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WIDESPREAD PHAGOCYTOSIS OF CILIATES AND OTHER PROTISTS BY MARINE MIXOTROPHIC AND HETEROTROPHIC THECATE DINOFLAGELLATES[1]

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ABSTRACT

*An electron microscopic examination of large amorphous inclusions located in a variety of photosynthetic thecate dinoflagellates (*Alexandrium ostenfeldii *(Paulsen) Balech et Tangen,* Gonyaulax diegensis *Kofoid,* Scrippsiella *sp.,* Ceratium longipes *(Bailey) Gran, and* Prorocentrum micans *Ehrenberg) and a nonphotosynthetic thecate species (*Amylax *sp.) revealed each inclusion to be a food vacuole, the majority of which were ingested ciliate prey. Recognizable features of these ciliates included linear arrays of basal bodies and cilia consistent with oligotrich polykinetid structure, characteristic macronuclei, chloroplasts (evidently kleptoplastids), cup-shaped starch plates, and cylindrical extrusomes. Three species contained (apparent) nonciliate prey:* Scrippsiella *sp., whose food vacuoles consistently contained unusual and complex extrusome-like cylindrical bodies having a distinctive six-lobed, multilayered structure;* P. micans, *which contained an unidentified encysted cell; and a single* A. ostenfeldii *cell, containing a* Dinophysis *sp. dinoflagellate cell. Several food vacuoles of ciliate origin had a red hue. This, together with the resemblance of* A. ostenfeldii *cells to planozygotes, suggests that similar structures previously identified as accumulation bodies may in fact be food vacuoles and that feeding may in some cases be associated with sexual processes.*

Key index words: Alexandrium ostenfeldii, Amylax *sp.*; Ceratium longipes; *ciliates; food vacuole ultrastructure*; Gonyaulax diegensis; *heterotrophic dinoflagellates; mixotrophy; phagocytosis*; Prorocentrum micans; *Pyrrophyta*; Scrippsiella *sp.*

Dinoflagellates are an important group of marine phytoplankton, best known for toxic red tides caused by a few photosynthetic species. The importance of phagotrophy is well known in the aplastidic (nonphotosynthetic) species that constitute approximately half of all known dinoflagellates. Among them, a remarkable variety of phagotrophic strategies are found (as reviewed by Schnepf and Elbrachter 1992). However, little is known of either the prevalance of phagotrophy (mixotrophy) among photosynthetic forms or their feeding mechanisms. Prior accounts of mixotrophy involve either athecate cells, which, having no thecal wall to act as a barrier to ingestion, can readily engulf prey (Biecheler 1952), or thecate species having either a large ventroposterior (sulcal) opening (as in *Ceratium*) through which intact prey organisms can pass (Bockstahler and Coats 1993) or a smaller cytostome through which food is "pumped" piecemeal by myzocytosis via a peduncle (as in *Dinophysis,* Jacobson and Andersen 1994). Because ingested prey items often resemble either large fatty storage inclusions or accumulation bodies or autophagic vesicles (i.e. the PAS bodies of Schmitter and Jurkiewicz 1981), it is only by transmission electron microscopy (TEM) or, in special cases, the use of silver staining techniques (Bockstahler and Coats 1993) that the identity of these prey can be determined. Here we present light and electron microscopic evidence for widespread phagotrophy in thecate dinoflagellates, including phototrophs not previously known to feed (*Alexandrium, Gonyaulax, Scrippsiella,* and *Prorocentrum,*), evidently using a novel feeding strategy. We also extend the record of phagotrophy in the genus *Ceratium* to *C. longipes* and describe the ultrastructural features (and, for some, the identity) of the ingested food. In addition to these mixotrophs, we have observed phagotrophy in an aplastidic species of *Amylax,* a genus related to *Gonyaulax,* and in *Gonyaulax alaskensis* (also aplastidic, to be reported elsewhere). Mixotrophy is clearly far more common in dinoflagellates, especially among thecate forms, than previously recognized.

MATERIALS AND METHODS

The following species were isolated simultaneously from dockside surface plankton tows in West Boothbay Harbor, Maine, taken in June 1993: *Alexandrium ostenfeldii* (Paulsen) Balech et Tangen, *Amylax* sp. (resembling *A. longicornu* of Campbell 1973), *Ceratium longipes* (Bailey) Gran, *Gonyaulax diegensis* Kofoid, *Gonyaulax grindlyi* Reinecke, and *Scrippsiella* sp. *Prorocentrum micans* Ehrenberg was collected in 1992 from the same locality. *Alexandrium ostenfeldii* was identified on the basis of its large size (39–50 μm) and distinctive tabulation, including a very large ventral pore, whereas *G. diegensis* was distinguished by its characteristic thecal texture (visible only in squashed, disarticulated thecae) and cell shape. An *Alexandrium* sp. and *Gonyaulax* cf. *spinifera* Claparede & Lachmann were found in Eel Pond, Woods Hole, Massachusetts. Cells that had been concentrated with a 20-μm Nitex sieve were transferred via micropipette from a settling slide on

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a Ziess inverted compound microscope to the fixation mixture (2% glutaraldehyde in 0.1 M cacodylate buffer) in depression wells. After 30 min at 20° C, the selected cells were mounted as juxtaposed clusters of five or six cells within small drops of 1.5% agarose, cut into small blocks, and postfixed in 1% OsO_4. After ethanol dehydration and infiltration with Spurr's resin, the agar blocks were transferred to and properly oriented in a clear silicon rubber mold and heat-cured. Serial sections were cut on a Reichert ultramicrotome using a Diatome diamond knife, contrasted with uranyl acetate and lead citrate stains, and examined with either a Zeiss 902A or Zeiss 10CA transmission electron microscope. Five or six cells of known identity were examined on the same section. Light micrographs were taken with differential interference microscopy on an Olympus microscope (40× objective).

RESULTS AND DISCUSSION

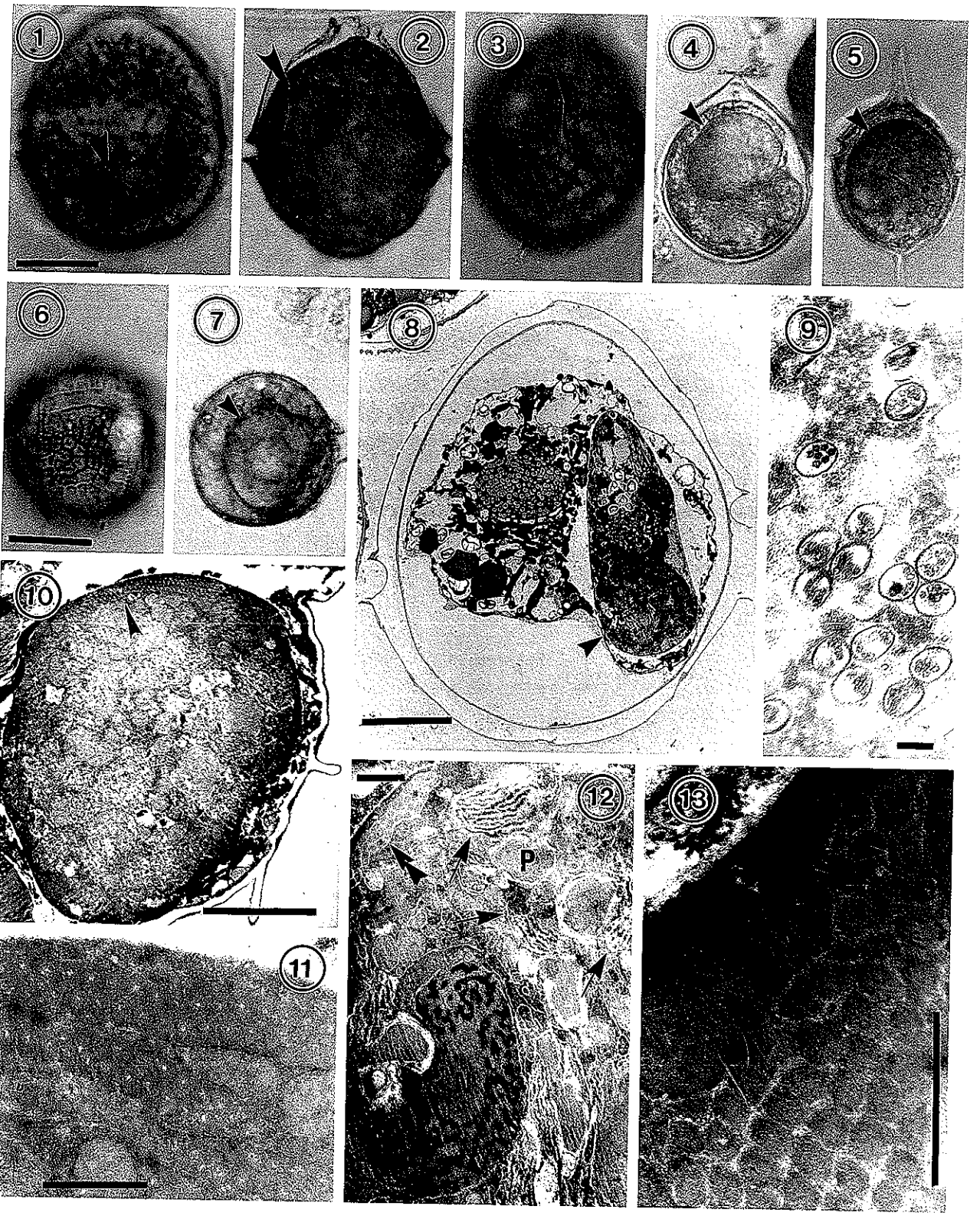
Food vacuoles found in these thecate dinoflagellates numbered from one to three per cell and ranged in size from 8 to 35 μm, representing from 20 to 82% of the predator diameter. These vacuoles fell into three main categories according to their light microscopic appearance. The first category was characterized by amorphous, moderately refractile rounded bodies (often irregularly shaped) that lacked internal structure visible with differential interference contrast (DIC) optics (Figs. 1, 2). While these inclusions often appeared pigmented within the confines of a plastidic cell, they usually appeared colorless when isolated from a crushed cell. The second category of food vacuoles, exemplified by all those found within *Scrippsiella* sp., were rounded, had a pale green hue, and contained inconspicuous linear striations (which proved to be extrusome-like organelles) visible with DIC microscopy (Fig. 4). Several food vacuoles did not conform to these two categories, including the following: 1) elongate, wedge-shaped inclusions found in two cells of *A. ostenfeldii,* 2) a uniformly rounded inclusion containing a refractile central spot in *Prorocentrum micans,* and 3) three red vacuoles encountered in *Ceratium longipes, Amylax* sp. (Fig. 5), and an *Alexandrium* sp. (see later). Two species with colorless food vacuoles have not yet been examined with TEM: *Gonyaulax grindleyi* (Figs. 6, 7) and *Gonyaulax spinifera* (not shown).

The ultrastructure of all category 1 food vacuoles identifies them as the remains of ciliates. The number of cells (n) for each species examined by TEM is given later. Ciliates were observed in *Alexandrium ostenfeldii* (n = 7) (Figs. 10–16) and *Gonyaulax diegensis* (n = 2) (Figs. 21–23). Ciliate remains within the *A. ostenfeldii* and *G. diegensis* vacuoles usually lacked intact cilia but contained highly ordered double rows of basal bodies that appeared as juxtaposed electron-dense, amorphous round bodies, each with a small electron-lucent core (Fig. 11; see also Figs. 22, 23). In one cell, intact cilia exhibited barely discernible axonemal microtubules (Fig. 13). Ciliary or basal body remnants also appeared as homogeneously electron-dense cylinders, as in *Amylax* sp. (Figs. 19, 20) or *C. longipes* (Fig. 24). These partially degraded basal body arrays were often located in a single peripheral region of a given food vacuole and may represent the oral polykineties of an oligotrich ciliate (i.e. *Strombidium*). Co-occurring with these polykineties were nuclei having a bold heterochromatin pattern resembling that of ciliate macronuclei (Fig. 12) as well as cylindrical extrusome-like organelles (Figs. 14, 15) and chloroplasts and associated pyrenoids (Fig. 12). Electron-lucent inclusions were also present, having either a round form with membrane-like invaginations in *A. ostenfeldii* and *C. longipes* (Figs. 16, 17) or the distinctive cap shape of starch plates in *Amylax* sp. (Figs. 18, 19). Both the cylindrical extrusome-like structures and starch plates resembled those routinely observed in *Dinophysis acuminata* food vacuoles, which, though they lacked kineties, were thought to be derived from ciliate prey (Jacobson and Andersen 1994).

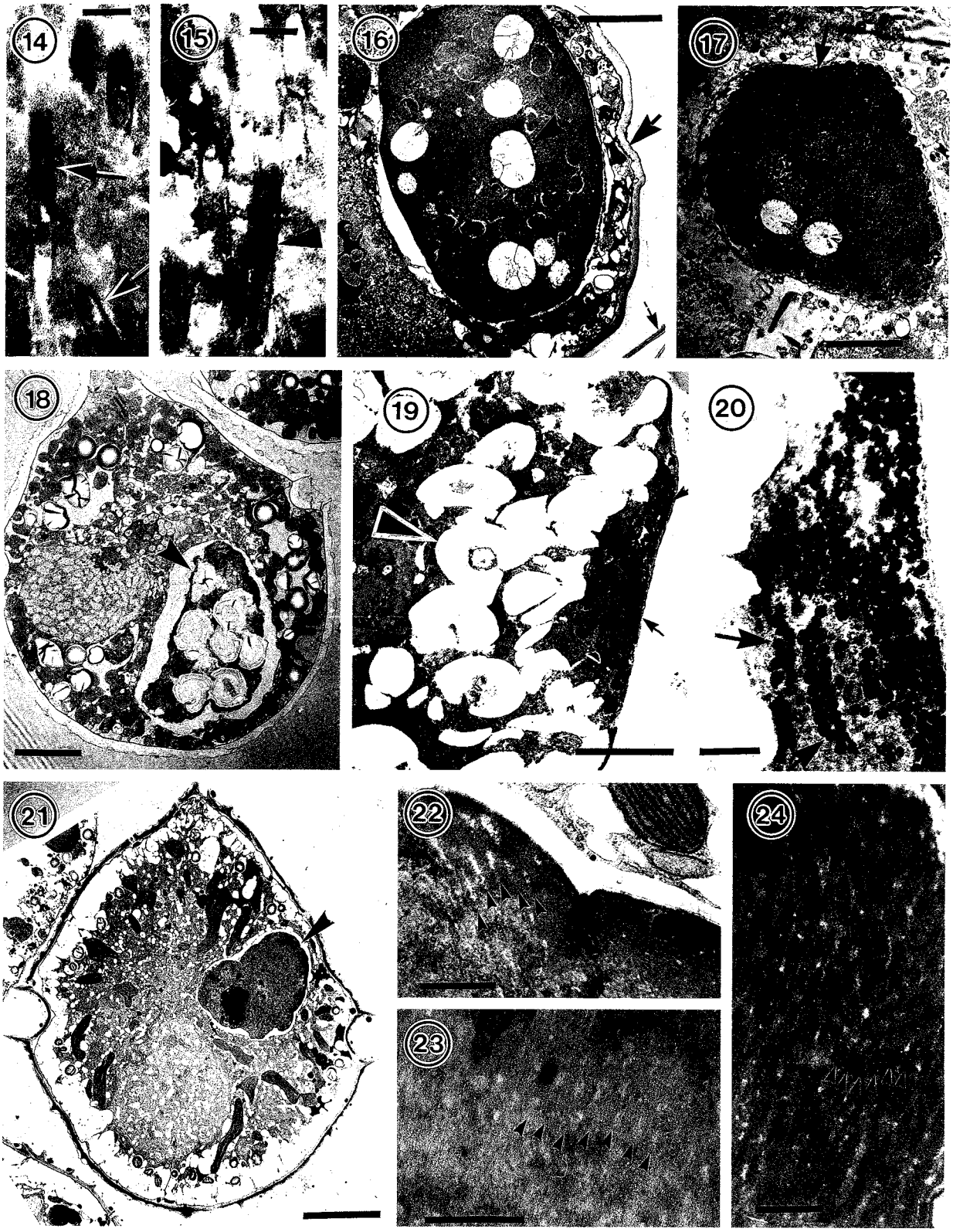
Interestingly, all *A. ostenfeldii* cells examined had an inner cyst-like wall (ranging in thickness from 160 to 715 nm) (Figs. 8, 16). Such a thick cyst-like wall was absent in all other species except *Scrippsiella* sp., which had a thinner 110-nm wall. The *Scrippsiella* sp. cells co-occurred with two types of *Scrippsiella* zygotic cysts, still suspended in surface water. This suggests that *A. ostenfeldii* and *Scrippsiella* sp. cells containing food vacuoles were in the process of encystment (to be discussed further later).

The second category of food vacuoles was found in two species, *Scrippsiella* sp. (n = 5) (Figs. 25–27) and a nonphotosynthetic species, *Gonyaulax alaskensis* (n = 5) (Fig. 28). These 10 cells were all found to have similar and highly distinctive food vacuole contents dominated by 7–8-μm cylindrical organelles. These extrusome-like structures were 400 nm in diameter and had a distinct six- to eight-lobed cross-sectional shape (Figs. 27, 28). Details of cross-sectioned extrusome varied, having either a sandwiched, laminar ultrastructure (Fig. 27) or a multilayered, concentric structure with a cusp-like central protrusion (Fig. 28). These distinctive structures occurred either alone (Fig. 25) or together with a flat, disc-shaped plate or scale-like structures and hollow cylindrical scales (Fig. 26). The identity of these 10 food inclusions is yet unknown, despite such elaborate internal structures. However, one plastid, perhaps a kleptochloroplast, was found (Fig. 26). Because ciliates appear to be the most numerous kleptoplastidic marine protist, these enigmatic inclusions should be scrutinized further for the presence of basal bodies or nuclei. The degree of prey selectivity revealed by these food inclusions was striking: all five *Scrippsiella* sp. cells and all but one of six *G. alaskensis* cells contained matching food vacuoles. *Gonyaulax alaskensis* collected elsewhere contained food vacuoles of a very different sort (unpubl. observ.).

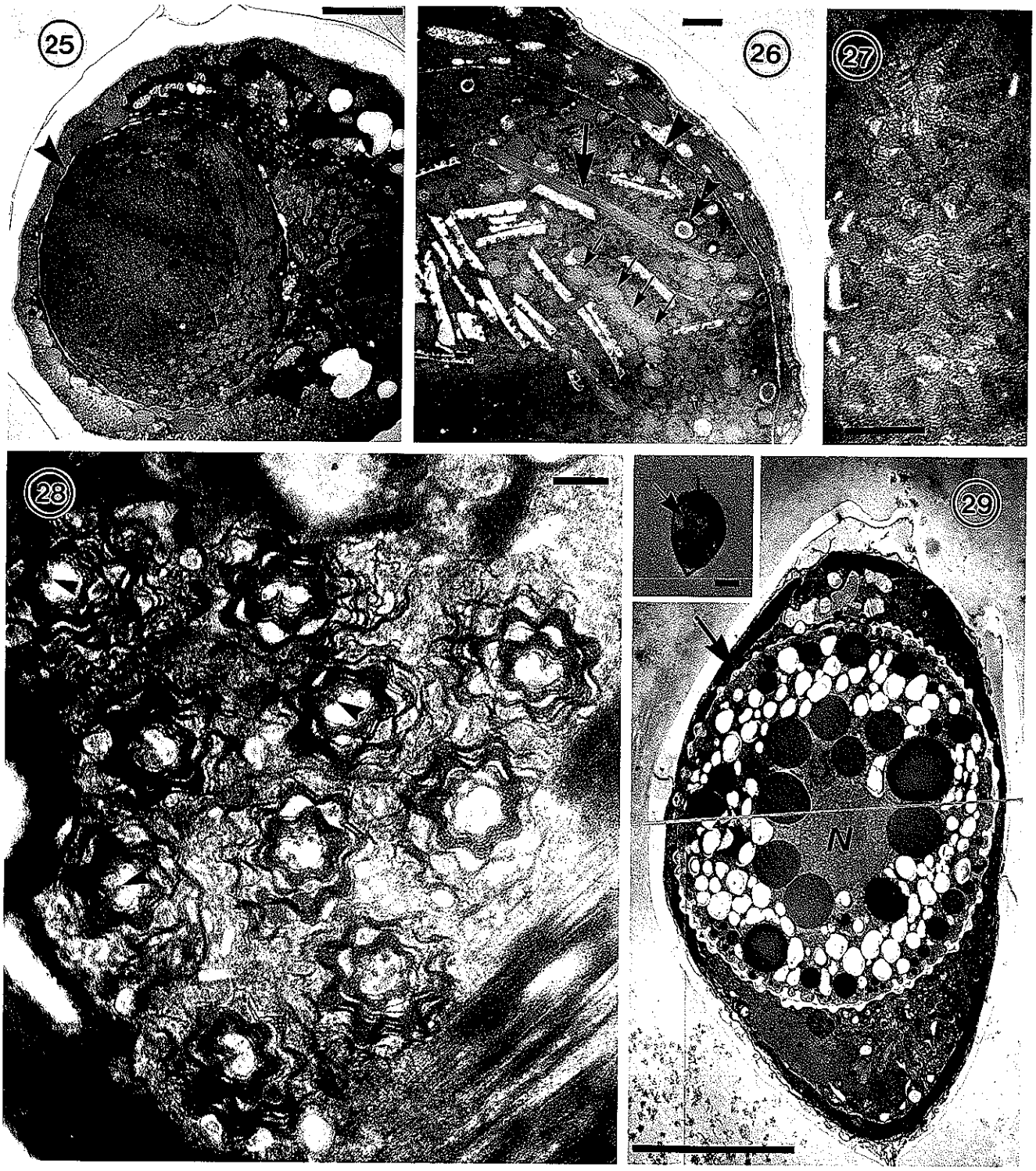
In addition to the two preceding classes of food vacuoles, several *Prorocentrum micans* cells from a *P.*



NOTE: Scale bar = 1 μm unless otherwise indicated. FIGS. 1–13. Phagotrophy in thecate dinoflagellates. FIGS. 1–7. Dissolved inorganic carbon light micrographs of cells containing food vacuoles (arrowheads). Scale bars = 20 μm. FIG. 1. *Alexandrium ostenfieldii*. FIGS. 2, 3. Two focal planes of *Gonyaulax* cf. *diegensis*. FIG. 4. *Scrippsiella* sp. FIG. 5. *Amylax* sp. (cf. *A. longicornu*) with an unusually large food vacuole. FIG. 6. *Gonyaulax grindleyi* with distinctive thecal ornamentation. FIG. 7. *Gonyaulax grindleyi*. FIGS. 8–13. Transmission electron micrographs. FIG. 8. *A. ostenfieldii* containing *Dinophysis* in food vacuole (arrowhead). Scale bar = 10 μm. FIG. 9. Detail of rhabdosomes within *Dinophysis*. Scale bar = 0.2 μm. FIG. 10. Food vacuole (ciliate) within *A. ostenfieldii* (note linear kinety array on the upper margin of large inclusion, arrowhead). Scale bar = 5 μm. FIG. 11. Detail of linear kinety arrays in food vacuole shown in Figure 10. FIG. 12. Ciliate nucleus (N), cilia (double arrowhead) and plastids (arrows), and pyrenoids (P) within *A.* cf. *ostenfieldii* food vacuole. FIG. 13. Details of cilia (same cell as in previous figure) some of which contain intact axonemal microtubules (arrows).



FIGS. 14–24. Category 1 food vacuoles with the exception of Figs. 17 and 24. FIGS. 14, 15. Extrusome-like inclusions (arrows) in *A. ostenfeldii* food vacuole shown in Figure 10. Scale bar = 0.2 μm. FIG. 16. *A. ostenfeldii* cell with cyst-like wall (arrow) and outer theca (small arrow) containing food vacuole containing characteristic starch plates or vacuoles (arrowhead) (cf. Fig. 17). Scale bar = 5 μm. FIG. 17. *Ceratium longipes* red pigmented food vacuole (arrow) with abundant cilia and vacuoles (arrowhead) (see Fig. 24 for anterior detail). Scale bar = 5 μm. FIGS. 18–20. *Amylax* cf. *longicornu*. FIG. 18. Whole cell containing food vacuole with compound starch plates (arrowhead). Scale bar = 5 μm. FIG. 19. Food vacuole containing starch plates (arrowhead) and electron-dense basal bodies (arrows). Scale bar = 5 μm. FIG. 20. Detail of basal bodies (arrow) of Figure 19. FIGS. 21–23. *Gonyaulax diegensis*. FIG. 21. Whole cell containing food vacuole (arrow). Scale bar = 5 μm. FIGS. 22, 23. Details of food vauole of Figure 21, showing basal bodies (arrowheads). FIG. 24. Detail of cilia (arrowheads) of Figure 17 in *Ceratium longipes*.



FIGS. 25–29. Food vacuoles in *Scrippsiella* and *Prorocentrum*. FIG. 25. *Scrippsiella* sp. food vacuole (arrowhead) with six-lobed cylindrical inclusions (arrows). Scale bar = 5 μm. FIG. 26. *Scrippsiella* sp. food vacuole (arrowhead) containing disc-shaped, cylindrical plates (double arrowheads) and extrasome-like bodies in cross-section (small arrows) and in longitudinal section (large arrow). FIG. 27. Detail of three six-lobed cylindrical bodies, identical to those found also in *Gonyaulax alaskensis*. Scale bar = 0.2 μm. FIG. 28. Cluster of six-lobed bodies in *Gonyaulax alaskensis* (interspersed with scales or plates like those in Fig. 26). Note inward cusps (arrowhead). Scale bar = 0.2 μm. FIG. 29. *Prorocentrum micans* with large food vacuole containing central nucleus (N). Inset: Light micrograph of different cell containing food vacuole (arrow). Scale bars = 10 μm.

micans bloom in West Boothbay Harbor in 1992 contained refractile circular inclusions having a nonrefractile central spot. One of these cells contained a nonphotosynthetic cell bounded by an ornamented cyst-like wall containing abundant starch-like grains and lipid-like storage bodies (Fig. 29). The central nucleus was amorphous, devoid of heterochromatin. The identity of this protistan inclusion is unclear, and the possibility that it is an encysted intracellular parasite (similar to those documented by Canter-Lund and Lund (1995) in a freshwater *Ceratium*) cannot be entirely ruled out because the cyst cytoplasm was not degraded. However, *P. micans* possesses a microtubular basket typical of an ingestion apparatus (Schnepf and Winter 1990), and one of us has directly observed phagotrophic behavior in this species (D.M.J., unpubl. observ.).

Two cells (both *Alexandrium ostenfeldii*) contained atypical, elongate food vacuoles, one of which was sectioned. The food vacuole was a dinoflagellate of the genus *Dinophysis*, identifiable by virtue of its characteristic wedge shape, mesokaryotic nucleus, and abundant rhabdosomes (Vesk and Lucas 1986) (Fig. 8). The *Dinophysis* cell also contained chloroplasts and a spherical food vacuole-like structure. Cross-sections of these rhabdosomes showed five to seven fiber profiles (Fig. 9), compared to eight fiber profiles found in *D. acuminata* and *D. norvegica* (unpubl. observ.). The theca of the prey dinoflagellate was missing, having been either removed or digested. Because this food vacuole maintained its normal shape, the *Dinophysis* cell had probably been ingested as a thecate cell. This therefore appears to represent the first case of the ingestion of a toxic dinoflagellate by another toxic dinoflagellate (Hansen et al. 1992).

Our identification of red food vacuoles in *C. longipes* and *Amylax* sp. suggests an alternative interpretation of red bodies routinely found within planozygotes of various dinoflagellates (Dale 1983). In addition, we have earlier seen very large, food vacuole-like red inclusions in *Alexandrium* sp. having a yellow autofluorescence like that seen in smaller "PAS bodies" in *Gonyaulax polyedra* (Schmitter and Jurkiewicz 1981). While we have not yet conclusively demonstrated the presence of red food vacuoles in planozyogotes, all *A. ostenfeldii* cells containing food vacuoles had an elongate cell form (Fig. 1) characteristic of *Alexandrium* planozygotes as well as a cyst-like wall, suggesting that these mixotrophic cells were preparing to encyst. We hypothesize that some of the smaller red bodies may be the digested remains of ingested ciliates or other prey. In theory it would be advantageous for a zygote to augment its nitrogen or phosphate (etc.) storage prior to encystment and dormancy, especially because sexuality is often triggered by nitrogen or phosphate limitation (Pfeister and Anderson 1984).

Phagotrophy in the context of the entire dinoflagellate community appears to be important: of the 20 most abundant dinoflagellate species found in a plankton tow from West Boothbay Harbor in early June 1993, only 9 were photosynthetic, and of these 9 only 2, *Heterocapsa triquetra* and *Amylax triacantha*, completely lacked food vacuoles. However, phagotrophy among mixotrophs may be temporally patchy. For example, a period of 2 weeks' duration beginning in early June, when food vacuole-containing cells of *A. ostenfeldii* were abundant (12%, $n = 50$), was followed by several weeks during which no food vacuoles could be detected even though *A. ostenfeldii* continued to be abundant. Eventually, a single food-containing *A. ostenfeldii* cell (Fig. 1) was found in early July. This pattern was duplicated by *Scrippsiella* sp., whose food-inclusion rate had reached 8% ($n = 187$) in mid-June but was followed by an absence of food vacuoles. Clearly, these apparent episodic patterns of phagotrophy deserve further investigation.

Most phagotrophic dinoflagellates ingest food through their sulcal region. Until now, fully thecate phagotrophic dinoflagellates lacking the large sulcal apertures found in the genus *Ceratium* were known only to utilize special feeding pseudopodia, which emerge from a small sulcal pore. These pseudopodia take either the form of a narrow sucking tube called a peduncle, which is used to ingest prey cytoplasm in small discrete packets (i.e. *Dinophysis*, Hansen 1991) or of a widely spreading, enveloping pseudopodium called a pallium, which can surround and digest large armored prey such as diatoms (i.e. *Protoperidinium*, Jacobson and Anderson 1986). Neither of these two mechanisms results in the ingestion of intact organisms. To these two unique thecate feeding strategies, we therefore add a third strategy, the ingestion of large, whole prey by peridinioids, gonyaulocoids, and prorocentroids. While the mechanism of this mode of phagocytosis has not been observed, it must involve one of three mechanisms: selected plates (probably in the sulcal region) are "hinged" and open (this has been seen during sexual fusion of *Ceratium cornutum* gametes, Pfeister and Anderson 1984), sulcal plates are selectively dissolved to form a temporary cytostome, or the cell undergoes ecdysis (complete shedding of the theca) prior to the actual ingestion of prey. Indeed, ecdysis is a conspicuous feature in *A. ostenfeldii, G. diegensis, G. alaskensis*, and *Amylax* sp., although ecdysis as a consequence of physical disturbance or sudden changes in the environment cannot be equated with "unprovoked" ecdysis. When one reflects on the elaborate feeding strategies employed (evidently) to accommodate the thecal barrier without sacrifice of the theca, an ecdysis-based feeding strategy is strikingly straightforward and comparatively wasteful. It may also increase the vulnerability of the feeding cell to predation and parasitism. However, loss of the theca during feeding is yet to be directly documented.

Our observations show that ciliates are ingested by diverse gonyaulacoid dinoflagellates, adding to the early reports by Biecheler (1952) and the recent reports of *Oxyphysis oxytoxoides* (Inoue et al. 1987)

and of gymnodinioid and ceratioid dinoflagellates (Bockstahler and Coats 1993). Certain constituents of the ciliate food vacuoles, including cylindrical extrusome-like organelles in *A. ostenfeldii* and abundant starch plates in *Amylax* sp., resemble those found within the food vacuoles of mixotrophic *Dinophysis* species (Jacobson and Andersen 1994), suggesting that diverse dinoflagellates may be preying on a common pool of ciliates.

Until recently, the armored or thecate photosynthetic dinoflagellates were considered obligate autotrophs, with the exception of species of *Ceratium,* with its apparent sulcal modification for phagotrophy (Dodge and Crawford 1970, Bockstahler and Coats 1993), and of mixotrophic *Dinophysis* spp. (Jacobson and Andersen 1994). Our observations of the ingestion of large particles by representatives of three additional thecate lineages (gonyaulacoid, peridinioid, and prorocentroid) demonstrates that mixotrophy in this group is far more common than previously thought. While it is possible that some plastidic dinoflagellates exist that never ingest particulate food, our data add weight to the notion that dinoflagellates are fundamentally and overwhelmingly a phagotrophic lineage.

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