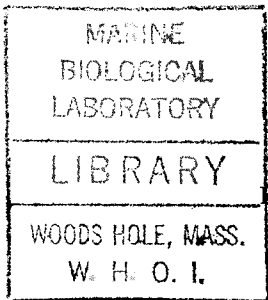THE ECOLOGY OF COLONIAL RADIOLARIANS: THEIR COLONY MORPHOLOGY,

TROPHIC INTERACTIONS AND ASSOCIATIONS, BEHAVIOR, DISTRIBUTION,

AND THE PHOTOSYNTHESIS OF THEIR SYMBIONTS

by

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                  Woods Hole Oceanographic Institution

This dissertation is dedicated to my mother, Marian Swanberg

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Submitted to the Department of Biology

August, 1979 in partial fulfillment of the requirements

for the Degree of Doctor of Philosophy

ABSTRACT

Colonial radiolarians (Spumellaria) are among the most common and abundant large zooplankton, but they have been little studied by modern biologists. Colonies were found on 98% of epipelagic diving stations in the period from 1977 to 1979. Measured abundances ranged from .04 to 540 colonies per m^3. Colony morphology of common genera and species is described and three new shell-less species which reach a length in excess of 1 m are discussed in detail. Some simple behavioral responses are documented, including control of colony buoyancy and position of algae in the colonies. Radiolarians feed on a wide variety of planktonic organisms including tintinnids, copepods, appendicularians, mollusc larvae and hydromedusae. They are hosts to parasitic hyperiid amphipods, particularly those of the genus *Hyperietta*. Radiolarians are prey of the amphipod *Oxycephalus clausi*, an unidentified turbellarian and possibly the Harpacticoid copepods *Miracia efferata* and *Sapphirina* sp. Colonial radiolarians are also hosts to symbiotic dinoflagellates.

Experiments were done at sea on the net incorporation of CO_2 by these algae using ^{14}C labelled $NaHCO_3$. Data from these experiments were related to content of carbon and chlorophyll as a function of colony size (cell number). Carbon content of colonies related well with colony size. Mean values were 50, 85, 100 and 200 ng C per radiolarian cell for *Collozoum inerme*, *C. longiforme*, *Acrosphaera spinosa* and *Collozoum radiosum* respectively. Chlorophyll content varied widely between colonies and chlorophyll per radiolarian cell decreased with increasing colony size in *Acrosphaera spinosa*. Net carbon incorporation increased with colony size at given light intensities as did photosynthetic assimilation (mmoles $CO_2 \cdot$mg Chl $a^{-1} \cdot hr^{-1}$) in *A. spinosa*. In experiments on the effect of light intensity on photosynthesis, there was no evidence for photoinhibition at high intensities in *Acrosphaera spinosa*. Replicate pieces of the large colonies of *C. longiforme* were incubated together, each colony at a different light intensity. Representative pieces were measured and used for chlorophyll carbon and nitrogen analysis and counted for abundance of radiolarian and algal cells and tintinnid prey. Incorporation per unit length varied little within colonies. Photosynthetic assimilation followed no predictable pattern as a function of light intensity. However, it related directly to abundance of tintinnid prey remains. This effect apparently overrides that of light intensity. Total photosynthesis incorporation was only 0.1 to 0.8% of the total colony carbon per hour. The contribution of colonial radiolarians to total productivity of the regions studied was insignificant. However, the radiolarians' productivity is available to a unique

portion of the planktonic food web. Because of their size and abundance

radiolarians are important as substrates in their environment.

Name and Title of Thesis Supervisor: G. Richard Harbison, Associate
                                        Scientist

PREFACE AND ACKNOWLEDGEMENTS

For eight years a number of researchers have been observing and col-

lecting oceanic plankton *in situ* through the use of SCUBA. In addition

to the task of convincing their colleagues that the method was worthwhile

these diving scientists have often been faced with the problem of simply

recognizing the new or unknown organisms as such in their own environment.

Often the *in vivo* morphology of planktonic animals is different from that

of preserved specimens. This problem has often been made more difficult

by the sheer abundance of "elusive" or "rare" species. One hardly expects

to find the most abundant organism to be unknown.

The inadequacy of conventional sampling techniques is underscored

when one realizes that many of the "new" organisms are not new at all,

but merely forgotten. All too often have we found our exciting discover-

ies elegantly drawn in some dusty 19th century monograph. The radio-

larians are an excellent example of this. Quite a number of experienced

investigators have mistaken the colonial radiolarians for mollusc egg

masses to which they bear a superficial resemblance. I, too, thought they

were egg masses until February of 1975 in the Sargasso Sea when I suddenly

realized that "egg masses" were the most common thing in the ocean, yet

nothing ever seemed to lay them. Oblivious to the näiveté of that idea

(and the fact that it took me about 150 open-ocean dives to realize it),

I decided that anything that was that common was worth closer examination.

As luck would have it, the first specimen I chose to examine was a new

species and very different in morphology from what is expected from a

radiolarian (this species is described in this work as *Collozoum* sp. A).

Great credit goes to my good friend, Ronald Gilmer, who suggested on

that cruise that the organisms might have been radiolarians. I also thank

Georges Merinfeld of Dalhousie University, who confirmed this and intro-

duced me to some of the key literature for the group. Dr. G. Richard

Harbison, my thesis advisor, has had a great deal to do with recognizing

the most important directions of this research and is to be commended for

somehow keeping me from becoming too side-tracked. His generous financial

and intellectual support has been completely indispensible in this under-

taking.

I am grateful to Drs. Jean and Monique Cachon and to Professor André

Hollande for their patient suggestions and assistance, and to Dr. Susumu

Honjo and Margaret Goreau for the fixation of specimens for transmission

electron microscopy and for doing the scanning electron microscopy.

Dr. O. Roger Anderson provided valuable expertise, sectioning, viewing and

giving many helpful comments in interpreting the transmission electron

micrographs.

I especially thank Anita M. Brosius, whose labor of love allowed this

work to appear in its present form. Her invaluable assistance on two

cruises with diving, routine laboratory procedures and photography enabled

me to accomplish a great deal more than otherwise would have been possible.

She did all of the graphics and often lent a patient ear and an encouraging

voice. I also thank Jane Peterson for her patient and expert typing and

my good friend, Dr. Laurence P. Madin for his patient and critical listening

during the writing process. All of those who dove with me, assisted in

collecting and especially the members of the crews of the R/V ATLANTIS II

and R/V OCEANUS have helped a great deal throughout the years. Finally, I would be remiss if I did not express my gratitude to Dr. W. M. Hamner, whose insight pioneered the *in situ* work on zooplankton. His generosity enabled me to participate in plankton research as an undergraduate at the University of California and his enthusiasm kindled my interest in the plankton.

GENERAL INTRODUCTION

Over most of the past 100 years our knowledge of planktonic life in the epipelagic environment has been limited to our interpretation of preserved collections, and to the natural history and behavioral observations made by scientists in the latter quarter of the nineteenth century. For a host of reasons, the primary emphasis in the research of the past 60 years has been placed on quantitative investigations of the plankton. One artifact of this approach has been the disappearance of a few groups from the modern plankton literature. It is well known (Harbison et al., 1978) that ctenophores, siphonophores and some other soft-bodied (gelatinous) metazoan organisms break up or become unrecognizable in formalin preparations. It is perhaps less well known that colonial radiolarians dissolve in formalin or even that radiolarians form colonies. All these groups were heavily studied in the last century.

Recently, *in situ* observations and the collection of intact healthy organisms for experimentation have inspired a different perspective on the oceanic planktonic community.

This research began with the realization in the spring of 1975 that the organisms most frequently encountered by divers in the surface waters of the Atlantic Ocean were colonial radiolarians. The overwhelming feature of this fact is that these protozoans are practically unknown as components of the oceanic food chain and go unreported in most plankton samples. This research will attempt to place the colonial radiolarians in proper perspective with the rest of the epipelagic planktonic community by describing their size, abundance, functional morphology, trophic relationships and primary productivity.

Biologists who are unfamiliar with the radiolaria will find the following brief description of their taxonomy, morphology and life history useful.

The super-class Actinopoda is divided into four major classes (Cachon and Cachon, in prep.).[1] These are Acantharia, Phaeodaria, Polycystina and Heliozoa. The "radiolaria" are the Phaeodaria and Polycystina. The Polycystina are characterized by a skeleton of spines and shells made of silicon dioxide. They have an axopodial system which issues from axoplasts, usually through pores called fusules in a capsular membrane made of a glycoprotein substance (Hollande et al., 1970). This separates the inner part of the cell, or central capsule, from the remainder. Frequently there are symbiotic dinoflagellates in the extracapsular region.

There are two orders of Polycystina: Spumellaria and Sphaerellaria. The order Spumellaria (Peripylea) is characterized by spherical central capsules and uniformly distributed fusules. The sub-order Collodaria (Sphaerocollida) includes a number of species of colonial radiolarians. The shells or spines are relatively simple. There are a number of families including the Sphaerozoidae (forming spicules or no skeleton) and Collosphaeridae (forming spherical shells) which group together all the colonial forms. Detailed cytological studies support this classification scheme for the radiolarians (Cachon and Cachon, 1971, 1972a, b, 1976). There is some evidence that other radiolarians, specifically certain deep

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[1]The levels of these taxa are in dispute. Cachon and Cachon (personal communication) have provided the best and most recent classification scheme for the radiolaria. Older parallel forms are provided in parentheses where appropriate.

living Tuscaroridae (Phaeodaria) form colonies also (Haecker, 1908,

personal observation). Colonial radiolarians in this report will be con-

sidered to be those collodarian radiolarians in the families Sphaero-

zoidae and Collosphaeridae (Hollande and Enjumet, 1953) forming multi-

cellular gelatinous masses.

Within the central capsules of colonial Collodaria are found the

nuclei, vacuoles, mitochondria, endoplasmic reticulum, Golgi apparatus,

and often one or several oil droplets (Figure 1). Many form crystals of

strontium sulfate (Hollande and Martoja, 1974) in the later phases of

their reproductive cycle. Some species (particularly in the family

Collosphaeridae) form blue or violet pigment granules in the reproductive

stage (Brandt, 1885). The reader is referred to Anderson (1976a,b,c;

1978), Hollande and Enjumet (1953), Hollande et al. (1970) and Cachon

and Cachon (1976) for more detailed morphological information on the

Collodaria.

Outside of the central capsule is the extra-capsular region enclosing

the cytoplasm. In the Sphaerozoidae and Collosphaeridae this region al-

ways encloses zooxanthellae (dinoflagellates), which belong either to the

genus *Amphidinium* or *Endodinium* (Hollande and Carré, 1974; Taylor, 1974).

These encysted dinoflagellates are non-motile and have no external fla-

gellar structure. Extracapsular bodies are also found in the ectocytoplasm

of many radiolarian species (Brandt, 1885, 1902). These are thought to

be storage bodies.

Skeletal structures of simple or complex spines are found in the

extracapsular region, usually immediately surrounding the central cap-

sule, but occasionally, as in the case of some species of *Sphaerozoum* and

Figure 1. A central capsule of *Collozum* (= *Myxosphaera*) *coeruleum* in the reproductive stage of its life cycle. Visible are the crystals of $SrSO_4$ (C), blue pigment granules (P), the large oil droplet (ϕ), the central capsule membrane (CM) and the symbiotic zooxanthellae (Z). Scale = 10 μm.

Figure 2. A single cell of *Sphaerozoum* sp. showing the siliceous spicules gathered around the central capsule. S = spicule, Z = zooxanthella. Scale = 50 μm.

Figure 3. *Collosphaera huxleyi*, showing the spherical shell (Sh) perforated by pores. Shell is 105 μm diameter.

Figure 4. A reproductive colony of *Siphonosphaera tenera* showing the central capsules scattered over the surface of a single large alveolus. Colony is 4.5 mm diameter.

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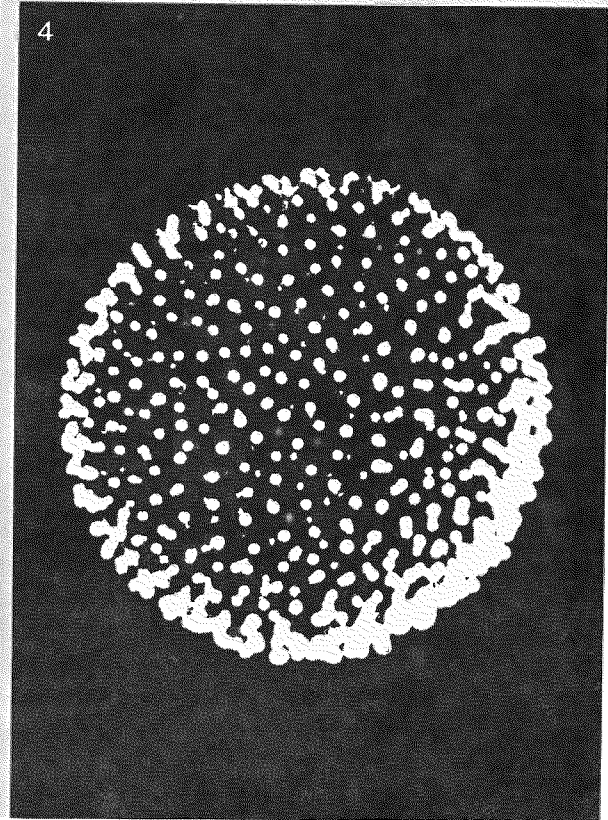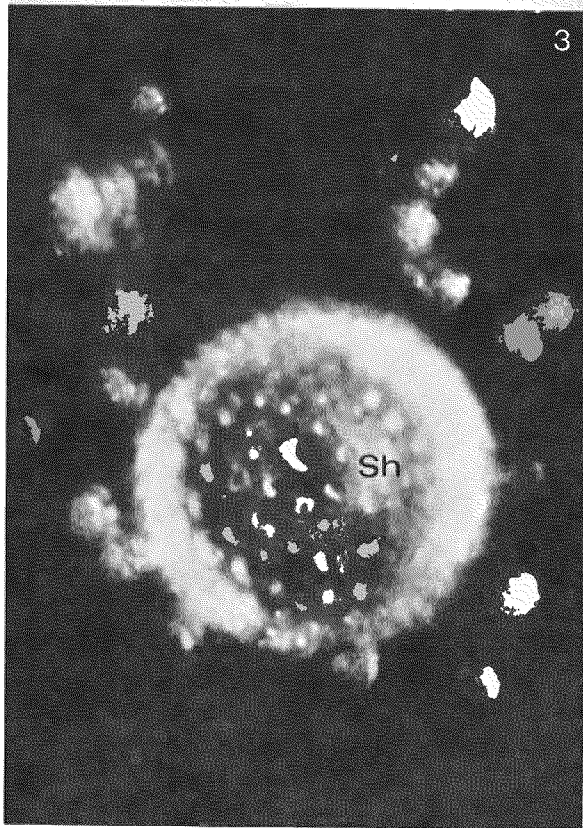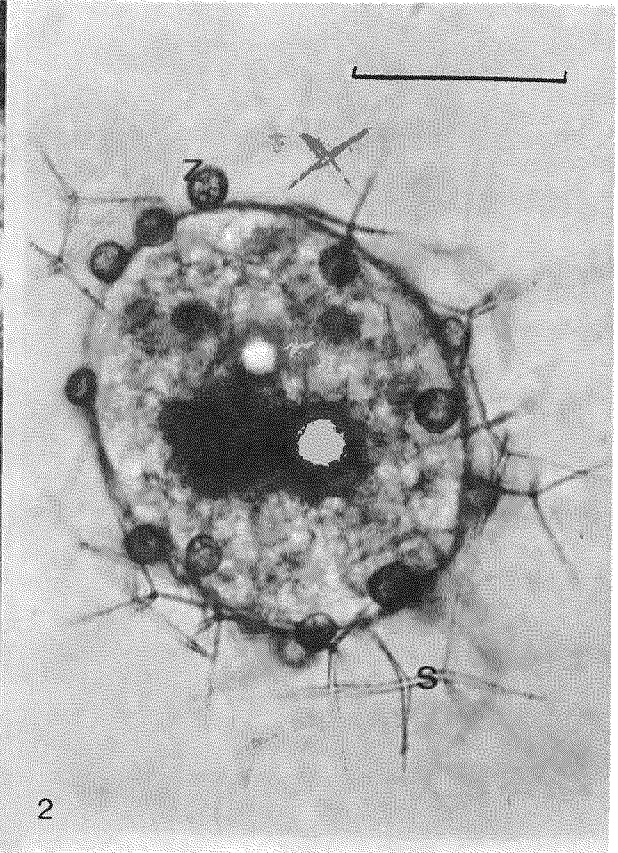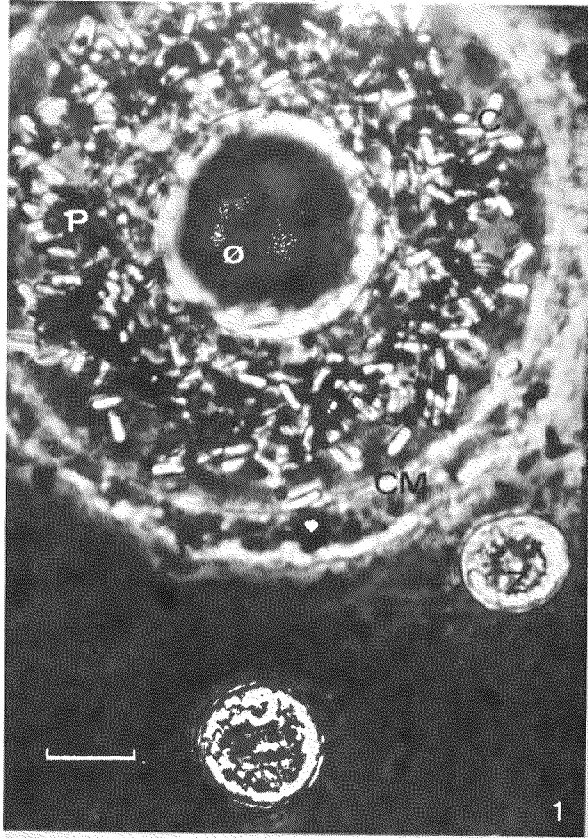
Rhaphidozoum, they are scattered widely through the colony. They may

take the form of simple or complex spicules (*Rhaphidozoum* and *Sphaero-*

zoun; Figure 2) or complete shell structures in the form of a simple

sphere perforated with holes (*Collosphaera*; Figure 3), and sometimes

bearing spines (*Acrosphaera*), protrusions (*Siphonosphaera* and *Soleno-*

sphaera) or invaginations (*Bucinosphaera*). All of the taxonomy common-

ly used is based on the details of shell morphology described by

Haeckel (1887). At least one genus (*Collozoum*) forms no shell. The

cells are held together in a colony by a network of interlacing rhizo-

podia and by extra-cellular secretions of sulfated mucopolysaccharides

(Hollande and Hollande, 1975).

The colonies usually show well-defined structure. The rhizopodia

extend to a fringe around the entire colony and there are usually large

alveolar structures present (Figure 4). Anderson (1976c) showed these

to be enclosed by a thin envelope of cytoplasm with mitochondria in it,

and thus to be part of the radiolarian cell. These alveoli occupy a

large part of the volume of the colony and may largely affect its appear-

ance. Their contents are unknown. Although colonies occur in a very

wide range of shapes and sizes, the overall appearance and organization

are relatively consistent within given stages of most species.

The life cycle of the radiolarians is poorly understood. The young

solitaries of the genus *Thalassophysa*, *T. sanguinolenta*, *T. spiculosa*

and *T. pelagica*) are known to reproduce vegetatively as the central cap-

sule ramifies and divides to form a colony (Brandt, 1902; Hollande and

Enjumet, 1953) [these colonies were described earlier as separate

species in separate families]. This is followed by changes in the

separate central capsules of the colonies which are associated with the development of isospore swarmers like those produced in the solitary Collodaria *Thalassicolla*, *Thalassoxanthium*, etc. Each swarmer contains a nucleus, lipid granules, mitochondria, crystals of $SrSO_4$ and two flagella (Hollande, 1974). Events subsequent to isospore swarming are unknown in any group of the Collodaria.

The single cell stage is not known for any shelled species, although it is axiomatic that the colonies must in fact originate from a unicellular stage if they send out reproductive swarmers. It is recognized that the family Sphaerozoidae is a totally artificial category and that the members may all be polyzoic stages of described solitary species (Hollande and Enjumet, 1953). Until those stages are recognized they must be treated as a separate group. As will be seen, the polyzoic stage is certainly the most prominent in the plankton.

PART I

MORPHOLOGY, DISTRIBUTION, BEHAVIOR, TROPHIC

RELATIONSHIPS AND ABUNDANCE

2

INTRODUCTION

The least understood feature of the biology of colonial radiolarians
is the fact that they are not microscopic. Although the colonies are
composed of hundreds or thousands of protozoan cells, in many ways they
act as discrete organisms. Their structure is well defined, they respond
to external stimuli in an organized manner and some exhibit behavior
comparable to that of simple metazoan organisms.

During the past four years I have collected many specimens and made
many observations of radiolarian behavior and trophic activity, both *in
situ* and in the laboratory. It soon became apparent that some of the
radiolaria were different both qualitatively and quantitatively than any
of the descriptions suggest. I found radiolarians with surprising fre-
quency and abundance once I started actively looking for them; I also en-
countered colonies of gigantic proportions. The largest radiolarian pre-
viously described is *Collozoum moebii* Brandt (1905) which can reach the
size and shape of a cylinder 40 cm long and 1 mm in diameter. I frequent-
ly encountered specimens of several other species in excess of 1 m in
length; the largest was 3 m long.

This section deals with the radiolarians in terms of their morphology,
their trophic relationships with the rest of the plankton and their abun-
dance. Most of the species discussed here were described in the 19th
century, but several of the more unusual forms have not been described.
I was compelled to deal with these species systematically, but wish to
defer formal description for later publication. Accordingly, I will de-
scribe them here and designate them by letter code. Before doing so I

will briefly review some of the problems in the systematics of colonial radiolarians.

The colony morphology is not known for many radiolaria. Many species have been described solely from the morphology of isolated shells found in the sediments and plankton catches. There is a great deal of variability in the shell morphology within a species and even within a colony (Hilmers, 1906). This was not realized until rather late in the 19th century when Haeckel (1887) refused to accept the systematics of the geologist Ehrenberg (1860, 1872a,b) because it was based on morphological criteria which had no relationship to biological species.

Haeckel's own system was largely based on the CHALLENGER material from sediments and net collections. Although he was familiar with living material he still did not allow for very much variability of shell morphology within a species, nor did he consider colony morphology. Haeckel listed 84 species of colonial radiolaria in 17 genera and 3 families. Each of these families was in a separate order.

Brandt's monograph (1885) on the ecology of the colonial radiolarians of the Gulf of Naples emphasized the importance of studying the morphology and development of the living colonies in addition to central capsule and shell morphology for systematic work. Brandt (1905) also wrote a major systematic work on the colonial radiolarians. He submerged a number of Haeckel's genera and species and modified the classification scheme to include the colonial radiolarians in one order or suborder (Sphaerozoeën) with two family groups. Brandt's students Hilmers (1906) and Breckner (1906) only slightly modified his system and Haecker (1908) and Popofsky (1917) accepted it. Very little systematic work has been

done within the group since then; the French worker Tregoubouff (1953) modified the classification of Brandt and wrote a key for the Mediterranean species and the micropaleontologist Campbell (1954) inexplicably returned to much of Ehrenberg's classification.

This thesis is not a systematic work. In this first section I present morphological information relevant to my other work. It is introduced here to provide the reader with an understanding of the scale and range of colony morphology to be expected from the radiolarians. It will also provide the necessary perspective for an appreciation of the uniqueness of the gigantic colonies I have described.

There has not been sufficient time in this study to examine all of the collected material in detail. The species which I have studied thoroughly are in the genera *Collozoum, Acrosphaera, Solenosphaera* and *Siphonosphaera*. I have not yet thoroughly studied the species of *Sphaerozoum* and have little to add to Breckner (1906), who reviewed the genus. He organized it into 7 groups of forms (*Formenkreise*) including 15 species. The groups were based on colony and cell morphology as well as the shape and distribution of the siliceous spicules. Strelkov and Reshetnyak (1971) found only four species in their collections, two of which were new. It is possible that they overemphasized spicule structure and did not pay enough attention to cell and colony morphology. In the case of *Rhaphido-zoum*, no one has altered Brandt's (1905) reduction of the genus to two species; *R. neapolitanum* and *R. acuferum*; the former has simple spicules, the latter branched ones. The morphology of these genera in my material did not differ significantly from that described by earlier workers.

In the genus *Collosphaera*, Haeckel reported nine species. Hilmers (1906) combined all of these into *C. huxleyi* because he found much shell

variability within colonies. Strelkov and Reshetnyak (1971) accepted a wide range of shell morphology in *C. huxleyi* but also resurrected two of Haeckel's species. Until these are studied more carefully I have chosen to follow Hilmers, who studied living material and described colony morphology in detail.

Although I will present new data on *Acrosphaera* and *Solenosphaera*, I have concentrated on studies of the genus *Collozoum*.

Species of the genus *Collozoum*, which form no shell, are much less likely to have been described from net collections and, of course, leave no trace in the sediments. Thus they are known only from living specimens, mostly in the Mediterranean. The three largest of the new oceanic species mentioned in this text are in the genus *Collozoum*. These species of *Collozoum* seem to be much different ecologically than any of the small shelled species. Since these will be discussed at length in this section and since more is known of the life cycle of species of *Collozoum* than any shelled species it would be appropriate to review the state of knowledge of the systematics and life cycle of these species before proceeding.

Quoy and Gaimard (1824) described the organism *Lemniscus marginatus* from Ombai in the Alors group north of Timor (10°S x 123°E). The transparent gelatinous ribbon which they described was 2 feet long and 1 1/2 inches wide; it had no openings or visible internal structure, and it broke apart when they collected it. The morphology grossly matches that of one of the species described in this report except that their description includes a reddish border. They described no microscopic examination or cell structure. Colonial radiolarians were not discovered until Meyen (1834) described *Physematium*, so there was no reason to suspect that it might have been a protozoan. In the 816 dive stations occupied by my

colleagues and me since 1971, primarily in the Atlantic and Indian Oceans, nothing has been seen other than the radiolaria which could match the descriptions of Quoy and Gaimard. The organism was not described well enough to warrant priority, but it raises the interesting possibility that the first colonial radiolarian reported might have been one of the giant *Collozoum* species.

In his monograph, Haeckel (1862) separated the genus *Collozoum* from *Sphaerozoum* and described three species; *Collozoum inerme*, *C. pelagicum*, and *C. coeruleum*. Brandt (1885) adopted two of these, *C. pelagicum* and *C. inerme* and added two of his own: *C. fulvum* and *C. hertwigi*. Haeckel had described most of his species solely on the form of the central capsules. Brandt (1885) based his systematics on studies of the cellular morphology, histology and *in vivo* studies of the colony shape and changes undergone during reproduction. Included in the latter were some erroneous observations of the development of "anisospores" which are actually protozoan infections (Hollande and Enjumet, 1953).

Brandt described two basic colony shapes in *Collozoum*. *Collozoum hertwigi* and *C. fulvum* were reported to be small (4 mm dia.) spherical colonies; *C. pelagicum* and *C. inerme* were elongated cylindrical colonies, the latter somewhat segmented by large alveoli. Brandt separated *C. coeruleum* from the genus *Collozoum* and erected the genus *Myxosphaera* which he placed in the family Collosphaeridae with the shelled species.[2]

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[2] Having seen *Myxosphaera coerulea* (and often confused it with collosphaerids) I share Brandt's intuition that this species belongs with the Collosphaeridae, but I cannot defend such an opinion with fact. The argument Brandt believed strongest was that the development of anisospores paralleled that in shell-bearing species. While there may be some species-specific biological interaction controlling these "infusorien," the development of parasitic infections really should not be used to erect a new genus. Accordingly I refer to it as *Collozoum coeruleum*.

Later, in the CHALLENGER reports, Haeckel (1887) recognized 13 species and 5 subgenera of *Collozoum* and separated the genus from the Sphaerozoidae, forming the new family Collozoidae. Most of these species were based on preserved material from the CHALLENGER expedition, although he certainly drew upon his own experience in Messina, the Canaries and the Indian Ocean. Unfortunately Haeckel paid no attention to colony formation; his taxonomic system, like that for the shelled species, reveals little about and has little bearing on living organisms. A few other species were added by later workers (Haswell and Hedley, 1907; Enriques, 1919), but no major changes were made in the genus after Brandt (1905).

Brandt (1902) first observed the transformations from solitary collodarians to polycyttarians (colonial forms). He followed the development of *Thalassophysa sanguinolenta* and *T. pelagica* (3 specimens each) over a period of 3 months. During the transformations, which take about three days, both species change shape radically as the solitary central capsule elongates. After elongation the capsule begins to fragment into separate "individual" central capsules forming a colony with serpentine cells. Brandt (1902, 1905) proceeded to synonymize Haeckel's *Collozoum pelagicum*, *C. serpentinum*, *C. contortum* and *C. vermiforme* with the aforementioned species, although he did not specify which *Thalassophysa* developed into which *Collozoum*. He did specify that Haeckel's *C. pelagicum* as described matched *T. sanguinolenta's* polyzoic stage and that *C. ameboides* was probably also a polyzoic stage. Brandt commented that the *C. inerme* as figured by Haeckel (1887) was not identical with *C. inerme* Haeckel, 1862, but with *C. pelagicum* , and he resurrected his own *C. radiosum* (Brandt, 1885) which he originally tentatively placed with *C. pelagicum*. Hollande and Enjumet (1953) reported the same findings as Brandt (1902) for

T. sanguinolenta and *T. spiculosa*. Many or possibly all of the members of the genus *Collozoum* are derived from monozoic stages of collodarians. This has not yet been observed for any of the shelled species.

After describing the morphology of the colonies I have seen, I will present data on behavior, trophic relationships and abundance of the radiolarians.

MATERIALS AND METHODS

Colonial radiolarians were collected and observed by SCUBA divers on the following cruises: R/V CHAIN 122 (23 May to 7 June 1975), R/V CHAIN 123 (13 to 23 June 1975), R/V CHAIN 125 (31 July to 18 August 1975), R/V KNORR 53 (14 November to 2 December 1975), R/V COLUMBUS ISELIN 76-2 (29 January to 13 February 1976), S/V LA CURIEUSE 7601-7605 (26 February to 21 April 1976), R/V SUBSIG II (8 to 16 June 1976), CGC DALLAS (21 June to 1 July 1976), R/V OCEANUS 11 (23 July to 1 August 1976), R/V KNORR 58 (18 August to 7 September 1976), R/V OCEANUS 22 (5 to 30 March 1977), R/V OCEANUS 30 (17 to 27 July 1977), R/V OCEANUS 33 (6 to 19 September 1977), R/V THOMAS WASHINGTON BMET (22 November to 19 December 1977), R/V ATLANTIS II 98 (27 February to 11 March 1978), R/V ATLANTIS II 101 (19 June to 20 July 1978), R/V OCEANUS 52 (28 October to 23 November 1978), R/V ANTON DOHRN at the Naples Zoological Station (7 August to 7 September 1978), and on the M/V PIERCE 79-1 (17 June to 16 July 1979). These cruises include dive stations (Harbison et al., 1978) 353 to 816 (see Appendix I) in the Atlantic Ocean from 7°S to 40°N lat., in the California Current and in the equatorial Indian Ocean at 55°30'E long. There were some of these cruises on which I did not go. These were only used for distributional

information when preserved samples were available or when the records of the cruise were judged sufficiently good to be sure of presence or absence of the species in question. This was generally the case for very large or otherwise unusual colonies.

Detailed information was collected at 212 stations between station 417 and 774; 82 of these were within 10° of the Atlantic or Indian Oceans' geographic equator. North Atlantic maps were made for the distribution of common genera and some of the more common species. Since negative stations could not always be relied upon for accuracy, the distributions are presented as stations where radiolaria were collected and stations where the species in question was collected. Superimposed on the maps are faunal provinces of mesopelagic fish (Backus and Craddock, 1977; Backus et al., 1977). These provinces are based on physical oceanographic discontinuities and observed faunal changes in fish. They have also been used in distributional studies of epipelagic ctenophores (Harbison et al., 1978).

At each dive station where radiolarians were encountered those collected were studied *in vivo* and representative specimens preserved. Colonies were generally preserved as discrete samples and notes made of their *in vivo* morphology. The preservatives recommended by Brandt (1885) were tried and found to work for a number of species (*Collozoum inerme, C. serpentinum, Acrosphaera spinosa, Siphonosphaera tenera, Sphaerozoum* sp., *Rhaphidozoum neapolitanum, R. acuferum,* and *Collosphaera huxleyi*). They are cumbersome to use at sea, however, and the best preservative found was a 4% solution of Formalin in distilled water saturated with picric acid and mixed 1:1 with seawater and specimens. This generally preserved the details of colony morphology lost with conventional preservative such as Formalin; however, there was some shrinkage. Whenever possible, colonial forms were

photographed *in vivo* at sea in a Wild M-5 stereomicroscope with trinocu-
lar head assembly. Individual central capsules and details of cell
morphology were photographed *in vivo* in a Leitz Ortholux compound micro-
scope equipped with phase optics. Both systems used a Wild microscope
camera and automatic electronic flash.

Shelled species were examined ashore after digestion of organic matter
from the siliceous shells using the method of Hasle and Fryxell (1970).
For identification of species I have used the figures and descriptions of
Strelkov and Reshetnyak (1971) extensively. I have also referred to
Haeckel (1862, 1887), Brandt (1885, 1905), Breckner (1906), and Hilmers
(1906). The latter three works are probably the best on colonial radio-
larians, but they are in the German language and are difficult to obtain.
Possibly for this reason, many researchers have referred to Haeckel (1887)
which is readily available in the English language.

Fixation for transmission electron microscopy was done by Dr. Susumu
Honjo's laboratory at Woods Hole. Sectioning and transmission electron
microscopy was done in Tübingen by Dr. O. Roger Anderson of the Lamont-
Doherty Geological Observatory. Dr. Anderson summarized his methods:
The "semi-thin section was obtained with an ultra microtome, transferred
to a slide, stained with 1.5% toluidine blue O solution prepared in 10%
ethanol solution. The stain was warmed on the slide to improve penetra-
tion and after washing and drying was mounted with Canada balsam... The
ultra-thin sections were obtained with a diamond knife in a Reichert ultra
microtome. The sections were thin silver to silver gold in thickness,
picked up on uncoated upper grids, and post stained with Reynold's lead
citrate stain for 5 min. They were observed with a Zeiss EM9 electron

microscope." Scanning electron microscopy of shells was done by Margaret Goreau in Dr. Honjo's laboratory.

Whenever possible, interactions between radiolarian colonies and other components of the epipelagic community were also recorded on film. Colonies were frequently collected and preserved with various species of prey in their gelatinous matrix. In addition, external and internal commensal associates were preserved and photographed as encountered. Some attempts were made to feed radiolarians to fish, isopods, siphonophores and other plankters. Opportunistic observations were made on the behavior of the radiolarians in response to mechanical and photo stimulation, including their control of density and algal distribution.

Amphipods of the family Hyperiidae were identified to species by Dr. G. R. Harbison, using the key and descriptions of Bowman (1973). Copepods (Harpacticoida) of the genus *Miracia* were identified to species using the keys and descriptions of Lang (1948) and Wells (1970). Crustaceans were measured using the method described by Harbison (1976).

At most stations density of radiolarian colonies was visually estimated by divers using the drift rate calculations described by Harbison et al. (1978). These stations were ranked according to their relative abundance as 1, 10, 100, 1000, corresponding approximately to the density of colonies per 1000 m^3. On OCEANUS 30 and LA CURIEUSE 7601-7605 densities were measured by a method similar to that used by Swanberg (1974) for ctenophores. A 0.5 m^2 hoop made of plastic hosing was used and radiolarian colonies in a 10 m path were counted as they passed through the grid. Path length was determined by a measured line. In one instance this was compared to a measured drift tow on OCEANUS 30. Occasionally, in surface swarms in the Indian Ocean, colonies were counted in a 0.5 m^2 grid

placed horizontally on the surface. Because of extreme vertical strati-
fication and horizontal patchiness, absolute density measurements were
not heavily emphasized in this work.

RESULTS

Morphology and Distribution

There are six basic forms which colonies of radiolarians normally
assume. They can be spherical, ellipsoidal (flattened), cylindrical,
lemniscal (ribbon-shaped), toroidal, and shaped like a very complicated
pretzel. There are variations on these shapes and they present a be-
wildering array to the observer who first sees a dense aggregation of
colonies.

None of the basic shapes are species-specific. Nor are very many of
the species shape-specific. This does not mean, however, that one cannot
use structure in the identification of species. There are suites of other
features of secondary structure, such as distribution of alveoli and tex-
ture of gelatin, which are easily recognizable and may in some cases by
species-specific. These features are best described as they apply to each
species. Following are brief descriptions and observations on the species
encountered during this work. Special emphasis is given to those which
are new or unusual.

Family Sphaerozoidae

Genus *Collozoum*

The genus *Collozoum* was the most widespread of any of the genera en-
countered. Specimens were collected at 191 of 212 stations recorded (90%).

The genus is particularly noteworthy because it includes all of the species which form large colonies. With very few exceptions the described species of *Collozoum* form cylindrical or spherical colonies.

Collozoum inerme

This species is the textbook example of a colonial radiolarian (Grell, 1973). The most common of the *Collozoum* species, it was collected on 85 of 212 stations (40%). It was well described by Haeckel (1862) and very extensively studied by Brandt (1885). The ultrastructure was reported by Anderson (1976a).

The colonies are cylindrical, 2-5 mm diameter and 1-4 cm in length. They are dominated by large alveoli which give the appearance of segmentation (Figure 5). Occasionally toroidal colonies were seen. The radiolarian cells are spread evenly over the surface of these alveoli and the whole colony is surrounded by a fringe of rhizopodia and gelatin which extends about .5 mm beyond the cell layer. The gelatin is fairly firm in the young colonies; in older colonies it is softer and the colony stretched at the cytoplasmic connections between the alveoli, giving it the appearance of a string of spheres (Figure 6). Central capsules are 60 to 80 um in diameter, and no central capsular membrane is visible *in vivo* (Figure 7). There are 1000-5000 central capsules per colony.

Collozoum inerme occurred infrequently on the equator (19 of 82 dives within 10° of the equator) but I did find it commonly in the Gulf Stream and Central Gyre, as far north as 40° lat. (Figure 9). It is reported to have occurred as far north as 75° (Pavshtiks, 1956).

Stations: 403, 407, 417, 419, 420, 422-426, 455, 463, 469, 470, 472, 477-479, 481, 513, 514, 516, 517, 521, 524, 526, 531, 536, 537, 542, 544, 547-549,

Figure 5. A typical colony of *Collozoum inerme*, showing the segmental appearance caused by the large alveoli. Diameter of colony is approximately 3 mm.

Figure 6. An older colony of *Collozoum inerme* in which the gelatin is softer and the colony is stretched at the cytoplasmic connections between alveoli. Diameter of colony is 2.5 mm.

Figure 7. A single central capsule of *C. inerme*. There is no membranar structure visible. Scale = 50 μm.

Figure 8. A portion of a colony of *Collozoum pelagicum* (= *Thalassophysa sanguinolenta*), showing the fuzzy border and the irregular distribution of central capsules. Diameter of colony is 2.0 mm.
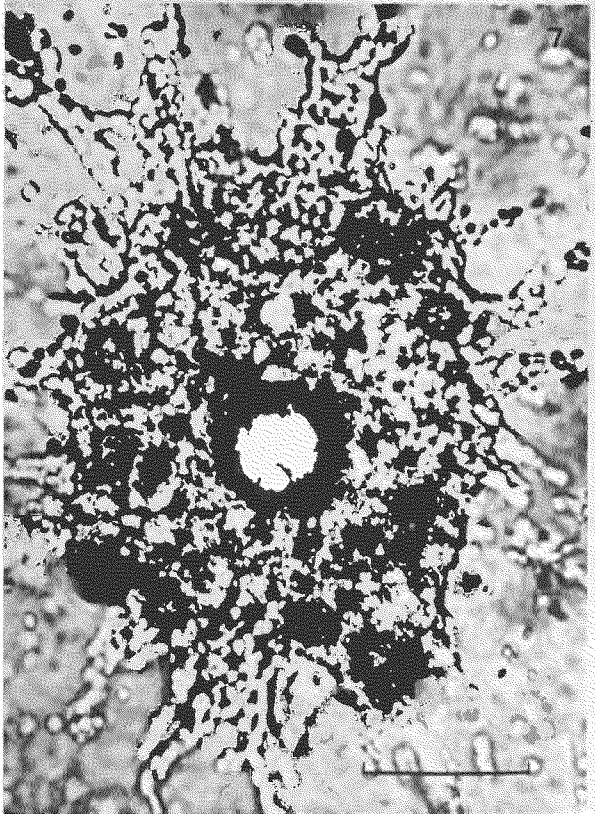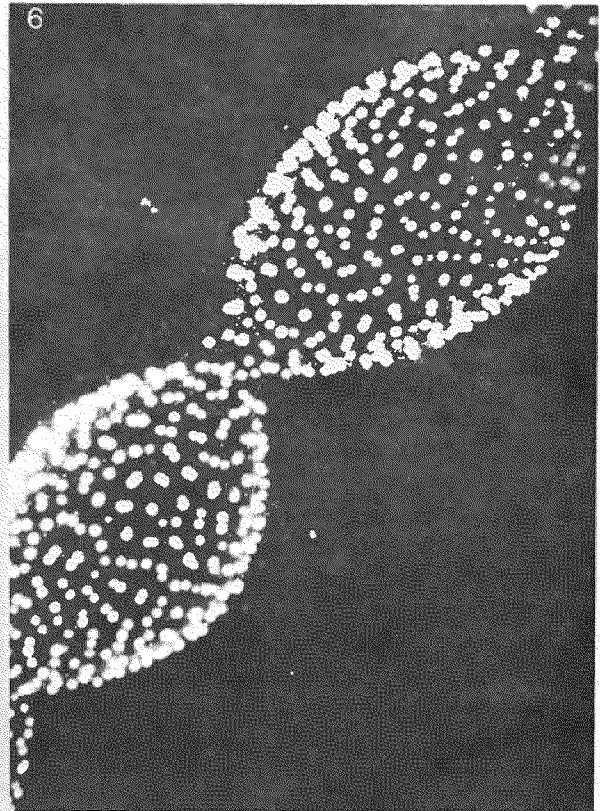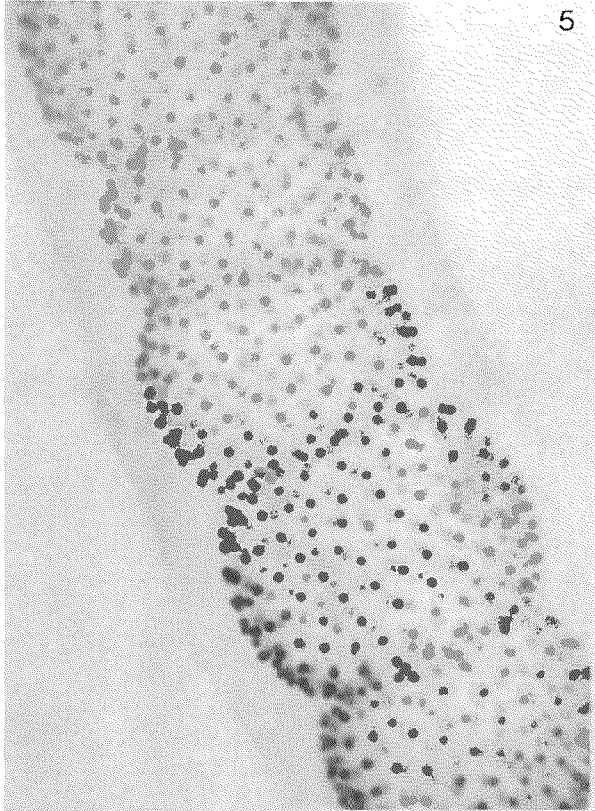
Figure 9. Map showing locations of stations in the North Atlantic

Ocean where specimens of *Collozoum inerme* were collected (●), and

stations where other radiolarians were collected (+). Forty stations

were made where no radiolarians were recorded; many of these were

coastal (see Figure 75). Boundaries shown are for faunal provinces

defined by Backus and Craddock (1977). The provinces are:

1 - Atlantic Subarctic, 2 - Northern Gyre, 3 - Slope Water, 4 - Azores-

Britain, 5 - Mediterranean Outflow, 8 - Northern Sargasso Sea,

9 - Southern Sargasso Sea, 10 - Northern North African Subtropical Sea,

11 - Southern North African Subtropical Sea, 12 - Lesser Antillean,

14 - Caribbean Sea, 15 - Amazonian, 16 - Guinean, 19 - Mauritanian

Upwelling.
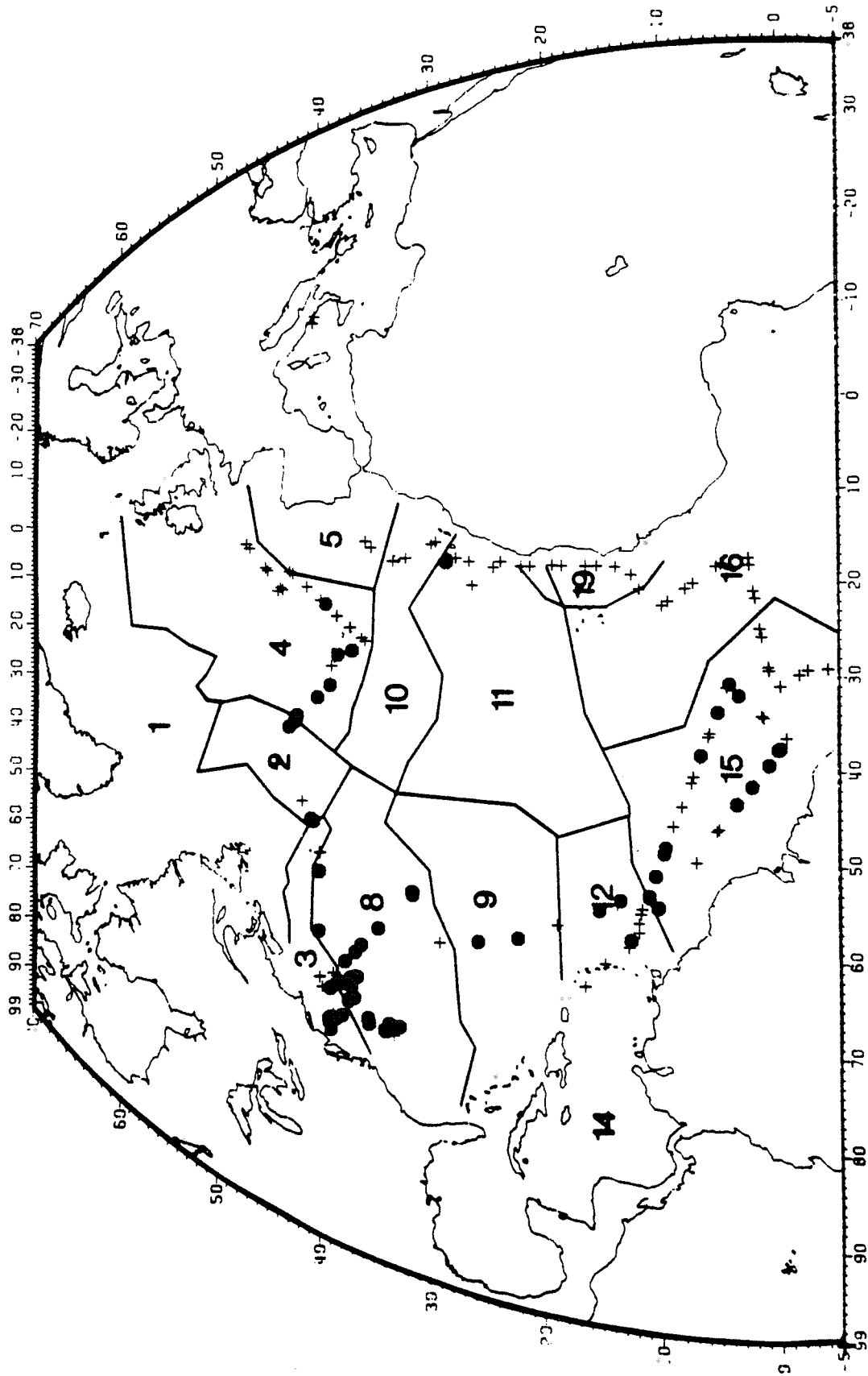
553, 555, 557, 560, 566-571, 574, 577-583, 585-597, 611, 613, 615, 616, 624-631, 632, 640, 643, 652, 656, 659-675, 682, 684, 703, 737, 774.

Thalassophysa sp. group (*Collozoum pelagicum, C. serpentinum, C. vermiforme, C. ameboides, C. stellatum* and *C. contortum*)

This group of species was synonymized with the solitary collodarian *Thalassophysa sanguinolenta* by Brandt (1902; Introduction, this section). My material includes all of these forms, but I am not convinced that they are all stages of *T. sanguinolenta*.

Collozoum pelagicum forms cylindrical or occasionally toroidal colonies 2-4 mm diameter by 1-4 cm in length with a very fuzzy border (Figure 8), soft gelatin, and many small spherical alveoli. The cells are spherical or oval (Haeckel, 1862, claimed that they were polygonal) and 20-80 μm diameter. Extra-capsular bodies (Brandt, 1885) could be found around the central capsules. There may be many species which are closely allied to this and which have similar stages. They are among the most difficult of radiolarians to identify as there are few distinctive features which are diagnostic.

Stations: 417, 467, 523, 527, 542, 547, 550, 567, 580, 585, 586, 587, 589, 592, 594, 612, 615, 616, 630-633, 642-645, 649, 650, 655-658, 660, 662, 663, 671, 675, 679, 682, 702, 716, 726.

The colonies with elongate or serpentine cells were either spherical (approximately 5 mm diameter) with a single alveolus, or cylindrical (1-2 cm long) with many small alveoli. There were different types of serpentine cells (Figures 10, 11) but the types did not necessarily correspond to the descriptions of Haeckel (1887) for *C. serpentinum* or *C. vermiforme*.

Stations: 395, 459, 465, 470, 472, 476, 514, 516, 517, 519-521, 526-528, 537, 557, 591, 613, 614, 616, 644, 679, 682, 695, 741, 744, 769.

Figure 10. A serpentine central capsule of *Collozoum serpentinum*? (= *Thalassophysa* sp.) showing oil droplets (arrow) and surrounding alveoli (A). Scale = 100 µm.

Figure 11. Another colony (*C. vermiforme*?) which forms serpentine cells. The cells can be several mm long. Scale = 200 µm.

Figure 12. A spherical colony of *Collozoum contortum*? with many alveoli in its center. Diameter of colony is 4.2 mm.

Figure 13. A larger view of the cells of the colony shown in Figure 12. Some of the cells are larger, opaque and spherical. Scale = 200 µm.

Figure 14. These opaque cells from the colony in Figure 13 are reproductive, forming swarmers. Scale = 100 µm.

Figure 15. A segment of a colony of *Collozoum radiosum*. Many other species of radiolarian have morphology similar to this. Colony is 2.0 mm in diameter.

Figure 16. A few cells of *Collozoum ellipsoides*, showing the multiple oil droplets. Scale = 100 µm.

Figure 17. Cells of *Collozoum* (= *Myxosphaera*) *coeruleum* are very regular and distinctively spherical. Scale = 100 µm.
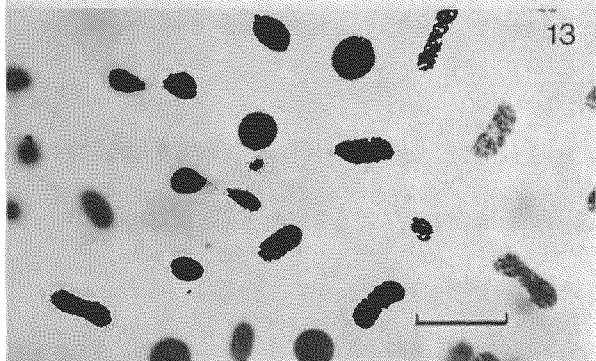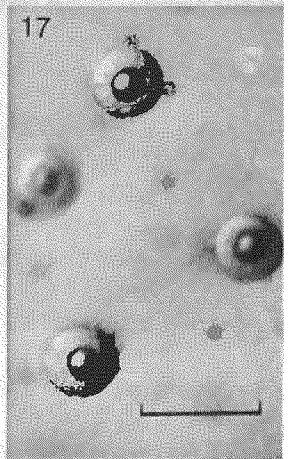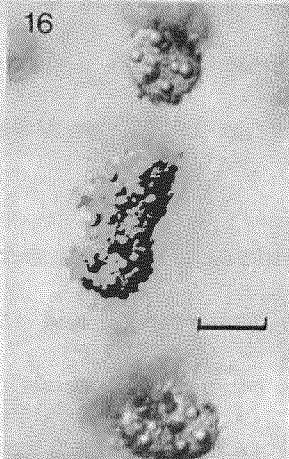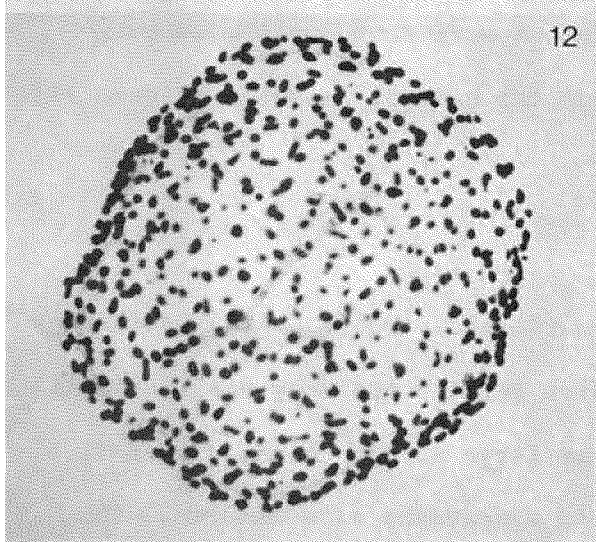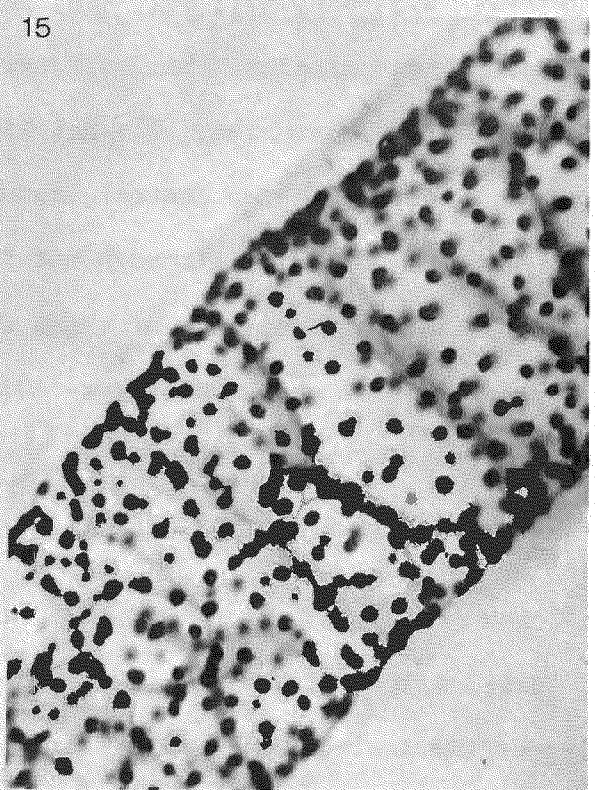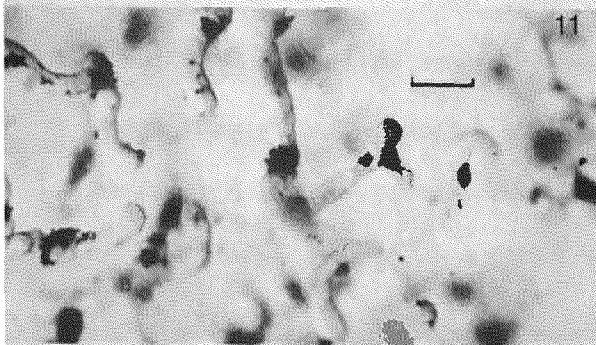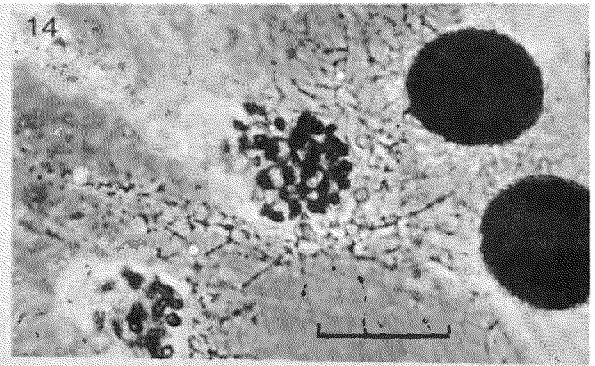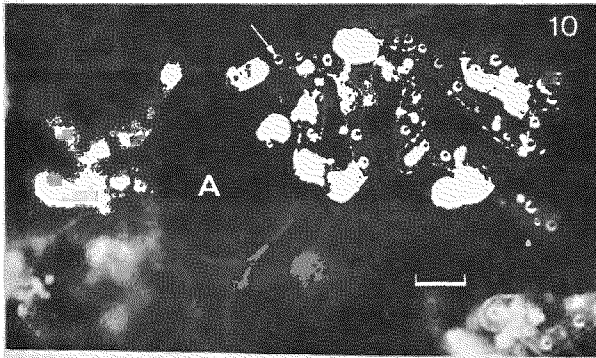
A few colonies (11) were found with lobes of cytoplasm extruded from the central capsules. These may be specimens of *C. ameboides* and *C. stellatum*. All but two of these colonies possessed the cylindrical segmentation of *C. inerme*. Those two were flattened elliptical colonies. One of these contracted to a spherical mass upon capture.
Stations: 473, 569, 571, 612, 616, 681, 706, 708.

Collozoum contortum. Six colonies were caught which matched the description of *C. contortum*. The colonies were spherical with many small alveoli (Figure 1). The central capsules were mostly elongate (60 µm dia., 150-200 µm long), although not "c" or "s: shaped as described by Haeckel (1887). In several of these colonies there were also opaque spherical central capsules (Figure 13) which were reproductive as evidenced by the presence of swarmers inside the central capsules (Figure 14).
Stations: 681, 695.

Collozoum radiosum

Originally mistaken for *C. pelagicum* (Brandt, 1885), *C. radiosum* forms long cylindrical colonies with fairly firm gelatin and many small alveoli (Figure 15). In some the alveoli were as large as the colony diameter, although they did not acquire the segmented appearance of *C. inerme*. The colonies I found were up to 50 mm long; Brandt (1885) reported colonies as large as 260 mm.

The spherical central capsules were a little larger than those of Brandt's figures (60 - 100 µm diameter), and included a single large oil droplet. They were surrounded by a thick mesh of rhizopodia.

I found colonies in abundance, especially on ATLANTIS II 101 in the summer of 1978 in the vicinity of the Azores. They were hardy and abundant

enough there to be a useful subject for experimentation. Data on their

algal photosynthetic rates will be presented in Part II.

Stations: 419, 424, 425, 455, 464, 471, 477, 523, 548, 589, 630, 632,

652, 653, 654, 656, 660, 661, 663-666, 673, 675, 676, 679, 681, 747.

Collozoum ellipsoides

This species was characterized by Haeckel (1887) as having large cen-

tral capsules (300-400 μm long, 200 μm wide), each provided with many oil

droplets. I found one type of colony which characteristically had such

elliptical central capsules (Figure 16). Although the capsules were small-

er (80x 80-300 μm) and had fewer oil droplets, they were consistent in

their morphology and matched no other described species. The colonies

were cylindrical with many small alveoli. They were always drawn to a

point at each end. This was noticeable enough to allow successful recog-

nition *in situ*.

Stations: 557, 560, 613, 649, 660, 716, 770.

Collozoum (= Myxosphaera) coeruleum

This species forms two types of colonies; long cylinders and hollow

spheres. In the vegetative stage the cylindrical colony resembles that of

C. radiosum. There are many small spherical alveoli and the cells are

scattered among them. The colonies of the reproductive stage are hollow

spheres with the cells only on the surface. The central capsules of this

species were very easily recognized as defined spheres with clear central

capsule membranes and very little visible cytoplasm outside the central

capsule (Figure 17).

I saw the transition from vegetative cylinder to reproductive sphere

at the Zoological Station of Naples in August, 1978. It occurred exactly

as Brandt (1885) described it. Vegetative specimens were collected in the Gulf of Naples and placed in glass jars on 23 August. The next day all the cells in the vegetative colonies (approximately 4 cm long) were on the surface of the cylinders which had become irregular in contour. Within hours the cylinders had shrunk to hollow blue spheres 5-10 mm in diameter. Stations: 571, 635, 657, 663, 670, 673, 675, 708, 727, 729.

Collozoum longiforme sp. nov. (Swanberg and Harbison, 1979 - see Appendix II).

The vegetative colonies of this species are cylindrical, 5-7 mm in diameter and 1 cm to 3 m in length (Figure 18). The colonies have a distinct, but slightly irregular border and are rounded at the ends; occasionally small colonies were shaped like a lobed torus. Each colony had a translucent core composed of small alveoli ($\sim$ 1 mm in diameter), central capsules, and zooxanthellae which comprised about four-fifths of the colony diameter (Appendix II, Figure 1). The core was surrounded by a transparent zone of gelatin in which rhizopodia and often captured prey were found. Early vegetative colonies had spherical or elongated central capsules 50-80 μm in diameter (Figure 19) with small oil droplets (8 μm). There were from 14-28 algae per central capsule and an average of 130 central sapsules per mm length. Thus a 1 m long colony had 10^5 cells. Late vegetative colonies had spherical central capsules 80-120 μm in diameter with a single large oil droplet of 35-55 μm (Figure 20). In these colonies, there were up to 50 algae per central capsule. The solitary and reproductive stages are unknown. The gelatin is very firm.

24

Figure 18. An elongate specimen of *Collozoum longiforme*. There is a large core of alveoli and cells surrounded by a thin margin of rhizopodia and gelatin. This specimen is about 15 cm long x 6 mm in diameter.

Figure 19. An early vegetative central capsule of *Collozoum longiforme*. There is no visible oil droplet and in this specimen only 17 algae surround the central capsule. Note the thin proximal ectoplasm (e). Scales = 20 μm.

Figure 20. A late vegetative central capsule of *Collozoum longiforme*. There is a large oil droplet (∅) and very numerous algae. Scales = 20 μm.
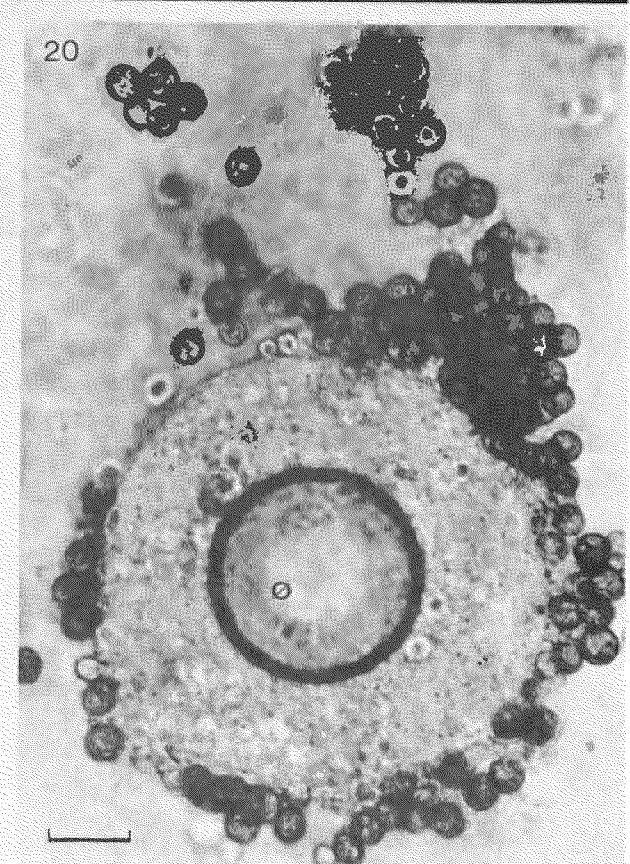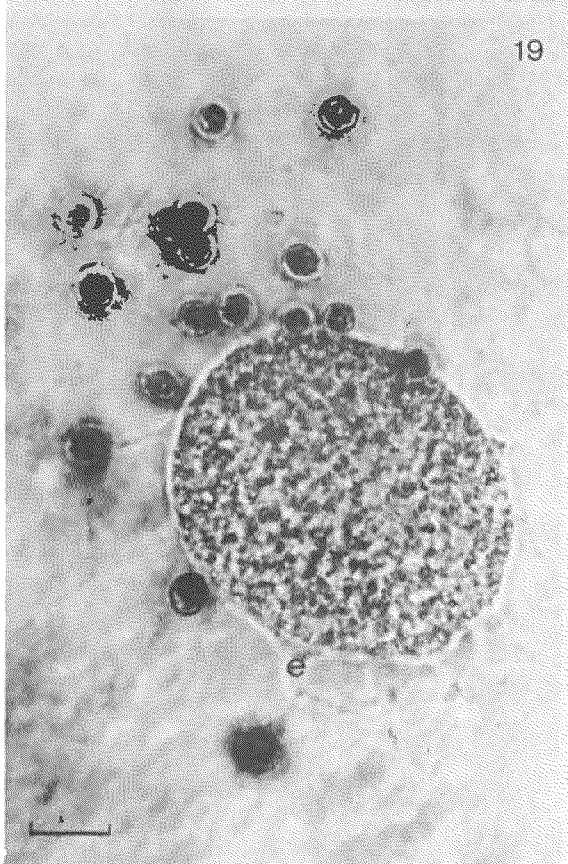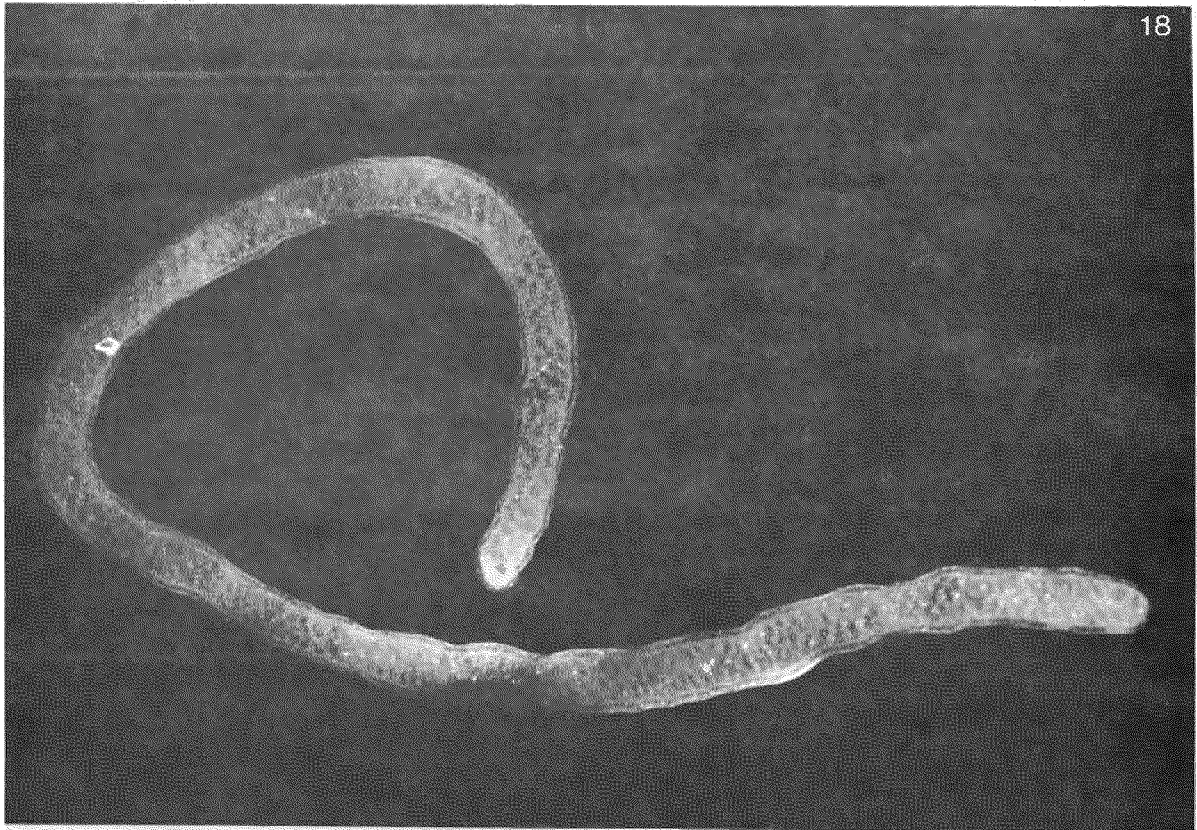
Figure 21. Map showing locations of stations in the North Atlantic

Ocean where specimens of *Collozoum longiforme* were collected (●) and

stations where other radiolarians were collected (+). The species was

not encountered on any of the stations in the Indian or Pacific Oceans.

Boundaries as in Figure 9.
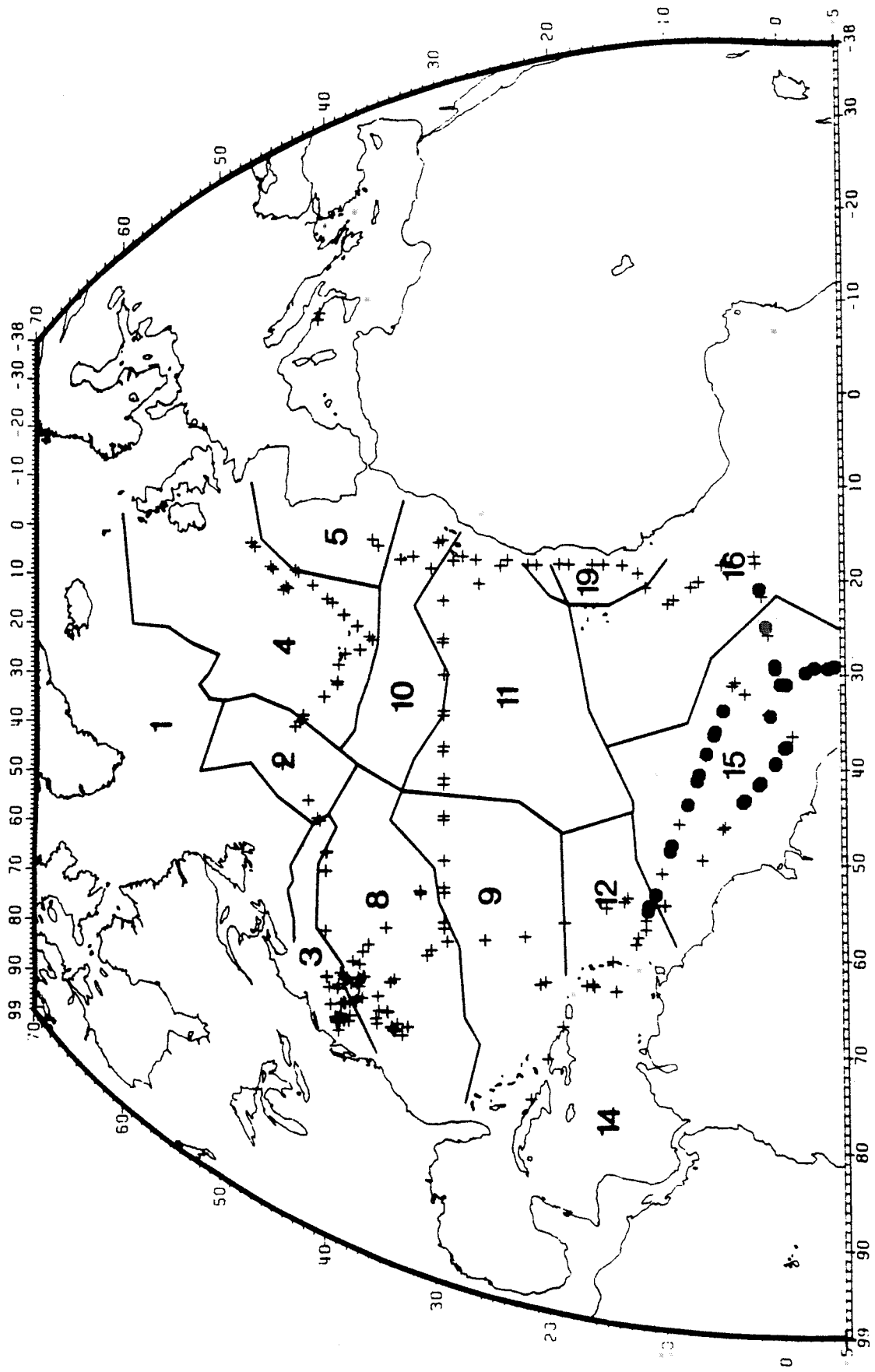
Specimens were found on 33 stations in the equatorial epipelagic region known as the Amazon Province (Backus et al., 1977) east of the north coast of Brazil to Saints Peter and Paul Rocks (Figure 21).

Stations: 542-549, 551, 557-560, 562-564, 566, 567, 571-573, 700, 702, 704-713.

Collozoum sp. A.

The best diagnostic feature of this species is the colony morphology. The colony, which may reach a length of 2 m, consists of a core of radiolarian central capsules densely packed with algae and surrounded by alveoli 1 - 2 mm in diameter. This species had more algae per radiolarian cell than any other species collected. There were 250-350 algae per central capsule (see Part II). The core is surrounded by a gelatinous sheath equal in thickness to the diameter of the core itself ($\sim$ 5 mm). Figure 22 shows a typical small specimen. The most characteristic feature of the species is the formation of a fecal strand at either end of the colony (Figure 22, arrow). The colonies were occasionally seen as large toroids or more complicated structures probably generated by the fusion upon contact of separate portions of the colony. The central capsules are characteristically large, 150-300 μ in diameter, translucent, with a few oil droplets in early stages. These droplets were coalesced in more advanced stages. The earlier stages had oval or oblong central capsules, the latter ones were spherical. There is no shell.

I was unable to follow the developmental stages of *Collozoum* sp. A because the species is so delicate. However, I have seen several stages from which I infer that its development parallels that of *T. sanguinolenta* (= *Collozoum pelagicum*, *C. serpentinum*, *C. contortum*, etc.). Only one

Figure 22. A small specimen of *Collozoum* sp. A, curled up in a dish. The core of large central capsules and algae is clearly visible. This is surrounded by a thick gelatinous sheath. One fecal strand (arrow) dangles at each end. This specimen was about 10 cm long.

Figure 23. A detailed view of the core, showing the large alveoli (A), the central capsules (C) with their large oil droplets, and the rhizopodia (R) and abundant zooxanthellae. Scale = 200 µm.

Figure 24. A high magnification phase-contrast photograph of the central capsule of one late stage *Collozoum* sp. A shows the platelets (P). These are purple *in vivo*. Their function is unknown. Scale = 20 µm.

Figure 25. A microscope photograph taken of the strand-forming region of a specimen of *Collozoum* sp. A. Veliger larvae and tintinnids are clearly visible as they are incorporated into the fecal strand (T). When these strands reach a length of several cm they appear like threads hanging from the end of the colony. Scale = 1 mm.
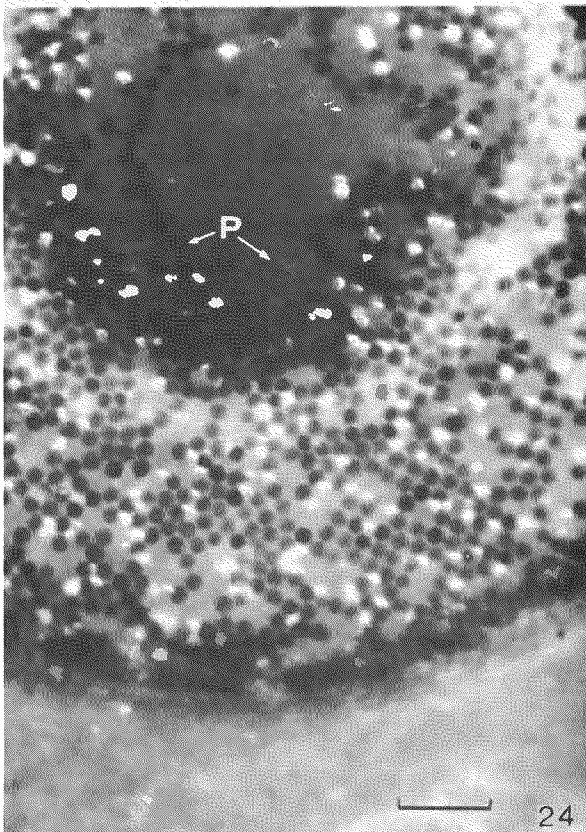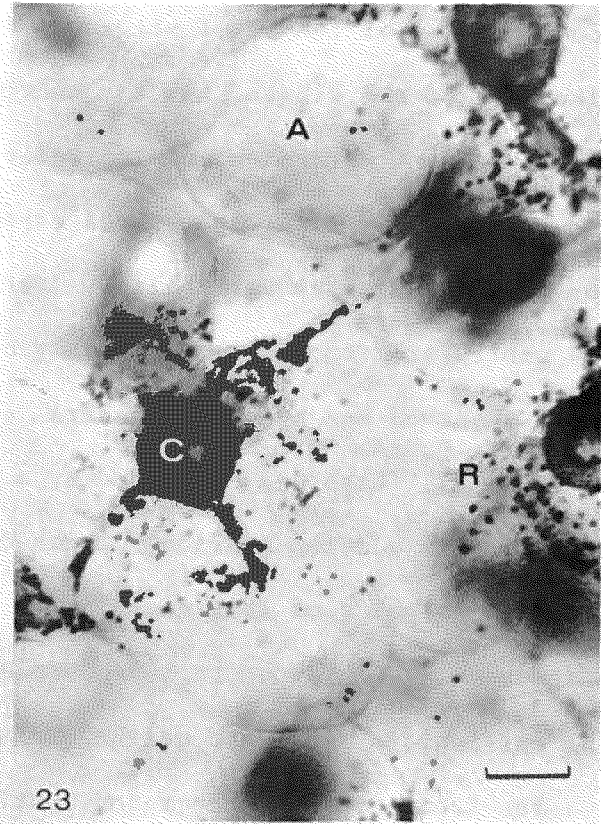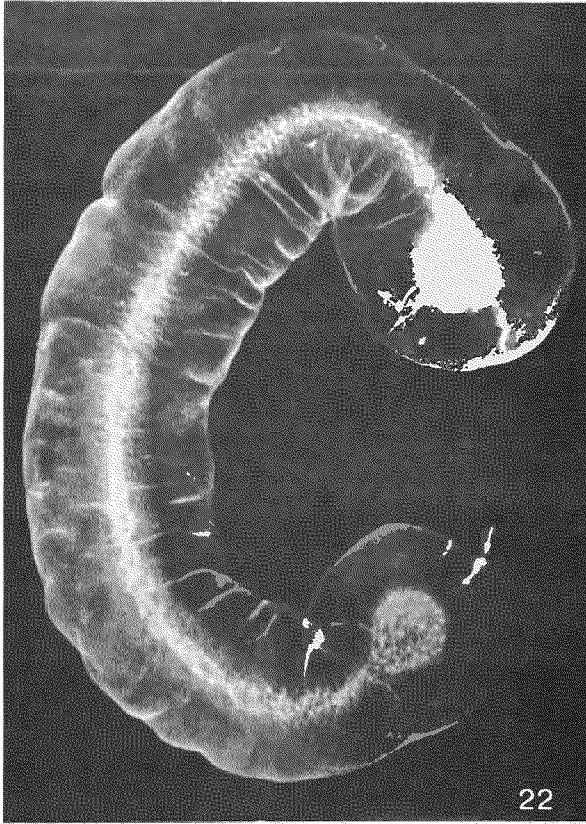
good specimen of the first stage was found. The colony morphology was like that of the others, but the central capsules were connected together by transparent extensions of the cells like those of *T. sanguinolenta*. A second stage had discrete central capsules with a diameter of 130-200 μm. The central capsules were oblong, irregular or subspherical in shape with 2-4 vesicular structures (presumably oil droplets) in them. The third stage observed had spherical central capsules with a diameter of 200-300 μm (Figure 23). Each was dominated by a large oil droplet (160 μm in diameter). This and the previous stages described were amber in color, but I also saw colonies of this description which had purple central capsules. Under the light microscope this purple color appeared as an array of regular particulate platelets on the surface of the central capsule (Figure 24).

The fecal strand is composed mostly of the empty loricae of tintinnids, mollusc veliger shells and other undigested prey remains. Figure 25 shows the incorporation of this debris into the strand. The strand elongates and pieces fall off. In very few instances did fecal strands emerge from along the length of the colony, although occasionally more than one stub or start was seen near the ends.

The fine-structure of one colony with purple pigment granules was typical for the genus *Collozoum* (Anderson, 1976a). The diameter of the cell in Figure 26 is 250 μm. It is multi-nucleate and dominated by the large lipid reserve body (160 μm) in its center. The cytoplasm does not present the radiating columnar profiles (Anderson, 1976a) found in *C. inerme*. The endoplasmic region (Figure 27) includes nuclei (N) surrounded by vacuoles (V) and motochondria (M). Figures 28, 29 and 30 show details of this region including a Golgi body (GB), probable microbodies (MB) and endoplasmic reticulum (ER). The nuclei closely resemble those of *C. inerme*,

Figure 26. A light micrograph of a thin section of *Collozoum* sp. A.
The center of the cell is dominated by a large electron-dense body, pre-
sumably a lipid reserve body (R). All the major cell organelles are in
the periphery of the cell, inside the cell wall. Visible in this section
are the nuclei (N), vacuoles (V), and outside the central capsule, the
symbiotic zooxanthellae (Z). Magnification = 270 X, Scale = 100 μm.

Figure 27. The peripheral region of the cell shown in Figure 26. This
electron micrograph shows the nucleus (N) surrounded by vacuoles (V) and
mitochondria (M). The dense granules (G) near the plasma membrane and
capsule wall are also surrounded by mitochondria. Magnification = 3600 X,
Scale = 2 μm.

Figure 28. High magnification of the region near a nucleus showing the
Golgi body (GB) and a probable microbody (MB). Magnification = 20,000 X,
Scale = 1 μm.

Figure 29. Edge of nucleus (N) showing microtubules (MT) and endoplasmic
reticulum (ER). Magnification = 21,000 X, Scale = 1.0 μm.

Figure 30. Higher magnification view of Figure 29 showing endoplasmic
reticulum (ER), microtubules (MT) and the nuclear membrane in detail.
Nuclear membrane is composed of inner membrane (IM) and outer membrane
(OM). Microtubules attach to inner membrane. Magnification = 53,000 X,
Scale = 0.5 μm.
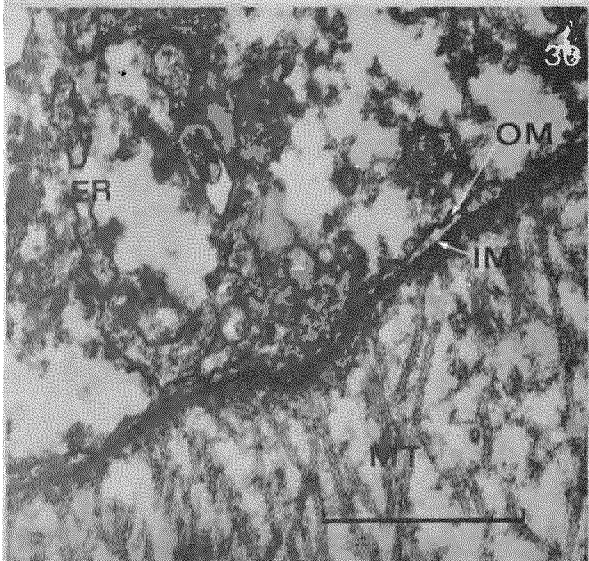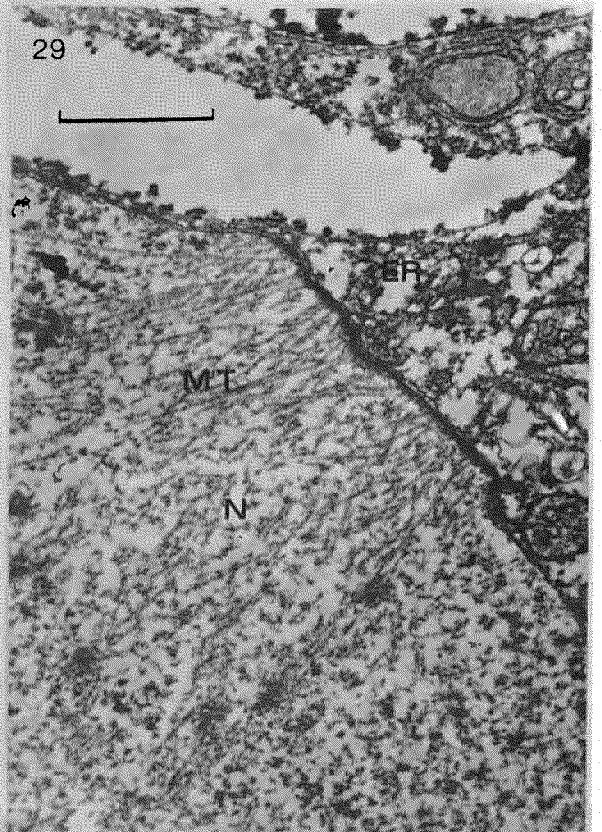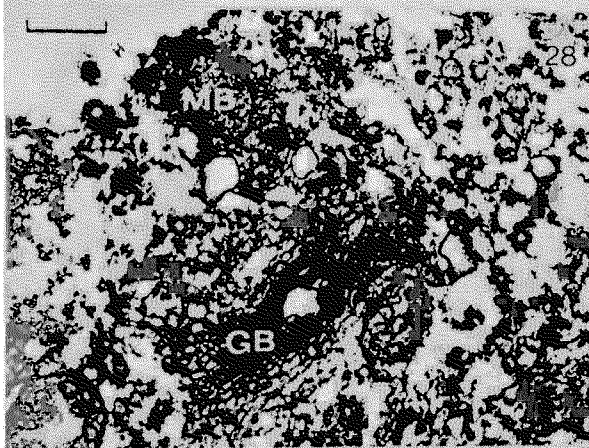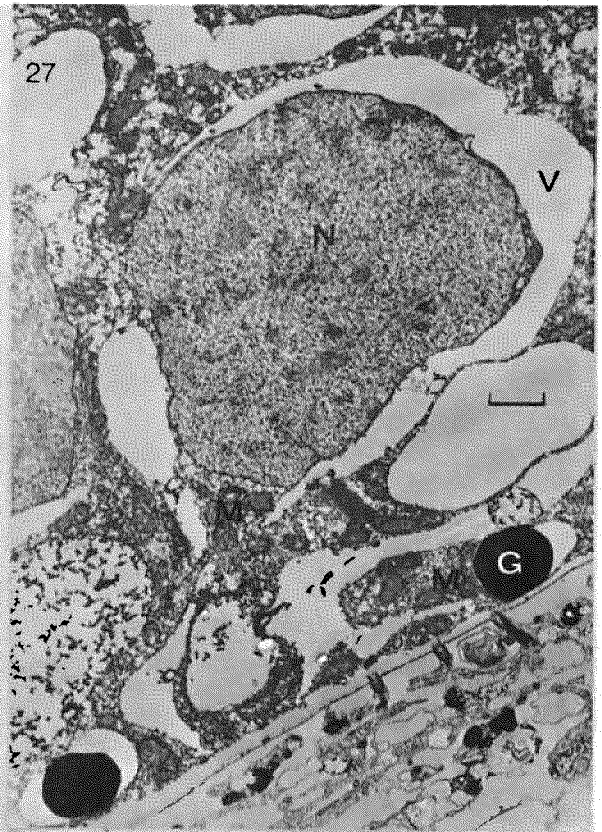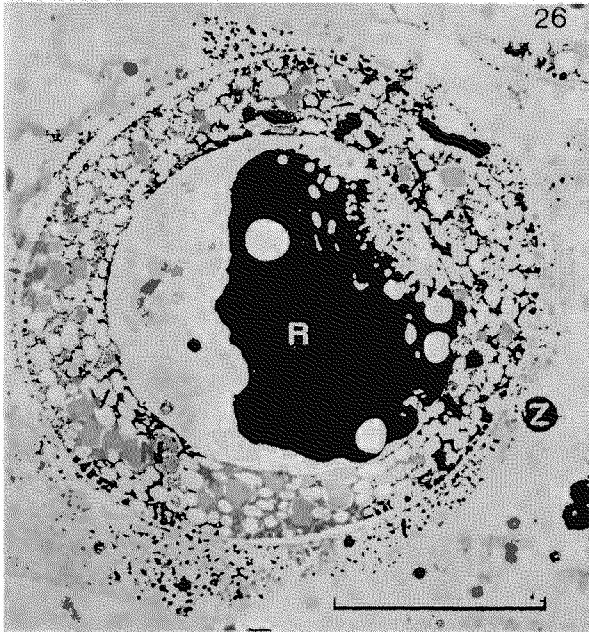
possessing a double membrane and fine fibrils of chromatin suspended in the nucleoplasm. As in *C. inerme* the microtubules (MT, Figure 30) are attached to the inner surfaces of the nuclear membrane (Anderson, 1976a) and not to the cytoplasmic surface. They also attach to granular chromatin masses (Figure 29) exactly as in *C. inerme*. This is much different from the structure in the nuclei of *Collosphaera globularis* which contained cord-like strands of chromatin (Anderson, 1978). Outside the plasma membrane (PM, Figure 31) lies the central capsule wall (CW, central capsule membrane of old literature) with fusules (F) providing continuity between endo- and ectoplasm. In this section the fusule is separated from the plasma membrane. It looks somewhat different from that of *C. inerme* (Anderson, 1976a) because of the capsule wall lying outside of the plasma membrane surrounding the fusule. In *C. inerme* there is no such wall.

Along the central capsule wall are seen fissures (S). Anderson (1976c) hypothesized that these were points for the central capsular wall to break at swarmer release in *Sphaerozoum punctatum*. Just inside the plasma membrane all around the periphery of the central capsule are found vacuoles with dense granular inclusions (G, Figure 27). The one in figure 31 measured 2.5 μm in diameter. No structure such as these is seen in *Collozoum inerme* (Anderson, personal communication, 1979). They occupy the same position and are as numerous as the purple "platelets" visible *in vivo*. Although they are near the resolution limit for light microscopy, the platelet diameter was approximately 2.9 μm *in vivo*.

The function of these organelles is unknown. If they are the colored pigment granules one might compare them with the blue pigment granules which develop in reproductive collosphaerids and in *Collozoum* (= *Myxosphaera*) *coeruleum*. They are not known to develop in any other species of *Collozoum*.

Figure 31. High magnification of the periphery of a central capsule of
Collozoum sp. A showing the cell wall (CW), a fusule (F) and the small
pores in the cell wall (S). Also visible are mitochondria (M) and the
dense granules (G) inside vacuoles (V), possibly identical with the pig-
mented platelets shown in Figure 24. Magnification = 20,000 X.
Scale = 0.5 μm.

Figure 32. Overview of a symbiont. The prominent structures are the
nucleus (N), the pyrenoid lobes (PY) with their starch sheaths and the
numerous chloroplasts (CH) and starch bodies (S). Outside of the cell
are seen host cytoplasm (C) and the host mitochondria (HM), all enclosed
in the gelatinous envelope (GE). Magnification = 5400 X. Scale = 2 μm.

Figure 33. Details of the cell of the algal symbiont showing chloroplasts
(CH), pyrenoid (PY) with starch sheaths (SH), mitochondria (M), reserve
bodies (R), nucleus (N) and vacuole containing hair-like structures (F).
Magnification = 11,000 X. Scale = 1 μm.

Figure 34. Details of a chloroplast continuous with a pyrenoid (PY) which
is penetrated by a membrane system (CM) resembling chloroplast thylakoids.
Visible as a continuous line is the algal thecal wall (T) separating the
algal cell contents from the host cell. Magnification = 18,000 X.
Scale = 0.5 μm.

Figure 35. Sketch from photograph of an unidentified solitary radiolarian
which forms a strand-like structure like those of *Collozoum* sp. A.
Approximate length, without strand is 1 cm.
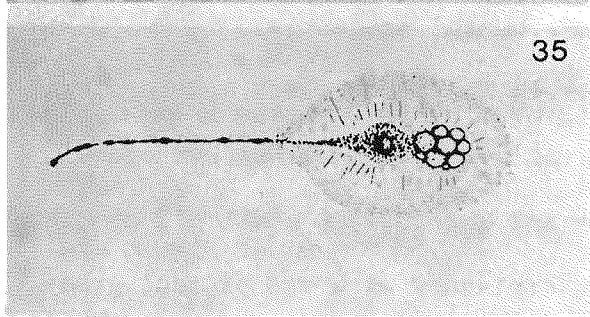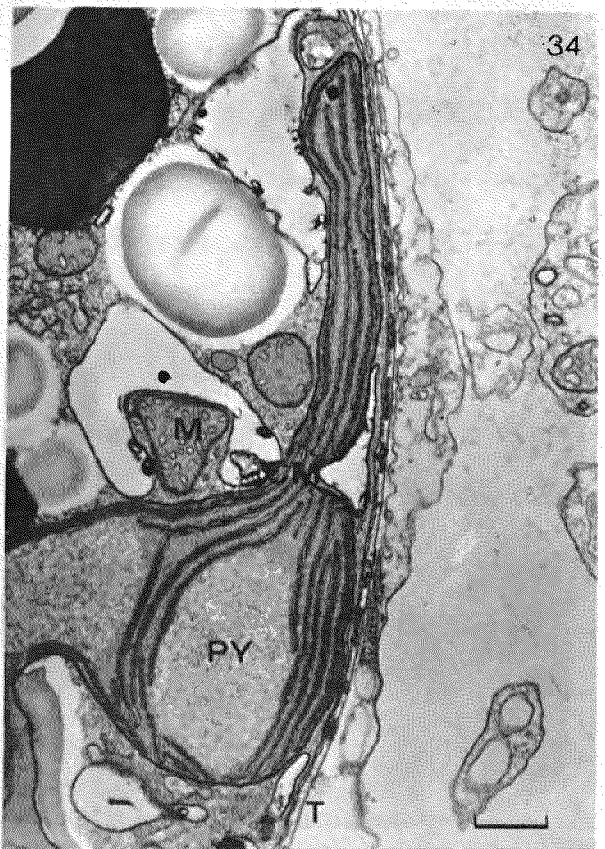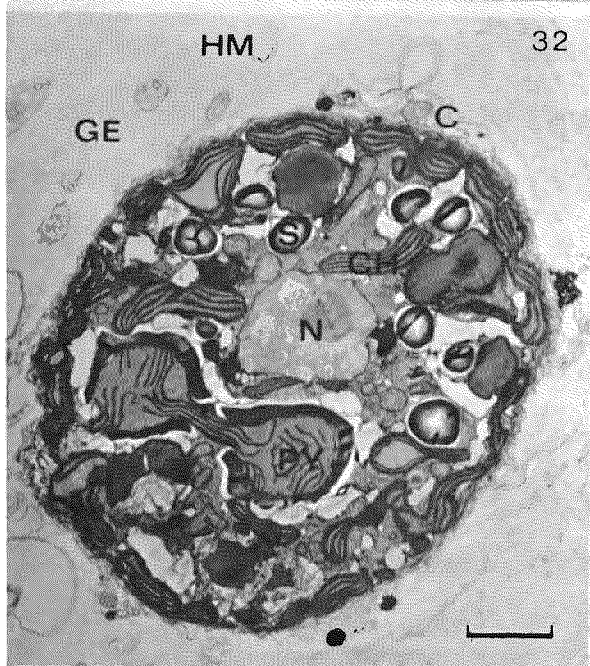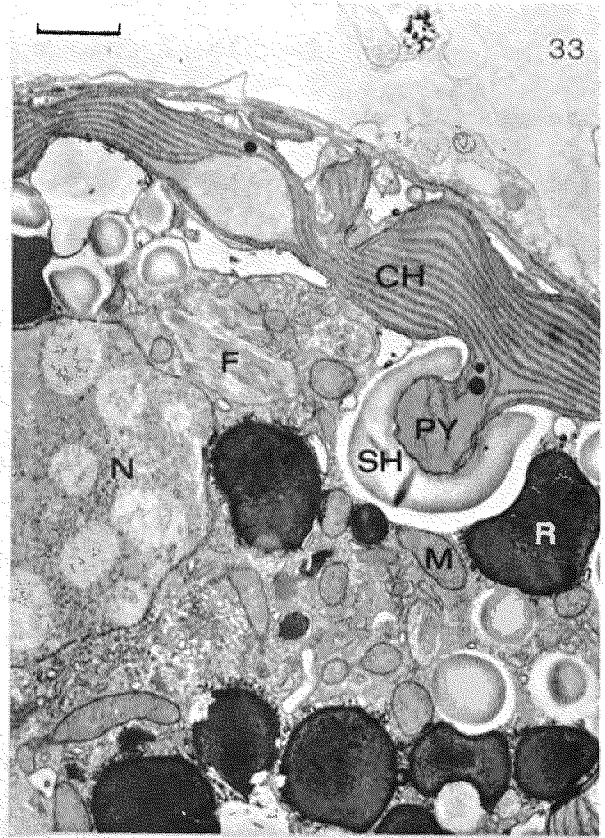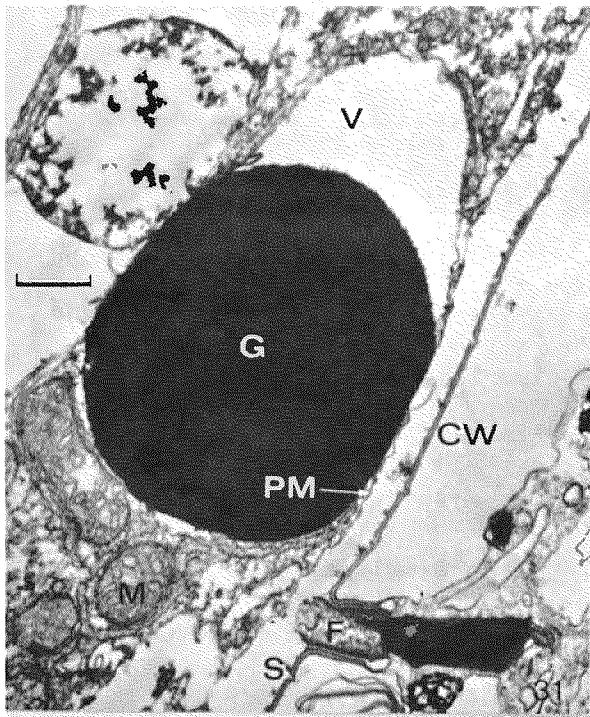
The zooxanthellae (12 μm diameter) occur in the radiolarian gelatinous envelope (GE) outside the central capsule (Figure 32). The host cytoplasmic sheath (C), including mitochondria (HM) is seen surrounding the cell. The pyrenoid lobes (PY) seen in the alga are surrounded by starch sheaths. There are numerous starch grains (S) and chloroplasts (CH) and one central nucleus (N). High magnification (Figure 33) shows a pyrenoid with its starch sheath (SH), mitochondria (M), and in this specimen, dense reserve bodies (R). There is also a vacuole with hair-like structures (F) like those described by Anderson (1978) in the symbiont of *Collosphaera globularis*. These fine filaments are believed to be Golgi-derived and appear to be deposited on the surface of the flagella in free-living dinoflagellates (Anderson, personal communication). Figure 34 shows the thecal wall (T) which separates the alga from its host's ectocytoplasm. In the alga cell a chloroplast lobe lying in the cytoplasm is continuous with a pyrenoid (PY) which is penetrated by a membrane system (CM) resembling chloroplast thylakoids.

This radiolarian is a species of *Collozoum*. The resemblance of the nuclei to those of *C. inerme* and the absence of a shell are strong evidence for inclusion in this genus. The inferred events of the life cycle strongly resemble the transformation of *T. sanguinolenta* to *C. pelagicum*. A few solitary forms with fecal strands were collected (Figure 35) which could be likely candidates for the developmental precurser.

Haeckel (1887) described two species of *Collozoum* which have central-capsules as large as *Collozoum* sp. A. *Collozoum nostochinum* has opaque central capsules 300-500 μm in diameter and has 200-300 small oil droplets. The central capsules were described as "distended with red pigment granules" (type locality; Indian Ocean off Socotra). *Collozoum volvocinum* has

Figure 36. Map showing locations of stations in the North Atlantic Ocean

where specimens of *Collozoum* sp. A were collected (●) and stations where

other radiolarians were collected (+). Included in this map are stations

from the M/V PIERCE in province 8. Although the samples from this recent

cruise have not yet been studied, these stations could be included be-

cause the species is easily recognizable *in situ*. This species was col-

lected on 15 of 29 equatorial Indian Ocean stations and was not collected

on the R/V THOMAS WASHINGTON off the California Coast. Boundaries as in

Figure 9.
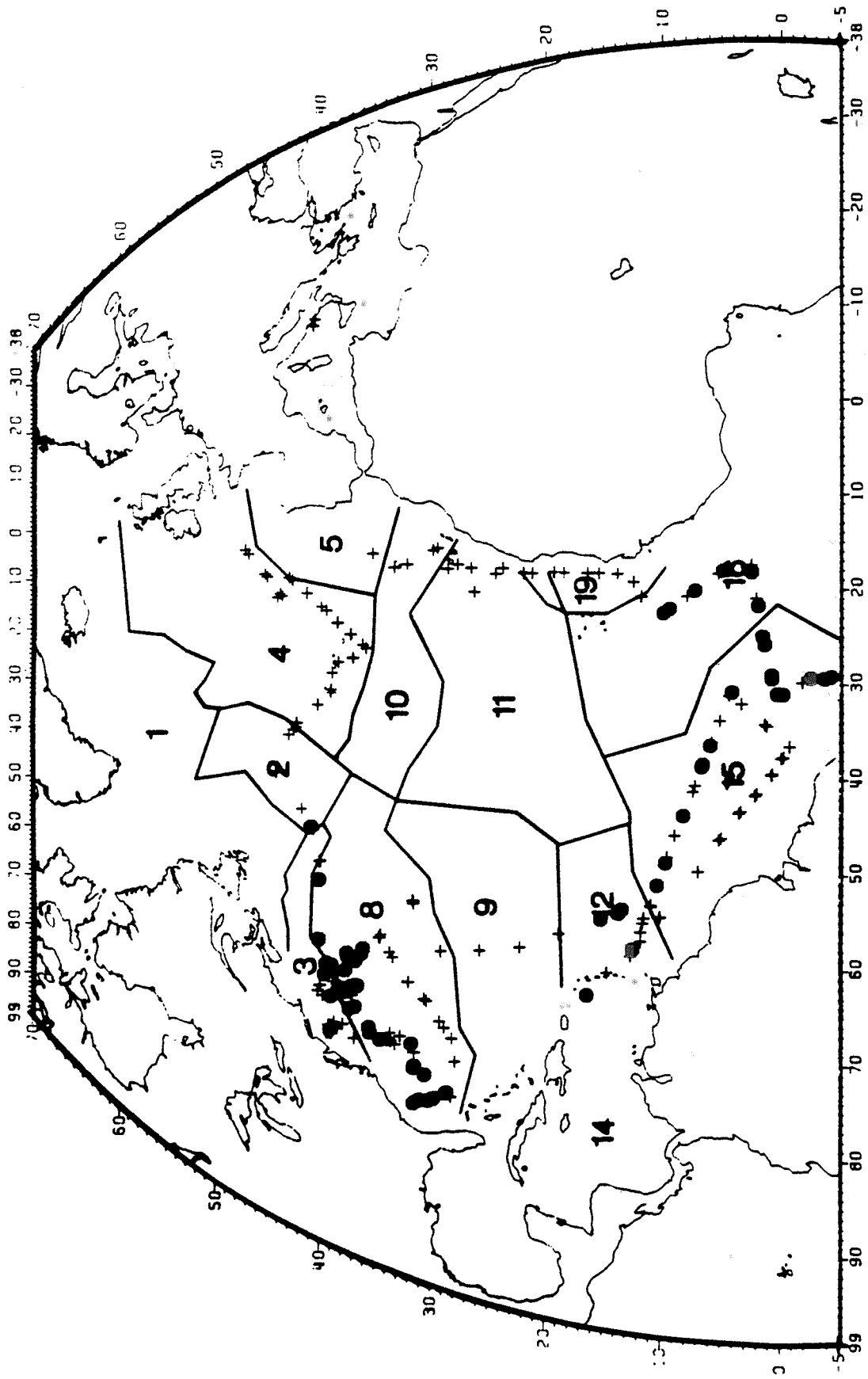
opaque central capsules 200-300 μm in diameter and 10-30 small oil drop-
lets (from the CHALLENGER station 272). Neither of these species is
adequately described for comparison. It is conceivable that *Collozoum*
sp. A could be one of these, but I have never seen the central capsules
opaque or to have so many oil droplets.

The species was found at 94 stations. Figure 36 shows the distribu-
tion of the colony in the Atlantic; in addition it was found on 15 out of
29 stations (57%) between 03°0'S and 02°0'N at 55°30'E in the Indian Ocean
during LA CURIEUSE cruise 7601-5.

Stations: 417, 426, 427, 458, 460, 469-476, 478-481, 483, 555, 559-561,
564, 567, 568, 574, 577, 582, 583, 585, 587-589, 591-594, 596, 608, 610,
612, 613, 624-631, 643, 752, 753, 755, 757, 759, 761-767, 769-771, 773,
774, 776, 778, 780, 783-791, 793, 807, 809-815.

Collozoum sp. B.

On 10 occasions I have encountered large ribbon-shaped colonies (Figure
37), usually about 1 m x 3-5 cm x 4-5 mm. The largest was approximately
3 m long (Station 577).

These colonies showed no special organization, but had a region of
cells and small alveoli dominating the mass of the colony. This was sur-
rounded by a gelatinous fringe around the entire colony. The central
capsules were 100-200 μm in diameter and without shell or spicules. Pre-
served central capsules are difficult to distinguish from those of *Collo-
zoum* sp. A. No ultrastructural study was done. *In vivo* the cells also
resembled *Collozoum* sp. A and the appearance of the alveoli in the colony
is similar. Both were collected in the vegetative and reproductive stages
however, and although the reproductive ribbons had large oil droplets I

Figure 37. A photograph (*in situ*) of a lemniscal colony of *Collozoum* sp. B. This colony was approximately 80 cm in length.

Figure 38. The rhizopodia of a colony of *Collozoum* sp. B contract in defined regions giving the border a striated appearance; the colonies frequently fragment after this. Scale = 1 mm.

Figure 39. A close-up view of the radiolarian central capsules in Figure 38 showing the algae densely packed around the central capsules. Scale = 250 μm.

Figure 40. Detailed light microscope view of the central capsules (C) of the same specimen in Figures 38 and 39. Note the dense rhizopodia (R) and the symbionts (Z). Scale = 100 μm.
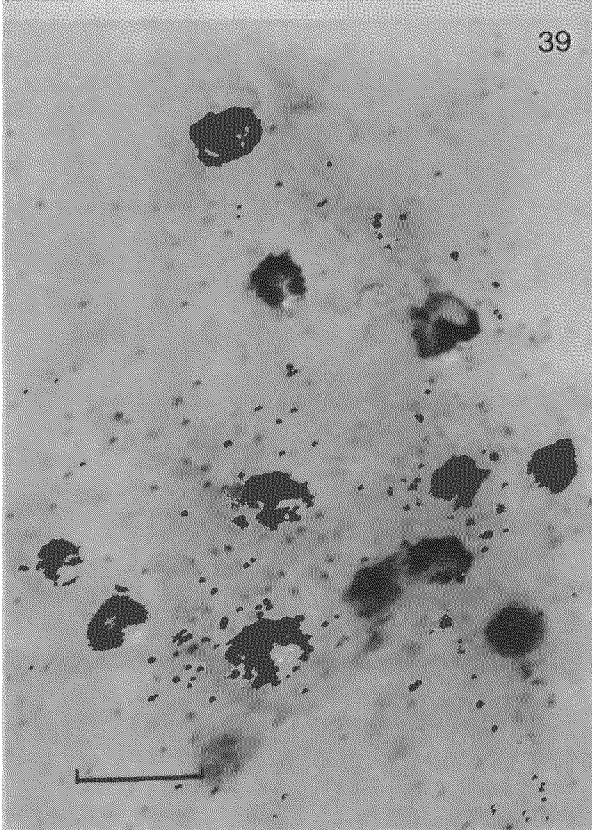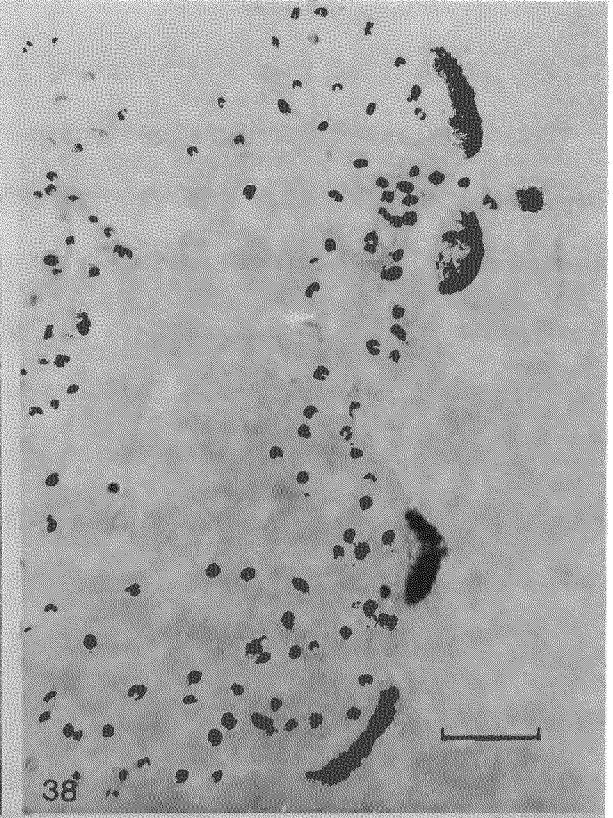
did not see any of them with pigment or fecal strands.

These colonies were virtually impossible to collect intact; they fragmented very readily and when pieces were collected the rhizopodia contracted into dense masses and the colony disintegrated (Figure 38). The algae were very abundant (Figure 39) and were drawn close to the cell as the rhizopodia contracted. In the microscope the vegetative central capsules appeared quite simply with very dense rhizopodia (Figure 40). Extracapsular bodies were common. These colonies were seen or collected mostly on the equator and in the Gulf Stream. One was found near the Canary Islands. This species bears a resemblance to *Leminiscus marginatus* described by Quoy and Gaimard (1824).

Stations: 519, 522, 523, 527, 528, 737, 762, 769, 770, 771

Genus *Sphaerozoum*

Colonies of *Sphaerozoum* sp. were found at 92 of 212 stations (43%) and 26 of 82 equatorial stations (32%) (Figure 45). They were almost always either cylindrical (segmented, like *Collozoum inerme*, or smooth, like *C. radiosum*) or spherical (Figure 41). Occasionally toroidal or oval-shaped colonies were found. Species of *Sphaerozoum* are easily recognizable by the presence of spicules, usually double triradiate, in the colony. These may be on the central capsules (Figures 2, 42) or scattered throughout the gelatin of the colony (Figures 41, 43). This distribution may have taxonomic significance. The spicule morphology varied widely within a colony and is probably only good in a very general sense as a diagnostic feature.

Figure 41. View of a colony of *Sphaerozoum* sp. showing spicules dis-
tributed throughout the gelatin. There is a prey organism caught in the
periphery of the colony. Scale = 0.5 mm.

Figure 42. A central capsule showing spicules tightly packed around a
cell of *Sphaerozoum* sp. Scale = 100 μm.

Figure 43. Spicules scattered in the gelatin of a colony of *Sphaerozoum*
sp. Note the secondary spinules on the branches of the spicules. Scale =
100 μm.

Figure 44. In this colony of *Sphaerozoum* sp. all the central capsules
drew together and left the spicules behind like empty shells. Scale =
200 μm.

41

42

43

44

45
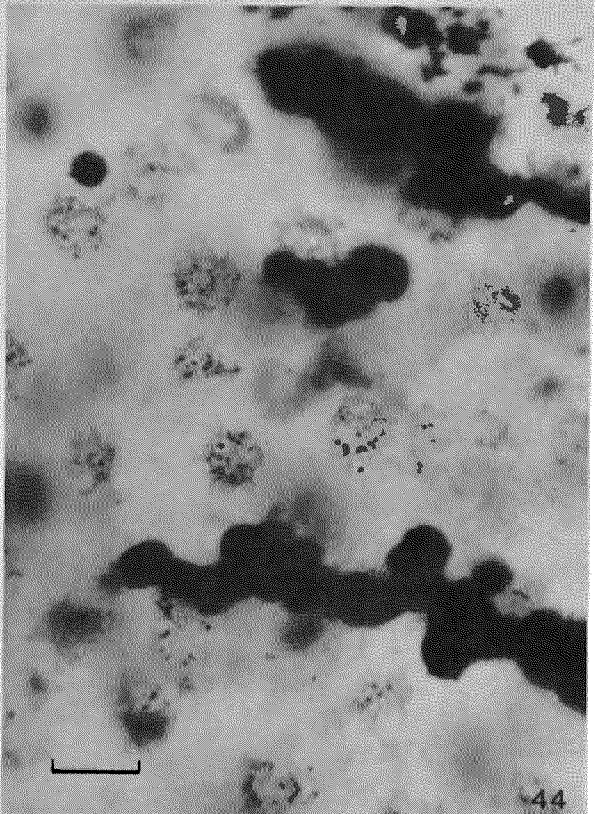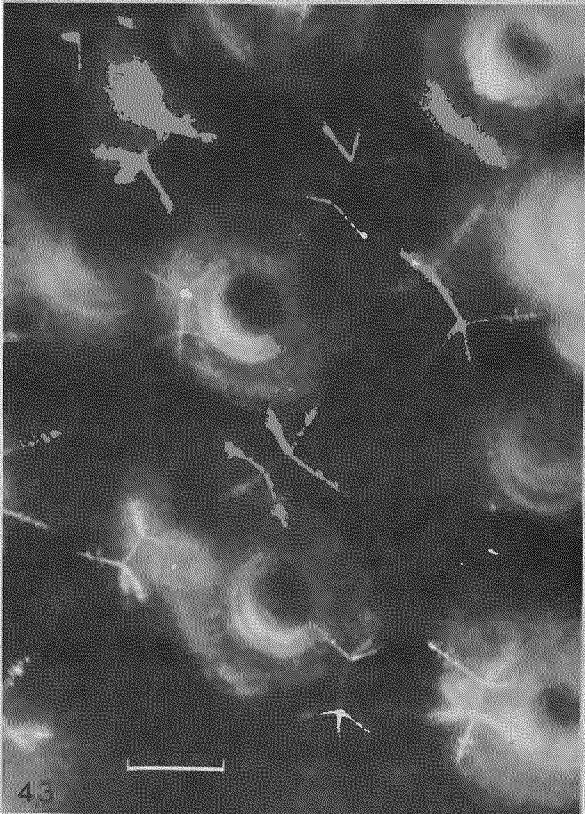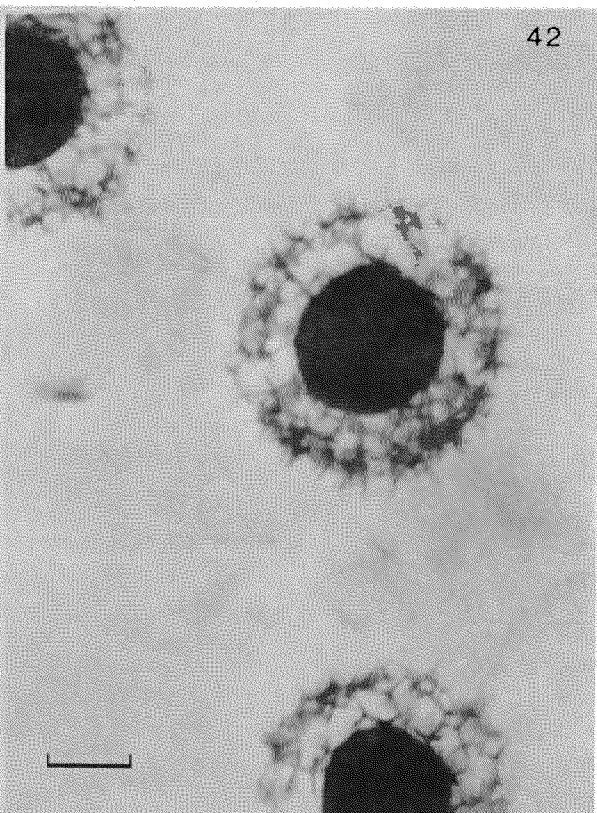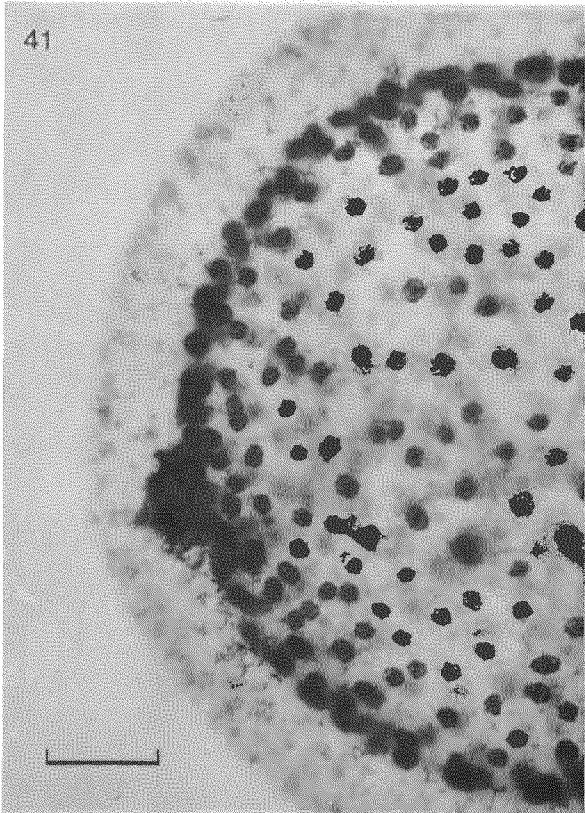
Figure 45. A map showing locations of stations in the North Atlantic

Ocean where specimens of *Sphaerozoum* sp. were collected (●) and stations

where other radiolarians were collected (+). The genus was encountered

on 14 of 29 stations in the equatorial Indian Ocean. Boundaries as in

Figure 9.

47
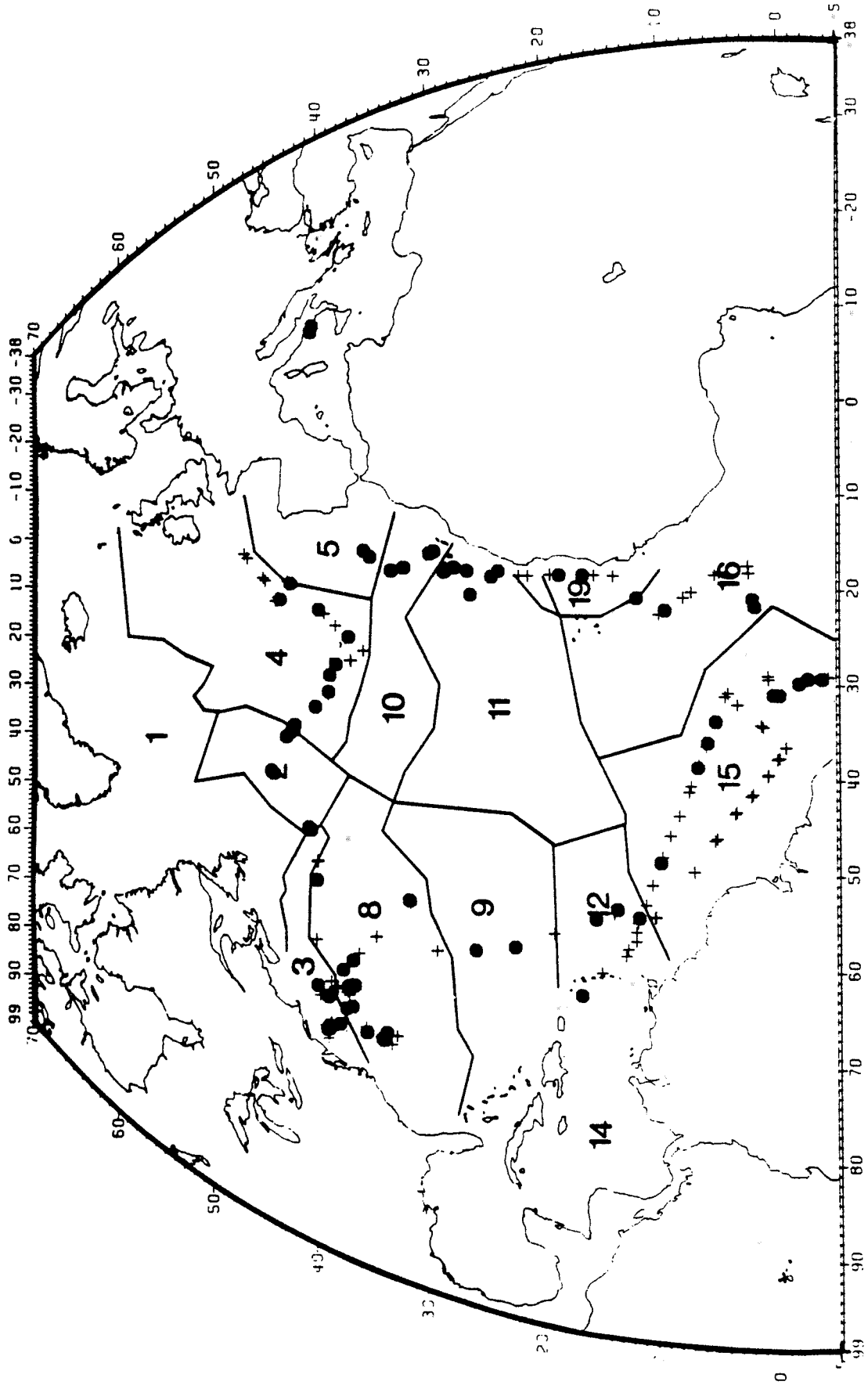
A few colonies had very unusual distribution of spicules. One, a pre-
served specimen, had large smooth quadri-radiate spicules (30-40 μm central
axis) distributed in a hemispherical pattern around the central capsules.
The smallest spicules (10-20 μ) were at the periphery of the cell's gelatin-
ous matrix. In this specimen the algae were also distributed in the same
pattern. The colony was fragmented.

A specimen of *Sphaerozoum* sp. collected on OCEANUS 52 (Station 731)
was stained with neutral red and photographed two to three hours after
capture. In this colony the opaque central capsules drew together leaving
behind their surrounding spicules and zooxanthellae (Figure 44).
Stations: 420, 423-426, 458, 460-462, 464, 467, 469, 471, 475-478, 481,
483, 515, 521, 531, 533, 557, 558, 561, 567, 571, 572, 577, 579, 583,
585-596, 608, 611, 613, 615, 616, 618, 631, 640, 641, 650, 652, 659-664,
672, 679-682, 694, 705, 711, 715, 727-729, 731-742, 746, 747, 751, 753,
760, 761, 766-770.

Rhaphidozoum

Species of the genus *Rhaphidozoum* were collected on 54 of 212 stations
(25%). Almost all of the colonies collected were flat and disc-shaped
(Figure 47), from 1 to 6 cm in diameter, although a few were simple
cylinders like *C. radiosum*.

Rhaphidozoum neapolitanum

This species is distinguished by its simple, straight or curved spines.
These were difficult to see without the compound microscope. Some colon-
ies were collected which were cylindrical; most were discoidal. The cells
resembled those of *Collozoum* (Figure 64a,b).

Figure 46. A map showing the locations of stations in the North Atlantic

Ocean where specimens of the genus *Collosphaera* were collected (•) and

stations where other radiolarians were collected (+). The genus was

encountered on 14 of 29 stations in the equatorial Indian Ocean.

Boundaries as in Figure 9.
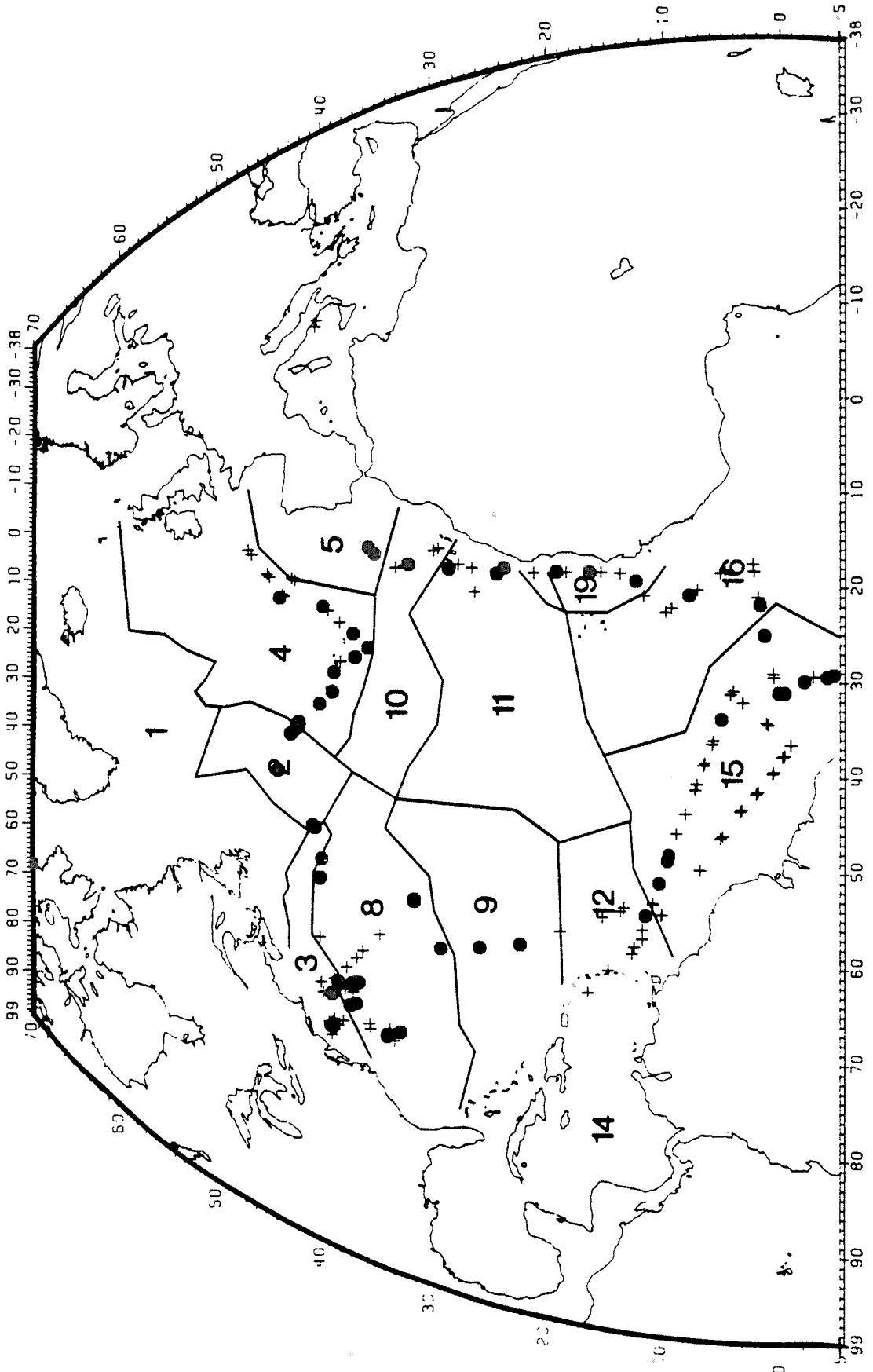
Figure 47. A disc-shaped colony of *Rhaphidozoum* sp. Diameter of disc is approximately 4 cm.

Figure 48. A view of the central capsules of *Collosphaera huxleyi*, showing shell (Sh), extra-capsular bodies (EB) and zooxanthellae (Z). Scale = 100 μm.

Figure 49. A section of a cylindrical colony of *Acrosphaera spinosa*. Note the similarity to *Collozoum radiosum* (Figure 15). Diameter of colony is 3 mm.

Figure 50. Central capsules of *Acrosphaera murrayana* showing the characteristic small spines (Sp) emerging from the central capsules, and the extra-capsular bodies (EB). Scale = 100 μm.

Figure 51. A segment of a dense mat of very large cells of *Acrosphaera* sp. A, showing the strands of cells interwoven together.

Figure 52. A scanning electron micrograph of a shell of *Acrosphaera* sp. A showing the spines emerging from the shell. Scale = 200 μm. Magnification = 100 X.
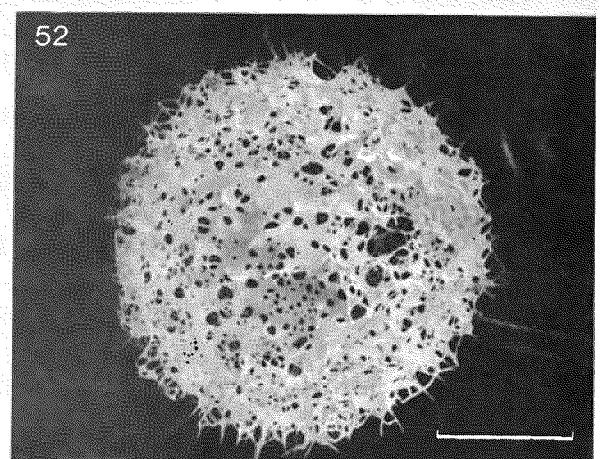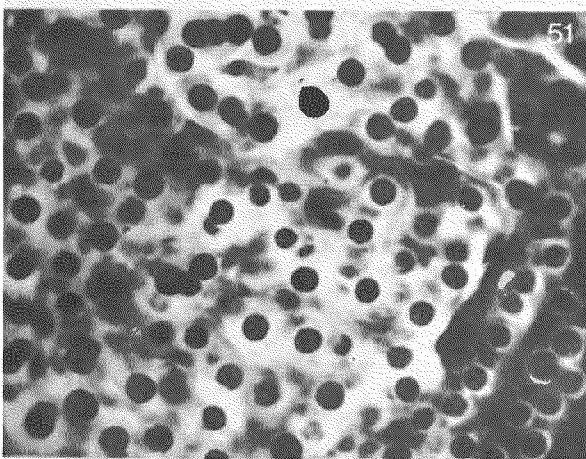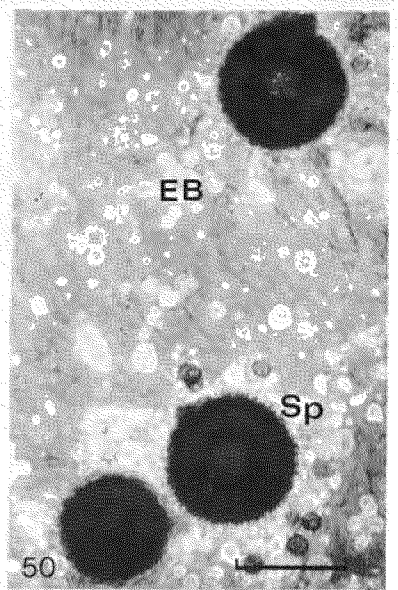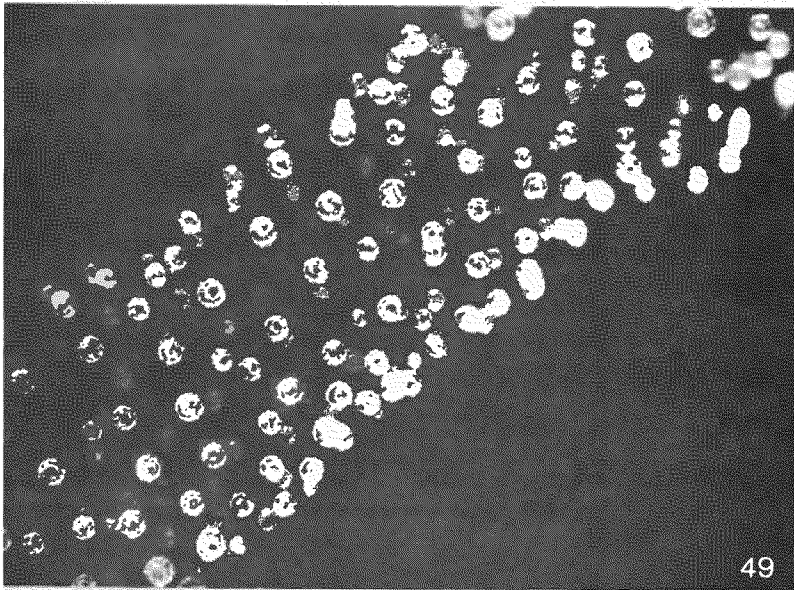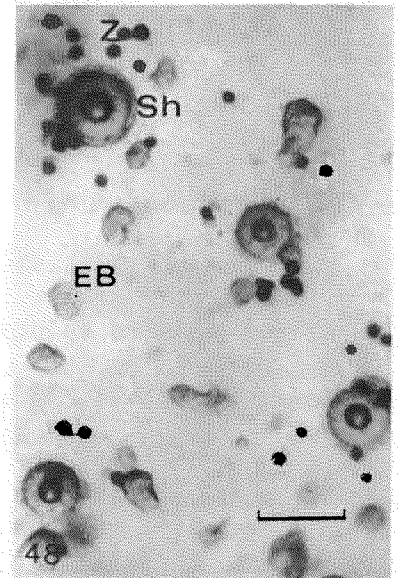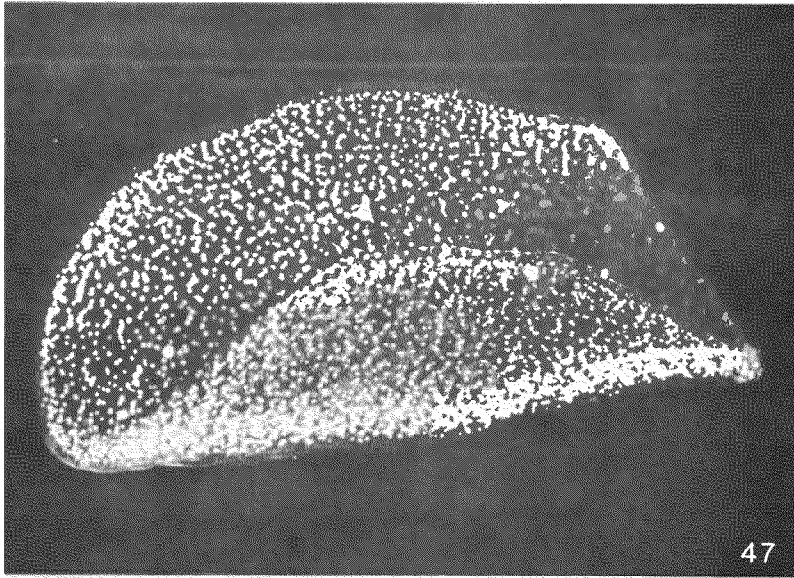
Stations: 406, 466-468, 473, 557, 581, 585, 592, 596, 613, 630, 649, 657, 660, 684, 696, 712, 713, 728.

Rhaphidozoum acuferum

This species is distinguished by the spicules, which are branched, having two or more spines. All the colonies collected were disc-shaped. Stations: 418, 421, 523, 572, 578, 591, 628-630, 649, 657, 682, 687, 712.

Rhaphidozoum sp. A.

Several reproductive colonies were collected on ATLANTIS II 101 which were spherical or oblate spheroid in shape and had orange pigment around the central capsules. The spines were simple, but in no other way did the colonies resemble *R. neapolitanum*. The orange pigment gave the colony a fluorescent appearance underwater.

Station: 712.

Family Collosphaeridae

Genus *Collosphaera*

Specimens of *Collosphaera* were collected frequently (83 stations, 39%) except in the Amazonian Province (Backus et al., 1977) east of Brazil (Figure 46). Almost all of these were *C. huxleyi*). The genus is characterized by the possession of a smooth spherical shell perforated by pores (Figure 3). Occasionally the shell is crumpled slightly. The size and distribution of the pores are used to distinguish the species, but there is a great deal of plasticity in this character. The species *C. huxleyi* and *C. polygona* were found.

Collosphaera huxleyi

Three types of colonies were found; spherical, cylindrical and discoid-al. The most common were flattened discs. Specimens were found which resembled the variety *C. huxleyi tuberosa* (Hilmers, 1906) and the species *C. armata*; these were cylindrical. The shells were usually readily visible in the microscope surrounding the central capsules (Figure 48). Extracapsular bodies were common.

I collected 12 colonies believed to be *C. huxleyi* which appeared to be in the process of shell formation. These had transparent spherical structures distended from the central capsules. Most of the colonies were spherical; 3 were cylindrical. When the organic matter was digested, some of the structures were completely oxidized and some left a delicate shell-like lattice. Many of these collapsed when they were dehydrated. In one specimen, which was a flattened disc, a region running around the equator of the disc included central capsules with delicate shells. No other cells in the colony had shells or presumptive shells.

C. huxleyi was collected almost everywhere.

Stations: 406, 419, 422, 424, 457, 458, 460, 462, 467, 469-472, 474, 476-481, 515, 520, 528, 533, 557, 566, 568, 572, 580, 581, 585, 587, 592, 593, 600, 615-617, 628-633, 635, 641, 644, 649, 650, 654, 657, 660, 663, 666, 671, 673, 675, 676, 681, 690, 695, 696, 706, 708, 735, 738.

Collosphaera polygona (?)

On 11 stations I collected cylindrical colonies (20-100 cm in length) of a diaphanous nature. They offered no resistance to deformation; a diver could pass his finger right through the colony and not feel it. They were very difficult to collect. The ones which were collected seemed to disappear in the collecting vessels, until it was discovered that they had

shrunken to a very dense mass of cells which had sunk to the bottom (Figure 61). These cell masses were cylindrical and so dense that they were completely opaque to transmitted light in the dissecting microscope.

The preserved shrunken colonies had very small central capsules; their diameter, 20-30 µm, only slightly larger than that of their commensal algae. No shells were evident, although some did have the appearance of an inflated membrane around the central capsule which looked very much like a shell. The cells always appeared to be vegetative, without large oil droplets. No ultrastructural study was done.

Some colonies which were collected had slightly denser gelatin. In these were found some central capsules with shells, although most were as described above. Digestion of organic matter in one colony showed the shells to be like those in *Collosphaera polygona* and *Collosphaera macropora*, although their size range was smaller (50-100 µm). The colony structure has not been described for either of these species (Streklov and Reshetnyak, 1971).

Although I have no developmental evidence, the circumstances suggest that these are not *Collozoum*, but young *Collosphaera* colonies developing their shells.

Stations: 471, 472, 567, 572, 573, 580, 617, 632, 641, 706, 770.

Genus *Acrosphaera*

Species of the genus *Acrosphaera* were found commonly (72 of 212 stations, 33%), much more so in the central gyre than on the equator (11 of 82 stations, 13%) or in the Gulf Stream area (17 of 52 stations, Figure 53). Five species were encountered, one of which was new: *Acrosphaera*

Figure 53. A map showing locations of stations in the North Atlantic

Ocean where specimens of *Acrosphaera* were collected (•) and stations

where other radiolarians were collected (+). The genus was encountered

on 8 of 29 stations in the equatorial Indian Ocean. Boundaries as in

Figure 9.
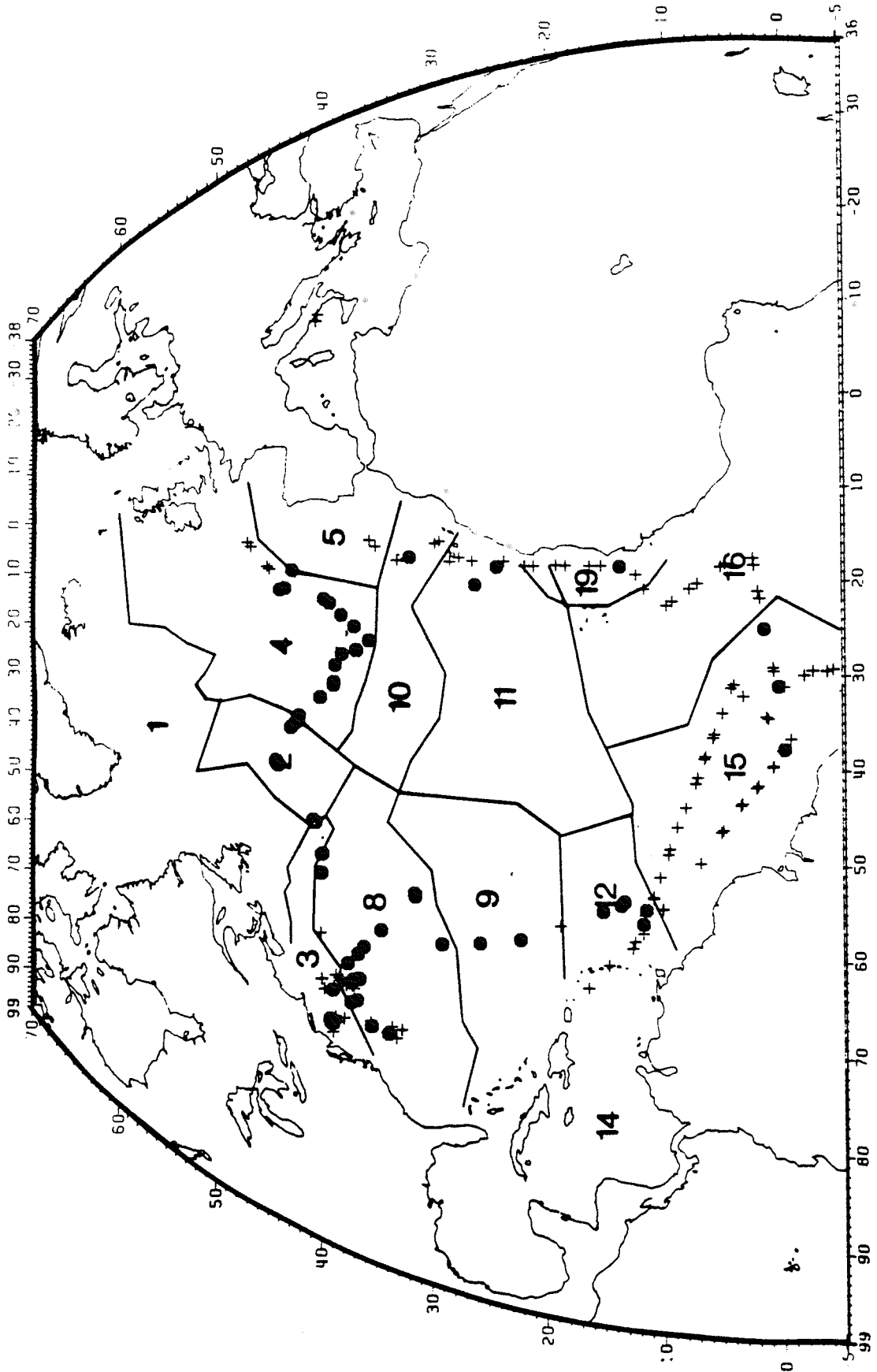
spinosa, *A. circumtexta*, *A. murrayana*, *A. cyrtodon* and *Acrosphaera*
sp. A. The diagnostic feature for the genus is the presence of spines
protruding from the spherical shells, which are perforated with holes,
as in *Collosphaera*. The shape and distribution of the spines are con-
sidered to be diagnostic species characters. The reader is referred to
Strelkov and Reshetnyak (1971) for taxonomic information.

Acrosphaera spinosa

I collected colonies which were spherical and some which were cylindri-
cal. The spherical colonies ranged in diameter from 3.2 to 6.8 mm (Figure
72). Small colonies always had a single alveolus; spherical colonies
larger than 5 mm occasionally enclosed several alveoli, and in some of
these the central capsules were found inside the sphere among the alveoli
as well as on the surface of the sphere. Although the whole shells are
difficult to see, the large spines are often visible as points emerging
from the proximal ectoplasm of the central capsules. Occasionally spheri-
cal colonies of *Acrosphaera spinosa* occurred in great swarms near the sea
surface. On calm days they were found touching the surface film of the
air-water interface. Because of its abundance and the symmetry of its
colonies, *A. spinosa* was used for shipboard photosynthetic incorporation
measurements. These data will be presented in Part II.

The cylindrical colonies resembled *C. radiosum* in size and appearance
(Figure 49). The shells match the description and figures of Strelkov and
Reshetnyak (1971), but their shell structures for *A. spinosa* accept a wide
range of spine morphology. It may be that further study will show that
there is more than one species represented in this material.

Stations: 401. 467, 473, 478, 482, 483, 523, 527, 549, 577-582, 595, 611,
616, 629, 631, 632, 634, 636, 640, 644, 645, 648, 650, 655, 657, 660, 663,

666, 671, 673, 675, 676, 679, 681, 682, 686, 690, 695, 699, 703, 706, 708, 713, 716, 749.

Acrosphaera murrayana

This species was not encountered often. It is easily recognizable by the abundant small spines emerging from the shells. The colonies were always spherical and in many cases there were extra-capsular bodies present in the ectoplasm (Figure 50). The layer of gelatin and rhizopodia was thicker than in *A. spinosa*. This was reduced in the reproductive stage. No experiments or further observations were made.

Stations: 426, 515, 517, 587, 613, 615, 616, 617, 740.

Acrosphaera circumtexta

Like *A. spinosa*, this species formed both cylindrical and spherical colonies — although some were toroidal — and the cells were about the same size. The pores of the shells were surrounded by ridges; the diagnostic feature is that many of the ridges have cross-members or interconnections of thin bars. This feature is not visible without digestion of the organic material. In some instances shells like *A. spinosa* were found in colonies of *A. circumtexta*.

Stations: 470, 479, 577-579, 581, 596, 631, 633, 675, 687, 696

Acrosphaera cyrtodon

Only two specimens were collected. The species is characterized by the presence of a few simple small spines emerging from isolated pores in the shells which resemble those of *Collosphaera*. The specimens collected formed flattened oblong colonies.

Stations: 612, 657.

Acrosphaera Sp. A

Only one specimen was collected. The colony was a large mat composed of an intricately woven cylindrical strand or strands of cells (Figure 51). The opaque central capsules were 300-400 μm in diameter (Figure 52). Digestion of organic matter revealed an extremely delicate lattice of silica threads with fine spines extending 40-50 μm beyond the shell. Many of the spines were branched or had complex cross members as in *A. lappacea*, but were much larger and much more delicate than in that species.
Station: 534.

Genus *Siphonosphaera*

This genus was not encountered often (31 of 212 stations, 15%), nor was it common on the equator (5 of 82 stations within 10°). The genus is characterized by the presence of solid-walled tubules emerging from some of the pores in the shell. Four species were found: *S. tenera*, *S. socialis*, *S. macropora*, and *S. cyathina*.

Siphonosphaera tenera

This was the most common of the species (23 stations). The colonies, shaped as spheres or small cylinders, appeared much like those of *Acrosphaera*, but their shells easily distinguished them (Figure 54). A number of spherical colonies were found with extra-capsular bodies like those in *A. murrayana*. Blue pigment granules were found in the reproductive stage.
Stations: 417, 418, 424, 467, 515, 521, 523, 525, 527, 567, 568, 577, 585, 600, 611, 616, 666, 671, 673, 675, 735, 738, 740.

Figure 54. Two central capsules of *Siphonosphaera tenera* showing the shell and tubules (T) emerging from it. Scale = 50 μm.

Figure 55. A colony of *Solenosphaera collina* which assumes a very complicated shape, somewhat like that of a pretzel. Diameter of whole colony is approximately 5 cm.

Figure 56. Another colony showing a simpler pretzel-shape. Length of colony is approximately 3 cm.

Figure 57. Three shells of *Solenosphaera collina*. Note the shell in their midst. Scale = 100 μm.

Figure 58. An *in vivo* light micrograph of central capsules of *Solenosphaera collina*, showing the same curious shell as in Figure 57. Scale = 100 μm.

Figure 59. A scanning electron micrograph of the shell of Figures 57 and 58. As yet unidentified, shells like this were found in 32 of 32 colonies of *S. collina* examined. See text for details. Scale = 50 μm.
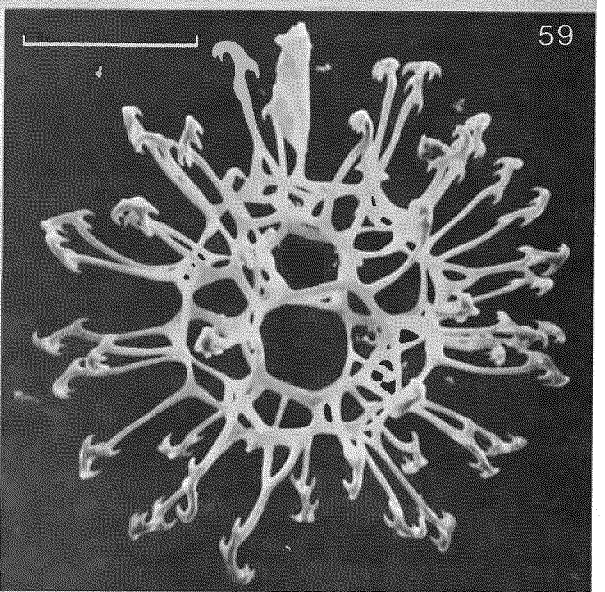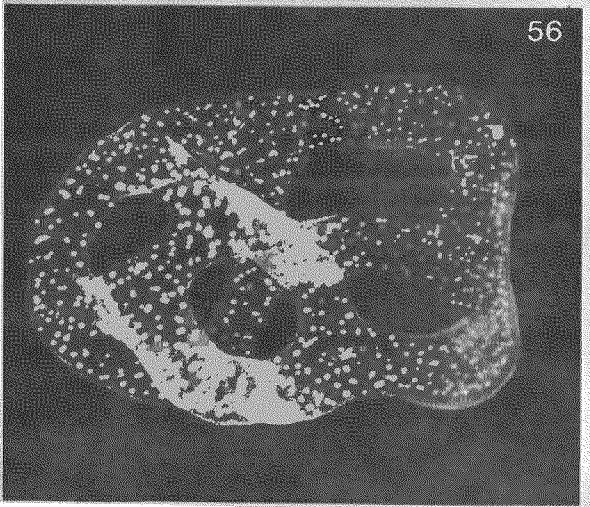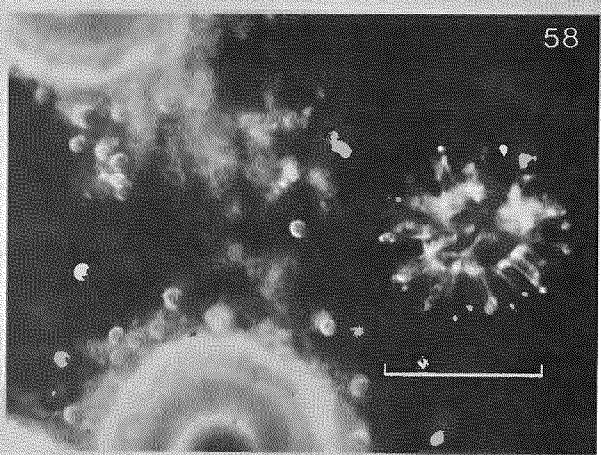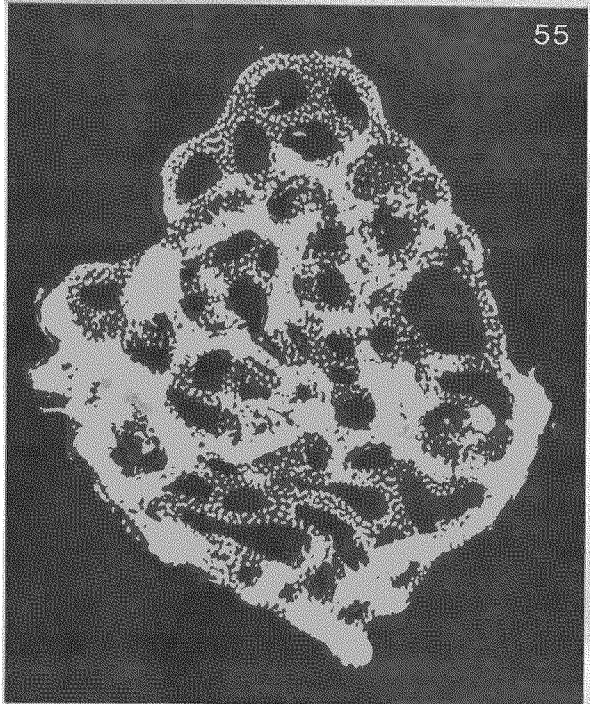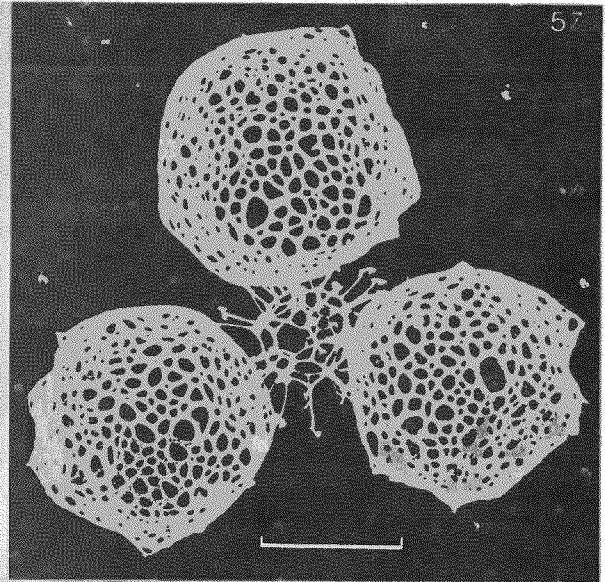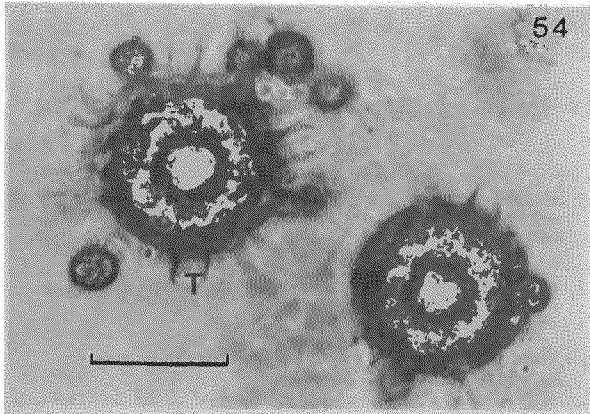
Siphonosphaera socialis

This species was encountered less frequently than *S. tenera*. It also
formed cylindrical and spherical colonies. The short cylindrical colonies
resembled *C. inerme* with its large spherical alveoli. The shells are
characterized by the presence of a few (2-16) contorted tubules (Strelkov
and Reshetnyak, 1971). These may flare out or taper and may terminate
irregularly. They are not as readily visible *in vivo* as in *S. tenera*.
The one reproductive colony seen had two adjacent spherical alveoli with
pinkish cells on their surfaces. Strelkov and Reshetnyak (1971) reported
that spherical colonies of *S. socialis* were among the most frequently en-
countered in their tropical plankton collections. I found it at 40°N in
the Atlantic.
Stations: 656, 657, 666, 673, 675.

Siphonosphaera macropora (Strelkov and Reshetnyak, 1971)

Shells matching the description of this species were found in spherical
colonies on ATLANTIS II 98. Strelkov and Reshetnyak reported it from the
tropical Pacific plankton and Indian Ocean sediments. The shells are
spherical with pores as large as the interporous septae. Some of the
pores are elongated into short tubules. The colonies collected had many
extra-capsular bodies. Unfortunately the photographs (and with them the
morphological information) were lost due to a camera malfunction.
Station: 616

Siphonosphaera cyathina

One specimen was collected in the Indian Ocean. The colony morphology
was not noted and the structure did not survive preservation. The shells

have all their pores elongated into short cylindrical tubules.

Station: 467.

Genus *Solenosphaera*

This genus was rare in my material. The shell surface has either

tubules perforated by pores or tapered processes terminating in an

aperture. Four species were collected: *S. pandora*, *S. zanguebarica*,

S. chierchiae, and *S. collina*.

The first three of these species were represented by only four speci-

mens. I have no information on the colony form in *S. pandora* (station

465). *Solenosphaera zanguebarica* (station 644) was cylindrical. One

specimen of *S. chierchiae* was a 1 mm diameter sphere, the other was a

cylinder 3 cm long and 2 mm in diameter (stations 421, 608).

The fourth species was encountered more commonly and assumed an un-

anticipated form.

Solenosphaera collina

This species is known primarily from isolated shells in the plankton

and sediments (Strelkov and Reshetnyak, 1971), although Hilmers (1906) re-

ported young vegetative cylindrical colonies 5-14 mm long. It was not en-

countered very frequently (20 stations), but when present, often several

colonies were found. Colonies of *S. collina* were always shaped like a very

complicated pretzel (Figures 55, 56) as large as 10 cm in diameter. On

station 766 I observed that all colonies were oriented with the plane of

the colony parallel to the sea surface, presenting the largest profile to

the incident light.

Examination of the colonies with a light microscope showed the characteristic *Solenosphaera* shells (Figure 57) which take the form of spheres perforated with pores, with tapered points spaced out over the surface. Each is provided with a "tooth" (Strelkov and Reshetnyak, 1971). The gelatin is firm but brittle.

In 32 of the 32 colonies examined there were also siliceous shells of another shape (Figures 57-59). I never saw these in any other radiolarian colony. Although usually in amongst the central capsules, they were sometimes found at the outside of the gelatin as though being rejected from the colony. There were two colonies collected in which there were no *Solenosphaera* shells. Both of these had the pretzel morphology, had shells as in Figure 59 and in one of them the shells contained the central capsules of the colony.

Solenosphaera collina was found in eastern and equatorial waters of the Atlantic (Figure 60).

Stations: 406, 514, 534, 548, 562, 566, 572, 599, 664, 667, 737, 741, 745, 747, 750, 754, 758, 766, 768, 770.

Behavior and Trophic Interactions
==================================

The radiolarians I studied demonstrated various behavior in response to mechanical and light stimulation. The response to mechanical stimulation was rapid and dramatic in some species. *Collosphaera polygona* (p.54) shrunk to a fraction of its length when collected. A colony of 30 cm length shrunk to approximately 2 cm (less than 10% of its original length). The diameter was reduced from 4-5 mm to 1 mm. Shrinking proceeded as a single peristalsis from one point in the colony to the extremities (Figure 61). The whole process was not timed, but was usually

Figure 60. A map showing locations of stations in the North Atlantic

Ocean where specimens of *Solenosphaera collina* were collected (●) and

stations where other radiolarians were collected (+). The species was

not encountered in the equatorial Indian Ocean. Boundaries as in

Figure 9.
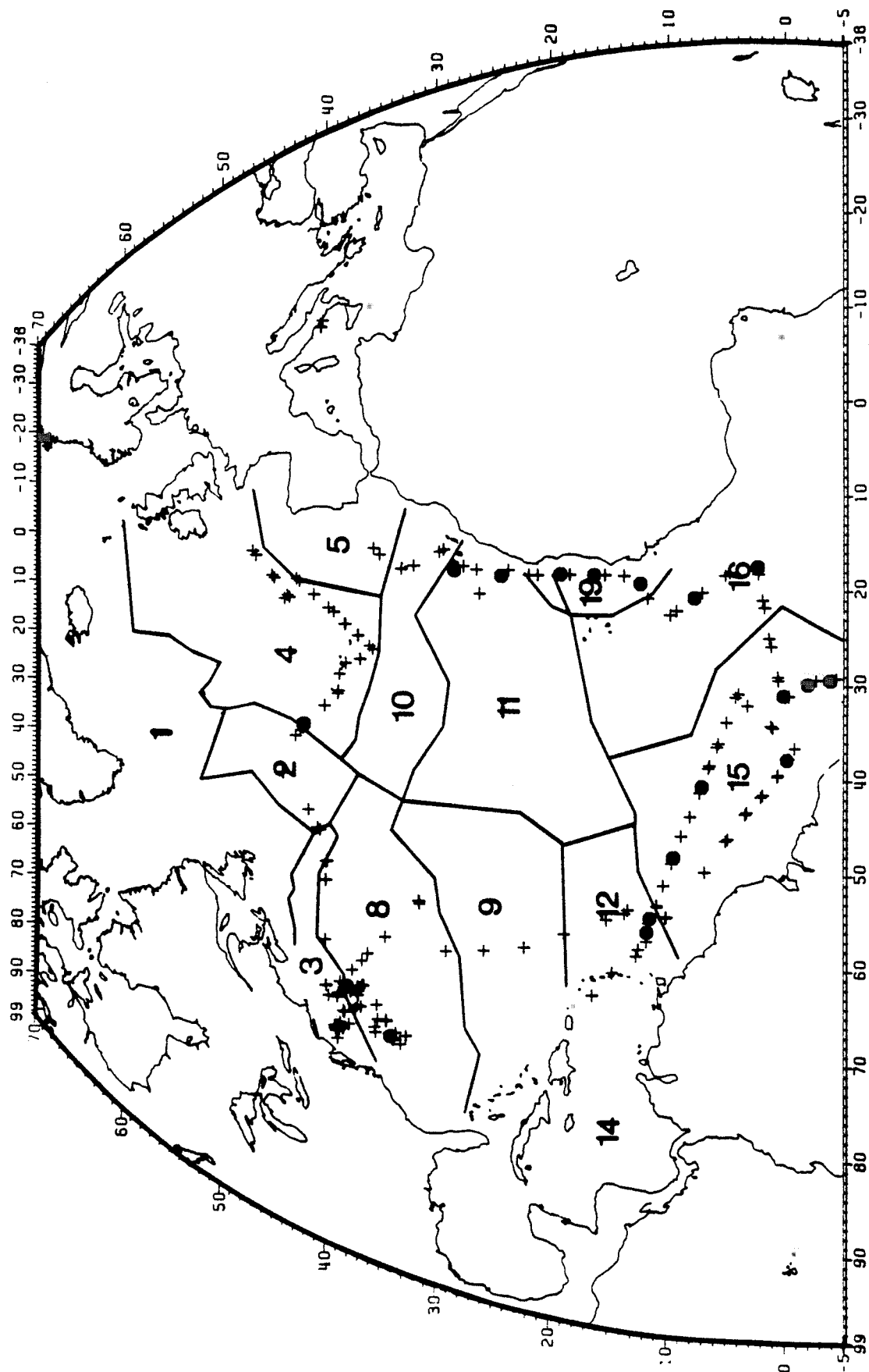
accomplished before specimens were aboard ship (less than 30 minutes).
One colony had several hyperiid amphipods embedded in it in two regions.
In those regions occupied by the hyperiids the colony did not shrink,
giving it a dumbbell-like appearance. Ultimately the region with one
amphipod contracted to 2 mm although the region with two amphipods did
not contract.

I have seen similar shrinking behavior in a number of large radio-
larians. A phenomenon very similar to that in *Collosphaera polygona* was
observed in *Collozoum* sp. A (Figure 62), although less commonly and to a
lesser degree. Some pretzel-shaped colonies of *S. collina* collected on
OCEANUS 52 were observed to simultaneously shrink in three dimensions to
approximately one-tenth of the original colony volume within five hours.
A second shrunk and re-expanded from 13 mm diameter to 40 mm diameter in
two hours. It was not clear what stimulus caused the colony to re-expand.
Shrinking generally occurred in response to physical handling.

Another response to mechanical stimulation which may be related to
shrinking was colony re-organization. Many of the shelled species which
form a spherical colony with a single alveolus (*Siphonosphaera tenera* and
Collosphaera huxleyi) gathered all the central capsules on one or two
poles of the colony which then fragmented. A similar phenomenon was seen
in *Collozoum* sp. B and *Collosphaera huxleyi* (discs). The central capsules
grouped in defined regions frequently around the border of the colony fol-
lowed by fragmentation. Some colonies which were never identified had a
single row of elongated central capsules. These contracted their rhizopodia
and forced the alveoli towards the outer region of the colony (Figure 63).
In all of these cases the cells were gathered together and the alveoli
"squeezed out" towards the seawater. No shrinking or re-organization was

Figure 61. A close view of the point in a colony of *Collosphaera polygona*(?) where shrinking is occurring. Shrinking proceeds as a single peristalsis down the length of a colony. Scale = 1.0 mm.

Figure 62. A shrinking phenomenon similar to that shown in Figure 61 occurs, although less frequently, in *Collozoum* sp. A. This specimen was approximately 15 cm long.

Figure 63. An alternate method of shrinking was observed in which the rhizopodia contracted around the central capsules (C) leaving the alveoli (A) exposed to the seawater-like large balloons. Specimen of unknown identity. Scale = 250 µm.

Figure 64. Colonial radiolarians move their algae in response to light. a) Algae are spread far from each other after exposure to light in *Rhaphidozoum* sp. b) After exposure to dark for 3 hours the algae in the same specimen were all tightly packed around the central capsules. The effect was reversible. Scales = 250 µm.
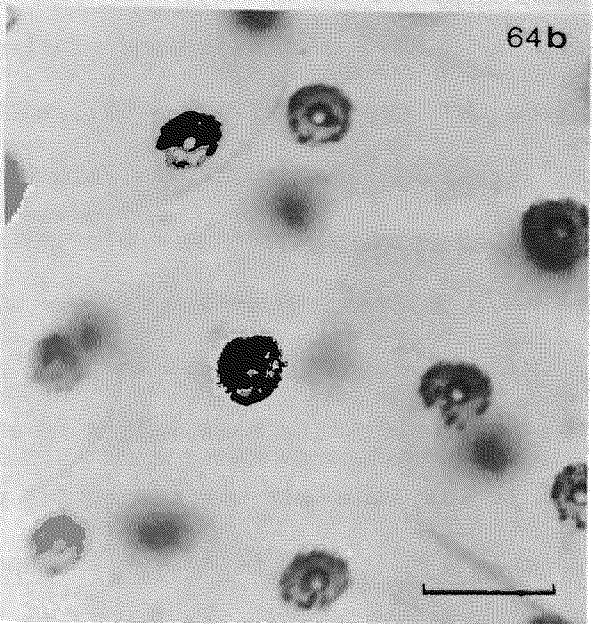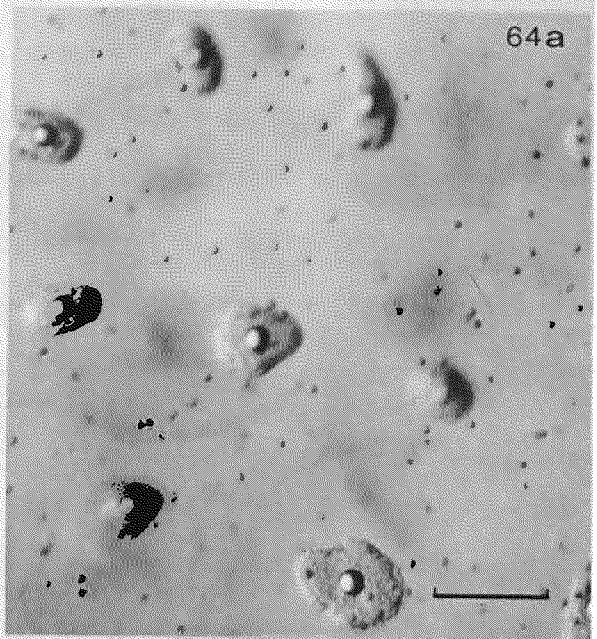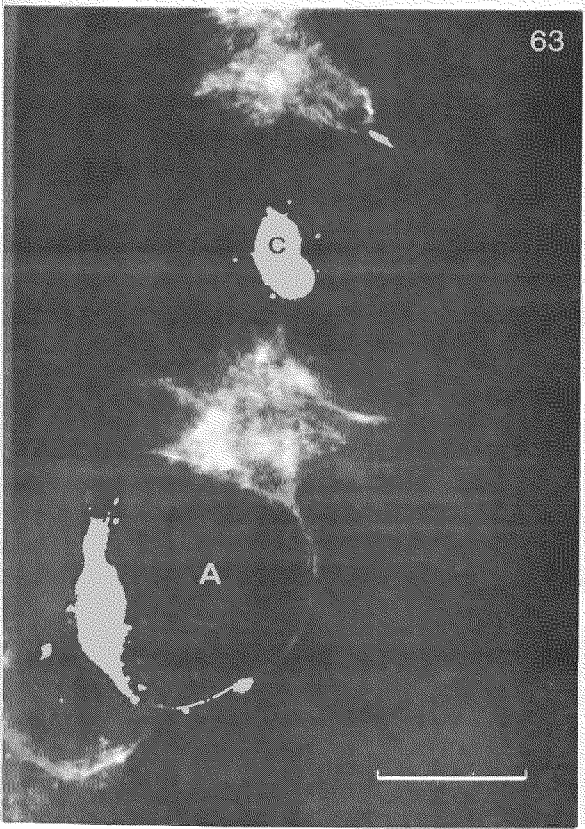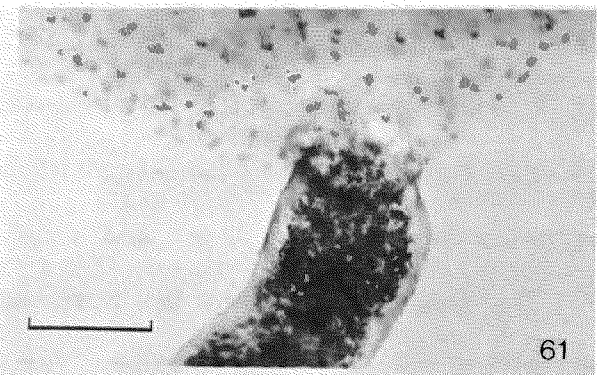
ever seen in *Collozoum inerme*, *C. radiosum*, *C. ellipsoides*, *C. longiforme*, or *Aerosphaera murrayana*. In response to rigorous mechanical stimulation *Solenosphaera collina* bioluminesced in the dark. There were relatively bright points of blue light and a diffuse light of lower intensity.

The response to light was more subtle. When colonies of *Rhaphidozoum* sp. were placed in total darkness for several hours, the distribution of the symbiotic zooxanthellae changed. In the light the algae were spread far from the radiolarian cells and from each other (Figure 64a). After three hours in the dark they were all tightly packed around the radiolarian central capsules (Figure 64b). The effect was reversible after one additional hour of light. This type of experiment was done four times with *Rhaphidozoum* sp. and *Collozoum* sp. A and the results were the same.

Prey

I have fed copepods and *Artemia salina* to various radiolarian colonies in the laboratory and observed the feeding process in the field. In addition I have commonly found tintinnids (Figure 25; see also Appendix II, Figure 2b), copepods (Figure 65), mollusc larvae (Figure 66), ostracods and larvaceans in radiolarian colonies (in order of frequency). I have also found probable *Nitschia closterium* around the radiolarian central capsules of *Collozoum radiosum* (Figure 67), *Ceratium* sp. in *Collozoum pelagicum* (= *Thalassiophysa sanguinolenta*) one Atlantid heteropod and one unidentified chaetognath with its head lodged in a colony of *Sphaerozoum* sp. In the last case it was not clear who was eating whom. I have found siphonophore nematocysts in a colony of *Collozoum* sp. and have seen a colony of *C. pelagicum* stuck to a siphonophore in the field. On two occasions I observed small jellyfish which were stuck to colonies (*C. inerme* and *C. ameboides*). In

Figure 65. A copepod being digested by a colony of *Collozoum radiosum*.
Scale = 0.5 mm.

Figure 66. A larval mollusc shell in a colony of *Collozoum inerme*.
Scale = 0.5 mm.

Figure 67. The diatom *Nitschia closterium*(?) was found in the gelatin-
ous matrix of *Collozoum pelagicum*.   Scale = 50 µm.

Figure 68. An unidentified hyperiid amphipod resting on the outside of
a colony of *Solenosphaera collina*.   Scale = 1.0 mm.

Figure 69. An adult male amphipod, *Hyperietta luzoni*, on the outside of
a colony of *Collozoum longiforme*.   The second, third and fourth periopodia
are placed behind it to grip the gelatin of the colony.   Note tintinnid
prey (arrows).   Scale = 1.0 mm.

65

66

68

67

d

69
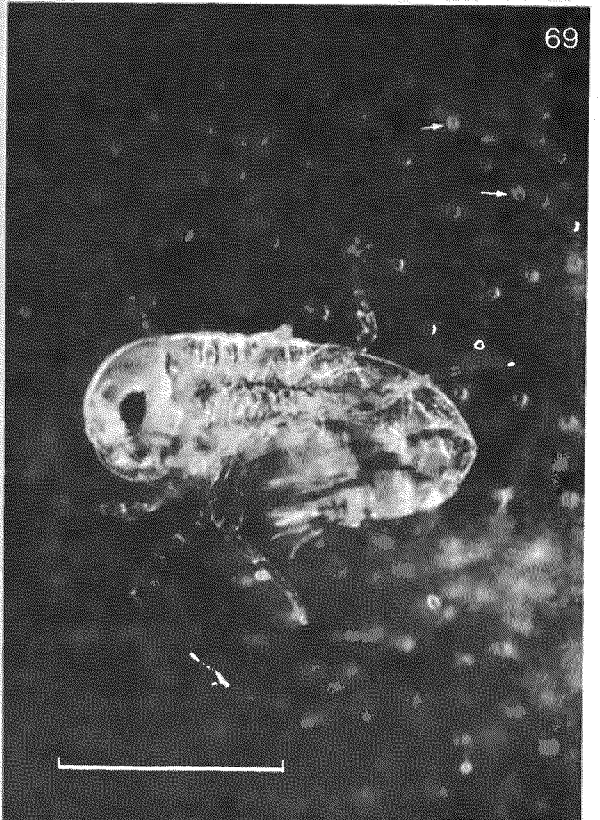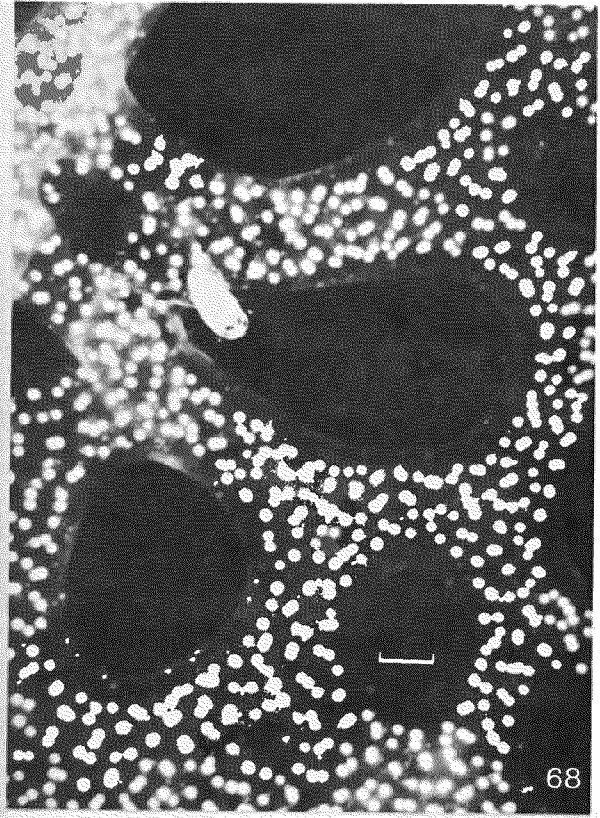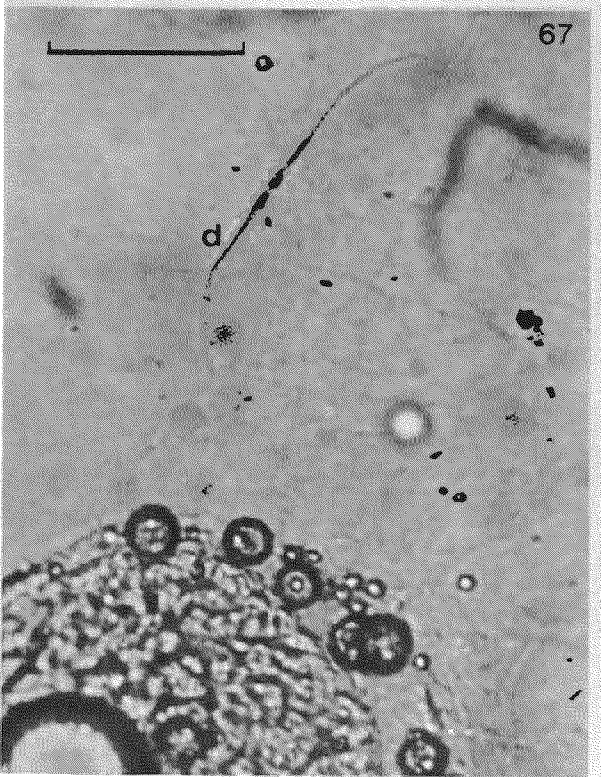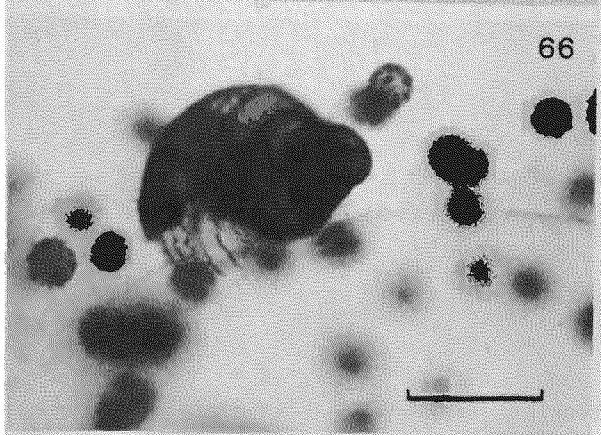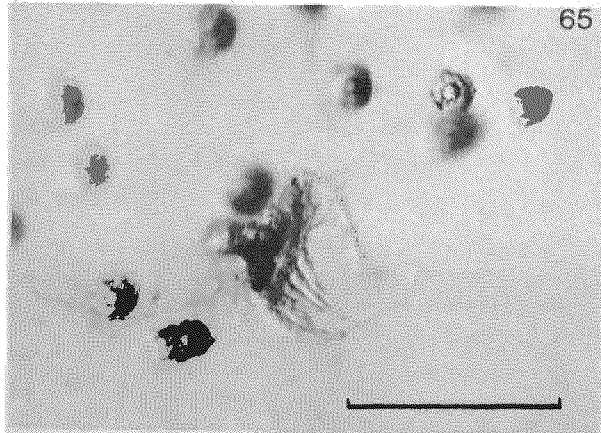
one such instance where the colony of *C. inerme* and a *Pelagia noctiluca* ephyra were caught, the jellyfish was approximately one-third digested after 5 hours. I have never found any organism larger than approximately 1 cm in a radiolarian colony. No experiments were done on the rate of prey capture; this is assumed to be density dependent. In colonies of *C. longiforme*, however, 5-25 tintinnid loricae were found per mm colony length in six colonies (see Table 3, Appendix II). Thus a 1 m long colony had captured $5 - 25 \times 10^3$ tintinnids. This certainly could be significant both in the nutrition of the radiolarian and in its impact on the tintinnid population, depending on the time span in which the prey were captured.

When medusae and siphonophores were first caught with radiolarian colonies it was thought that they were feeding on the radiolarians. This later proved to be incorrect. There is no known predator of radiolarian colonies in the true sense of the word. Strelkov and Reshetnyak (1971) and Khmeleva (1967) reported that radiolarians were repugnant to fish, although they offered no proof. I have tried to feed various radiolarians to a number of fish, including *Fundulus* sp., *Poecilius* sp. (guppies), and *Tetragonurus cuvieri*. None of these would accept colonies after mouthing them. Neither did the isopods *Idothea* sp. One small fish was found associated with a large unidentified radiolarian colony in the Indian Ocean, swimming around the outside of the colony, but I do not know what it was doing; it did not appear to be feeding.

Although the search for a large predator has proved fruitless, a number of small organisms fed on radiolarian colonies, perhaps more as parasites than as predators.

Amphipods

The most common of these are the amphipods of the family Hyperiidae. Hyperiids were collected on 143 colonies at 92 of 224 stations. No calculation of infestation rate was made since there was a bias towards collection of amphipod associations. The stations at which hyperiids were found were scattered throughout the ocean without apparent pattern.

Most of the amphipods I collected on radiolarian colonies were in the genus *Hyperietta* (Table I; also Table 4, Appendix II). Adult *Hyperietta stephenseni* were found on all species with amphipods; *H. luzoni* was found on *Sphaerozoum* sp., *Collozoum longiforme* and *Collozoum* sp.; *H. stebbingi* was found on *Collozoum* sp., and possibly *H. parviceps* on *Acrosphaera spinosa* (the amphipod identification is tentative). Many of the juveniles were not identifiable to species. Adult *Hyperietta* sp. were usually found on the outside of a host colony (Figure 68). Frequently they placed the dorsal region of their pereon against the colony and periopods 3-6 were embedded in the gelatin of the radiolarian (Figure 69). Occasionally specimens were found which had modified the contour of the radiolarian colony to fit their bodies (Figure 70a,b). One *Lestrigonus* sp. was found molting in the peripheral region of a colony of *Collozoum inerme* (Figure 71). Adults were also found holding on to the outside of spherical colonies (Figure 72) and post-juvenile stages were inside the gelatinous alveoli; crawling around in an invisible structure. Usually a hole could be found in the colony where an amphipod had bored into the alveolus. Juveniles (.53 to 1.9 mm) were found embedded in colonies, often in groups of as many as 23 (Appendix II, Figure 6). Those amphipods inside the colonies rarely separated voluntarily from the radiolarian; those on the outside did so readily. On several occasions I saw the

TABLE I. Associations of hyperiid amphipods with radiolarians. Species in the genus *Hyperietta* are obligate parasites of radiolarian colonies during early development and are found embedded in the centers of the colonies. Identifications of some small juveniles are questionable (see Appendix text for explanation). Probable species are footnoted. Size in mm. Each station number represents a single colony.

Station	Host species	Amphipod species or group	Males No. (size)	Females No. (size)	Juveniles No. (size)
417	*Collozoum inerme*	Hyperiidae			9 (0.7)
424	*Collozoum inerme*	*Hyperietta stephenseni*		1 (2.4)	
426		*Hyperietta* sp.*			1 (1.4)
477		*Hyperietta* sp.[1]			1 (1.5)
478		*H. stephenseni*	1 (3.4)		
517		*Hyperietta* sp.[2]			1 (1.3)
544		*Hyperietta* sp.[1]		1 (1.2)	
549		*Hyperietta* sp.[1]	2 (1.2,1.5)	2 (1.3,1.4)	
549		*Oxycephalus clausi*		1 (9.3)	
568		*Lestrigonus* sp.?			2 (1.1,1.2)
		Hyperietta sp.[1]			4 (1.6)
568		*Hyperietta* sp.[1]			3 (1.3)
568		**Hyperietta* sp.[1]			1 (1.1)
580		*H. stephenseni*?	1 (1.9)		
582		*H. stephenseni*?		1 (1.7)	
585		*Hyperietta* sp.[1]		1 (1.3)	
586		*Hyperietta* sp.?			4 (.95-1.0)
666		*H. stephenseni*		1 (1.4)	
547	*Thalassophysa sanguino-lenta = C. pelagicum*	**Hyperietta* sp.[1]			3 (1.2-1.3)
467		*Lestrigonus* sp.?			1 (1.3)
527		Hyperiidae			7 (.94)
542		**H. luzoni*		1 (1.3)	
569		*Hyperietta* sp.			1 (1.1)
571		**Hyperietta* sp.			4 (0.9)
586		*Hyperietta* sp.?			18 (-)
587		*Hyperietta* sp.?			23 (1.0-1.1)

TABLE I (Continued)

Station	Host species	Amphipod species or group	Males No. (size)	Females No. (size)	Juveniles No. (size)
592		Hyperiidae			6 (.8)
592		Hyperiidae			6 (.7-.8)
592		Hyperiidae			4 (.9-1.0)
594		H.luzoni			
616		H. stephenseni	1 (1.9)	1 (2.3)	4 (1.1-1.3)
644		Hyperietta sp.			1 (1.5)
679		H. stephenseni			6 (1.2)
523	Collozoum radiosum	Hyperiidae			3 (-)
548		Hyperietta sp.			11 (1.2)
558		Lestrigonus sp.?			1 (0.7)
653		Hyperiidae			
557	Collozoum ellipsoides	Oxycephalus clausi			
716		H. stephenseni	3 (2.0)	1 (9.3)	
472	Collozoum sp.	H. stebbingi		1 (3.0)	
666		H. stephenseni		1 (1.8)	
649		Hyperiidae			2 (1.1)
684		Hyperiidae			2 (.68)
690		H. luzoni			
716		H. stephenseni	1 (2.0)	3 (1.5-1.7)	
559	Collozoum sp. A.	Hyperietta sp. 1	1 (1.8)		
592		H. stephenseni	1 (3.8)		
592		Hyperietta sp.* 1			11 (1.1)
593		Hyperietta sp. 1	1 (1.6)		
593		Hyperiidae			many
594		H. stephenseni	1 (2.8)		
462	Sphaerozoum sp.	Hyperietta			
558		Hyperiidae			
571		Hyperietta sp.			2 (1.0)
583		Lestrigonus	1 (3.0)		3 (.8-1)
591		Hyperietta sp.?			2 (1.2,1.4)

TABLE I (Continued)

Station	Host species	Amphipod species or Group	Males No. (size)	Females No. (size)	Juveniles No. (size)
592		Hyperiidae			2 (.95–1)
592		H. stephenseni	1 (4.2)	1 (3.7)†	
613		H. luzoni			
643		Hyperietta sp.			1 (1.2)
644		H. stephenseni		1 (1.3)	
657		Brachyscelus rapacoides		1 (2.1)	
716		H. stephenseni ?	2 (1.9)		6 (1.8–2.0)
716		H. stephenseni ?			
406	Rhaphidozoum neapolitanum	Oxycephalus sp.	?		
581		**Hyperietta sp.			1 (1.6)
596		Hyperiidae			1 (1.8)
523	Rhaphidozoum aciferum	Brachyscelus rapacoides		1 (2.4)	
563		Oxycephalus clausi		1 (9.1)	
471	Collosphaera huxleyi	Lestrigonus crucipes	1 (2.3)		
477		Hyperiidae			1 (.8)
477		Hyperiidae			1 (.53)
478		Hyperiidae			1 (1.9)
480		Hyperiidae			1 ( )
481		Hyperiidae			1 (.82)
580		H. stephenseni	1 (1.4)		
581		Hyperietta sp.3		1 (1.7)	
592		H. stephenseni		1 (2.4)‡	
632		Hyperiidae			1 (1.9)
573	C. polygona?	Hyperietta sp.2			8 (1.3–1.6)
424	Siphonosphaera tenera	Hyperietta sp.1			1 (1.3)
467		H. stephenseni		1 (2.7)	
523	Acrosphaera spinosa	Hyperietta			1 (1.4)
549		Hyperietta sp.2			1 (1.7)
578		Hyperiidae	1 (1.8)	1 (1.5)	
579		H. stephenseni	2 (1.9,2.0)		
		Hyperietta sp.			1 (1.3)
579		Hyperietta sp.			1 (1.1)

TABLE I (Continued)

Station	Host species	Amphipod species or group	Males No. (size)	Females No. (size)	Juveniles No. (size)
580		H. stephenseni		1 (2.1)	
581		Hyperietta sp.	1 (2.0)		
581		H. stephenseni		1 (2.2)§	
648		Hyperietta sp.[1]			1 (1.3)
657		Brachyscelus sp.	1 (2.0)		
690		Hyperiidae			1 (1.9)
690		Hyperietta sp.*		1 (1.8)	
695		H. parviceps (?)		1 (2.4)	
699		H. parviceps (?)		1 (2.3)	
706		Hyperietta sp.[4]		1 (1.7)	
716		H. stephenseni	1 (1.5)		
716		H. stephenseni			
716		H. stephenseni	2 (2.0,2.1)	2 (2*0,2.1)	
716		H. stephenseni	1 (1.9)		
579	A. circumtexta	Hyperiidae			1 (1.7)
579		Hyperietta sp.			1 (1.0)

*Co-occurred with Miracia efferata.

**Co-occurred with Sapphirina sp.

[1]Probably Hyperietta luzoni or H. vosseleri.

[2]Probably H. stephenseni or H. stebbingi.

[3]Probably Hyperietta stephenseni or H. parviceps.

†Gravid female with 19 eggs.

‡Gravid female with 17 eggs.

[4]Probably Hyperietta stephenseni or H. parviceps.

§Gravid female with 7 eggs.

Figure 70. a) A hyperiid amphipod embedded in the outer region of a colony of *Solenosphaera collina*, its dorsal perion against the colony. b) The amphipod has left the colony, showing the deformation it has created in the gelatin. Diameter of colony is 2.5 mm.

Figure 71. A hyperiid amphipod, *Lestrigonus* sp., is molting in the external region of *Collozoum inerme*. Molt (M), rhizopodial fringe (R). Scale = 1 mm.

Figure 72. A spherical colony of *Acrosphaera spinosa* with an unidentified adult amphipod on the outside. Colony diameter is 5 mm.

Figure 73. A juvenile hyperiid embedded in a colony of *Collozoum* sp. A. Note the copepod carapace (c). Scale = 0.5 mm.

Figure 74. Ectocommensals of radiolarian colonies. a) The copepod *Miracia efferata* waves its rear thoracic appendages as it grips the gelatin of a colony of *Sphaerozoum* sp. with its first legs. Scale = 100 μ. b) Two turbellarian flatworms cruise over the outside of an unidentified radiolarian colony. They were abundant both as ectocommensals and free-living in surface waters between Lisbon, Portugal and the Canary Islands on R/V OCEANUS 52. Scale = 0.5 mm.

70a

71

70b

73

72

74a

74b
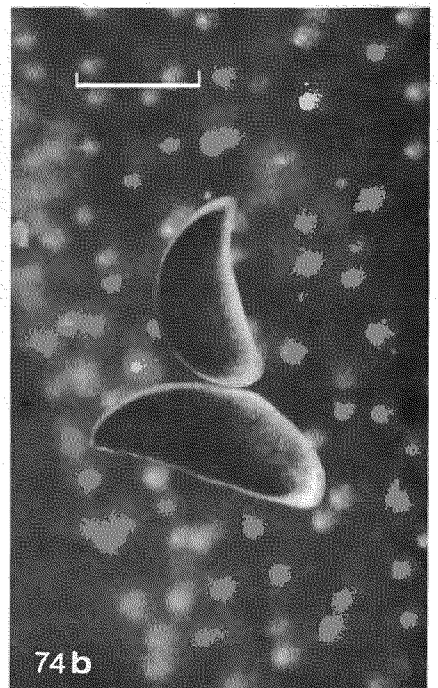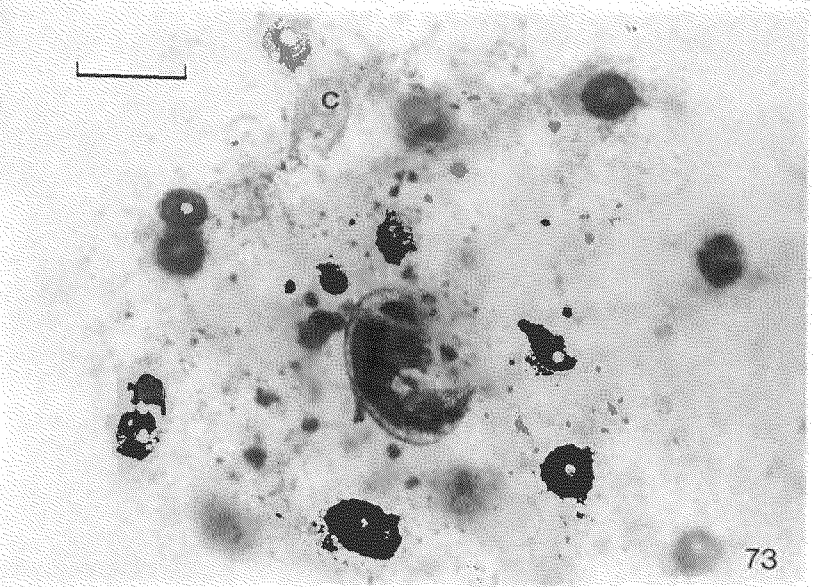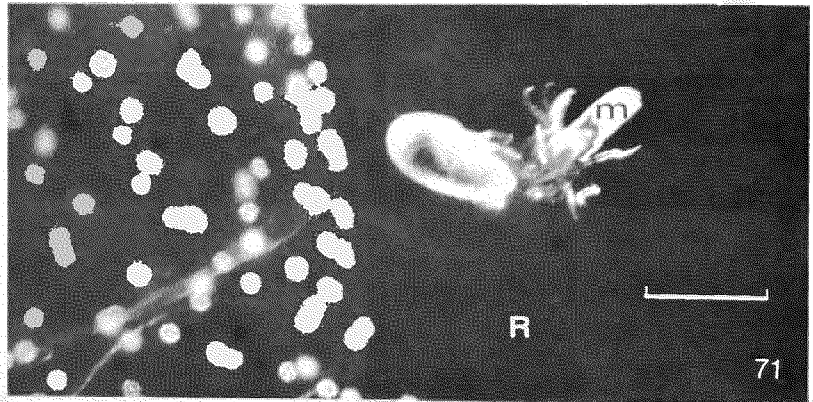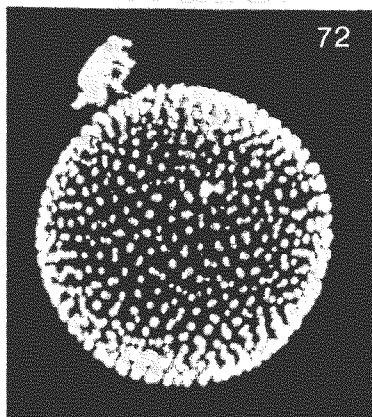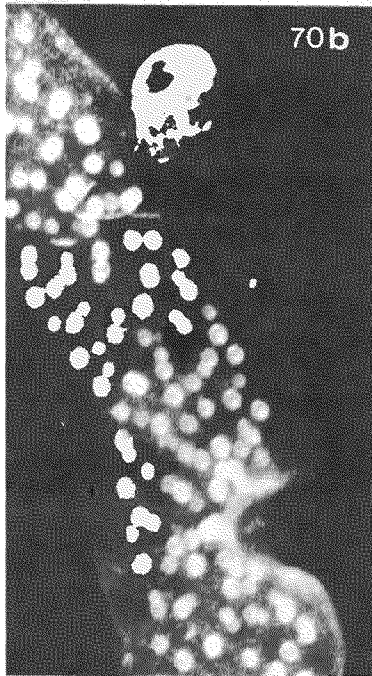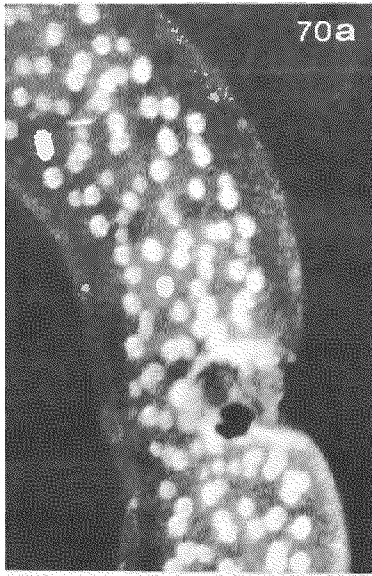
amphipods embedded in the colonies feeding on the radiolarian central capsules; in *Collozoum* sp. A, the juvenile amphipods were only slightly larger than the central capsules and looked very similar to them (Figure 73).

Species of *Oxycephalus* were always found resting on the outside of the colonies. *Oxycephalus* could be described as a predator because of its wide feeding habits (Madin and Harbison, 1977; Harbison et al., 1977).

Copepods

Other crustacean predator/parasites associated with radiolarians were found. Most common of these was the harpacticoid copepod, *Miracia efferata*. *Miracia efferata* was found on 31 of 224 stations. This species was found on the outside of colonies, as many as 96 individuals on a single colony of *C. longiforme* (Appendix II, Table 5). It was also found on *Collozoum inerme*, *Collozoum* sp., *Acrosphaera spinosa*, *Rhaphidozoum* sp., *Collosphaera huxleyi*, *Sphaerozoum punctatum*, and *Solenosphaera chierchia*. *Miracia efferata* planted its first, second and third thoracic legs in the gelatin of the colony and waved its remaining thoracic appendages (Figure 74a). It appeared to use its first legs and mouth parts to probe in the gelatin of the colony for food. It may feed on gelatin, algae or prey organisms caught by the radiolarian. These copepods are in turn frequent hosts to parasitic stalked protozoans which reside on their thorax and head.

Stations: 421, 424, 455, 477, 478, 484, 514, 515, 521, 542, 550, 553, 557, 558, 561, 563, 567-569, 581, 585, 592, 595, 610, 611, 631, 753, 754, 760, 761, 773.

Also found in a similar position were juvenile decapods (probably penaeids), phyllosome larvae and other Harpacticoida. Of these, the harpacticoid *Sapphirina* was the most common. It was found at 18 stations. The hosts were *Collozoum inerme*, *Collozoum* sp., *Collosphaera huxleyi* and *Solenosphaera chierchia*. The activity of the copepods or the other crustaceans was not observed because they separated from the colonies upon capture.

Stations (*Sapphirina*): 417, 519, 520, 537, 568, 579, 586, 587, 589, 608, 675, 679, 687, 734, 736, 769, 771, 774.

Turbellarians

On 12 stations I found turbellarians affixed to the exterior of various radiolarian colonies. The flatworms (Figure 74b) moved freely around the exterior of the radiolarian with their oral surface against the colony. On OCEANUS 52 from Lisbon to the Carnaries these turbellarians were encountered in abundance on the first nine station, both free-living and on the outside of salps and radiolarians. They were most abundant on radiolarians. I could not observe whether they were feeding, but on two occasions they deposited yellowish granular fecal masses. In one of these I found a radiolarian central capsule. They contained chlorophyll and what appeared to be plastid structures. Specimens were examined by Dr. S. Collard of Florida State University and sent to the U.S. National Museum. They have not yet been identified. They were also encountered in the Indian Ocean on the equator and once in the Gulf Stream. Stations: 424, 483, 689, 690, 731-739, 745.

It was not unusual to find infestations of ciliated protozoans in
radiolarian colonies. This was especially prevalent on ATLANTIS II 98
in March of 1978 in the Southern Sargasso Sea. At times infestation was
very heavy, and once invaded, the colonies seldom survived long. I have
little information on ciliate infestations since they are very difficult
to see aboard ship unless the investation is severe. Their impact on the
colonies and the rapidity with which they spread to other colonies sug-
gests that they could be important in the ecology of the radiolarians.

Frequency and Abundance

Radiolarians have been found on 402 of 452 stations (89%) on which
they have been investigated since 1975 (Figure 75). I have found them on
98% of stations in the period of intensive study since 1977. Table II
lists the stations and shows the relative abundance and frequency of
radiolaria on each cruise since 1975. They were abundant or very abun-
dant (> $1/100$ m^3) on 114 of these stations (29%). They were most abun-
dant in summer in the central gyres in calm weather and most sparse in
relatively eutrophic coastal stations at any time of year.

Measurements of abundance were made at 18 stations and are presented
in Table III. Stations 420-425 were in the Sargasso Sea and stations
466-481 were near the geographic equator in the Indian Ocean between the
northwest and southwest monsoons. The other stations were in the North
Atlantic central gyre and the Sargasso Sea. At most of these stations
radiolarians were assessed as "abundant" or "very abundant" and ranked
100-1000. In Table III the total number of radiolarians counted is noted
and in some cases the sample size was too small to be meaningful. For
example, on station 469 only one colony was counted in five 5 m^3 samples

TABLE II. The number of stations by cruise where radiolarians were present. The frequency distribution of stations in the relative abundance categories is also given; the numbers 1000, 100, 10, 1, 0 refer to approximate densities per 1000 m^3. Cruises on which I did not participate are marked with an "*". Cruises are in chronological order.

Cruise	Stations	No. of stations	Stations with radio-larians	Relative Abundance					
				(%)	1000	100	10	1	0
CHAIN 122*	355-381	27	21	78	2	11	4	2	6
CHAIN 123*	382-394	13	5	38	–	2	3	–	8
CHAIN 125	395-414	20	14	70	0	8	3	3	6
KNORR 53	417-431	15	12	80	1	3	4	3	3
COLUMBUS ISELIN*	432-454	23	19	83	–	–	13	4	4
LA CURIEUSE 7601-5	455-483	29	28	93	6	4	5	13	1
SUBSIG II*	484-492	9	1	11	–	–	–	–	8
ADVANCE*	493-495	3	0	0	–	–	–	–	3
DALLAS*	496-503	8	8	100	–	–	6	1	–
OCEANUS 11*	504-512	9	5	56	–	3	2	–	4
KNORR 58-2	513-523	11	11	100	1	1	4	3	–
KNORR 58-3	524-533	10	9	90	0	0	2	7	1
OCEANUS 22	534-576	41	40	98	0	2	19	19	1
OCEANUS 30	577-584	8	8	100	3	3	1	1	–
OCEANUS 33	585-601	17	17	100	1	7	5	4	0
THOMAS WASHING-TON*	602-607	6	4	67	0	1	1	2	2
ATLANTIS II 98	608-617	10	10	100	0	2	6	2	0
ATLANTIS II 101	618-726	104	101	97	8	43	37	0	3
ANTON DOHRN	727-729	3	3	100	0	0	3	0	0
OCEANUS 52	731-774	44	44	100	0	4	20	20	0
PIERCE	775-816	42	42	100	0	14	22	6	0
TOTAL		452	402	89	22	106	157	90	50

TABLE III. Measurements of abundance of radiolarians are expressed as rads/m³. Column 5 shows total number of colonies counted. Densities from stations with low values in column 5 must be interpreted with caution. Surface count at station 472 was in a patch approximately 100 m in diameter. At station 473 one-third to one-half of colonies counted were *Collozoum* sp. A.

Station No.	Rank	Sample volume m³	No. counts (n)	Total No. of rads counted	Mean No. rads/count	s	Rads/m³	Method	Depth of counts (m)
420	1000	4.5	4	20	5	-	1.1	grid	15
423	100	4.5	7	6	.9	-	.2	grid	-
425	100	4.5	3	4	1.7	-	.4	grid	15
425	100	4.5	2	6	3	-	.7	grid	8
425	100	4.5	2	4	2	-	.4	grid	5
466	10-100	5	5	5	1	-	.2	grid	10
467	100	5	5	4	.8	-	.2	grid	10
468	10	5	5	1	.2	-	.04	grid	-
469	1000	5	5	1	.2	-	.04	grid	10
469	1000	.005	23	62	2.7	2.1	540	grid	surface
470	100	5	10	29	2.9	1.4	.6	grid	10
470	100	5	10	27	2.7	1.4	.5	grid	2-3
471	1000	5	10	7	.7	-	.1	grid	10
471	1000	5	10	12	1.2	-	.2	grid	1
471	1000	.05	9	51	5.7	3.5	113	grid	0.10
472	1000	5	10	3	.3	-	.06	grid	10
472	1000	5	9	3	.3	-	.07	grid	1
472	1000	.05	3	33	11	-	220	grid	surface

TABLE III (Continued)

473	10	5	20	21	1.05	1.1	.22	grid 10
474	1000	5	12	118	9.8	3.4	2.0	grid 10
474	1000	5	10	46	4.6	2.3	.92	grid 1
478	1000	.3	36	156	4.3	5.0	14	grid –
481	100	.005	53	40	.75	.98	150	grid surface
578 (Parflux)	100	900	1	61	61	–	.07	net 0-10
592	100	1.4	1	4	4	–	3	net 0-20

Figure 75. A map showing the locations of stations in the North Atlantic Ocean where radiolarians were collected (+) and stations where no radiolarians were found (●). Boundaries as in Figure 9.
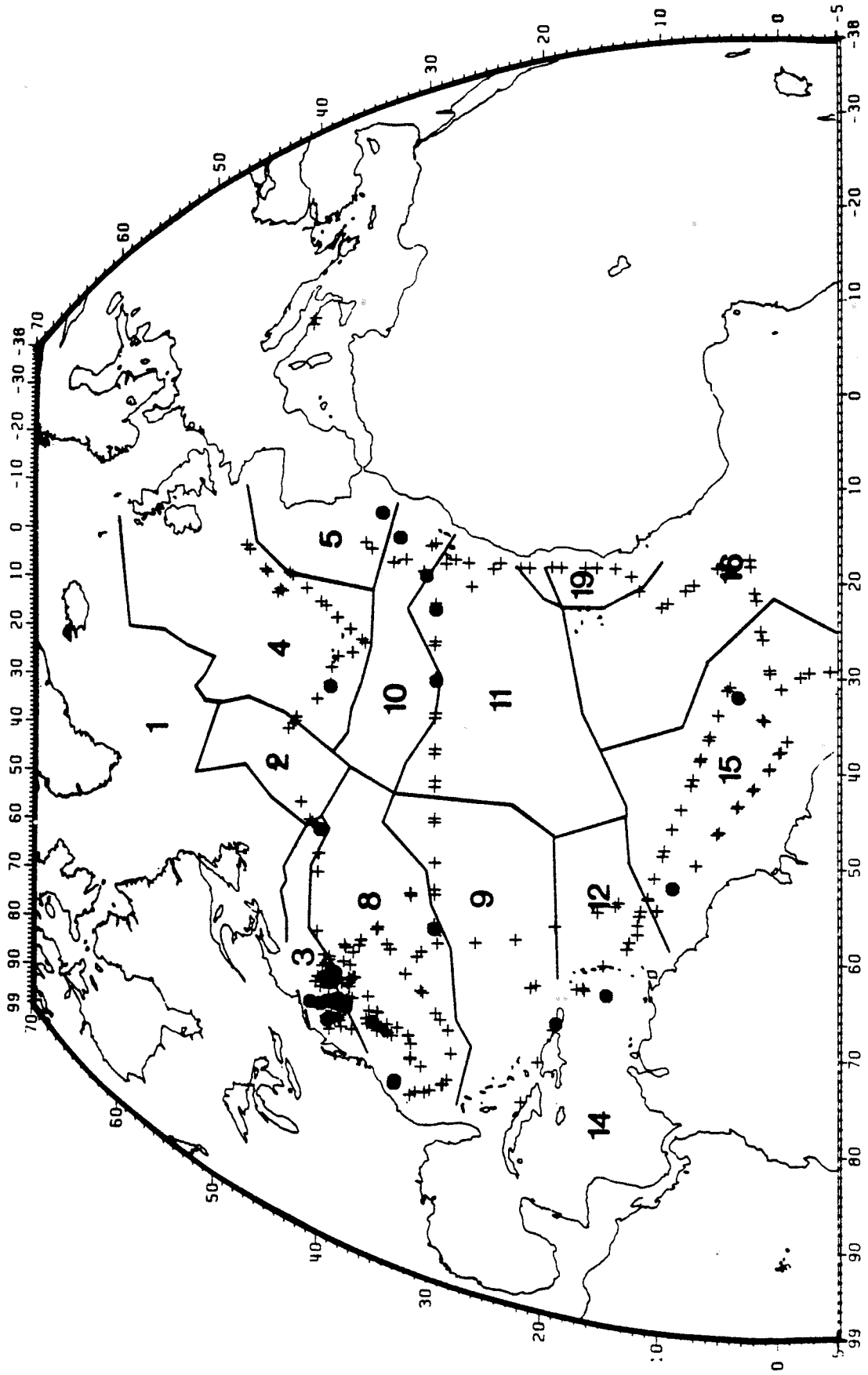
at 10 m but an average of three were counted within the hoop on the sur-
face (n = 23) for a density of 540 colonies/m^3 in the top few cm of water.
Extreme vertical stratification and horizontal patchiness of the radio-
larians on calm days is the rule and underlies the problem in measuring
their density. For these stations the density of radiolarians ranged from
.04 to 1.1 colonies/m^3 in the water column. On calm days any measure is
meaningless since most radiolarians will be on the air-water interface.

DISCUSSION

I have shown that although many colonial morphologies are convergent,
there are some which are characteristic of or specific for a given species.
A few of the species of colonial radiolarians described are identifiable
in situ, even by the novice. They may be recognized by their colony
morphology from a distance of several meters. This is especially true
for *Collozoum longiforme*, *Collozoum* sp. A, *Collozoum* sp. B and *Soleno-
sphaera collina*. It is also true for *Collosphaera polygona* (shrinking
colony) and *Collozoum ellipsoides*. Several other forms are easily recog-
nizable to the trained eye, but may be confused with other species. These
are *Collozoum inerme* (segmented colony, easily confused with *Sphaerozoum*
and some *Siphonosphaera* species), *Rhaphidozoum neapolitanum* and *R. acuferum*
(disc-shaped, similar to *Collosphaera huxleyi*), *Acrosphaera spinosa*
(hollow sphere, resembles some *C. huxleyi* and *A. murrayana*) and *Collozoum*
(=*Myxosphaera*) *coeruleum* (blue reproductive sphere, may be confused with
reproductive *Siphonosphaera tenera*). The colony shape of *Collozoum
radiosum* and *C. pelagicum* is not a good diagnostic character as a many
shelled species have convergent morphology. A brief examination under

the microscope will usually resolve any confusion to the level of genus.

Colony morphology is determined by the consistency of the gelatin and the size and distribution of the buoyancy alveoli. The gelatin chemistry probably varies from species to species since response to histological fixatives varies (Brandt, 1885). The distribution of the alveoli could be controlled by the rhizopodia. Numerous colonies were observed to reorganize the alveolar distribution upon capture and this changed the appearance of the colony. The degree of response and the mechanism of reorganization also varied systematically; some species shrunk uniformly or peristaltically, some squeezed their alveoli to the colony surface and others did not visibly respond to mechanical stimulation. All those species examined (and I believe most other species as well) responded to light by moving their symbiotic algae. The same behavior occurs in the foraminiferan *Globigerinoides sacculifer* which moves its algae into its test at night and out during the day (Anderson and Bé, 1976). There may be functional significance to both of these types of behavior.

The simplest hypothesis to explain the movement of the algae in response to light is that the radiolarian optimizes the photosynthetic output of the algae. In ample light, even spacing of the algae would reduce product inhibition of the dark reactions of photosynthesis and reduce shading. As light intensity diminishes, moving the cells closer to the radiolarian central capsules would bring them closer to the center of host mitochondrial activity, optimizing the use of their diminished output. This might also increase the level of nutrients in the micro-environment of the algae.

The possible adaptive value of the various shrinking responses is fairly obvious. Brandt (1895a,b) showed that the alveoli ("Vacuolen")

functioned as buoyancy organelles, and that they are manipulated to contact the external medium so that the buoyant substance can diffuse out when the organism needs to go down. He did not report the kind of shrinking described here for *C. polygona*. Brandt (1885) determined that many Collosphaeridae have gelatinous substances in their alveoli and that species of *Collozoum* have substances which are more fluid. He suggested (1895b) that reinflation of the alveoli is caused by osmotic pressure and that the buoyancy is caused by the presence of a CO_2 solution of osmolarity equal to that of seawater.[3] Regardless of the mechanism of buoyancy, Brandt (1895a,b) observed that disturbance and shrinking are followed by sinking of the colonies. In one instance the presence of embedded hyperiids locally interfered with the shrinking process of *Collosphaera polygona*. This, and the fact that it frequently occurs in a peristalsis means that the shrinking is an active process by the radiolarian and not simply a passive result of physical disruption. I reported that radiolarians were often found contacting the air-water interface on calm days (see also Brandt, 1885 and Khmeleva, 1967). Their sensitivity to mechanical irritation allows them to respond to changes in weather and sink before it is severe enough to damage the colonies. Since they also respond to light, I suggest that they may inflate the alveoli in response to diminishing light intensity. This would allow them to seek a position in the water column optimal for the prevailing conditions by balancing the stimuli of light and wave motion.

Their size and the ability to maintain their buoyancy make the radiolarians excellent platforms for other organisms in the plankton. Brandt

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[3]This is doubtful. It is more likely that an ion exchange mechanism replaces heavy Ca^{++} and Mg^{++} ions with lighter ones such as Na^+, H^+ and NH_4^+ (Hochachka and Somero, 1973).

(1885) reported the occurrence of *Hyperia* sp. in the large alveolus of
Collozoum (= *Myxosphaera*) *coeruleum*. The genus *Hyperia* has been extensive-
ly revised since then (Bovallius, 1889; Bowman, 1973) and Brandt's iden-
tification is probably only valid to the level of the family Hyperiidae.
The presence of gravid female and juvenile hyperiid amphipods embedded in
colonies suggests that the radiolarians may be very important to the life
cycle of the amphipods. Although at present there does not seem to be
much specificity of amphipod species to radiolarian species, the *Hyperietta*
are only found on colonial radiolarians (Harbison et al., 1977) and accord-
ing to Swanberg and Harbison (Appendix II) three of the five species of
Hyperietta have now definitely been found on radiolarians.

Radiolarians are effective carnivores and feed abundantly on a wide
range of prey organisms. The amphipods, copepods and turbellarians must
either be immune to the radiolarian capture device or behaviorally adapted
to avoid predation. Some hyperiids are known to live among the tentacles
of medusae and siphonophores (Harbison et al., 1977) and may have a waxy
cuticle protecting them from predation (Harbison and Madin, personal com-
munication). The other ectocommensal associates may simply avoid the
rhizopodia. Brandt (1885) reported finding the remains of diatoms, peri-
dinians, small radiolarians and sometimes ostracods, copepods, decapod
larvae, appendicularians and echinoderm larvae in radiolarian colonies.
Although he observed the digestion of one ostracod by *Sphaerozoum punctatum*
and admitted that radiolarians were capable of digesting other organisms,
Brandt did not believe that these were a natural food source. The reasons
for this were 1) he always collected radiolarians in nets and could not
separate the net artifact from natural conditions and 2) he observed
hyperiids living in the colonies. Since these were not digested he could

not conclude that the radiolarians had digested the organisms whose shells
he so often found embedded in colonies. He also observed that when less
plankton was caught, fewer of these "prey" organisms were found in the
colonies. He concluded that the algae fulfill the nutritive requirements
of the radiolarians.

While his caution in interpreting his net data is to be commended,
Brandt was definitely wrong. I have described hard-body remains of
organisms found in countless hand-collected radiolarians. Most of these
were unquestionably captured prey. One notable exception is the siliceous
shells found in *Solenosphaera collina* (Figures 57-59). Since these were
found in 100% of the colonies of *S. collina* and never in any other radio-
larian species I do not think they were prey. Nor is it likely that they
were predators or parasites since they were nearly always empty. That
they were the only shells in two colonies which resembled *S. collina* in
morphology and that in one of these they enclosed central capsules argues
circumstantially that they are a stage in the life cycle of this radio-
larian. Hilmers (1906) did not report the presence of such shells in the
young vegetative colonies, but I found them throughout the range of
S. collina.

Solenosphaera collina was found mostly in the eastern and equatorial
regions of the Atlantic. Two of the other species of radiolarians showed
interesting patterns of distribution: *Collozoum longiforme* was confined
to the Amazonian Province (Backus et al., 1977); *Collozoum* sp. A was found
only in the equatorial and Gulf Stream regions. I do not know what fac-
tors cause the apparent specificity of the distribution of *Collozoum* sp. A
and *C. longiforme.* According to Backus et al. (1977), the "Amazonian

Province is somewhat warmer, saltier, has more dissolved oxygen, and is less productive than the Guinean Province [to the east]...in some parts of the Amazonian Province variation [in surface temperature] is almost nil, although a range of about 2°C is more general." The 14° isotherm for 200 m separates the Lesser Antilles Province to the north from the Amazonian Province. Equatorial and Gulf Stream surface temperatures are higher than those of surrounding water masses. It may be that temperature or variability in temperature makes these species water-mass specific and that *C. longiforme* is more sensitive to such factors than *Collozoum* sp. A.

Three Russian workers have described great numbers of colonial radiolarians. Pavshtiks and Pan'kova (1966) report that the abundance of *Collozoum* in the top 50 m in the Davis Straits in September 1964 was 3000-4000 colonies$\cdot$m^{-3}. Khmeleva (1967) found 16-20,000 colonies of *Collozoum* per m^3 in the Gulf of Aden. The data I presented indicate that abundances are orders of magnitude lower in the open ocean and that radiolarian colonies are patchy and show strong vertical stratification in their distribution. Thus reliable estimates of abundance cannot be made without sampling large volumes of water. Unfortunately, present economically feasible techniques of large volume sampling are inappropriate for collecting colonial radiolarians since they destroy or fail to catch such delicate organisms.

Low absolute abundance does not necessarily mean that an organism is unimportant (Harbison and Gilmer, 1976). Radiolarians occupy the same size range as do salps and ctenophores in the epipelagos and they are more common and abundant than either (Harbison et al., 1978). Their size may confer an advantage for the trapping of prey, but it also provides a

stable platform for some organisms in an environment which has few sur-
faces. In some ways they are analogous to the reef building corals:
they provide structure to the epipelagic environment, they feed on plank-
tonic organisms and they are host to symbiotic algae.

In Part II, I will present data on the photosynthesis of the algal
symbionts and consider the role the radiolarians may play in the produc-
tivity of the open ocean.

PART II

PHOTOSYNTHESIS OF THE SYMBIONTS

INTRODUCTION

Perhaps the most striking feature of colonial radiolarians is the consistent presence of the symbiotic algae in the extracapsular matrix of the colony. While solitary forms may shed their extracapsularium and regenerate it, producing an aposymbiotic condition (Hollande and Enjumet, 1953), this has not been observed with polycyttarian forms. Algal abundance ranges from a few algae to several hundred per radiolarian cell. The association is interesting primarily because radiolarians seem to be very successful in extremely oligotrophic pelagic waters where few if any other large organisms survive. The algal symbiosis may be vital to the radiolarians' successful survival in the open sea.

The notion of symbiont host organisms acquiring their nutrition from their algal symbionts in exchange for nutrient-rich waste products dates back at least as far as Geddes (1882). He offered the hypothesis of symbiosis in opposition to Cienkowski's (1871) hypothesis of parasitism. Although his evidence was flimsy, most researchers of the time accepted it as a probable theory. Geddes's hypothesis is especially appealing in the open sea where it has long been held that nutrient limitation controls productivity in lower latitudes. A great deal of work has been done to demonstrate the validity of Geddes's hypothesis. Brandt (1883) showed with numerous invertebrate-algal associations, including one radiolarian, that the animals survived longer and were healthier when

kept in the light than in the dark. More recent experiments have shown

net oxygen production by corals in the light (Yonge et al., 1932; Odum

and Odum, 1955; Kanwisher and Wainwright, 1967) and translocation of

products (Muscatine and Hand, 1958; Muscatine and Lenhof, 1963;

Muscatine, 1965; Von Holt and Von Holt, 1968a; Trench, 1971a) from

symbiont to host. Other researchers have identified specific products

(Von Holt and Von Holt, 1968b; Trench, 1971b,c; Schmitz and Kremer,

1977; Muscatine, 1965, 1967) translocated from the algae and shown en-

hancement of calcification in corals by photosynthetic activity of

zooxanthellae (Goreau, 1959, 1961; Goreau and Goreau, 1959; Pearse

and Muscatine, 1971).

With his work on *Tridacna*, Fankboner (1971) showed grazing by the

host on its symbionts and the same process has been demonstrated in

radiolarians by Anderson (1976a) on the basis of cytochemistry in

Collozoum inerme. No recent work, with the exception of Anderson's

(1976a,b,c, 1978) has dealt with radiolarians. Droop (1963), citing

Brandt (1883) and Yonge (1944), stated that radiolarians are an example

of a symbiotic host which survives in the adult stage without feeding.

There has been a great deal of work on symbiosis in corals and the reader

is referred to several excellent reviews for detailed information (Buchner,

1953; Yonge, 1944; Droop, 1963; McLaughlin and Zahl, 1966; Muscatine,

1973; Taylor, 1973, 1974; Trench, 1979). The consensus of workers is

that while there is certainly a continuum between types of associations,

from parasitism by algae to grazing by the host, the primary beneficiary

is usually the alga (Droop, 1963; McLaughlin and Zahl, 1966). This is

not to say that the host does not benefit. Coral reefs are thought to

succeed largely because of their zooxanthellae. Their growth and $CaCO_3$ secretion are substantially influenced by photosynthetic processes (Goreau, 1961; Pearse and Muscatine, 1971). It is probable with the abundance of demersal plankton on coral reefs and the relatively high local productivity, that the coral reef does not present the desert habitat faced by the radiolarians in the open ocean central water masses. As Goreau (1961) stated, this may simply be due to the ability to erect a substrate available to other animals. In this way corals have been able to modify their environment far more than the radiolarian could.

One Russian worker has investigated the productivity of colonial radiolarians. Khmeleva (1967) found that colonies of *Collozoum inerme*, which existed in very high densities in the Gulf of Aden produced up to three times the amount of carbon/m^3 as the surrounding phytoplankton populations. Unfortunately she did not present her data in terms which could be more directly related to the radiolarian colonies. I calculated from her table an average of 0.68 nmoles CO_2/colony/hr over her 24 hour natural light incubation. She reported that colonies usually have 180-200 central capsules, thus they were incorporating about 3.4 pmoles CO_2 per hour per radiolarian cell at 27-28°C. While this may be a useful starting point, Khmeleva's production numbers raise more questions than they answer. She incubated in full sunlight and she states without support that colonial radiolarians are not light inhibited in full sunlight as are most algae. There may indeed be something to this. In calm weather radiolarians rest directly at the air-water interface (see p.; also Brandt, 1885; Khmeleva, 1967). They certainly could have evolved some mechanism to circumvent photo-inhibition of their algae. One likely

candidate as Khmeleva suggests is the gelatinous tissue of the host. Khmeleva reported her data as g $C \cdot m^{-3} \cdot day^{-1}$. The volume specific "productivity" of the colonial radiolarians may indeed be high in dense patches of colonies, but this may be meaningless, since although swarms of radiolarian colonies are not infrequent, they are still the exception rather than the rule and typically show much vertical stratification and horizontal patchiness (p. 90). Another approach is certainly needed.

Taylor (1973) points out that the physiological significance of excess O_2 production by a marine symbiotic system is questionable since few associations occur in environments likely to realize oxygen stress. Net photosynthetic production could be underestimated by the oxygen method due to host and algal respiration. Even so, when Kanwisher and Wainwright (1967) converted oxygen flux to carbon productivity they found that net productivity is much higher than in free-living algae. This suggests that it should be revealing to study the physiology of photosynthetic incorporation in the symbiosis in units which can be easily compared to measurements for other groups of algae.

The units in which photosynthetic incorporation has been reported seem to number almost as many as the investigators who have reported them. The literature of plant physiology uses primarily units of molar values of product (O_2) or substrate (CO_2) per unit mass of chlorophyll per hour. Some of the plankton literature uses this, although it is more common to find units of carbon mass or oxygen volume, and the ecological literature frequently uses g $C \cdot m^{-2} \cdot day^{-1}$ or yr^{-1}. These values have very different biological meanings. Kanwisher and Wainwright (1967)

suggest that the maximum obtainable photosynthetic assimilation rate (P, mg C$\cdot$mg Chl $a^{-1}\cdot$hr^{-1}), has no meaning ecologically since photosynthetic potential may be independent of actual achievable photosynthesis in natural light flux. While it is true that "photosynthetic potential" does not mean that photosynthesis can occur without sufficient light, the usual interpretation of the light-saturated photosynthetic potential is that it is determined by the dark reactions of photosynthesis, and that saturation by definition indicates that light is not limiting. Still, if one recognizes that light flux is the actual physical parameter to which an organism can respond, the area-specific photosynthetic incorporation could be a measure of the integration of the other components of the photosynthetic apparatus.

In this section I will present data taken to assess the rate of light-activated $H^{14}CO_3^-$ incorporation in radiolarian colonies. It is important to report the relationship between photosynthesis and light intensity in order to show that light saturation is reached and to evaluate the effects of higher light intensities. In order to simplify comparison with the units of plant physiology as well as the measurements of biological oceanographers, I will express my data as pmoles $CO_2\cdot$radiolarian cell$^{-1}\cdot$hr^{-1} and nmoles $CO_2\cdot$hr^{-1} as a function of colony size and light intensity. These data will be compared to other data on the content of carbon and nitrogen, chlorophyll and phaeophytin in the radiolarian colonies.

MATERIALS AND METHODS

All specimens used for experimental purposes were hand-collected by SCUBA divers using glass jars. In most instances individual colonies were used within 2-3 hours of collection. All colonies were collected from the upper 30 m of water during daylight hours. Damaged or unhealthy appearing colonies were not used.

The selection of species for experimental work was of necessity opportunistic. Radiolarians were used which were locally abundant, easily identified, and hardy enough to endure experimental treatment. In addition the constraint was applied that the colonial stage under investigation be morphologically symmetrical and simple enough to allow estimation of the number of central capsules in the colony. The number of central capsules was used as an index of size.

With the exception of the very large colonies of *Collozoum longiforme* and *Collozoum* sp. A, the measurement and calculation of the central capsule number was done from micro-photographs of individual specimens. The method of calculation varied according to colony morphology. Spherical colonies with single vacuoles (*Acrosphaera spinosa*, see p. 58) have their central capsules and algae all on the sphere's surface. These were photographed at 4X and 18X magnification in a Wild M-5 stereomicroscope equipped with a trinocular head and camera. The diameter of a colony was measured in several co-planar axes on a 35 mm format negative and calculated using a conversion factor obtained by photographing a metric scale under the same optical system. From this value the total surface area in mm^2 was calculated and multiplied by the central capsule

density counted on the colony surface in two to three replicate negatives for each colony. Simple linear colonies (*Collozoum radiosum*, see p. 21) with small vacuoles and central capsules scattered along the length of the colony were photographed at 9X and central capsule density per unit length measured. This density was multiplied by the length of the colony as measured directly. Segmented colonies, such as vegetative *Collozoum inerme* (see p. 13) were photographed at 4X and 18X for diameter and central capsule density. The surface area was calculated by assuming that the colony approximated a cylinder with discs at the interfaces of the spheres created by the vacuoles; this surface corresponds to the distribution of the central capsules.

Collozoum longiforme sp. nov. (Swanberg and Harbison, 1979; see Appendix II) was the largest and most gelatinous organism worked with extensively. In the early stages of the work it was not clear which was the best size parameter to use with such colonies. In early experiments colony volume was used but later cylindrical pieces of colony were excised and preserved and experimental pieces of the same colony were measured for length. Once ashore, the preserved sections with their gelatinous matrix dissolved in formalin, were counted for radiolarian cell number in a Sedgwick-Rafter chamber and for algae number in a Palmer-Maloney chamber. These counts were then correlated to measurements of carbon and nitrogen, chlorophyll or ^{14}C incorporation per unit length. The same method was used for *Collozoum* sp. A (see p. 28).

Measured sections of the colonies were wrapped in precombusted aluminum foil, dried at 50°C and frozen. Samples were analyzed ashore for carbon and nitrogen on a Perkin-Elmer Model 240 CHN analyzer.

For chlorophyll analysis colonies were measured and disrupted by grinding in a Potter-Elvehjem tissue homogenizer in approximately 1 ml seawater. The homogenate was centrifuged 8-10 minutes in an IE clinical centrifuge at 3100 rpm. To assure complete retention of algal cells the supernatant was filtered through a .45 μ Millipore filter and discarded. The filter and pellet were resuspended in 3 ml of 90% Spectranalyzed® (Fisher Chemical Company) acetone with approximately 10 mg of $MgCO_3$ in a 1- ml Nalgene ® centrifuge tube. The tubes were wrapped in aluminum foil and extracted in a dark refrigerator for 12-24 hours. Extraction experiments showed no increase in fluorescence after 15 hours. After extraction the tubes were shaken and centrifuged again. The supernatant acetone extract was decanted into a fluorometer cuvette and serially diluted with 90% acetone to read on a Turner Model 111 fluorometer equipped with 5-60 and 2-64 primary and secondary filters. Dilution was usually 10^{-1} or 10^{-2}. Phaeopigments were determined according to Strickland and Parsons (1972). The fluorometer was zeroed on each door on an equivalent serial dilution of a Millipore filter "extracted" in 90% acetone. Recovery of chlorophyll showed no appreciable quenching by the gelatin of the colony. The Turner fluorometer was calibrated on extracts from cultures of *Thalassiosira pseudonana* (Guillard clone 3H) in Woods Hole by measuring a 90% acetone extract in a Perkin Elmer model 124 dual beam scanning spectrophotometer and serially diluting the extract by four orders of magnitude to read on the fluorometer according to Strickland and Parsons (1972).[4] The factor τ was obtained as the mean value from acidification

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[4] Strickland and Parsons' formula was used for chlorophyll: $C_{chl\ a} = 11.6\ E_{665} - 1.31\ E_{645} - 0.14\ E_{630}$ where C is μg/ml for a 1 cm cell (see Jeffrey and Humphrey, 1975).

of chlorophyll extracts from six unialgal cultures (Guillard clones

SYN, 715, NONO, ISO, ACTIX, and COCCO). One extract of *C. longiforme* was

made in high enough concentration to scan at sea on the Perkin-Elmer

spectrophotometer.

Experiments on the uptake of labelled carbon were done on colonies

measured as outlined above. $NaH^{14}CO_3$ was obtained from New England

Nuclear (lot Nos. 670-079, 670-080) in sealed glass ampoules of 5 and 10

$\mu Ci/ml$ (50 and 100 μg carbon, 1 ml, pH 9.5). Freshly bucketed seawater

was filtered through a .45 μ Millipore® filter (HAWP) and dispensed

into unused disposable 125 ml clear glass surplus bottles. On OCEANUS 22

125 ml Erlenmeyer flasks were used. Labelled seawater stock was added

to make 0.01 $\mu Ci/ml$ or .02 $\mu Ci/ml$ final solution. After mixing labelled

incubation seawater, measured radiolarian colonies were added to each num-

bered bottle through a modified Pasteur pipet with as little seawater as

possible. The bottles were then incubated in appropriate light conditions.

Carbon-14 activity was measured by adding .5 ml aliquots of incubation

seawater to 0.5 ml 1 M NH_4OH and 10 ml Aquasol® and counted as below.

Preliminary experiments were done in an incubator at low light levels

under artificial lighting (10^3 $\mu W\cdot cm^{-2}$; Sylvania "Cool-White"® fluorescent

lights) and for long periods (up to 24 hours). Later experiments were

done in a 12-liter cylindrical clear, Nalgene® aquarium set in natural

light on the deck of the ship and cooled with flowing seawater. Bottles

were placed upright in a clear plexiglass holding rack and the tank

covered with 0 to 4 fitted grey fiberglass window screens. Each screen

filtered 40% of the incident light. Incubations were done between 1000

and 1500 hours, usually for 2-3 hours. Dark uptake controls were done

for every experiment and uptake by killed (frozen) colonies of *Acrosphaera*

spinosa was measured. Light was measured with a United Detector Technology

40X Opto-Meter® (s/n 45879) fitted with a radiometric head and set to read in units of power ($\mu W \cdot cm^{-2}$), with a 39 mm 4X neutral density Nikon photographic filter and one layer of fiberglass screening material over the sensor. This meter measures light in the region from 450 to 910 nm. Temperature was monitored and kept within $1^o C$ of ambient surface temperature by flowing seawater from the ship's lines through the incubation chamber. Light levels were recorded whenever possible with a Perkin-Elmer model 56 chart recorder.

After incubation, colonies were removed from labelled seawater with a pipet and frozen in liquid scintillation vials. Ashore, frozen samples of radiolarians were acidified and left for one hour: 1 ml Protosol® was then added and allowed to work 24 hours. Ten ml Aquasol® was added, the solution shaken and placed in the dark for 24 hours to eliminate chemiluminescence. Samples were counted on a Beckman LS 100 C liquid scintillation counter on channels ratio and corrected for quenching. No measurements were made of alkalinity or total CO_2 in the seawater. Carbon uptake calculations were made assuming 90 mg CO_2/l seawater (Steeman-Nielsen, 1952).

Spectrophotometric scans of absorption were made on the gelatin from several species of radiolarians. Gelatin was separated from central capsules and algae by centrifugation of colonies. Scans were done on the Perkin-Elmer 124 with a reference cell of seawater.

RESULTS

With most species, data were of necessity obtained in different

categories on different individual colonies. Thus chlorophylls and ^{14}C

incorporation were taken on separate groups of measured colonies. As a

check on the precision of colony measurement carbon and nitrogen content

was measured.

Carbon and Nitrogen Content

Carbon and nitrogen data were collected for *Acrosphaera spinosa* and

Collozoum inerme on OCEANUS 30 and ATLANTIS II 101, for *Collozoum radio-

sum* on ATLANTIS II 101 and for *Collozoum longiforme* on OCEANUS 52. Data

are presented as µg C as a function of colony size (total central capsule

number or length) and C:N ratio. Figures 76-78 show carbon as a function

of central capsule number for *C. inerme*, *A. spinosa* and *C. radiosum*.

These had about 50, 100 and 200 ng C·central capsule^{-1} respectively; C:N

ratios were 11.0 (s = 3.2, n = 11) for *C. inerme*, 8.3 (s = 1.7, n = 13)

for *A. spinosa* and 8.4 (s = .76, n = 13) for *C. radiosum*. Only three

colonies were measured for carbon and nitrogen content in *C. longiforme*.

Mean values were 4.9 µg C·mm^{-1} (s = .80, n = 5), 14 µg C·mm^{-1} (s = .60,

n = 3), and 8.7 µg C·mm^{-1} (s = .40, n = 4). After allowing for difference

in central capsule abundance per unit length the carbon contents were 67,

93, and 96 ng C·(central capsule)$^{-1}$ respectively ($\bar{x}$ = 85 ng C·(central

capsule)$^{-1}$). The mean C:N ratio was 8.6 (s = .54, n = 12).

The carbon and nitrogen data correlate well with cell number, although

it is not clear to what extent the gelatin contributes. Similar sorts of

measurements were done for chlorophyll *a* to determine whether colony size

could be used to predict chlorophyll content.

Figure 76. Colony carbon content (µg C) by CHN analysis in *Collozoum*
inerme as a function of radiolarian colony size (radiolarian cell
number x 10^{-3}). Carbon (µg) = [3.6 x 10^{-2}]·(cell no.) + 31. r = .89.

Figure 77. Colony carbon content (µg C) by CHN analyais in *Acrosphaera*
spinosa as a function of radiolarian colony size (radiolarian cell
number x 10^{-2}). Carbon (µg) = [8.5 x 10^{-2}]·(cell no.) + 10. r = .94.

Figure 78. Colony carbon content (µg C) by CHN analysis in *Collozoum*
radiosum as a function of colony size (length, mm). Mean number of
central capsules per mm length was 17 (s = 5.6; n = 18). Carbon (µg) =
[3.4]·colony length (mm) + 4. r = .69.

Figure 76. Carbon (µg) versus Colony Size (cell no. x 10³).

Figure 77. Carbon (µg) versus Colony Size (cell no. x 10²).

Figure 78. Carbon (µg) versus Colony Length (mm).
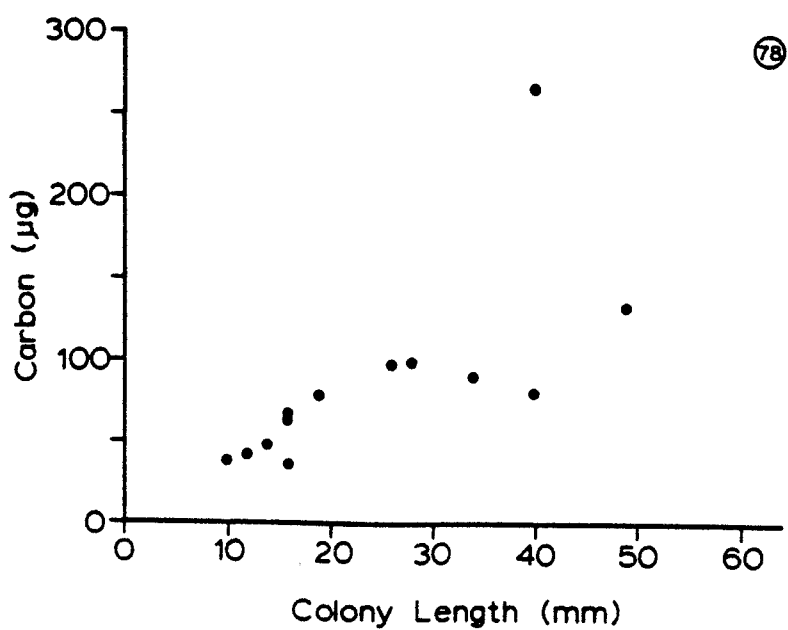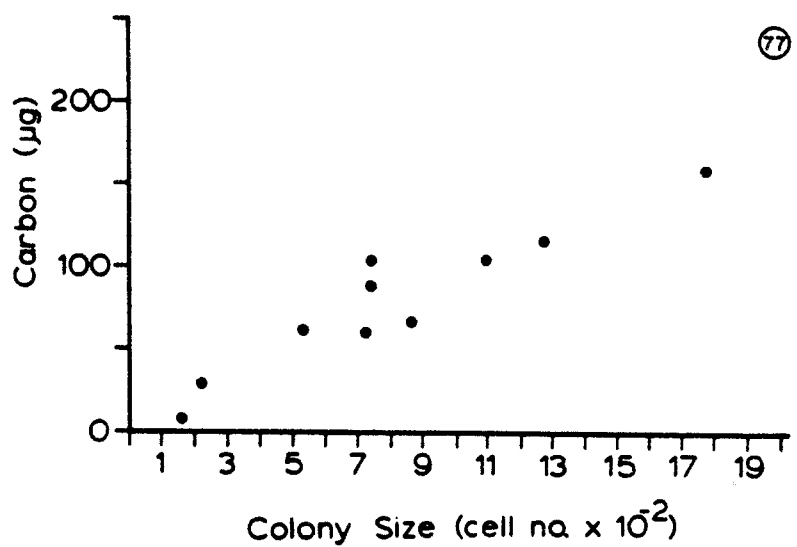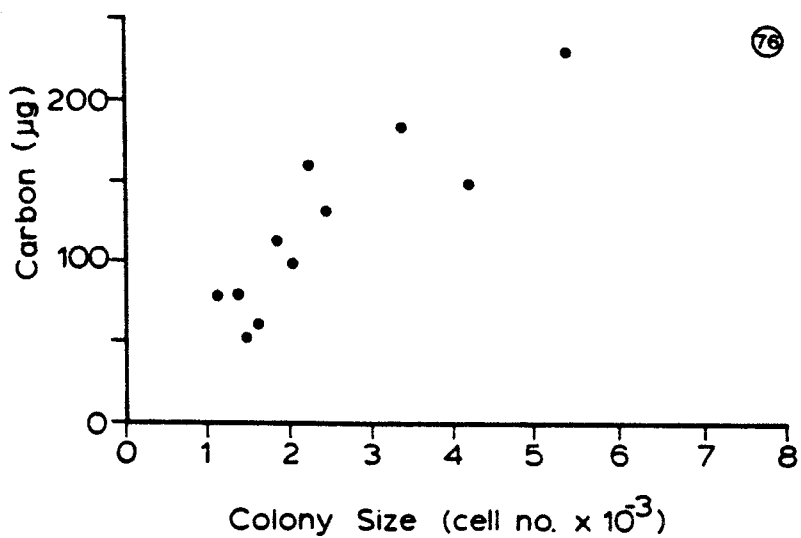
Chlorophyll *a* Content

Chlorophyll *a* as measured fluorometrically is shown in Figure 79 for *Collozoum inerme* as a function of colony size (central capsule number). Most of these data are from early cruises where phaeophytin was not measured. Chlorophyll *a* has been calculated using a ratio of fluorometer readings for phaeopigment of 1.9, typically obtained with this species on later cruises (ATLANTIS II 101 and OCEANUS 52). For this reason phaeopigments are not plotted with these data. The result shows about 10 pg Chl *a* per central capsule ($\bar{x}$ = 9.7, s = 3.3, n = 12.)

Figure 80 is a similar plot for *Collozoum radiosum*. These data are ng Chl *a* as a function of length on a log plot. The mean was 1.0 ng Chl *a* $\cdot$ (mm length)$^{-1}$ ($\bar{x}$ = 1.02, s = .62, n = 8). Because of a camera malfunction photographs of colonies used for chlorophyll were lost, so backup linear measurements were substituted. It was later found that central capsule density varied enough and was sufficiently unpredictable to exclude the possibility of accurately reporting these data as a function of central capsule number. When an estimate of 17 central capsules$\cdot$mm^{-1} was used (x = 16.9, s = 5.6, n = 18) I calculated 60 pg Chl *a*$\cdot$central capsule^{-1} ($\bar{x}$ = 60, s = 37, n = 8, range 25-120 pg Chl *a*$\cdot$(central capsule)$^{-1}$).

For *Acrosphaera spinosa* the situation was more complicated. Figure 81 shows a log plot of Chlorophyll *a* as a function of total central capsule number. The scatter was very high. At a given colony size, chlorophyll varied as much as two-fold, but increased little with increasing size. Fairly good correlations were obtained with this species between carbon and nitrogen content and central capsule number, so I consider it unlikely that the variability was due to estimation of central

Figure 79. Chlorophyll content (ng Chl a) by fluorometric analysis of colonies of *Collozoum inerme* as a function of colony size (radiolarian cell number x 10^{-3}). Data are from OCEANUS 22 (●), OCEANUS 33 (◖), OCEANUS 52 (▲), and ATLANTIS II 98 (■). Chl a (ng) = [8.0 x 10^{-3}]·(cell no.) + 5.14. r = .71.

Figure 80. Chlorophyll content (ng Chl a) by fluorometric analysis of colonies of *Collozoum radiosum* as a function of colony length (mm). Data from ATLANTIS II 101. Chl a (ng) = [1.3]·colony length (mm) + 4.9. r = .46.

Figure 81. Chlorophyll content (ng Chl a) by fluorometric analysis of *Acrosphaera spinosa* as a function of colony size (radiolarian cell number x 10^{-2}). Data from ATLANTIS II 101.

Figure 82. Chlorophyll a content (pg) per radiolarian cell in *Acrosphaera spinosa* as a function of colony size (radiolarian cell number x 10^{-2}). Data from Figure 8. Chl. a (ng) = [-3.6 x 10^{-2}]·(cell no.) + 42. r = .67.
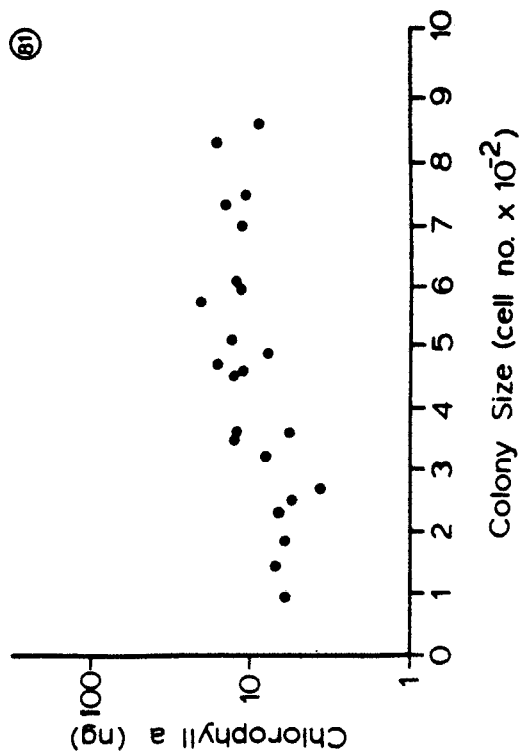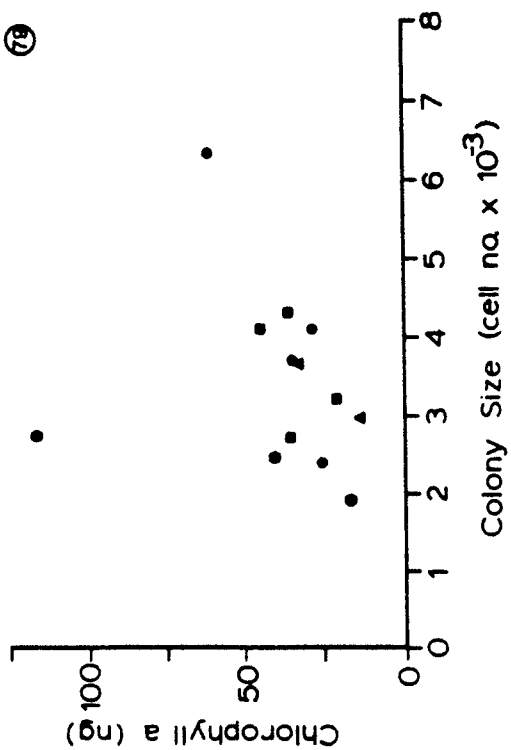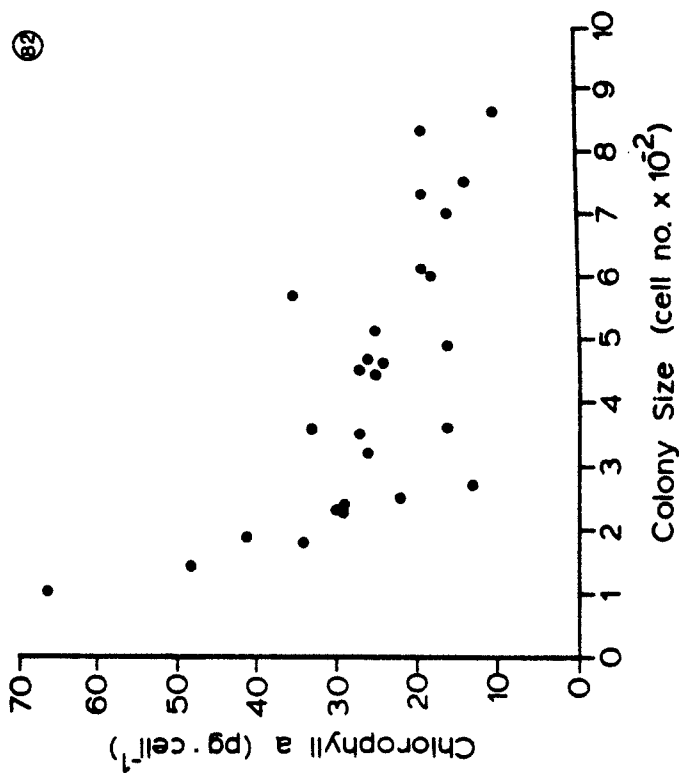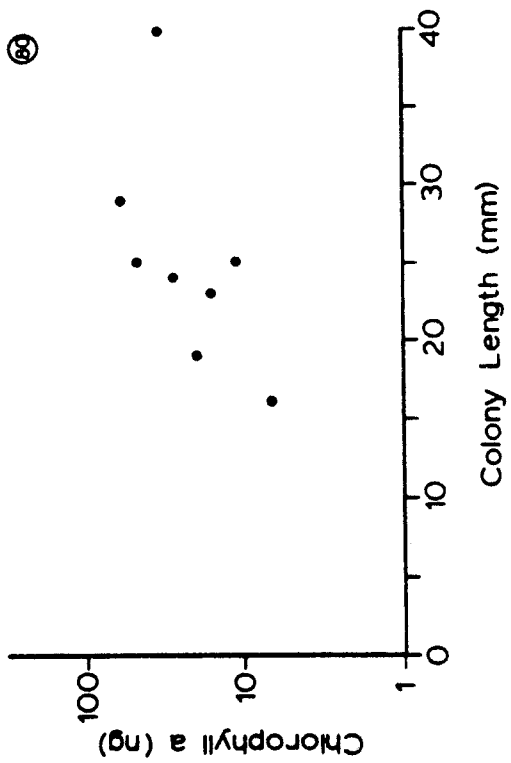
capsule number. Figure 82 shows the same data normalized to central

capsule number. Either the chlorophyll content per algal cell decreased

or the number of algae per central capsule decreased with increasing

colony size.

Collozoum longiforme was measured for chlorophyll a on OCEANUS

cruises 22 and 52. On OCEANUS 22 phaeophytin was not measured and there

was not a one-to-one correspondence between the colonies used for chloro-

phyll a analysis and ^{14}C uptake experiments. There were more late vege-

tative colonies present on this cruise and the number of algae·(mm

length)$^{-1}$ and pigment·(mm length)$^{-1}$ was high. A spectrophotometric scan

of a chlorophyll extract of *C. longiforme* was made. Although the ab-

sorbance was low, I calculated Chl a = 2.8 μg, Chl b = 0 μg and Chl c =

1.4 μg for a piece of colony approximately 3 cm long. One late vegeta-

tive colony had 47 algae·(central capsule)$^{-1}$ and 320 central capsules·

(mm colony length)$^{-1}$. On OCEANUS 52 only early vegetative colonies were

studied. When a colony was cut into 8 pieces and analyzed for chlorophyll

a, Chl a·mm^{-1} varied by a factor of 3 ($\bar{x}$ = 1.8 ng Chl a·mm^{-1}, s = .60);

the variation between colonies was much greater (six-fold; $\bar{x}$ = 2.8, s =

1.8, n = 6). Central capsule density and algal density were related

(Figure 83) so that the algae:cell ratio varied from 14 to 28 ($\bar{x}$ = 19,

s = 3.4, n = 6). There was no relationship between Chl a·mm^{-1} and algae·

mm^{-1}. Thus Chl a levels in the algal cells were variable. Most of the

measurements for *C. longiforme* are summarized in Table 3 in Appendix II.

There was no discernible relationship between phaeophytin and

colony size in *A. spinosa* or *C. radiosum*. Most colonies (22 of 33)

showed levels of phaeophytin between .25 and .75 of chlorophyll a.

Several (7) were less than .25 and four had more phaeopigments than
chlorophyll. In *C. inerme*, on ATLANTIS II 98 and OCEANUS 52, phaeo-
pigment was always .13-.50 of chlorophyll. Phaeophytin did not vary
much in *C. longiforme* (see Table IV), but chlorophyll did, so the ratio
varied from .20-.83 except for two values which were higher in phaeo-
pigment than chlorophyll. Plots of total pigment did not look much dif-
ferent than those of chlorophyll a for any species.

Chlorophyll a was also measured for a few species for which no other
data were taken. For *Siphonosphaera tenera* the mean of 8 determinations
was 9.2 pg Chl $a \cdot$(central capsule)$^{-1}$ (s = 4.2; central capsule number
varied from 540 to 740 and showed no linear trend with chlorophyll a).
For *Sphaerozoum* sp. the mean was 16 pg Chl $a \cdot$(central capsule)$^{-1}$ (s = 5;
n = 3). Measurements of chlorophyll in *Collozoum* sp. A (p. 28) were not
always taken with central capsule number. The mean was 6.6 ng Chl $a \cdot mm^{-1}$
(length) from ATLANTIS II 101 (n = 3) and 10.2 ng Chl. $a \cdot mm^{-1}$ (2.8 ng
Chl. $a \cdot$(central capsule)$^{-1}$ from OCEANUS 52 (n = 6). The mean of three
preserved measured specimens was 58 central capsules per cm and 311 algae
per central capsule (range 250-350 algae/central capsule, 40-70 central
capsules per cm).

To evaluate the transparency of the gelatin, samples from several
species of radiolarians were scanned spectrophotometrically on OCEANUS 22
and KNORR 58. *Collozoum inerme*, *C. serpentinum* and *Collozoum* sp. A all
showed absorption peaks around 300 nm, usually with a shoulder or bulge
at 330 nm. *Collozoum longiforme* showed a large peak at 330 nm which
shadowed the 300 nm peak. Absorption below 300 nm in all colonies was
lower. No gelatin showed any absorption in the visible spectrum.

In general either the precision of measurement of chlorophyll a was not sufficient or chlorophyll varied a great deal between colonies. It could not be reliably predicted from colony size by a factor better than 2-4. Because of this P (mmoles $CO_2 \cdot$mg Chl $a^{-1} \cdot hr^{-1}$) may be inappropriate as a measure of photosynthesis. The values will be presented but must be used cautiously.

Incorporation of Labelled Carbon

Measurements of incorporation of $H^{14}CO_3^-$ in *Collozoum inerme* were made under low-level artificial light (10^3 $\mu W \cdot cm^{-2}$) on OCEANUS 30 in an incubator at 25^oC. The net incorporation rate was 3.3 pmoles $CO_2 \cdot$(central capsule)$^{-1} \cdot hr^{-1}$ ($\bar{x}$ = 3.32, n = 10, s = 1.0). The data for total incorporation as a function of colony size are presented in Figure 84. Figure 85 shows the incorporation per cell as a function of colony size. Carbon incorporation per cell decreased with increasing colony size and with increasing central capsule density. No useful data were obtained for this species in experiments on the effect of higher light intensities. Such data were obtained in deck incubation experiments which began with *Collozoum radiosum* on ATLANTIS II 101.

Figure 86a and b show plots of net carbon incorporation for *C. radiosum* as measured by ^{14}C uptake. Both experiments were done on 4 July 1978 near the Azores ($42^o12'N$, $35^o26'W$); duration of each was 2 hours. Figure 86a, at full sunlight (1124-1324 hours local, mean light intensity estimated at 1.7×10^4 $\mu W \cdot cm^{-2}$) shows less net uptake ($\bar{x}$ = 51.4 pmoles $CO_2 \cdot$(central capsule)$^{-1} \cdot hr^{-1}$, s = 12, n = 8) than that shown in Figure 86b ($\bar{x}$ = 76.1 pmoles $CO_2 \cdot$(central capsule)$^{-1} \cdot hr^{-1}$, s = 11, n = 8) at 0.6×10^4 $\mu W \cdot cm^{-2}$ (1340-1540 hrs).

Figure 83. Algal density (cells·mm^{-1}) as a function of radiolarian cell density (cells·mm^{-1} colony length) in *Collozoum longiforme*. Data from OCEANUS 52. Algae (cells·mm^{-1}) = [28]·radiolarian cells (cells·mm^{-1}) - 1200. r = .99.

Figure 84. Net incorporation rates (●) of CO_2 (nmoles CO_2·hr^{-1}) in *Collozoum inerme* at 10^3 μW·cm^{-2} as a function of radiolarian colony size (cell number x 10^{-3}). Dark control incorporation rates are shown (▲). Data from OCEANUS 30. Incorporation (nmoles CO_2·hr^{-1}) = [4.6 x 10^{-3}]·(cell no.) = 6.3. r = .10.

Figure 85. Net incorporation rates per radiolarian cell of CO_2 (pmoles CO_2·cell^{-1}·hr^{-1}) in *Collozoum inerme* as a function of colony size (cell number x 10^{-3}). Data from Figure 84. Incorporation (pmoles CO_2·cell^{-1}·hr^{-1}) = [- 1.1 x 10^{-3}]·(cell no.) + 5.9. r = .74.

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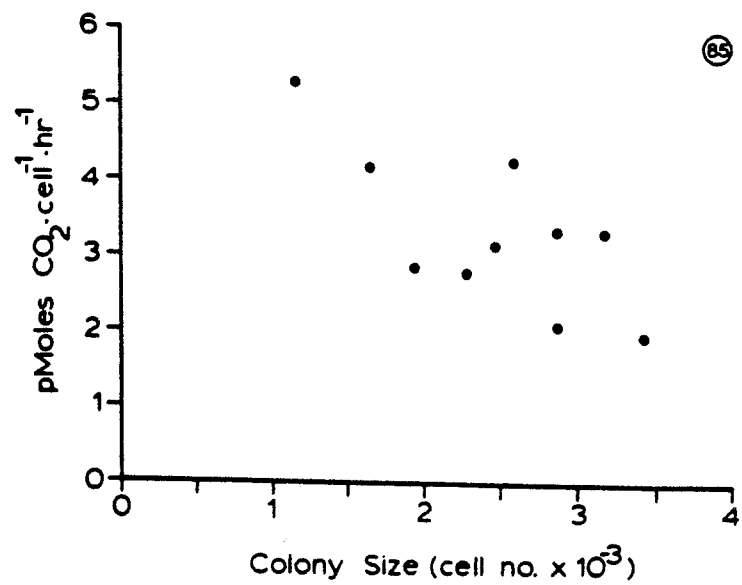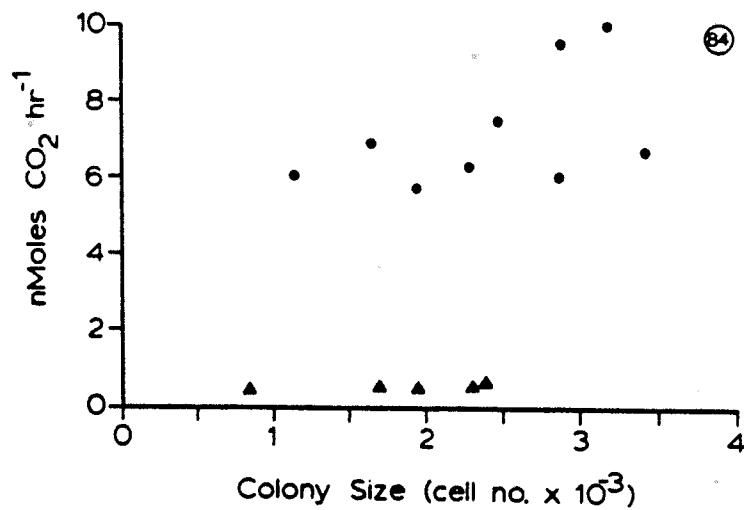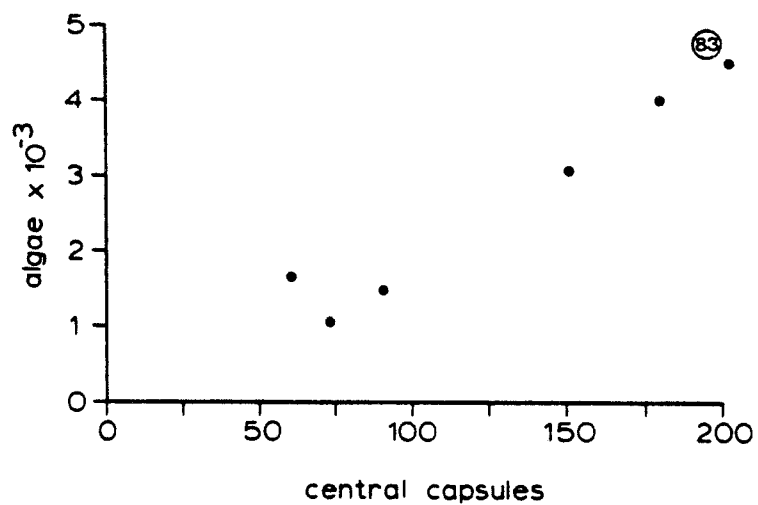
Figure 86. Net incorporation rate (●) of CO_2 (nmoles $CO_2 \cdot hr^{-1}$) as a function of colony size (cell number x 10^{-2}) in *Collozoum radiosum*. Dark control rates are shown (▲). Data from ATLANTIS II 101.

a) at 17 x 10^3 $\mu W \cdot cm^{-2}$. Incorporation (nmoles $CO_2 \cdot hr^{-1}$) = $[4.9$ x $10^{-2}] \cdot$ (cell no.) + 1.4.   r = .85.

b) at 6 x 10^3 $\mu W \cdot cm^{-2}$. Incorporation (nmoles $CO_2 \cdot hr^{-1}$) = $[7.7$ x $10^{-2}] \cdot$ (cell no.) - 1.3.   r = .90.
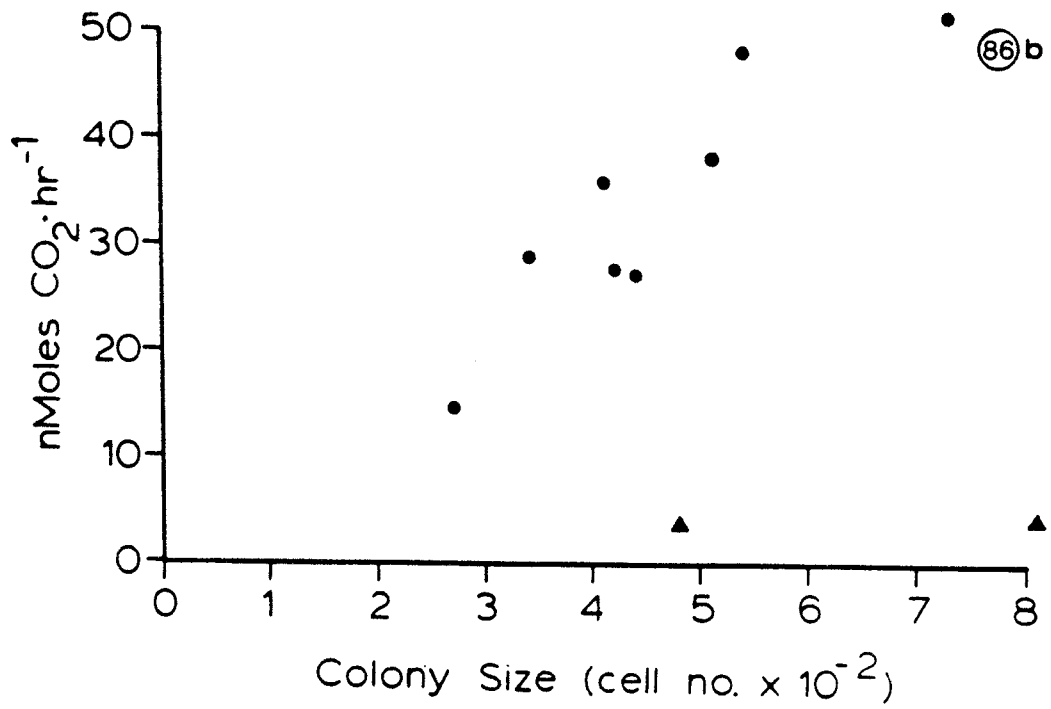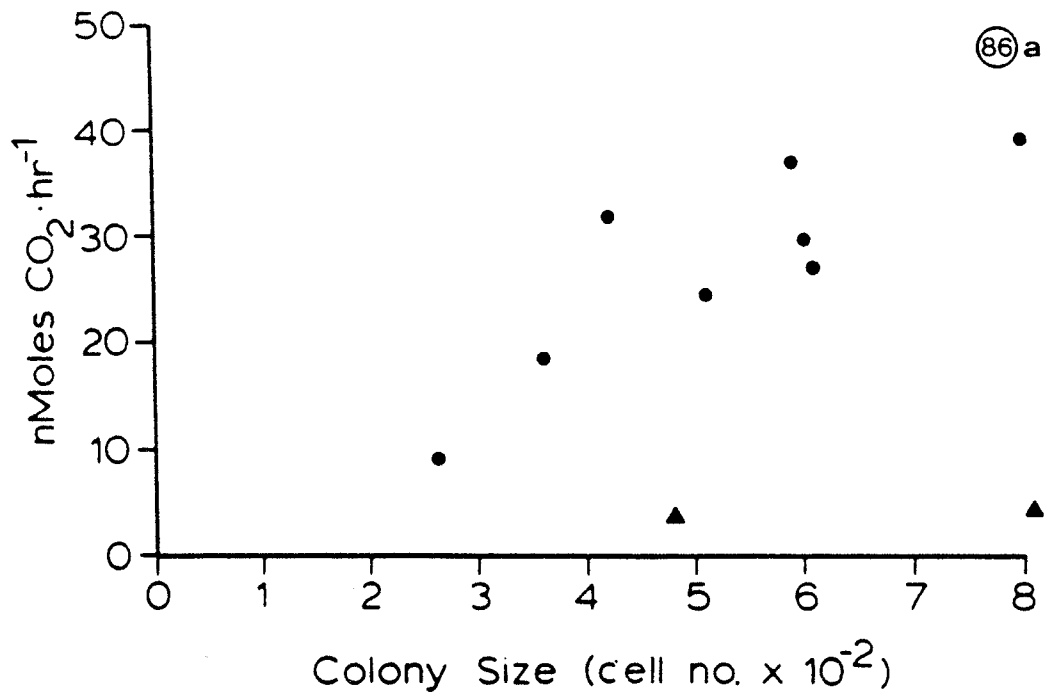
Five experiments were done with *Acrosphaera spinosa*, one each at full sun intensity (4.4×10^4 $\mu W \cdot cm^{-2}$), one screen (1.9×10^4 $\mu W \cdot cm^{-2}$), two screens (1.4×10^4 $\mu W \cdot cm^{-2}$), and four screens ($.42 \times 10^4$ $\mu W \cdot cm^{-2}$) on ATLANTIS II 101 near the Azores and one experiment at 10^3 $\mu W \cdot cm^{-2}$ on OCEANUS 30 under artificial light. These data are shown in Figure 87a-d and summarized in Table IV. No data are plotted for the experiment at 1.9×10^4 $\mu W \cdot cm^{-2}$ since there were only two points. In general, total CO_2 incorporation increased with increasing colony size. There was considerably more scatter at full illumination than at lower light intensities. There was no relationship between the central capsule-specific uptake rate (pmoles $CO_2 \cdot$(central capsule)$^{-1} \cdot hr^{-1}$) and colony size. Data for dark uptakes and killed colonies incubated in light which were indistinguishable from dark colonies are plotted in Figure 87a. Dark uptake "rates" for Figure 87b,c were as high as low net rates, although the absolute values were equivalent to those of the longer experiment.

Six experiments were done on carbon uptake in *C. longiforme*. Five of these were done in natural light on OCEANUS 52 and one at low-level artificial light on OCEANUS 22. Data were taken in terms of CO_2 incorporation per mm colony length of segments of the long colonies. Each experiment represents a separate colony. Figure 88 shows the net CO_2 incorporation per unit length as a function of light intensity. The maximum value obtained was approximately 6.5 nmoles $CO_2 \cdot$(mm colony length)$^{-1} \cdot hr^{-1}$ at about one third of full sunlight intensity (1.7×10^4 $\mu W \cdot cm^{-2}$).

Representative data from the $H^{14}CO_3^-$ incorporation experiments in all four species are summarized in Table V. They ranged from 3.3 to 64 pmoles ($CO_2 \cdot$(central capsule)$^{-1} \cdot hr^{-1}$. Also shown are carbon content (by CHN analysis) and chlorophyll *a* content per central capsule.

Figure 87. Net incorporation rates (●) of CO_2 (nmoles $CO_2 \cdot hr^{-1}$) in *Acrosphaera spinosa* as a function of colony size (cell number x 10^{-2}). Dark control rates are shown (▲) in a, b, c from ATLANTIS II 101 and killed rates (■) in d from OCEANUS 30.

a) $I = 1 \times 10^3$ μW·cm^{-2}. Incorporation (nmoles $CO_2 \cdot hr^{-1}$) = $[2.2 \times 10^{-3}] \cdot$ (cell no.) + .86. r = .90.

b) $I = 4.2 \times 10^3$ μW·cm^{-2}. Incorporation (nmoles $CO_2 \cdot hr^{-1}$) = $[7.9 \times 10^{-3}] \cdot$ (cell no.) + 1.0. r = .83.

c) $I = 14 \times 10^3$ μW·cm^{-2}. Incorporation (nmoles $CO_2 \cdot hr^{-1}$) = $[9.1 \times 10^{-3}] \cdot$ (cell no.) + 1.9. r = .82.

c) $I = 44 \times 10^3$ μW·cm^{-2}. Incorporation (nmoles $CO_2 \cdot hr^{-1}$) = $[6.9 \times 10^{-3}] \cdot$ (cell no.) + 3.9. r = .53.
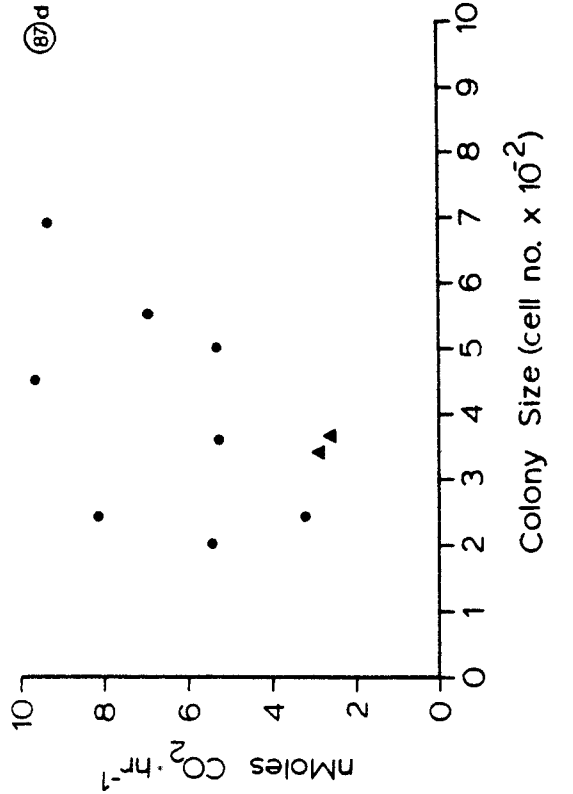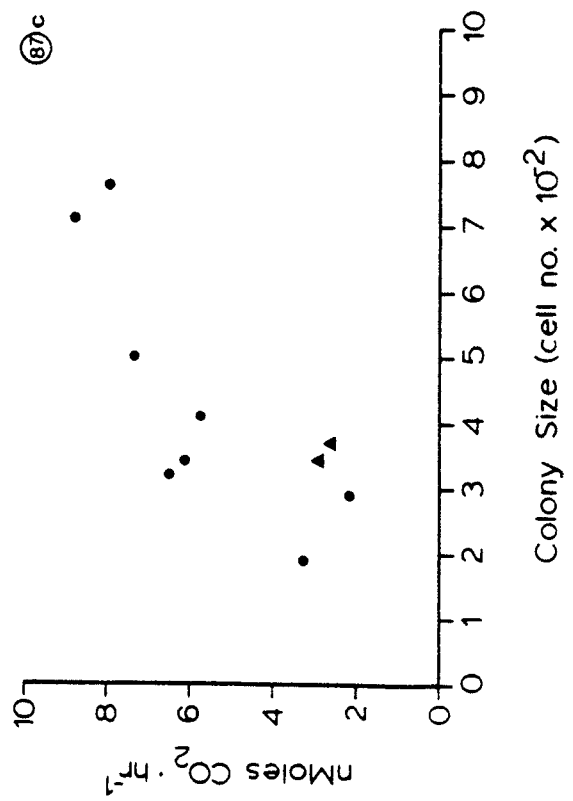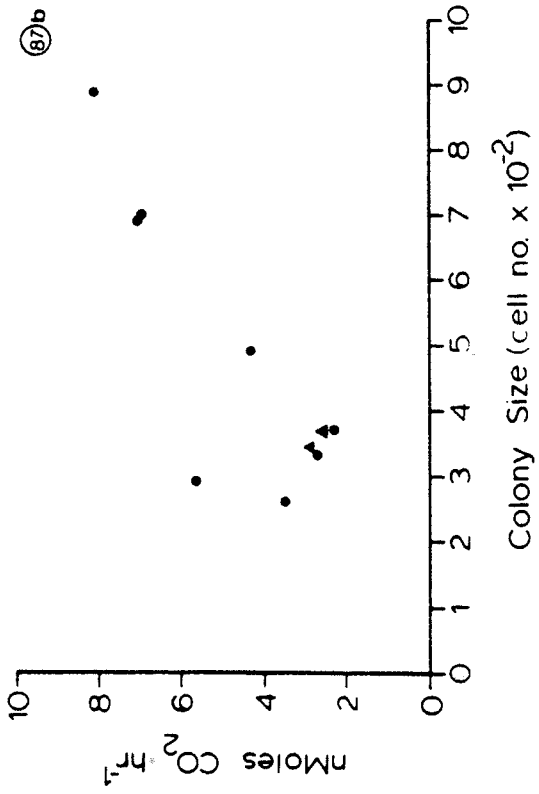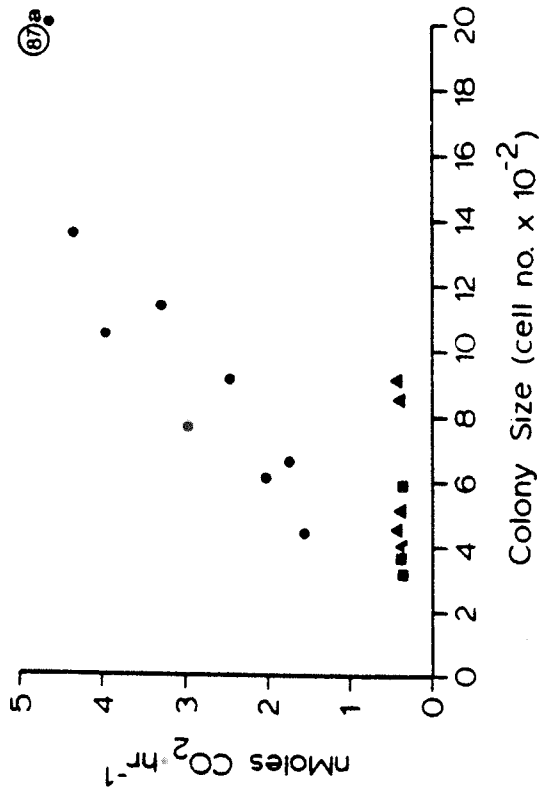
TABLE IV. $^{14}CO_2$ uptake experiments on *Acrosphaera spinosa* under various lighting conditions. Uptake values are net incorporations, dark values are those from OCEANUS 30 and are very similar to the dark incorporations from ATLANTIS II 101. Artificial light experiments are denoted with an asterisk (*).

Incident light intensity $\mu W/cm^2$ x 10^{-3}	Number of screens	Screened intensity $\mu W/cm^2$ x 10^{-3}	Incorporation pmoles/cell/hr; $\bar{x}$, s, n
44	0	44	18.2, 8.2, 8
32	1	19	20.9, -, 2
44	2	14	14.3, 4.3, 9
33	4	4.2	10.4, 3.9, 9
1*	-	1.0	3.16, .57, 9
0	dark	0	0.77, .23, 13

Figure 88. Net incorporation rates of CO_2 per unit length of colony (nmoles $CO_2 \cdot mm^{-1} \cdot hr^{-1}$) in *Collozoum longiforme* as a function of light intensity. I ($uW \cdot cm^{-2}$ x 10^{-3}) of incubation. Error bars shown are 95% confidence limits for the mean. Data from OCEANUS 52.
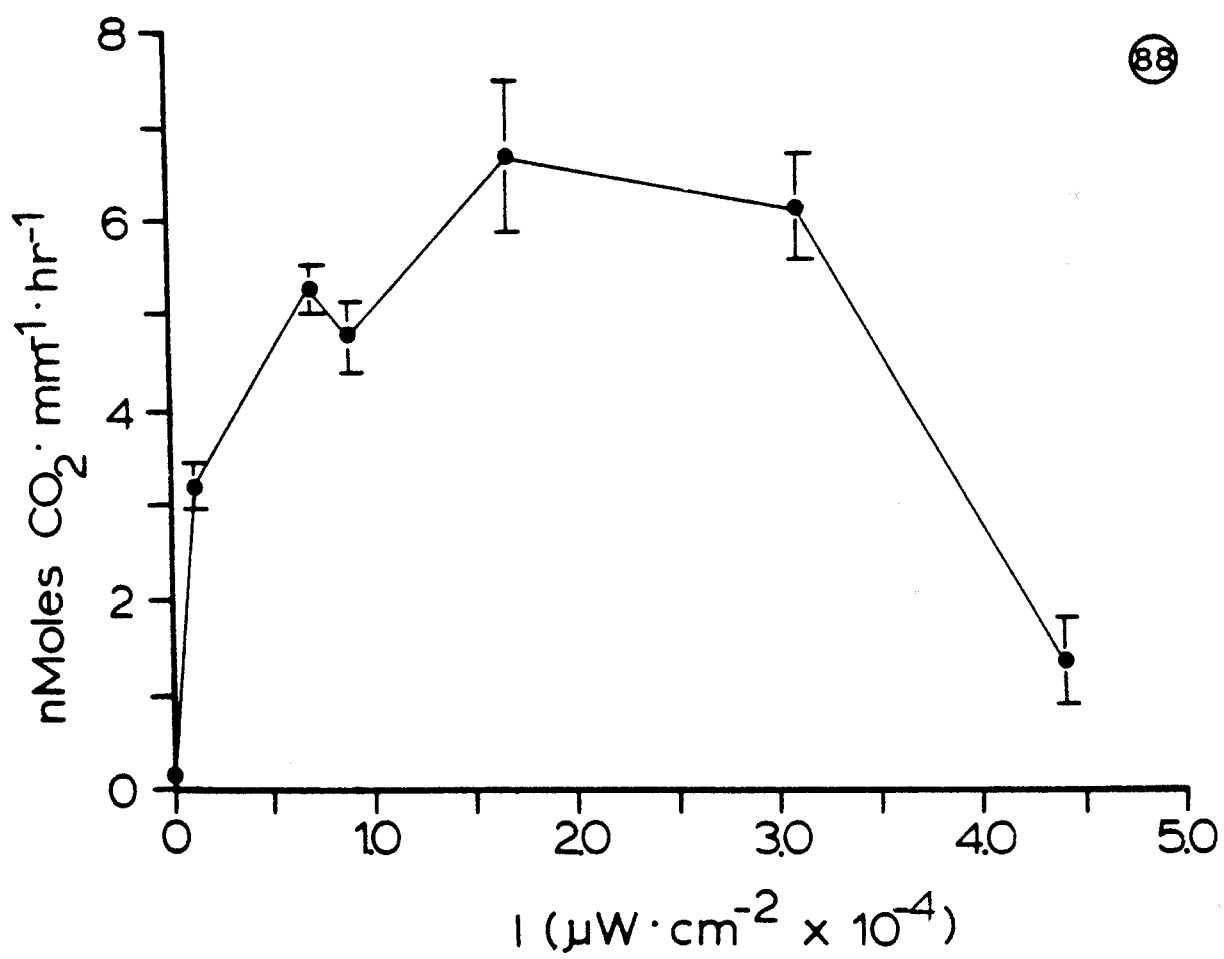
TABLE V. Summarized data from the experiments on the incorporation of labelled carbon. Range of mean values are given for light intensities above 10% sunlight.

Species	Incorporation (pmoles CO_2/central capsule/hr)	Carbon content (ng C)	Chlorophyll content (pg Chlorophyll a/ radiolarian cell)	Typical colony size (cell No.)
Collozoum inerme	3.3*	50	9.7	2500
C. radiosum	51,76	200	60	350
Acrosphaera spinosa	10-21	100	10-50	300
C. longiforme	18-53	85	25	65,000

*Low light level

DISCUSSION

The data I have presented here are not measurements of productivity. Since I considered it likely that the physiology of the symbiont would be altered when out of the host (Smith et al., 1969; Trench, 1971b) I measured the carbon incorporation of the intact radiolarian-algal system. There are some complications associated with this approach. Carbon-14 measurements of photosynthetic activity in algal systems may not really measure gross or net photosynthesis because of loss of label due to respiration in the light and due to "leaking" of soluble products. This situation could be exacerbated when dealing with a symbiotic system because of host respiration of algal photosynthate. In an intracellular symbiosis the situation is much more complex than in free-living algae (Conover and Francis, 1973). The turnover of carbon between host and symbiont cannot be measured from outside the colony. However, the soluble products are probably not as readily lost in a symbiotic system because of the proximity of the host metabolic machinery. If this is so then ^{14}C uptake may approximate net photosynthesis over a short term experiment. Net photosynthesis could be seriously underestimated if the respiration of the host were high (fixed products respired as CO_2). Anderson's (1978) experiments with hand-separated ^{14}C incubated cells show that significant translocation occurs after 1.5 hours incubation of *Collosphaera globularis*. This suggests that unless host respiration rates are low, one measures at best a minimum net value of photosynthesis.

Keeping this caveat in mind, one can still calculate the values of P(mg C or mmoles $CO_2 \cdot$mg Chl $a^{-1} \cdot hr^{-1}$) from the data on ^{14}C incorporation

and chlorophyll content of the four species of radiolarians studied (Table V). For *A. spinosa* and *C. longiforme*, I will present P as a function of light intensity, I ($\mu W \cdot cm^{-2}$).

Using 3.3 pmoles $CO_2 \cdot$central capsule$^{-1} \cdot hr^{-1}$ and 9.7 pg Chl. $a \cdot$ central capsule^{-1} in *C. inerme*, the value of P was .34 mmoles $CO_2 \cdot$mg Chl. $a^{-1} \cdot hr^{-1}$ at low light level. For *C. radiosum* the mean of 60 pg Chl. $a \cdot$central capsule^{-1} and the values of 51 and 76 pmoles $CO_2 \cdot$central capsule$^{-1} \cdot hr^{-1}$ give .85 and 1.3 mmoles $CO_2 \cdot$mg Chl. $a \cdot hr^{-1}$, respectively.

In *Acrosphaera spinosa* I found that chlorophyll/central capsule decreased with increasing colony size. This imposed a relationship between P and increasing size of colonies. Hence P as a function of central capsule number in a colony showed an increase (Figure 89a-d) in all but the full sunlight experiment. It was not possible to take chlorophyll a data and ^{14}C incorporation data on the same individual colony, so these curves were based on a regression for chlorophyll (Figure 82). If the assimilation rate does change with colony size then P is a poor measure of photosynthetic rate: it would be meaningless to plot P as a function of I (intensity) without first removing the variable of colony size. Each experiment would be biased by the size distribution of the colonies used. Incorporation per central capsule was independent of colony size. Accordingly the photosynthetic rate was normalized to central capsule density in units of pmoles $CO_2 \cdot$(central capsule)$^{-1} hr^{-1}$ as a function of light intensity. A plot of this in Figure 90 shows a typical P-I curve form with the exception that there was no clear photoinhibition as commonly seen in such curves. Unfortunately the errors were so large, especially at higher light intensities that very little can be said about the

Figure 89. Photosynthetic assimilation, P (mmoles $CO_2 \cdot mg$ Chl $a^{-1} \cdot hr^{-1}$) as a function of colony size (radiolarian cell number x 10^{-2}) in *Acrosphaera spinosa*. Data from ATLANTIS II 101.

a) 1 x 10^3 uW·cm^{-2}. P = 7.6 x 10^{-5} (cell no.) + .18. r = .42.

b) 4.2 x 10^3 uW·cm^{-2}. P = 7.8 x 10^{-4} (cell no.) + .11. r = .77.

c) 14 x 10^3 uW·cm^{-2}. P = 6.2 x 10^{-4} (cell no.) + .31. r = .69.

d) 19 x 10^3 uW·cm^{-2} ■

44 x 10^3 uW·cm^{-2}. P - 1.1 x 10^{-4} (cell no.) + .73. r = .1.
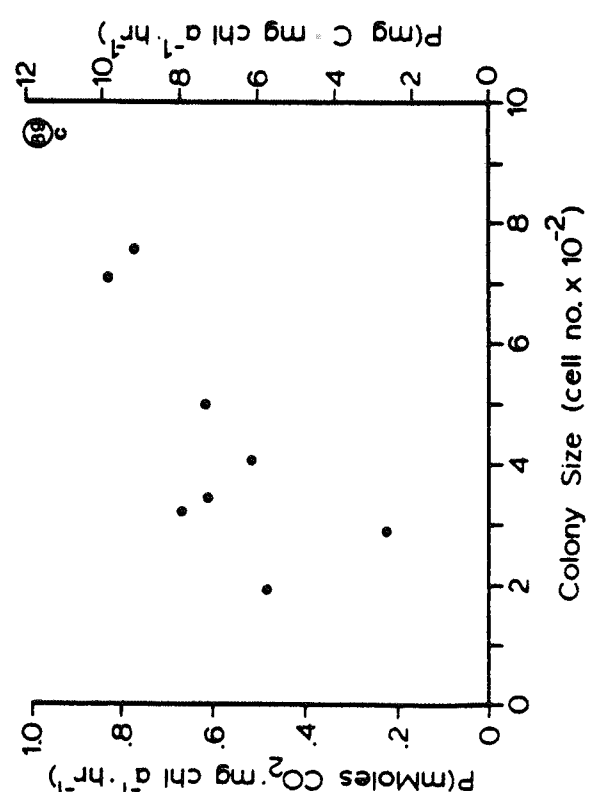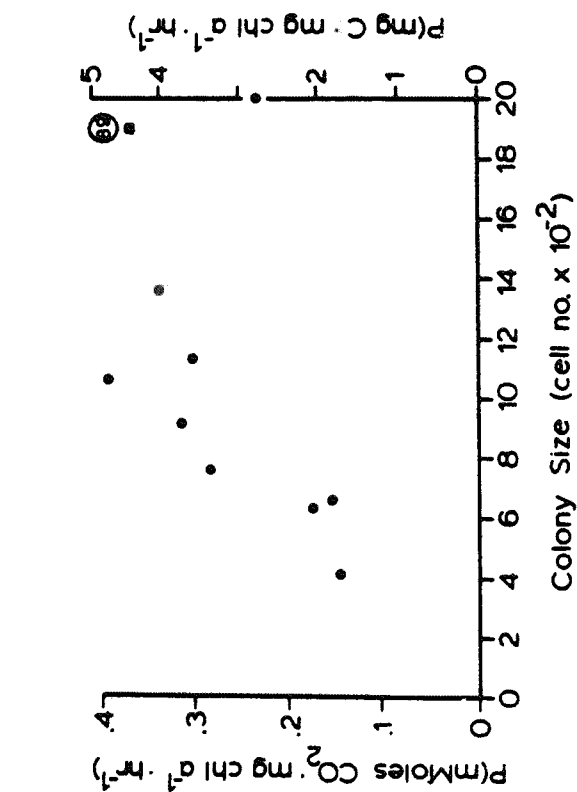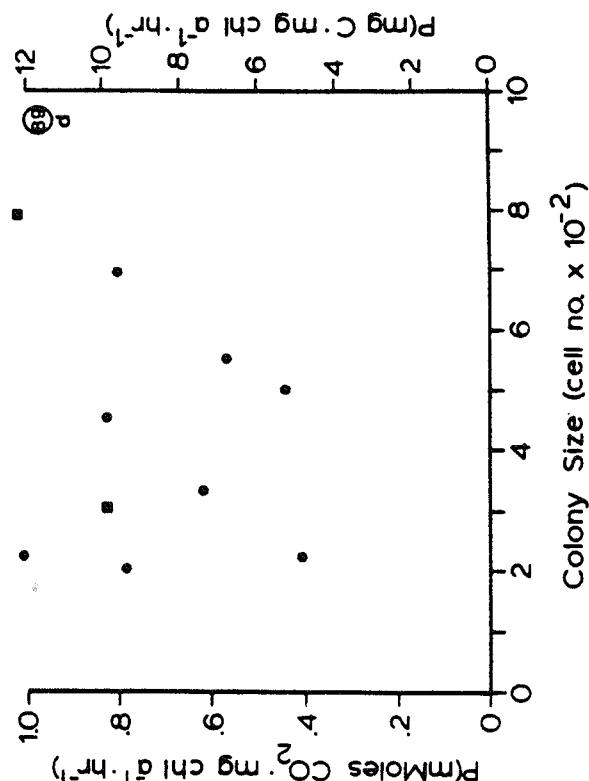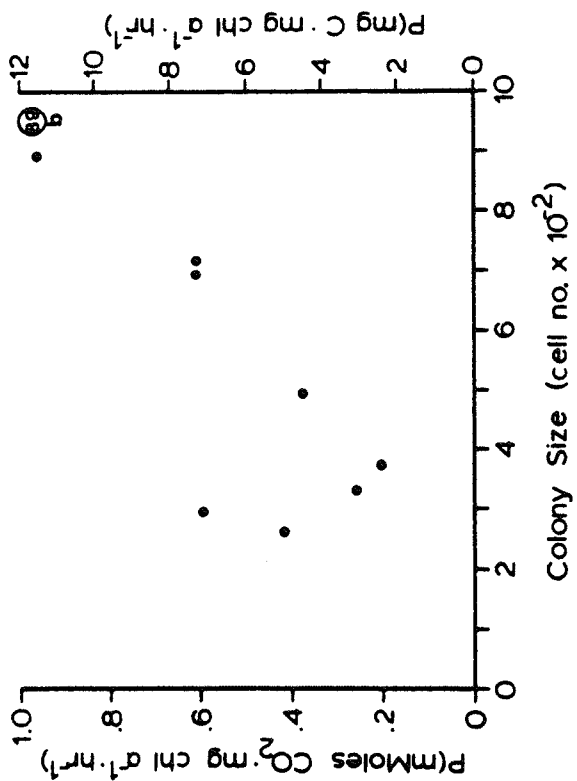
curve except that even in the extreme situation photosynthetic inhibition appears to be only about 50%.

In *Collozoum longiforme* the data of Figure 88 appear to fit a typical P-I curve as in Figure 90. However, if the true assimilation curve normalized to chlorophyll is constructed (Figure 91), there is no trend. With *A. spinosa* it was easy to run replicate colonies at fixed light intensity, so each experiment represented a cross-section of age distribution for the colonies. The experiments on *C. longiforme* were each done with replicates within a single large colony. Some factor other than light intensity may have affected P as did colony size (age?) in *A. spinosa*. I looked at the possible effects of previous feeding history on assimilation. Tintinnids were the most frequently found prey organisms in colonies of *C. longiforme* (Appendix II, Table 3). A positive relationship was observed between the abundance of tintinnid loricae in the colonies and the assimilation rate (Figure 92). I do not know the time span involved in the accumulation of this material. If this is the total capture of tintinnids for the lifespan of the colony, then it either represents cumulative predatory success or simply age. Alternatively, it could be recent prey capture; some species eject their prey remains (p. 31). It appears that nutritional history overrides the effects of high light intensities on the photosynthetic assimilation rate. Size of *A. spinosa* may also coincide with predatory success. In both examples the increase in P was caused by a decrease in chlorophyll *a* rather than a decrease in ^{14}C incorporation. Other than this the results were as one might predict; larger colonies fixed more CO_2 than did smaller ones and the values for P, although supposedly minima, were high. The maximum

Figure 90. Net photosynthetic incorporation, P (pmoles CO_2·radiolarian cell^{-1}·hr^{-1}) in *Acrosphaera spinosa* as a function of the light intensity. I (uW·cm^{-2} x 10^{-4}) of incubation. Error bars are the 95% confidence limits for the mean. Data from ATLANTIS II 101.

Figure 91. Net photosynthetic assimilation. P (mmoles CO_2·mg Chl a^{-1}· hr^{-1}) in *Collozoum longiforme* as a function of light intensity. I (uW· cm^{-2} x 10^{-4}) of incubation. Error bars are 95% confidence limits for the mean. Data are from OCEANUS 52.

Figure 92. Net photosynthetic assimilation. P (mmoles CO_2·mg Chl a^{-1}· hr^{-1}) in *Collozoum longiforme* as a function of the abundance of prey tintinnids (cells·mm^{-1}) in the colonies of the incubations in Figure 18.
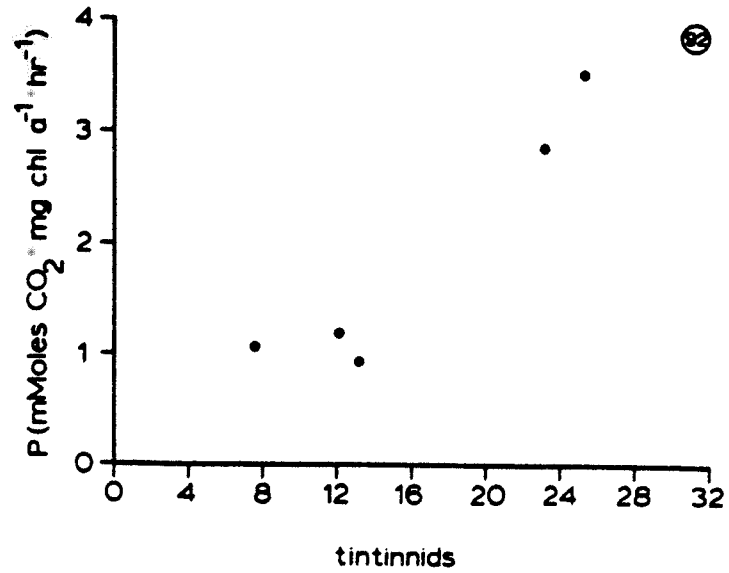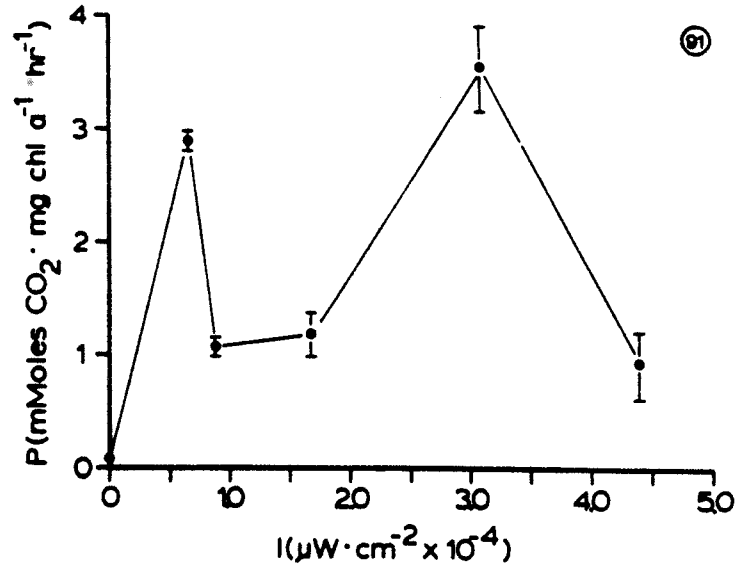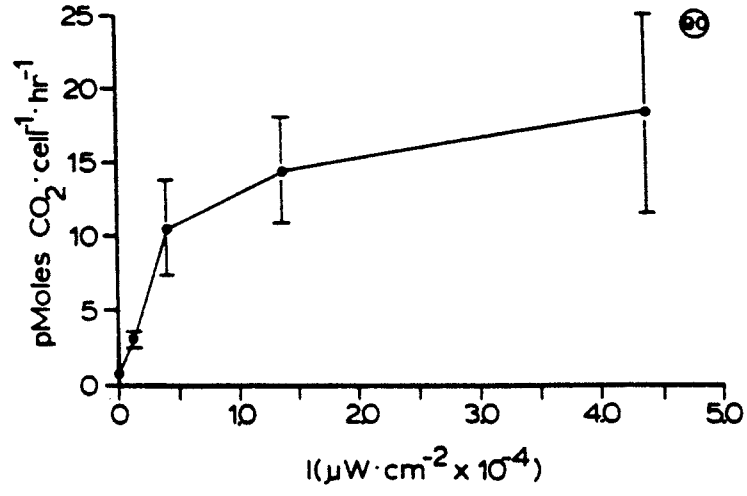
values obtained for P were 3.5 mmoles $CO_2 \cdot$mg Chl. $a^{-1} \cdot hr^{-1}$ for *C. longiforme* and 1.0 mmoles $CO_2 \cdot$mg Chl. $a^{-1} \cdot hr^{-1}$ for *A. spinosa*.

The value of the assimilation number, P, varies tremendously between species and under different environmental conditions. In general it increases with increasing light until saturation is achieved (Ryther, 1956) and levels off or decreases with higher light intensities. The maximum photosynthetic rate in this curve, P_{max}, is influenced by temperature (Aruga, 1965; Platt and Jassby, 1976), culture light conditions (Yentsch and Lee, 1966) and nutrient conditions (Ichimura and Aruga, 1964; Ichimura et al., 1962; Yentsch and Lee, 1966; Ichimura, 1967). The consensus is that P_{max} is determined by the dark reactions of photosynthesis (Yentsch and Lee, 1966; Parsons and Takahashi, 1973) and thus limited by substrate removal and enzyme titer and kinetics. Typical values range from less than 1.0 mg C$\cdot$mg Chl. $a^{-1} \cdot hr^{-1}$ for populations under Antarctic ice (Bunt, 1964) to 20 mg C$\cdot$mg Chl. $a^{-1} \cdot hr^{-1}$ for diatoms in warm eutrophic ponds (Ichimura and Aruga, 1964). The values obtained for the dinoflagellates of radiolarian colonies ranged from 1 to 3.6 mmoles $CO_2 \cdot$mg Chl. $a^{-1} \cdot hr^{-1}$ (12-43 mg C); up to roughly twice the highest reported values for free-living algae.

If nutrients do cause an increase in P_{max} then there would be every reason to expect a high value in a symbiotic system. McLaughlin and Zahl (1966) reported unpublished results of theirs showing a two-fold increase in ^{14}C uptake in *Gymnodinium* (= *Symbiodinium*) *microadriaticum* with the addition of uric acid to the medium. The effect was not seen in other free-living flagellate cultures. It is known that the nutrient requirements of the symbionts in culture are vigorous (McLaughlin and Zahl, 1957, 1966).

Lee and Zucker (1969) showed a higher photosynthetic rate in fed *Archais* (a symbiont-bearing foraminiferan) than in starved ones. It may be that symbiosis can produce a nearly optimal environment for photosynthesis, both by supplying nutrients and by removing products. I compared these data for assimilation with Eppley's (1972, Figure 9) family of curves for maximum expected photosynthetic rate. Although I do not have the appropriate measurements of C:Chl on the algae, all the points fall on or between the lowest and highest curves at 20° and 27°C.

None of the experiments were designed to test a relationship between P and prey consumption. The increase of P with size in *A. spinosa* was discovered fairly early, but it was not until experiments were done with *C. longiforme* that the relationship with prey consumption could be extracted. For the *Acrosphaera* experiments there is a cross section of colony sizes for each experiment, but no information on algal and prey densities. That information is known for the *C. longiforme* experiments, but each colony was incubated at only one light intensity, so the effect of prey history cannot be separated from that of light intensity.

More experiments should be done with fed and starved colonies in different lighting conditions. Should the relationship between P and prey history be supported by further experimentation, it suggests that either nutrients are limiting or there is a feedback between the algal photosynthetic apparatus (chlorophyll level, enzyme titer) and the host nutrient condition. A study of the time response of P to feeding the host would distinguish between these two possibilities. Such a relationship underscores the importance of predation to the colony. It is not possible to evaluate the role of the algal photosynthesis in the nutrition of the

radiolarians without information on their respiration and growth rates.
However, one can calculate that the photosynthetic rates in Table V repre-
sent only 0.1 to 0.8% of the colony carbon per hour. Even though trans-
location of algal products may be as much as 60% of total photosynthesis
in dinoflagellate-invertebrate systems (Trench, 1979), it seems unlikely
that this could fulfill a significant portion of the radiolarians' nutri-
ent requirements relative to predation. A single adult copepod may have
10-100 µg carbon content (Marshall and Orr, 1955; Parsons et al., 1969).
Figures 75-77 showed that colonies of *C. inerme*, *C. radiosum* and *A. spinosa*
had a total carbon content of 100-200 µg. Thus the capture of 1 or 2
large copepods may equal hundreds of hours of algal photosynthesis for
the radiolarians.

Low $^{14}CO_2$ incorporation and translocation to the radiolarians, how-
ever, does not necessarily mean that the radiolarians do not benefit from
the presence of the algae. In an oligotrophic environment with scarce
prey, a low but reliable "income" of energy may be valuable to the host,
especially if it has a low subsistence metabolic rate, characteristic of
passive predators. Low-level algal photosynthesis may supplement the
radiolarians' opportunistic predation.

The symbionts might also secrete substances protective to the colonies.
This has been shown with the zooxanthellae of a number of gorgonians
(Ciereszko et al., 1960, 1962) which secrete terpenoid substances. These
substances are toxic to potential predators such as the parrot fish
(Ciereszko et al., 1962) but not to the snail *Cyphoma gibbosa*, one of the
few predators of the gorgonians. Such an hypothesis may apply to the
radiolarians. If so it might explain why there are apparently so few

predators and why most of the amphipods are in just one genus, *Hyperietta*.
It is easy to see why such a strategem might be important for the radio-
larians which otherwise would be very vulnerable to predation as highly
visible, non-motile, floating food particles in the transparent environ-
ment of the central gyres.

SIGNIFICANCE

I have shown that radiolarians are among the most common and abun-
dant macrozooplankton; they form some of the largest planktonic entities
in the ocean. Their trophic position as planktivores harboring symbionts
is similar to that of corals and foraminifera.

Despite their abundance, radiolarians are not particularly important
as primary producers. The data of Table II showed that the abundance of
radiolarians was between .04 and 540 colonies per m^3. The greatest pro-
portion of these was between 0.1 and 1.0 ($\bar{x}$ = 0.4) colonies per m^3. At
such densities they contribute an insignificant amount to the total pro-
ductivity of the area. Table VI shows the estimated "productivity" by
radiolarian algae for a 30 m water column (> 10% light). The highest
value shown is 2 $\mu gC \cdot m^{-2} \cdot hr^{-1}$ ($\sim$ 24 μg $C \cdot m^{-2} \cdot day^{-1}$). In tropical waters
primary productivity is typically about 50 $gC \cdot m^{-2} \cdot yr^{-1}$ ($\sim$ 140 mg $C \cdot m^{-2} \cdot day^{-1}$;
Ryther, 1956). I have no estimate of the radiolarians' secondary produc-
tivity.

Althouth the productivity may be miniscule, it is packaged in such
a way that it is available to a unique portion of the food web. When one
considers the associations other organisms have with the radiolarians the
analogy with corals is strengthened. The harpacticoid copepods *Miracia*
efferata and *Sapphirina* sp. and the turbellarians rest or prey on the

colonies, and amphipods of the genus *Hyperietta* are associated with them for much of their life cycle. Some of these associates practically live a benthonic existence on the colonies. In this way the radiolarians, like the corals, provide structure to their environment. This and the fact that they are large and ubiquitous and demonstrate behavior complex for a protozoan, make the colonial radiolarians significant components of the oceanic plankton.

More research should be done on this group. The relationship between feeding by the radiolarians and photosynthesis by the algae should be further studied and the extent of influence on photosynthesis by the host evaluated. The mechanism of buoyancy and its regulation in response to environmental stimuli should be investigated. The respiration and growth rate of the radiolarians should be measured and used to calculate the role of algal photosynthesis in their nutrition. The possibility of chemical defense substances being secreted by the algae should be investigated since there seem to be few predators of colonies.

Almost nothing is known of radiolarian life cycles or the mechanism of the inoculation of the symbionts into the colony. These may be studied and the inconsistencies in the systematics of the radiolarians should be resolved. Colonial radiolarians are primarily surface organisms, although their maximum depth distribution is not known. There are deep-living radiolarians (Tuscaroridae) whichproduce equally complex aggregate structures. Their source of nutrition is completely unknown. There are no reported deep-living shell-less forms. If the results of this *in situ* study are any indication of what lies deeper, then there may be some major surprises from the radiolarians in mesopelagic ecology.

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APPENDIX I

List of stations made during the period 1975 to 1979. Columns are, in order left to right, latitude, longitude, presence or absence of radiolarians, relative abundance, and station number. Latitude and longitude are in degrees and hundredths of a degree. Latitudes north of 0° and longitudes east of 0° are positive. In column 3 a "1" indicates that no radiolarians were seen or collected. See page 11 for explanation of relative abundances.

34.27	-10.78	1	0	355
32.68	-13.38	1	0	356
30.56	-17.95	∩	100	357
30.33	-18.50	1	0	358
29.48	-21.70	∩	100	359
29.48	-22.45	1	0	360
29.50	-26.07	∩	100	361
29.55	-26.52	∩	100	362
29.47	-30.22	∩	10	363
29.47	-30.22	∩	10	364
29.43	-30.62	1	0	365
29.47	-34.33	∩	100	366
29.52	-34.88	∩	100	367
29.50	-38.43	∩	10	368
29.55	-39.00	∩	1000	369
29.48	-42.05	∩	1	370
29.52	-42.78	∩	1000	371
29.50	-46.37	∩	100	372
29.52	-46.83	∩	1	373
29.47	-51.42	∩	1	374
29.50	-54.50	∩	1	375
29.45	-55.07	∩	100	376
29.50	-58.45	∩	100	377
29.50	-58.98	1	0	378
29.48	-59.15	∩	100	379
30.63	-61.82	∩	10	380
31.02	-62.48	∩	100	381
34.25	-66.35	∩	10	382
34.27	-66.40	1	0	383
34.25	-66.40	∩	100	384
33.90	-65.90	∩	100	385
37.32	-68.33	1	0	386
37.30	-68.43	1	0	387
38.78	-70.18	1	0	388
38.70	-70.20	∩	10	389
39.38	-70.53	1	0	390
39.67	-70.62	1	0	391
39.67	-70.62	∩	10	392
39.32	-70.25	1	0	393
38.43	-69.95	1	0	394
38.42	-69.97	∩	10	395
38.47	-70.00	∩	1	396
37.12	-68.92	∩	1	397
35.35	-68.30	∩	100	398
35.27	-69.97	∩	100	399
34.52	-69.90	∩	100	400
34.53	-69.85	∩	10	401
34.47	-69.95	∩	100	402
34.50	-69.90	∩	100	403
34.15	-71.55	∩	100	404
34.18	-71.63	∩	100	405
34.15	-71.62	∩	10	406
34.13	-71.63	∩	100	407
34.93	-71.22	1	0	408
37.37	-70.18	1	0	409
38.00	-70.05	1	0	410
38.17	-70.08	1	0	411

38.33	-70.08	∩	1	412
39.08	-70.10	1	0	413
39.18	-70.18	1	0	414
39.77	-70.65	1	0	415
35.53	-70.97	∩	10	417
32.75	-71.18	∩	10	418
32.72	-71.15	∩	1	419
33.65	-71.05	∩	1000	420
33.22	-72.28	∩	1	421
33.92	-71.77	∩	1	422
33.82	-71.90	∩	100	423
33.92	-71.98	∩	10	424
34.02	-71.88	∩	100	425
35.45	-71.57	∩	100	426
38.12	-67.17	∩	10	427
38.92	-67.73	1	0	428
38.92	-67.77	1	0	429
38.92	-67.97	∩	1	430
39.43	-67.28	1	0	431
21.83	-76.67	∩	10	432
20.37	-72.02	∩	10	433
19.07	-68.32	∩	10	434
18.80	-67.63	1	0	435
21.00	-64.00	∩	10	436
21.00	-64.00	∩	10	437
21.00	-64.00	∩	1	438
21.00	-64.00	∩	10	439
21.00	-64.00	∩	10	440
21.00	-64.00	∩	10	441
21.00	-64.00	∩	10	442
21.00	-64.00	∩	10	443
20.55	-63.70	∩	10	444
17.03	-63.63	∩	10	445
16.38	-63.67	∩	10	446
14.50	-64.00	∩	1	447
14.50	-64.00	1	0	448
14.50	-64.00	∩	1	449
14.50	-64.00	1	0	450
14.50	-64.00	∩	1	451
14.50	-64.00	∩	1	452
14.50	-64.00	∩	1	453
14.50	-64.00	1	0	454
-2.48	55.48	∩	1	455
-2.00	55.50	1	0	456
-3.00	55.50	∩	1	457
-3.00	55.50	∩	1	458
-1.50	55.50	∩	1	459
-1.00	55.50	∩	1	460
.50	55.50	∩	1	461
2.00	55.50	∩	1	462
1.00	55.63	∩	100	463
.18	55.50	∩	1	464
.17	55.50	∩	1	465
-3.00	55.83	∩	100	466
-2.50	55.50	∩	100	467
-1.00	55.50	∩	10	468
.50	55.50	∩	1000	469
2.05	55.50	∩	100	470
1.25	55.50	∩	1000	471
-3.00	55.50	∩	1000	472

-1.50	55.50	∩	10	473
-3.00	55.50	∩	100	474
-2.50	55.50	∩	1000	475
-1.50	55.50	∩	10	476
-1.00	55.50	∩	10	477
.50	55.50	∩	1000	478
2.00	55.50	∩	10	479
1.50	55.50	∩	10	480
.00	55.50	∩	100	481
-.50	55.50	∩	1	482
-2.00	55.50	∩	1	483
38.05	-69.48	1	0	484
38.33	-69.67	1	0	485
38.10	-69.67	1	0	486
40.73	-70.77	1	0	487
38.30	-69.63	1	0	488
37.92	-69.75	1	0	489
37.90	-69.73	∩	1	490
38.05	-69.48	1	0	491
38.05	-69.48	1	0	492
33.02	-77.70	1	0	493
32.97	-77.40	1	0	494
32.97	-77.40	1	0	495
38.83	-72.52	∩	10	496
38.00	-72.08	∩	10	497
38.95	-72.40	∩	1	498
39.05	-72.38	∩	10	499
38.93	-72.48	∩	1	500
39.08	-72.33	∩	10	501
39.00	-72.27	∩	10	502
39.15	-72.25	∩	10	503
37.00	-65.00	∩	100	504
37.00	-65.00	∩	100	505
37.00	-65.00	∩	100	506
37.00	-65.00	∩	10	507
37.00	-65.00	∩	10	508
38.65	-66.35	1	0	509
38.62	-66.50	1	0	510
38.37	-66.43	1	0	511
38.58	-66.47	1	0	512
39.15	-72.18	∩	1	513
39.13	-72.63	∩	1	514
39.08	-72.47	∩	1	515
38.47	-72.02	∩	1	516
39.17	-72.38	∩	10	517
38.95	-72.40	∩	1	518
39.12	-72.23	∩	1000	519
38.83	-72.45	∩	100	520
38.92	-71.98	∩	10	521
39.07	-72.00	∩	10	522
39.25	-72.00	∩	10	523
38.93	-72.37	∩	1	524
38.97	-72.38	∩	1	525
38.95	-73.52	∩	1	526
38.95	-72.42	∩	10	527
38.78	-71.78	∩	1	528
38.73	-71.46	∩	1	529
38.43	-72.12	∩	1	530
37.92	-71.43	∩	10	531
39.15	-72.42	1	0	532

38.87	-72.32	∩	1	533
11.92	-56.27	∩	1	534
11.92	-57.27	∩	1	535
10.25	-54.55	∩	1	536
10.30	-54.63	∩	10	537
9.00	-52.17	'	0	538
7.08	-49.65	∩	10	539
5.35	-46.33	∩	1	540
5.17	-46.12	∩	1	541
3.68	-43.48	∩	1	542
3.55	-43.30	∩	1	543
2.35	-41.63	∩	1	544
2.22	-41.42	∩	1	545
.98	-39.47	∩	10	546
.92	-39.33	∩	10	547
.18	-37.73	∩	10	548
.00	-37.63	∩	10	549
-.53	-36.50	∩	1	550
1.37	-34.37	∩	10	551
1.53	-34.17	∩	10	552
3.50	-32.03	∩	1	553
3.60	-31.92	'	0	554
4.28	-30.80	∩	1	555
4.53	-31.17	∩	1	556
5.27	-33.83	∩	100	557
5.95	-36.07	∩	10	558
6.07	-36.45	∩	1	559
6.70	-38.42	∩	10	560
6.78	-38.70	∩	1	561
7.33	-40.67	∩	1	562
7.50	-41.30	∩	10	563
8.32	-43.85	∩	10	564
9.05	-45.93	∩	10	565
9.70	-48.23	∩	1	566
9.83	-48.82	∩	10	567
10.52	-51.23	∩	10	568
10.52	-51.23	∩	10	569
11.07	-53.37	∩	1	570
11.07	-53.53	∩	100	571
11.67	-54.77	∩	1	572
11.77	-55.30	∩	10	573
12.60	-58.15	∩	10	574
12.78	-58.88	∩	10	575
37.63	-64.80	∩	10	577
34.62	-60.08	∩	100	578
31.65	-55.25	∩	1000	579
31.58	-55.33	∩	1000	580
31.58	-55.58	∩	1000	581
36.18	-62.45	∩	100	582
36.73	-63.43	∩	100	583
38.75	-66.55	∩	1	584
36.93	-66.75	∩	100	585
38.98	-68.50	∩	10	586
39.00	-68.43	∩	10	587
37.77	-67.48	∩	10	588
37.32	-69.37	∩	100	589
37.30	-69.50	∩	100	590
36.78	-68.95	∩	10	591
37.13	-66.75	∩	100	592
37.13	-66.63	∩	1000	593

36.55	-66.37	n	100	594
36.58	-66.37	n	100	595
36.71	-66.37	n	100	596
37.05	-67.67	n	1	597
37.25	-67.38	n	10	598
38.13	-66.93	n	1	599
38.45	-66.77	n	1	600
39.77	-68.57	n	1	601
32.60	-120.25	1	0	602
32.60	-120.48	1	0	603
32.56	-120.46	n	1	604
32.55	-120.48	n	1	605
32.57	-123.89	n	10	606
32.54	-123.88	n	100	607
16.52	-63.42	n	1	608
14.30	-60.83	n	10	609
13.50	-54.00	n	1	610
13.50	-54.00	n	10	611
13.78	-54.42	n	10	612
15.33	-55.18	n	10	613
18.92	-57.07	n	10	614
22.33	-58.97	n	10	615
25.82	-59.87	n	100	616
29.20	-60.58	n	100	617
40.00	-67.45	n	1	618
40.02	-67.38	n	1	621
40.10	-61.82	n	100	624
40.07	-54.47	n	100	628
40.08	-54.52	n	100	631
39.97	-52.12	n	10	634
40.05	-52.20	n	10	637
39.87	-49.22	1	0	639
40.62	-48.40	n	10	640
40.83	-48.15	n	100	643
41.70	-46.07	n	10	646
44.10	-41.77	n	10	647
44.13	-41.72	n	10	649
44.17	-41.77	n	10	650
42.95	-36.92	n	1000	652
42.50	-36.27	n	100	658
42.50	-36.27	n	100	659
42.25	-35.92	n	100	661
42.17	-35.38	n	100	664
42.20	-35.43	n	100	667
40.23	-33.00	n	100	669
40.20	-33.00	n	100	672
39.00	-31.47	n	100	675
38.97	-31.43	1	0	678
38.97	-31.13	n	100	679
38.87	-29.07	n	1000	680
38.28	-27.73	n	1000	682
36.97	-27.25	n	100	684
36.93	-27.30	n	10	687
35.78	-26.10	n	100	689
36.08	-25.72	n	100	691
37.15	-24.40	n	100	694
37.18	-24.45	n	1000	697
38.35	-22.97	n	1000	698
38.40	-23.00	n	100	701
39.42	-21.43	n	100	703

39.90	-20.92	∩	1000	705
44.02	-19.40	∩	100	707
41.25	-19.15	∩	10	709
42.60	-17.35	∩	1	711
42.88	-17.03	∩	10	713
43.57	-19.27	∩	100	715
43.77	-18.98	∩	100	717
45.02	-16.60	∩	10	719
45.23	-16.23	∩	10	721
46.78	-13.37	∩	10	723
47.08	-12.78	∩	10	725
40.70	14.05	∩	10	727
40.67	13.98	∩	10	728
40.50	14.75	∩	10	729
35.75	-14.10	∩	10	731
35.22	-14.93	∩	10	732
33.25	-16.73	∩	10	733
32.15	-16.47	∩	100	734
29.88	-15.05	∩	100	735
29.50	-14.80	∩	10	736
28.58	-17.22	∩	10	737
27.73	-16.78	∩	10	738
26.55	-17.22	∩	10	739
26.28	-19.93	∩	100	740
24.40	-18.00	∩	10	741
23.78	-17.40	∩	1	742
22.00	-18.00	∩	1	743
21.22	-18.03	∩	1	744
19.30	-17.98	∩	1	745
18.47	-18.08	∩	1	746
16.47	-18.15	∩	10	747
15.50	-18.18	∩	1	748
13.88	-18.30	∩	1	749
12.52	-19.17	∩	1	750
11.88	-20.73	∩	10	751
10.00	-22.50	∩	1	752
9.47	-22.05	∩	1	753
8.00	-20.70	∩	10	754
7.32	-20.13	∩	1	755
5.38	-18.33	∩	1	756
5.00	-18.02	∩	1	757
2.65	-17.40	∩	1	758
2.58	-18.15	∩	1	759
2.25	-20.92	∩	10	760
2.08	-21.68	∩	10	761
1.72	-24.92	∩	10	762
1.53	-25.78	∩	1	763
.97	-29.00	∩	1	764
.92	-29.35	∩	1	765
.50	-30.98	∩	10	766
.00	-31.02	∩	1	767
-1.63	-29.77	∩	1	768
-2.36	-29.27	∩	100	769
-3.53	-29.32	∩	10	770
-4.05	-29.10	∩	10	771
-5.62	-31.13	∩	10	772
-6.13	-31.77	∩	10	773
-7.65	-34.23	∩	10	774
38.08	-71.80	∩	100	775
37.85	-72.82	∩	100	776

36.87	-72.75	⌒	10	777
34.53	-72.12	⌒	100	778
33.59	-72.03	⌒	100	779
31.78	-71.78	⌒	10	780
31.75	-71.82	⌒	100	781
31.53	-72.68	⌒	100	782
31.52	-74.31	⌒	10	783
31.58	-74.47	⌒	100	784
31.60	-74.28	⌒	100	785
30.63	-75.03	⌒	10	786
31.12	-78.05	⌒	10	787
31.60	-78.57	⌒	10	788
30.30	-77.85	⌒	1	789
29.85	-77.47	⌒	100	790
28.78	-76.53	⌒	10	791
28.77	-76.43	⌒	10	792
28.67	-76.48	⌒	10	793
28.33	-76.85	⌒	10	794
27.95	-72.78	⌒	1	795
28.23	-70.23	⌒	1	796
28.23	-70.23	⌒	10	797
28.92	-69.20	⌒	10	798
29.33	-68.55	⌒	100	799
30.47	-66.50	⌒	10	800
30.67	-66.33	⌒	100	801
32.03	-64.70	⌒	1	802
33.37	-62.17	⌒	10	803
33.68	-61.65	⌒	100	804
34.47	-59.77	⌒	10	805
34.52	-60.12	⌒	100	806
36.05	-61.80	⌒	10	807
36.00	-61.72	⌒	100	808
37.45	-63.07	⌒	10	809
37.55	-62.75	⌒	10	810
39.42	-64.52	⌒	10	811
38.95	-64.58	⌒	10	812
38.95	-64.97	⌒	10	813
39.27	-65.50	⌒	10	814
39.58	-65.92	⌒	10	815
40.23	-68.12	⌒	1	816

STOP 0
END

APPENDIX II

The ecology of *Collozoum longiforme* sp. nov., a new colonial radiolarian
from the equatorial Atlantic Ocean. Submitted to Deep-Sea Research.

The ecology of *Collozoum longiforme*, sp. nov., a new colonial radiolarian from the equatorial Atlantic Ocean[*]

N. R. Swanberg and G. R. Harbison[†]

Abstract — A new species of colonial radiolarian (*Collozoum longiforme*) is described from the equatorial Atlantic Ocean. It forms elongate colonies (up to 3 m long). The carbon mass of the colony relates well with the density of central capsules; the number of algal cells per central capsule is relatively constant. Incorporation of ^{14}C per unit chlorophyll a is largely independent of light intensity, and is most strongly affected by the feeding history of the predatory radiolarian cells. Radiolarians feed on a wide variety of planktonic organisms, as determined by remains found in the colony matrix; remains of tintinnids predominate. Colonies serve as hosts for several hyperiid amphipods and the harpacticoid copepod *Miracia efferata*. *Collozoum longiforme* has been found only in oligotrophic equatorial Atlantic waters, and the colonies may serve as largely self-contained islands in the open ocean ecosystem.

INTRODUCTION

Colonial radiolarians are an artificial group of the Rhizopoda, Order

Spumellaria (Peripylea), composed of at least two families (Hollande

and Enjumet, 1953). The complete life history of any species is unknown,

although for a few the colonial and solitary stages have been matched.

Brandt (1902) first observed the transformation of the solitary *Thalasso-*

physa sanguinolenta (and *T. pelagica*) into a colonial *Collozoum pelagicum*;

Hollande and Enjumet (1953) documented this phenomenon thoroughly with

T. sanguinolenta and *T. spiculosa*. Brandt (1902) and Hollande and Enjumet

(1953) synonymized a number of species of the shell-less genus *Collozoum*

with several species of *Thalassophysa*. Although it is likely that other

Sphaerozoidae (colonial or polycyttarian radiolarians) are also polyzoic

stages of monocyttarians (Hollande and Enjumet, 1953), they must be

treated as distinct species and genera until the solitary stages are

linked with their colonial stages.

Colonial radiolarians possess a dense gelatinous matrix secreted by

the individual cells. As with other radiolarians, their protoplasm is

divided into two regions. The capsular (endocytoplasmic) region contains

the cell nuclei, mitochondria, and often crystalline material and oil

droplets. The extracapsular (ectocytoplasmic) region forms the rhizopodia,

and contains symbiotic dinoflagellates and some digestive organelles

(Brandt, 1885; Anderson, 1976a,b,c). Like the hermatypic corals, radio-

larians are predators which feed on small zooplankton such as copepods,

larvaceans, tintinnids and ostracods.

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While diving, we have encountered colonial radiolarians more frequently than any other group of large organisms in the open sea. They appear to be most common in oligotrophic regions, such as the Mediterranean and Sargasso Seas (Brandt, 1885; Haeckel, 1887; Anderson, 1976; our own observations). Although considerable research was done on this group in the latter part of the nineteenth century, they have received relatively little attention until recently. They are not usually reported from the results of conventional plankton sampling programs, since the colonial structure disintegrates when the organisms are placed in Formalin. As a result of direct observation and collection, their prominence in the open ocean has become apparent.

As prominent members of the oceanic plankton, radiolarians represent the most widespread symbiotic algal system in the world. Although most often studied by geologists for their shells the novel and highly successful adaptations of colonial radiolarians make them worthy of more attention from plankton biologists than they have enjoyed. In this paper we describe a gigantic new colonial species collected in the equatorial Atlantic. In order to help define its role in the open ocean ecosystem, we present measurements of the ^{14}C incorporation rates of the associated zooxanthellae and document some of the interactions the colonies have with other members of the plankton.

MATERIALS AND METHODS

Collection methods

Colonies were collected in one-liter hand-held glass jars by divers on R/V OCEANUS cruises 22 and 52 (Figure 1). Colonial radiolarians have been

studied during 397 of the diving stations occupied since the summer of 1975. Positions of dive stations through 1977 are given by Harbison et al. (1978); stations from 1977 through 1978 are listed in Table I. The abundance of radiolarian colonies in the field was estimated by experienced divers using drift-rate calculations as described by Harbison et al. (1978). Specimens were transported to the ship in the dark and transferred to larger volumes (12 liters) within 1-2 hours of capture.

Taxonomic methods

Colonies were examined and photographed at sea with a Wild M-5 stereomicroscope with a trinocular head assembly, camera, and automatic strobe. Individual radiolarian central capsules and associated algae were examined and photographed with a Leitz Ortholux compound microscope equipped with phase optics. Those with hyperiid amphipods or copepods were preserved. Amphipods of the genus *Hyperietta* were identified to species using the key and descriptions of Bowman (1973). Copepods of the genus *Miracia* were identified to species using the keys and descriptions of Lang (1948) and Wells (1970). Crustaceans were measured using the method described by Harbison (1976).

To obtain estimates of cells per unit length of a colony, measured sections were disintegrated and preserved in formalin. Algal cells were counted with a Palmer-Maloney chamber and a Whipple disc in a Wild M-20 compound microscope; radiolarian cells and tintinnid prey were counted with a Sedgwick-Rafter chamber. In all experiments on OCEANUS 52 representative sections of each colony used were photographed and preserved in Formalin and in a picric acid fixative. A 4% solution of formalin, saturated with picric acid and added 1:1 to the specimen worked best to preserve the gelatinous structure.

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Experimental methods:

For analysis of chlorophyll, measured sections of colonies used for radioactive incorporation experiments were ground in a Potter-Elvehjem tissue homogenizer in approximately 1 ml seawater. Microscope examination showed disruption of radiolarian cells but algal cells appeared intact. The homogenate was centrifuged 8-10 minutes in an IE clinical centrifuge at 3100 rpm; the supernatant was filtered through a .45 micron Millipore filter and discarded. The filter and the pellet were resuspended in 3 ml of 90% Spectranalysed® acetone with approximately 10 mg $MgCO_3$ in a 15 ml Nalgene centrifuge tube and extracted in the dark at $4^{o}C$ for 24 hours. Extraction experiments showed no increase in fluorescence after 15 hours. The samples were centrifuged again and chlorophyll *a* was measured on a Turner 111 Fluorometer (Strickland and Parsons, 1972). Dilution was usually 10^{-1} or 10^{-2}. Phaeopigment was also measured according to Strickland and Parsons (1972). The fluorometer was zeroed on each door on an equivalent dilution of a Millipore filter extracted in 90% acetone. Recovery of chlorophyll showed no appreciable quenching by the gelatin of the colony. The fluorometer was calibrated on extracts from cultures of *Thalassiosira pseudonana* (Guillard clone 3H) by measuring a 90% acetone extract in a Perkin Elmer model 124 dual beam scanning spectrophotometer and serially diluting the extract by 4 orders of magnitude to read on the fluorometer according to Strickland and Parsons (1972). The Strickland-Parsons equations for 90% acetone were used to calculate chlorophyll concentration as outlined by Jeffrey and Humphrey (1975). The factor $\mathcal{J}$ was obtained as the mean value from acidification of chlorophyll extracts from six unialgal cultures (Guillard clones SYN, 715, NONO, ISO, ACTIX, and COCCO).

Measured sections of the colonies were wrapped in pre-combusted aluminum foil, dried at 50°C and frozen. Ashore samples were analyzed for carbon and nitrogen content on a Perkin Elmer model 240 CHN analyzer.

Uptake experiments used $NaH^{14}CO_3$-inoculated seawater, in which measured sections of colonies (1-3 cm) were placed. Microscopic examination revealed that the pieces recover rapidly after being cut. On OCEANUS 22 incubations were done in 125 ml closable Erlenmeyer flasks placed in a culture box containing 50 ml 0.45 μ Millipore-filtered bucketed seawater with .01 μCi/ml ^{14}C (New England Nuclear lot #670-080, sealed glass ampoules). Temperature was 24°C and illumination was at 10^3 μW/cm^2 (Sylvania "cool white" fluorescent lights). Incubations on OCEANUS 52 were done in natural light in a 12 liter cylindrical clear Nalgene® aquarium cooled with flowing seawater. Incubation bottles were placed upright in a clear plexiglass rack and the tank was placed on deck and covered with 0 to 4 fitted gray nylon window screens. Each screen decreased incident light by 40%. Dark controls were run. No killed colonies of *C. longiforme* were used, although killed colonies of *Acrosphaera spinosa* were indistinguishable from dark *A. spinosa* (Swanberg, unpublished data). Portions of each colony were used for ^{14}C incorporation, CHN analysis, chlorophyll *a* and phaeophytin analysis and cell counts. ^{14}C concentration was twice that used in experiments on OCEANUS 22 (NEN lot #670-079). Incubations were between 1000 and 1400 hours (local time) for 2-3 hours at 27 ± 1°C.

Carbon-14 activity was measured by adding 0.5 ml aliquots of incubation seawater to 0.5 ml 1 M NH_4OH and 10 ml Aquasol®. After incubation, colonies were removed with pipettes and frozen in liquid scintillation vials. Ashore, samples were thawed, acidified for 1 hour (0.1 ml 2 M HCl), then digested in Protosol® for 24 hours. All samples were counted in

a Beckman LS 100 C liquid scintillation counter after 24 hours in darkness and corrected for quenching by channels-ratio counting. No measurements were made of alkalinity or total CO_2 in the seawater; the assumption of 90 mg CO_2/liter seawater was used (Steeman-Nielsen, 1952).

For incubation experiments light intensity was measured with a United Detector Technology 40X Opto-meter equipped with a radiometric head and a 4X ND Nikon photographic filter to measure in $\mu W/cm^2$ in the spectrum from 450 to 910 nm. Gelatin was obtained from the colonies by centrifugation and scanned spectrophotometrically. It showed no absorption in the visible spectrum.

Collozoum longiforme sp. nov.

Diagnosis

Form of colony cylindrical, 5-7 mm diameter with distinct but slightly irregular border, rounded at ends, occasionally branched. Central capsules without shells, roughly spherical, may be elongate in early vegetative stage, diameter of central capsules 50-120 μm. Central capsule wall thin but visible, thin proximal ectoplasm. Small oil droplets in early vegetative stage; large oil droplet in late vegetative stage. No spicules present. Gelatin firm. Abundant zooxanthellae; 14 to 50 algae per central capsule.

Description

The vegetative colonies of *C. longiforme* make it one of the most easily recognizable species of *Collozoum*. They range from 1 cm to 3 m in length; most arebetween 30 cm and 1 m; very small colonies (3-5 cm) may be shaped like a lobed torus. Each colony (Figure 2a) has a translucent core composed of small alveoli (approximately 1 mm in diameter), central capsules and zooxanthellae which composes about four-fifth's of the colony diameter.

The core is surrounded by a transparent zone of gelatin (Figure 2b) in which dense rhizopodia are found and often algae and captured prey. Early vegetative colonies have central capsules 50-80 μm in diameter with small oil droplets (8 μm). There are from 14-28 algae per central capsule (Table 2). Late vegetative colonies have central capsules 80-120 μm in diameter with a single large oil droplet (35-55 μm). In these colonies, there are up to 50 algae per central capsule. The solitary and reproductive stages are unknown. The gelatin is very firm; a diver can gently grasp a 1 m long colony in the middle region and drag it along while swimming slowly. The colony keeps its shape in a small dish and does not break when dangled from a smooth rod. We know of no other cylindrical radiolarian colony which is this durable. The gelatin is poorly fixed with chromic acid or with I_2/EtOH. In formalin the colony disintegrates after several days. In picric acid/formalin the colony form is preserved indefinitely.

Type locality

Equatorial epipelagic region east of the North coast of Brazil to St. Peter and Paul Rocks (Holotype and Paratypes sta. 773; 6°08'S, 31° 46'W).

Holotype

A holotype specimen will be deposited with the U.S. National Museum. Station Numbers: 542-549, 551, 557-560, 562-564, 566, 567, 571-573, 760, 762, 764-773.

Comments

From studies of living radiolarians, we have found the following characters to be of taxonomic importance: 1) colony shape (spherical, cylindrical), 2) colony diameter (1-2 mm, 2-5 mm, 5-7 mm), 3) central capsule shape

(spherical, serpentine, polygonal, ameboid) and size (< 50 μm, 50-150 μm, > 150 μm), and 4) appearance of the central capsule wall (delicate, thin, or thick, stout). These characters have been used by previous researchers to distinguish *Collozoum* species (Brandt, 1885; Haeckel, 1862, 1887). All but character 2 may usually be observed in carefully preserved material. There are a number of other useful characters that may vary with developmental stage or are more subjective: 1) size and arrangement of alveoli (segmentation in cylindrical colonies), 2) number of layers of nuclei (single or double), 3) thickness of proximal ectoplasm ("Pseudopodienmutterboden", Brandt, 1885) and presence of absence of "Assimilationsplasma" (osmiophilic substance in proximal ectoplasm), 4) thickness and abundance of pseudopodia, 5) consistency of gelatin; its reaction to fixatives (dissolves in formalin, fixed in $Cr_2O_3^{-2}$ and I_2/EtOH etc.), its firmness and transparency (firm, soft; visible, invisible) and the sharpness of the colony border (distinct or fuzzy with rhizopodia), 6) the number of algae per central capsule (< 10, 10-100, >100) and 7) the number and distribution of oil droplets (1, a few, many). All but character 5 may be observed in carefully-preserved material.

There are several other characters which we consider useless: 1) algal cell distribution (on central capsules or in gelatin matrix), 2) presence or absence of oil droplets, 3) the development of anisospores (shown to be parasites by Hollande and Enjumet, 1953), 4) color of oil droplets, and 5) presence or absence of spicules.

Using descriptions in the literature and the "good" characters, *C. longiforme* can be separated from all previously-described species (Table 2). *Collozoum fulvum, C. hertwigi, C. serpentinum, C. vermiforme* and *C. ameboides*

all form spherical colonies. *Collozoum coeruleum, C. inerme, C. radiosum, C. moebii* and *C. minus* all have smaller diameters than *C. longiforme. Collozuom nostochinum, C. volvocinum, C. ovatum* and *C. ellipsoides* all have larger central capsules. *Collozoum pelagicum, C. discoideum* and *C. stellatum* have polygonal or assymetrical central capsules. Brandt (1885) described 8 additional forms of *Collozoum*, none of which he named, and none of which resemble *C. longiforme*. Neither do the forms described from preserved material by Haswell and Hedley (1907). The longest colony of *Collozoum* hitherto reported was that of *C. moebii* (Brandt, 1905) which reaches a length of 40 cm. The vegetative stage of *Collozoum* (*=Myxosphaera*) *coeruleum* as figured by Brandt (Taf I, Figure 40, 1885) resembles *C. longiforme*, but the diameter of the colony is 2.5 mm. The central capsules are very regular spheres. The largest are slightly smaller than early vegetative *C. longiforme* (45-67 μm), the algae:central capsule ratio is lower (1-4:1) and the membrane is thick and heavy.

Distribution

Since 1975 we have made 434 stations. Of these, the presence or absence of radiolarian colonies was studied in 397 (Station numbers 355-381, 395-414, 417-774). Radiolarians were found on 355 dives (89% of stations since 1975). However, using the stations where they have been intensively studied since the Fall of 1976 they were found on 98% of 248 dives. Thus, we conclude that they are ubiquitous in the temperate, subtropical and tropical oceanic environment. *Collozoum longiforme*, however, has been found only in one area of the Atlantic (Figure 1) which we have visited on two cruises. This area is termed the "Amazonian Province" (Backus and Craddock, 1977)

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RESULTS

Photosynthesis

Experiments were done only on early vegetative colonies; the results below may differ from late vegetative colonies. In order to compare colonies, and to measure variation within individual colonies, all measurements are expressed per unit length. Carbon and nitrogen content per mm of colony length seems to be related to the number of central capsules/mm (Table 3). Carbon and nitrogen values varied little within colonies, but great differences were seen between colonies. Mean carbon/central capsule values were 67, 93 and 96 ng C/cell. The overall mean C:N ratio was 8.6 (s = 0.54, n = 12). Central capsule density and algal density were related (Figure 3); the algae:cell ratio varied from 14-28. Within single colonies, chlorophyll a/mm varied threefold ($\bar{x}$ = 1.8 ng chl a/mm, s.d. = 0.6, n = 8). There was no relationship among colonies in the ratio of chlorophyll a/mm to algae/mm (Table 3). Thus, chlorophyll a levels within the algal cells are variable and probably depend on factors such as the age of the algal cells, their nutritional state, or some other unknown factor. Phaeophytin values did not vary much between colonies.

In six experiments (five on OCEANUS 52 and one on OCEANUS 22) we measured $H^{14}CO_3$ uptake. Data are expressed as $^{14}CO_2$ incorporation (dpm) per mm for cut-up segments of single colonies. At different light intensities these data resemble a typical P-I curve for dinoflagellates (Figure 4). If $^{14}CO_2$ incorporation/mg chl a is plotted as a function of light intensity, there is no evidence (Figure 5) suggesting saturation or inhibition. Three of the experiments could only be represented by one sample for chlorophyll. The

fact that chlorophyll did vary as much as three-fold within those colonies

which were represented by more than one sample could account for the apparent

discrepancy. Notwithstanding this variation in chlorophyll within colonies,

^{14}C incorporation per unit length within a colony varied very little. At

full intensity the range was .72 to 2.4 nmoles/mm/hr, but at lower intensity

the ranges were 5.5-7.2, 5.3-7.7, 4.5-5.3 and 5.0-5.6 nmoles/mm/hr. It seems

possible that another factor is influencing P.

We found at least five different species of hyperiid amphipods with

C. longiforme (Table 4). The bulk of specimens that could be identified to

genus were *Hyperietta*. Few of the smaller specimens could be identified to

species with certainty. We have provisionally ascribed several small speci-

mens of *Hyperietta* to *H. luzoni* and *H. stebbingi*, based on the presence or

absence cf a strong spine on the anterdistal corner of s5 of pereiopods 5-7

and on the pattern of spines on pereiopods 1 and 2 (Bowman, 1973). These

identifications must remain uncertain until developmental studies are done,

and they are indicated by a question mark in Table 5.

These results are in agreement with a previous report on the specificity

of the genus (Harbison et al., 1977). Three of the five species of

Hyperietta, *H. luzoni*, *H. stephenseni* and *H. stebbingi* are now known to be

symbionts on colonial radiolarians. It appears likely that the entire genus

is associated with colonial radiolarians as obligate parasites in their

juvenile stages. At Station 562, we found large numbers of juveniles, which

we could identify as belonging to the family Hyperiidae (on the basis of a

well-developed pereiopod 7). These juveniles were embedded in the center of

the colony (Figure 6). Their poorly developed pleopods and urosome indicate

that they cannot be free-swimming. We believe that these juveniles belong

to the genus *Hyperietta*, since we have found identifiable juveniles embedded

in other radiolarian colonies. Adult *Hyperietta* have never been found embedded in radiolarian colonies. We have seen both adults and juveniles eating radiolarian central capsules.

We have also found *Oxycephalus clausi* on *C. longiforme* (Table 4). This amphipod appears to be predatory on a wide variety of gelatinous zooplankton, including salps, ctenophores, medusae, siphonophores and heteropods (Madin and Harbison, 1977; Harbison et al., 1977; unpublished observations). No juveniles smaller than 5 mm have been found on colonial radiolarians, however. This is in accord with the hypothesis that small juvenile *Oxycephalus* are obligate parasites on ctenophores (Harbison et al., 1978).

At station 563, we collected a specimen of *C. longiforme* that had two juvenile *Brachyscelus* sp., a juvenile *Lycaea* sp. and a juvenile *Oxycephalus clausi*. Species of *Brachyscelus* appear to be general predators on gelatinous organisms (Madin and Harbison, 1977; Harbison et al., 1977), but species of *Lycaea* are highly specific parasites of salps (Madin and Harbison, 1977).

Besides hyperiid amphipods, we have also found the harpacticoid copepod, *Miracia efferata*, living on *C. longiforme* (Table 5). It is interesting to note that we have found none of the naupliar stages living on either *C. longiforme* or other species of colonial radiolarians. We have also collected *Miracia efferata* living on and eating *Rhizosolenia* mats (Carpenter et al., 1977). It appears that the adult copepods feed opportunistically on large aggregations of plant material in the open sea. On Station 557 infestation was especially heavy and as many as 96 individuals associated with one colony (Table 5). The copepods appear to feed on the jelly or on food particles lodged in the peripheral pseudopodia.

DISCUSSION

In an oligotrophic environment, the waste products of the digestion of prey consumed by the host may significantly enrich the algal symbionts, affecting the $^{14}CO_2$ incorporation rate. The remains of prey in the colony may serve as an index of the feeding history, provided that there is little or no defecation of the undigested material. We found the remains of tintinnids more frequently than other prey (appendicularians, pteropod larvae, copepods, unidentified protozoans) in this species. Although other species of *Collozoum* eject the undigested remains of prey, we have never seen *C. longiforme* do so. Thus we have used tintinnid density as an index of the past feeding history of the radiolarian colony. A positive relationship between $^{14}CO_2$ incorporation/unit chlorophyll a (P) and tintinnid density is observed (Figure 7), suggesting that nutritional state overrides the effects of high light intensities.

It appears that the amount of food caught by the radiolarians drastically affects the photosynthetic rates of the algal cells. This hypothesis depends on whether the tintinnid shells are a good index of the amount of feeding by the radiolarians. When radiolarian colonies were fed brine shrimp, remains of the exoskeletons were not ejected after a few days, nor have we ever seen *C. longiforme* eject their natural prey. Therefore we assume that the number of tintinnids is a reasonably good estimate of recent feeding history. The actual residence time of undigested material within the colonies must be established before we can know how good an estimator this parameter actually is.

The relationship between tintinnid density and photosynthetic rate is in accord with the results of Lee and Zucker (1969), who demonstrated that fed *Archais angulatus* (Foraminifera) had higher photosynthetic rates than starved ones. Added nutrients enhance the photosynthetic rates of cultures of the common symbiont *Symbiodinium* (= *Gymnodinium*) *microadriaticum* (McLaughlin and Zahl, 1966). It appears that the zooxanthellae of *C. longiforme* benefit from the excretion of the radiolarians, as do the algal symbionts of other invertebrates (Droop, 1963; Taylor, 1974; Trench, 1979).

The assimilation rates we have measured are very high, with rates up to 3.6 mmoles CO_2/mg Chl *a*/hr. This is about twice the highest value reported for free-living algae (Ichimura and Aruga, 1964), but even the highest assimilation rates we have measured fall within the projected maxima calculated by Eppley (1972). It is reasonable to expect that symbiotic algae, which are in an extremely nutrient-rich environment, should have higher assimilation rates than free-living ones.

The benefit of the algae to the host is less clear. In *C. longiforme* the total mass of algal cells is much less than the mass of radiolarian cells and the total carbon fixed per hour constitutes only .4 to .7% of the total carbon content of the colony. Presumably only a fraction of the phososynthate is available to the radiolarians. Trench (1979) reports that 20 to 59% of the photosynthate is transported from the alga *Symbiodinium* (= *Gymnodinium*) *microadriaticum* to its hosts. Anderson (1978) demonstrated translocation in the radiolarian *Collosphaera globularis* and we calculate from his numbers that it was as high as 60% of the total photosynthate assuming 10 algae central capsule^{-1}. It is impossible to evaluate the role

this plays in the nutrition of the host without information on host respiration and growth rate or total prey ingestion. It seems unlikely that the algae provide much of the food for the radiolarian cells considering their total fixation rate. The possibility that the algae provide essential vitamins or protective secondary compounds, as is the case with gorgonians (Ciereszko, 1962), is promising and needs study. Nevertheless, it appears that the autotroph is the primary beneficiary in the radiolarian-algal symbiosis, in contrast to terrestrial symbioses, such as lichens, where it is the heterotroph that is the primary beneficiary (Smith et al., 1969).

Although the assimilation rates for *C. longiforme* zooxanthellae are high, the colonies contribute little to the overall productivity of the equatorial waters, since they are so sparsely distributed. A 50 cm colony fixes about 36 µg C/hr at 10% or more of full sun intensity (Figure 4). At a density of 10^{-3} colonies/m^3 and a 10% light depth of 27 m (25 m Secchi) this is about 4 mg C/m^2/yr. Even the most oligotrophic regions produce about 50 g C/m^2/yr (Ryther, 1969). However, *C. longiforme* is only a single, rather rare species of the many colonial radiolarians we find in equatorial waters. As a group, colonial radiolaria may contribute significantly to the total productivity of these areas. Khmeleva (1967) reported that the productivity of dense aggregations of *Collozoum inerme* in the Gulf of Aden was as much as three times that of the free phytoplankton.

The major role of *C. longiforme*, and other colonial radiolarians, in the open ocean ecosystem may not be their contribution to the total productivity, but their presence as highly concentrated packages of nutrients for symbiotic algae and food for predators. We have found both hyperiid amphipods

and harpacticoid copepods living directly on *C. longiforme* colonies. It is likely that there are other predators, but we have not observed them. Strelkov and Reshetnyak (1971) reported that radiolarian colonies repelled fish, perhaps adding support to the speculation that the zooxanthellae produce protective secondary compounds. Certainly, both of the crustacean predators we have observed on *C. longiforme* have well-developed eyes characteristic of visual, rather than chemotactic predators. We are only beginning to understand the intricacies of the planktonic community. In many ways, *C. longiforme* and other radiolarian colonies appear to be analogous to coral reefs, both intheir trophic position and in the structuring they impose on the pelagic environment.

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Table 1. Stations occupied in 1977 and 1978

Station Number	Position	Surface temperature (°C)	Date	Start dive
585	36°56'N, 66°45'W	27.8	7 September 1977	1345
586	38°59'N, 68°30'W	25.4	9 September 1977	1025
587	39°00'N, 68°26'W	25.5	9 September 1977	1510
588	37°46'N, 67°29'W	26.6	10 September 1977	1030
589	37°19'N, 69°22'W	27.2	11 September 1977	1030
590	37°18'N, 69°30'W	27.2	11 September 1977	1545
591	36°47'N, 68°57'W	27.1	12 September 1977	1030
592	37°08'N, 66°45'W	27.0	13 September 1977	1032
593	37°08'N, 66°38'W	26.8	13 September 1977	1520
594	36°33'N, 66°22'W	26.5	14 September 1977	1110
595	36°35'N, 66°22'W	26.5	14 September 1977	1545
596	36°43'N, 66°22'W	26.3	15 September 1977	1036
597	37°03'N, 67°40'W	24.8	16 September 1977	1038
598	37°15'N, 67°23'W	25.2	16 September 1977	1535
599	38°08'N, 66°56'W	26.4	17 September 1977	1036
600	38°27'N, 66°46'W	-	17 September 1977	1530
601	39°46'N, 68°34'W	24.8	18 September 1977	1035
602	32°36'N, 120°15'W	16.8	24 November 1977	1000
603	32°36'N, 120°28'W	16.8	25 November 1977	1323
604	32°34'N, 120°27'W	17.1	1 December 1977	1010
605	32°33'N, 120°29'W	16.3	2 December 1977	0955
606	32°34'N, 123°53'W	16.6	5 December 1977	1332
607	32°32'N, 123°53'W	16.6	7 December 1977	1010
608	16°31'N, 63°25'W	26.5	27 February 1978	1017
609	14°48'N, 60°50'W	26.7	28 February 1978	1017
610	13°30'N, 54°00'W	26.5	2 March 1978	1525
611	13°30'N, 54°00'W	26.5	3 March 1978	1637
612	13°47'N, 54°25'W	26.0	4 March 1978	1327
613	15°20'N, 55°11'W	25.7	5 March 1978	1031
614	18°55'N, 57°04'W	26.6	6 March 1978	1020
615	22°20'N, 58°58'W	24.8	7 March 1978	1021
616	25°49'N, 59°52'W	23.0	8 March 1978	1018
617	29°12'N, 60°35'W	20.7	9 March 1978	1019
618	40°00'N, 67°27'W	15.5	21 June 1978	1015
619	" "	15.5	21 June 1978	1045
620	" "	15.8	21 June 1978	1133
621	40°01'N, 67°23'W	17.5	21 June 1978	1450
622	" "	17.5	21 June 1978	1602
623	" "	17.5	21 June 1978	1615
624	40°06'N, 61°49'W	22.0	23 June 1978	1330
625	" "	22.0	23 June 1978	1405
626	" "	22.0	23 June 1978	1500
627	" "	22.0	23 June 1978	1600

Table 1 Continued - 2

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Station Number	Position	Surface temperature (^{o}C)	Date	Start dive
628	40°04'N, 54°28'W	22.7	25 June 1978	1019
629	" "	22.7	25 June 1978	1047
630	" "	22.7	25 June 1978	1132
631	40°05'N, 54°31'W	22.8	25 June 1978	1405
632	" "	22.8	25 June 1978	1544
633	" "	22.8	25 June 1978	1610
634	39°58'N, 52°07'W	20.6	26 June 1978	0930
635	" "	20.6	26 June 1978	1002
636	" "	20.6	26 June 1978	1044
637	40°03'N, 52°12'W	20.8	26 June 1978	1340
638	" "	20.8	26 June 1978	1455
639	39°52'N, 49°13'W	19.6	27 June 1978	1620
640	40°37'N, 48°24'W	22.4	28 June 1978	0955
641	" "	22.4	28 June 1978	1030
642	" "	22.4	28 June 1978	1116
643	40°50'N, 48°09'W	22.5	28 June 1978	1500
644	" "	22.5	28 June 1978	1542
645	" "	22.5	28 June 1978	1620
646	41°42'N, 46°04'W	21.0	29 June 1978	0955
647	44°06'N, 41°46'W	17.5	30 June 1978	1035
648	" "	17.5	30 June 1978	0957
649	44°08'N, 41°43'W	17.5	30 June 1978	1121
650	44°10'N, 41°46'W	18.0	30 June 1978	1340
651	" "	18.0	30 June 1978	1433
652	42°57'N, 36°55'W	20.7	2 July 1978	1035
653	" "	20.7	2 July 1978	0956
654	" "	20.7	2 July 1978	1115
655	" "	20.7	2 July 1978	1500
656	" "	20.7	2 July 1978	1515
657	" "	20.7	2 July 1978	1609
658	42°30'N, 36°16'W	21.0	3 July 1978	0515
659	42°30'N, 36°16'W	21.0	3 July 1978	1000
660	" "	21.0	3 July 1978	1100
661	42°15'N, 35°55'W	21.1	3 July 1978	1507
662	" "	21.1	3 July 1978	1540
663	" "	21.1	3 July 1978	1640
664	42°10'N, 35°23'W	21.0	4 July 1978	0522
665	" "	21.0	4 July 1978	0605
666	" "	21.0	4 July 1978	0650
667	42°12'N, 35°26'W	21.0	4 July 1978	0900
668	" "	21.0	4 July 1978	0855
669	40°14'N, 33°00'W	20.3	5 July 1978	0952
670	" "	20.3	5 July 1978	-
671	" "	20.3	5 July 1978	1110
672	40°12'N, 33°00'W	21.3	5 July 1978	1349
673	" "	21.3	5 July 1978	1422
674	" "	21.3	5 July 1978	1530

Table 1, Continued - 3

Station Number	Position	Surface temperature (°C)	Date	Start dive
675	39°00'N, 31°28'W	20.2	6 July 1978	1002
676	" "	19.5	6 July 1978	-
677	" "	19.8	6 July 1978	1115
678	38°58'N, 31°26'W	20.3	6 July 1978	1350
679	38°58'N, 31°08'W	20.3	6 July 1978	1650
680	38°52'N, 29°04'W	19.5	7 July 1978	0923
681	" "	19.5	7 July 1978	0925
682	38°17'N, 27°44'W	20.5	7 July 1978	1754
683	" "	20.1	7 July 1978	1755
684	36°58'N, 27°15'W	20.7	8 July 1978	0955
685	" "	21.2	8 July 1978	0950
686	" "	20.5	8 July 1978	1050
687	36°56'N, 27°18'W	20.5	8 July 1978	1253
688	" "	21.2	8 July 1978	1305
689	35°47'N, 26°06'W	21.2	9 July 1978	0940
690	" "	21.3	9 July 1978	0957
691	36°05'N, 25°43'W	21.0	9 July 1978	1345
692	" "	20.7	9 July 1978	1450
693	" "	20.5	9 July 1978	1330
694	37°09'N, 24°24'W	19.7	10 July 1978	0950
695	" "	19.5	10 July 1978	0948
696	" "	19.7	10 July 1978	1045
697	37°11'N, 24°27'W	19.7	10 July 1978	1332
698	38°21'N, 22°58'W	19.8	11 July 1978	0950
699	" "	19.7	11 July 1978	0958
700	" "	19.7	11 July 1978	1047
701	38°24'N, 23°00'W	20.0	11 July 1978	1335
702	" "	20.0	11 July 1978	1500
703	39°25'N, 21°26'W	19.6	12 July 1978	0950
704	" "	19.6	12 July 1978	1000
705	39°54'N, 20°55'W	19.7	12 July 1978	1452
706	" "	19.6	12 July 1978	1459
707	44°01'N, 19°24'W	18.5	13 July 1978	0950
708	" "	18.5	13 July 1978	1000
709	41°15'N, 19°09'W	18.5	13 July 1978	1320
710	" "	18.5	13 July 1978	1337
711	42°36'W, 17°21'W	18.2	14 July 1978	0955
712	" "	18.2	14 July 1978	1000
713	42°53'N, 17°02'W	18.0	14 July 1978	1318
714	" "	17.8	14 July 1978	1320
715	43°34'N, 19°16'W	18.8	15 July 1978	0945
716	" "	18.8	15 July 1978	1000
717	43°46'N, 18°59'W	18.5	15 July 1978	1323
718	" "	18.5	15 July 1978	1318

Station Number	Position	Surface temperature (°C)	Date	Start dive
719	45°01'N, 16°36'W	17.0	16 July 1978	0950
720	" "	17.0	16 July 1978	0957
721	45°14'N, 16°14'W	17.1	16 July 1978	1320
722	" "	17.0	16 July 1978	1330?
723	46°47'N, 13°22'W	16.6	17 July 1978	0948
724	" "	16.6	17 July 1978	0950
725	47°05'N, 12°47'W	16.2	17 July 1978	1415
726	" "	16.2	17 July 1978	1425
727	40°42'N, 14°03'E	>20	23 August 1978	0900
728	40°40'N, 13°59'E	>20	23 August 1978	0940
729	40°30'N, 14°45'E	>20	30 August 1978	–
730	–	–	–	–
731	35°45'N, 14°6'W	21.0	30 October 1978	1030
732	35°13'N, 14°56'W	21.3	30 October 1978	1530
733	33°15'N, 16°44'W	21.3	31 October 1978	1010
734	32°09'N, 16°28'W	22.0	31 October 1978	1641
735	29°53'N, 15°03'W	22.3	1 November 1978	1025
736	29°30'N, 14°48'W	22.9	1 November 1978	1500
737	28°35'N, 17°13'W	22.9	2 November 1978	0920
738	27°44'N, 16°47'W	22.7	2 November 1978	1616
739	26°33'N, 17°13'W	23.5	3 November 1978	1030
740	26°17'N, 19°56'W	23.3	3 November 1978	1522
741	24°24'N, 18°00'W	23.3	4 November 1978	1025
742	23°47'N, 17°24'W	22.3	4 November 1978	1553
743	22°00'N, 18°00'W	22.7	5 Novmeber 1978	1020
744	21°13'N, 18°02'W	23.2	5 November 1978	1545
745	19°18'N, 17°59'W	24.5	6 November 1978	1035
746	18°28'N, 18°05'W	25.3	6 November 1978	1552
747	16°28'N, 18°09'W	26.5	7 November 1978	1030
748	15°30'N, 18°11'W	27.0	7 November 1978	1520
749	13°53'N, 18°18'W	27.5	10 November 1978	1523
750	12°31'N, 19°10'W	28.0	11 November 1978	1025
751	11°53'N, 20°44'W	28.8	11 November 1978	1550
752	10°00'N, 22°30'W	28.3	12 November 1978	1022
753	9°28'N, 22°03'W	28.5	12 November 1978	1445
754	8°00'N, 20°42'W	28.4	13 November 1978	1020
755	7°19'N, 20°08'W	29.7	13 November 1978	1520
756	5°23'N, 18°20'W	28.2	14 November 1978	1015
757	5°00'N, 18°01'W	27.8	14 November 1978	1420
758	2°39'N, 17°24'W	27.2	15 November 1978	1020
759	2°35'N, 18°09'W	27.2	15 November 1978	1522
760	2°15'N, 20°55'W	27.0	16 November 1978	1019
761	2°05'N, 21°41'W	27.0	16 November 1978	1520
762	1°43'N, 24°55'W	26.2	17 November 1978	1020

Table 1, Continued - 5

Station Number	Position	Surface temperature (°C)	Date	Start dive
763	1°32'N, 25°47'W	—	17 November 1978	1540
764	0°58'N, 29°00'W*	25.8	18 November 1978	0945
765	0°55'N, 29°21'W*	—	18 November 1978	1600
766	0°30'N, 30°59'W	26.6	19 November 1978	1027
767	0°00'N, 31°01'W	26.8	19 November 1978	1518
768	1°38'S, 29°46'W	26.2	20 November 1978	1025
769	2°21.4'S, 29°16'W	26.0	21 November 1978	1025
770	3°32'S, 29°19'W	26.0	21 November 1978	1025
771	4°03'S, 29°06'W	26.5	21 November 1978	1545
772	5°37'S, 31°08'W	26.2	22 November 1978	1025
773	6°08'S, 31°46'W	26.5	22 November 1978	1525
774	7°39'S, 34°14'W	26.7	23 November 1978	1020

*
St. Peter and St. Paul Rocks

Table 2. Some of the best diagnostic characters of Collozoum species from description in the literature; values marked with an asterisk are taken from figures. Several poorly described species are omitted, especially those of Haeckel (1887). These are dealt with in the text. The cell-shape abbreviations are: sphere, spherical or subspherical; serp., serpentine or contorted; amoeb, amoebiform, with cytoplasmic protrusion; lens, lenticular, strongly flattened; poly, polygonal; and oval - elongate sphere. Species we have seen are marked with a dagger.

	Colony shape	Colony diameter (mm)	Reported length (cm)	Central capsule shape	Central capsule size (mm)	Central capsule wall	Algae/cc	Gelatin consistency	Source
C. fulvum	sphere	1.5-4	---	sphere	90-140	fine	220	---	Brandt, 1885
C. hertwigi	sphere	2-3	---	sphere	120-220	stout	"numerous"	---	Brandt, 1885
C. serpentinum†	sphere	13*	---	serp.	100x 1-40 mm	---	---	---	Haeckel, 1887
C. vermiforme†	sphere	2*	---	serp.	120x .6-6 mm	---	---	---	Haeckel, 1887
C. ameboides†	sphere	1*	---	amoeb.	40-80	fine	---	---	Haeckel, 1887
C. inerme†	cyl.	3	2	lens	70-170	absent	"numerous"	firm	Brandt, 1885 Haeckel, 1862
C. radiosum†	cyl.	.7-2.5	26	sphere	40-80	fine	2-6:1	soft	Brandt, 1885
C. pelagicum†	cyl.	2-4	4	poly.	20-80	fine	2-6:1	very soft	Haeckel, 1887,1ε
C. moebii	cyl.	2-2.5	40	lens	90-110	fine	15-20:1	sticky	Brandt, 1905
C. (M.) coeruleum†	cyl.	2.5*	10	sphere	45-67	stout	1-4:1	---	Brandt, 1885
C. minus	cyl.	1-2	2	lens	40-80	fine	variable	---	Enriques, 1919
C. longiforme†	cyl.	5-7	300	sphere or oval	50-120	fine	14-50:1	very firm	

Table 3. Measurements of early vegetative colonies of C. longiforme. Each column represents a colony. The first five are those used in photosynthetic experiments from full sun intensity (left) to 7 x 10³ uW/cm² (second from right) respectively. The values for all numbers are means of multiple counts of one sample. Asterisked values are calculated quantities.

Length (cm)	39	30	50	25	11	29
$ugC \cdot mm^{-1}$ + S.D.	4.9 + 0.8	14 + .6	-	8.7 + .4	-	-
Central capsules $\cdot mm^{-1}$ + S.D.	73 + 16	151 + 32	180 + 39	91 + 23	210 + 45	60 + 10
Alga $\cdot mm^{-1}$ + S.D. x 10^{-3}	1.0 + .5	3.0 + 1.6	4.0 + 2.3	1.5 + 13	4.4 + 2.3	1.7 + .6
Algae $\cdot$ central capsule^{-1}*	14	20	22	16	21	28
ng Chlorophyll $\cdot mm^{-1}$ (h)	1.4 (3)	1.7 (3)	5.6 (1)	4.6 (1)	1.8 (1)	1.8 (8)
ng Phaeophytin $\cdot mm^{-1}$	1.0	.87	1.1	1.8	.52	1.2
pg Chlorophyll $\cdot$ alga^{-1}*	1.4	.55	1.4	2.8	.41	1.1
Central capsule diameter (u)	61 (5)	60 (3)	68 (5)	59 (7)	61 (5)	-
Alga diameter (n)	12 (6)	11 (5)	11 (5)	11 (4)	11 (3)	-
Tintinnids $\cdot mm^{-1}$ + S.D.	13 + 4	25 + 11	12 + 7	7.5 + 4	23 + 13	5.4 + 3

Table 4. Associations of hyperiid amphipods with C. longiforme. Species in the genus Hyperietta are obligate parasites of radiolarian colonies during early development, and are found embedded in the centers of the colonies. See text for an explanation of questionable identifications. Size in mm. Each station number represents a single colony.

Station	Genus and Species	Males No. (size)	Females No. (size)	Juveniles No. (size)
546	Hyperietta luzoni	1 (2.7)		
546	Hyperietta luzoni		2 (2.8-3.1)	
547	Hyperietta luzoni	3 (2.6-3.1)	1 (3.1)	
549	Hyperietta luzoni	2 (3.6,3.7)	1 (2.7)	
557*	Hyperietta stephenseni		1 (2.8)	
557*	Oxycephalus clausi	1 (13.7)		
557	Hyperietta luzoni?			1 (1.7)
562	Hyperiidae			18 (0.9-1.1)
562	Hyperiidae			2 (1.0)
562	Hyperiidae			14 (1.0-1.2)
562	Hyperiidae			13 (0.8)
562	Hyperietta luzoni		1 (3.1)	
563	Hyperietta luzoni		1 (3.0)	
	Hyperietta stephenseni		1 (2.7)	
563	Hyperietta luzoni?			1 (1.5)
563*	Brachyscelus sp.			2 (2.4)
	Lycaea sp.			1 (3.0)
	Oxycephalus clausi			1 (7.0)
764	Hyperietta luzoni?		1 (2.2)	
770	Hyperietta luzoni?	1 (2.0)		
770	Hyperietta luzoni?		1 (2.1)	
771	Hyperietta luzoni?			1 (1.2)
771	Oxycephalus clausi	2 (5,6,6.5)		
771	Oxycephalus clausi		1 (6.7)	
771	Hyperietta stebbingi?			1 (1.4)
771	Oxycephalus clausi		1 (6.6)	

*Co-occurred with M. efferata.

Table 5. Associations of the harpacticoid copepod, Miracia efferata, with C. longiforme. Only adults and copepodids V were sexed. The juveniles all belonged to earlier copepodid stages. No naupliar stages have been found on C. longiforme. $\overline{X}$ = length in mm. Each station number represents a single colony.

Station No.	Males			Females			Juveniles		
	No.	$(\overline{X})$	Range	No.	$(\overline{X})$	Range	No.	$(\overline{X})$	Range
557	28	(1.4)	1.4-1.6	12	(1.7)	1.6-2.0	---		---
557[**]	76	(1.4)	1.2-1.6	18	(1.7)	1.4-1.8	---		---
557[*]	7	(1.3)	1.2-1.4	---		---	---		---
557	57	(1.4)	1.2-1.8	16	(1.7)	1.6-1.9	---		---
557	21	(1.5)	1.3-1.7	4	(1.8)	1.6-1.8	---		---
557	89	(1.5)	1.2-1.7	7	(1.8)	1.7-1.9	---		---
558	---		---	---		---	1		1.3
563[***]	---		---	---		---	1		1.2
563	---		---	---		---	2		0.5-0.6
573	1		1.5	---		---			

[*] Co-occurred with H. stephenseni

[**] Co-occurred with O. clausi

[***] Co-occurred with Brachyscelus sp., Lycaea sp. and O. clausi

FIGURE CAPTIONS

Fig. 1. Locations where *C. longiforme* has been collected (•). Stations
where other radiolarians were collected (+). Forty-one stations
were made where no radiolarians were recorded. Many of these
were coastal. *C. longiforme* was not seen in the equatorial
Indian Ocean (Stations 455-483), although other radiolarians
were collected on 27 of these stations. Lines denote boundaries
of Atlantic Faunal Province of Backus and Craddock (1977).

Fig. 2. a). A small vegetative colony of *C. longiforme* showing alveoli
(A), prey copepods (P), and the commensal *Miracia efferata* (M).
Colony length is approximately 30 mm. 5x. Photo by A. M.
Brosius.

b). Transparent region of gelatin of another colony showing
colony border (B), tintinnid prey (T), and radiolarian central
capsules (R) surrounded by zooxanthellae. 40x.

Fig. 3. Algal density (cells/mm) as a function of radiolarian (central
capsules) density.

Fig. 4. The incorporation of labeled carbon per unit length of colony
as a function of the light intensity (I) of the incubation.
Error bars show 95% confidence limits for the mean of n deter-
minations of carbon uptake from each colony. From left to
right n = 20, 19, 6, 9, 9, 8, 8.

FIGURE CAPTIONS (Continued)

Fig. 5. Assimilation (P) (mMoles CO_2/mg Chl. *a*/hr) vs. (I) (μW/cm^2 x 10^{-3}). Error bars show 95% confidence limits for the mean of n determinations of carbon uptake, n as in Fig. 4. The value at 10^{-3} μW/cm^2 is not shown since no chlorophyll measurement was taken. Error bars do not include chlorophyll error.
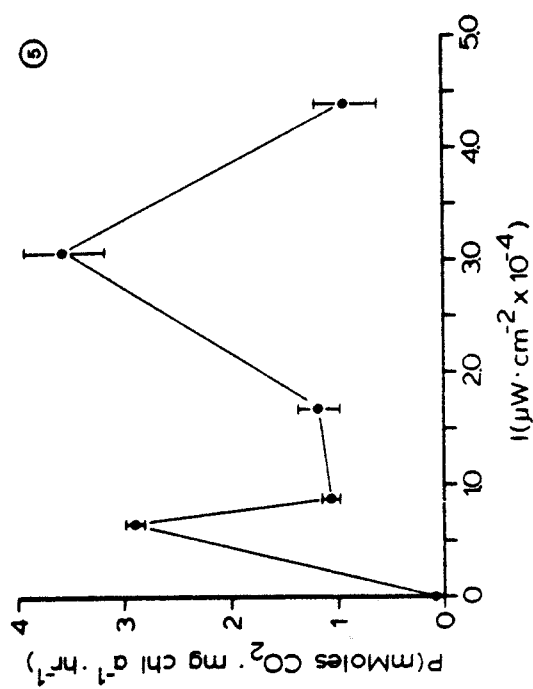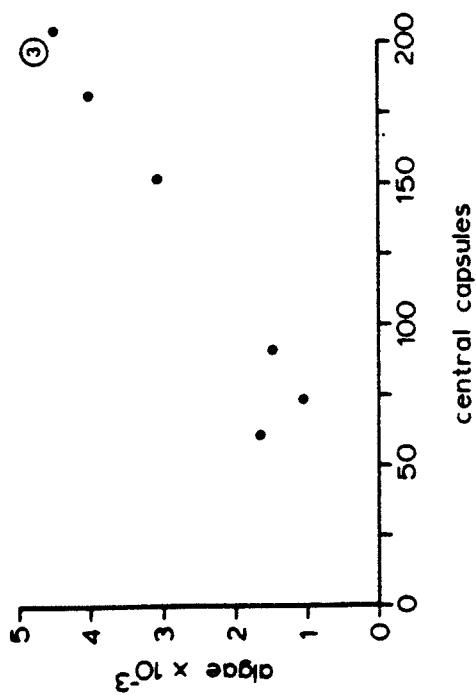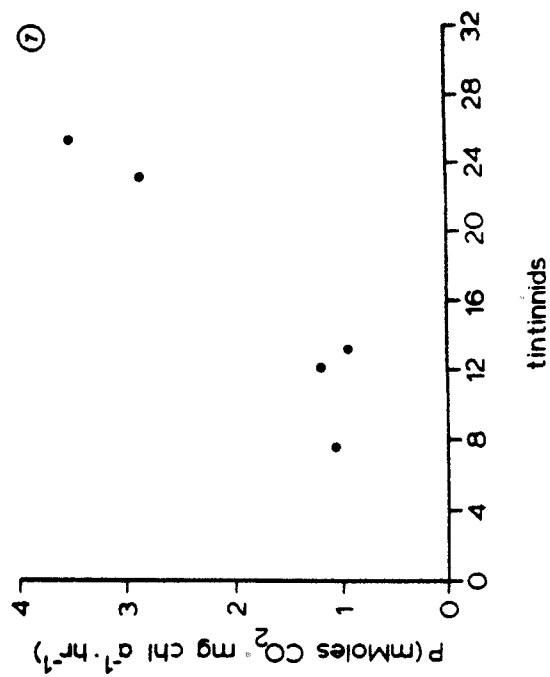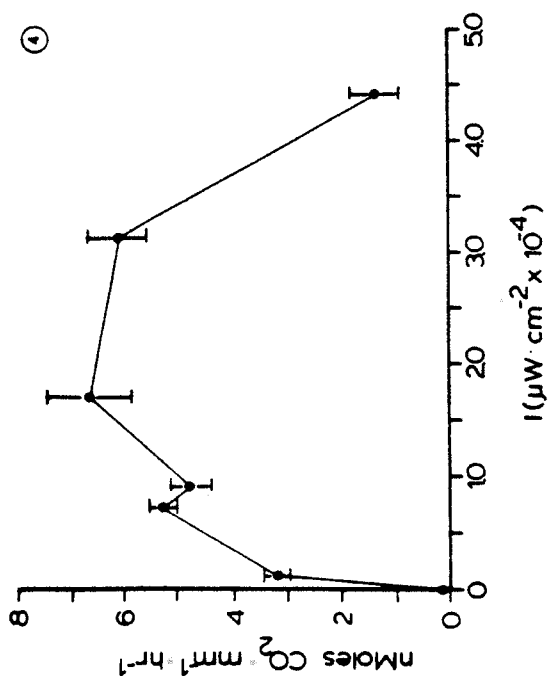
Fig. 6. Juvenile amphipods of the genus *Hyperietta* embedded in a colony of *Collozoum pelagicum* (= *Thalassophysa sanguinolenta*). The same behavior is observed in *C. longiforme*.

Fig. 7. P (mMoles CO_2/mg Chl. *a*/hr) vs. density of tintinnid prey (cells/mm) in each of the colonies from Fig. 5.
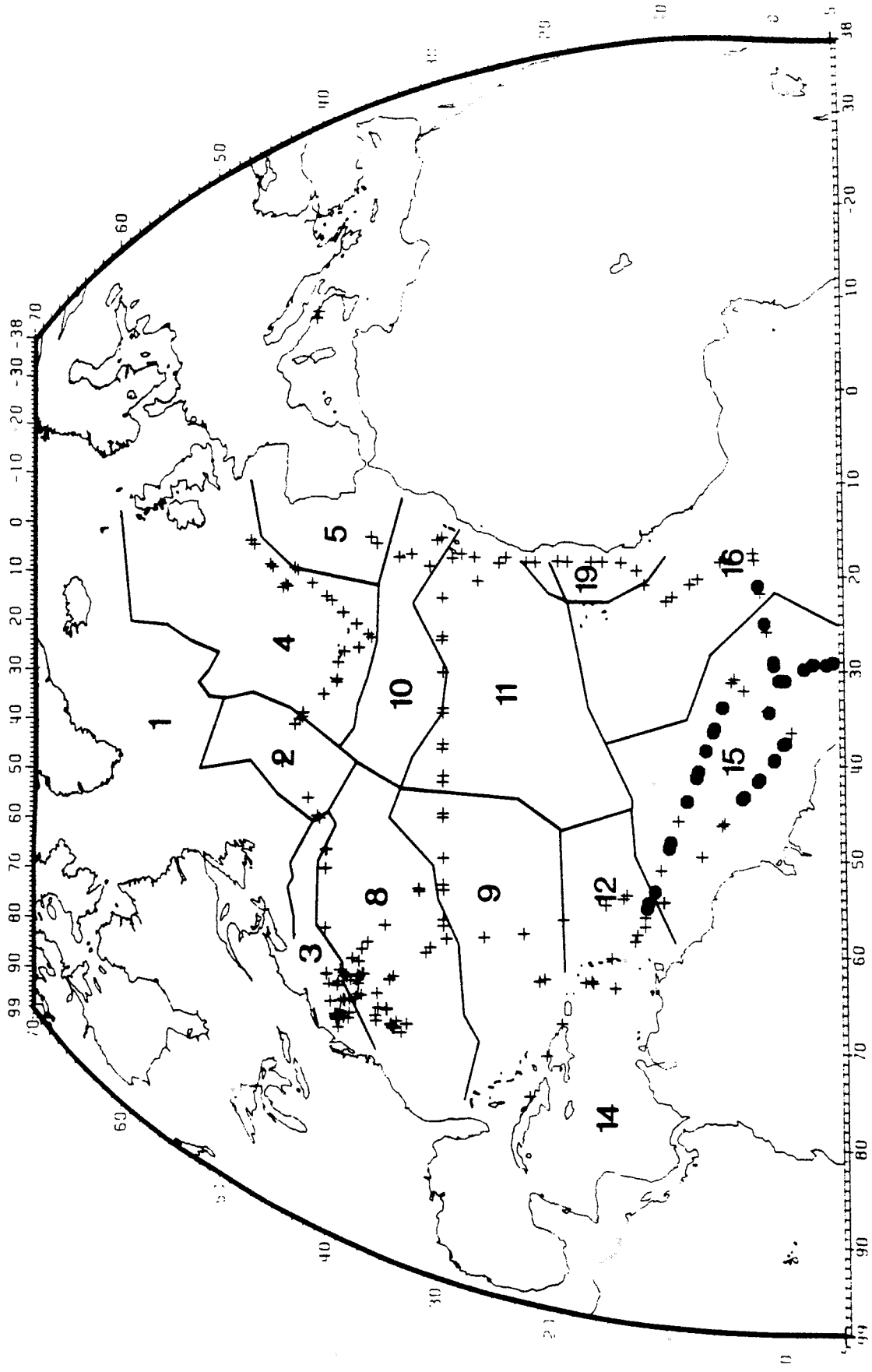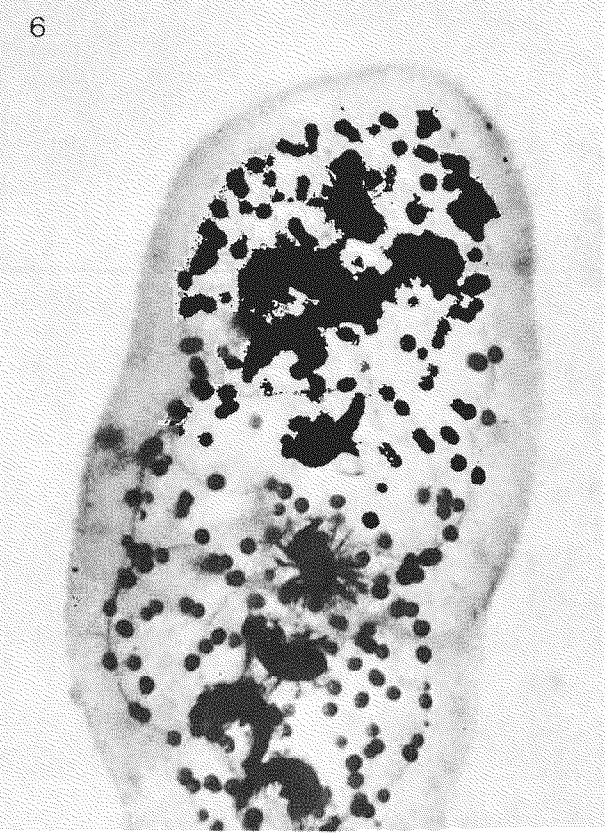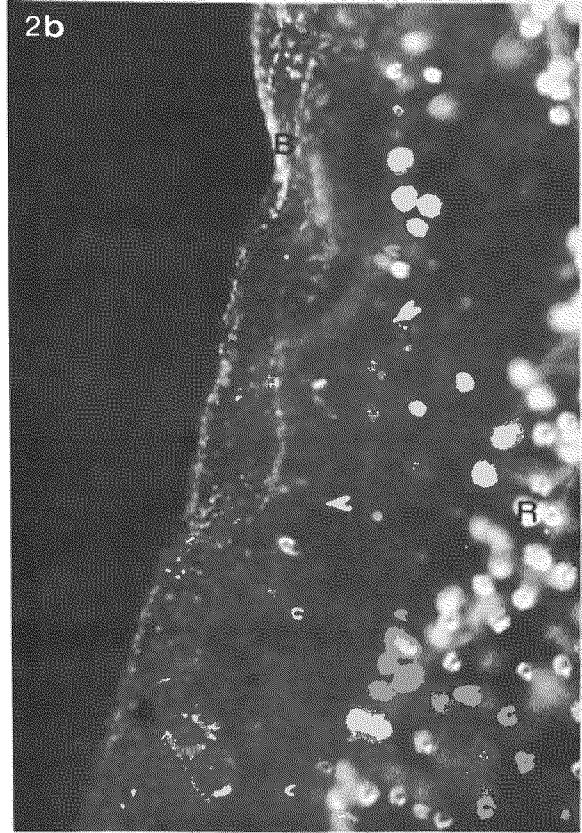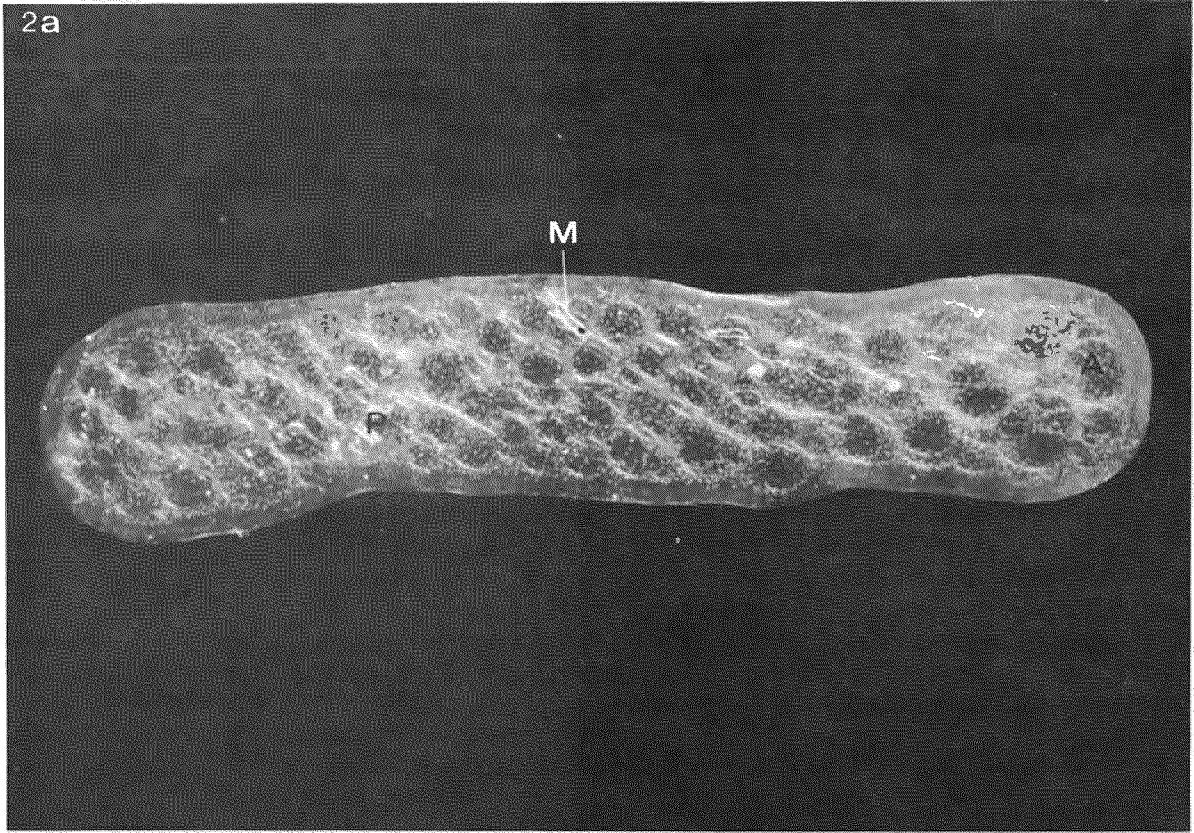
BIOGRAPHY

I was born on June 14, 1951 in Oakland, California. My childhood
was spent in several small towns in the San Francisco Bay area; a
memorable part of that period was spent exploring the wonders of Pacific
tidepools. Intrigued by what lay beyond the shore, I bought my first
set of mask and fins in 1957 and became an avid skin diver. Even at
that age I wanted to become a marine biologist. I am told I was an
irritatingly precocious child, more occupied by my books than by my
peers or toys. In my defense, I must point out that I did indulge in
the usual small-boy activities such as war games, fighting, and manipu-
lations of helpless invertebrates.

My childhood goals survived my adolescent diversions with some de-
lays, and I began to realize a true interest in biology. In anticipa-
tion of leaving the intellectual vacuum of high school I had carefully
made plans to go to the University of California at San Diego, followed
by graduate studies at the Scripps Institution of Oceanography (at that
age I had not discovered the world outside of California). All these plans
were disrupted by an amorous involvement with a young lady from the
University of California at Davis who convinced me of the academic superi-
ority of that campus. The decision to matriculate at Davis had a profound
influence on my career which far outlived the affair *d'amour*.

I was somewhat distracted by the political and cultural turmoil of the
campuses in the late 1960's, but never enough to seriously affect my edu-
cation. I was very frustrated by the discrepancy between the subjects I
wanted to learn and those the University required that I study. This

frustration was alleviated when I began to study zoology in my second year under Dr. William Hamner. My eagerness carried me off to the Bodega Marine Laboratory for a spring semester of benthic ecology. While there, Bill Hamner invited me to participate in a year-long expedition he was forming to study plankton *in situ* in the Bahamas. Always a romantic, it did not take me long to accept.

I spent a fruitful year at the Lerner Marine Laboratory on Bimini; it was a major landmark in my life. I developed a great interest in and some knowledge of the marine macro-zooplankton as well as a better understanding of research itself. This helped me to continue my studies when I returned to the University. My remaining years at Davis were relatively uneventful and are remembered mostly as hard work. Nearing graduation, I faced some indecision about which course to follow: I had always planned to do graduate study, but I wasn't sure which school or field I wanted. I applied to several graduate schools and of those which accepted me, the Woods Hole Oceanographic Institution was the most attractive, offering the opportunity to go to sea, the romanticism of oceanography and a solid academic framework in its connection with Massachusetts Institute of Technology. Some of the type of research begun by Dr. Hamner was being done at Woods Hole by Richard Harbison and Larry Madin. I still had a strong interest in plankton, and decided to go to Woods Hole. It was not long before I was back in blue oceanic water, diving and studying plankton. The rest is described in this thesis.

CURRICULUM VITAE

NEIL RALPH SWANBERG

BIRTH: 14 June 1951

EDUCATION:

   B.S., University of California, Davis. Zoology. Summa cum laude,
          1974
   Ph.D., Woods Hole Oceanographic Institution/Massachusetts Institute
          of Technology. Joint degree. Expected September 1979

POSITIONS HELD:

   Undergraduate Research Trainee, Lerner Marine Laboratory, Bimini,
          Bahamas, 1971-1972
   Research Fellow, W.H.O.I.-M.I.T. Joint Program in Oceanography,
          1974-present

RESEARCH INTERESTS:

   Behavior, ecology and trophodynamics of neritic and pelagic cteno-
   phores; studies on microstructure of oceanic plankton communities;
   physiology and ecology of living radiolarians. Productivity of
   algal-invertebrate symbiotic systems; distribution, behavior,
   natural history, functional morphology and commensal associations
   of sphaerozoid radiolarians

RESEARCH SUPPORT:

   Education Department, W.H.O.I., 1974-1977
   National Science Foundation, Biological Oceanography Program, 1978
   Education Department, W.H.O.I., 1979

SEA EXPERIENCE:

1974	R/V JOHNSON	July	Florida Current: W. Palm Beach-W. Palm Beach
	R/V ATLANTIS II 84	August	Equatorial Atlantic: Barbados-Woods Hole
	R/V ATLANTIS II 85	October	Sargasso Sea: Bermuda-Bermuda
1975	R/V ATLANTIS II 86	February	Caribbean Sea: San Juan-Fort-de-France
	R/V CHAIN 125	August	Gulf Stream: Woods Hole-Woods Hole
	R/V KNORR 53	November	Gulf Stream, Sargasso: Woods Hole-Woods Hole
1976	S/V LA CURIEUSE	Feb-May	Equatorial Indian Ocean: Mahe-Mahe, Sez.
	R/V KNORR 58-2	August	New York Bight, Hudson Canyon: Woods Hole-
	R/V KNORR 58-3	August	Woods Hole
1977	R/V OCEANUS 22	Feb-Mar	Equatorial Atlantic: Barbados-Barbados
	R/V OCEANUS 30	August	Sargasso Sea: Woods Hole-Woods Hole
	R/V OCEANUS 33	October	Gulf Stream: Woods Hole-Woods Hole
1978	R/V ATLANTIS II 98	March	W. Atlantic: San Juan-Woods Hole
	R/V ATLANTIS II 101	June-July	N. Atlantic: Woods Hole to Glasgow
	R/V OCEANUS 52-2	Oct-Nov	E. Atlantic, Equatorial Atlantic: Lisbon-Dakar-Recife

PUBLICATIONS:

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        colonial radiolarian (*Collozoum longiforme* sp. nov.) from
        the equatorial Atlantic Ocean. In review.

REFERENCES:

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