	5.4 – 11.6	19
Sebae clownfish	3.5	–	1
Mandarin goby	3.8	–	1
Imperator	6.4	–	1
Flame angelfish	5.1	–	1

Species	Incubation temperature	Incubation time (d)	Dinospore life span (d)
Red drum			
SERF	18–27	2–20	2–14
BH	20–28	3–5	2–10
VC	18–31	2–7	2–6
Sebae clownfish	24	2–3	5–6
Mandarin goby	21	2	1–14
Imperator	21–24	2–5	6
Flame angelfish	21	2	?

bation temperature of tomonts, length of time to dino-spore emergence, and dinospore life span are shown in Table 2. Of the fixation methods tried, the most effective one for determining plate structure of the dinospore of *A.* cf. *ocellatum* was the GTA/osmium tetroxide combination cold fix (Fig. 1). The other fixation methods used resulted in 'blown' dinospores in which at least 2 outer membranes were totally 'stripped', leaving a smooth surface (Fig. 2), or they resulted in distortion, leaving a thick nodular surface (Fig. 3).
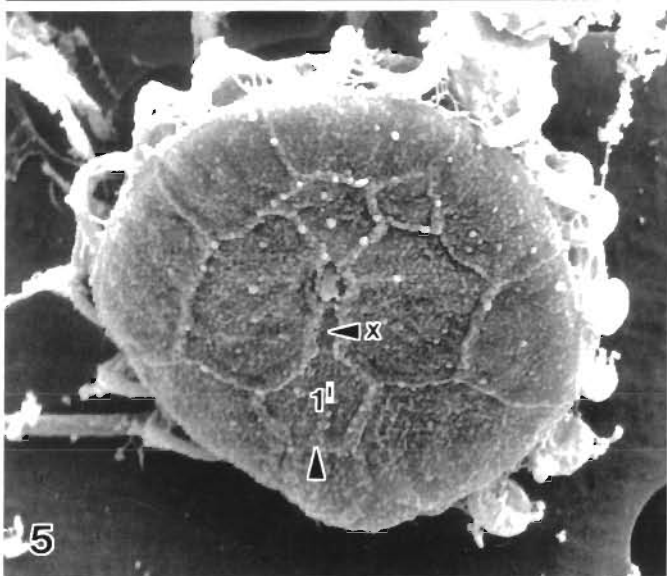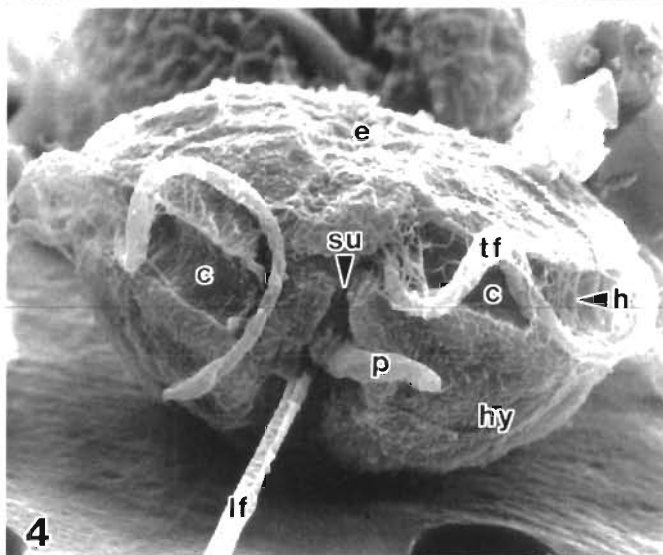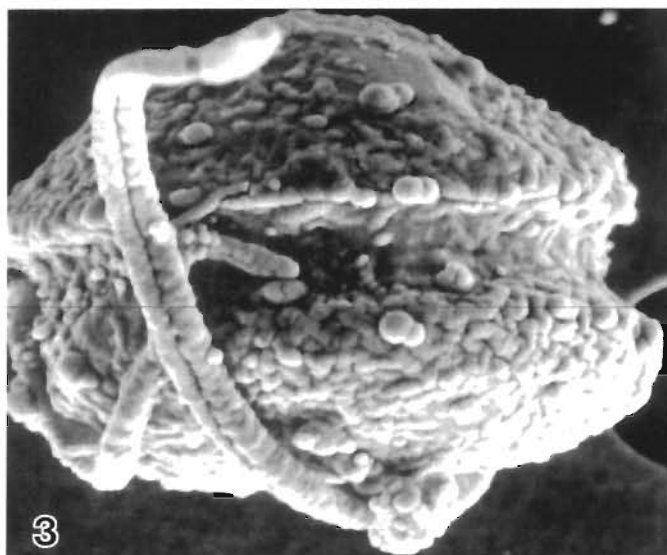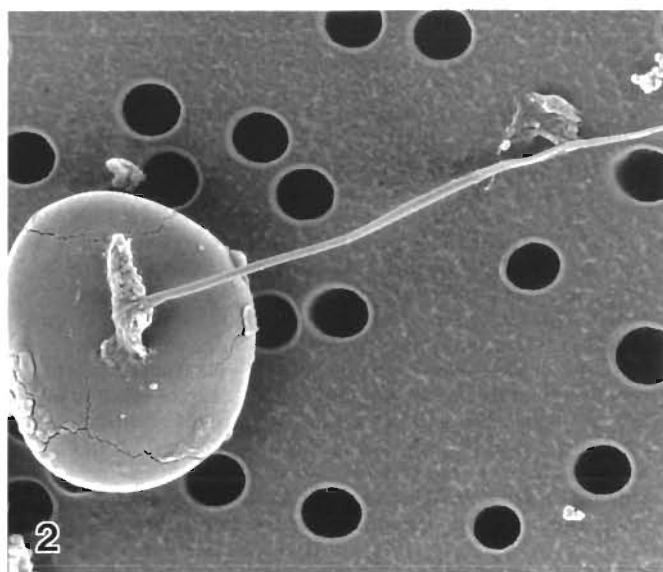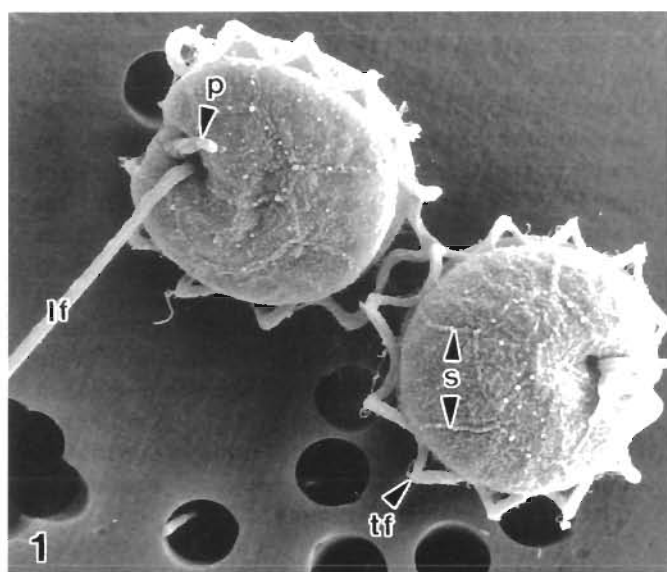
The *Amyloodinium* cf. *ocellatum* dinospore is a small, anteroposteriorly compressed, thinly armored peridin-ioid type, having an epitheca that is slightly shorter than the hypotheca (mean epitheca length = 2.7 ± 0.2 µm, mean hypotheca length = 3.3 ± 0.6 µm, n = 9) (Fig. 4). The dinospore plate pattern and tabulation of *A.* cf. *ocellatum* isolated from red drum, sebae clownfish and mandarin goby were the same. Dinospores were 6.1 ± 0.8 µm in length, 11.7 ± 0.5 µm in width, and 11.1 ± 1.2 µm in depth (n = 11). Of the several hundred individual dinospores evaluated, all were found to have a plate pattern and tabulation conforming to that of the free-living Peridiniales. The plate formula is Po, Cp, x, 4', 1a, 7", 6 to 8?c, ?s, 5''', 2'''' (Figs. 5 to 8). The plate formula varied in some specimens by having 8 precingulars (Fig. 9) or 6 postcingulars (Fig. 10). The cell is 'hamburger-shaped', with a deeply excavated cingulum that is displaced 1 to 1.5× (Fig. 4). In apical view, the right side appears deeper than the left be-cause of the extension of the 1' beyond the cingular margin of the 1" plate. The 1' is in contact with the x plate of the apical pore complex (APC; Figs. 5 & 7) and lies directly over the sulcus (Fig. 11); it is typically rhomboid (Fig. 9), or has a postmedian horizontal suture (Figs. 5 & 7). The Po is elongate and is posi-tioned under the rims of the 2' and 4'; it abuts the 3' (Figs. 5, 9 & 11). The closing or cover plate of the APC is elongate, irregular in outline, and the anterior margin appears crenulate or dentate (Fig. 12). The x plate is directly below the Po and in direct contact

with 1' (Figs. 5, 9 & 11). Plates 1", 2', 4', and the 7" (or 8") overlap the 1', which is sometimes slightly dis-placed to the left (Fig. 11). The hypotheca has a typical peridinioid plate pattern (Figs. 6, 8 & 10).

The thecal complex appears rugose and nodular to vermiculate, and although there are cytoplasmic trichocysts in the dinospore (Landsberg et al. unpubl.), there are no obvious external trichocyst pores even at ×34 196 (Fig. 12). The dinospore surface has numerous nodules of various sizes (Fig. 13), and the plate sutures are slightly raised (Figs. 1, 5 & 6). The sulcus is narrow distally and is about 3 times as wide proximally (Fig. 4). The widest part is excavated between the 1''' and 5''' plates. This excavation houses the peduncle and a rhizoid-like complex that appears to protrude from under the plate(s) in the right sulcal area (Figs. 6 & 14). The longitudinal flagellum is located below the peduncle (Fig. 14) and is 20 to 25 µm long (Fig. 15). It has a prominent longitudinal groove that separates 2 components (Fig. 16), of which 1 sometimes extends approximately 5 µm beyond the other (Fig. 15). The transverse flagellum is located in the cingulum, and fine hairs (Figs. 1, 4, 5 & 9) along its length attach it to the cell surface.

DISCUSSION

Based on their morphology, dinospores of *Amylo-odinium ocellatum* were described as naked gymno-dinioid types of dinoflagellate (Brown 1934, Nigrelli 1936, Lom 1981). Recently, the original description of the dinospore morphology of *A. ocellatum* has been questioned. Brown (1934) and Brown & Hovasse (1946) described the dinospore of *A. ocellatum* isolated from the Zoological Aquarium in London as being elongate and having the epicone smaller than the hypocone. Nigrelli (1936) reported *A. ocellatum* on marine fish in the New York Aquarium and described the dinospore as having an epicone that was slightly smaller than the hypocone. Brown (1934) and Brown & Hovasse (1946) reported the presence of a stigma in the hypocone, but Nigrelli (1936) described a stigma in the epicone. Dinospore measurements were 12.5 × 9.0 µm or 15.0 × 14.0 µm (Brown 1934) or 12.0 long × 8.0 µm wide (Nigrelli 1936). Lawler (1980) found that the shape of *A. ocellatum* dinospores isolated from the Gulf of Mexico differed from that of the earlier descriptions. Dinospores described in his paper were more antero-posteriorly flattened, had a red stigma in the hypocone, had an epicone shorter than the hypocone, had 1 flagellum with an undulating beat in a very distinct girdle, had a longer longitudinal flagellum, had a body 11.6 to 15.4 long × 10.4 to 14.5 µm wide, and could survive in a free-living stage for at least 15 d. Trophont
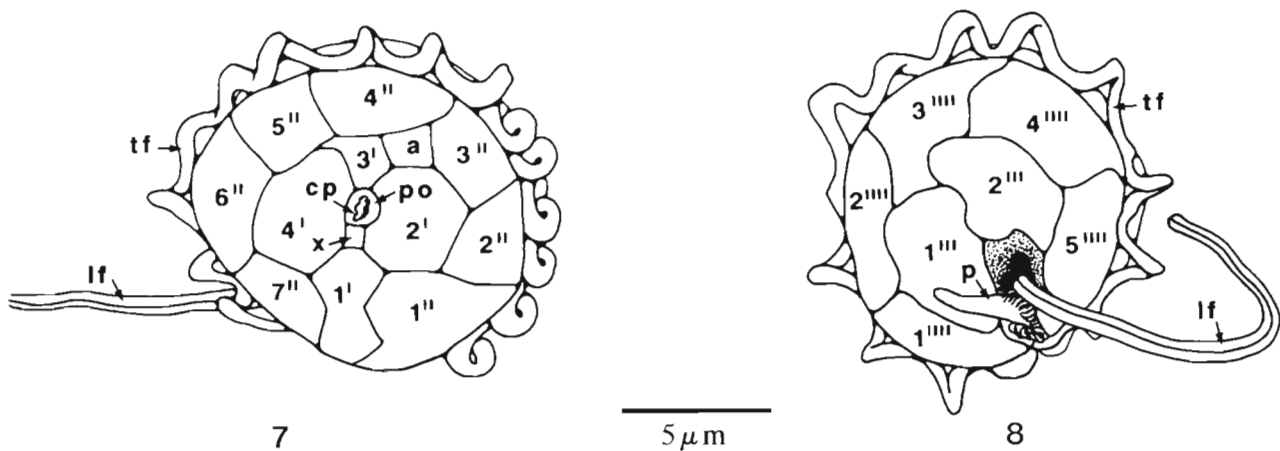
Figs. 1 to 6. *Amyloodinium* cf. *ocellatum*. Scanning electron microscope micrographs. Fig. 1. Hypothecal view of 2 dinospores showing longitudinal flagellum (lf), peduncle (p), sutures (s), and transverse flagellum (tf); × 3890. Fig. 2. 'Blown' dinospore with smooth surface; × 2190. Fig. 3. Poorly fixed dinospore with thick nodular surface and flagellum; × 8960. Fig. 4. Ventral view of dinospore showing displacement of cingulum (c), sulcus (su), longitudinal flagellum (lf), peduncle (p), transverse flagellum (tf) with attached hairs (h), epitheca (e), and hypotheca (hy); × 7760. Fig. 5. Epithecal view of dinospore showing 1st apical plate (1'), x plate (x), and postmedian horizontal suture (arrow); × 6580. Fig. 6. Hypothecal view of dinospore; × 5830

and tomont morphological characteristics were similar to those given in the original descriptions of *A. ocellatum*. Bower et al. (1987) also commented on the pronounced anteroposterior flattening of dinospores of the *A. ocellatum* (DC-1) strain isolated from clownfish (*Amphiprion ocellaris*), whereas the other life-cycle stages conformed to the original descriptions. Noga et al. (1991) mentioned apparent differences in the dinospore structure of *A. ocellatum* isolated from a natural outbreak of amyloodiniosis in hybrid striped bass in North Carolina, and they discussed the potential existence of different strains or species. In that report, dinospores were described as anteroposteriorly flattened and were 8.0 long × 13.8 μm wide. These recent descriptions seem to conform more closely to the dinospore structure discussed herein than to the original description.
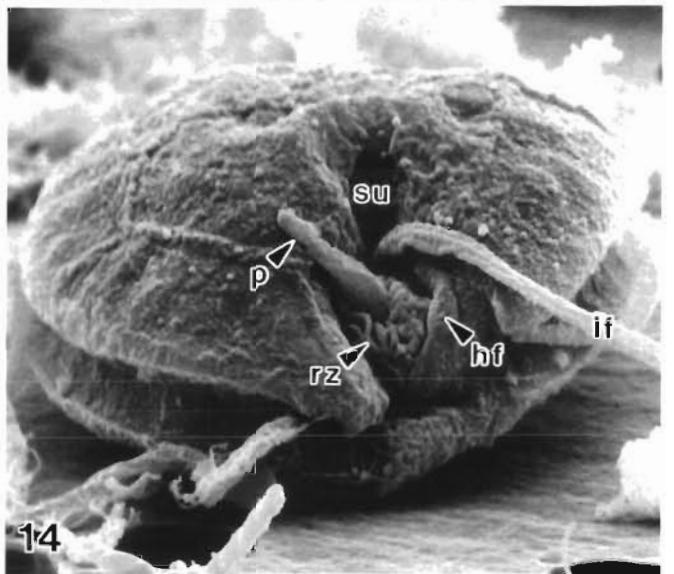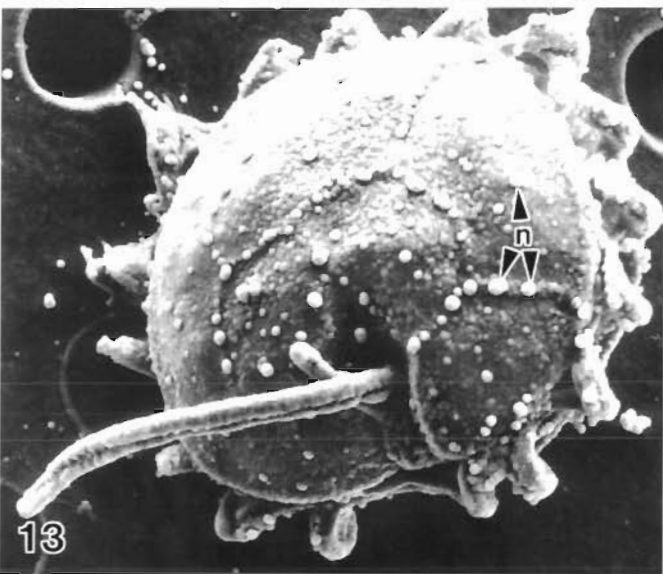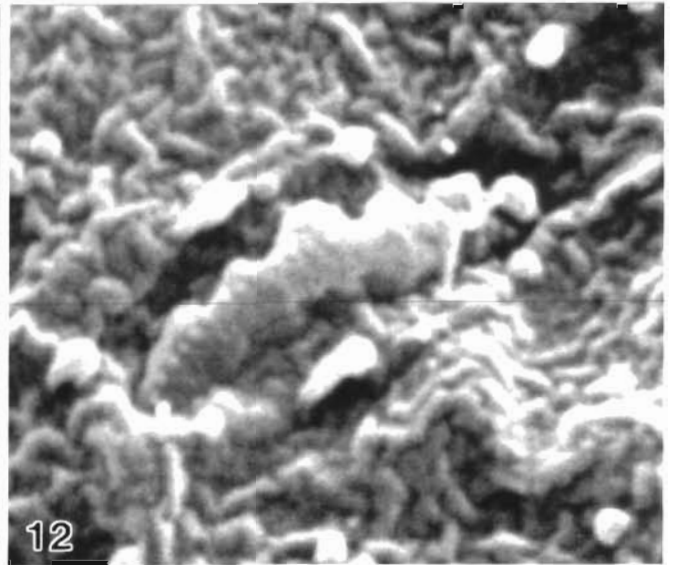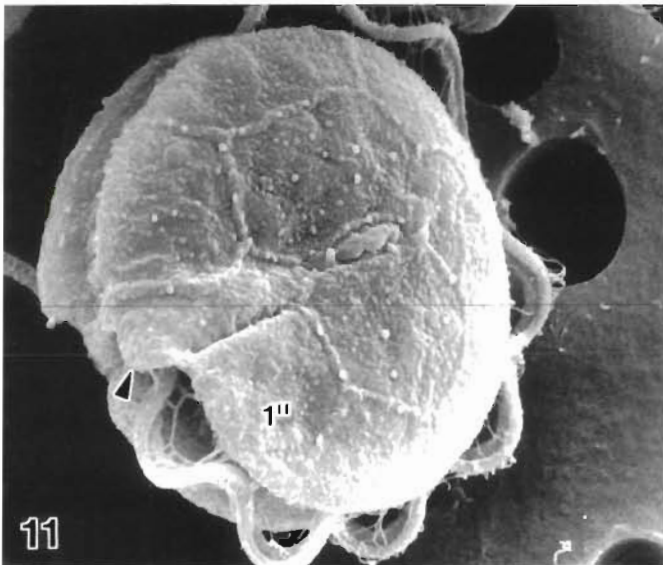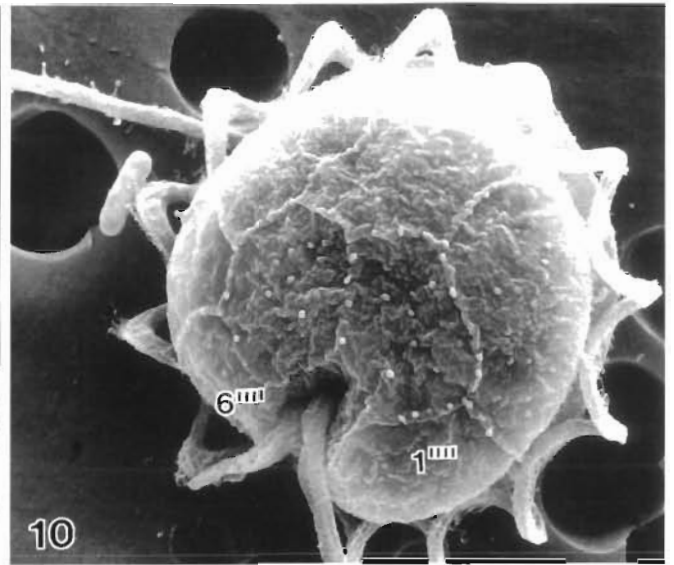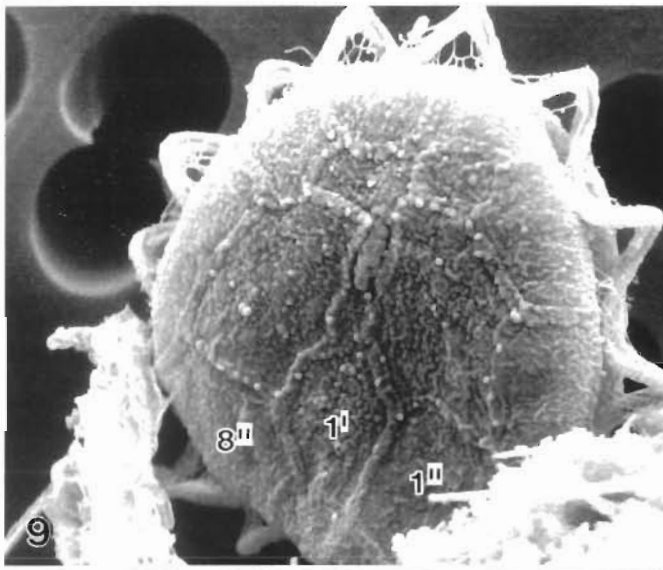
From the time of its original description using light microscopy until its recent description using electron microscopy, the structure of the dinospore of *A. ocellatum* had still not been confirmed. Cheung et al. (1981) published scanning electron micrographs of dinospores having a smooth surface and remarked on the poor quality of the pictures. We believe that poor fixation and preparation methods may have precluded the detection of the exact structure and that in fact, their

micrographs showed disrupted dinospores (Cheung et al. 1981) such as those in Fig. 2. The question of the relationship between *A. ocellatum* and *A.* cf. *ocellatum* remains. The original London Aquarium isolates of *A. ocellatum* were obtained from coral reef fish from Bermuda and the East Indies (Brown 1934). *A. ocellatum* from the New York Aquarium was found on fish from the East Indies as well as from 15 local host species of naturally infested fish from Sandy Hook Bay, New Jersey, USA. The *A. ocellatum* dinospores of Lawler (1980) and Bower et al. (1987) seem to be more closely related to *A.* cf. *ocellatum* than to the organism originally described as *A. ocellatum*. Type material of *A. ocellatum* is lacking. If specimens can again be obtained from Sandy Hook Bay, then the relationships of these variously reported species might be clarified.

The presence of a peduncle and an associated rhizoid-like complex in a motile dinospore stage is reported here for the first time. A stomopode and rhizoid complex are known in the trophont stage of some parasitic dinoflagellates (Lom & Lawler 1973). Rhizoids anchor the trophont to the host's epithelium, and the stomopode injects lytic substances into the prey (Lom & Lawler 1973). Presumably, the peduncle of *Amyloodinium* cf. *ocellatum* extends to form the stomopode after attachment. This can be seen by com-
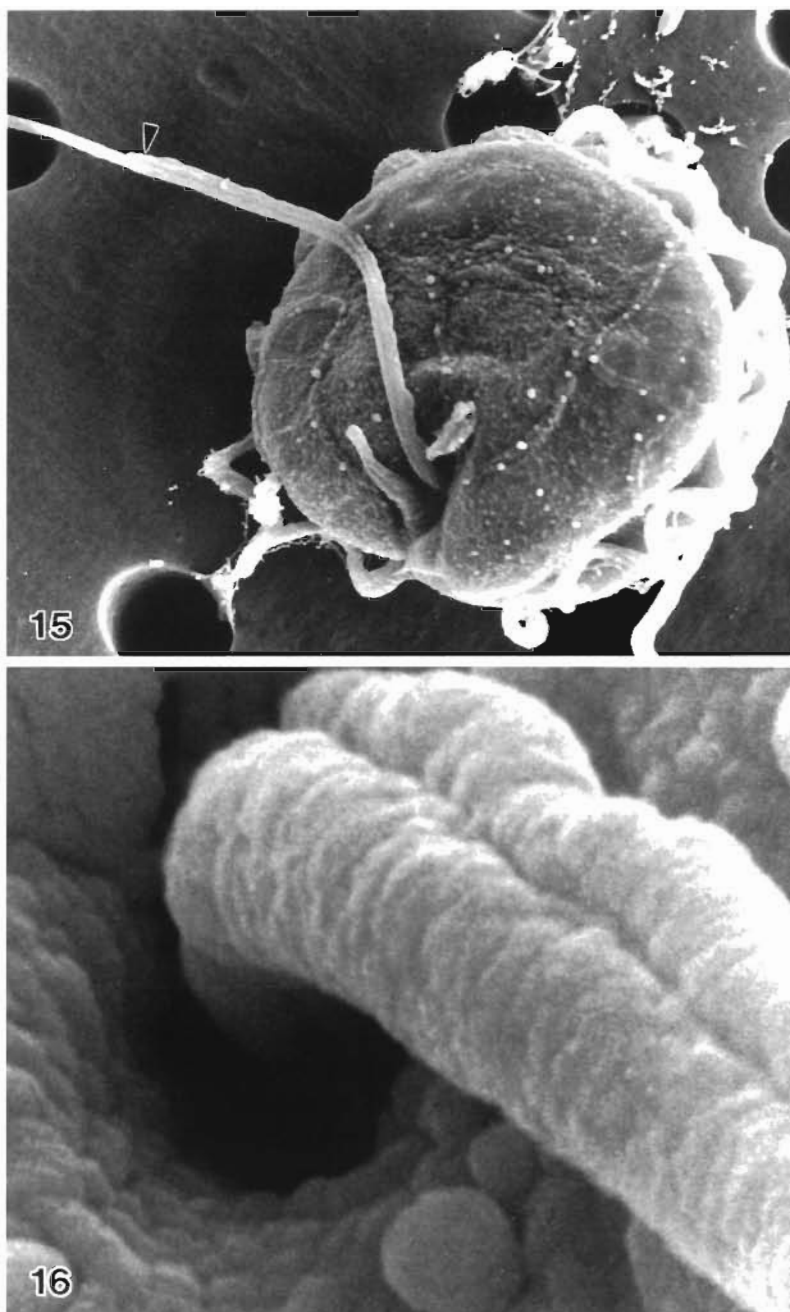

Figs. 7 & 8. *Amyloodinium* cf. *ocellatum*. Schematic drawings of micrographs of Figs. 5 & 6. Fig. 7. Epithecal plate tabulation showing apical pore (Po), closing plate (Cp), and canal plate (x), 1st to 4th apical plates (1' to 4'), anterior intercalary (a), 1st to 7th precingular plates (1" to 7"), transverse flagellum (tf), and longitudinal flagellum (lf). Fig. 8. Hypothecal plate tabulation showing 1st and 2nd antapical plates (1''', 2'''), 1st to 5th postcingular plates (1'''' to 5''''), peduncle (p), longitudinal flagellum (lf), and transverse flagellum (tf)

Figs. 9 to 14. *Amyloodinium* cf. *ocellatum*. Scanning electron microscope micrographs. Fig. 9. Variation of epithecal tabulation showing the 1st and 8th precingular plates (1" & 8") and 1st apical plate (1'); ×6600. Fig. 10. Variation of hypothecal tabulation showing the 1st and 6th postcingular plates (1"" & 6""); ×5550. Fig. 11. Epithecal/ventral view of dinospore showing extension of the 1st apical plate (arrow) beyond the cingular margin of the first precingular plate (1"); ×6270. Fig. 12. Apical pore complex showing ridged closing plate; ×34 200. Fig. 13. Dinospore surface with numerous, variably sized nodules (n); ×5730. Fig. 14. Hypothecal/ventral view showing peduncle (p), rhizoid-like (rz) complex, hood-like flange (hf), deep sulcal groove (su), and longitudinal flagellum (lf); ×8310

paring the transmission electron microscope (TEM) micrographs of the microtubular basket in both dinospores and trophonts (Landsberg et al. unpubl.) with those of the stomopode in *Amyloodinium* sp. trophonts (Lom & Lawler 1973). A peduncle is usually associated with heterotrophic or mixotrophic forms of nutrition in dinoflagellates, and the microtubular basket complex of phagotrophs is well documented (Schnepf & Elbrächter 1992). The grooved longitudinal flagellum (Figs. 15 & 16) of *A.* cf. *ocellatum* has not previously been recorded in parasitic dinoflagellates. The accessory portion may consist of a paraxial rod similar to the ventral flagellum of *Oxyrrhis marina* (Dodge & Crawford 1971) and to the longitudinal flagellum of some other dinoflagellates. For example, spiral packing material (or a paraxial rod equivalent) has been described from TEM micrographs in free-living *Amphidinium cryophilum* (Wilcox et al. 1982), *Ceratium tripos* (Maruyama 1982) and *Gymnodinium* sp. (Leadbeater & Dodge 1967). In addition, SEM micrographs of other dinoflagellates such as *Peridinium cinctum* f. *westii* (Berman & Roth 1979), *Gymnodinium splendens* (Herman & Sweeney 1977), *Gymnodinium* sp. (Roberts 1986) and *Symbiodinium* spp. (Trench & Blank 1987) seem to indicate grooved, 2-portioned longitudinal flagella.

Traditionally, the dinospore of parasitic dinoflagellates has been described as unarmored (naked) and as having gymnodinioid, gyrodinioid or cochlodinioid forms that are important for parasite classification (Chatton 1938). Some studies have questioned the need to use dinospore structure as a taxonomic criterion, since it is too plastic and unstable for classification (Cachon & Cachon 1987). We believe that char-

Figs. 15 & 16. *Amyloodinium* cf. *ocellatum*. Scanning electron microscope micrographs. Fig. 15. Hypothecal view of dinospore showing tapering longitudinal flagellum (arrow); ×5840. Fig. 16. High magnification of grooved structure of longitudinal flagellum; ×64 430

acterization of parasitic dinoflagellates from morphological study of the dinospore is critical. Only a few parasitic dinoflagellates having an armored dinospore have been identified, e.g. *Protoodinium poucheti* (Cachon & Cachon 1971a), but even in these, the plate tabulation and patterns have not been described. Ultrastructural studies of *Oodinium fritillariae*, *P. poucheti*, *O. dogieli* and *Amyloodinium* sp. trophonts have shown that there are thecal plates in the thecal vesicles (= periplast alveoli or amphiesmal vesicles) (Cachon & Cachon 1971b, Lom & Lawler 1973), which would indicate that plates should be detectable in the dinospore stage. Gonocytes of the endoparasite *Haplozoon axiothellae*, found in the polychaete *Axiothella rubrocincta*, also contain thin plates in thecal vesicles (Siebert & West 1974). TEM micrographs of the parasitic phagotroph *Paulsenella* sp. show diagonal sutures, yet these features were not discussed (Schnepf et al. 1985). Our preliminary studies suggest that the dinospore is an extremely useful stage for classificatory purposes. Dinospore and trophont morphology and ultrastructure should be used together to classify parasitic dinoflagellates. The acceptance of these classificatory criteria has very important taxonomic implications. By judging the morphology of these dinospores solely at the light level, it would be easy to incorrectly describe them as unarmored and related to the Gymnodiniales. However, improved ultrastructural fixation techniques for *Amyloodinium* cf. *ocellatum* revealed the presence of thin plates arranged in Kofoidian series and having a tabulation typical of the Peridiniales (Loeblich 1982). Further study of the cingular and sulcal areas for total number of plates and arrangement is necessary for this species to fully characterize the pattern and tabulation. Use of refined fixation techniques may show that plates in Kofoidian series could be more prevalent than previously thought in both parasitic and free-living dinoflagellates. Dinospores of other parasitic dinoflagellates should be scrutinized for similar diagnostic characters. The relationship and affinities of *A.* cf. *ocellatum* to other parasitic genera classified in the Blastodiniales, as well as to free-living genera classified in the Peridiniales, require further study. Differences in life cycles, trophic strategies and behavioral adaptations of these 2 orders currently determine placement into separate taxa (Loeblich 1982).

This type of evaluation is probably also applicable to some other small, free-living, and symbiotic 'gymnodinioid' dinoflagellates that have been previously classified as unarmored types. For example, *Gymnodinium estuariale* appears to have an apical pore complex typical of armored species (Gardiner et al. 1989), and motile cells of *Gyrodinium lebouriae* apparently have thecal plates (Lee 1977). In addition, the symbiotic

Symbiodinium spp. have thin thecal plates in vesicles (Trench & Blank 1987) and a definite plate tabulation has been described in *S. microadriaticum* (Loeblich & Sherley 1979), yet they are still classified in the Gymnodiniales (Trench & Blank 1987). Actually, *Symbiodinium* spp. seem to be transitional between unarmored and armored dinoflagellates in that they have an apical groove (= acrobase) rather than an APC (as in armored species), about 62 plates, and a 2-tiered plate series like some *Woloszynskia* spp. Further studies are needed to clarify the evolutionary relationships among free-living, symbiotic, and parasitic dinoflagellates and to allow characterization of their structure in relation to trophic adaptations.

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