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FEEDING ADAPTATIONS OF THE FORAMINIFERAN *CIBICIDES REFULGENS* LIVING EPIZOICALLY AND PARASITICALLY ON THE ANTARCTIC SCALLOP *ADAMUSSIUM COLBECKI*

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ABSTRACT

The calcareous foraminifer *Cibicides refulgens* is a conspicuous and abundant component of the epifaunal community living on the valves of the free-swimming Antarctic scallop, *Adamussium colbecki*. Examination of this association using light microscopy, scanning electron microscopy, radiotracer, and resin-casting/sectioning techniques, demonstrates that the foraminifer possesses a combination of morphological and physiological adaptations, unique among benthic calcareous foraminifera, which enhance its ability to acquire nutrients in an otherwise oligotrophic and seasonal environment. Three distinct modes of nutrition are employed: (1) grazing the algae and bacteria living upon the scallop shell surface, (2) suspension feeding through the use of a pseudopodial net deployed from a unique superstructure of agglutinated tubes which form an extension to the calcareous test, and (3) parasitism by eroding through the scallop's shell, and using free amino acids from the highly concentrated pool in the extrapallial cavity.

INTRODUCTION

A variety of benthic foraminiferal species are known to live most, or part of their lives, epizoically on a wide range of organisms. Examples include *Rosalina globularis* d'Orbigny, *R. anomala* Terquem, *R. carnivora* Todd, *Cibicides refulgens* Montfort, *C. lobatulus* Walker and Jacob, *C. pseudoungerians* (Cushman), *Discorbis wrighti,* and *Discorbinnella* sp. which firmly attach to macroscopic algae and metazoans such as hydroids, bryozoans, tunicates, crustaceans, isopods, amphipods, decapods, pycnogonids, brachiopods, gastropods, and bivalves (Nyholm, 1961; Todd, 1965; DeLaca and Lipps, 1972; Hayward and Haynes, 1976; Zumwalt and DeLaca, 1980; Mullineaux and DeLaca, 1984; Alexander, 1985; Moore, 1985).

The most important association in terms of numbers of foraminifera appears to involve filter feeding invertebrates, particularly free-swimming bivalves. Hayward and Haynes (1976) reported 998 individual foraminifers on one specimen of the commercial scallop *Clamys opercularis* (Linneaus) of which 765 were *Cibicides lobatulus.* Similarly, Mullineaux and DeLaca (1984) noted an average of 1386 foraminifers on 21 specimens of the Antarctic scallop *Adamussium colbecki,* 901 of which were *C. refulgens.*

For the majority of associations between filter feeding invertebrates and epizoic

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foraminifers, the host shell may provide not only a firm substrate for attachment, but also the added advantage of a relatively silt-free environment. In motile bivalves living in areas of strong currents and wave action, the shell may provide further protection against sand shifting and possible burial with fatal consequences (Dobson and Haynes, 1973; Hayward and Haynes, 1976). Even sessile molluscs such as *Mytilus* can provide a relatively silt-free substrate (Allen, 1953), and *Notocorbula* living in the silt-laden Mississippi delta, offers a preferred habitat for *Hanzawaina* sp. by crawling above the layers of accumulating flocculent material (Bock and Moore, 1969). Furthermore, life activities of the host can enhance the availability of nutrients to the epizoic foraminifers; for example seven species living on the shell of the brachiopod *Tichosina floridensis* Cooper, are thought to benefit from suspended food material transported by the inhalant and exhalent feeding currents (Zumwalt and DeLaca, 1980).

The means by which foraminifera attach themselves to the shells of their hosts varies considerably. Some adhere simply, with no detectable effect or marking on the substrate (Bock and Moore, 1969; Zumwalt and DeLaca, 1980), while others extensively pit and erode the subsurface layers (DeLaca and Lipps, 1972) and even penetrate the entire shell to reach the mantle cavity (Todd, 1965).

In this paper we use radiotracer techniques, light and scanning electron microscopy, resin casting, and sectioning methods to describe the remarkable morphological and physiological adaptations of a large Orbitoidacean, *Cibicides refulgens*, to its specialized epizoic habit on the free-swimming Antarctic scallop, *Adamussium colbecki*.

The study site

The study site at Explorers Cove (approximately 77.6 S, 163.5 E), McMurdo Sound, Antarctica, was used previously by Stockton (1984) and Mullineaux and DeLaca (1984).

The sediment is homogeneous fine silt mainly deposited from the late austral summer/early autumn freshwater input to the locality via streams originating from the Commonwealth and Wales glaciers (DeLaca, unpub. obs.). The virtual absence of currents (Mullineaux and DeLaca, 1984) prevents any reworking of the sediments and results in a seasonal accumulation of fine silt. *Adamussium colbecki* occurs in densities of up to 90 m^{-2} and forms 90% of the available hard substrate in the area (Stockton, 1984); it resides within depressions in the sediment which are caused by the light, non-locomotory flapping action of its valves (Mullineaux and DeLaca, 1984; Stockton, 1984).

The benthic community of Explorers Cove is thought to resemble the deep sea in species diversity, abundance of individual organisms, sediment relief, and long-term stability of temperature, salinity, and oxygen (Dayton and Oliver, 1977). The austral summer is accompanied by an increase in primary productivity by ice algae living within the lower 10 cm of sea ice, and is followed in late summer by release of the algae into the water column from the melting ice. Thus a seasonal pulse of organic material is contributed to the developing *in situ* productivity in shallow-water (DeLaca, unpub. data).

MATERIALS AND METHODS

Living specimens of *A. colbecki* were collected from 20 to 27 m by scuba diving through holes blasted in the 3 m thick sea ice, and maintained in an aquarium at *in situ* temperature and salinity (−1.8°C and 34‰ S).

Most material used for scanning electron microscopy (SEM) was coated with gold and/or carbon and examined in a Cambridge Stereoscan MK 2 operated at 20 kV; images were recorded on Ilford FP4 35mm film developed in Microphen.

Scallop shells with epifaunal communities were embedded in Spurr's low viscosity resin (Polysciences Inc.), then ground and polished using carborundum, diamond, and aluminum oxide abrasives until the desired plane of section was reached. Azure II/methylene blue, and methylene blue in borax (Richardson *et al.*, 1960) was used to stain organic material. Other scallop shells, cleared of epifauna by boiling in 20 vol. hydrogen peroxide, were gradually embedded in Spurr's over three days to penetrate the fine cavities of the shell material. After polymerization, the block was fractured along the plain of the shell so that the upper block retained only a thin translucent layer of calcite. Alternating treatments of 0.1 *N* HCl at room temperature, and 3% aq. sodium hypochlorite at 60°C, removed calcite and organic layers, respectively; the exposed face of the lower block forms a perfect cast of the scallop shell dorsal surface and the canals and cavities within the calcite itself. Observations were made with an ETEC Autoscan SEM at the Wadsworth Center for Laboratories and Research, Albany, New York.

For SEM examination of substrate pitting, agglutinated tube morphology, and pseudopodial deployment, six scallops with epifauna were fixed for 2 h in 6% glutaraldehyde buffered with 0.1*M* sodium cacodylate at pH 7.4. Dorsal valves were rinsed five times with distilled water, rapidly frozen at −40°C, and freeze dried in an inverted position. Other *C. refulgens* were picked from all size classes of *A. colbecki* (Stockton, 1984) and examined for gross morphology, aperture, and spiral face detail; attachment zones were fractured and the exposed calcite laminae studied for evidence of pitting or tunneling. Etched (using 0.1*N* HCl) and non-etched inner valve surfaces were examined for perforations.

To determine the rate of substrate pitting and agglutinated tube formation, foraminifera were picked from the dorsal valves of *A. colbecki,* cleaned of extrathalamous material, and placed in semi-enclosed, transparent plastic chambers attached to areas of non-pitted dorsal valves from recently killed scallops (50% of which had most of their microflora removed). It was not possible to use living *A. colbecki* since the frantic flapping of collected specimens prevented the introduction and subsequent attachment of *C. refulgens* to the upper valves. Such violent movements are not usual in the normal habit of *A. colbecki* (Mullineaux and DeLaca, 1984; Stockton, 1984). The valves with experimental foraminifers were returned to the collection site for 3 months; the containing chambers did not alter ambient light levels and a loose fitting lid prevented silt accumulation but permitted exchange of dissolved materials.

ATP analysis (DeLaca, 1986) was used to distinguish living from dead foraminifera and to measure foraminiferal biomass. A carbon to ATP ratio of 300 was tentatively assumed for application to ATP values from *C. refulgens,* since recent work shows that this ratio is remarkably constant between the two taxonomically distant rhizopod species, *Gromia oviformis* (order Testacida) and *Astrammina rara* (order Foraminiferida) (DeLaca, 1986). Cellular nucleotides were extracted with phosphate/citrate buffer at 100°C, and data were used for normalizing experimental results.

Labeled amino acids (^{14}C) in the same proportions as a typical algal protein hydrolysate (Amersham corporation, product CFB.25; see table I), were used to demonstrate uptake through the pecten shell by individual foraminifers. Plastic containers (12 ml volume) were sealed to the inner valve surface with silicon vacuum grease, and the seawater within enriched with 2.5 μCi radio-labeled amino acids at 100 μM final concentration. This concentration of amino acids is approximately 25 times lower than that recorded for free amino acids within the extrapallial cavity (see Re-

sults) and 14.7 times greater than at the sediment/water interface (DeLaca, 1982). Incubations lasted up to four days, and controls with containers on both faces of the shell (one contained label; the other retained any diffused label) measured leaching through non-pitted shell and passive diffusion into heat killed (30°C for 30 min), attached foraminifers. To establish the viability of animals harvested, 10 specimens from each experimental group were analyzed for ATP content.

To measure influx rates of dissolved amino acids, individual animals were removed from pecten shells, cleared of all extraneous materials, and allowed to recover from handling for 24 hours prior to experimentation. These animals were incubated in experimental medium [10 ml filter sterilized seawater (FSSW) with labeled and unlabeled compounds (depending upon experiment)]. Incubated specimens were washed in 5–6 serial baths of FSSW (~1 min each) until wash water registered no significant radioactivity over background levels. Influx was determined by measuring the level of accumulated radioactivity in experimental animals (homogenized in Aquasol 2) with a Beckman LS 6800 liquid scintillation counter. "Time zero" and heat killed controls were used.

To measure grazing rates of *C. refulgens*, epiflora of the dorsal valves were labeled *in situ* with [^{14}C] sodium bicarbonate in light at temperatures between −1.8 and 0°C for 12 hours; individual cleaned and heat killed *C. refulgens* were placed on these shells prior to labelling. After incubation, the scallop shells with foraminifers were washed in serial baths of FSSW until the radioactivity of wash water was not significantly over background levels. Twenty individual diatoms, living foraminifers, and heat killed foraminifers were selected as time-zero samples and extracted in 1.0 ml of hot (100°C) phosphate/citrate buffer. After removal of 10 μl of supernatant for ATP analyses, the extract was dried and digested with 0.3 ml of 0.2 *N* perchloric acid prior to adding Aquasol 2. Subsequent specimens were sampled at three 6-h intervals, and similarly processed. Radiation counts obtained from the time zero specimens were subtracted, and the results used to calculate the number of cells ingested. Experimental protocols for isolating, washing, and determining ^{14}C uptake by single algal cells were taken after Rivkin and Seliger (1981).

Suspension feeding was investigated using radiolabeled bacteria and diatoms. Bacteria were isolated from the sediments of New Harbor and further isolated on 2216 Marine Agar (Difco). Selected cultures were then labeled with [^{14}C] leucine (ICN) at log growth in Marine Broth (2216 Difco). Labeled bacteria were washed free of extraneous label by repeated centrifugation and resuspension in FSSW, until supernatant radioactivity was not significantly over background levels. Cell concentrations were determined with a Petroff-Hauser counting cell, and disintegrations per cell measured by liquid scintillation using Aquasol 2. *Nitzchia cylindricus* cultures, provided by Dr. C. W. Sullivan (University of Southern California), were grown with Alga-grow media (Carolina Biol. Suppl. Co.) in FSSW and labeled with [^{14}C] sodium bicarbonate. These cultures were concentrated and washed on nitex screen and resuspended to the desired concentration (measured using a plankton counting cell).

Four dorsal valves of living *Adamussium colbecki* were removed, and the agglutinated portions of 50 *C. refulgens* were gently but thoroughly removed from the test, leaving the foraminifers securely attached to the shells. Two of the shells were maintained at temperatures between −1.8 and 0°C, and the others were warmed to 30°C for 30 min (heat killed controls); shells were suspended upside down for 6 h in a culture vessel with a suspension (maintained with a small stream of air) of labeled diatoms in seawater. This configuration was duplicated to measure bacterial capture. At t_0 and hourly intervals, samples of both diatom and bacterial suspensions were taken (by centrifugation and filtration with nitex screen, respectively) to check for

dissolved label and to measure cell concentration. Following incubation, 30 foraminifers with agglutinated tubes, and 30 foraminifers without, were detached, cleaned of extraneous material (if necessary), washed through 10 serial washings of FSSW, extracted in citrate/phosphate buffer, and processed as described above.

Cell dimensions were measured using light microscopy. Approximate cell volumes were calculated by appropriate geometric formulae corresponding to the cell shape. Carbon content was also calculated (Strathmann, 1967).

Small volumes of fluid were sampled from the extrapallial cavity of *A. colbecki* (between the mantle and inner surface of the shell) by passing a blunt cannula attached to a syringe through a window cut in the 0.5–0.7 mm thick shell. Separation, identification, and quantification of free amino acids in selected samples were accomplished using high pressure liquid chromatography (HPLC) after fluorescence derivitization with ortho-pthaldialdehyde (see Stephens, 1982).

Results

The dorsal surfaces of *Adamussium colbecki* living in sedimentary environments are encrusted with attached foraminifera (Fig. 1) including *C. refulgens*. The force required to dislodge an individual of *C. refulgens* from the surface of a bivalve shell increases with size of the individual, as does the extent and depth of substrate erosion. Juvenile *C. refulgens* (Fig. 2) are easily dislodged using a fine needle, whereas adult specimens (Figs. 3–6) must be pried off with a stout microprobe. A random sample of shell surfaces under *Cibicides refulgens* demonstrated that only 45% (n = 200 on each of 5 shells) of foraminifers had caused etching. Similar sampling near the umbo revealed that 92% of the foraminifers resided in etched concavities whereas only 12% of those foraminifers nearer the shell margins were attached over etched shell (100 foraminifers examined on each of 5 shells). No significant etching was detected after three months on shells artificially infested with *C. refulgens* (Fig. 7).

A progression in the extent of substrate pitting caused by increasing sizes of foraminifers and the age of the shell is clearly visible using a dissecting microscope. Use of the SEM demonstrated that pits caused by younger *C. refulgens* generally extend no deeper than the uppermost laminae of the valve. At this stage the striations visible on the shell surface (Stockton, 1984) and the smaller perpendicular 'ribs' connecting them (Fig. 8) are removed completely in the area of the pit, and the exposed calcite is eroded to appear as irregular granules with multitudinous 'micro-canals' (Figs. 9, 10). Further pitting results in enlargement of the microcanals to form distinct canal openings which penetrate several calcite layers, and are to some extent guided by planes of weakness within, or between, the layers (Figs. 11, 13). This phenomenon is dramatically illustrated by resin casts which show the pit erosion in reverse, producing a 'cathedral effect' from the pattern of channels within the scallop shell material (Fig. 12). The distributions of canal openings within the substrate pits as a whole do not exhibit any noticeable pattern.

The bond between the test wall of the umbilical face of *C. refulgens* and the uppermost calcite layer in the pit is sufficiently strong so that when a specimen is forcefully detached from the shell, a layer of shell material will often remain attached to the foraminifer. It is then possible to observe deeper canals ramifying through the shell; these canals are generally fewer in number than the more superficial canals, but are larger in diameter (10–14 μm) and more conspicuous.

Fracturing a scallop shell directly through a substrate pit allows for detailed SEM study of groups of canals in the middle and lower layers (Fig. 22). Scanning electron micrographs (Figs. 13, 14, 16) demonstrate conclusively that the canals do not funda-

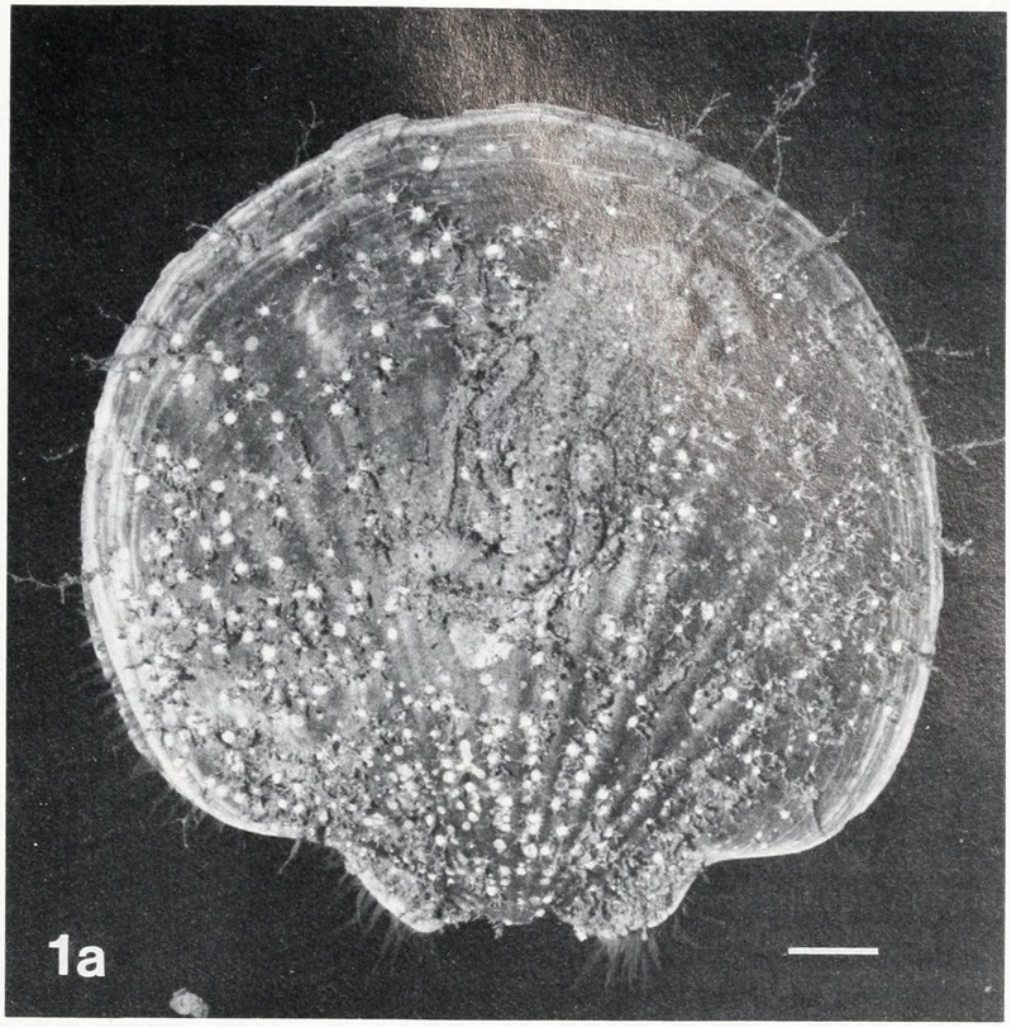


FIGURE 1a. The free swimming Antarctic scallop *Adamussium colbecki* with characteristic epizoic growth. Conspicuous attached faunal components include the agglutinated tube of a large polycheate, hydrozoans, bryozoans, and commonly four or more species of benthic foraminifera. The most abundant and conspicuous species is *Cibicides refulgens* with its agglutinated tubes. Scale bar = 1 cm. b. Oblique view of the dorsal valve of *A. colbecki* with attached *C. refulgens* and associated agglutinated tubes reaching into the overlying water. Vertical tubes may extend to 5 mm and exhibit three orders of branching. Scale bar = 5 mm.

mentally follow lines of weakness within the shell, and therefore it appears that the foraminifer's cytoplasm can control both the extent and direction of the dissolution process. The thick resin cross-sections of *C. refulgens* attached to the valve surface revealed many visible canals extending from the base of the pit through most of the calcite layers perpendicular to the plane of the laminae (Figs. 17, 18). However as a

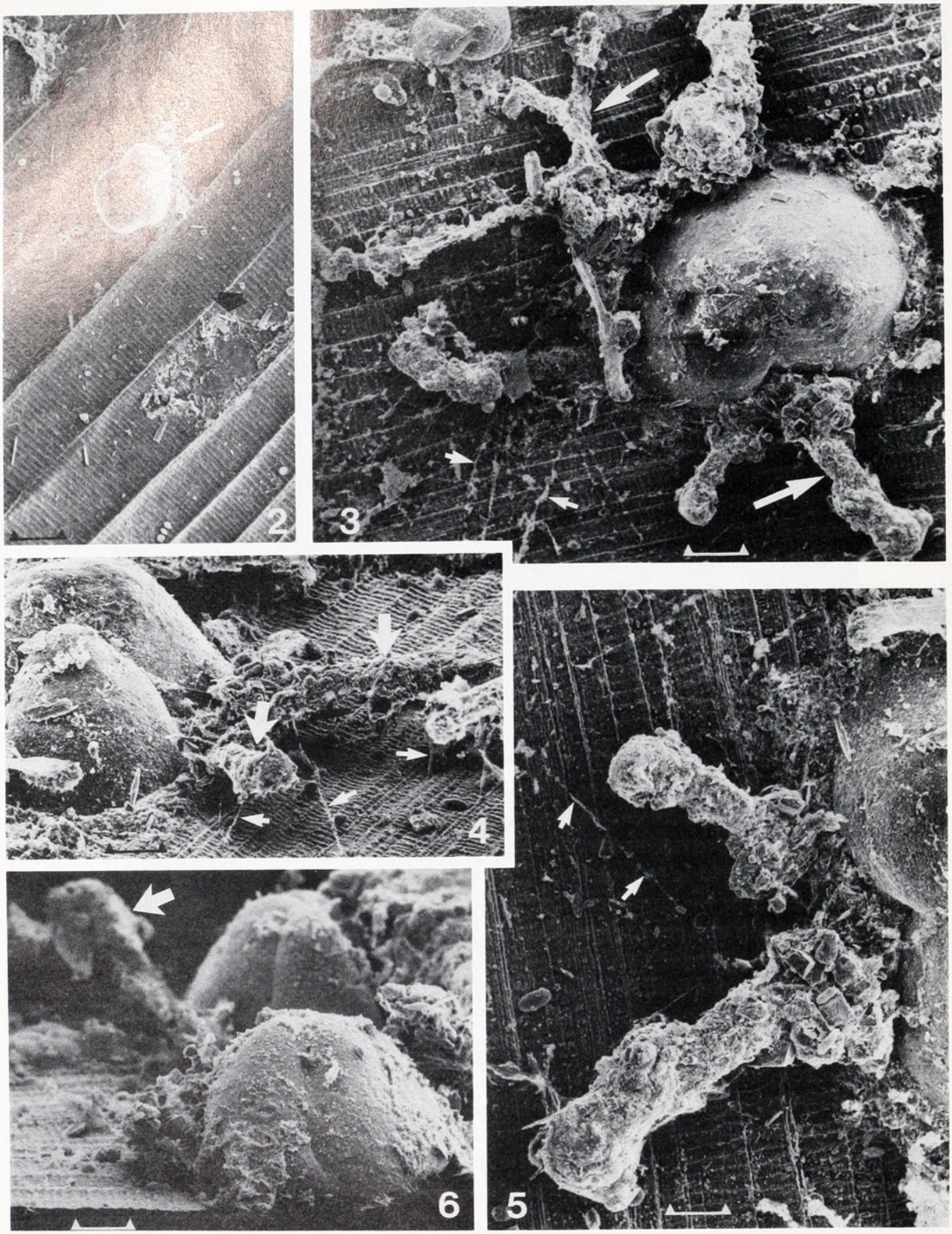


FIGURE 2. Juvenile *Cibicides refulgens* attached to surface of *A. colbecki* dorsal valve. A rudimentary peripheral agglutinated tube has been built (white arrow). Vertical tubes are not present. Two juveniles have been removed to show the shallow surface etching of the shell (black arrows). Scale bar = 163 μm.

FIGURE 3. Plan view of an attached adult with a well developed agglutinated tube system (large arrows) and net of pseudopodia on the scallop shell surface (small arrows). Scale bar = 200 μm.

FIGURE 4. Oblique view of specimen in Figure 3. Pseudopodia (small arrows) can be seen traversing the space between the agglutinated tubes (large arrows) and the substrate. Scale bar = 143 μm.

FIGURE 5. Detail of Figure 3 showing composition of agglutinated tubes and the presence of a fine pseudopod (arrows) radiating away from the foraminifer, across the shell surface. Scale bar = 102 μm.

FIGURE 6. Oblique view of two attached adult *Cibicides refulgens*. An agglutinated tube can be seen clearly raised away from the scallop shell surface (arrow). Scale bar = 154 μm.

result of the curvature of the canals, and the limited depth of field, it was not possible to photograph a single element traversing the complete shell thickness without interruption. The canal walls are significantly smoother than the adjacent calcite exposed at the fracture zone (Figs. 16, 22), but there is no evidence of an actively secreted lining.

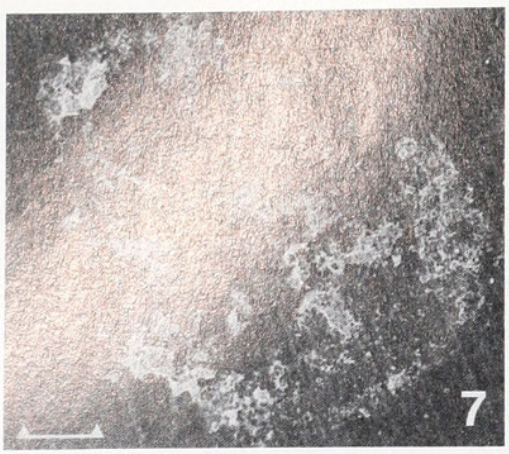
The inner valve surface is generally lined with overlapping, angular, tile-like calcite crystals (Fig. 23), between which are many naturally occurring pores leading to the lamina beneath (Fig. 24). Upon careful scrutiny of this inner layer in the SEM, circular areas (approximately 15–50 μm in diameter) with significantly enlarged pores (Fig. 23) are evident marking the area above which an individual foraminiferan is attached on the outer valve surface. After etching for 5 to 10 minutes with 0.1 *N* HCl, the outermost calcite layer is removed and those salient markings are revealed more clearly (Figs. 19, 20). High magnification detail shows them to be closely spaced canal openings (Fig. 21), and there remains little doubt that these openings are continuous with the canals which originate in the surface pit, and penetrate deep into the bivalve's shell.

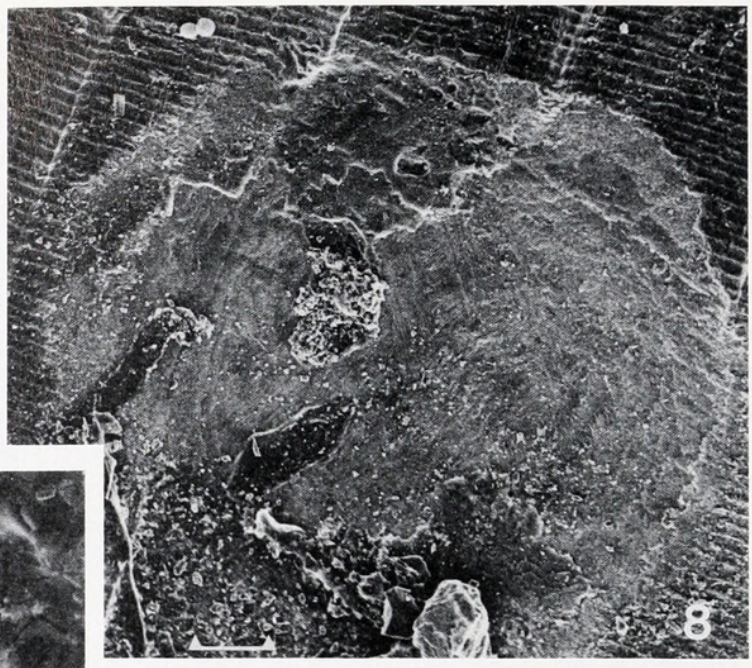
Examination of the exposed face of an adult *C. refulgens* detached from the substrate (Fig. 25, 26) reveals that the spiral face is not adhered to the shell material over its complete area due to a pattern of grooves radiating from the primary aperture to the peripheral test margins. The roof of each groove is the spiral test face, and the floor is formed by the etched shell material of the pit floor. Typically, four to five such grooves of approximately 30 to 50 μm width connect areas immediately adjacent to the primary aperture (Figs. 25, 29) with those more remotely situated on the opposite test margins. Etched bivalve shell which forms the base of the grooves often exhibits a pattern of fine channels (5–10 μm wide) running parallel with the main trend of the groove (Fig. 30), giving the impression of the streamlines oriented with the direction of the main cytoplasmic flow within the grooves. In addition, the lumina of the radial grooves are continuous with that of the peripheral tube encircling the test at its point of contact with the substrate (Figs. 25, 26).

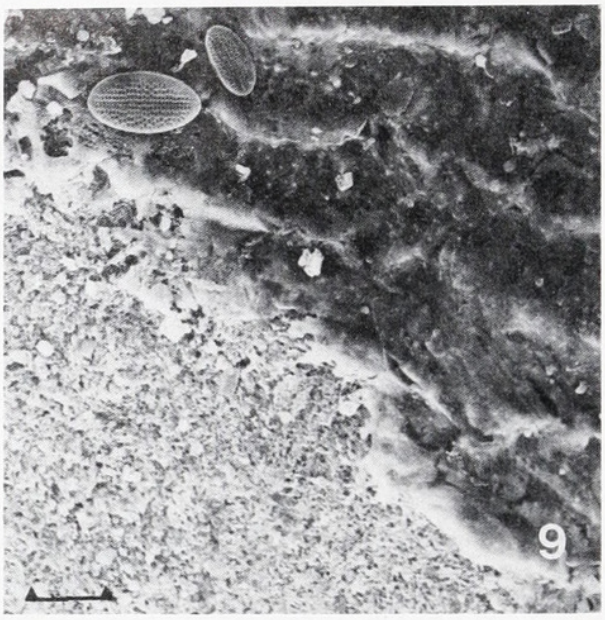
Cibicides refulgens secondarily forms an elaborate agglutinated tube system around, and extending from, its attached test. The agglutinated tube system typically is comprised of: (1) a peripheral tube encircling most, if not all, of the lateral test margin at the point of contact between it and the substrate (Figs. 2, 3, 25, 26), and (2) radial tubes attached to the substrate and test, extending over the shell surface and vertically away from it (Figs. 1b, 3, 4, 27). These tubes often form several branches (Fig. 3).

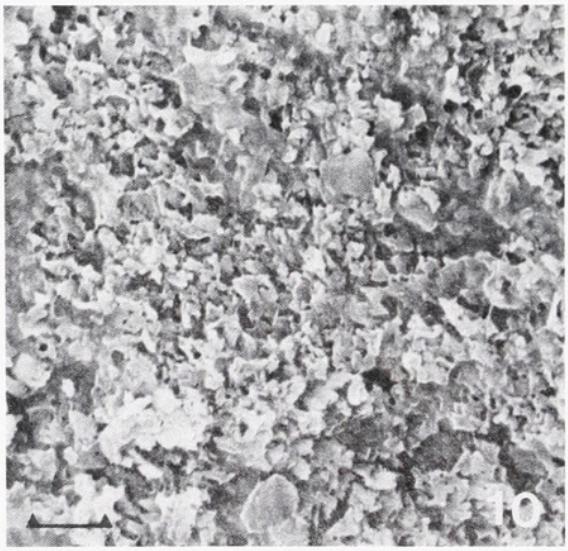
All radial tubes originate from the peripheral tube, either dividing from it without any observable thickening, or arising from a distinct node at a particular point. Tubes extending horizontally along the shell surface and vertically into the overlying water may branch from the same nodes. There is no obvious organization of the branching patterns of *C. refulgens*. Typically, *C. refulgens* has from 1 to 6 ($x = 3$, $n = 50$) agglutinated tubes extending vertically up to 5 millimeters ($x = 2.5$, $n = 50$) from their points of origin at the peripheral tube. Vertical tubes may exhibit up to three orders of branching, and tube diameter does not vary consistently with length or distance from the test/substrate; thickenings or nodes can occur at any point along a tube. The interior tube surface is smoother than the outer surface (Fig. 26), and in freeze dried specimens it is partially covered with a layer of cytoplasm.

Intact tubes, when viewed in the SEM, do not show clearly defined apertures; openings are inferred by the presence of pseudopodia which extend from many points along the tubes to either the shell surface, test surface, or other tubes. Apparent aper-









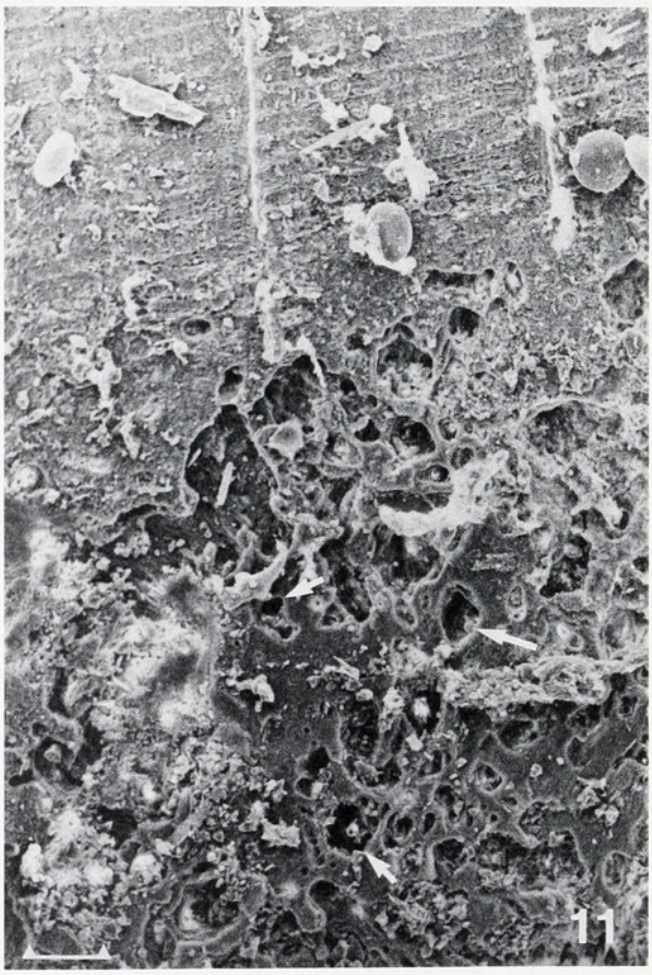


FIGURE 7. Substrate markings caused by an adult *Cibicides refulgens* after three months of attachment. There is no visible etching of the shell surface, but adhesion was great enough to break away some test material upon removal of the foraminifer. Scale bar = 200 μm.

FIGURE 8. 'Early stages' of substrate pitting. The striae of the scallop shell have been removed, and from two to three laminae have been eroded. There is no evidence of boring to form canals. Scale bar = 110 μm.

FIGURE 9. Detail of peripheral region of an early stage pit. The surface lamina has been etched away (lower left) and the calcite beneath has been partially eroded to form fine, angular granules. Scale bar = 11 μm.

tures such as that shown in Figure 31 are caused by tube breakage during collecting or transport of the scallops.

Removal of specimens from the water causes the vertical tubes to collapse against and adhere to the substrate, forming what then appears to be a system of surface tubes which resemble polycheate worm tubes. However, cytologically fixed and freeze dried tubes are able to partially support themselves thereby almost maintaining their natural positions (Figs. 4–6), and thus facilitating examination in the SEM.

The walls of all tubes are clearly agglutinated and comprise fine (silt- and clay-sized) mineral particles, diatom frustules, fine organic detritus, and occasional sponge spicules (Figs. 5, 26–28, 31). The cementing material is not clearly distinguished from the agglutinated particles and does not cover their outer surfaces. Wall thickness varies considerably but is generally from one to four particles thick with no evidence of layering or selection of specific particle size for construction. Particle recruitment by foraminiferal cytoplasm during tube construction seems to be dependent on the availability of sedimentary material on the scallop shell surface. Similarly, the incorporation of specific diatom frustules into the tubes is related to the dominant flora growing upon the scallop shell, and perhaps, the diet of the foraminifer.

Extrathalamous cytoplasm and pseudopodia were studied for gross morphology using both living and freeze dried specimens attached to pectin shells. An extensive pseudopodial net was observed spread over most of the shell surface in areas densely populated by *C. refulgens* (Fig. 32). The dorsal test surface of *C. refulgens* usually is partially covered with cytoplasm in the form of tangled strands (Figs. 32, 33). From this, randomly branching and anastomosing networks of pseudopodia emanate and connect with neighboring tests, agglutinated tubes, and/or clumps of algal or detrital material. Trunk pseudopods are usually found closer to the substrate, originating from peripheral or vertical agglutinated tubes, and traversing portions of the shell while remaining suspended above it (Figs. 3, 4, 5). Fine pseudopodial elements branch at apparently random points along trunk pseudopods and connect with others nearby (Fig. 34), or attach to the substrate beneath. These elements often merge with a finer net system attached to the substrate at raised points such as striae, and spread over most of the shell surface in the vicinity of the adult *C. refulgens* (Fig. 35). The rectilinearity and patterning of elements forming the fine nets and the limited extent of sagging when they are bearing dense mineral particles is indicative of tension within the system. The larger trunk pseudopods often visibly sag when crossing spaces between neighboring foraminifers and clumps of detrital material.

Vertical agglutinated tubes also give rise to trunk pseudopods and finer branching elements suspended freely in the water space immediately surrounding and above the tubes. Relative movement of the water in this space causes the pseudopods to bend and wave freely, demonstrating extreme flexibility in response to water movement.

All of the pseudopodia have a sticky quality when touched with single hair brushes or steel microprobes; once adhered they stretch considerably under tension before breaking. Diatoms, sedimentary particles, and organic debris are commonly observed attached to pseudopodia (Figs. 36, 37), and large clumps of detrital material were

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FIGURE 10. Detail of pit base in Figure 9. Note the fine 'pores' visible between the angular calcite granules. Scale bar = 2.8 μm.

FIGURE 11. A well developed substrate pit (bottom half of micrograph) with characteristic deep borings visible (arrows) penetrating several laminae of the scallop shell. Scale bar = 62 μm.

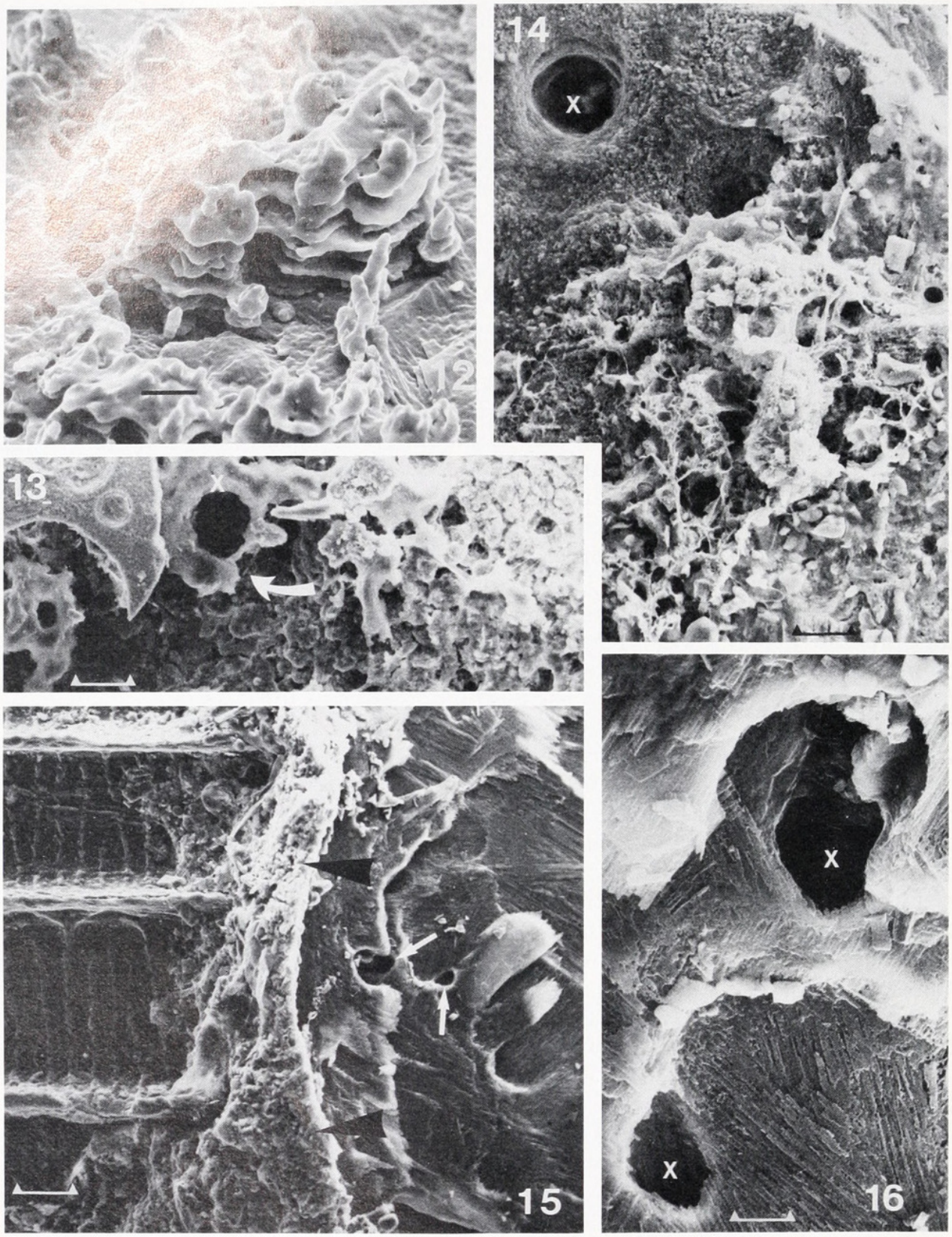

FIGURE 12. A resin cast of the central portion of a substrate pit formed by an adult *Cibicides refulgens;* the raised central area represents channels within the scallop shell which were originally occupied by foraminiferal cytoplasm. Scale bar = 20 μm.

FIGURE 13. Irregular etching of calcite at the pit edge. A bored hole in upper calcite layer (×) has been undercut by subsequent dissolution of lower layers (arrow). Scale bar = 31 μm.

FIGURE 14. Peripheral area of a deep substrate pit showing transition from scallop shell surface (bottom right) to extensively etched pit base (top left) and a circular vertical boring (×). Scale bar = 18 μm.

FIGURE 15. Transition from normal scallop shell surface (left) to a deep pit (right) eroded by a large adult *Cibicides refulgens.* Removal of the foraminifer has torn away the uppermost calcite layer, exposing

often observed suspended above the substrate within pseudopodial nets. Such inclusions may be partially engulfed by cytoplasm and/or suspended by a pattern of reticular 'subnets' formed between main pseudopodial elements (Fig. 36).

Figure 40 presents the results of three experiments to further examine the sources of particulate organic material used as a nutrient source by *Cibicides refulgens*. Though patchy in distribution, benthic diatoms (primarily *Cocconeis* sp. approximately 15 μm in length) represent a potentially significant resource to grazing organisms living on the surface of the bivalve. Time course studies monitoring the consumption of radio-labeled benthic algae by *C. refulgens* demonstrated average grazing rates of 54.5 diatoms mg^{-1} h^{-1} (n = 60, min = 14, max = 1030). The relatively large differences in uptake rate can be accounted for by the proximity of the foraminifer's attachment site to benthic diatoms on the surface of the bivalve shell. Two other experiments examined the rate of capture of suspended bacteria and diatoms. These experiments were additionally designed to determine the relative importance of the agglutinated tubes in suspension feeding. In both of these experiments half of the attached foraminifers were cleaned of all agglutinated tubes to evaluate the importance of these structures to suspension feeding efficiency. While suspended cultures of *Nitzchia cylindricus* (5–10 μm at concentrations of 8×10^4 cells ml^{-1}) were taken at rates of 153 cells mg^{-1} h^{-1} (n = 15, min. = 82, max. = 284) by foraminifers with their arborescent agglutinated tube structures intact, those without this superstructure averaged rates of only 62 cells mg^{-1} h^{-1} (n = 15, min. = 32, max. = 141). Similarly, suspended bacteria (unidentified gram negative rods 1.2×2 μm at 2×10^6 cells ml^{-1}) were consumed in greater numbers by *C. refulgens* with agglutinated tubes ($x = 4.2 \times 10^2$ cells mg^{-1} h^{-1}, n = 15, min = 1.1×10^2, max. = 6.7×10^2) than those without agglutinated tubes (x = 69 cells mg^{-1} h^{-1}, n = 15, min. = 21, max. = 1.7×10^2).

The discovery of pronounced etching channels penetrating through the shell clearly placed foraminiferal cytoplasm in contact with the nutrient-rich extrapallial space formed between the mantel and the inner surface of the shell, and suggested a parasitic relationship. Our studies using radio-labeled amino acids demonstrated the 0.5–0.7 mm thick unetched bivalve shell is not permeable to free amino acids. However, when the inner surface of the bivalve shell opposite attached *C. refulgens* was bathed with radio-labeled amino acids (100 μM), the foraminifers consistently became radioactive within a few hours. These experiments were duplicated with heat (30°C for 30 min) killed *C. refulgens* and no radioactivity was detected.

Figure 39 presents the uptake of uniformly ^{14}C labeled mixture of amino acids from seawater at various concentrations. This curve is clearly hyperbolic and suggests that the transport system for amino acids in *Cibicides refulgens* can be described by the Michaelis-Menten equation. The data have therefore been analyzed by a Hanes-Woolf plot (where substrate concentration divided by rate of influx is plotted against substrate concentration). As shown in Figure 40, J_{max} is 3.59×10^{-3} μmoles mg^{-1} (wet weight of protoplasm) h^{-1} and the K_t (substrate concentration at which the rate of uptake = $J_{max}/2$) is 10.43 μM.

Analysis of the fluid filling the extrapallial cavity were conducted using high pres-

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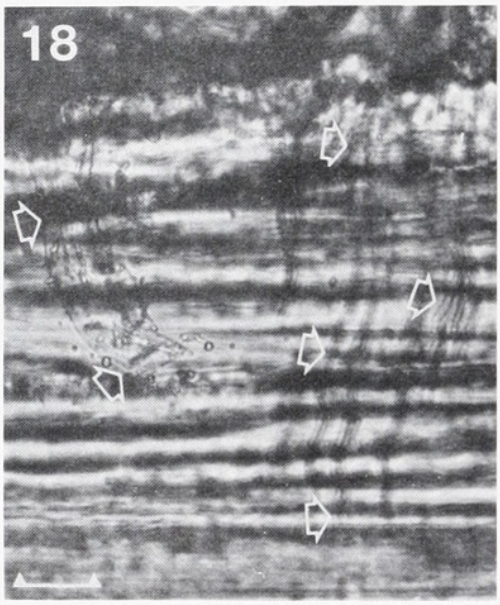
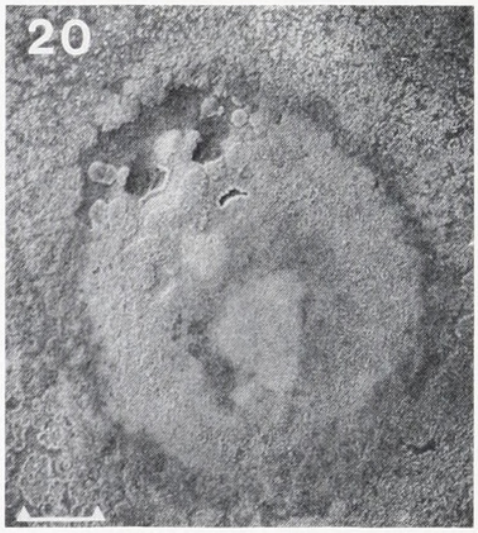
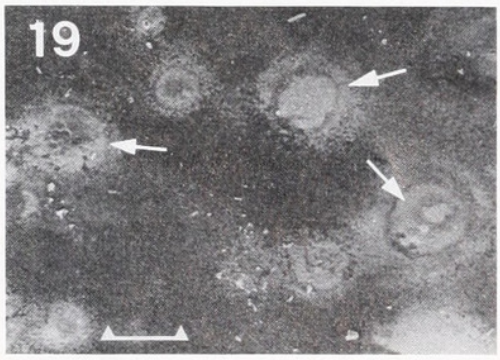
unetched laminae beneath and canals penetrating deeper into the shell material (arrows). Part of the agglutinated peripheral tube remains secured to the shell surface (large arrowheads). Scale bar = 36 μm.

FIGURE 16. Detail of Figure 15 demonstrating the distinct canal borings (×) in shell material beneath the attached foraminifer. Scale bar = 6.7 μm.







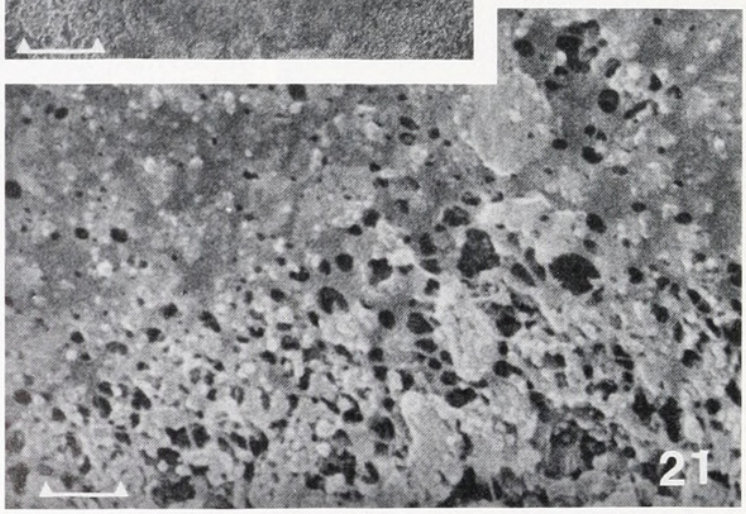


FIGURE 17. Thick cross section through a resin-embedded adult *Cibicides refulgens* attached to *Adamussium colbecki*. Groups of canals are discernible originating from the base of the pit and passing through most of the shell thickness (arrows). Scale bar = 200 μm.

FIGURE 18. Detail of Figure 17 showing the canals to be continuous through to the inner-most laminae of the scallop shell (arrows). Scale bar = 480 μm.

FIGURE 19. Acid etched inner shell surface with foraminifers attached to the opposing face. Each mark (arrows) corresponds to groups of canals penetrating the shell from the surface pits above. Scale bar = 250 μm.

sure liquid chromatography. The results (Table I) revealed concentrations of 2527 μM (2.527 mM) free amino acids with extremely high concentrations of glycine (2066.3 μM).

Discussion

The rarity of loosely attached or 'roaming' *C. refulgens* on the surfaces of scallop shells strongly suggests that the sessile habit is preferred by this species. The poorly eroded pits beneath juveniles and the extensive pits associated with adults, leads to the assumption that pitting progresses with growth at least until the adult stage is reached (data on the life span of *C. refulgens* are unavailable). Specimens experimentally placed on a previously unmarked scallop shell became firmly attached to the substrate and began to construct agglutinated tubes. However, the lack of significant etching after three months raises several interesting questions: is this the typical rate of etching which would be observed by those specimens attached to live *A. colbecki?* Alternatively, is it significantly lower in response to the absence of specific cues? We have demonstrated that amino acids do not normally leach through the shell material, thus it seems unlikely that this would act as a cue to initiate excavation; cues could conceivably come from a variety of stimuli, such as rates of sediment accumulation on the shell surface, the presence or absence of organic materials from scallop excretion, and the presence/absence of water movements over the shell surface. Extensive further studies are required to investigate the role (if any) of environmental cues in initiating substrate erosion by *C. refulgens.*

Parasitism

Our investigations have shown that 50% of attached *C. refulgens* significantly erode the surface of the scallop's shell and excavate channels to the extrapallial cavity. Though the scallop shell normally is not permeable to dissolved amino acids, radiolabeled studies have consistently shown uptake of amino acids by attached foraminifers. This uptake could only have been mediated by pseudopodia penetrating through the shell. The nutritional significance of dissolved amino acids to several marine invertebrate species has been discussed by other workers (Southward and Southward, 1972; Stephens, 1981) including foraminifera (DeLaca *et al.*, 1981; DeLaca, 1982). *Cibicides refulgens* has the ability to absorb free amino acids at relatively low substrate concentrations (K_t = 10.43 μM). However, concentrations of free amino acids within the extrapallial space are more than two hundred times higher (2527 μM, [2.527 mM]) than the half saturation concentration (K_t). Therefore, a logical assumption that the foraminifer has little difficulty realizing its maximal rate of influx (J_{max} = 3.59×10^{-3} μg, mg^{-1}, h^{-1}) from the scallop, and presumably this source of material would be available to the foraminifer year-round.

A wide range of associations between individuals of different species in which one

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FIGURE 20. Detail of Figure 19 showing salient features directly beneath a substrate pit on the opposing shell surface. Scale bar = 60 μm.

FIGURE 21. Detail of Figure 20 showing fine perforations present in laminae exposed by etching with HCl. Scale bar = O.9 μm.

FIGURE 22. Detail of canals exposed during fracture of the shell through a pit. These canals are approximately midway through the dorsal shell material and contain precipitated material, most probably cytoplasm. Scale bar = 23 μm.

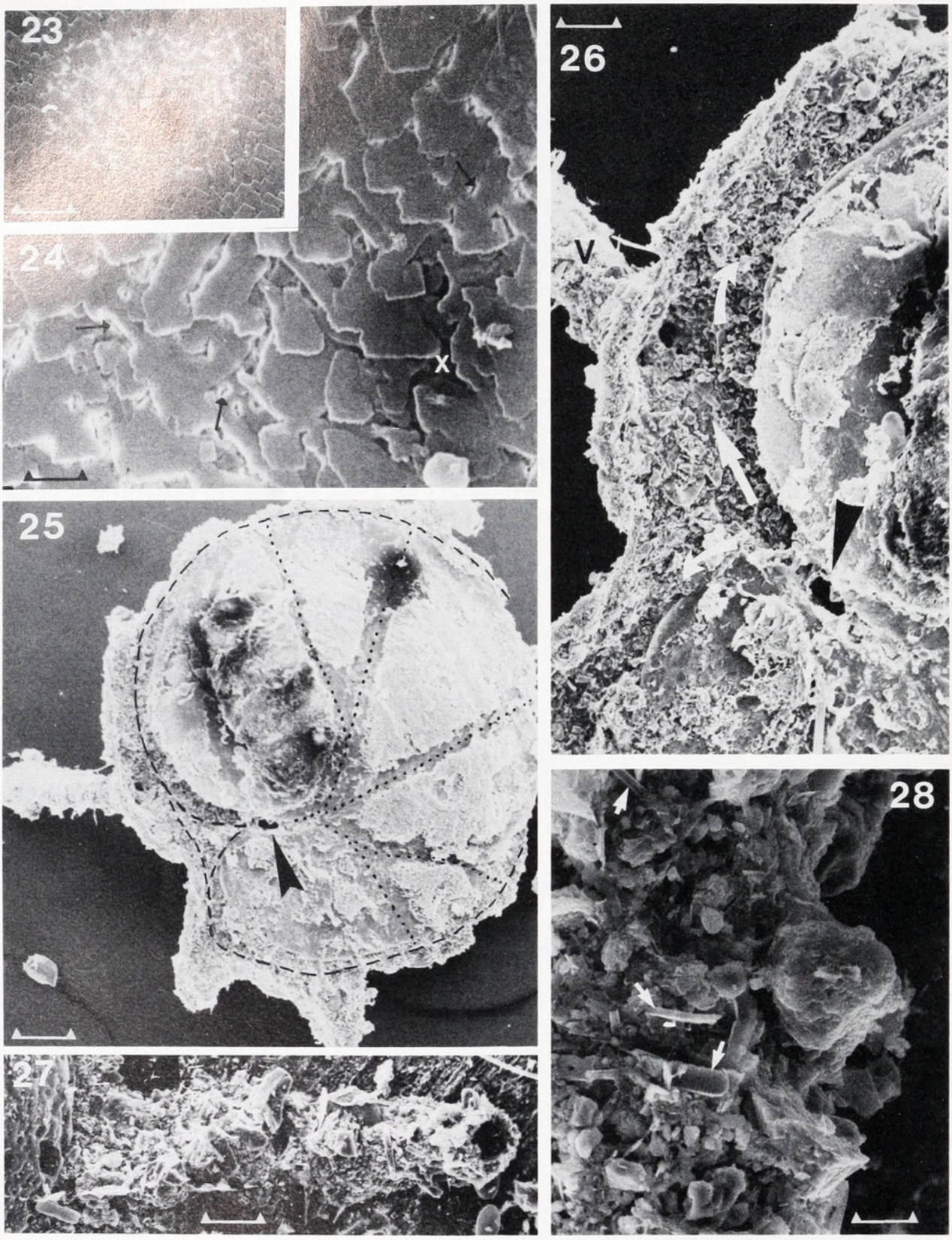

FIGURE 23. Inner surface of dorsal scallop valve showing marking which is often observed when the opposing surface is heavily colonized with *Cibicides refulgens*. Scale bar = 6.2 μm.

FIGURE 24. Detail of Figure 23 demonstrating enlarged 'pore' between calcite plates (×) and numerous 'micropores' located peripherally (arrows). Scale bar = 1.0 μm.

FIGURE 25. Umbilical view of an adult *Cibicides refulgens* removed from the valve surface. The primary aperture (arrow head) opens into (a) the lumen of the peripheral agglutinated tube (dashed line) and (b) grooves created between the umbilical face and the base of the pit (dotted lines). Scale bar = 150 μm.

or both derive benefit from the other have been described in the literature. They range from being obligate to being facultative (each partner being able to live without the involvement of the other), and the grades of association within this range often are not distinct. For convenience the relationships are frequently termed commensal and parasitic. By definition, a parasite always lives to the detriment of its host. Parasitic life styles are frequently specialized and lead to development of morphological as well as physiological adaptations which ensure efficiency. The relationship between *C. refulgens* and *A. colbecki* is very similar to that described by Todd (1965) for *Rosalina carnivora* and *Lima angolensis*. Unlike Todd's work however, the present study presents unambiguous evidence that *C. refulgens* does derive nourishment from the mantel of its host. Whether the cumulative affects of approximately 900 attached *C. refulgens* (~400 [45%] of which may have created channels through the shell) have a detrimental affect on the bivalve in this marginal environment remains unknown, but seems likely.

Grazing

Morphological test elaboration in the form of a constructed horizontal tube systems on the scallop shell surface effectively increases the distance that pseudopodia can gather food without severely increasing risk of cytoplasmic loss to predation or other causes. For example, we have observed tanaid crustaceans living in tubes on the scallop shell and feeding on unprotected cytoplasm of extended pseudopodia from *C. refulgens*. Of course, cytoplasm within the agglutinated tubes of the foraminifer is contiguous with cytoplasm in the lumen of the last formed chamber and thus the tubes are regarded as an extension of that chamber. Whereas most calcareous foraminifera are compelled to withdraw all extrathalamous cytoplasm into the test when unfavorable conditions or predators are encountered, *C. refulgens* individuals need only withdraw pseudopodia into the agglutinated tubes for protection. Thus the total volume of cytoplasm deployed, and therefore the total area grazed, is vastly increased without much risk of cytoplasmic loss. Most calcareous foraminifera use only the cytoplasm present in the last formed, penultimate and sometimes the antepenultimate chamber for pseudopodia and extrathalamous cytoplasmic activity (Anderson and Be, 1978; Anderson, 1983; Alexander and Banner, 1984; Alexander, 1985), and therefore may gather food at limited distances from the test without considerable risk to cytoplasm.

Adamussium colbecki shells typically are colonized by benthic diatoms and bacteria, but their concentrations, diversity, and percentage of surface coverage, however, vary from specimen to specimen. This heterogeneity is typical in New Harbor both spatially and temporally on large and small scales, and organic productivity in this portion of McMurdo Sound is extremely seasonal; our observations indicate that pronounced shallow-water productivity may be limited to as little as 2½ months. (DeLaca, unpub. data). Although approximately six months of continuous sunlight

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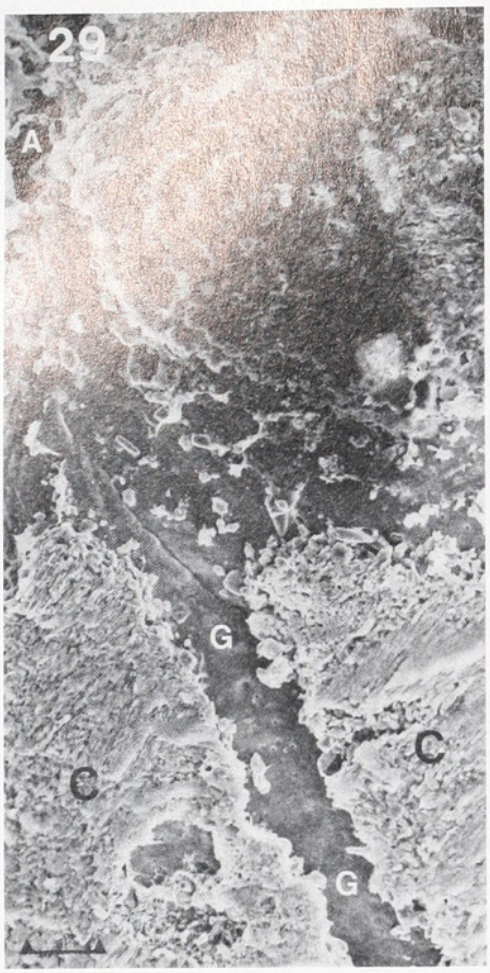
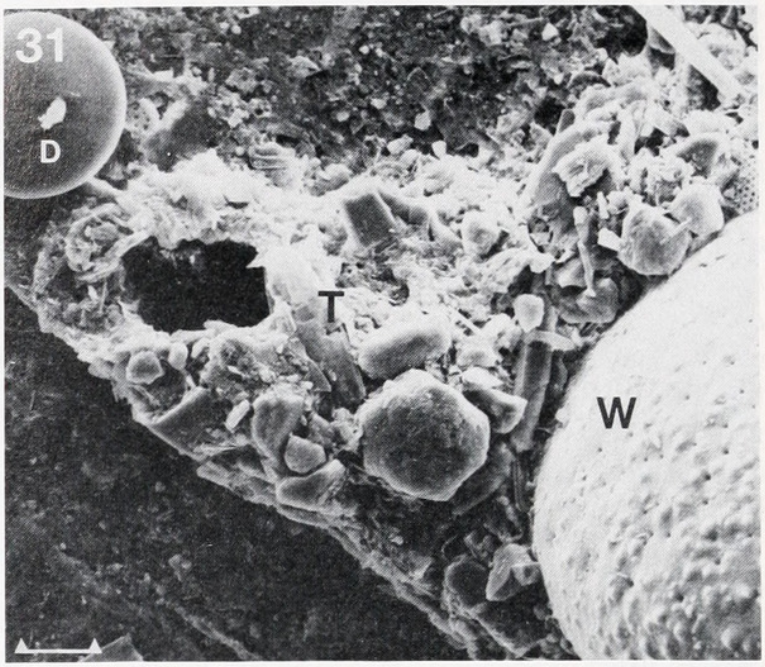
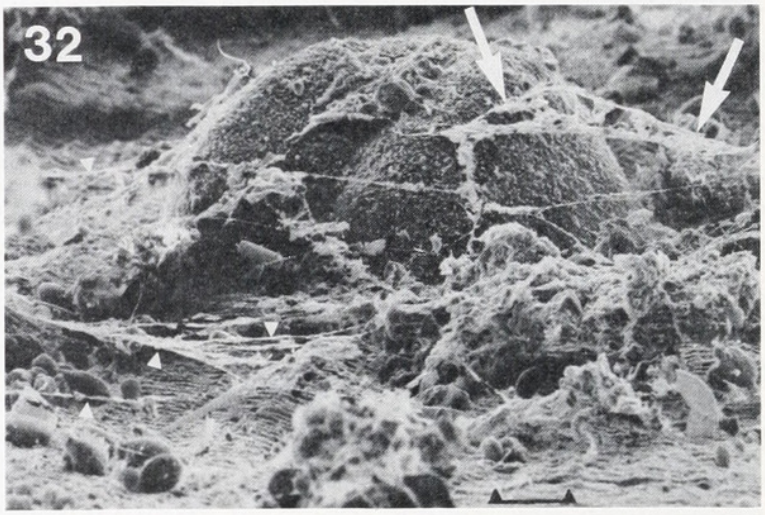
FIGURE 26. Detail of Figure 25, demonstrating continuity of the primary aperture (arrow head), with the lumen of the peripheral agglutinated tube (arrows) and that of a vertical agglutinated tube (V). Scale bar = 67 μm.

FIGURE 27. Surface morphology of a typical agglutinated tube (in this case, radial and in contact with the substrate). Scale bar = 67 μm.

FIGURE 28. Detail of typical agglutinated material forming tube walls. Arrows = diatom frustules. Scale bar = 12 μm.







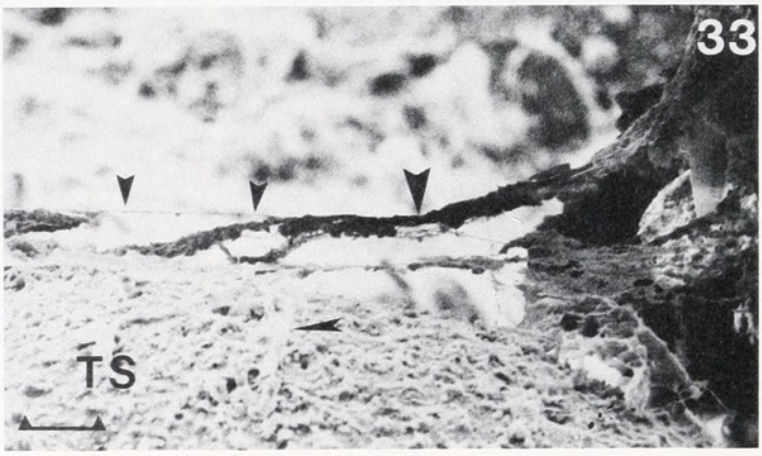


FIGURE 29. Detail of Figure 25 showing a radial umbilical 'groove' (G) which exists between the substrate surface in the pit and the umbilical test wall. A = primary aperture; C = Calcite broken away from pit base. Scale bar = 48 μm.

FIGURE 30. A typical eroded 'channel' (Ch) commonly observed on calcite which forms the base of umbilical 'grooves' in attachment pits. Scale bar = 4.2 μm.

FIGURE 31. Detail of agglutinated tubes (T) formed by juvenile *Cibicides refulgens* in Figure 2. D = Diatom; W = test wall of last formed chamber. Scale bar = 18 μm.

FIGURE 32. Oblique view of adult *Cibicides refulgens* attached to dorsal scallop valve. An extensive net of pseudopodia (arrow heads) is visible over the substrate and extending from the dorsal test surface (arrows). Scale bar = 83 μm.

is available annually, the combination of low angle of incident radiation, sea ice, and snow cover reduces the period of primary productivity further (see Dayton and Oliver, 1977).

Benthic diatoms on the scallop shell surface, as well as amorphous organic material and sediment, were attached to and transported by pseudopodia. Our experiments using *in situ* ^{14}C-labeled attached, and motile benthic diatoms, demonstrate that the foraminifers graze upon the naturally occurring 'lawns' of algae, and that relatively high numbers ($x = 54$ diatoms mg^{-1} h^{-1}) are consumed. Through the approximation of biomass and conversion to carbon content (Strathmann, 1967), it is estimated that if rate of harvest remained constant, those benthic diatoms would have contributed approximately 1×10^{-3} μg C mg^{-1} h^{-1}. That value is approximately one-half the amount of carbon obtained through the uptake of dissolved amino acids; thus grazing microorganisms from the surface of the scallop shell appears to be an important factor in *C. refulgens* nutrition. The discorbid foraminifer, *Rosalina globularis*, also forms deep pits in its preferred substrate (DeLaca and Lipps, 1972), and grazes upon algae in the immediate vicinity; however, in conditions of low food concentration it roams in search of algae (Sliter, 1965). In view of the patchy distribution of algae on *A. colbecki*, the selection of a sedentary habit by *C. refulgens* seems to have potentially reduced its grazing abilities. This disadvantage is more than compensated for by the permanent, or semi-permanent attachment between the scallop shell and the foraminifer, which virtually eliminates the risk of being swept off the shell during swimming movements of the scallop, and enables further morphological and physiological adaptations to the epizoic habit.

The radial grooves existing between the spiral side of the foraminifer's test and the surface of the pits increases the efficiency of this greater cytoplasmic volume through provision of a short line of communication between the primary aperture and the lumen of the peripheral tube on the opposite test side; this facilitates rapid exchange of cytoplasmic organelles and inclusions such as mitochondria, phagocytosed material, and energy substrates between the most distal pseudopodia and the intrathalamous cytoplasm. These internal-external lines of communication between deeply situated cytoplasm and the external milieu, are considered important in foraminiferan cell systems (Brasier, 1982).

Suspension feeding

Using the vertical agglutinated tubes as conduits for streaming pseudopodia and as anchors for pseudopodial nets, *C. refulgens* exploits suspension feeding as a third trophic mechanism. Figure 38 depicts the most typical arrangement of pseudopodia in an undisturbed living specimen; free pseudopodia are not rigid structures, but yield to water movement. Pseudopodial nets are randomly arranged and thus form a wide range of mesh sizes. Construction of the nets is initiated by the extension of pseudopodia from apertures along the vertical tubes, followed by contact with other tubes or nearby structures, and elaboration through bi-directional cytoplasmic flow. While unsupported pseudopodia of *C. refulgens* also have been seen projecting into the water, the construction of an agglutinated tube system provides scaffolding for further suspended pseudopodia within the water column, as well as a reservoir of protected

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FIGURE 33. Dorsal test surface (TS) of an adult *Cibicides refulgens* showing cytoplasmic strands (arrow heads) reaching to adjacent detrital material (far right). Scale bar = 3.2 μm.

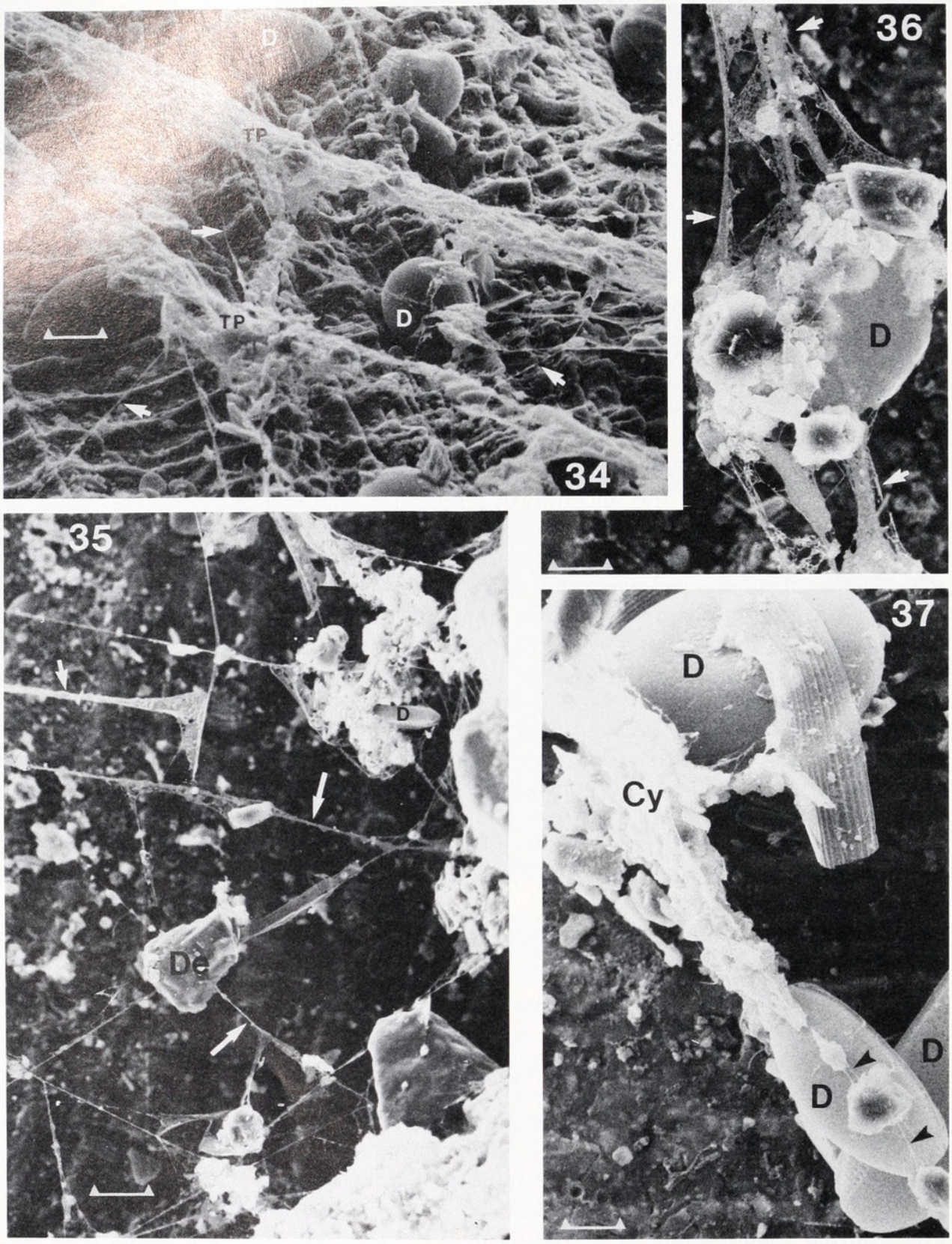

FIGURE 34. Trunk pseudopodia (TP) crossing the scallop shell surface and radiating away from a large adult *Cibicides refulgens*. Fine pseudopodia can be seen branching from the main trunk and attaching to the substrate (arrows). D = diatoms. Scale bar = 16.6 μm.

FIGURE 35. Finely branching pseudopodia (arrows) forming a net above the substrate. Detrital material (De) and diatoms (D) are entrained by pseudopodia. Scale bar = 17.2 μm.

FIGURE 36. Diatom (D) and attached detritus suspended above substrate by a fine anastomosing pseudopodia (arrows). Scale bar = 6.9 μm.

FIGURE 37. Cytoplasm (Cy) of pseudopod which has adhered to several diatoms (D) on the substrate surface. Note fine cytoplasmic threads (arrow heads). Scale bar = 8 μm.

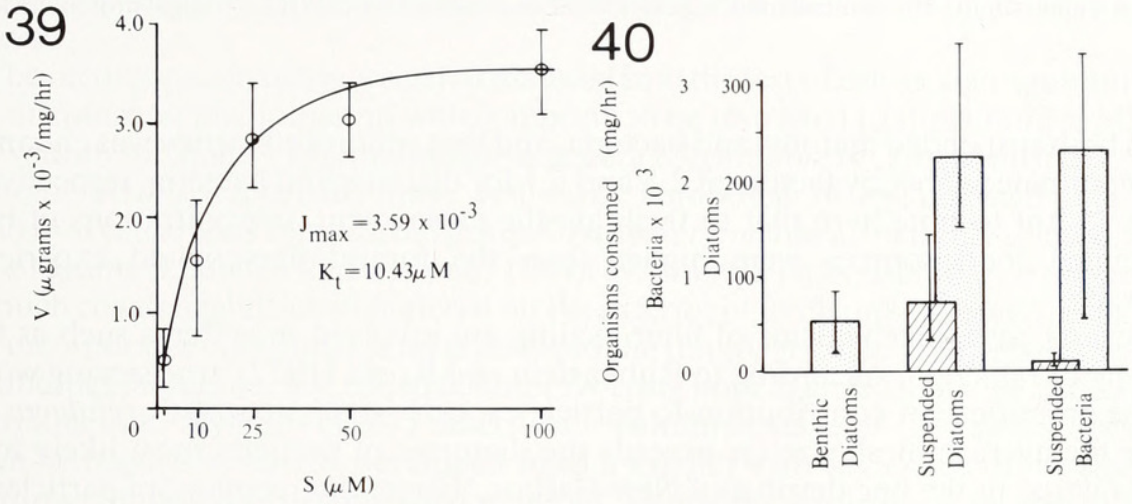

FIGURE 38. *Cibicides refulgens* attached to the shell of *Adamussium colbecki*, with pseudopodia deployed from agglutinated structures. (Not to scale.)

FIGURE 39. Velocity of uptake as a function of the concentration of dissolved amino acids in seawater. The values for J_{max} (μgrams/mg h) and K_t were obtained from a Hanes-Wolff linear transformation of the data. Each point is the mean of 10 replicates; bars represent the range of measurements.

FIGURE 40. Numbers of bacteria or diatoms taken (organisms/mg h) by *C. refulgens* through grazing (first bar) or suspension feeding. All agglutinated material was removed from half of the attached foraminifers (diagonal lines) while the remaining subpopulation was undisturbed (stippling) in order to determine if suspension feeding was facilitated by the agglutinated test extensions. Bar heights represent mean values (15 replicates for each suspension experiment and 60 replicates for the grazing experiment); error bars depict the range of values for each experiment.

cytoplasm. Agglutinated tubes radiate away from the substrate and have been measured to heights of five millimeters, and pseudopodia have been measured to extend an additional three millimeters from the tips of these tubes. The resulting canopy of branching tubes and pseudopodia potentially increases the volume of water available to suspension feeding by a factor of 10 to 20. Suspension feeding efficiency is further enhanced by the near proximity of other foraminifers and their tubes.

Our experiments using radio-labeled prey demonstrated that *C. refulgens* cap-

TABLE I

Free amino acids present in the extrapallial space of Adamussium colbecki

Amino acid	Concentration of AA in extrapallial cavity μM	Percent AA in ^{14}C protein hydrolysate*
Alanine	87.1	9.3
Arginine	165.5	6.3
Asparagine	11.0	0.0
Glycine	2066.3	4.6
Histidine	0.0	4.0
Phenylalanine	26.5	6.7
Proline	—	5.6
Serine	76.8	4.8
Tyrosine	11.8	3.6
Glutamic acid	24.1	11.8
Valine	13.1	6.8
Isoleucine	8.9	4.8
Leucine	12.7	11.8
Lysine	17.3	5.1

* An analysis given by Amersham Corporation for its product CFB.25 ([U-^{14}C]algal protein hydrolysate).

tured both suspended diatoms and bacteria, and that capture efficiency was enhanced by agglutinated tubes by factors of 2.5 and 6.1 for diatoms and bacteria, respectively. It is relevant to note here that to facilitate the experiment, concentrations of both suspended food sources were higher than the foraminifers would experience naturally.

Several basic mechanisms of filter feeding are involved in systems such as that used by *C. refulgens*. According to Rubenstein and Koehl (1977), true sieving would not be an important contribution to particle capture in the nets of *C. refulgens* because the average mesh size far exceeds the diameter of particles most likely to be encountered in the fine detritus of New Harbor. 'Direct interception' of particles by the sticky pseudopodia would form a large part of the filtering process, as would 'motile particle deposition' of, for example, motile algae and bacteria. 'Gravitational deposition' of particles resuspended by the non-locomotory flapping motion of the scallops, is likely to provide an important source of captured material. The requirement for water movement to allow filter feeding through the pseudopodial sieve must be satisfied almost entirely by movements of scallops, either locomotory (which occurs infrequently; see Mullineaux and DeLaca, 1984), non-locomotory, or by low velocity localized turbidity currents observed by DeLaca *et al.* (1980).

How material is entrapped by pseudopodia of *C. refulgens* and transported to the agglutinated tubes or the cell body, has not been previously investigated. However, detailed information is available on the ultrastructural aspects of particle/prey entrapment and transport by pseudopodia of the Antarctic foraminifer *Astrammina rara* (see Bowser and DeLaca 1985a, b; Bowser *et al.*, 1986), and *Allogromia* sp. (Bowser and McGee-Russell, 1982). In *Allogromia* sp. attachment is mediated by 'ultramicrospikes' and 'ultramicrowebs' which possess special adhesive properties (Fig. 3, in Bowser and McGee-Russell, 1982; McGee-Russell *et al.*, 1982). Structures almost identical to the ultramicrowebs of *Allogromia* sp. were observed in *C. refulgens*. These structures were found at the points of pseudopodial bifurcation, and in areas where particles were suspended (see Fig. 37) by the pseudopodia. That these structures sur-

vived the crude freeze-drying techniques available to us in Antarctica, without low calcium treatment and critical point drying, suggests that they may be even more extensive than our results indicate. These two taxonomically distant species appear to employ a similar mechanism for particle entrapment.

Suspension feeding has been reported for a number of benthic foraminiferal genera, most of which possess elevated stalk-like tests anchored at one end to the substrate (See Christiansen, 1971; and Lipps, 1982; 1983 for reviews); in addition, two species of the benthic rotaliid *Elphidium* have been observed with three-dimensional pseudopodial networks extending into the seawater medium, which would be efficient collectors of free-floating food particles (Jepps, 1942; Sheehan and Banner, 1972). In addition, the arborescent foraminifer *Notodendrodes antarctikos* DeLaca, living in New Harbor, captures bottom sediments which are brought into suspension by activities of larger benthic invertebrates (DeLaca *et al.*, 1980) and, as with *C. refulgens*, this specialized mode of feeding is regarded as being an adaptation to an unusual oligotrophic environment. The availability of resuspended organic material could provide a more consistent source of food during the dark austral winter when benthic diatom productivity is low, and as such would compliment nutrients obtained by other mechanisms such as the uptake of free amino acids from the sediment and surrounding seawater in the case of *N. antarctikos*, and parasitism in the case of *C. refulgens*.

The incorporation of agglutinated material into the test of calcareous foraminifera is an uncommon phenomenon which appears to be restricted to the suborder Miliolina. Within the family Miliolidae, three genera (*Sigmoilopsis*, *Ammomasilina*, and *Schlumbergerina*) reportedly have test walls composed of agglutinated material bound by a calcareous cement; the genus *Denstostomina* has an external agglutinated layer of grains (Loeblich and Tappan, 1964). Within the Nubeculariidae, *Nubeculina* has much coarse agglutinated material on the exterior of its chambers, and *Nodobacularia* incorporates occasional sand grains into the test (*opera. cita.*). However, among the suborder Rotaliina, test construction involving both agglutinated and calcareous material is rare. Nyholm (1961) described a coniform stage of *Cibicides lobatulus* (which he regards as having developed from a zygote) with associated "tube-shaped structures composed of agglutinated material" extending vertically from the apex of the test, or occasionally, basally branching and leading from the aperture. Nyholm (1961) noted that an interspace of a few microns exists between the cytoplasm and the agglutinated wall of the coniform test; this may be morphologically analogous to the lumen of the circular agglutinated tube at the periphery of the test in *C. refulgens*. Indeed, regardless of which part of *C. lobatulus*' life cycle these agglutinated tubes are associated, it is apparent that they are, in some respects, structurally similar. Nyholm (1961) did not suggest a function for the agglutinated tubes which project into the water above the attached sarcode (although he states that the agglutinated coniform test determines the form of the outer calcareous chambers), but in light of our findings with *C. refulgens*, it is tempting to speculate that they are also concerned with the deployment of pseudopodia into the surrounding water as a mechanism for suspension feeding.

The taxonomic and phylogenetic significance of extensive agglutinated additions to the tests of members of the genus *Cibicides* is not understood and remains an interesting question for taxonomists.

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LITERATURE CITED

ALEXANDER, S. P. 1985. The cytology of certain benthonic foraminifera in relation to test structure and function. Unpublished Ph.D. thesis, Univ. of Wales, Cathays Park, Cardiff, Wales. 365 pp.

ALEXANDER, S. P., AND F. T. BANNER, 1984. The functional relationship between skeleton and cytoplasm in *Haynesina germanica* (Ehrenberg). *J. Foraminiferal Res.* **14**(3): 159–170.

ALLEN, E. J. 1953. Observations on the epifauna of the deep-water muds of the Clyde Sea Area, with special reference to *Clamys septemradiata* (Muller). *J. Anim. Ecol.* **22** pt. 2: 240–260.

ANDERSON, O. R. 1983a. *Radiolaria.* Springer-Verlag, New York.

ANDERSON, O. R. 1983b. Cellular specialization and reproduction in planktonic foraminifera and radiolaria. Pp. 35–66 in *Significances of Plankton Cycles in Population Survival and Dispersal,* K. Steidinger and L. Walker, eds. Chemical Rubber Co. Press, Cleveland Ohio.

ANDERSON, O. R., AND A. W. H. BE. 1976. A cytochemical fine structure study of phagotrophy in a planktonic foraminifer *Hastigerina pelagica* (d'Orbigny). *Biol. Bull.* **151**: 437–449.

ANDERSON, O. R., AND A. W. H. BE. 1978. Recent advances in foraminiferal fine structure research. Pp. 121–202 in *Foraminifera,* Vol. 3, R. H. Hedley, and C. B. Adams, eds.

BOCK, W. D., AND D. R. MOORE. 1969. A commensal relationship between a foraminifer and a bivalve mollusk. *Gulf Res. Rep.* **2**: 273–277.

BOWSER, S. S., AND T. E. DeLACA. 1985a. Skeletal elements involved in prey capture by the Antarctic foraminiferan *Astrammina rara. Proc. 43rd Ann. Meet. Electron. Microsc. Soc. Am,* G. W. Bailey, ed. Pp. 484–485.

BOWSER, S. S., AND T. E. DeLACA. 1985b. Rapid intracellular motility and dynamic membrane events in an Antarctic foraminifer. *Cell Biol. Int. Rep.* **9**(10): 901–910.

BOWSER, S. S., AND S. M. McGEE-RUSSELL. 1982. EM Cytochemical study of phagotrophy in the benthic foraminifer, *Allogromia sp.* (N. F. Lee). *J. Protozool.* **29**: 474.

BOWSER, S. S., T. E. DeLACA, AND C. L. RIEDER. 1986. Novel extracellular matrix and microtubule cables associated with pseudopodia of *Astrammina rara,* a carnivorous antarctic foraminifer. *J. Ultrastruct. Mol. Struct. Res.* **94**: 149–160.

BRASIER, M. D. 1982. Architectures and evolution of the foraminiferan test a theoretical approach. Pp. 1-41 in *Aspects of Micropaleontology,* F. T. Banner and A. Lord, eds.

BUCHANAN, J. B., AND H. R. HEDLEY. 1960. A contribution to the biology of *Astrorhiza limicola* (Foraminifera). *J. Mar. Biol. Assoc. U. K.* **39**: 549–560.

CHRISTIANSEN, O. 1971. Notes on the biology of foraminifera. *Vie Milieu, Suppl.* **22**: 465–478.

DAYTON, P. K., AND J. S. OLIVER. 1977. Antarctic soft-bottom benthos in oligotrophic and eutrophic environments. *Science* **197**: 55–58.

DeLACA, T. E. 1982. Use of dissolved amino acids by the foraminifera *Notodendrodes antarctikos. Am. Zool.* **22**: 683–690.

DeLACA, T. E. 1986. Determination of benthic rhizopod biomass using ATP analyses. *J. Foraminiferal Res.* **16**: 285–291.

DeLACA, T. E., AND J. H. LIPPS. 1972. The mechanism and adaptive significance of attachment and substrate pitting in the foraminiferan *Rosalina globularis* (D'Orbigny). *J. Foraminiferal Res.* **2**: 68–72.

DeLACA, T. E., J. H. LIPPS, AND R. R. HESSLER. 1980. The morphology and ecology of a new large agglutinated antarctic foraminifer (Textulariina: Notodendrodidae nov.). *J. Linn. Soc. Lond. Zool.* **69**: 205–224.

DeLACA, T. E., D. M. KARL, AND J. H. LIPPS. 1981. Direct use of dissolved organic carbon by agglutinated benthic foraminifera. *Nature* **289**: 287–289.

DOBSON, M., AND J. HAYNES. 1973. Association of foraminifera with hydroids on the deep shelf. *Micropaleontology* **19**(1): 78–90.

HAYWARD, J. J. B., AND J. R. HAYNES. 1976. *Clamys opercularis* (Linneaus) as a mobile substrate for foraminifera. *J. Foraminiferal Res.* **6:** 30–38.

JEPPS, M. W. 1942. Studies on *Polystomella* Lamark (Foraminifera) *J. Mar. Biol. Assoc. U. K.* **25:** 607–666.

LEE, J. J. 1983. Perspective on algal endosymbiosis in larger foraminifera. *Int. Rev. Cytol. Suppl.* Cytology supplement 14d.

LENGSFELD, A. M. 1969. Nahrungsaufauhme und verdauung bei der Foraminifera, *Allogromia laticollaris. Helgol. Wiss. Meeresunters.* **10:** 385–400.

LIPPS, J. H. 1982. Biology/paleontology of foraminifera. Pp. 1–21 in *Notes for a Short Course,* M. A. Buzas and B. K. Gupta, eds. Univ. of Tennessee, Department of Geological Sciences, Studies in Geology 6.

LIPPS, J. H. 1983. Biotic interactions in benthic foraminifera. Pp. 331–376 in *Biotic Interactions in Recent and Fossil Benthic Communities,* M. J. J. Tevez and P. L. McCall, eds. Plenum Publishing Co., New York.

LOEBLICH, A. R., JR., AND H. TAPPAN. 1964. Sarcodina, chiefly "Thecamoebians" and Foraminiferida. Pp. 1-900 in *Treatise on Invertebrate Paleontolgy,* Part C, Protista 2, R. C. Moore, ed. University of Kansas Press, Lawrence.

MCGEE-RUSSELL, S. M., S. S. BOWSER, AND S. T. KOURY. 1982. Motility organizing vesicles (MOV's) in *Allogromia* a new concept and term in cell motility. *J. Cell Biol.* **95:** 329a.

MOORE, P. G. 1985. *Cibicides lobatulus* (Protozoa: Foraminifera) epizoic on *Astacilla longicornis* (Crustacea: Isopoda) in the North Sea. *J. Nat. Hist.* **19:** 129–133.

MULLINEAUX, L. S., AND T. E. DELACA. 1984. Distribution of Antarctic benthic foraminifers settling on the pecten *Adamussium colbecki. Polar Biol.* **3:** 185–189.

NYHOLM, K. G. 1961. Morphogenesis and biology of the foraminifer *Cibicides lobatulus. Zool. Bidr. Uppsala* **33:** 157–192.

RICHARDSON, K. C., L. JASRETT, AND E. H. FINKE. 1960. Embedding in epoxy resins for ultrathin sectioning in electron microscopy. *Stain Technol.* **35:** 313–323.

RIVKIN, R. B., AND H. H. SELIGER. 1981. Liquid scintillation counting for ^{14}C uptake of single algal cells isolated from natural samples. *Limnol. Oceanogr.* **26:** 780–785.

RUBENSTEIN, D. I., AND M. A. R. KOEHL. 1977. The mechanisms of filter feeding: some theoretical considerations. *Am. Nat.* **111:** 981–994.

SHEEHAN, R., AND F. T. BANNER. 1972. The pseudopodia of *Elphidium incertum. Rev. Esp. Micropaleontol.* **4**(1): 31–63.

SLITER, W. V. 1965. Laboratory experiments on the life cycle and ecologic controls of *Rosalina globularis* d'Orbigny. *J. Protozool.* **12:** 210–215.

SOUTHWARD, A. J., AND E. C. SOUTHWARD. 1972. Observations on the role of dissolved organic compounds in the nutrition of benthic invertebrates. III. Uptake in relation to organic content of the habitat. *Sarsia* **50:** 29–46.

STEPHENS, G. C. 1982. Recent progress in the study of "Die Ernahrung der Wassertiere und der Stoffhaushalt der Gewasser." *Am. Zool.* **22:** 611–619.

STOCKTON, W. L. 1984. The biology and ecology of the epifaunal scallop *Adamussium colbecki* on the west side of McMurdo Sound Antarctica. *Mar. Biol.* **78:** 171–178.

STRATHMANN, R. R. 1967. Estimating the organic carbon of phytoplankton from cell volume or plasma volume. *Limnol. Oceanogr.* **12:** 411–418.

TODD, R. 1965. A new *Rosalina* (Foraminifera) parasitic on a bivalve. *Deep-Sea Res.* **12:** 831–837.

ZUMWALT, G. S., AND T. E. DELACA. 1980. Utilization of brachiopod feeding currents by epizoic foraminifera. *J. Paleontol.* **54:** 477–484.