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The ebridian flagellates *Ebria* and *Hermesinum*

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Abstract: Ebridian flagellates have a long geological history, but only two extant species: *Ebria tripartita* and *Hermesinum adriaticum*. The former species feeds extensively on diatoms and has a widespread distribution in coastal oceans; the latter species is mixotrophic and possibly autotrophic, with numerous *Synechococcus*-like endosymbiotic cyanobacteria, and is restricted to warmer waters associated with hypoxic or anoxic conditions. Ebridians were previously classified erroneously with dinoflagellates, but their nuclear structure is similar to that of euglenoid flagellates. These relict flagellates exhibit a distinct dichotomy in their structure, distribution, and trophic status. Their role in coastal ecosystems and their proper taxonomic classification is unclear since they have yet to be grown *in vitro*, but their occasional abundance suggests they may have an impact on nanoplankton and picoplankton biodiversity and microbial loop processes.

Key words: ebridian, flagellate, *Ebria*, *Hermesinum*, endosymbiosis

Introduction

The ebridian flagellates are a small group of marine microplankton with a rather long geological history. The first fossils attributed to this group are Cretaceous in age and the biodiversity maximum for ebridian genera was the late Eocene to early Miocene (Ernissee & McCartney 1993; Tappan 1980), about 40–20 Ma, with at least 25 genera reported during these epochs (Dell'agnese & Clark 1994; Loeblich et al. 1968; Gombos 1982). With many of these fossil genera, assignation to the ebridian group must be considered tentative. In the recent coastal plankton only four species have been reported worldwide: one species of *Ebria*; one species of *Hermesinella*; and two species of *Hermesinum*. Although *Ebria tripartita* (Schumann) Lemmermann is commonly reported worldwide from coastal plankton environments, *Hermesinum adriaticum* Zacharias is found only rarely, and both *H. platense* Frenguelli and *Hermesinella reliqua* Frenguelli et Orlando have been reported only once.

The general characteristics of ebridians are these: no external cell wall; an internal, three-dimensional siliceous skeleton composed of various solid elements whose triaxial or tetraxial nomenclature is well-established (Deflandre 1934); two slightly unqual flagella, subapically inserted; centrally located nucleus with condensed chromosomes during interphase; phagotrophic nutrition; no known sexual reproduction. Their taxonomic classification is confused: they have been regarded as a botanical class (Ebriophyceae) in the dinoflagellate division Pyrrhophyta (Sournia 1986); as the order Ebriida in the zoological phylum Sarcomastigophora (Lee et al. 1985); or as a class (Ebridea) in the novel phylum Neomonada (Cavalier-Smith, 1996/1997). Although not a diverse group, ebridians can play a role in plankton dynamics of coastal waters, since they can reach concentrations in excess of 10^5 cells/liter (Conover 1956; Hargraves & Miller 1974). The vast majority of studies on this group are micropaleontological, and mostly restricted to skeletal and stratigraphic description. Published research on extant ebridians is rare. The fortuitous presence of both extant ebridians in local waters over several years, coupled with supplementary material from elsewhere, provided an opportunity for closer examination.

Materials and Methods

Samples for study came from: Narragansett Bay, Pettaquamscutt River, and contiguous waters (Rhode Island, U.S.A.); embayments on Long Island (New York, U.S.A.); Chesapeake Bay (Virginia, U.S.A.); Indian River Lagoon (Florida, U.S.A.); the coastal waters of Shimizu (Japan); the Humboldt Current (Peru); and Golfo de Nicoya (Costa

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Rica). Light photomicrography (brightfield, epifluorescence, phase contrast, interference contrast) was done with a Zeiss Photomicroscope-II. Electron microscopy was done with a Zeiss EM9S2 and JEOL-STEM. For SEM and LM, samples were examined live or oxidized in hydrogen peroxide and air-dried onto stubs or cover slips. For TEM, samples were fixed in 1% glutaraldehyde/isotonic seawater, postfixed in 1% OsO_4, and gravity-concentrated for several hours. Individual cells were then picked, negative-stained (1% PTA) or imbedded in Spurr's resin, sectioned, and post-stained in Pb-citrate according to common protocols.

Results

The main morphological distinction between the two genera is that *Ebria* has three primary branches to its internal siliceous skeleton (triaxial), and *Hermesinum* has four primary branches (tetraxial). The nomenclature of the siliceous parts is based on that for sponge spicules, as proposed by Deflandre (1934). This terminology was more recently summarized by Ernissee & McCartney (1993) and Tappan (1980). The main longitudinal rod is the rhabde, the principal branches (three [triode] in *Ebria*, four [triaene] in *Hermesinum*) called actines, and peripheral bifurcations of the skeleton called clades.

In *Hermesinum adriaticum* (Fig. 1–13) skeletal morphology corresponds to the type description of Zacharias (1906), although there is variability in the degree of spininess of the siliceous branches and in the length of the major segments. The length of individual cells is 32–64 μm, and the width is 16–24 μm. The L/W ratio varies from 2.0 to 2.9. The most commonly seen morphological variation of the skeleton is a bend in the lower rhabde of about 80–90° (Fig. 6), with a frequency of <5%. Skeletons are duplicated internally prior to mitosis and cytokinesis, as described by Hovasse (1932). On one occasion in the Pettaquamscutt River, RI, 40% of all *H. adriaticum* cells in a preserved sample had paired skeletons. It is unclear whether this was a case of synchronous division or whether, as Hovasse (1932) suggests, cell division is inhibited if fusion of daughter skeletons occurs during silicon deposition. The fused skeletons of these cells were completely formed, at an angle of 80–110° to each other (Fig. 5), binucleate, but with just two flagella.

Examination of live cells reveals the beaded appearance of the nucleus (Fig. 2) enclosed within the actines, which led many investigators to ally ebridians with the dinoflagellates. This beading is due to the persistence of chromatin in a condensed state during nuclear interphase. To the eye, the color of the cell is slightly yellowish, or lacks color entirely. A transverse section at midlength of the cell is shown in Fig. 7. The sectioned actines and rhabde of the skeleton show fractures from the knife. The interphase nucleus is characterized by condensed chromatin, and a single prominent nucleolus is present. Mitochondria ('m' in Fig. 7) are consistently rounded in section, with tubular cristae. The lack of any sections with substantially elongated mitochondrial sections suggests that there is no mitochondrial reticular complex, but simply ovoid or subspherical units. Three membranes surround the nucleus (Fig. 8, 9) but one membrane is probably a continuous part of the endoplasmic reticulum. The outer periplast consists of dense fibrillar material, which becomes thickened in the region of the flagellar pore (Fig. 9). Scattered throughout the cell, but more numerous close to the cell membrane, are many cyanobacteria closely resembling *Synechococcus* (Fig. 7, 8, 10, 11). These cyanobacteria are slightly cylindrical or rod-shaped and typically are 1.1–1.4 μm in length and 0.8–1.0 μm in

Fig. 1–13. *Hermesinum adriaticum.* (LM=light microscopy; SEM=scanning electron microscopy; TEM=transmission electron microscopy).

Figures 1–5: scale bar = 10 μm. Figures 6, 7, 9–11, 13: scale bar=1.0 μm. Figures 8, 12: scale bar=0.1 μm.

Fig. 1. Entire skeleton, cytoplasm removed by chemical oxidation. LM/phase contrast.

Fig. 2. Living cell with 'beaded' nucleus; arrow=nucleus, arrowheads=flagella. LM/interference contrast.

Fig. 3. Living cell with ingested diatoms (arrowheads). The alveolate valve indicates this diatom is *Cyclotella.* LM/interference contrast.

Fig. 4. Entire skeleton, cytoplasm removed by chemical oxidation. SEM.

Fig. 5. Recently divided cells with skeletons still fused at an angle of 80–110°; cytoplasm removed by chemical oxidation. LM/brightfield.

Fig. 6. Antapical portion of rhabde bent at ca. 90°. SEM.

Fig. 7. Median thin section, ten *Synechococcus*-like cells visible, with two in division (indicated by *); siliceous skeleton (arrows) showing fracturing by the knife; m=mitochondrion. Typical nucleus structure with condensed chromatin and nucleolus. TEM.

Fig. 8. Single *Synechococcus*-like cell; portion of nucleus at left. TEM.

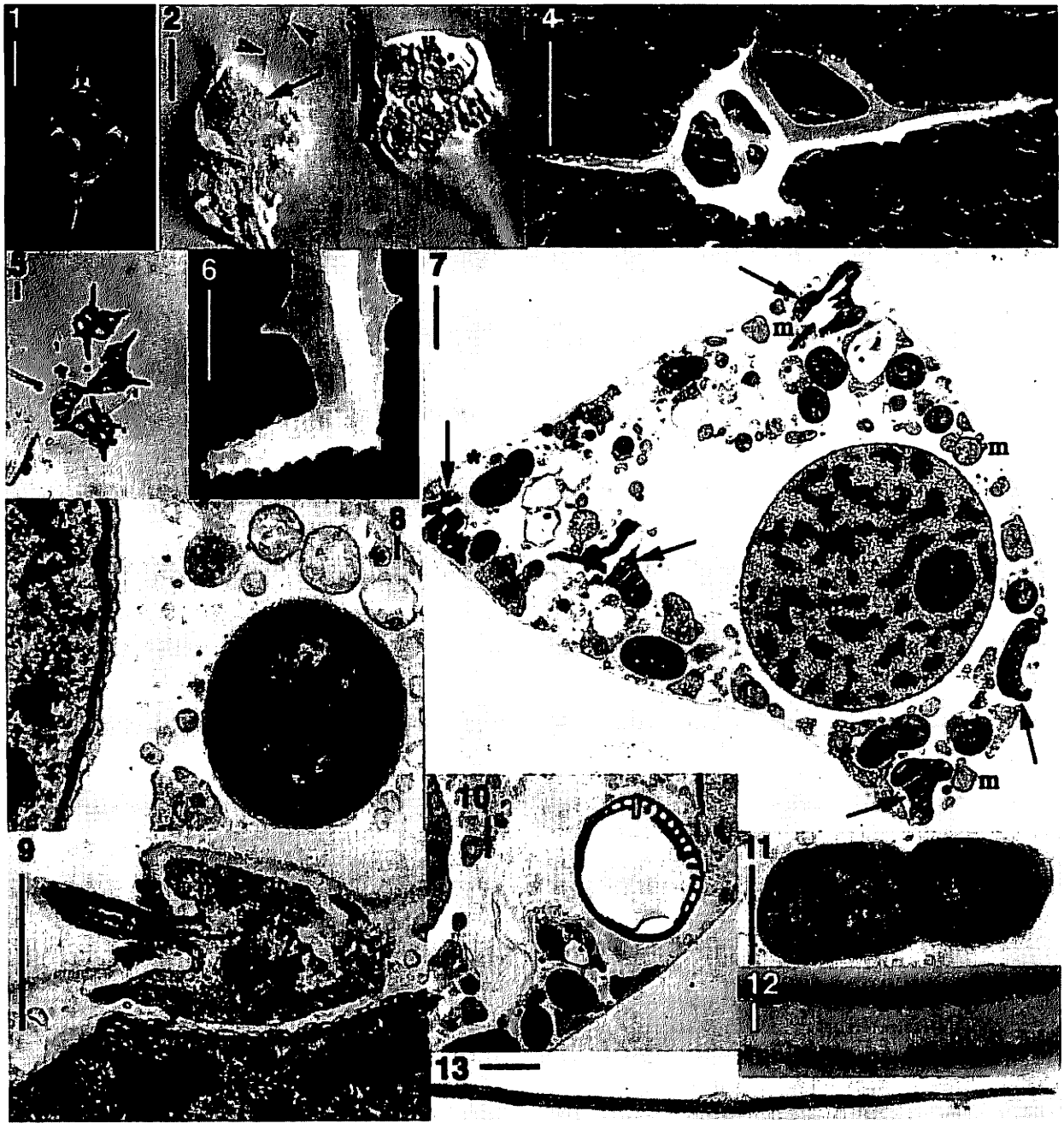
Fig. 9. Flagellar bases and kinetosomes adjacent to nucleus; flagella emerging at divergent angle from the cell; thickened portion of pellicle sround flagellar pore. TEM.

Fig. 10. Siliceous remains of an ingested cell of the diatom *Thalassiosira* (as indicated by the areolar and fultoportula structure). Two *Synechococcus*-like cells (at bottom) and portion of nucleus(at left) are also visible. TEM.

Fig. 11. Dividing *Synechococcus*-like cell. TEM.

Fig. 12. Median portion of flagellum. TEM/negative stained.

Fig. 13. Distal portion of flagellum. TEM/negative stained.



diameter. That these cyanobacteria are living and not merely ingested is clear from the frequent appearance of dividing cells (Fig. 7, 11). Most of the cyanobacterial cells have four thylakoids surrounding a central area with chromatin and carboxysomes (Fig. 8). With epifluorescent light microscopy they are visible in the *Hermesinum* cell as multiple orange/red bodies of micrometer size. All *H. adriaticum* cells examined from Rhode Island and Long Island waters contained cyanobacteria; cells examined from other locations either lacked cytoplasm or were preserved inappropriately for epifluorescence and electron microscope examination. Although *Hermesinum* can ingest diatoms (Fig. 3, 10), this is apparently an uncommon occurrence, with a frequency of <0.1% in several thousand cells examined.

The flagella of *H. adriaticum* are subapically inserted and slightly unequal in length, giving the cell a wobbling rotatory or helical motion in the water. Both flagella are smooth (Fig. 12) and taper gradually toward the tip with no hairpoint (Fig. 13). Flagellar bases and kinetosomes (Fig. 9) are in close association with the nucleus and emerge from the cell at strongly divergent angles from a slight promontory on the cell surface.

Geographic distribution of *H. adriaticum* is disjunct (Table 1). Most records are from subtropical or tropical environments, or from temperate localities during warmer months. Where quantitative data are available, maximum population density is well in excess of 10^5 cells per liter (Hargraves & Miller 1974; Vilicic et al. 1996/97). The envi-

Table 1. Known *Hermesinum adriaticum* Distribution

Location	Reference
* Northern Adriatic Sea	Zacharias, 1906; Vilicic et al., 1996/97
*Black Sea	Bodeanu, 1969
*Nile River mouth	Halim, 1960
Suez Canal	M. Elbrächter, pers. com., 1991
*Pettaquamscutt River, RI (USA)	Hargraves & Miller, 1974
*Coastal Long island, NY (USA)	Caron et al., 1989
*Chesapeake Bay, VA (USA)	Rhodes & Gibson, 1981; and pers. obs.
*Taylor's Creek, Beaufort NC (USA)	J. Burkholder, pers. com., 1995
*Indian River Lagoon, FL (USA)	J. Lackey, pers. com., 1973; and pers. obs.
*Salton Sea, CA (USA)	Carpelan, 1962; M. Tiffany, pers. com.,1999
*Golfo de Nicoya, Costa Rica	Pers. obs., 1994
*Pacific coast, COLOMBIA	C. Carbonell-Moore, pers. com., 2000
Shimizu (Shizuoka) Japan	Pers. obs., 1985
*Varano Lagoon, Italy	Caroppo, 2000

* Associated with hypoxic or anoxic conditions and/or stratification.

ronments where *H. adriaticum* is found are frequently characterized by hypoxic or anoxic subsurface conditions, either permanently or seasonally as a result of intense stratification. Interestingly, a recent study (Zav'yalova and Mikaelyan 1997) in the Black Sea where *H. adriaticum* was formerly abundant (Bodeanu 1969) failed to reveal its presence. Since the Black Sea has undergone considerable recent change in its pelagic ecosystem structure (Zaitsev 1992), *Hermesinum* may have been a casualty of biodiversity changes resulting from introduced species.

The more common *Ebria tripartita* has a rounded, slightly elliptical skeletal shape (Fig. 14). The variation in skeletal size is 24–34 μm in length, and 22–31 μm in width, based on samples from Narragansett Bay, Long Island, Chesapeake Bay, California (all USA), Japan, Peru, and the Pacific coast of Canada. The length/width ratio is about 1.1. Cells are biflagellate, with subapical flagellar insertion. The flagella are slightly unequal in length, and impart a wobbling rotatory motion to living cells (hence the genus name, from Latin ebrius='drunken'). The cells are quite sensitive to mechanical and thermal disturbance, and flagella are readily cast off. No flagellar ultrastructural details were apparent in the limited number of thin sections available. Form variations of the skeleton are due partly to the comparative completeness during formation, and partly due to variability of silicification. Both robust and thin skeletons may appear in the same population, without regard to skeleton size. During their initial formation skeletons appear as triradiate structures, with silicon deposition apparently progressing outward from the triradiate central portion of the skeleton (Fig. 15). Skeletal duplication takes place following mitosis. The paired skeletons are somewhat offset in *Ebria* (Fig. 18) rather than angled to each other as in *Hermesinum* (Fig. 5).

The nuclei of living cells of *Ebria tripartita* also show a beaded appearance (Fig. 19) but less distinctly so than those of *Hermesinum* (Fig. 2). A transverse section of *Ebria* (Fig. 16) shows the similarity of condensed chromatin in nuclei of the two genera. A single nucleolus is present (Fig. 17), but not visible in all thin sections (cf. Fig. 16). The nucleus is bounded by two membranes. The cytoplasm is highly vacuolate and vesiculate, with no trace of endosymbiotic cyanobacteria (nor were any detected by epifluorescence), and the outer cell membrane has a thin layer of fibrillar material on both the interior and exterior surfaces of the cell (Fig. 20). *Ebria* appears to be an obligate phagotroph, feeding on a variety of diatoms, including *Detonula*, *Leptocylindrus*, *Skeletonema* (Fig. 21) and *Thalassiosira* (Fig. 22). In the case of long chain-forming diatoms *Ebria* attaches to the chain and feeds progressively along its length, sometimes maintaining its flagella or even undergoing mitosis while attached. The details of this feeding process remain unknown. Although there are reports of *Ebria* feeding on dinoflagellates, only diatoms were seen as food in this study.

The geographic distribution of *Ebria* is quite extensive compared to that of *Hermesinum*. It appears most frequently in coastal waters and mesohaline portions of estuaries at temperatures of 6–22°C throughout the world. It is apparently absent from the Antarctic and Arctic oceans, although it was found at −1°C in the boreal North Atlantic (Smayda 1958) and is occasionally found in the tropics. Although it may become a significant part of the protist plankton in unusual circumstances (Conover 1956), *Ebria* rarely exceeds concentrations of 10^4 cells per liter. Geologically, both *E. tripartita* and *H. adriaticum* appeared first in the Miocene.

Discussion

Ebridians are commonly assumed to be herbivorous and/or bacterivorous, and for *Ebria tripartita* this is proba-

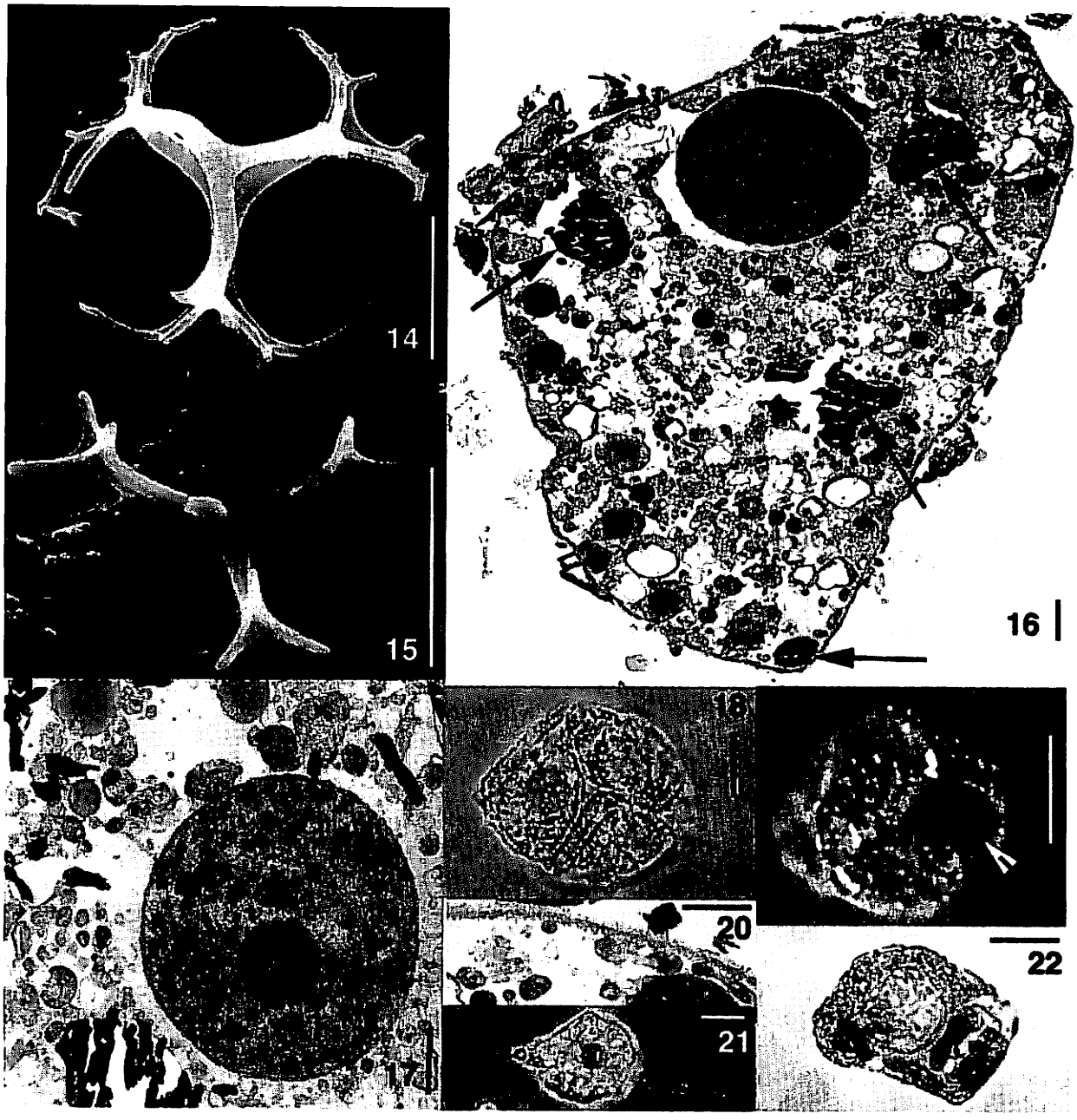


Fig. 14–22. *Ebria tripartita.* (LM=light microscopy; SEM=scanning electron microscopy; TEM = Transmission electron microscopy).

Fig. 14, 15, 18, 19, 21, 22: scale bar=10 μm. Fig. 16, 17: scale bar=1.0 μm. Fig. 20: scale bar=0.5 μm.

Fig. 14. Entire skeleton, cytoplasm removed by chemical oxidation. SEM.

Fig. 15. Partially formed skeleton, cytoplasm removed by chemical oxidation. SEM.

Fig. 16. Median thin section, silicon skeleton (arrows) showing fracturing by the knife. TEM.

Fig. 17. Detail of nucleus with nucleolus. Fragments of fractured silicon skeleton are scattered over the section. TEM.

Fig. 18. Recently divided cell with offset skeletons. LM/brightfield.

Fig. 19. Living cell with 'beaded' nucleus (arrowhead). LM/interference contrast, from a video frame.

Fig. 20. Detail of the cell membrane; fibrillar material on inner and outer surface. Compare with Fig. 9. TEM.

Fig. 21. Living cell attached to a chain of the diatom *Skeletonema costatum*. LM/phase contrast.

Fig. 22. Living cell with two ingested cells of the diatom *Thalassiosira*, one cell in girdle view, one cell in valve view. LM/brightfield.

bly true: a variety of diatoms are ingested, and others have observed dinoflagellates as food. In contrast, evidence of grazing on other planktonic protists was quite rare in *Hermesinum adriaticum*. It is clear that *Hermesinum* is mixotrophic, and perhaps is primarily autotrophic. The ultrastructural evidence suggests that the intracellular cyanobacteria are true endosymbionts rather than kleptoplastids, for reasons that are both physiological (they divide *in situ*, and no stages of digestion were seen) and semantic (they are entire cells, not plastids). The identity of the cyanobacteria is not unequivocal, but most probably they are members of the form-genus *Synechococcus*. The generic limits of many cyanobacteria are ill-defined, and in the classification scheme presented by Rippka et al. (1979) the only alternative to *Synechococcus* is *Synechocystis*, which differs in that it divides in three planes. Both genera are common in temperate coastal areas. *Synechococcus* is a common endosymbiont in sponges, opisthobranch molluscs and some dinoflagellates, where it can provide photosynthetic products and fixed nitrogen to the host (Paerl 1992). One may speculate on the value of photosynthetic endosymbionts to *Hermesinum* in relation to its restricted environment. In many places where it has been found, hypoxic conditions are persistent or frequent (Table 1.). The presence of oxygen-producing endosymbionts may provide such fortunate species with a competetive advantage over other protists where oxygen levels may be reduced to nil. In the Pettaquamscutt River where *Hermesinum* attains $>10^5$ cells/liter, two co-dominant protists are the ciliate *Perispira ovum* with euglenoid kleptochloroplasts (Johnson et al. 1995), and an undescribed species of the ciliate *Mesodinium* with internal phycocyanin-containing *Hemiselmis* cryptomonads (pers. obs.). The ability of these protists with photosynthetic endosymbionts or kleptoplastids to maintain populations under such environmental conditions may provide a partial refuge from predators and reduce competition for limited nutrient resources.

The inability to cultivate ebridians in the laboratory leave many unanswered questions regarding the details of cell division and life cycle. No resting stages (cysts) have been seen in either species, although they have been reported from fossil ebridians, and attributed to a developmental stage in sexual reproduction (Tappan 1980). The lack of apparent resting stages becomes a quandary in the case of *H. adriaticum*. As discussed in Hargraves & Miller (1974), this species is temporally and ecologically restricted, and must annually endure stressful conditions in a confined basin where it is unable to grow during much of the year, yet forms no identifiable resting stages: does it persist in an unrecognized form? Such is the case with the taxonomically unrelated silicoflagellate *Dictyocha speculum*. It forms motile and ameboid stages lacking an internal siliceous skeleton, which may be unrecognizable as silicoflagellates in natural populations (Moestrup and Thomsen 1990).

Until quite recently ebridians have been allied with the dinoflagellates in both botanical and zoological classification schemes. The primary justification for this view has been the perceived similarity (in the light microscope) of interphase chromosomes between dinoflagellates and ebridians. Secondarily, the presence of internal siliceous skeletons in dinoflagellates such as *Actiniscus* and *Dicroerisma* (Hansen 1993; Taylor & Cattel 1969) has been proposed as indication of a taxonomic relationship. The evidence presented here shows that the nuclear structure in both *Ebria* and *Hermesinum* is quite unlike that of dinoflagellates, which have nuclei with condensed chromosomes that are also fibrillar in appearance (Fensome et al. 1993). Moreover, nuclear structure suggests that ebridians are not closely related to siliceous radiolarians, as originally suggested by Hovasse (1932), nor as intermediate between dinoflagellates and radiolarians as suggested by Taylor (1990). Ebridian nuclei show considerable structural similarity to those of the euglenoid flagellates (e.g., Gavrila 1996; Leedale 1967; Sluiman 1993) but differ in other cytological characters, such as having mitochondria with tubular cristae (as opposed to mitochondrial reticula with flattened cristae in euglenoids, Walne & Kivic, 1990), lack of a euglenoid-like pellicle, and lack of unilateral hairs on the flagella. Further, Kivic & Walne (1984) have hypothesized a relationship between euglenoid flagellates and Kinetoplastidea based in part on ultrastructure, and there are other flagellates of unknown affinity with similar nuclei, e.g. *Cryothecomonas* (Thomsen et al. 1991). The structure of the outer periplast in both ebridian genera consists of fibrillar material; more dense in *Hermesinum* then in *Ebria* (it is somewhat subjective to decide exactly when fibrillar material is dense enough to be called a cell wall). In both genera the periplast bears a superficial resemblance to, among others, the Cryptophyceae, but no relationship to this class is implicit or explicit. Until ebridians are brought into culture, allowing additional cytological detail, mitotic patterns, and molecular genetics to be compared with these other groups, any relationships among them remains speculative. At present, ebridians are most appropriately placed *Incertae Sedis*.

It is likely that only two extant ebridians are found in modern seas. The other two species reported from contemporary marine waters are questionable. Both were described from the southern hemisphere. The first, *Hermesinella reliqua*, was described from the northern Palmer Peninsula in Antarctica by Frenguelli & Orlando (1958). This ebridian, of which only one example was seen, is from an area rich in Miocene deposits and has not been recorded since the original description, which is both incomplete and gives no evidence that it was living at time of collection. One must conclude that *Hermesinella reliqua* is a fossil form, probably reworked from the local Miocene sediments. Likewise, *Hermesinum platense* is probably a fossil. It was described as a single specimen from the Río de la Plata (Argentina) by Frenguelli (1942). This river drains portions of South America rich in fossil deposits of various Mesozoic and

Cenozoic ages, and Frenguelli again gives no evidence that the skeleton of his new species (which closely resembles *H. adriaticum*) is a living species. Recent examination of plankton materials from the same area (A. Gayoso, pers. com.) failed to reveal the presence of *H. platense*. Regardless of the taxonomic validity of the species, it does not appear to be extant.

Apart from distributional mention these flagellates have been overlooked in most studies. But a field study involving *H. adriaticum* showed a grazing rate of 4 microalgae (2–3 μm size) per hour per cell (Caron et al. 1989), which at maximum ebridian abundance of 10^5 cells per liter would unquestionably have a significant impact on nanoplankton and picoplankton diversity and abundance, and microbial loop processes. These relict flagellates exhibit a distinct dichotomy in their structure, distribution, habitat, and trophic status. Eventual success at laboratory cultivation will provide answers to the many questions arising from this dichotomy.

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