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THECATE HETEROTROPHIC DINOFLAGELLATES: FEEDING BEHAVIOR AND MECHANISMS[1]

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ABSTRACT

*The feeding of 18 species of thecate heterotrophic dinoflagellates from three genera (*Protoperidinium, Oblea, Zygabikodinium*) can all be described within one general framework. These species engulf diatoms and other prey with a pseudopod (herein termed a "pallium") which originates at the flagellar pore in the sulcus. The pallium is a highly plastic, membranous organ which easily stretches to accommodate spines and other protrusions, and has been observed to enclose as many as 58 diatom cells in a chain. The contents of the phytoplankton prey are liquified and transported through the pallium typically within 7 to 30 minutes of capture (although feeding may last 2 h) leaving an intact but empty cell wall or frustule. Thus far, with few exceptions,* Protoperidinium *species have been observed feeding only on diatoms, whereas two diplopsaloid species feed on dinoflagellates and prasinophytes as well. In four species from the three genera studied, a capture filament has been observed that connects the food to the dinoflagellate prior to extension of the pallium, sometimes allowing the cell to pull the food while swimming. A distinctive precapture swimming behavior is also described for six species, suggesting that the dinoflagellates are selective grazers.*

Key index words: heterotrophic dinoflagellates; microzooplankton grazing; pallium; Protoperidinium; *pseudopod feeding, diatoms*

Thecate heterotrophic dinoflagellates equipped with a rigid cell wall or theca have long been an enigma in the planktonic community. They are widely abundant and have attracted much study, but their feeding mechanisms, preferences, and rates remain a mystery. Holozoic dinoflagellates which lack a cellulose theca are regularly observed to contain phagocytosed food particles, but the thecate species show no evidence of food ingestion. One exception is an account by Bursa (1961) of a *Protoperidinium* ingesting a flagellate, which is reinterpreted below. The most likely food uptake orifice through the theca—the flagellar pore—is too small for the passage of any particle larger than a bacterium (Abé 1981). Other feeding strategies that have been considered are uptake of dissolved materials (osmotrophy) or uptake of decaying organic matter (saprotrophy). Osmotrophy seems unlikely since surface-to-volume ratios suggest that it would be difficult for an organism as large as a dinoflagellate to compete with bacteria for dissolved organic carbon in the sea (Morey-Gaines and Elbrächter 1986). The recent report of the feeding behavior of two *Protoperidinium* species by Gaines and Taylor (1984) did much to resolve the mystery as they described a large "feeding veil" that the dinoflagellates deployed to completely envelop relatively large diatoms whose cell contents were then dissolved. The veil was deployed over a large area, only a portion of which was occupied by the diatom food. The work reported here, based on observations of 18 species from three genera, demonstrates that feeding is far more selective than the "feeding veil" description would suggest.

MATERIALS AND METHODS

Organisms were captured with net tows from Perch Pond or Vineyard Sound, Massachusetts (average salinities 26 and 32‰, respectively). The <80 μm plankton fraction was incubated at 15° C for 2 to 16 hours, with added diatoms, in 15 mL polypropylene centrifuge tubes mounted on a slowly rotating apparatus. When the ratio of thecate heterotrophic dinoflagellates to detritus was too low, desired cells were transferred via micropipette to filtered seawater, with cultured diatoms or natural phytoplankton assemblages added. Such short term "cultures" typically yielded 0–5% feeding dinoflagellates at a given time. Feeding cells were either monitored with a Nikon dissecting microscope or transferred to wet mounts for observation with the phase and Nomarski optics of a standard Zeiss compound microscope. For ease of relocation, 6 mm coverslips, supported by small lumps of modeling clay, were used. Nomarski optics simplified analysis of thecal plate arrangements needed for taxonomic assignment, but two species (*Protoperidinium* species A and B) could not be identified and may constitute new species. Cells with deployed pseudopodia had to be manipulated gently as they readily aborted feeding by retracting or detaching their pseudopod when disturbed. Use of 2 mL settling slides with a Zeiss inverted compound microscope allowed direct observations to be made on samples at high magnifications without the need for further isolation. Feeding durations were determined either by continuous surveillance of an undisturbed cell held in a 15 mL petri dish or by transferring cells seen to have recently captured food (i.e. those with long attachment filaments) to microwell plates so that several individuals could be monitored simultaneously. Swimming velocities and trajectories were determined from videotaped recordings by tracing from the video monitor. Bouin's fixative was used to preserve the pseudopod apparatus intact. For documentation, a Nikon photomicrography system, a JVC S-100CH color camera with a Panasonic ½ inch VCR and an MTI black and white video camera with a Panasonic ¾ inch VCR were employed. For preliminary transmission electron microscopy, single isolated cells were added to a mixture of 2% cacodylate-buffered glutaraldehyde and 1% osmium tetroxide at 0° C for 30 min, washed in seawater, embedded in 1% agar and passed through dehydration and Epon-Araldite infiltration series. Cells were ultimately flat-embedded and then

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excised and reoriented on a resin stub for microtomy. Thin sections were stained with uranyl acetate and lead citrate.

RESULTS

To date, 18 species of thecate heterotrophic dinoflagellates have been observed to employ a pseudopodal mechanism to feed on living particulate food. With the exception of *Protoperidinium pyriforme* and possibly *Protoperidinium* species B (an organism resembling a colorless *Scrippsiella*), the food consumed by *Protoperidinium* species consists exclusively of diatoms, whereas two diplopsaloid species fed on diatoms, dinoflagellates and prasinophytes (Table 1). While hundreds of dinoflagellates have been seen feeding on intact phytoplankters, several cells of *Oblea rotunda* and *Zygabikodinium lenticulatum* have also been seen to capture and envelop small transparent detrital particles. Several bacteria were seen on one such particle stained with DAPI. The list of acceptable food species varies according to the number of observations made on the various dinoflagellates. In many instances, the dinoflagellates consumed prey much larger than themselves. This typically involved consumption of diatom chains but, on occasion, large cells (e.g. *Coscinodiscus*) were enveloped and digested individually. Spines on bristly food species such as *Chaetoceros* presented no obstacle to the enveloping pseudopod. No diel variation in feeding has yet been detected; most observations were made during the organisms' light phase.

Feeding behavior in the species observed follows a consistent pattern marked by distinctive precapture, capture, pseudopod deployment, digestion, and pseudopod retraction phases.

Precapture

Precapture behavior has been observed in six species (*Oblea rotunda, Zygabikodinium lenticulatum, Protoperidinium spinulosum, Protoperidinium punctulatum, Protoperidinium conicum* and *Protoperidinium claudicans*). Other species may also have this same behavior but the likelihood of witnessing the initial moments of feeding events (which seem to occur infrequently) is extremely small. Most cells swim in a relatively straight course, occasionally changing direction, but passing by diatoms that are close to the swimming path without outwardly indicating recognition or attraction. However, a cell is sometimes seen that, when it encounters a diatom, swims in tight circles about the prey for usually one minute or less, occasionally up to 2 min. The path of *P. spinulosum* around a chain of *Chaetoceros* traced from a video recording illustrates this behavior (Fig. 1A–

TABLE 1. *Predator/prey relationships in thecate heterotrophic dinoflagellates.*

Predator species	Size[a]	Food speecies	Size[a]	Type[b]
Oblea rotunda	30	*Pyramimonas* sp. (13-10)	10	pras
		Micromonas sp. (DW8)	8	pras
		Heterocapsa triquetra	30	dino
		Prorocentrum minimum	25	dino
		Dinophysis acuminata	40	dino
		Gonyaulax tricantha	35	dino
		Protoperidinium pellucidum	45	dino
		Oblea rotunda	30	dino
		Nitzchia closterium	30	s.d.
		Amphiprora sp.	120	s.d.
		Ditylum brightwellii	80	s.d.
		Leptocylindrus danicus		c.d.
		Eucampia zoodiacus		c.d.
		colorless detrital particle	50	
Zygabikodinium lenticulatum	50	*Prorocentrum scutellum*	30	dino
		Heterocapsa triquetra	30	dino
		Coscinodiscus sp.	60	s.d.
		Amphiprora sp.	120	s.d.
		Ditylum brightwellii	80	s.d.
		Nitzchia sp.	35	s.d.
		Licmophora sp.	40	s.d.
		Chaetoceros sp.		c.d.
		Thalassiosira sp.		c.d.
		Guinardia flaccida		c.d.
		colorless detrital particle	40	
Protoperidinium spinulosum	45	*Chaetoceros affinis*		c.d.
		C. curvetus		c.d.
		Leptocylindrus danicus		c.d.
		Skeletonema costatum		c.d.
		Eucampia zoodiacus		c.d.
P. pellucidum	45	*Licmophora* sp.	40	s.d.
		Thalassiosira sp.		c.d.
		Asterionella japonica		c.d.
		Leptocylindrus danicus		c.d.
		Chaetoceros sp.		c.d.
P. conicum	55	*Corethron hystrix*	35	s.d.
		Thalassiosira sp.		c.d.
		Chaetoceros sp.		c.d.
		Lithodesmium sp.		c.d.
P. cf. *hirobis*	25	*Leptocylindrus danicus*		c.d.
P. species A	50	*Chaetoceros* sp.		c.d.
P. punctulatum	55	*Rhizosolenia* sp.	200	s.d.
		Leptocylindrus danicus		c.d.
P. curtipes	60	*Ditylum brightwellii*	80	s.d.
P. achromaticum	35	*Leptocylindrus danicus*		c.d.
P. minutum	40	*Licmophora* sp.	40	s.d.
		Guinardia flaccida		c.d.
		Chaetoceros sp.		c.d.
P. pentagonum	50	*Lauderia* sp.		c.d.
P. excentricum	60	*Ditylum brightwellii*	80	s.d.
		Coscinodiscus sp.	50	s.d.
P. claudicans	60	*Chaetoceros curvetus*		c.d.
P. quarnerense	40	*Thalassiosira* sp.		c.d.
P. oblongum	60	*Chaetoceros* sp.		c.d.
P. pyriforme	40	*Protogonyaulax tamarensis*	40	dino
		Heterocapsa triquetra	35	dino
		Scrippsiella sp.	40	dino
		Nitzchia sp.	30	s.d.
P. species B	30	*Oblea*-like cell	17	

←

[a] Diameters in μm.

[b] pras = prasinophyte; dino = dinoflagellate; s.d. = solitary diatom; c.d. = colonial diatom, with lengths ranging from 100–400 μm.

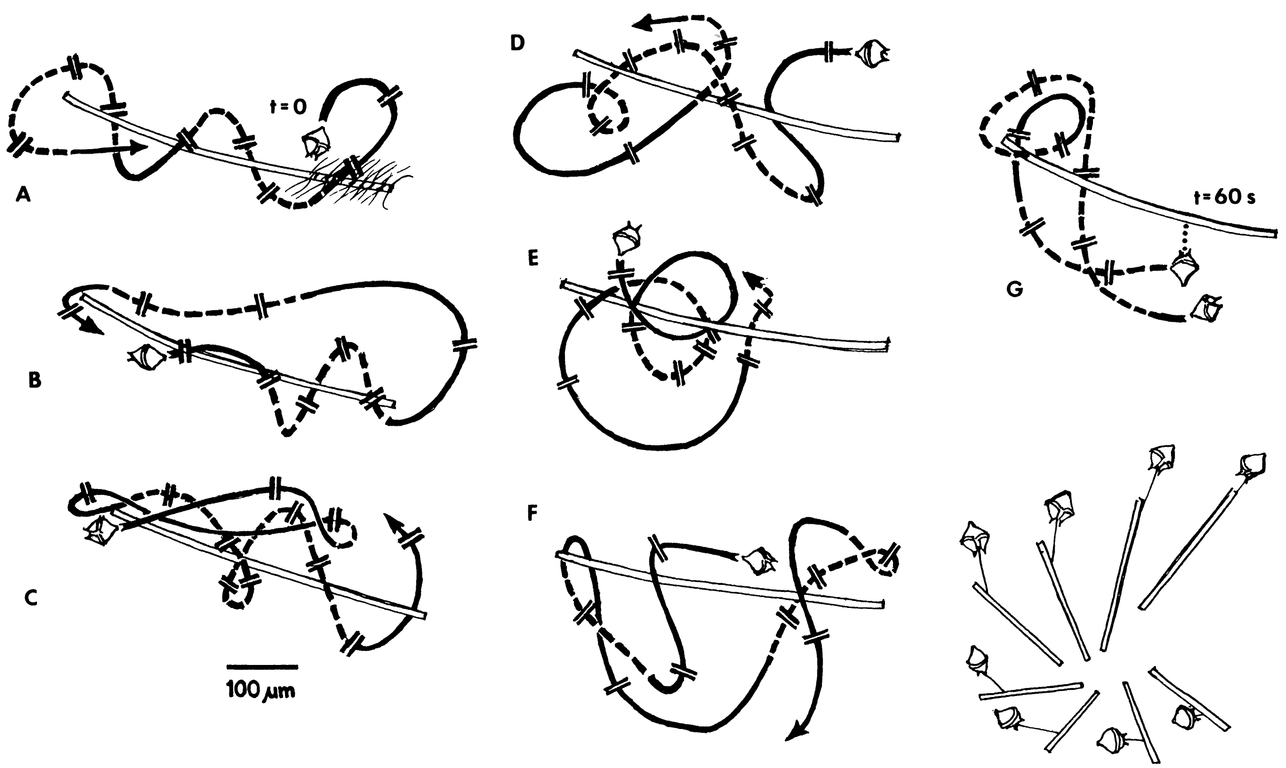

FIG. 1A–F. Sequence of 60 s duration showing swim path of *Protoperidinium spinulosum* immediately prior to capture of *Chaetoceros* chain. Frame A depicts portion of diatom spines. Dashes signify one second intervals. Each frame commences at dinoflagellate symbol (drawn to scale) and concludes with arrow. Dashed lines indicate sawtooth swimming behavior (see text for details). Frame G indicates location of pseudopod attachment. Last frame shows dinoflagellate with slender pseudopodal attachment slowly pulling (foreshortened) diatom.

F). With the exception of *P. punctulatum,* the species listed above display a characteristic, punctuated swimming pattern as they circle the prey. This pattern, symbolized in Figure 1 by the dashed line, consists of a series of small pulses as the cell pitches its apex in a sawtooth pattern at a rate of three or four cycles per second. Their swimming speed in this mode is typically reduced from 350 $\mu m \cdot s^{-1}$ to 100 or 150 $\mu m \cdot s^{-1}$. The conspicuous "sawtooth" behavior was not observed in *P. punctulatum,* whose swim path around a chain of *Leptocylindrus danicus* was a smooth, uninterrupted spiral. *Oblea rotunda* is distinctive because of its high velocity swimming behavior around its typically small prey. The swim path is punctuated by brief jerks or twitches, comparable to the slower sawtooth pattern of larger species but more difficult to resolve.

Capture

Precapture behavior flows directly into capture, except when the cell abandons its potential prey item and departs, returning to straight swimming. While diatoms are obviously passive, other prey may be able to escape capture. An individual *O. rotunda* cell was observed as it attacked quiescent *Heterocapsa triquetra* cells, but in each of five successive encounters, the potential food organisms distanced themselves from the predator with brief pulses of swimming, thereby evading capture.

Successful captures occur as follows. Without pausing from spiraling and sawtooth-swimming, a cell may resume straight swimming with the prey suddenly trailing behind. Clearly, a linkage was established in a fraction of a second in the form of a filament too thin to detect with a dissecting microscope. The moment of filament attachment is often signaled by particularly rapid, high frequency twitches of the predator. Unfortunately, the erratic and rapid swimming of dinoflagellates makes observation with higher magnifications of the brief, infrequent capture event impractical. However, observations of the capture behavior of *O. rotunda* with dark field illumination allowed both the longitudinal flagellum and the "tow filament" to be simultaneously visible. These two thread-like appendages appear to have the same diameter of approximately 1 µm. The tow filament has also been observed during food capture in *P. spinulosum, P. conicum,* and *Z. lenticulatum.* As illustrated in Figure 2A–C, the emerging pseudopod appears to extend along the filament; at the same time the filament is either contracted or retracted, pulling the prey closer. Similar, previously unreported filament-assisted capture behavior has been frequently observed both in *Oxyrrhis*

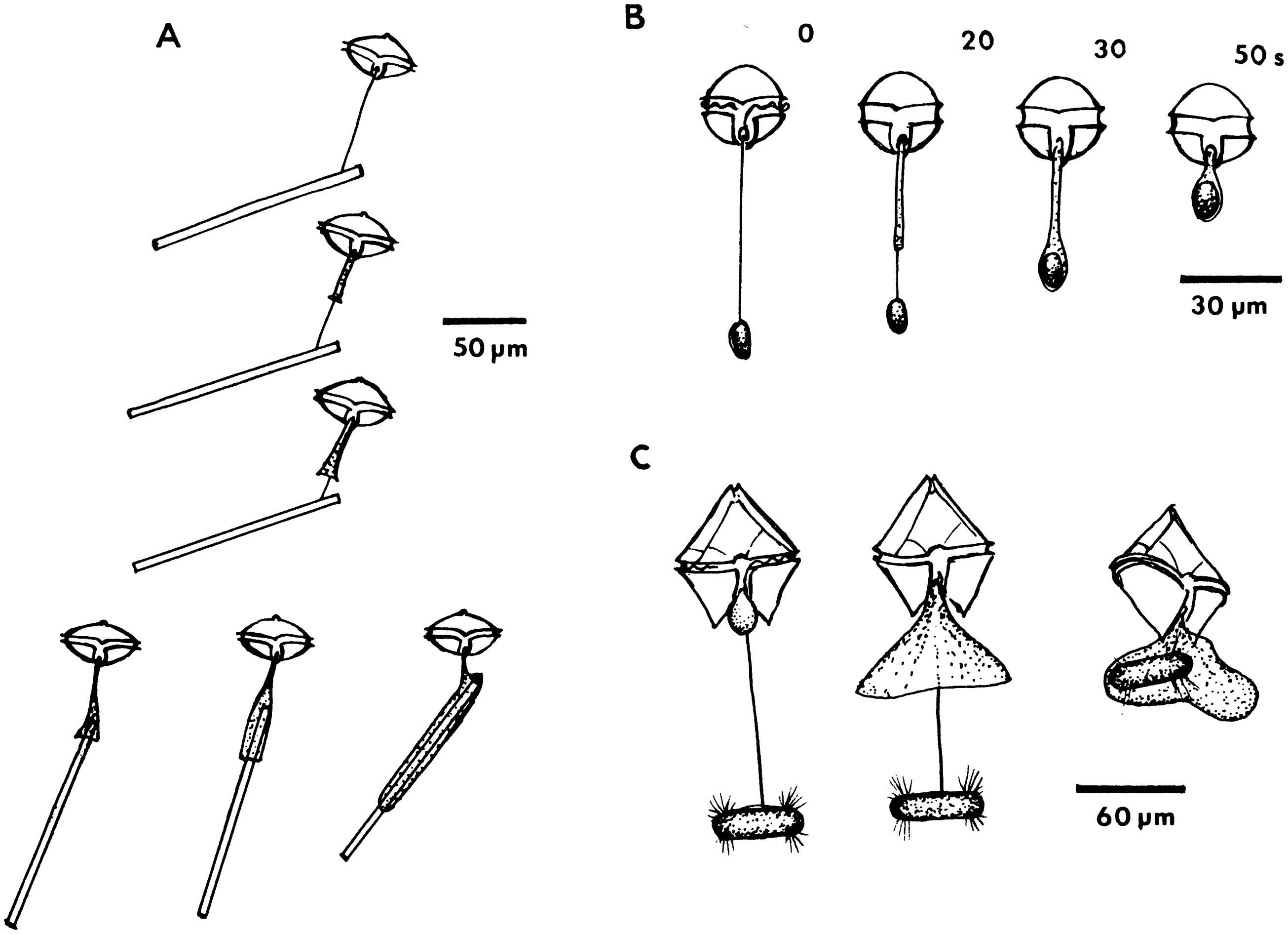

FIG. 2A–C. Pseudopod deployment in thecate heterotrophic dinoflagellates. (A) Sequence of approx. 3 min duration showing pseudopod deployment of *Zygabikodinium lenticulatum* feeding upon *Leptocylindrus danicus.* Note primary attachment filament. (B) Similar sequence of *Oblea rotunda* feeding on *Pyramimonas* sp., with times given. (C) *Protoperidinium conicum* feeding on *Corethron hystrix.* Note broadness of emerging pallium.

marina and *Gyrodinium* cf. *dominans.* These naked heterotrophic dinoflagellates promptly phagocytosed their filament-anchored food cells (unpubl. obs.). On three occasions a filament was not observed during capture by *P. spinulosum.* One such instance is depicted in Figure 1. After a minute of looping around a *Chaetoceros* chain, the cell halted, then rolled and pitched so that its antapex was directed toward the diatom, then extended its tongue-like pseudopod toward the diatom. It is possible that a filament was present. However, the dinoflagellate did not pull the diatom until the pseudopod had become attached, so that the existence of a primary filament attachment could not be established.

Pseudopod Deployment

In *P. pellucidum, P. punctulatum, O. rotunda* and *Z. lenticulatum,* the pseudopod appears to emerge from the sulcal pore as a narrow tongue, advancing at a rate of 2–6 $\mu m \cdot s^{-1}$. In *Z. lenticulatum,* the leading edge of the pseudopod was observed to flare as it approached its prey, broadening from a diameter of 6 μm to 12 μm (Fig. 2A–C). This broadening can be more pronounced in *P. conicum,* in which a pseudopod reached 75 μm laterally as it approached a filament-tethered *Corethron* cell (Fig. 2C). A recently excysted cell of *Protoperidinium* sp. A (closely related to *P. leonis*) rapidly protruded a lobate pseudopod when compressed beneath a coverslip (Fig. 8). An ovoid body next to the large sac pusule was darkly stained by Lugol's iodine solution; the nature of this body is not known. Most frequently, however, the pseudopod maintains a narrow (5–10 μm) cylindrical form resembling an umbilical cord (Figs. 2 and 12) until it contacts the diatom, over which it spreads, forming a close-fitting envelope. This hyaline envelope is usually inconspicuous and can easily escape detection by an observer. The pseudopod conforms to projections such as spines, coating them in a thin sheath (Figs. 6, 7, 21). The long slender projections that follow and enclose spines can expand to form a continuous sheet around peripheral particles (Fig. 22A, B). Filopodia may project from a pseudopodal envelope enclosing a spineless diatom; on spinose

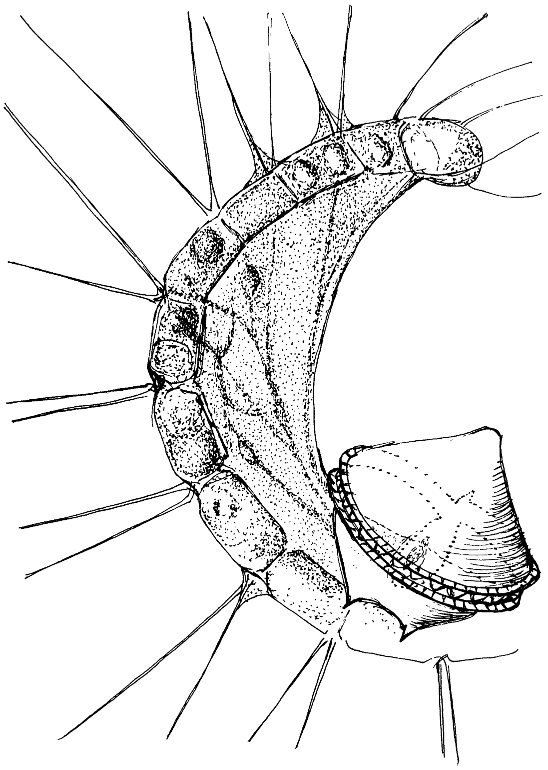

FIG. 23. *Protoperidinium spinulosum* feeding on *Chaetoceros curvetus,* illustrating radial fibrillar structure within web-like pallium. From video recording.

appear, from our observations, to be unified by their feeding behavior, sharing similar precapture behavioral patterns, capture mechanisms (involving the use of a previously unreported filament) and pseudopod deployment and digestion techniques. The capture filament, only briefly manifested, will probably be discovered in other species; the four species in which it has been detected are also the species whose feeding behavior has been most extensively observed. The manner in which the pseudopod tightly fits the prey organism, and the close proximity of the dinoflagellate to its food (so that the pseudopodal attachment is hidden) conspire to make feeding behavior inconspicuous, and helps explain why this phenomenon has for so long been unknown.

The pseudopod structures described above are clearly similar to those reportd by Gaines and Taylor (1984). They observed *P. depressum* as it deployed a disc-shaped pseudopodal sheet that spread broadly to form a circular "feeding veil." One edge of the veil made contact with a diatom which was drawn close to the dinoflagellate when the veil was retracted, somewhat like the entrapment of fish within a purse seine. Our interpretation of their observations is that of a pseudopod spreading evenly across the glass slide upon which the dinoflagellate had settled. The appearance of a veil covering a large area lacking diatoms may be due to the proximity of the smooth, flat surface of the glass slide, and may not have formed had the cell been suspended in water. In only one case (involving *P. conicum*) out of the dozens of captures we observed (none of which occurred against a glass surface) was the pseudopod laterally expanded prior to diatom engulfment. In other capture events involving *P. conicum,* as well as *O. rotunda, Z. lenticulatum, P. spinulosum* and *P. punctulatum,* the emerging pseudopod held the form of a narrow cylinder, spreading laterally only after contact was made with the prey. The presence of a capture filament helps explain how the pseudopod is directed towards its target. We have not yet observed capture behavior in *P. depressum* (the species described with a feeding veil by Gaines and Taylor 1984) but in cells observed in the process of feeding, the pseudopod appeared as a close-fitting envelope, as is the case for the other species we have observed.

The search and capture behavior described above shows that swimming thecate heterotrophic dinoflagellates, which persistently spiral tightly around potential prey items before effecting their capture, are not nonspecific predators using a broad net mechanism to obtain food randomly. Rather, they actively select a particular prey item, anchor themselves to this particle with a filament, and then deploy their pseudopod.

The sudden contraction of the cytoplasm of a captured diatom occurring after pseudopodal attachment as described earlier for *Ditylum* is very similar to a phenomenon described by Drebes and Schnepf (1982) occurring during the peduncular feeding of the naked dinoflagellate *Paulsenella* sp. upon the diatom *Steptotheca.* This phenomenon very likely reveals the rapid release of an enzyme from the pseudopod or peduncle that can alter the permeability of the diatom membranes.

The pseudopodal feeding mechanism of thecate heterotrophic dinoflagellates has been described as "extra-cellular digestion" (Gaines and Taylor 1984). Strictly speaking, if the pseudopod membrane is able to surround a prey item completely, digestion is intra-cellular since it occurs within a feeding vacuole, albeit a vacuole outside the theca. If the pseudopod can engulf only a portion of an elongate prey, digestion occurs in an extra-cellular manner. The distinctions between "extra-cellular," "intra-cellular," and phagotrophic feeding are in this case rather artificial.

Large, colonial diatoms are currently believed to be grazed only by organisms at least the size of copepods, while microzooplankters such as oligotrich ciliates are thought to be limited to small, often flagellated phytoplankters. This study helps to establish a new trophic link within the marine planktonic food web, that is, the grazing of thecate heterotrophic dinoflagellates upon large diatoms.

Pseudopodia are not new to flagellates. Amoeboflagellates are heterotrophs akin to "true" amoebae, except for a brief flagellated stage prior to encystment (Schuster 1963). A number of photosynthetic chrysophytes (*Rhizochrysis, Chrysamoeba, Rhizochromulina*) and a xanthophyte (*Rhizochloris*) apparently have flagellate/amoeboid alternation life cycles, the persistent amoeboid form displaying radiating filopodia (Hibberd and Chretiennot-Dinet 1979). In *Chrysamoeba* alone is the amoeboid stage flagellated, but the flagellum does not contribute to cell motility (Hibberd 1971). Small, bactivorous monads are certainly phagotrophic, and diminutive pseudopodia have been described in *Cercomonas* (Mignot and Brugerolle 1975). From this brief survey it becomes clear that the thecate heterotrophic dinoflagellate pseudopod is unlike that of any flagellate yet described. The pseudopod is manifest in flagellated, vegetative, motile cells, and is certainly more elaborate than those observed in other flagellates.

Pseudopodal structures as elaborate as those described here are found in foraminiferans and radiolarians. Filopodia are conspicuous in these "rhizopoda," and are often elaborated into anastomosing reticulopodial networks (Leidy 1879, Anderson 1983). The pseudopodia of thecate heterotrophic dinoflagellates do form filopodia but they are few in number. Occasionally they can converge and fuse to form lamellipodia in a manner similar to that of reticulopodia. However, a comparison of the details of food engulfment as revealed by transmission electron microscopy accentuates the unique nature of this pseudopod. In radiolaria, Anderson (1983) has described how reticulopodia that contact food develop thickened, microfilament-rich "coelopods" that envelop and forcibly rupture the prey exoskeleton. This allows pseudopods to gain access to the internal tissue of such prey as copepods. In foraminiferans, Anderson and Bé (1976) reveal reticulopodia that surround food such as copepods and secrete an adhesive substance to anchor the prey item in place. Reticulopodia find their way within the exoskeleton and transport bits of tissue and oil droplets to the large cell aperture and on into the endoplasm. In contrast, thin sections through a feeding dinoflagellate cell (unpubl. data) show that the transparent envelope surrounding the diatom food is composed merely of empty membrane vesicles within a continuous membrane sheath (Fig. 13). This delicate structure apparently cannot rupture a diatom frustule. Instead, degenerative enzymes presumably diffuse through the diatom pores to liquify the prey cytoplasm, which then diffuses out through the pores, leaving the silica frustule intact. This situation is reminiscent of arachnid feeding, in which the contents of captured arthropods are liquified and ingested, leaving an empty exoskeleton.

The uniqueness of the thecate heterotrophic dinoflagellate pseudopod leads us to propose a new term, "pallium," Latin for the sheet-like garment worn in ancient Greece. This term emphasizes the manner in which the membranous pseudopod envelops food particles.

Further analysis of the pallium and comparisons with different protists must wait for ultrastructural/cytochemical work (in progress) to be completed. The organization of the pallium, especially in regard to microtubules, and the spatial relationships between the internal manifestations of the pallium, the sac and collecting pusules, and the two flagella, all of which are associated with the flagellar pore, will be of particular interest.

The observation of size changes of the sac pusule in *Z. lenticulatum* suggests that this organelle may play a role in feeding. The sac pusule, the larger of two, is most conspicuous in thecate heterotrophic dinoflagellates (Kofoid 1909), much less so in naked heterotrophic and most photosynthetic dinoflagellates. In some heterotrophs the sac pusule can occupy as much as half of the cell volume, yet it appears to contain only seawater. The pusules, despite much attention and imagination, are still in want of a proven function. One of the most convincing hypotheses is one of excretion or osmoregulation (Dodge 1972) but uptake of dissolved substances (Kofoid and Swezy 1921) and buoyancy (Norris 1966) have also been proposed. The streaming of cytoplasm out of and into the theca through the flagellar pore during feeding suggests a different function for the sac pusule, that of volume regulation. One might expect its volume to increase upon deployment of the pallium or its volume to decrease during import of food materials and pallium retraction. Indeed, a decrease in sac pusular volume of approximately 50% has been observed during digestion in a cell of *Z. lenticulatum.* Further work is needed to test this hypothesis; considerable care must be taken to avoid artifacts because of the sensitivity of the pusule to stresses associated with microscopic observation.

The description made by Bursa (1961) of a *Protoperidinium* sp. ingesting a flagellate, which is illustrated by a drawing, matches the appearance of a cell retracting its pallium. The drawing shows irregular protrusions that radiate from a mass at the sulcus, which we reinterpret to be its pallium. Drawings by Schütt (1895) which depict cells of *Podolampus bipes* and *Blepharocysta splendor-maris* with pseudopodal extensions protruding through the flagellar pore lead us to suggest that the pallium may be present in these tropical dinoflagellates as well. Indeed, such a phenomenon was again observed by Steidinger et al. (1967) in *Blepharocysta splendor-maris.*

The 17 predator species listed in Table 1 have widely differing numbers of prey species; as mentioned before, this is primarily an artifact of the number of observations. At this time little can be said of selection among diatom species; prey species tend to be amongst the most abundant diatoms at the time of capture. However, a clear pattern emerges with regard to diatoms vs. non-diatom species. Generally speaking, *Protoperidinium* species graze exclusively on diatoms, while the two diplopsaloid species (*O. rotunda* and *Z. lenticulatum*) also take dinoflagellates, and in the case of *Oblea*, prasinophytes as food. While this hypothesis holds true, so far, for 14 species of *Protoperidinium,* two other species, *P. pyriforme* and *Protoperidinium* sp. B may feed on dinoflagellates. It is interesting that while *P. pyriforme* frequently fed on *Protogonyaulax* (= *Gonyaulax*) *tamarensis,* this toxic species was not preyed upon by *O. rotunda* even when offered as its sole food. *O. rotunda* will consume other dinoflagellates of similar size.

The fact that *O. rotunda* and *Z. lenticulatum* and perhaps other species can capture and feed upon detrital "marine snow" type particles shows that bacterial consumption undoubtedly occurs. Consumption of diatoms alone would also result in assimilation of bacterial carbon, as well as other commensal organisms living on or near diatoms. The intensity of bactivory among thecate heterotrophic dinoflagellates is not clear, and may be most significant in diatom-poor regions. This may explain uptake of labeled bacterial carbon by thecate heterotrophic dinoflagellates observed by Lessard and Swift (1985).

Although thecate heterotrophic dinoflagellates are delicate, fastidious organisms that reveal their secrets only after prolonged coaxing, much has been learned of them. In summary, three genera have been found to share the pallium feeding system, including the use of a filament to initially secure their prey. Swimming behavior prior to capture indicates that the predators are potentially selective grazers. Indeed, while the genus *Protoperidinium* restricts its diet almost entirely to diatoms, two diplopsaloid species also prey upon dinoflagellates and prasinophytes, as well as bacteria-colonized detrital particles.

Much remains to be discovered of the ultrastructure, chemosensory abilities, diel feeding patterns and trophic rates of these remarkable microzooplankters.

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