

## SYMBIOSES IN MARINE MICROPLANKTON

BY

F. J. R. TAYLOR \*

KEY-WORDS : Symbiosis.  
Microplankton.  
Associations.  
Primary productivity.

MOTS CLÉS : Symbiose.  
Microplancton.  
Associations.  
Productivité primaire.

### Abstract

Symbioses in marine microplankton are common, particularly in tropical waters, but are usually noted only in passing in studies on other aspects. The literature on them is therefore very scattered. This paper brings together information on more than 40 non-parasitic associations. They range from adventitious, non-specific epibioses, to highly integrated, specific symbioses in which both partners are completely dependant on each other. Most of the ecologically important symbionts are photosynthetic, living in non-photosynthetic hosts, but there is little information on the exchange of materials between them. The best known cases are those involving foraminifera, radiolarians and ciliates. The most strongly integrated association, involving the temperate, autotrophic ciliate *Mesodinium rubrum* Lohm., is also one of the most ecologically important, particularly in upwelling areas where it has been responsible for the highest micro-organismal primary productivity on record.

### Résumé

#### Les symbioses dans le microplancton marin.

Les symbioses sont fréquentes dans le microplancton marin, et particulièrement dans celui des zones tropicales, mais elles ne sont que signalées lors d'études diverses. La bibliographie les concernant est de ce fait très dispersée. Ce travail fournit des informations au sujet de plus de 40 associations non parasitaires allant d'épibioses accessoires non-spécifiques à des symbioses hautement intégrées spécifiques dans lesquelles les deux partenaires sont complètement dépendants l'un de l'autre. La plupart des symbiontes qui sont écologiquement importants sont photosynthétiques et vivent dans des hôtes non-photosynthétiques, mais on a peu de données quant aux échanges qui ont lieu entre eux. Les symbiontes les mieux connus sont ceux qui concernent les Foraminifères, les Radiolaires et les Ciliés. L'association la plus intimement intégrée qui concerne un Cilié autotrophe des eaux tempérées, *Mesodinium rubrum* Lohm., est aussi celle qui est la plus importante du point de vue écologique, surtout dans les zones de upwelling où elle est responsable de la productivité primaire la plus élevée connue parmi les microorganismes.

\* Departments of Oceanography and Botany, University of British Columbia, Vancouver, B.C., Canada, V6T 1W5.

« For a vegetable cell no more ideal existence can be imagined than within the body of an animal cell ... and conversely for an animal cell there can be no more ideal existence than to contain a sufficient number of vegetable cells constantly removing its waste products, supplying it with oxygen and starch, and being digestible after death. »

Patrick GEDDES,

1882, p. 387.

## 1. INTRODUCTION

### 1.1. Aims of the review.

No microscopist who has studied tropical microplankton can fail to be impressed by the numerous instances of organisms living on or in the cells of others that one sees. However, if much further information is searched for in the literature, disappointment follows. Although many of the associations have been known for one hundred years or more, few have received more than cursory study. Often this is because they have been seen only in preserved material. The great majority of papers on marine symbioses almost exclusively deal with larger, more readily studied host organisms. Only in recent years have the radiolarian and foraminiferan symbioses begun to receive experimental study, and the other microplanktonic symbioses noted here are recorded as scattered notes throughout the literature.

This paper attempts to bring information on non-parasitic physical associations in marine microplankton together in the hope that it will stimulate more deliberate studies on these fascinating, sometimes ecologically significant associations. Although an attempt has been made to cover the full spectrum of associations it has not been feasible to cite all the minor, passing references to each association. Because many involve the uniting of photosynthetic with non-photosynthetic partners, leading to a partially or wholly autotrophic consortia, the topic has not been restricted to microzooplankton *per se*, but includes all symbioses involving unicellular marine plankton, regardless of animal or plant affinity. Similarly, although the term microplankton usually refers to organisms larger than 20  $\mu\text{m}$ , it is not used in such a restrictive sense here.

SIEBURTH (1979) has included several of the cases which follow in his valuable compilation of marine micro-organisms. Two early papers dealing with some examples of ectocommensalism are those of SCHRÖDER (1914) and PAVILLARD (1916 *b*). NORRIS (1967) has

reviewed some photosynthetic symbionts (principally cyanobacterial), but unfortunately in a very obscure publication. Further useful partial reviews are cited in the text where appropriate.

### 1.2. Some remarks on terminology.

As noted, this review will not include parasitic associations. The term *symbiosis* is currently used in three different ways: in its widest sense, to include all physical associations regardless of benefit or harm, chiefly by American authors such as HENBY, (1966) or STARR, (1975); in its narrowest sense, applying only to associations of mutual benefit (i.e. as a synonym for *mutualism*), or to non-parasitic associations in which *commensalism* (no benefit or harm to the host) and *mutualism* (mutual benefit) are subdivisions. The latter seems to be the most widely used sense. The existence of gradients and even periodic shifts in the balance between organisms makes the application of many of these terms simplistic (see STARR, 1975 for a lengthy discussion of such matters), and they will be avoided here where possible, particularly as so little is known of these associations.

A simple distinction can be made between *epi-* and *endosymbionts*, depending on whether they live on or in their hosts, regardless of the nature of their interactions, if any. Although the former is relatively unambiguous (and is more apt than « *ectosymbiont* »), the latter has been used to refer to the inhabitants of such disparate habitats as the guts, circulatory or lymphatic systems, coelomic cavities or within the host cells. All the present cases of endobiosis are intracellular, either in vacuoles or embedded in the cytoplasm. TAYLOR (1979) has suggested that the inhabitants of cells of other organisms be referred to as *cytobionts* (approximately equivalent to the *endocytobionts* of SCHWEMMLER, 1980, and others: the « *endo* » seems to be superfluous except when used to distinguish *epi-* from *endocytic* symbionts).

## 2. EPIBIONTS

The principal epibionts of microplankton are listed in Table 1. Details are given below.

## 2.1. Colonisers of planktonic diatom walls.

The silica walls of diatoms are usually free of foreign organisms. However, under some circumstances, particularly in benthic species (e.g. *Melosira* spp.) and tropical planktonic communities, a variety

of epibionts may occur. Because the surface is not covered by cytoplasm it seems to offer an excellent surface for sessile micro-organisms and the interest is almost greater in finding out why they are not more colonised than why they are.

Bacteria are commonly present on some (but by no means all) benthic diatoms, such as *Melosira*, but are usually only obvious on planktonic cells when they are dead (DROOP and ELSON, 1966, and personal obs.). As the parent wall is shared by the daughter cells

TABLE 1. — Principal epibionts of marine microplankton (see text for details).

Epibiont ( ) = No. of spp.	Host(s) *	Notes
Bacteria	Diatoms	Rare on healthy cells.
Cyanobacteria :		
<i>Richelia</i> (1)	DT- <i>Chaetoceros</i>	Filamentous, usually cytotibiotic.
<i>Calothrix</i> ? (1)	DT- <i>Rhizosolenia</i> <i>Hemiaulus</i>	Possibly <i>Richelia</i> .
<i>Synechococcus</i> (1)	DN- <i>Ornithocercus</i> , <i>Parahistioneis</i> <i>Histioneis</i> <i>Ciltharistes</i> ?	Coccioid, living between the girdle lists; sometimes a special chamber; endosymbiotic in <i>Amphisolenia</i> (DN).
<i>Synechocystis</i> (1)	DN- <i>Parahistioneis</i> , <i>Histioneis</i>	Coccioid; endosymbiotic in a diatom and a silicoflagellate ?
Prymnesiomonads :		
<i>Emiliana</i> (coccol.) (1)	DT- <i>Thalassiosira</i> , <i>Planktoniella</i>	Diatom originally called <i>Brenneckella</i> .
<i>Phaeocystis</i> (1)	DT- <i>Chaetoceros</i>	Motile settles on setae.
Chrysomonads ? :		
<i>Ruttnera</i> (1)	DT- <i>Chaetoceros</i> , <i>Bacteriastrum</i> Diatoms	Motile settles on setae.
<i>Bicosoeca</i> (1 ?)		Belongs in separate group.
Xanthomonad ? :		
<i>Solenicola</i> (1)	DT- <i>Leptocylindrus</i>	Host formerly <i>Dactyliosolen</i> ; parasite ?
Dinoflagellates :		
<i>Dissodinium</i> (1 ?)	F- <i>Hastigerina</i> + others	On bubble capsule; parasitic ?
<i>Pyrocystis</i> (2)	DT- <i>Chaetoceros</i>	Probably parasitic.
<i>Paulsenella</i> (1)		
Diatoms :		
<i>Nitzschia</i> (1)	PM- <i>Phaeocystis</i> DT- <i>Chaetoceros</i>	On the palmelloid stage.
<i>Chaetoceros</i> (2)	CL- <i>Eulintinnus</i>	On lorica; phoresy.
<i>Pseudoannotia</i> (1)	CL- <i>Eulintinnus</i>	On lorica; phoresy.
Giliates :		
<i>Vorticella</i> (2 ?)	DT- <i>Chaetoceros</i>	On girdle.
<i>Vaginicola</i> (3)	DT- <i>Chaetoceros</i> , <i>Rhizosolenia</i> , <i>Coscinodiscus</i>	On girdle. On girdle. On valve.
<i>Zoothamnium</i> (1-?)	DT- <i>Rhizosolenia</i>	On girdle; phoresy.

\* : CL, Ciliate; DN, Dinoflagellate; DT, Diatom; F, Foraminiferan; PM, Prymnesiomonad.

this does not seem to be due to the inadequacy of time for colonization, but rather an active discouragement of external colonisers. As bacteria are known to be generally highly efficient in the uptake of nutrients and may even compete with phytoplankton for inorganics such as phosphate (RHEE, 1972; SIEBURTH, 1976), this might outweigh any immediate benefits from regeneration in the vicinity of the wall. Numerous phytoplankters, particularly diatoms, have been shown to produce antimicrobial compounds, although only a few of these have been characterized. *Skeletonema costatum* (Grev.) Cleve has been shown to produce dimethyl beta-proprionethin (DMPT), a sulphonium compound which hydrolyses to dimethyl sulphide and acrylic acid (cf. BURKHOLDER, 1974, and GLOMBITZA, 1979, for numerous other references), the latter being a powerful antibiotic. Unsaturated fatty acids can also play this role in some diatoms (e.g. *Asterionella glacialis* Castr. = *A. japonica*, and *Chaetoceros teres* Cl., and in many macroalgae (PESANDO, 1972, AUBERT *et al.*, 1979). In a few diatoms an organic « coat » is present which may play a role. Obviously much more information is required on the interaction between diatoms and potentially colonizing bacteria.

Cyanobacteria (« blue-green algae ») are better known as intracellular inhabitants of some diatoms (see 3.2) but there are records of the filamentous species *Richelia intracellularis* Schm. occurring on the valves and setae of *Chaetoceros compressum* Laud. (= *Ch. contortum*) e.g. by KARSTEN (1907) and SOURNIA (1968), from the tropical Indian Ocean and NORRIS (1961) from the tropical Pacific near Fiji. LEMMERMANN (1905) described a filamentous form from the exterior of *Rhizosolenia* sp. near Hawaii which is remarkably similar to *Richelia* but has a smaller diameter (filament cell 1.5-3.5  $\mu\text{m}$  instead of 4-8  $\mu\text{m}$ , heterocyst 3-6  $\mu\text{m}$  instead of 8-12  $\mu\text{m}$ ). It also has a sheath. He named it *Calothrix rhizosoleniae* Lemm. As it has not been seen again his size data and sheath presence may be erroneous. SOURNIA (1970) has reproduced Lemmermann's figures. NORRIS (1967) has reported coccoid cells on *Leptocylindrus mediterraneus* but these may be a stage of *Solenicola* (see below).

Choanoflagellates (non-photosynthetic « collar flagellates ») may occur as either free-swimming or attached forms, depending on the species. The latter are common on inanimate surfaces (including the surface film) but are also common on benthic algae, including diatoms. On rare occasions they can be

found adhering to planktonic diatoms (this author has observed the non-colonial genus *Monosiga* evenly distributed on cells of a chain of *Chaetoceros* sp. in British Columbia waters) and on the marine ciliate *Zoothamnium* (LAVALL, 1971; see 2.3). More elaborate forms, with costate « baskets », are often observed in enrichment cultures but are usually more associated with inanimate surfaces, showing no obvious affinities for the cells in the culture.

Coccolithophorids can also occur on the surface of diatoms, apparently in a relatively unspecific manner. When first observed, on the surface of centric diatom walls resembling *Thalassiosira* (*Coccolithodiscus*) *eccentrica* by LOHMANN (1912), he believed that both were unique and assigned the diatoms to a new genus, *Brenneckella*, and the coccolithophorid to a new species of the (renamed) common genus *Pontosphaera*. The coccolithophorid cells were either concentrated in a belt around the girdle or/and scattered over the valve surfaces (fig. 14). GAARDER and HASLE (1962) summarised these and later observations, including their own, which indicate that the association is not as specific as earlier authors had maintained. Most of the coccolithophorid cells are referable to *Emiliana* (*Coccolithus*) *huxleyi* (Lohm.) HAY & MOHL., the commonest oceanic coccolithophorid species in both temperate and tropical waters, with a few specimens of *Syracosphaera pulchra* Lohm., *Gephyrocapsa oceanica* Kampt., *Michaelarsaria* sp., *Acanthoica* sp. and *Ophiaster* sp. The diatoms are *Planktoniella sol* (Wall.) Schütt, *Th. eccentrica* (Ehr.) Cleve (possibly including wing-less *P. sol*, the valves of which are extremely similar to *Th. eccentrica*) and a few planktonic pennate diatoms. All are tropical to warm temperate in distribution. There is no evidence for any interaction between the commensals.

The motile, biflagellated cells of the photosynthetic prymnesiomonad (= Haptophyte) *Phaeocystis pouchetii* (Har.) Lagerh. can be seen occasionally attached to the highly branched setae of *Chaetoceros radicans* Schütt (unpubl. obs., British Columbia), but there is no evidence to show that this is an obligatory phase in the life-cycle. In Indo-West Pacific waters a very similar, more common phenomenon involves the taxon first described as *Ruttnera pringsheimii* SUBRAHMANYAN (1962). The biflagellated « swimmers » of this organism have been observed to settle only on the setae of *Chaetoceros lorenzianum* Grun. (fig. 1), *Ch. curviselum* Cleve and *Bacteriastrium varians* Laud. Although the flagella are subequal in

length one appears thicker than the other with the light microscope and beats differently. SUBRAHMANYAN (1962) gave the dimensions of the flagellates as 4 to 6  $\mu\text{m}$  in length and 3  $\mu\text{m}$  in narrow width. However, a population observed on *Ch. lorenzianum* by the present author while studying Andaman Sea phytoplankton (fig. 1 and unpubl. UNESCO rept., 1973) reached a maximum length of 12  $\mu\text{m}$ . According to SUBRAHMANYAN the flagellates rapidly lose their flagella, begin to produce mucilage, and divide repeatedly to produce palmelloid colonies in which up to 256 cells may be embedded. The colonies become detached before reaching full size. With the exception of the lack of a visible haptonema, and the palmelloid cells being embedded throughout the colony rather than only at the periphery, this is remarkably like *Phaeocystis*. However, electron microscopy will be required to determine the most appropriate allocation of the tropical species. SUBRAHMANYAN assigned it to the chrysoomonads, but at that time (1962) the distinction between the latter and prymnesiomonads (= Haptophyceae = Prymnesiophyceae) was not established. Benthic samples need to be taken in future to see if the species only carries out its life-cycle on diatoms. It is interesting to note that one of the diatom species was the same in both the west coast of India, and eastern Andaman Sea occurrences.

Another chrysoomonad-like ectocommensal is *Bicoeca*\*, a non-photosynthetic flagellate which forms a lorica resembling that of some ciliates, the lorica being attached to various inanimate or animate surfaces by a stalk. It is extremely common in fresh-water ponds. PAVILLARD (1916 b) described *B. mediterranea*, a colonial marine species, which he observed on the surface of *Skeletonema costatum* (Grev.) Cleve, *Chaetoceros lorenzianum* Grun., *Ch. anastomosans* Grun., *Cerataulina bergonii* Per., *Thalassiothrix frauenfeldii* Grun. and several planktonic *Nitzschia* spp. CUPP (1943) illustrated a non-colonial form on *N. pacifica* Cupp and it is not clear if this is the same species as that of Pavillard. The diatoms usually look healthy and there appears to be little interaction

between the diatoms and their ectocommensals. SIEBURTH (1979) has provided a recent compilation of illustrations and references to the marine bicosoecids.

PAVILLARD (1916 b) named another epibiont, first seen by GRAN (1908), which has a much more specific association and which points up the difficulty in determining the basis of the host-symbiont relationship in many cases. The curiously shaped organism, occurring in a mass encircling the girdle of *Leptocylindrus (Dactyliosolen) mediterraneus* (Perag.) Hasle was named *Solenicola setigera* because of an unusual flagellum-like projection protruding from the cytoplasm (fig. 2). It has been classified as a member of the order Mischococcales of the yellow-green Xanthophyceae but it requires more detailed study before assigning it with any certainty to this or any other group. The « host » is almost invariably empty of cell contents when *S. setigera* is present. *L. mediterraneus* has been reported as possessing a few « not very small » chloroplasts (e.g. CUPP, 1943, who also illustrates cells infested by *S. setigera*), but the present author has never seen any contents in hundreds of cells observed from the Indian and Pacific Oceans, and HASLE (1975) also notes not being certain of ever seeing any in her considerable amount of material. Another peculiar feature, revealed by scanning electron microscopy, is that there is either an extremely delicate, membranous covering over the reticulated surface of the diatom wall, or (improbably) no covering at all (HASLE, 1975). It seems possible that *S. setigera* parasitises the diatom, as suggested by GRAN (1908) or, a stranger possibility, the massed cells on the outside may be part of the diatom life-cycle! HASLE refers to « the actively swimming epiphyte propelling the diatom along » and so it could also be a phoretic type of association.

There is only one dinoflagellate that seems to occur attached to diatom walls: *Paulsenella chaetoceratis* (Pauls.) Chatton, but there is evidence to suggest that it is parasitic (CHATTON, 1930). It can be seen attached to the setae of several species of *Chaetoceros* (e.g. *Ch. decipiens* Cleve) in cold temperate coastal waters (east coast of Greenland; British Columbia).

Diatoms can even occur on other diatoms. For example, *Nitzschia granii* Hasle, which is commonly found on the surface of *Phaeocystis* colonies in the North Atlantic (HASLE, 1964) and off British Columbia (unpubl. obs.), can also occur on the setae of several species of *Chaetoceros* (unpubl. obs.). Small, slender species of *Nitzschia* have also been seen on a variety

\* Commonly spelled *Bicoeca*, which derives from Stein's modification, *Bikoeka*, of James-Clark's original spelling. Both these variants are incorrect according to modern nomenclatural practice set out in the Codes of Nomenclature (e.g. Art. 73 of the Botanical Code specifies that the original spelling of a generic name must be used except to correct a typographical error).

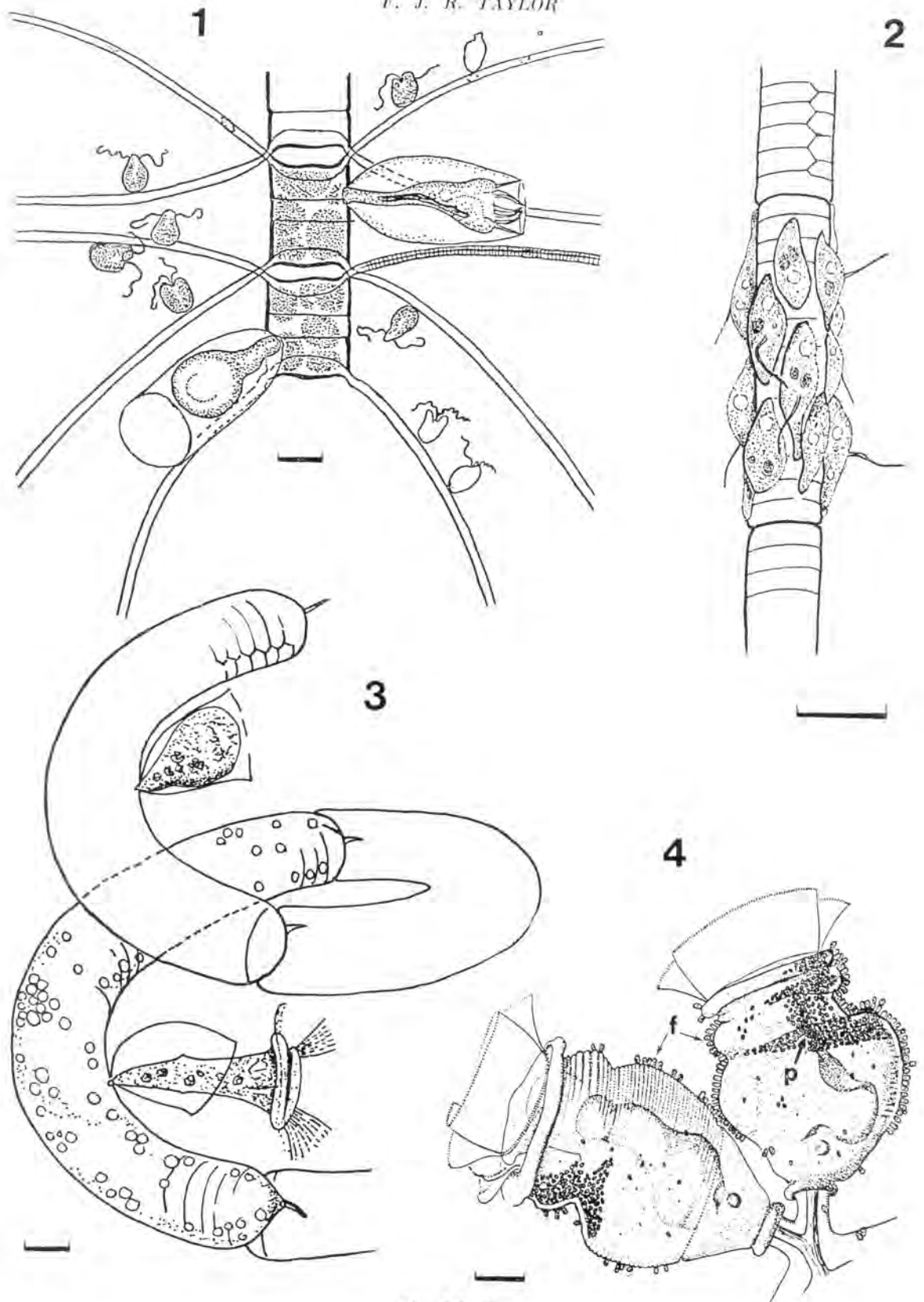


FIG. 1 TO 4.

of other diatoms, such as *Thalassiosira hispanica* Pauls., *Thal. subtilis* (Ost.) Gran, *Thal. gravida* Cleve (= *Thal. rotula*) and *Ch. socialis* Laud. by MARGALEF *et al.* (1955) in the Ria de Vigo, Spain.

Other than the fact that these diatoms, occurring on others of the same group, are small pennate *Nitzschia* species, and that planktonic *Nitzschia* are capable of gliding movement when they come in contact with a solid surface due to the presence of a raphe, there is little that can be said of these usually rare instances (occurrence on *Phaeocystis* colonies being more common).

## 2.2. Ciliate - Diatom Associations.

Within the marine plankton one finds instances both of ciliates living on diatoms and diatoms attached to ciliates. The first case involves various sessile peritrich ciliates and the second, tintinnids.

Sessile peritrichs, such as *Vorticella*, *Vaginicola* and *Zoothamnium* spp. are found attached to a wide variety of marine substrates, both animate and inanimate (numerous examples in KAHL, 1930). Therefore it might be expected that they occur rather indiscriminately on planktonic as well as benthic diatoms. However, even if the association is not highly integrated, the partners involved are relatively predictable in the microplankton.

Species of *Vorticella* (usually attributed to *V. oceanica* Zach., which KAHL did not recognise as a legitimate species), identifiable by their non-colonial organisation, with contractile stalks, have been seen many times on two species of *Chaetoceros*: *Ch.*

*coarctatum* Laud. (e.g. by POUCHET, 1894, SCHRÖDER, 1914, CUPP, 1943; MARGALEF, 1957; CURL, 1959; TAYLOR, unpubl. — Andaman Sea; etc.) and *Ch. densum* Cleve (e.g. DANGEARD, 1927, MARGALEF & DURAN, 1953). These two *Chaetoceros* species are very similar to one another and can be easily confused if entire chains are not present. A single chain may support twenty or more of the ciliates and the motion of the ciliary beating moves the chains in an irregular manner. On the west coast of Thailand the author observed three different species of the loricate genus *Vaginicola* (fig. 1, 3) attached in a predictable manner to several diatoms.

Individuals resembling *V. ingenta* (O. F. Müll.) Ehr. were present on the girdle bands of *Ch. lorenzianum* Grun., usually one per cell (fig. 1). A second species, apparently undescribed previously, was found consistently on the inner curve of the coiled cells of *Rhizosolenia phuketensis* Sundström (very similar to *Rh. stollerfothii*; fig. 3). A third species, judging by lorica form, was attached to the valve centres of the large diatom *Coscinodiscus centralis* Ehr.. As with the vorticellids, these ciliates can move their hosts through the water, but not very efficiently compared to the tintinnids (below). Species of *Zoothamnium* may also occur on planktonic diatoms. This author has seen a large colony attached to the diatom *Rhizosolenia alata* f. *indica* (Perag.) Ost. in Andaman Sea samples.

Observations of diatoms attached to the loricae of tintinnids extend back nearly a century (DADAY, 1887; FAMINTZIN, 1889). Several tintinnid genera build loricae of foreign material cemented together, and some of these frequently contain diatom frustules

FIGS. 1-4. — All scales indicate 10  $\mu$ m.

FIG. 1. — A chain of the diatom *Chaetoceros lorenzianum* infested by the flagellate *Ruttnera pringsheimii* and the loricate peritrich ciliate *Vaginicola* (*ingenta*?). Andaman Sea. Orig.

FIG. 2. — *Solenicola setigera* on the wall of the diatom *Leptocylinthus mediterraneus*. Orig., after Pavillard.

FIG. 3. — Two individuals of *Vaginicola* sp.; upper individual contracted; on the diatom *Rhizosolenia phuketensis*. Andaman Sea. Orig.

FIG. 4. — Two zooids of *Zoothamnium pelagicum* with numerous epibiotic cyanobacteria; f, cyanobacteria; p, pigment granules; modified from LAVAL (1968), with permission.

FIG. 1-4. — Toutes les échelles indiquent 10  $\mu$ m.

FIG. 1. — Une chaîne de la Diatomée *Chaetoceros lorenzianum* infestée par le Flagellé *Ruttnera pringsheimii* et par le cilié péritriche loriqué *Vaginicola* (*ingenta*?). Mer d'Andaman; original.

FIG. 2. — *Solenicola setigera* sur la paroi de la Diatomée *Leptocylinthus mediterraneus*. D'après Pavillard.

FIG. 3. — Deux individus de *Vaginicola* sp., celui du haut contracté, sur la Diatomée *Rhizosolenia phuketensis*. Mer d'Andaman; original.

FIG. 4. — Deux zoïdes de *Zoothamnium pelagicum* avec de nombreuses algues bleues épibiontes. f, algues bleues; p, granules pigmentaires. Modifié d'après LAVAL (1968), avec l'autorisation des Éditeurs.

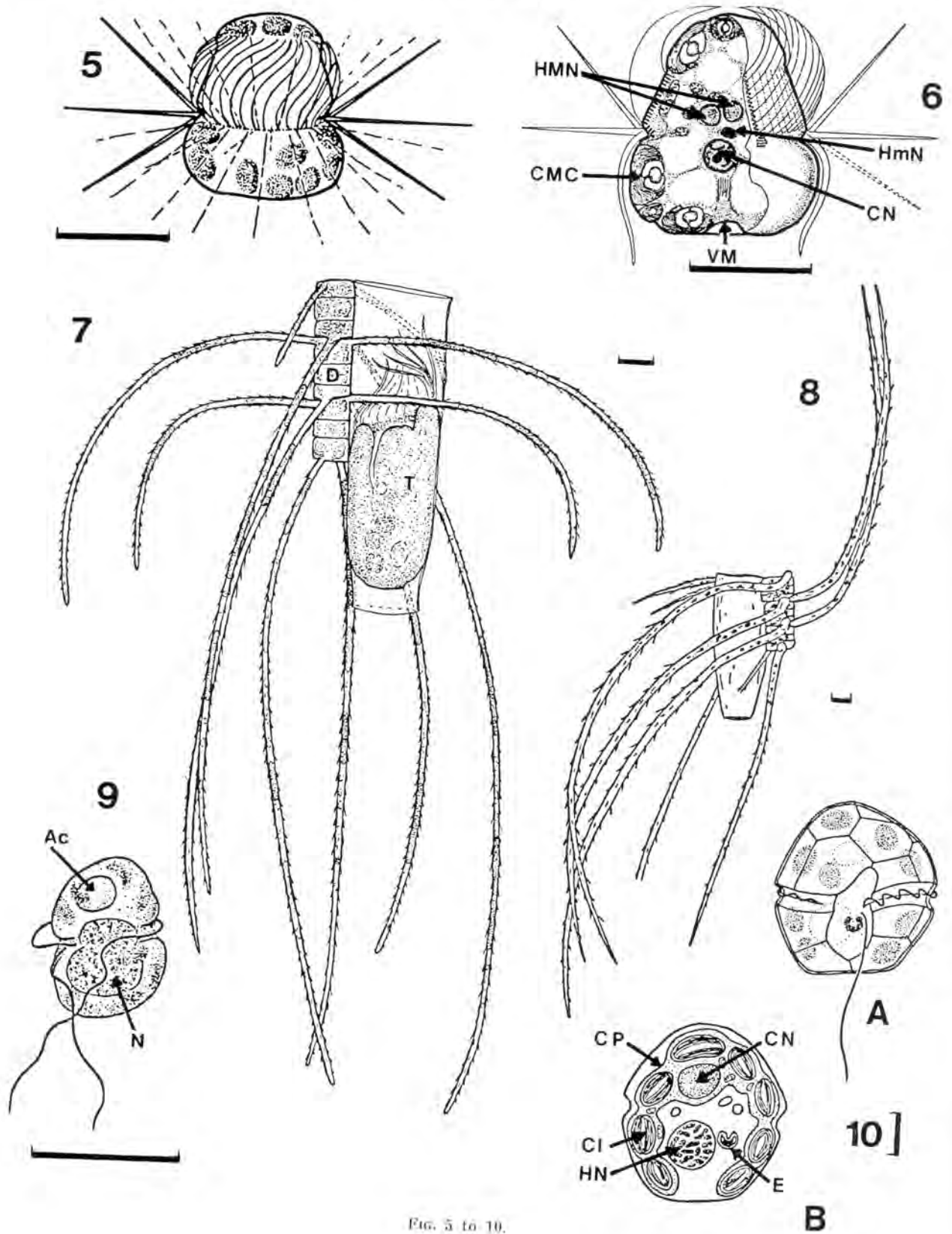


FIG. 5 TO 10.



(e.g. *Codonellopsis* spp., shown in scanning electron micrographs by TAYLOR, 1972, and several more recent authors). However, these are empty, often fragmented walls and are presumably scavenged from food. However, in several instances the diatoms are evidently healthy and may acquire a phoretic benefit from the association.

The most striking of these are the associations between members of the diatom genus *Chaetoceros* and the tintinnid genus *Eutintinnus*. *Ch. tetrastichon* Cl. and *Ch. dadayi* Pav. (fig. 5, 6) are closely related members of the subgenus *Phaeoceros* (with thick, hollow setae), forming short chains that are almost invariably only three cells long. They differ in the orientation of some of the setae « embracing » the lorica of *E. apertus* (K & C.), *E. pinguis* (K. & C.) or *E. lusus-undae* (Entz) \*, e.g. PAVILLARD (1916 a),

\* Many authors have attributed the tintinnid partner to *Tintinnus inquilinus* (O.F. Müll.) but this species, the first tintinnid described, has been claimed to have a closed aboral end (e.g. by KOFOD and CAMPBELL, 1929). Because this is debatable (unpubl. observations by this author) some nomenclatural revisions may be necessary later.

FORTI (1922), CUPP (1943), GAARDER (1946), MARGALEF and DURAN (1953), TAYLOR (1980 b). The diatom chain is invariably on the outer lorica surface adjacent to the oral lip. Observations on living cells (Andaman Sea and Caribbean Sea, unpubl.) indicate that the tintinnid is capable of swimming rapidly through the water, despite the diatom clinging to its back (reminiscent of the old man clinging to Sindbad in the « Arabian Nights »), and so Pavillard's conclusion that the association was « phoretique » is quite justified. Although one can infer that the diatom may benefit from the added flow of water over its surface, on a greater scale than in the *Vaginicola* associations above, it seems doubtful that the tintinnid benefits in any way. Further study is needed to determine if there is any physiological interaction, and to discover how a transfer of diatom cells to a new lorica is achieved. Furthermore, one wonders if the ciliate's behaviour is altered by the association. For example, does it remain in the euphotic zone, or does it drag the cumbersome passenger into unlit depths (its own food is principally euphotic) ?

The chain-forming pennate diatom, *Pseudoeunotia doliolus* (Wall.) Grun. is most commonly free in the

FIGS. 5-10. — All scales indicate 10  $\mu$ m.

- FIG. 5. — *Mesodinium rubrum*; external view showing extended cirri: from TAYLOR (1979), with permission.
- FIG. 6. — Half cut-away section of *M. rubrum*, showing the two ciliate macronuclei (HMN), micronucleus (HmN), cytobiont nucleus (CN) and chloroplast-mitochondrial complexes (CMC), and vestigial cytostome (VM); modified from TAYLOR et al. (1971), with permission.
- FIG. 7. — *Chaetoceros tetrastichon* attached to the lorica of the tintinnid *Eutintinnus pinguis*. D, diatom chain; T, tintinnid cell body. Orig., Andaman Sea.
- FIG. 8. — *Chaetoceros dadayi* on *Eutintinnus apertus*. From CUPP (1943), with permission.
- FIG. 9. — Motile cell of *Zooxanthella nutricula* Brandt. From HOLLANDE and CARRÉ (1974; after HOLLANDE and ENJUMET, 1953), with permission.
- FIG. 10. — *Kryptoperidinium foliaceum*. A, External, ventral view. B, Internal organisation. Cl, chloroplast; CN, cytobiont nucleus; CP, cytobiont plasmalemma. E, eyespot; HN, host nucleus. From TAYLOR (1979), with permission.

FIG. 5-10. — Toutes les échelles indiquent 10  $\mu$ m.

- FIG. 5. — *Mesodinium rubrum*; vue externe, montrant les cirres en extension. D'après TAYLOR (1979), avec l'autorisation des Editeurs.
- FIG. 6. — Coupe semi-évidée de *M. rubrum*, montrant les deux macronucleus du cilié (HMN), le micronucleus (HmN), le noyau du cytotiote (CN), les complexes chloroplaste-mitochondrie (CMC) et le cytotiote vestigial (VM). Modifié d'après TAYLOR et al. (1971), avec l'autorisation des Editeurs.
- FIG. 7. — *Chaetoceros tetrastichon* fixé à la lorica du Tintinnide *Eutintinnus pinguis*. D, chaîne de la diatomée; T, corps cellulaire du Tintinnide. Mer d'Andaman; original.
- FIG. 8. — *Chaetoceros dadayi* sur *Eutintinnus apertus*. D'après CUPP (1943), avec l'autorisation des Editeurs.
- FIG. 9. — Cellule mobile de *Zooxanthella nutricula* Brandt. D'après HOLLANDE & CARRÉ, 1974 (eux-mêmes, d'après HOLLANDE & ENJUMET, 1953) avec l'autorisation des Editeurs.
- FIG. 10. — *Kryptoperidinium foliaceum*. A, vue externe. B, organisation interne: Cl, chloroplaste; CN, noyau du cytotiote; CP, plasmalemma du cytotiote; E, tache oculaire; HN, noyau de l'hôte. D'après TAYLOR (1979), avec l'autorisation des Editeurs.

water, but several times it has been seen attached to the loricae of *Eulintinnus medius* (K. & C.) (PAVILLARD, 1935- as *E. apertus*; BALECH, 1962). Again, the diatom is usually at the anterior end, forming a collar (or « véritable manchon » — Pavillard), but a second chain has been seen near the posterior end in one instance, possibly prior to reproduction. A few other diatoms have been reported on *Eulintinnus* walls, but not as usual associates (*Isthmia*, *Planktoniella*, *Hemiaulus*). *Ps. doliolus* has also been seen attached to the bowl of *Codonellopsis indica* K. & C. by the present author (*Indian Ocean*, unpubl.), but this tintinnid has an agglutinated bowl and it could not be seen if the diatoms were alive.

### 2.3. Other epibionts on pelagic ciliates.

Although most members of the colonial peritrich ciliate *Zoothamnium* are epibionts themselves (previous section), *Z. pelagicum* Du Plessis is continuously pelagic. The cuticle of the latter regularly supports large numbers of minute epibionts particularly on the zooids (fig. 4). First described as microalgae (DRAGESCO, 1948), they are cyanobacteria (LAVAL, 1971). The nature of any interaction is unknown but LAVAL (1968) noted that there seemed to be a correlation between the degree of pigmentation of the zooids and the concentration of cyanobacteria, although the pigment is formed without their presence, after alteration and migration of intranuclear bacteria (LAVAL, 1970). In Villefranche Bay the epi-

biotic populations on *Z. pelagicum* are greatest in summer.

Small numbers of choanoflagellates may also be present on *Z. pelagicum* colonies. They feed on the cyanobacteria. This provided a favourable opportunity for LAVAL (1971) to study the ultrastructure of the flagellate, *Salpingoeca pelagica* L., coincidentally with that of the ciliate.

Prasinomonads are epibiotic on one tintinnid (LAVAL-PEUTO, pers. comm.).

### 2.4. The phaeosomes (coccoïd cyanobacteria) of dinoflagellates.

Coccoïd cyanobacteria, termed « phaeosomes » by SCHÜTT (1895), are regularly present on the cell surface or loosely attached to one another in the space between the upper and lower girdle lists (fig. 12) of some of the more elaborate dinophysoid dinoflagellate genera (reviewed recently by TAYLOR, 1980 a). GRAN (1912) believed that they were symbiotic, coccoïd stages of « brown flagellates ». After studying living material, including isolation and culture, NORRIS (1967) concluded that they were cyanobacteria (blue-green algae) and named two taxa: *Synechococcus carcerius* Norris (ellipsoid or elongate, pink to reddish, also endosymbiotic in *Amphisolenia*) and *Synechocystis consortia* Norris (spherical, blue-grey, also endosymbiotic in the diatom *Streptotheca thamesis* Shrubs, and the silicoflagellate *Dictyochoa speculum* Ehr.).

FIGS. 11-15.

FIG. 11. — Scanning electron micrograph of *Ornithocerus magnificus*. Orig., *Indian Ocean*,  $\times 1130$ .

FIG. 12. — Light micrograph, focussed to show the phaeosomes (arrows) filling the space between the girdle lists of *Ornithocerus magnificus*. Orig., *Barbados*,  $\times 1630$ .

FIG. 13. — *Histioneis dolon* (scanning electron micrograph). PC, phaeosome chamber formed by the upper and lower girdle lists. From TAYLOR (1972), with permission.  $\times 750$ .

FIG. 14. — Coccolithophorids (arrow) on the surface of the diatom *Planktoniella* sol. Orig., *Indian Ocean*.  $\times 500$ .

FIG. 15. — *Citharistes apsteinii*, a dinoflagellate in which the body has been greatly deformed to form the phaeosome chamber (PC) with the aid of the lower girdle list only. From TAYLOR (1976), with permission.  $\times 800$ .

FIG. 11-15.

FIG. 11. — Photographie en microscopie électronique à balayage d'*Ornithocerus magnificus*. Océan Indien; original.  $\times 1130$ .

FIG. 12. — Photographie en microscopie optique, avec mise au point sur les phéosomes (flèches) qui remplissent l'espace compris entre les deux membranes cingulaires d'*Ornithocerus magnificus*. La Barbade, original.  $\times 1630$ .

FIG. 13. — *Histioneis dolon* (microscopie électronique à balayage). PC, chambre à phéosomes, entre les deux membranes cingulaires supérieure et inférieure. D'après TAYLOR (1972), avec l'autorisation des Editeurs.  $\times 750$ .

FIG. 14. — Coccolithophorides (flèche) sur la surface de la Diatomée *Planktoniella* sol. Océan Indien; original.  $\times 500$ .

FIG. 15. — *Citharistes apsteinii* (Dinoflagellé). La chambre à phéosomes (PC) est ici limitée par la seule membrane cingulaire inférieure, du fait de la déformation du corps cellulaire. D'après TAYLOR (1976), avec l'autorisation des Editeurs.  $\times 800$ .

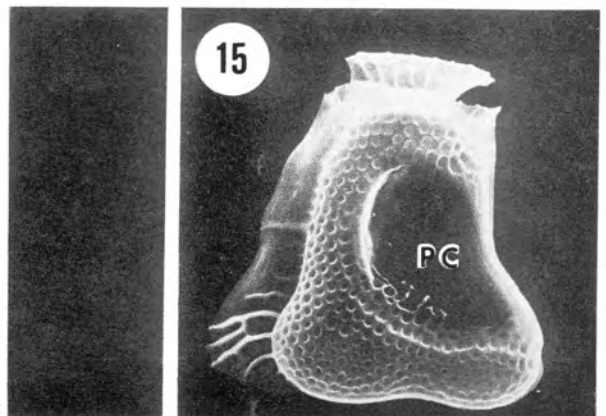
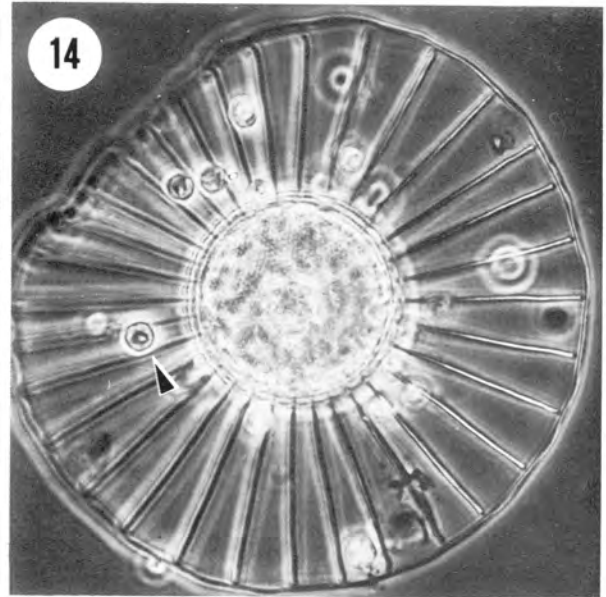
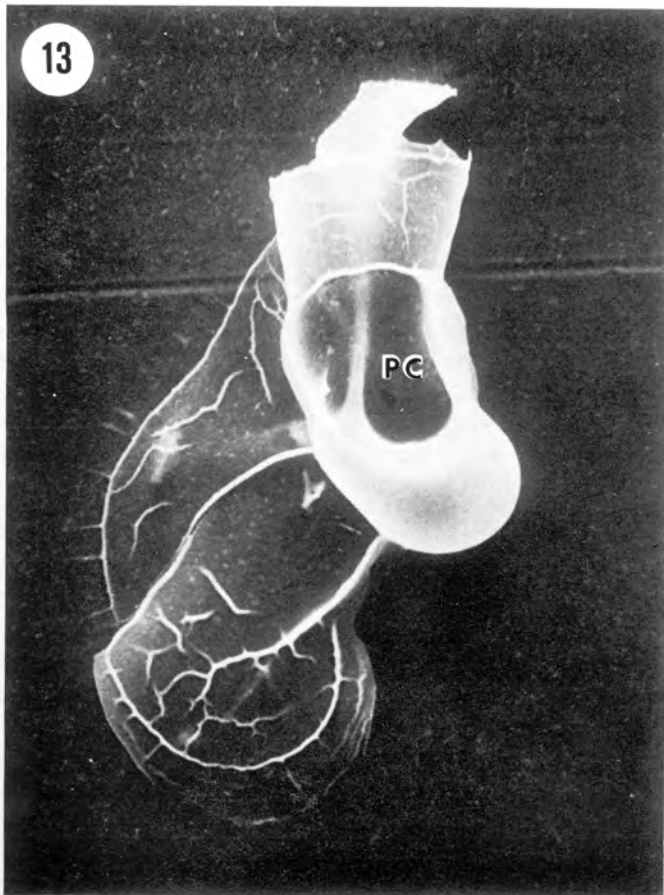
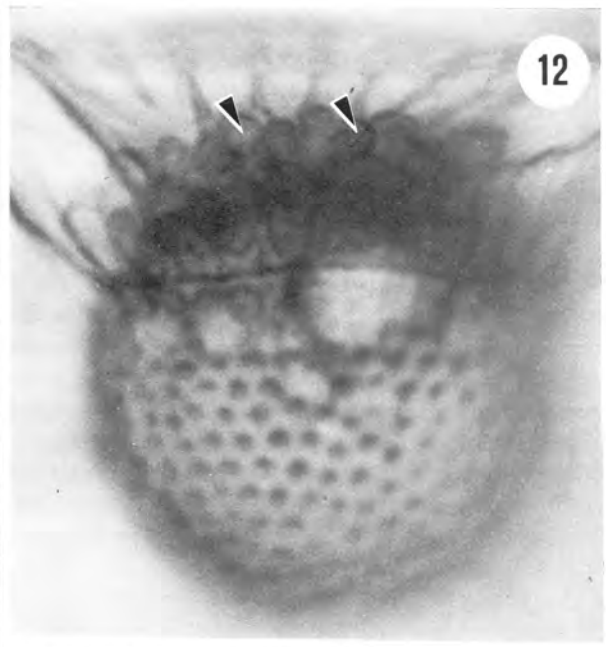
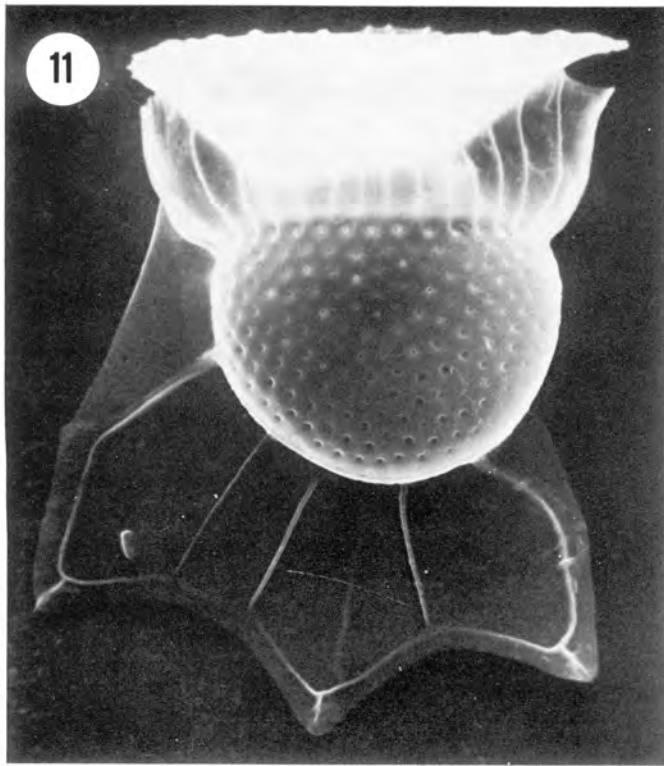


FIG. 11 TO 15.

They are epibiotic on four genera (Table 1) and the hosts seem to show progressively elaborate modifications of the body and girdle lists in response to the association, (SCHÜTT, 1895; TAYLOR, 1980 a), proceeding from *Ornithocercus* (fig. 11, 12), in which the girdle may have a more important hydrodynamic role, through *Parahistioneis*, *Histioneis* (fig. 13) to *Citharistes* (fig. 15). In *Histioneis* and *Citharistes* the space enclosed by the lists is termed the phaeosome chamber and resembles a « greenhouse », the translucent chamber usually filled with cells. The transverse flagellum of dinoflagellates normally runs in the space between the girdle lists and it is not known how the presence of the cyanobacteria affects it in these taxa. It is also not known what the physiological relationship is. Only non-photosynthetic dinophysoids are involved (TAYLOR, 1980 a), phaeosomes not being evident in photosynthetic genera such as *Dinophysis*. This, together with the morphological modifications, strongly indicates some nutritional benefit to the host. Phagotrophy has not been seen in the genera in question although the collar-like design of the lists in *Ornithocercus* seems to be formed to concentrate flow over the single, large flagellar aperture (TAYLOR, 1971). Although Norris cultured the cyanobacteria he did not publish any of their physiological features. The cells are larger than the free-living coccoid cyanobacteria now being discovered to be remarkably abundant in oceanic waters (cf. SIEBURTH, 1979), the latter being 2 to 3  $\mu\text{m}$  in maximum dimension, whereas the phaeosomes are 4 to 10  $\mu\text{m}$  or more in length. Some planktonic cyanobacteria within this size range have been seen by various authors (e. g. the « olivegrüne Zellen » of HENTSCHEL, 1936; SOURNIA, 1970). Occasionally these dinoflagellates may be found without phaeosomes and so the dependence on them by the dinoflagellates cannot be absolute.

### 2.5. Dinoflagellates on the surface of foraminifera.

Foreign organisms adhering to the outer cytoplasm of foraminifera are usually in the process of being ingested. However, in a study of the unique, « bubble-capsule »-forming planktonic species, *Hastigerina pelagica* (d'Orbigny), ALLDREDGE & JONES (1973) found that certain large dinoflagellates persisted in contact with the capsule of 80 % or more (84 % of 700 specimens seen by SPINDLER & HEMLEBEN, 1980)

of the foraminifera. The number of dinoflagellates per foraminiferan is approximately related to the size of the latter, averaging 0.5 per  $\text{mm}^2$  of surface when present. As many as 200 per foraminiferan have been seen (BÉ *et al.*, 1977; SPINDLER & HEMLEBEN, 1980). Three species of dinoflagellates are usually involved: *Dissodinium elegans* Pav., *Pyrocystis noctiluca* Murr. and *P. fusiformis* Murr. They all exist chiefly as non-motile, photosynthetic cyst-like forms, greatly expanded in size, with a large vacuole. They can reproduce while on the surface of the foraminiferan. Occasionally they have been seen attached to other planktonic foraminifera: *Globigerinoides ruber* d'Orb., *G. sacculifer* (Brady), *G. conglobatus* (Brady), *Globigerinella aequilateralis* (Brady), *Globorotalia truncatuloidea* (d'Orb.) and *Orbulina universa* d'Orb. With the exception of *G. truncatuloidea*, these also possess intracellular « zooxanthellae » (see 3.4).

The dinoflagellates involved are common, free-living inhabitants of the surrounding water, SPINDLER & HEMLEBEN (1980) found no difference in survival times for foraminiferans with or without them. No signs of their digestion have been seen although the foraminifera are active carnivores or omnivores (ANDERSON *et al.*, 1979). These dinoflagellates possess a thin, continuous, cellulose wall with an outer, chemically resistant layer (SWIFT & REMSEN, 1970) which may prevent the host from digesting them. There is no evidence to show benefit to either associant, although it can be speculated that the dinoflagellates may receive some nutrients from the host and possibly *vice versa*. At present it seems most likely that the dinoflagellates are trapped during normal feeding activities by the foraminifera. The latter cannot digest them and they continue to flourish and reproduce. In these cases any physiological benefits may be fortuitous, but much further data are needed.

Although not strictly within the scope of this review it may be pertinent to note that some motile dinoflagellates have been found consistently in very close proximity with planktonic foraminifera (an association which falls under the category of *parasitism* because it is not direct contact). The foraminifera are the same as those above, with the exception (so far) of *G. conglobatus* and *G. truncatuloidea*. The dinoflagellates are gymnodinoid or gyrodinoid in form. As many as 100 or more may be found swimming among the spines of the foraminiferan (SPINDLER & HEMLEBEN, 1980). At present it seems possible that they may be life-cycle stages of other

associants. They do not resemble the swimmers of the *Pyrocystis*.

The possibility also exists that parasitism may be involved in either or both of the above associations, although no host damage has been observed. Two species of *Dissodinium* are ectoparasitic on copepod eggs (ELBRÄCHTER & DREBES, 1978 who would like

to restrict the genus to parasitic forms, thus excluding *D. elegans* at present). One of the parabiotic motile cells is similar in size and form to the dinospore of the parasitic species *D. pseudolunula* Swift ex. Elbr. & Drebes (unpubl. obs. on Barbados material courtesy of A. BÉ, H. SPERO, C. HEMLEBEN & M. SPINDLER).

### 3. CYTOBIONTS

Because all microplankton are basically unicellular (some multinucleate, some colonial), all endobionts of this assemblage are intracellular, being located either within vacuoles or within the cytoplasm. This is clearly a much more intimate relationship than those in the preceding section, and requires much greater integrational co-ordination in order to persist. It is also within this category that some of the most ecologically important planktonic associations are to be found. *Table II* summarises the principal cytobioses in marine microplankton, with further details in *Table III*.

#### 3.1. Viruses and bacterial cytobionts.

As with the epibionts, little attention has been paid to bacteria (and to viruses in this case) within microplankton cells, the few records being mostly passing references.

Viruses are usually thought of by non-specialists as pathogenic, and so might not be thought of in a symbiotic context. However, latent viruses which persist in their host cells for long periods of time without evident harm (although possibly causing

TABLE II. — *Principal cytobionts in marine microplankton (excluding non-photosynthetic bacteria and viruses).*

Host ( ) No. of spp.	Cytobiont(s)	Notes
<b>Diatoms :</b>		
<i>Rhizosolenia</i> (8-12)	<i>Richelia</i> (cyanobact.)	Nitrogen fixation.
<i>Hemiaulus</i> (2)	<i>Richelia</i>	Nitrogen fixation.
<b>Dinoflagellates :</b>		
<i>Noctiluca scintillans</i>	<i>Pedinomonas noctilucae</i>	In vacuole.
<i>Peridinium balticum</i>	Chrysonomad ?	Fully autotrophic.
<i>Kryptoperid. foliaceum</i>	Chrysonomad ?	Fully autotrophic.
<b>Actinopods :</b>		
Polycystines - several families	<i>Zooxanthella</i> <i>Pedinomonas</i> in <i>Thalassolampe</i>	In ectoplasm, zx. encysted.
Nasselarians - several families (Phaeodarians)	Zooxanthellae ?	In ectoplasm, zx. encysted.
Acantharians	(Absent)	—
	Dinoflagellates in some,	In endoplasm.
	Prymnesiomonads in 3	In endoplasm.
<b>Foraminifera : (cf. Table 3)</b>		
spinose forms (7)	Dinoflagellates (1 prymn.)	Appear to be mastigote phase.
non-spinose forms (2)	Prymnesiomonads ?	Possibly coccolithophorids.
<b>Ciliates :</b>		
<i>Mesodinium rubrum</i>	Cryptomonad	Fully autotrophic.
<i>Prorodon</i> sp.	Chloroplasts only	Temporary, functional.
<i>Strombidium</i> sp.	Chloroplasts only	Temporary, functional.

harm later: « slow viruses » are extremely common and may have evolutionary, as well as physiological consequences (discussed further by TAYLOR, 1979 and references therein). Unless a virus can be isolated and shown to follow « Koch's Postulates », i.e. producing a similar effect on re-infection with re-isolation after passage through the host, it is not usually possible to prove that it is a virus, despite its suggestive appearance. Putative viruses seen in electron microscopical sections are usually referred to as VLP's (viral-like particles). In marine microplankton records are few, MANTON & LEADBEATER (1974) observed VLPs in a small prymnesiomonad, *Chrysochromulina* (technically a nanoplankton because it is less than 20 µm), PIENAR (1976) found VLPs in three coastal photosynthetic flagellates: *Hymenomonas (Cricosphaera) carterae* (Br. & Fagerl.) Mant. & Pel., *Cryptomonas* sp. and *Micromonas pusilla* (Butcher) Manton & Parke. In the former he noted abnormal morphology, but did not notice any evidence of harm in the other cases. However, MAYER & TAYLOR (1979) observed similar particles in *M. pusilla* from the same region (within 100 miles) and were able to show that they were true viruses, producing lethal lysis of the flagellate host (the first demonstration of viral destruction of a eukaryotic marine phytoplankton).

Further observations on VLPs in marine microplankton includes those found in the nucleus of *Platymonas* sp., a prasinomonad (PEARSON & NORRIS, 1974) and the large viral-like masses in the cytoplasm of the dinoflagellate *Gyrodinium resplendens* (type V1 of FRANCA, 1976). The hazards of interpretation are illustrated by the demonstration that the type V2 VLPs of Franca were sections through trichocyst-associated filaments of the dinoflagellate by SOYER (1978). The latter also reported VLPs from the nucleus of the dinoflagellate parasite of pelagic copepods, *Blastodinium* sp.

Despite this high assimilation rate SWANBERG & HARBISON (1980) calculated that this could provide only 0.4 to 0.7 % of the host cell carbon per hour. They also found that the nutritional state of the host had a considerable effect on the photosynthetic performance of the zooxanthellae, the latter being greater if the host had previously been well fed heterotrophically (judging by retained tintinnid loricae).

With the increasing use of transmission electron microscopy it has become evident that the presence of bacteria in the cytoplasm of protists is commonplace,

particularly in phagotrophs. Those inhabiting ciliates, and particularly those imparting « killer » properties to their host paramecia, have been fairly extensively studied, but there are only a few reports of bacteria in marine microplanktonic ciliates. LAVAL (1970) illustrated the presence of bacteria within the macronucleus of *Zoothamnium pelagicum* Du Plessis which later go to the cytoplasm. Others are in the vesicular reticulum of the tintinnids *Petalotricha ampulla* (Fol) and *Cyrtarocyclus brandti* K. & C. (LAVAL, 1972, LAVAL-PEUTO, 1975). Very few ultrastructural studies have been carried out on pelagic ciliates so far and it may be expected that cytoplasmic bacteria are equally commonplace in marine and freshwater ciliates. Their presence in the nucleus of these organisms is more extraordinary, considering that the nuclear envelope remains intact during mitosis in ciliates, but a one-way release from the macronucleus to the cytoplasm can occur each time macronuclei disintegrate following sexual reproduction when new macronuclei are formed from micronuclei. How do they get into the nucleus in the first place? LAVAL did not see them in micronuclei. What influence do they have, inhabiting such a sensitive organelle? The occurrence of bacteria within permanently closed nuclear envelopes is not unique to this case, having been observed in several groups, including freshwater euglenoids (LEEDALE, 1969).

Intracellular bacteria have also been reported from marine dinoflagellates. Light microscope observations of apparent bacteria in the vacuoles of dinoflagellates by GOLD & POLLINGER (1971) were not confirmed by electron microscopy: instead it revealed that they are rod- or chevron-shaped crystalline particles, usually referred to as « scintillons », present in many dinoflagellates (POKORNY and GOLD, 1973). This may also have been the nature of some of the bacteria-like bodies seen by SILVA (various refs. in SILVA, 1978). Others accompany decomposition in recently dead cells. SILVA (*loc. cit.*) was able to confirm the presence of intranuclear bacteria in *Gymnodinium sanguineum* Hir. (= *splendens* Leeb.) and *Kryptoperidinium (Glenodinium) foliaceum* (Stein) Lind. She noted no harmful effects in the host dinoflagellates after several months of infection in culture. A search of 32 strains of 20 other species of dinoflagellates did not reveal any further intracellular bacteria. Similarly, a search for bacteria within the toxic species *Gambierdiscus toxicus* Adachi & Fukuyo as a possible source of ciguatera has not revealed any obvious bacterial cytobionts (TAYLOR, unpubl.).

### 3.2. Cyanobacterial cytobionts.

Since its description by SCHMIDT (*in* OSTENFELD & SCHMIDT, 1901) the filamentous cyanobacterium (blue-green alga) *Richelia intracellularis* Schm. has been observed within the cells of planktonic diatoms by many authors (*fig. 20*). HUSTEDT (1930) illustrated and discussed it briefly in his monumental work on marine diatoms and SOURNIA (1970) has summarised earlier information in a general review of marine planktonic cyanobacteria. Although several species can act as hosts they are usually within a predictable spectrum. They are chiefly members of the genus *Rhizosolenia*: *Rh. acuminata* (Perag.) Gran, *Rh. castracane* Perag. (listed as questionable by SOURNIA but confirmed by this author on the basis of Andaman Sea material), *Rh. clevei* Ost., *Rh. cylindrus* Cl., *Rh. firma* Karst., *Rh. hebetata* Bail., *Rh. imbricata* Brightw., and *Rh. styliformis* Brightw. This author has observed a population of *Rh. bergonii* Perag. off the east coast of Africa that was infected more than 95% (TAYLOR, thesis, 1964, *unpubl.*). VERNICK (1974) noted that 94-98% of three *Rhizosolenia* species (*acuminata*, *hebetata*, *cylindrus*) found in 9 years of sampling the central Pacific were infected, whereas five other *Rhizosolenia* species, including some of the above which are infected in other regions (e.g. the Indian Ocean), were not. *Rh. stollerfothii* Perag. has never been seen to possess *R. intracellularis* and neither has *Rh. delicatula* Cl. although both co-occur with those above. SOURNIA (1970) lists the following as questionable records: *Rh. alata* Brightw., *Rh. setigera* Brightw., *Rh. similis* Karst., and *Rh. temperei* Perag. (all listed by HUSTEDT, 1930, but not subsequently confirmed). The filaments consist of six to 14 cells, with a larger, rounded terminal cell which has usually been referred to as a heterocyst. It generally resembles that structure as seen in other genera but differs in having only a marginally thicker wall than the normal cells and not showing as much pigment loss as is usual. It does have a pore-like opening on the filament side. Quite often only this body will be seen, particularly if the host cell is dead (often in empty frustules), suggesting that it can serve as an akinete (reproductive spore). KIMOR *et al.* (1978) found that this was the normal condition at the end of a bloom of *Hemiaulus membranaceus* Cl.

Within *Rhizosolenia* hosts the arrangement is always precise. Shortly following diatom division

*Richelia* is present at only one end. In narrow species, such as *Rh. hebetata*, there is only one filament at this stage, but in wider species (e.g. *Rh. castracane*) there can be as many as 11 at one end. The heterocyst is always at the pole (valve end). The filament is usually embedded in the host cytoplasmic strands, rather than in the large vacuole usually present. As it grows a heterocyst develops at the opposite end of the filament, the filament separates in the middle, and the daughter filament migrates to the opposite end without change in orientation, its heterocyst thus directed towards the opposite valve. This movement may be accomplished by the cytoplasmic streaming of the host which can be strong in some *Rhizosolenia* species. If this migration does not take place one of the subsequent diatom daughters will not receive the *Richelia*.

*R. intracellularis* is only present in tropical to subtropical waters. A particularly interesting aspect of VERNICK's study was the discovery that, although the host species can extend well beyond 38°N in the North Pacific, the cyanobacterium does not. Because of the heterocyst-like cell in the filament it has been natural to suspect that the species may be capable of nitrogen fixation, a definite asset for both partners in oligotrophic oceanic waters. MAGUE *et al.* (1974) demonstrated significant acetylene reduction (the most commonly used indirect index of nitrogen fixation) associated with a *Rhizosolenia* bloom infected by *R. intracellularis*. If any of this fixed nitrogen were available to the host diatoms (as yet unknown) this could be a key explanation for this otherwise unusual cytobiosis involving two photosynthetic partners (TAYLOR, 1979).

Although it is usually species of *Rhizosolenia* that act as hosts, there are occasional reports of the association in *Hemiaulus hauckii* Grun. (SOURNIA, 1970) and *H. membranaceus* (KIMOR *et al.*, 1978). As noted earlier, it can also occur rarely on the exterior of diatoms, or even more rarely, free in the plankton.

According to NORRIS (1967) the chloroplast-like bodies of the dinoflagellate *Amphisolenia globifera* Stein, the silicoflagellate *Dictyocha speculum* Ehr. and the diatom *Streptotheca thamesis* Shrubbs. (= *S. indica*) are coccoid cyanobacteria (« cyanelles »). If confirmed, this raises the question as to how many of the bodies assumed to be chloroplasts in related organisms are cyanelles (*see* KIES, 1980 for a review of well-established cyanelles in fresh-water organisms).

### 3.3. Photosynthetic cytobionts of Actinopods.

The photosynthetic cytobionts of radiolarians (polycystines) have been reviewed recently by ANDERSON (1980) and so only principal points, or features not discussed by him, are included here. The « gelbe Zellen » (yellow cells) of the colonial radiolarian *Collozoum inerme* J. Müller served as the type species for the genus *Zooxanthella*: *Z. nutricula* (commonly mis-spelled *nutricula*) Brandt. Although the original description was minimal it has been possible to re-examine the host species using electron microscopy, thus providing a much expanded description. The « zooxanthellae » from *Collozoum* in the Mediterranean (HOLLANDE & CARRÉ, 1974) and the Sargasso Sea (ANDERSON, 1976) are essentially similar except that the latter have been reported as being smaller (d. 7.5 µm) than the former (d. 11-14 µm). Those in *C. longiforme* are 11-12 µm (SWANBERG & HARBISON, 1980). Key features (other than common dinoflagellate ones) which can be used to recognise this genus are: cytobiont lacking amphiesmal vesicles (equivalent to a cyst stage), pyrenoids (2 to 8) with multiple stalks and penetrated by thylakoids. HOLLANDE & CARRÉ (1974) found that *Endodinium chattonii* Hovasse (1923), the zooxanthella from the siphonophore *Vellela*, is essentially similar, although a wall is less well developed (this is variably developed in various coelenterate hosts by the zooxanthella *Symbiodinium microadriaticum* Fr. (SCHOENBERG & TRENCH, 1980). The motile stage of *Z. nutricula* resembles the free-living dinoflagellate genus *Gymnodinium* Stein (fig. 8) although the transverse flagellum seems longer than normal (HOLLANDE & ENJUMET, 1953). D. TAYLOR (1974) has proposed that the nature of the motile cell (« mastigote ») should be the principal guide to the allocation of the species to genus. However, there is a significant life-cycle difference between the species of this zooxanthella genus (shared by another: *Symbiodinium* Freudenthal) and *Gymnodinium*. The latter divides only in the motile mastigote stage, whereas these zooxanthellae divide in the non-motile, cyst-like, amastigote stage. Greater emphasis is being placed on such differences in current dinoflagellate taxonomy than before (TAYLOR, 1980 a). D. TAYLOR (1971) has reported an *Amphidinium*-like motile stage for *Endodinium chattonii* and, if confirmed, this could provide a basis for distinguishing *Zooxanthella* from *Endodinium*. HOLLANDE & CARRÉ (1974) evidently did not consider it established, and

placed *Z. nutricula* BRANDT (1881) in the same genus with *E. chattonii* HOVASSE (1922), but inexplicably retained the name *Endodinium* instead of *Zooxanthella* although the latter clearly has priority. Most of the zooxanthellae from multicellular invertebrates conform in morphology to *Symbiodinium microadriaticum* Fr., the type species of *Symbiodinium*, differing from *Z. nutricula* in the possession of only one (rarely two) pyrenoids with single stalks and no penetration by thylakoids. Recently LÖEBLICH & SHERLEY (1979) have combined all these taxa into the genus *Zooxanthella*, without explanation for disregarding the distinction proposed by HOLLANDE & CARRÉ (1974). In this author's view the pyrenoid features are a sound basis on which to separate the genera in question, a view shared with SCHOENBERG & TRENCH (1980). The dinoflagellate zooxanthellae of several planktonic foraminifera appear to exist principally in a stage equivalent to the mastigote, recognisable by the presence of amphiesmal vesicles even though the flagella are not developed (section 3.4 and TAYLOR, 1980 a). This would exclude them from any of the above genera.

The zooxanthellae of actinopods occur in the ectoplasm of radiolarians (many spumellarians and nasse-larians, but not reported in any phaeodarians so far) and the endoplasm of many acantharians (Table III). Because of their evident photosynthetic nature and their life within non-photosynthetic hosts, it was natural to suppose that a close, cyclic, mutualistic relationship exists (e.g. GEDDES, 1882) with the waste or excess of one of the raw materials, for the other. However, as ANDERSON (1980) has noted, there is little direct evidence for this. He has found that they can fix <sup>14</sup>C, but has also obtained cytochemical and ultra-structural evidence for the digestion of the zooxanthellae by *Collozoum inerme* J. Müll., at least under some circumstances. The number of zooxanthellae per cell (usually approximately 20-30 although as many as 2,000 may be present in a colony), decreases in prolonged dark conditions. In *Collosphaera globularis* Hekl. he could find no signs of digestion of the zooxanthellae. Under some circumstances the cytobionts may outlive their hosts (GEDDES, 1882). As the zooxanthellae are not present in the gametes they must be taken up afresh after sexual reproduction.

Not all « zooxanthellae » (used in the usual loose sense to refer to any golden brown symbionts) in actinopods are dinoflagellates. HOLLANDE & CARRÉ (1974) noted that those in one species of *Acanthometra* were not similar to dinoflagellates in ultra-



structure, and FEBVRE & FEBVRE-CHEVALIER (1979) have shown that those of the acantharia *Lithoptera muelleri* Heckl., *Amphilonche elongata* J. Müll. and *Acanthometra pellucida* J. Müll., both large (ca. 15 µm) and small (7 µm), have ultrastructural features similar to the prymnesiomonads *Chrysochromulina* and *Prymnesium* (immersed pyrenoids traversed by tubular elements, occasional scales on the cytobiont surface, microtubular features). They are more likely to encounter the former in their habitat as the latter is a brackish water genus.

Green cytobionts are loosely termed « zoochlorellae » (after another genus proposed by BRANDT, 1881, but no longer recognised). NORRIS (1967) suggested that the zoochlorellae present in the ectoplasm of some spumellarians (taxa not specified) may be prasinomonads; possibly encysted stages of *Pyramimonas*. More recently CACHON & CARAM (1979) have demonstrated the prasinomonad nature of the minute zoochlorellae in the radiolarian *Thalassolampe margarodes* Heckl. They attributed it to a new species: *Pedinomonas symbiotica*. It is very similar to the *Pedinomonas* occurring within the dinoflagellate *Noctiluca* (see section 3.5) and to the free-living nanoplankton *Micromonas pusilla* (Butcher) Manton & Parke, but the latter is always uniflagellate whereas *Pedinomonas* may pass through a biflagellated stage.

Although BRANDT (1883) reported cryptomonad-like motile stages associated with some radiolaria and foraminifera, there are no modern critical identifications of cryptomonad cytobionts in these groups. A cryptomonad is cytobiotic in the ciliate *Mesodinium rubrum* Lohm. (Section 3.6).

Because of the relative abundance of acantharians in oligotrophic tropical oceanic waters, often not appreciated because they preserve very poorly, their strontium sulphate spicules dissolving rapidly after

death, and because many possess zooxanthellae (unpublished observations by this author on live populations north of Puerto Rico in February, 1978 indicated that 70 % of those in the upper 50 m possessed zooxanthellae), their potential contribution to the primary productivity of these impoverished waters deserves study.

Curiously, although subeuphotic foraminifera lack zooxanthellae (next section) KIMOR & WOOD (1975) found acantharians with zooxanthellae containing chlorophyll occurring deeper than 4,000 m. in the Eastern Mediterranean Sea. One of these was *Lithoptera muelleri* Heckl., a species with prymnesiomonad (coccolithophorid) zooxanthellae (see earlier).

### 3.4. Photosynthetic cytobionts of planktonic foraminifera.

The situation in foraminifera is generally similar to that in actinopods, i.e. zooxanthellae present in the cytoplasm of many (Table III). Zoochlorellae, in the usual sense of Chlorophyceae/Volvocales and Prasinophyceae cells, are restricted to benthic forms so far. The cytobionts of planktonic species have been recently reviewed by BÉ *et al.* (1977) and SPINDLER & HEMLEBEN (1980). Foraminiferal symbioses have generally received more experimental attention than actinopods, but this has been focussed mainly on the benthic forms, such as nummulitids and soritids (e.g. LEE *et al.*, 1979; LEE, 1980).

The number of recent, planktonic foraminiferal species is rather small (ca. 31 spp.). Most of those occurring predominantly within the euphotic zone have been found to support photosynthetic cytobionts (seven spinose and two non-spinose species reported so far: Table III), all predominantly warm water species.

TABLE III. — Cytobiont-containing planktonic Foraminifera.

Host	Cytobiont type	Cytobiont size
<i>Orbulina universa</i> d'Orb.	Dinoflagellate	5 × 8 µm
<i>Globigerinoides conglobatus</i> (Brady)	Dinoflagellate	5 × 8 µm
<i>Globigerinoides ruber</i> d'Orb.	Dinoflagellate	6-10 µm
<i>Globigerinoides sacculifer</i> (Brady)	Dinoflagellate	5 × 8 µm
<i>Globigerina cristata</i> H.-A. & Earl	Dinoflagellate	5 × 8 µm
<i>Globigerina bulloides</i> d'Orb.	Dinoflagellate (or absent)	5 × 8 µm
<i>Globigerinella aequilateralis</i> (Brady)	Prymnesiomonad ?	Small
<i>Globorotalia menardii</i> (d'Orb.)	Prymnesiomonad ? *	1.3-2.7 µm
<i>Pulleniatina obliquiloculata</i> (Parker & Jones)	Prymnesiomonad ? *	ca. 2.5 µm

\* Stated to be zoochlorellae by BÉ *et al.* (1977) but ultrastructure inconsistent with a prasinomonad or chlorophycean cytobiont.

Five of them contain dinoflagellate cytobionts (as indicated by their distinctive chromosomal structure plus other consistent features). Most of these are similar in size (length 8-10  $\mu\text{m}$ ) and are unusual in several related respects. The cells are pyriform or spindle-shaped, rather than semi-spherical or roundly ovoid. In a few, e.g. in *G. ruber*, there is a median constriction reminiscent of the girdle furrow of motile forms. In dinoflagellates the cyst is usually surrounded by a continuous, cellulosic wall with a sporopollenin-like layer, but the mastigote motile cell has a single layer of « amphiesmal vesicles » lying just beneath the cell membrane (discussed further by TAYLOR, 1980 a). The vesicles may be empty, or may contain a very thin, membranous layer, as in *Gymnodium fuscum* (Ehr.) Stein, or may be filled by substantial cellulose plates (in « armoured »/thecate dinoflagellates). In several of the published micrographs of planktonic foraminiferal zooxanthellae (eg. in *G. sacculifer* : ANDERSON & BÉ, 1976) it appears that there are peripheral amphiesmal vesicles containing very thin « plates », although it is difficult to be certain, i.e. the cells appear to correspond to the motile, rather than the non-motile, cyst-like stage in which most dinoflagellate zooxanthellae occur within their hosts, even though the flagella are not developed within the host. They also possess multiple pyrenoids like *Zooxanthella* Brandt, although they appear to have single stalks, and the life-cycle difference should be enough, in this author's view, to distinguish them from the latter genus. Their affinities can be sought among the free-living species in which multiplication is in the vesiculated (usually motile) stage. ANDERSON & BÉ (1976) and SPINDLER & HEMLEBEN (1980) have compared them with the free-living taxon *Aureodinium* Dodge. The latter is not generally recognised as distinct from *Gymnodinium* Stein by recent authors, now that it is realised that the type species of the latter possesses delicate, membranous structures within its amphiesmal vesicles. However, the type species, *A. pigmentosum* Dodge, does possess stalked pyrenoids.

*Globigerina bulloides* d'Orb. has been observed with (SPINDLER & HEMLEBEN, 1980) and without (LEE *et al.*, 1965; FEBVRE-CHEVALIER, 1971) cytobionts.

Three planktonic species were thought to possess zoochlorellae by BÉ *et al.* (1977) but are now known to have extremely small (less than 5  $\mu\text{m}$  diameter) coccoid cells with the ultrastructural characteristics of chryomonads or prymnesiomonads (= Hapto-

phyceae). Coccolithophorids (grouped with the prymnesiomonads) are the nanoflagellate group most likely to be encountered in the tropical oceanic environment. True chlorophycean cytobionts have been found in some benthic species (e.g. *Chlamydomonas* spp. in some soritids : LEE *et al.*, 1979) and other benthic associations involve diatom cytobionts which only develop their walls when cultured independently of their hosts (SCHMALJOHANN & RÖTTGER, 1976; LEE *et al.*, 1980). Benthic species can also support dinoflagellates, some of which resemble the very wide-spread taxon *Symbiodinium microadriaticum* Freudenthal).

There can be several hundred cytobionts per host foraminiferan, occurring in the peripheral rhizopodial network and/or in the shell chambers. ANDERSON & BÉ (1976) observed that there was a light-dependent circadian rhythm of ingress and egress of the zooxanthellae with relation to the host body : in the light they occur in the most centrifugal position, in rhizopodia extended far from the body, but are drawn into the body in the dark. Presumably such movements optimise illumination and exchange, but the events in each position have not been examined in detail yet. Deeper-occurring species lack photosynthetic cytobionts, e.g. *Globorotalia hirsuta* (d'Orb.).

All the cytobiont-containing foraminifera are omnivorous and it is possible to observe diatoms and zooplankton in evident states of digestion together with intact zooxanthellae. Unlike radiolarians, there has been no clear indication of the hosts digesting their cytobionts, although this cannot be ruled out. Like radiolarians the gametes do not possess cytobionts and the young foraminifera must be re-infected from their surroundings. Once again, the contributions of host to cytobiont and vice-versa can only be speculated about at present. In foraminifera there exists an added possibility of the cytobionts playing a beneficial role in shell calcification, but this is presumably more usable by heavily calcified, benthic forms. The cytobionts may contribute energetically, or facilitate the process by removing the phosphate thought to interfere with calcification.

### 3.5. Non-parasitic cytobionts of dinoflagellates.

Although dinoflagellates are the group most often cohabiting with other plankton organisms, they can play host to other organisms themselves. For example, although *Noctiluca scintillans* McCartney (= *miliaris*)

is a voracious phagotrophic predator on all manner of cells smaller (and occasionally slightly larger) than it, populations in the East Indies and off the coasts of India are frequently infected by large numbers of a minute prasinomonad, *Pedinomonas noctilucae* (Subr.) Sweeney. SUBRAHMANYAN (1954) thought it was a euglenoid and named it *Protoeuglena noctilucae*, but subsequent study (SWEENEY, 1971, 1976) revealed its real affinities. As many as 12,000 unflagellated cells, 2-6  $\mu\text{m}$  in length, can be found swarming and reproducing within the general vacuole of a single *Noctiluca*. Several authors, dating back to 1890 (see refs. in SUBRAHMANYAN, 1954) have observed the same phenomenon from the same region but not all *Noctiluca* in the Indo-West Pacific are thus infected. TAYLOR (1976) did not see any obviously infected *Noctiluca* in International Indian Ocean Expedition samples although those in a bloom off the mouth of the Irrawaddy River, Andaman Sea, were feeding on a poorly preserved microflagellate of similar size to *P. noctilucae*. SWEENEY (1971) found that infected *Noctiluca* can survive in the light, but not the dark, without an external food source. If fed *Dunaliella* they remained healthy, but lost the *Pedinomonas*. They retained their luminescent capacity.

Mention has been made earlier of NORRIS's (1967) claims of cyanelles in some dinophysoid dinoflagellates. In addition GEDDES (1882) cited a personal communication from « M. de Merejkowsky » (presumably C. Mereschkowsky of symbiotic-origin-of-chloroplasts fame, his Russian name being variously transliterated) to the effect that algal cells may occur in *Ceratium tripos* (O. F. Müller) Nitzsch. There have been no further observations on either of these.

Some better known, and more unusual, cytbionts are those occurring within *Peridinium balticum* (Lev.) Lemm. and *Kryptoperidinium (Glenodinium) foliaceum* (Stein) Lind. (fig. 10), both brackish-water, temperate species (reviewed by TAYLOR, 1979). In both cases it has been found that double nuclei were present, one typical of dinoflagellates, and one with a more common-place eukaryotic appearance (DODGE, 1971; TOMAS, COX & STEIDINGER, 1973). Subsequently it was discovered that both the ultrastructure and pigments of the chloroplasts of these two species were anomalous for dinoflagellates (full references cited by JEFFREY & VESK, 1976). These curious observations became more understandable when it was found that, in both, the chloroplasts were joined by a common cytoplasm to the non-dinoflagellate nucleus, separated by only a single membrane from

the dinoflagellate cytoplasm. They are therefore highly integrated, eukaryotic cytbionts ramifying throughout the host dinoflagellate. They make the host fully autotrophic. A further intriguing observation is that both host dinoflagellates appear to contain chloroplast vestiges in the form of eyespots surrounded by the distinctive three-membrane envelope of dinoflagellate (and euglenoid) chloroplasts indicating that they lost their own photosynthetic abilities in the past (TAYLOR, 1979). Both species can form dense blooms in brackish coastal waters (e.g. uninucleated *P. balticum* in pools on the Baltic coast of Denmark, July 1975, TAYLOR, 1979).

These are not the only dinoflagellates with two dissimilar nuclei. *Pseliodinium vaubanii* Sournia, a non-photosynthetic species, appears to have a second, non-dinoflagellate nucleus (see JACQUES & SOYER, 1977), but this has not been confirmed yet with electron microscopy.

### 3.6. Photosynthetic cytbioses in planktonic ciliates.

KAHL's (1935) general ciliate work contains many references to cytbiont-like bodies in marine species, but very few are planktonic. GEDDES (1882) and BRANDT (1883) refer to pigmented bodies in *Vorticella* sp.

A very similar condition to that described for the two dinoflagellates immediately above has been observed in the unusual gymnostome ciliate *Mesodinium rubrum* Lohm. (= *Cyclotrichium meunieri* Powers: see TAYLOR *et al.*, 1971 for details and fig. 5, 6, 18, 19 here). It has been recently reviewed in an evolutionary context by TAYLOR (1979). *M. rubrum* is a cosmopolitan neritic ciliate with a dark maroon colour due to the presence of from less than ten to more than 100 pigmented bodies within it. It is a common cause of non-toxic « red water » blooms in both temperate and warm coastal waters (principally upwelling zones in the latter: TAYLOR *et al.*, 1971, PACKARD *et al.*, 1978). In these areas it can be a significant primary producer (PACKARD *et al.*, 1978; SMITH & BARBER, 1979 and earlier refs. therein).

Ultrastructural studies (TAYLOR *et al.*, 1971; HIBBERD, 1977; OAKLEY & TAYLOR, 1978) have revealed that the pigmented bodies are chloroplasts with pyrenoids projecting towards the centre of the ciliate (fig. 19). Their ultrastructure, together with pigment characteristics and other ultrastructural features

(mitochondrial morphology, presence of curious structures resembling vestigial nuclei, termed « nucleomorphs ») leave little doubt that they are of cryptomonad origin. However, there are several very peculiar features of this association. Although there are a few cryptomonads with multiple chloroplasts recorded in the early literature, none have been confirmed by modern methods. There is one (sometimes two, possibly after division of the symbionts) large cryptomonad nucleus in the centre of the ciliate, close to the two macronuclei and single micronucleus of the latter (*fig. 6*). In a population from British waters examined by HIBBERD (1977) all the chloroplasts and other cryptomonad organelles were found to be in a common cytoplasmic matrix, separated from the ciliate by a single membrane, i.e. a situation very similar to that in the binucleate dinoflagellates described above. However, serial sectioning revealed that occasional « blebs » containing a single cryptomonad chloroplast and mitochondrion (and, possibly, nucleomorph) were not connected to the nuclear-chloroplast matrix. In populations from the coastal waters of British Columbia (TAYLOR *et al.*, 1971; OAKLEY & TAYLOR, 1978) most of the chlo-

roplasts and mitochondria exist in islands of cytoplasm separated from the cryptomonad nucleus and this may have been the case in a population off New Brunswick, Canada (WHITE *et al.*, 1977). This condition appears to be unique among symbioses.

The ciliate also exhibits modifications that appear to be adaptative responses: the oral cone is reduced, the mouth is vestigial, lacking the oral tentacles found in several closely related species (e.g. *M. pulex* Cl. & Lachm.), the pellicle is reduced and lacks alveoli, the ciliate swims with the oral end posterior instead of anterior, and it shows marked phototactic behaviour (although it avoids intense sunlight). It can sustain migration of 2-7 m per hr., an order of magnitude greater than flagellates (SMITH & BARBER, 1979) and, with beats of its cirri it can make « jumps » of 0.6-2.0 mm/sec. (PACKARD *et al.*, 1978). The cells disintegrate very easily, probably because of the lack of peripheral strengthening.

Although attempts to culture the consortium have been unsuccessful so far, information concerning its physiology and ecology has been obtained from intense ( $2 \times 10^6$  per L. or more), virtually mono-

---

 FIGS. 16-21.
 

---

- FIG. 16. — One end of a cell of *Rhizosolenia* sp. with several filaments of *Richelia intracellularis* (arrows) within its cytoplasmic strands. Orig., Andaman Sea.  $\times 300$ .
- FIG. 17. — Detail of several filaments of *R. intracellularis* from the interior of *Rhizosolenia castracanei*. H, « heterocyst ». From TAYLOR (1980 b), with permission.  $\times 500$ .
- FIG. 18. — A large individual of *Mesodinium rubrum*, preserved with Lugol's Iodine (which causes loss of the cirri and disorganisation of the cilia), containing numerous cytobiont chloroplasts. Arrows indicate starch sheaths. From TAYLOR (1980 b), with permission  $\times 1310$ .
- FIG. 19. — Cytobiont « island » from *M. rubrum*, containing a chloroplast (C.), mitochondrial sections (m) and a pyrenoid (p). Arrows in the chloroplast indicate plastoglobuli. Photo courtesy of B. OAKLEY.  $\times 19\,000$ .
- FIG. 20. — Portion of the outer cytoplasm of *Strombidium* sp., with chloroplasts (arrowed). Orig., from British Columbia.  $\times 10\,000$ .
- FIG. 21. — Vegetative cyst of *Zooxanthella nutricula* from the radiolarian *Collozoum inerme*. Photo courtesy of O. R. ANDERSON. Ac, accumulation body; Nu, nucleus; P, pyrenoid (only one of several stalks visible).  $\times 4\,700$ .

## FIG. 16-21.

- FIG. 16. — L'une des extrémités d'une cellule de *Rhizosolenia* sp.; plusieurs filaments de *Richelia intracellularis* sont visibles (flèches) dans les trabécules du cytoplasme de la Diatomée. Mer d'Andaman; original.  $\times 300$ .
- FIG. 17. — Détails de quelques filaments de *R. intracellularis* à l'intérieur de *Rhizosolenia castracanei*. H, hétérocyste. D'après TAYLOR (1980 b), avec l'autorisation des Editeurs.  $\times 500$ .
- FIG. 18. — Une grande cellule de *Mesodinium rubrum*, conservée au lugol iodé (ce qui provoque la perte des cirres et la désorganisation des cils), avec nombreux chloroplastes cytobiotiques. Les flèches indiquent les enveloppes d'amidon. D'après TAYLOR (1980 b), avec l'autorisation des Editeurs.  $\times 1\,310$ .
- FIG. 19. — Cytobionte « insulaire » de *M. rubrum*. C, chloroplaste; m, sections de mitochondries; p, pyrénioïde. Les flèches dans le chloroplaste montrent les plastoglobules. Microphotographie aimablement fournie par B. OAKLEY.  $\times 19\,000$ .
- FIG. 20. — Partie externe du cytoplasme de *Strombidium* sp. avec chloroplastes (flèches). Colombie Britannique; original.  $\times 10\,000$ .
- FIG. 21. — Cellule végétative de *Zooxanthella nutricula* associée au Radiolaire *Collozoum inerme*. Ac, corps d'accumulation; Nu, noyau; P, pyrénioïde (un seul des nombreux pédoncules est visible). Microphotographie aimablement communiquée par O. R. ANDERSON.  $\times 4\,700$ .

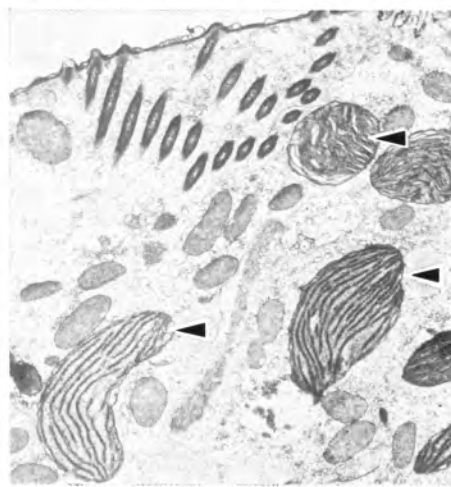
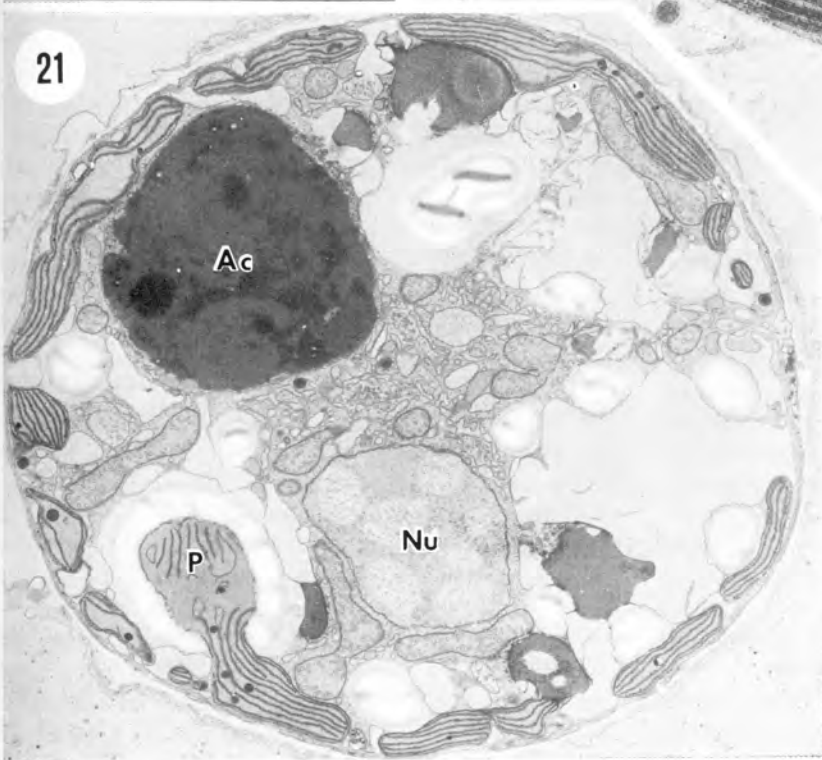
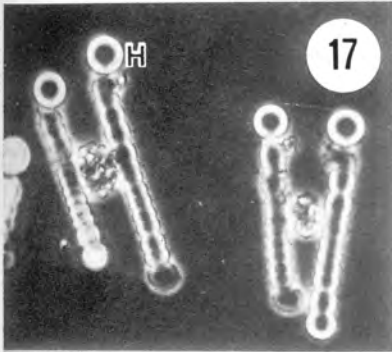
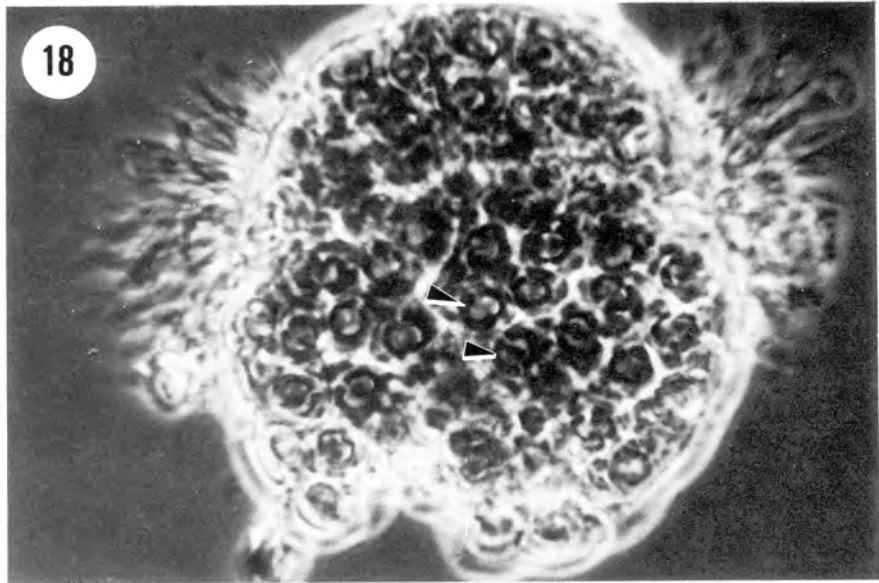
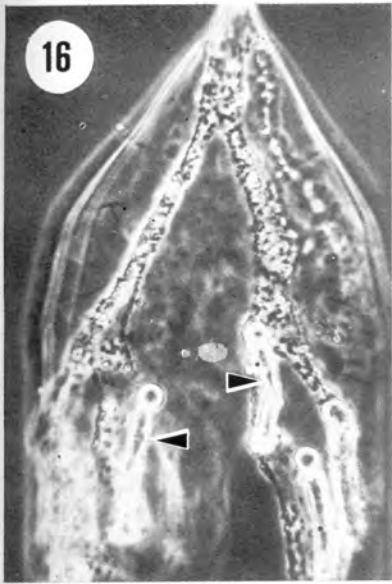


FIG. 16 to 21.

specific blooms. The consortium is a « functional autotroph ». BARBER *et al.* (1969) showed that such blooms fix  $^{14}\text{C}$ , evolve oxygen and incorporate  $^{32}\text{P}$ . PACKARD *et al.* (1978) found significant nitrate reductase activity (a key enzyme in the assimilation of nitrate by phytoplankton) produced by the consortium, an enzyme which has not been found previously in any animal association.

In upwelling zones *M. rubrum* is able to utilise its strong swimming ability (at high energetic cost) to exploit freshly upwelled water. It typically occurs on the downwelling side of convergence fronts (fig. 22). Of all the associations dealt with in this paper this species is the most ecologically significant as it is a

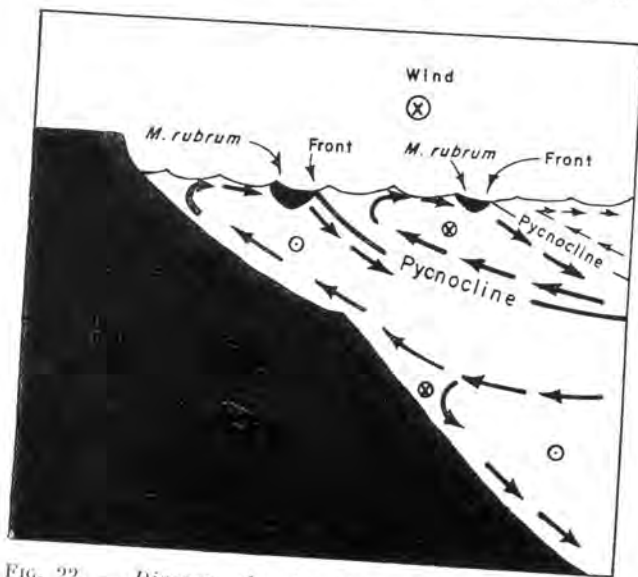


FIG. 22. — Diagram showing the relation of blooms of *Mesodinium rubrum* to upwelling water circulation cells off Baja California. The ciliate is able to swim against the descending flow at the fronts. From PACKARD *et al.* (1978), with permission.

FIG. 22. — Prolifération de *Mesodinium rubrum* dans les cellules hydrodynamiques de l'« upwelling » de Basse Californie. Dans les zones frontales, la motilité du Cilié lui permet de s'opposer au flux descendant. D'après PACKARD *et al.* (1978), avec l'autorisation des Editeurs.

major primary producer in upwelling regions, the dinoflagellate analogues being more distributionally restricted. It represents the greatest degree of integration between host and photosynthetic cytotient.

### 3.7. Chloroplast maintenance by planktonic ciliates.

Some of the pigmented bodies illustrated by KAHL (1935) and thought to be food bodies may be more interesting than that. With the aid of electron microscopy BLACKBOURN *et al.* (1973) discovered that the small, brownish, oval bodies within some individuals of the gymnostome *Prorodon* sp. and the oligotrich ciliate *Strombidium* sp. are chrysoomonad or diatom-like chloroplasts lying embedded in the cytoplasm (fig. 20). Most of these were in remarkably good condition, especially those near the periphery of the cells. In *Strombidium* there were signs of digestion of the chloroplasts near the base of the cytostome.

These seem to represent unicellular analogues to the better known cases of the maintenance of foreign chloroplasts in a temporarily functional state by sea hares (sacoglossan, opisthobranch molluscs — see TAYLOR, 1974, 1979; TRENCH, 1975, 1980). Although direct evidence for their functionality in ciliates is not available HOLM-HANSEN *et al.* (1970) found that a bloom of pigmented *Prorodon* (apparently the same species as that examined by BLACKBOURN *et al.*, 1973) at Barrow, Alaska, contained abundant chlorophyll *a* with very little phaeophytin (the breakdown product most commonly observed when phytoplankton are subject to digestion by zooplankters). The ultrastructural condition of the chloroplasts was as good, or better than that in chloroplasts known to be functional in the sea hares.

BURKHOLDER *et al.* (1967) have reported  $^{14}\text{C}$ -fixation during an oligotrich ciliate bloom near Puerto Rico which BLACKBOURN *et al.* (1973) have suggested may have been due to chloroplast maintenance.

## 4. DISCUSSION

In a recent review on the nutritional physiology of foraminifera LEE (1980) quantified existing data as « pitifully little ». This is undoubtedly apt. When one considers that nearly all the information he used was, by necessity, from studies on benthic species,

and that most of the studies on microzooplankton symbioses have concerned foraminifera, one gets an indication of the state of knowledge covered by this review. A lot of this discussion is speculative. It can only be justified by its role as a background against

which to examine new data or as a potential provocation of interest in these fascinating but neglected associations.

Even in superficial aspects it is evident that the examples included here cover as great a range of associational types as those conventionally studied;— from adventitious external attachments or chronic indigestion, to such strong integration that the cytobiont almost can be considered an organelle of the host;— from almost random attachment to strictly unispecific symbioses; from ecologically trivial to regionally significant. Another striking aspect is that the taxonomy is in a state of flux, as indicated by the abundance of names in parentheses throughout the text. The latter is due principally to the application of electron microscopy. Many of the cytobionts can only be identified by this means because their association leads to loss of distinctive gross features such as flagellation or sculptured walls. Also, the distinction between several groups, particularly among the microalgae, is based largely on ultrastructural features.

#### 4.1. Degree of interactions and specificity.

The epibionts, unsurprisingly, show the least interaction with the host and also, generally, the least specificity. Even here there are interesting questions to be pursued: what is the basis for the lack of bacterial or microflagellate growth on planktonic diatom walls? Are the coccoid cyanobacteria that live within the chamber-like lists of some dinophysoid dinoflagellates capable of nitrogen fixation? Is the occurrence of coccolithophorids on certain centric diatoms adventitious? The greatest specificity is shown by the occurrence of the mysterious organism *Solenicola* solely on the diatom *Leptocylindrus mediterraneus*. Is it a parasite, or perhaps even a life-cycle stage of the host? Although not quite as specific, the hosts in the tintinnid-*Chaetoceros* phoretic relationship are closely related (all *Eutintinnus*) and the two diatoms are morphologically very similar to each other. In some instances the epibionts may be trapped during normal feeding and neither digested, nor egested by the host. This may be the case for the large, cyst-like dinoflagellates (*Dissodinium*, *Pyrocystis*) adhering to the bubble capsule of the foraminiferan *Hastigerina pelagica*, although the reason they are not rejected may be partly related to some benefit to the host.

#### 4.2. Cytobiont adaptations.

Some epi-, or even cytobionts, show little or no apparent morphological adaptation to their association when compared with their close relatives. Habitually sessile organisms, such as the choanoflagellates, bicosoecids, and the loricate and non-loricate peritrich ciliates (*Vorticella*, *Vaginicola*) are already adapted, as groups, to a substrate associated existence, often with little difference as to whether it is animated or not, and do not undergo further, transient modifications. The least modified cytobiont species in the examples used here is the nanoflagellate *Pedinominas noctilucae*, which happily swims in the low pH vacuole of *Noctiluca* as if it were an internal sea. Even the pedinomonads in the cytoplasm of the radiolarian *Thalassolampe* show no obvious modifications.

Others show considerable departures from their close relatives that appear to be due to their associations. The morphological modifications that occur in endozoic microalgae tend to follow a general pattern (D. TAYLOR, 1973; TRENCH, 1979), with loss of flagella and a reduction in vegetative wall structure being the most commonly observed changes. The dinoflagellate zooxanthellae in spinose planktonic foraminifera appear to have lost only their flagella and some surface features, while retaining the vesiculated amphiesmal region typical of the motile form. The putative prymnesiomonad zooxanthellae in actinopods seem to have done the same, with a reduction in scales (but visible in some — FEBVRE & FEBVRE-CHEVALIER, 1979) or coccoliths. Other dinoflagellate zooxanthellae, such as *Zooxanthella nutricula* and *Symbiodinium microadriaticum* appear to have responded to an intracellular existence by forming a continuous cyst wall (to a varying extent even though they remain metabolically active « vegetative cysts »). They divide in this state rather than in the motile phase. The most radically modified cytobionts are those which occur in the dinoflagellates *Peridinium balticum* and *Kryptoperidinium foliaceum*, and in the ciliate *Mesodinium rubrum*. In these the cytobionts, separated only by a single membrane, ramify to such an extent that they are hardly recognisable as separate entities. Only the presence of a supernumerary nucleus calls attention to their presence. In *M. rubrum* the most extreme form of integration presently known, can occur (TAYLOR, 1979). In some populations the ramified cytobiont has appa-

rently fragmented, so that it exists as a number of blebs or « islands » of foreign cytoplasm (*fig. 19*), each containing one (rarely two) chloroplasts with accompanying mitochondria and « nucleomorphs ». One central island contains a very large cryptomonad nucleus. This raises all manner of questions concerning regulation and reproduction. Perhaps an explanation lies in the usual presence of a nucleomorph in each of the chloroplast-containing islands (chloroplast-mitochondrial complexes — CMCs; TAYLOR *et al.*, 1971). The nucleomorphs are enigmatic bodies thought to be vestigial nuclei (GILLOT & GIBBS, 1980) and if so, may retain enough information to support some of the activities of the CMCs.

Examples of the temporary maintenance of (apparently functional) chloroplasts from their food by ciliates were given in the previous section, serving as microplanktonic analogues to the better known cases involving sea hares. These are fundamentally different situations to that in *M. rubrum*, although this distinction has not been made clear by recent reviewers. The chloroplasts must be continuously replenished and the ciliates continue to feed.

#### 4.3. Mode of entry into the host.

This has been assumed to be principally by phagotrophy in the initial instance (e.g. MUSCATINE and POOLE, 1979) and there are plenty of examples to support this view in the spectrum of cytobioses here. Many of the associations appear to be facultative and « immature », some individuals lacking cytobionts, even within the same populations. This is largely due to the fact that the cytobionts are not transmitted in the gametes (radiolaria, foraminifera) and consequently must be taken up with each new sexual generation. In some, such as the colonial radiolaria, the cytobionts can be transferred during asexual reproduction. In facultative associations the rate of reproduction of the cytobiont relative to the host is not crucial, as long as it does not exceed the latter, and even then excess cells may be eaten or ejected. However, once the host depends on the cytobiont as its principal source of food (« biotrophy »), this regulation becomes crucial. Its mechanisms are little understood, even in much better known cases, such as the cytobiosis of *Chlorella* in the ciliate *Paramecium bursaria* (summarised by MUSCATINE & POOLE, 1979, who specifically deal with the basic question of cytobiont number regulation).

Phagotrophy is obviously not the mechanism by which the filamentous cyanobacterium *Richelia intracellularis* enters its silica-walled diatom hosts and this process remains a mystery although its transmission, once inside, is mechanistically understandable. If the host diatom dies the *Richelia* often persists as the heterocyst alone, but its eventual fate is unknown.

#### 4.4. Host adaptations.

As with cytobiont adaptations, the hosts also show a complete range from little or none, to considerable. Most of the epibiont hosts show no response to the presence of their passengers. However, the structurally elaborate, non-photosynthetic dinoflagellates (*Parahistioneis*, *Histioneis*, *Citharistes*) appear to have modified their girdle lists to form special chambers or pouches to act as « greenhouses » in which to cultivate (if one may excuse the anthropomorphism) the coccoid cyanobacteria known as « phaeosomes ». In *Ornithocercus* the girdle lists appear to be polyfunctional (TAYLOR, 1971, 1980 a). The actinopods and foraminifera do not seem to be structurally modified in any special way in response to symbiosis although the cytobionts are located in predictable regions of the host, depending on group. Benthic foraminifera do show window-like shell modifications in order to facilitate cytobiont illumination (LEE *et al.*, 1979).

The ciliate *M. rubrum* has a greatly reduced pellucid region, lacking alveoli and consisting of a single membrane over most of its non-ciliated surface. This could be related to illumination or, more probably, to facilitate exchange of dissolved materials, due to the high activity of the cytobiont. The chloroplasts line the periphery, with their broadest surfaces facing out and pyrenoids directed inwards. TAYLOR *et al.* (1971) noted that this arrangement could arise simply enough, as a centrifugal effect of host cell spin as it swims. The most extreme modification of *M. rubrum* is that the cytostome, situated on the end of an « oral cone » tipped with tentaculoids in its nearest relatives, is reduced to a shallow depression without tentaculoids. Trichites can still be seen within the cytoplasm below the mouth vestige.

Adaptation can be shown, not only in host structure, but also in behaviour, particularly when the cytobionts are photosynthetic. GÖTTES (1882) noted



movements to and from the surface by the large, colonial radiolaria such as *Collozoum*, and the vertical movements of other actinopods and foraminifera may be related to the need to illuminate their cytotobionts, even if they don't depend on them absolutely for food. Another form of behavioural adaptation which is shown by foraminifera is the circadian ingress and egress of the zooxanthellae from the rhizopodia, the cells being in an extended position in the light and contracted to the body at night (ANDERSON & BÉ, 1976; SPINDLER & HEMLEBEN, 1980). Interestingly, SWANBERG (1979) has also noted a dispersion and contraction of the zooxanthellae in the colonial radiolaria *Rhaphidozoum* sp. and *Collozoum* sp. that followed a similar light-dark pattern. Only those foraminifera which live in the euphotic zone possess photosynthetic cytotobionts. However, it should be noted that the bulk of potential food for these organisms is also concentrated in or at the bottom of the euphotic zone and there is, therefore, another good reason for them to occur in this depth range. The occurrence of zooxanthellae in acantharians 4,000 m deep (KIMOR & WOOD, 1975) is extraordinary.

Most of the dinophysoids that possess phaeosomes, with the exception of *Ornithocercus*, tend to occur in deep euphotic or subeuphotic water (TAYLOR, 1973). *M. rubrum* shows strong phototactic migration. Generally it rises near the surface in the morning but leaves it towards noon as it does not like intense light, returning to the surface in the afternoon before going deeper at night (TAYLOR *et al.*, 1971). Curiously, *M. rubrum* swims backwards compared to its non-photosynthetic relatives. It is evident why the latter should move with their cytostome forwards, but not why *M. rubrum* should reverse this.

#### 4.5. Metabolic interactions.

In most of the cases dealt with here there are almost no data on metabolic interactions, although one can assume a *potential* for cyclic exchange in the classical sense described by GEDDES (1882), in the quote which began this paper, when the host is non-photosynthetic. To what extent this is realised must vary with each situation. In most of the cases there is evidence that the association is facultative, the hosts supplementing any benefit they might obtain from their cytotobionts with captured prey (e.g. in radiolaria: ANDERSON, 1980; SWANBERG, 1979; and foraminifera: SPINDLER & HEMLEBEN, 1980). From studies on associations between the zooxanthella *Sym-*

*biodinium microadriaticum* and various invertebrate hosts (mostly coelenterates) an estimate of 20 to 59% transfer of photosynthate from cytotobiont to host has been obtained (TRENCH, 1979).

In the two dinoflagellates with ramifying photosynthetic cytotobionts (3.5), and in *Mesodinium rubrum*, the consortia are completely autotrophic. The cytotobiont pyrenoids of *M. rubrum* are usually surrounded by starch sheaths, indicating production in excess of the cytotobiont's needs. No data are available on the photosynthetic performance of the dinoflagellates, but from studies on dense, mono-specific blooms of *M. rubrum* assimilation rates from 4 to a high of 16.8 mgC (mg Chl. a)<sup>-1</sup>.hr<sup>-1</sup> have been obtained (PACKARD *et al.* 1978; SMITH and BARBER, 1979). This is within the normal range of phytoplankton. SWANBERG (1979), SWANBERG & HARBISON (1980) measured an extremely high rate while studying colonial radiolaria: 43.2 mgC (mg Chl. a)<sup>-1</sup>.hr<sup>-1</sup>, nearly an order of magnitude higher than most phytoplankton.

Despite this high assimilation rate SWANBERG & HARBISON (1980) calculated that this could provide only 0.4 to 0.7% of the host cell carbon per hour. They also found that the nutritional state of the host had a considerable effect on the photosynthetic performance of the zooxanthellae, the latter being greater if the host had previously been well fed heterotrophically (judging by retained tintinnid loricae).

Dinoflagellates produce an unusual sterol: dinosterol. However, the association of *Symbiodinium* with corals results in the production of a peculiar sterol: gorgosterol, which has a cyclopropyl-containing side chain. It is therefore intriguing to note that WITHERS *et al.* (1979) detected 4a-methylgorgostanol, together with dinosterol and several other sterols, in cultures of *Kryptoperidinium foliaceum* and *Peridinium balticum* containing their usual cytotobionts, suggesting that the unusual sterol is somehow involved in interactional membrane control.

Other associations have different potential interactions. The cyanobacterium *Richelia* which lives within photosynthetic diatom hosts, appears to be a nitrogen fixer (MAGUE *et al.*, 1974), a considerable asset in nitrogen-poor oceanic waters.

#### 4.6. Ecology.

Many of these associations, however fascinating they might be to the student of symbiosis, appear to be trivial from a synecological viewpoint. However, even with the limited information available it is

evident that some deserve wider attention and much further ecological study.

The majority of examples are from tropical waters, as is the case for symbioses in general. The same types of speculation used to account for other tropical associations can be used here, but all leave room for doubt. Is it a result of greater speciation and competition for niches? Is it that tropical waters are most stable, with slow reproduction under nutrient poor conditions (« K selection »), allowing associations to persist for longer periods before either partner dies? Is it that the oligotrophic conditions place a premium on rapid cycling, cytobioses offering the most rapid of all?

Despite this predominance of tropical associations, some of the most intimately integrated microplankton cytobioses are found in temperate waters, i.e. *P. balticum*, *K. foliaceum* and *M. rubrum* (which can occur in the tropics, but in cool, upwelled water; TAYLOR *et al.*, 1971). Not only are these autotrophic, but blooms of *M. rubrum* (noted in the previous section to have high assimilation rates) have been found to be highly productive: off Peru, SMITH & BARBER (1979) recorded an extremely high value of 2187 mgC. m<sup>-3</sup>. hr<sup>-1</sup>, with a maximum of 1,220 measured off Baja California by PACKARD *et al.* (1978). Because of strong swimming it might be expected that the respiration rate of *M. rubrum* might be high, but a figure of 4.6 % of carbon fixed is not excessive. These figures can be compared with those for the productivity of zooxanthellae as a whole, chiefly in larger hosts (MUSCATINE, 1980).

The role of actinopods in oceanic productivity may be seriously underestimated (KIMOR & WOOD, 1975). KHMELEVA (1967) considered that they were

major primary producers in the Gulf of Aden. In the southern Sargasso Sea the author found that acantharia were the major source of chlorophyll in the water between the surface (dominated by the cyanobacterium *Trichodesmium*) and the deep euphotic chlorophyll maximum (microflagellates and *Pyrocystis*; TAYLOR unpubl. obs., R. V. Endeavor cruise EN-018, Feb. 1978, courtesy of E. Swift). Although SWANBERG (1979) found such high assimilation rates for colonial radiolaria he concluded that their contribution to oceanic production may be relatively small due to the low numbers usually encountered in equatorial waters. However, they can occasionally reach concentrations as high as 540 colonies per m<sup>3</sup> and could be a major factor in production at such times.

The distribution of *Richelia intracellularis* in the North Pacific has received particular attention by VERNICK (1974). As noted in a previous section she found that the cytobiont had a more restricted, warm water distribution than its hosts, not occurring further north than 38°N. It would be interesting to know if this limit is set by temperature, availability of nutrients, or some other factor. In view of its demonstrated ability to fix nitrogen (MAGUE *et al.*, 1974) it is also of interest to enquire whether the consortium is of major or minor importance in the oceanic nitrogen cycle. MAGUE *et al.* (1977) calculated that the total contribution from all pelagic cyanobacteria (principally *Trichodesmium thiebautii*, which is not symbiotic although its colonies may be associated with a great variety of organisms, both large and small) could only supply 3 % of the nitrogen requirement of the primary producers of the Central North Pacific.

## REFERENCES

- ALLDREDGE, A. L., JONES, B. M., 1973. — *Hastigerina pelagica*: Foraminiferal habitat for planktonic dinoflagellates. *Mar. Biol.*, **22**: 131-135.
- ANDERSON, O. R., 1976. — Ultrastructure of a colonial radiolarian *Collozoum inerme* and a cytochemical determination of the role of its zooxanthellae. *Tissue Cell*, **8**: 195-208.
- ANDERSON, O. R., 1980. — Radiolaria. Chpt. I. In LEVANDOWSKY, M., HUTNER, S. H. (eds.), *Biochemistry and Physiology of Protozoa*, 2nd. Ed., **3**: 1-42. Academic Press, New York.
- ANDERSON, O. R., BÉ, A. W. H., 1976. — The ultrastructure of a planktonic foraminifer, *Globigerinoides sacculifer* (Brady), and its symbiotic dinoflagellates. *J. forami. Res.*, **6**: 1-21.
- ANDERSON, O. R., SPINDLER, M., BÉ, A. W. H., HEMLEBEN, C., 1979. — Trophic activity of planktonic foraminifera. *J. mar. biol. Ass. U.K.*, **59**: 791-799.
- AUBERT, M., AUBERT, J., GAUTHIER, M., 1979. — Antibiotic substances from marine flora. In HOPPE, H. A., LEVRING, T., TANAKA, Y. (eds.), *Marine Algae in Pharmaceutical Science*, de Gruyter, Berlin, New York, 267-291.
- BALECH, E., 1962. — Tintinnoina y Dinoflagellata del Pacifico. *Rev. Mus. Argent. Cienc. nat.*, « Bernardino Rivadavia », *Cienc. zool.*, **7**: 1-253.

- BARBER, R. T., WHITE, A. W., SIEGELMAN, H. W., 1969. — Evidence for a cryptomonad symbiont in the ciliate *Cyclotrichium meunieri*. *J. Phycol.*, **5** : 86-88.
- BÉ, A. W. H., HEMLEBEN, C., ANDERSON, O. R., SPINDLER, M., HACUNDA, J., TUNTIVATE-CHOY, S., 1977. — Laboratory and field observations of living foraminifera. *Micropal.*, **23** : 155-179.
- BLACKBOURN, D. J., TAYLOR, F. J. R., BLACKBOURN, J., 1973. — Foreign organelle retention by ciliates. *J. Protozool.*, **20** : 286-288.
- BRANDT, K., 1881. — Ueber das Zusammenleben von Thieren und Algen. *Verh. physiol. Ges. Berlin*, 1881-1882. **4/5** : 570-574 (reprint numbered 21-26).
- BRANDT, K., 1883. — Ueber die morphologische und physiologische Bedeutung des Chlorophylls bei Tieren. *Mit. zool. Stat. Neapel*, **4** : 191-302.
- BURKHOLDER, P. R., 1974. — The ecology of marine antibiotics and coral reefs. Chpt. 5. In JONES, O. A., ENDEAN, R. (eds.), *Biology and Geology of Coral Reefs*, **2** (Biology 1) : 117-182. Academic Press, N. Y. and London.
- BURKHOLDER, P. R., BURKHOLDER, L. M., ALMODOVAR, L. R., 1967. — Carbon assimilation of marine flagellate blooms in neritic waters of southern Puerto Rico. *Bull. mar. Sci. Gulf Caribbean*, **17** : 1-15.
- CACHON, M., CARAM, B., 1979. — A symbiotic green alga, *Pedinomonas symbiotica* sp. nov. (Prasinophyceae), in the radiolarian *Thalassolampe margarodes*. *Phycologia*, **18** : 177-184.
- CHATTON, E., 1920. — Les Péridiniens parasites. Morphologie, reproduction, ethologie. *Arch. Zool. exp. gén.*, **59** : 1-475 + 18 pl.
- CUPP, E. E., 1943. — Marine plankton diatoms of the west coast of North America. *Bull. Scripps Inst. Oceanogr.*, **5** : 1-238 + 5 pls.
- CURL, H., 1959. — The phytoplankton of Apalachee Bay and the Northeastern Gulf of Mexico. *Publ. Inst. mar. Sci. Univ. Texas*, **6** : 277-320.
- DADAY, E. VON, 1887. — Monographie der Familie der Tintinnodeen. *Mit. zool. Stat. Neapel*, **7** : 473-591 + pls. 18-21.
- DANGEARD, P., 1927. — Phytoplankton de la croisière du « Sylvara » (Février-Juin 1913). Mission Comte J. de Polignac-Louis Gain. *Ann. Inst. océanogr.*, N. S., **4** : 284-406.
- DODGE, J. D., 1971. — A dinoflagellate with both a mesokaryotic and a eukaryotic nucleus. 1. Fine structure of the nuclei. *Protoplasma*, **73** : 145-157.
- DRAGESCO, J., 1948. — Sur la biologie du *Zoothamnium pelagicum* (Du Plessis). *Bull. Soc. zool. Fr.*, **73** : 130-134.
- DROOP, M. R., ELSON, K. G. R., 1966. — Are pelagic diatoms free from bacteria? *Nature (Lond.)*, **211** : 1096-1097.
- ELBRÄCHTER, M., DREBES, G., 1978. — Life cycles, phylogeny and taxonomy of *Dissodinium* and *Pyrocystis* (Dinophyta). *Helgol. wiss. Meeresunters.*, **31** : 347-366.
- FAMINTZIN, A., 1889. — Beitrag zur Symbiose von Algen und Thieren. *Mem. Acad. sci. St. Petersbourg*, **7**(16) : 1-36 + 2 pls.
- FEBVRE, J., FEBVRE-CHEVALIER, C., 1979. — Ultrastructural study of zooxanthellae of three species of Acantharia (Protozoa : Actinopoda), with details of their taxonomic position in the Prymnesiales (Prymnesiophyceae, Hibberd, 1976). *J. mar. Biol. Ass. U.K.*, **59** : 215-226 + 6 pls.
- FEBVRE-CHEVALIER, C., 1971. — Constitution ultrastructurale de *Globigerina bulloides* d'Orbigny, 1826 (Rhizopoda-Foraminifera). *Protistologica*, **7** : 311-324.
- FORTI, A., 1922. — Ricerche su la flora pelagica (fitoplancton) di Quarto dei Mille (Mare Ligure). *Mem. R. Com. talassogr. Ital., Lab. mar. Quarto Mille Genova*, **97** : 1-248 + 13 pls.
- FRANCA, S., 1976. — On the presence of virus-like particles in the dinoflagellate *Gyrodinium resplendens* (Hulbert). *Protistologica*, **12** : 425-430.
- GAARDER, K. R., 1946. — Tintinninea from the « Michael Sars » North Atlantic Deep-Sea Expedition 1910. (*Reps. sci. Res.*, 2.1), 36 pp. + 5 tables. *Bergen Museum, Norway*.
- GAARDER, K. R., HASLE, G. R., 1962. — On the assumed symbiosis between diatoms and coccolithophorids in *Brenneckella*. *Nytt Mag. Bot.*, **9** : 145-149 + 1 pl.
- GEDDES, P., 1882. — On the nature and functions of the « Yellow Cells » of Radiolarians and Coelenterates. *Proc. R. Soc. Edinburgh*, **11** : 377-396.
- GILLOT, M., GIBBS, S. P., 1980. — The cryptomonad nucleomorph : its ultrastructure and evolutionary significance. *J. Phycol.*, **16** : 558-568.
- GLOMBITZA, K.-W., 1979. — Antibiotics from algae. In HOPPE, H. A., LEVING, T., TANAKA, Y. (eds.), *Marine Algae in Pharmaceutical Science* : 303-342, de Gruyter, Berlin, New York.
- GOLD, K., POLLINGER, U., 1971. — Occurrence of endosymbiotic bacteria in marine dinoflagellates. *J. Phycol.*, **7** : 264-265.
- GRAN, H. H., 1908. — Diatomeen. Chpt. 19. In BRANDT, K., APSTEIN, C., *Nordisches Plankton ; Botanische Teil*, 146 pp. *Lipsius und Tischer*, Kiel u. Leipzig.
- GRAN, H. H., 1912. — Pelagic plant life. Chpt. 6. In MURRAY, J., HJORT, J. (eds.), *The Depths of the Ocean* : 307-386. MacMillan, London.
- HASLE, G. R., 1964. — *Nitzschia* and *Fragilariopsis* species studied in the light and electron microscopes. I. Some marine species of the groups *Nitzschia* and *Lanceolatae*. *Skr. Norske vidensk.-Akad. Oslo, mar.-nat. Kl., N. S.*, **16** : 1-48 + 16 pls.
- HASLE, G. R., 1975. — Some living marine species of the diatom family Rhizosoleniaceae. *Beih. Nova Hedw.*, **53** : 99-140 + 13 pls.
- HENRY, S. M. (ed.), 1966. — Symbiosis, 1. Academic Press, New York, 478 pp.
- HENTSCHEL, E., 1936. — Allgemeine Biologie des südatlantische Ozeans. *Wiss. Ergebn. dt. atlant. Exped. « Meteor »*, **11** : 1-344.
- HIBBERD, D. J., 1977. — Observations on the ultrastructure of the cryptomonad endosymbiont of the red-water ciliate *Mesodinium rubrum*. *J. mar. Biol. Ass. U.K.*, **57** : 45-61.
- HOLLANDE, A., CARRÉ, D., 1974. — Les xanthes des Radiolaires Sphaerocollides, des Acanthaires et de *Vellela vellela* : infrastructure, cytochimie, taxonomie. *Protistologica*, **10** : 573-601.
- HOLLANDE, A., ENJUMET, M., 1953. — Contribution à l'étude biologique des Sphaerocollides et de leurs parasites. Chpt. 8. La nature des Zooxanthelles. *Ann. Sci. nat. Zool., 11<sup>e</sup> sér.*, **15** : 100-176.

- HOLM-HANSEN, O., TAYLOR, F. J. R., BARSDATE, R. J., 1970. — A ciliate red tide at Barrow, Alaska. *Mar. Biol.*, **7** : 37-46.
- HOVASSE, R., 1922. — *Endodinium chattonii* (nov. gen. et sp.). Son cycle de multiplication endogène. Variation du nombre de ses chromosomes. *C. R. Soc. biol., Paris*, **87** : 845-846.
- HUSTEDT, F., 1930. — Die Kieselalgen Deutschlands, Oesterreichs und der Schweiz. In : Rabenhorst, L. (ed.), *Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz*, **7** (1) : 1-920, Akademische Verlags., Leipzig.
- JACQUES, G., SOYER, M.-O., 1977. — Nouvelles observations sur *Pselodinium vaubanii* (Sournia), dinoflagellé libre planctonique. *Vie Milieu*, **A 27** : 83-90.
- JEFFREY, S. W., VESK, M., 1976. — Further evidence for a membrane-bound endosymbiont within the dinoflagellate *Peridinium foliaceum*. *J. Phycol.*, **12** : 450-455.
- KAHL, A., 1935. — Urtiere oder Protozoa I : Wimpertiere oder Ciliata (Infusoria). 4 Peritricha und Chonotricha. In DAHL, F. (ed.), *Die Tierwelt Deutschlands*, **30** : 1-886 (Gustav Fischer, Jena)
- KARSTEN, G., 1907. — Das Indische Phytoplankton nach dem Material der Deutschen Tiefsee-Expedition 1898-1899. *Wiss. Ergebn. dtsch. Tiefsee. Exped.*, **2** (2) : 1-548 + 20 pls.
- KHMELEVA, N. N., 1967. — Rol' radiolyarii pri otsenke pervichnoi produktii v Krasnom More i Adenskom Zalive. *Dokl. Akad. Nauk SSSR*, **172** : 1430-1433.
- KIES, L., 1980. — Morphology and systematic position of some endocyanomes. In SCHWEMMLER, W., SCHENK, H. E. A., *Endocytobiology; Endosymbiosis and Cell Biology : de Gruyter*, Berlin, New York, 7-19.
- KIMOR, B., REID, F. M. H., JORDAN, J. B., 1978. — An unusual occurrence of *Hemialus membranaceus* Cleve (Bacillariophyceae) with *Richelia intracellularis* Schmidt (Cyanophyceae) off the coast of Southern California in October 1976. *Phycologia*, **17** : 162-166.
- KIMOR, B., WOOD, E. J. F., 1975. — A plankton study in the Eastern Mediterranean Sea. *Mar. Biol.*, **29** : 321-333.
- KOFOLD, C. A., CAMPBELL, A. S., 1929. — A conspectus of the marine and fresh-water Ciliata belonging to the suborder Tintinninea, with descriptions of new species principally from the Agassiz Expedition to the Eastern Tropical Pacific 1904-1905. *Univ. Calif. Publ. Zool.*, **34** : 1-403.
- LAVAL, M., 1968. — *Zoothamnium pelagicum* Du Plessis, cilié péritriche planctonique : morphologie, croissance et comportement. *Protistologica*, **4** : 333-363 + 4 pls.
- LAVAL, M., 1970. — Présence de Bactéries intranucléaires chez *Zoothamnium pelagicum*. Abstr. 7<sup>e</sup> int. Congr. Micr. électr. Grenoble, 1970 : 403-404 (*Soc. Fr. Microsc. électr., Paris*).
- LAVAL, M., 1971. — Ultrastructure et mode de nutrition du choanoflagellé *Salpingoeca pelagica* sp. nov. Comparaison avec les choanocytes des spongiaires. *Protistologica*, **7** : 325-336.
- LAVAL, M., 1972. — Ultrastructure de *Petalotricha ampulla* (Fol). Comparaison avec d'autres Tintinnides et avec les autres ordres de Ciliés. *Protistologica*, **8** : 369-386.
- LAVAL-PEUTO, M., 1975. — Cortex, périmelle et réticulum vésiculeux de *Cyrtarocylis brandti* (Cilié Tintinnide). Les Ciliés à périmelle. *Protistologica*, **11** : 83-98.
- LEE, J. J., 1980. — Nutrition and physiology of the Foraminifera. Chpt. 2. In LEVANDOWSKY, M., HUTNER, S. H. (eds.), *Biochemistry and Physiology of Protozoa*, 2nd. Ed., **3** : 43-66. Academic Press, New York.
- LEE, J. J., FREUDENTHAL, H. D., KOSSOY, V., BÉ, A., 1965. — Cytological observations on two planktonic foraminifera, *Globigerina bulloides* d'Orb., 1826, and *Globigerinoides ruber* (d'Orbigny, 1839) Cushman, 1927. *J. Protozool.*, **12** : 531-542.
- LEE, J. J., McENERY, M. E., KAHN, E. G., SCHUSTER, F. L., 1979. — Symbiosis and the evolution of larger foraminifera. *Micropaleont.*, **25** : 118-140.
- LEEDALE, G. F., 1969. — Observations on endonuclear bacteria in euglenoid flagellates. *Oesterr. bot. Z.*, **116** : 279-294.
- LEMMERMANN, E., 1905. — Die Algenflora der Sandwich-Inseln. Ergebnisse einer Reise nach dem Pacific, H. Schauinsland, 1896-1897. *Engler bot. Jb. Syst. Pflanz.*, **41** : 607-663.
- LOEBLICH, A. R. III, SHERLEY, J. L., 1979. — Observations on the theca of the motile phase of free-living and symbiotic isolates of *Zooxanthella microadriatica* (Freudenthal) comb. nov. *J. mar. biol. Ass. U.K.*, **59** : 195-205.
- LOHMANN, H., 1912. — Untersuchungen über das Pflanzen- und Tierleben der Hochsee. *Veröff. Inst. Meeresk. Univ. Berlin, N.F.*, **1** : 1-92.
- MAGUE, T. H., MAGUE, F. C., HOLM-HANSEN, O., 1977. — Physiology and chemical composition of nitrogen-fixing phytoplankton in the central North Pacific Ocean. *Mar. Biol.*, **41** : 213-227.
- MAGUE, T. H., WEARE, N. M., HOLM-HANSEN, O., 1974. — Nitrogen fixation in the North Pacific Ocean. *Mar. Biol.*, **24** : 109-119.
- MANTON, I., LEADBEATER, B. S. C., 1974. — Fine structural observations on six species of *Chrysochromulina* from wild Danish marine nanoplankton, including a description of *C. campanulifera* sp. nov. and a preliminary summary of the nanoplankton as a whole. *Biol. Skr. Dan. vid. Selsk.*, **20** (5) : 1-26.
- MARGALEF, R., 1957. — Fitoplancton de las costas de Puerto Rico. *Inv. Pesq.*, **6** : 39-52.
- MARGALEF, R., DURÁN, M., 1953. — Microplancton de Vigo, de octubre de 1951 a septiembre de 1952. *P. Inst. Biol. Apl.*, **13** : 5-78.
- MARGALEF, R., DURÁN, M., SAIZ, F., 1955. — El fitoplancton de la ría de Vigo. *Inv. Pesq.*, **2** : 85-129.
- MAYER, J. A., TAYLOR, F. J. R., 1979. — A virus which lyses the marine nanoflagellate *Micromonas pusilla*. *Nature (Lond.)*, **281** : 299-301.
- MUSCATINE, L., 1980. — Productivity of zooxanthellae. In FALKOWSKI, P. (ed.), *Primary Productivity in the Sea* : Plenum Press, New York, 381-402.
- MUSCATINE, L., POOLE, R. R., 1979. — Regulation of numbers of intracellular legae. *Proc. R. Soc. Lond. B.*, **204** : 131-139.
- NORRIS, R. E., 1961. — Observations on phytoplankton organisms collected on the N.Z.O.I. Pacific cruise, September, 1958. *N.Z.J. Sci.*, **4** : 161-187.
- NORRIS, R. E., 1967. — Algal consortisms in marine plankton. In KRISHNAMURTHY, V. (ed.), *Proc. Seminar on Sea, Salt and Plants*, 1965 : 178-189 + 1 pl. Central Salt and Marine Chemicals Research Institute, Bhavnagar, India.
- OAKLEY, B. R., TAYLOR, F. J. R., 1978. — Evidence for a new type of endosymbiotic organization in a population

- of the ciliate *Mesodinium rubrum* from British Columbia. *Biosystems*, **10** : 361-369.
- ÖSTENFELD, C. M., SCHMIDT, J., 1901. — Plankton fra det Røde Hav og Adenbuchten (Plankton from the Red Sea and the Gulf of Aden). *Vid. Medd. Dansk. naturhist. For.*, Copenhagen, **1901** : 141-182.
- PACKARD, T. T., BLASCO, D., BARBER, R. T., 1978. — *Mesodinium rubrum* in the Baja California upwelling system. In BOJE, R., TOMCZAK, M. (eds.), *Upwelling Systems* : 73-89. Springer Verlag, Berlin, Heidelberg, N.Y.
- PAVILLARD, J., 1916 a. — Recherches sur les Diatomées pélagiques du golfe du Lion. *Trav. Inst. bot. Univ. Montpellier, Sér. Mixte*, **5** : 1-63 + 2 pls.
- PAVILLARD, J., 1916 b. — Flagellés nouveaux, épiphytes des Diatomées pélagiques. *C. R. Acad. sci., Paris*, **163** : 65-68.
- PAVILLARD, J., 1935. — Périodiniens et Diatomées pélagiques recueillis par Alain Gerbault entre les îles Marquises et les îles Galapagos. *Bull. Inst. Océanogr. Paris*, n° 669, 8 p.
- PEARSON, B. R., NORRIS, R. E., 1974. — Intranuclear virus-like particles in the marine alga *Platymonas* sp. (Chlorophyta, Prasinophyceae). *Phycologia*, **13** : 5-9.
- PESANDO, D., 1972. — Etude chimique et structurale d'une substance lipidique antibiotique produite par une diatomée marine : *Asterionella japonica*. *Rev. Int. Océanogr. méd.*, **25** : 49-69.
- PIENAAR, R. N., 1976. — Virus-like particles in three species of phytoplankton from San Juan Island, Washington. *Phycologia*, **15** : 185-190.
- POKORNY, K. S., GOLD, K., 1973. — Two morphological types of particulate inclusions in marine dinoflagellates. *J. Phycol.*, **9** : 218-224.
- POUCHET, G., 1894. — Histoire naturelle. Chpt. 10, in *Voyage de la Manche. Nonv. Arch. Miss.*, **5** : 155-218.
- RHEE, G.-Y., 1972. — Competition between an alga and an aquatic bacterium for phosphate. *Limnol. Oceanogr.*, **17** : 505-514.
- SCHMALJOHANN, R., RÖTTGER, R., 1976. — Die Symbioten der Grossforaminifere *Heterostegina depressa* sind Diatomeen. *Die Naturw.*, **10** : 486.
- SCHOENBERG, D. A., TRENCH, R. K., 1980. — Genetic variation in *Symbiodinium* (= *Gymnodinium*) *microadriaticum* Friedenthal, and specificity in its symbiosis with marine invertebrates. II. Morphological variation in *Symbiodinium* *microadriaticum*. *Proc. R. Soc. Lond. B.*, **207** : 405-427.
- SCHNÖDER, B., 1914. — Ueber Planktonepibionten. *Biol. Centralbl.*, **34** : 328-338.
- SCHÜTT, F., 1895. — Die Peridineen der Plankton-Expedition. *Ergebn. Plankt.-Exped. Humboldt-Stift.*, **4** : 1-170 + 27 pls.
- SCHWEMMLER, W., 1980. — Endocytobiology : a modern field between symbiosis and cell research. In SCHWEMMLER, W., SCHENK, H. E. A., *Endocytobiology, Endosymbiosis and Cell Biology* : 947-967. de Gruyter, Berlin.
- SIEBURTH, J. M., 1976. — Bacterial substrates and productivity in marine ecosystems. *Ann. Rev. Ecol. Syst.*, **7** : 259-285.
- SIEBURTH, J. M., 1979. — Sea Microbes. *Oxford Univ. Press*, New York, 491 pp.
- SILVA, E. S., 1978. — Endonuclear bacteria in two species of dinoflagellates. *Protistologica*, **14** : 113-119.
- SMAYDA, T. J., 1970. — The suspension and sinking of phytoplankton in the sea. *Oceanogr. mar. Biol. Ann. Rev.*, **8** : 353-414.
- SMITH, J. W. JR., BARBER, R. T., 1979. — A carbon budget for the autotrophic ciliate *Mesodinium rubrum*. *J. Phycol.*, **15** : 27-33.
- SOURNIA, A., 1968. — Diatomées planctoniques du Canal de Mozambique et de l'île Maurice. *Mém. O.R.S.T.O.M.*, **31** : 1-120 + 13 pls.
- SOURNIA, A., 1970. — Les Cyanophycées dans le plancton marin. *Ann. biol.*, **9** : 63-76.
- SOYER, M.-O., 1978. — Particules de type viral et filaments trichocystoïdes chez les Dinoflagellés. *Protistologica*, **14** : 53-58.
- SPINDLER, M., HEMLEBEN, C., 1980. — Symbionts in planktonic foraminifera (Protozoa). In SCHWEMMLER, W., SCHENK, H. E. A. (eds.), *Endocytobiology, Endosymbiosis and Cell Biology* : 133-140. de Gruyter, Berlin, N.Y.
- STAHR, M. P., 1975. — A generalized scheme for classifying organismic associations. In *Symbiosis; Symp. Soc. exper. Biol.*, **29** : 1-20.
- SUBRAHMANYAN, R., 1954. — A new member of the Euglenineae, *Protoeuglena noctilucae* gen. et sp. nov., occurring in *Noctiluca miliaris* Suriray, causing green discoloration of the sea off Calicut. *Proc. Ind. Acad. Sci.*, **39** : 118-127.
- SUBRAHMANYAN, R., 1962. — On *Rutilnera pringsheimii* sp. nov. (Chrysophyceae) from the coastal waters of India. *Arch. Mikrobiol.*, **42** : 219-225.
- SWANBERG, N. R., 1979. — The ecology of colonial radiolarians : their colony morphology, trophic interactions and associations, behavior, distribution and the photosynthesis of their symbionts. Ph. D. Thesis, Mass. Inst. Techn./Woods Hole oceanogr. Inst. W.H.O.I., **79-79** : 202 p.
- SWANBERG, N. R., HARBISON, G. R., 1980. — The ecology of *Collozoum longiforme*, sp. nov., a new colonial radiolarian from the equatorial Atlantic Ocean. *Deep-Sea Res.*, **27 A** : 715-732.
- SWEENEY, B. M., 1971. — Laboratory studies of green *Noctiluca* from New Guinea. *J. Phycol.*, **7** : 53-58.
- SWEENEY, B. M., 1976. — *Pedinomonas noctilucae* (Prasinophyceae), the flagellate symbiotic in *Noctiluca* (Dinophyceae in Southeast Asia). *J. Phycol.*, **12** : 460-464.
- SWIFT, E., REMSEN, C. C., 1970. — The cell wall of *Pyrocystis* spp. (Dinococcales). *J. Phycol.*, **6** : 79-86.
- TAYLOR, D. L., 1971. — Ultrastructure of the « zooxanthella » *Endodinium chiltonii* in situ. *J. mar. Biol. Ass. U. K.*, **51** : 227-234.
- TAYLOR, D. L., 1973. — Cellular interactions of algae-invertebrate symbiosis. *Adv. mar. Biol.*, **11** : 1-56.
- TAYLOR, D. L., 1974. — Symbiotic marine algae : taxonomy and biological fitness. In VERNBERG, W. (ed.), *Symbiosis in the Sea* : 245-262. Univ. S. Carol. Press, Columbia, S.C.
- TAYLOR, F. J. R., 1971. — Scanning electron microscopy of thecae of the dinoflagellate genus *Ornithocercus*. *J. Phycol.*, **7** : 249-258.
- TAYLOR, F. J. R., 1972. — Application of the scanning electron microscope to the study of tropical microplankton. *J. mar. Biol. Ass. India*, **14** : 55-60.
- TAYLOR, F. J. R., 1973. — General features of dinoflagellate material collected by the « Anton Bruun »

- during the International Indian Ocean Expedition. Chpt. 2.5. In ZEITZSCHEL, B. (ed.), *The Biology of the Indian Ocean* : 155-169. Springer, Verlag, New York.
- TAYLOR, F. J. R., 1974. — Implications and extensions of the serial endosymbiosis theory of the origin of eukaryotes. *Taxon*, **23** : 229-258.
- TAYLOR, F. J. R., 1976. — Dinoflagellates from the International Indian Ocean Expedition. *Bibliotheca bot.*, **122** : 1-234 + 46 pls.
- TAYLOR, F. J. R., 1979. — Symbioticism revisited : a discussion of the evolutionary impact of intracellular symbioses. *Proc. R. Soc. Lond. B.*, **204** : 267-286.
- TAYLOR, F. J. R., 1980 a. — On dinoflagellate evolution. *Biosystems*, **13** : 65-108.
- TAYLOR, F. J. R., 1980 b. — Basic biological features of phytoplankton cells. Chpt. 1. In MORRIS, I. (ed.), *The Physiological Ecology of Phytoplankton* : 3-55 (*Blackwell sci. Publs.*, Oxford, Studies in Ecology, 7).
- TAYLOR, F. J. R., BLACKBOURN, D. J., BLACKBOURN, J., 1971. — The red water ciliate *Mesodinium rubrum* and its « incomplete symbionts » : a review including new ultrastructural observations. *J. fish. Res. Bd. Canad.*, **28** : 391-407.
- TOMAS, R. N., COX, E. R., STEIDINGER, K. A., 1973. — *Peridinium balticum* (Levander) Lemmermann, an unusual dinoflagellate with a mesokaryotic and an eukaryotic nucleus. *J. Phycol.*, **9** : 91-98.
- TRENCH, R. K., 1975. — Of « leaves that crawl » : functional chloroplasts in animal cells. In *Symbiosis; Symp. Soc. exper. Biol.*, **29** : 229-265.
- TRENCH, R. K., 1979. — The cell biology of plant-animal symbiosis. *Ann. Rev. plant. Physiol.*, **30** : 485-531.
- TRENCH, R. K., 1980. — Uptake, retention and function of chloroplasts in animal cells. In SCHWEMMLER, W., SCHENK, H. E. A. (eds.), *Endocytobiology, Endosymbiosis and Cell Biology* : 703-727. de Gruyter, Berlin.
- VENRICK, E. L., 1974. — The distribution and significance of *Richelia intracellularis* Schmidt in the North Pacific Central Gyre. *Limnol. Oceanogr.*, **19** : 437-445.
- WHITE, A. W., SHEATH, R. G., HELLEBUST, J. A., 1977. — A red tide caused by the marine ciliate *Mesodinium rubrum* in Passamaquoddy Bay, including pigment and ultrastructural studies of the endosymbiont. *J. fish. Res. Bd. Canad.*, **34** : 413-416.
- WITHERS, N. W., KOKKE, W. C. M. C., ROHMER, M., FENICAL, W. H., DJERASSI, C., 1979. — Isolation of sterols with cyclopropyl-containing side chains from the cultured marine alga *Peridinium foliaceum*. *Tetrahedron Lett.*, **38** : 3605-3608.