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OBSERVATIONS ON NORTH AMERICAN *GOMPHONEIS* (BACILLARIOPHYCEAE).  
I. VALVE ULTRASTRUCTURE OF *G. MAMMILLA* WITH COMMENT ON THE  
TAXONOMIC STATUS OF THE GENUS<sup>1,2</sup>

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ABSTRACT

Recent questions concerning the taxonomic status of the diatom genus *Gomphoneis* Cleve have prompted critical examination of the valvar morphology of a species originally included in the genus. Light and electron microscopic observations on *G. mammilla* (Ehr.) Cl. show that the characteristics put forth by Cleve to delineate the genus are present in this taxon. Striae composed of two rows of simple areolae located in depressions on the valve and longitudinal lines formed by a broad internal axial plate were observed in *G. mammilla*. The presence of two apical spines on the headpole and the structure of a bilobed apical pore field located at the footpole are described, in addition to other valve features. Valve morphology of *G. mammilla* is compared with that of doubly-punctate *Gomphonema* species with the result that we recommend the two genera remain separate.

Key index words: axial plate; diatom ultrastructure; *Gomphoneis*; *Gomphonema*; longitudinal lines; taxonomy

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The diatom genus *Gomphoneis* was erected by Cleve in 1894 to segregate forms previously placed in the genus *Gomphonema*, but which differed in having striae composed of two rows of puncta (i.e. doubly-punctate striae) and a shadow line running longitudinally on each side of the axial area (i.e. longitudinal lines). Cleve (1894) originally transferred three species from *Gomphonema* to *Gomphoneis*, making the new combinations *Gomphoneis elegans* (Grun.) Cl., *G. herculeana* (Ehr.) Cl. and *G. mammilla* (Ehr.) Cl. Since that time additional *Gomphoneis* taxa have been described by Schmidt (1899), Skvortzow and Meyer (1928) and recently by Stoermer (in Reimer 1982).

Observations with light and electron microscopy have revealed species in the genus *Gomphonema* which also possess doubly-punctate striae. Hustedt (1942) described *G. intermedium* as possessing striae composed of two rows of puncta. Studies using electron microscopy have shown that taxa such as *G. olivaceum* (Lyngb.) Kütz. (Drum 1969, Helmcke and Krieger 1953, Dawson 1974), *G. quadripunctatum* (Østr.) Wisl. (Dawson 1974) and *G. curtum* (Lange-Bertalot 1978) also have this characteristic. Striae characteristics led Dawson (1974) and Lange-Bertalot (1978) to transfer these taxa to the genus *Gomphoneis*.

A reexamination of the *Gomphonema/Gomphoneis* question by Lange-Bertalot (1980) led him to sug-

gest the two genera be reunited. He based his opinion on observation of *Gomphonema angustatum* (Kütz.) Rabh. in which a single specimen was noted to have doubly-punctate striae, those composed of a single row of puncta, and those of intermediate structure. Variation in the number of rows of puncta per stria in other *Gomphonema* taxa have also been observed (Drum 1969, Drum and Hopkins 1966, Hustedt 1945, Krammer 1982b). Lange-Bertalot (1980) also cited an illustration from Patrick and Reimer (1975) of *Gomphoneis herculeana* var. *clavata* Cl., which shows no longitudinal lines. Lange-Bertalot (1980) argued that the two characteristics upon which Cleve (1894) established the genus *Gomphoneis* were not conserved and therefore the two genera should not be separated.

The present study describes the ultrastructure of *Gomphoneis mammilla*, one of the taxa originally included in the genus by Cleve.

#### MATERIALS AND METHODS

Collections of *G. mammilla* were taken from various lotic habitats in the Cascade Mountains and in Klamath County, Oregon and Shasta County, California. Diatoms were cleaned with HNO<sub>3</sub> and processed according to procedures described by Patrick and Reimer (1966).

*Light microscopy (LM).* Frustules were mounted in Hyrax (Custrom Research and Development, Inc., Auburn, CA) or Cumar R-9 (Holmes et al. 1981) and examined with a Leitz Dialux-20 or Zeiss RA light microscope.

*Scanning electron microscopy (SEM).* Frustules cleaned as above were air-dried onto aluminum stubs, sputter coated with 20 nm of gold and examined with an Hitachi 500 scanning electron microscope. All micrographs were taken at low angles (<5°) of stage tilt, but some specimens illustrated may lie at various angles because of their orientation on the stub.

*Transmission electron microscopy (TEM).* Carbon replicas of cell surfaces were made with frustules cleaned as above and air-dried on glass slides. Frustules were first coated with carbon using a vacuum evaporator and individual diatoms selected, transferred onto a Formvar-coated grid with a hair and gently immersed in 5% HF for 5 min. The grids were washed in distilled water, air-dried and the replicas examined with an Hitachi H-300 transmission electron microscope. Some acid-cleaned frustules were embedded in Spurr's low viscosity medium (Spurr 1969) and oriented to give a transapical plane for sectioning with a diamond knife. Sections were examined without staining the material.

Terminology of valve characteristics follows that of Ross et al. (1979).

#### RESULTS

Variations in valve dimensions and shape exhibited by *G. mammilla* are shown in Figures 1–4. Individuals within the examined populations ranged from 100–250  $\mu\text{m}$  in length and 25–45  $\mu\text{m}$  in breadth. Valve outline ranged from lanceolate in larger specimens to elliptical-lanceolate in the smaller ones. The headpole was either subrostrate (Figs. 1, 3) or broadly rounded (Figs. 2, 4). The distinct longitudinal lines (2 per valve) are located ca. one-fifth to one-quarter the distance from the valve margin to the axial area (Figs. 1–4, 8). The slightly radiate striae

number 7–9 in 10  $\mu\text{m}$  throughout the length of the valve and each is composed of two rows of areolae (Figs. 1, 2, 9–11). The striae extend onto the valve mantle and usually terminate in a single (i.e. isolated) areola (Figs. 6, 10). Areolae are located in pits or depressions on the valve face (Figs. 9, 11) and mantle (Fig. 10) giving the valve a rugose appearance. Within each depression, the external rim of the areola is slightly elevated (Fig. 12). Areolae are apparently without internal or subtending occlusions or perforations of any type (Fig. 12).

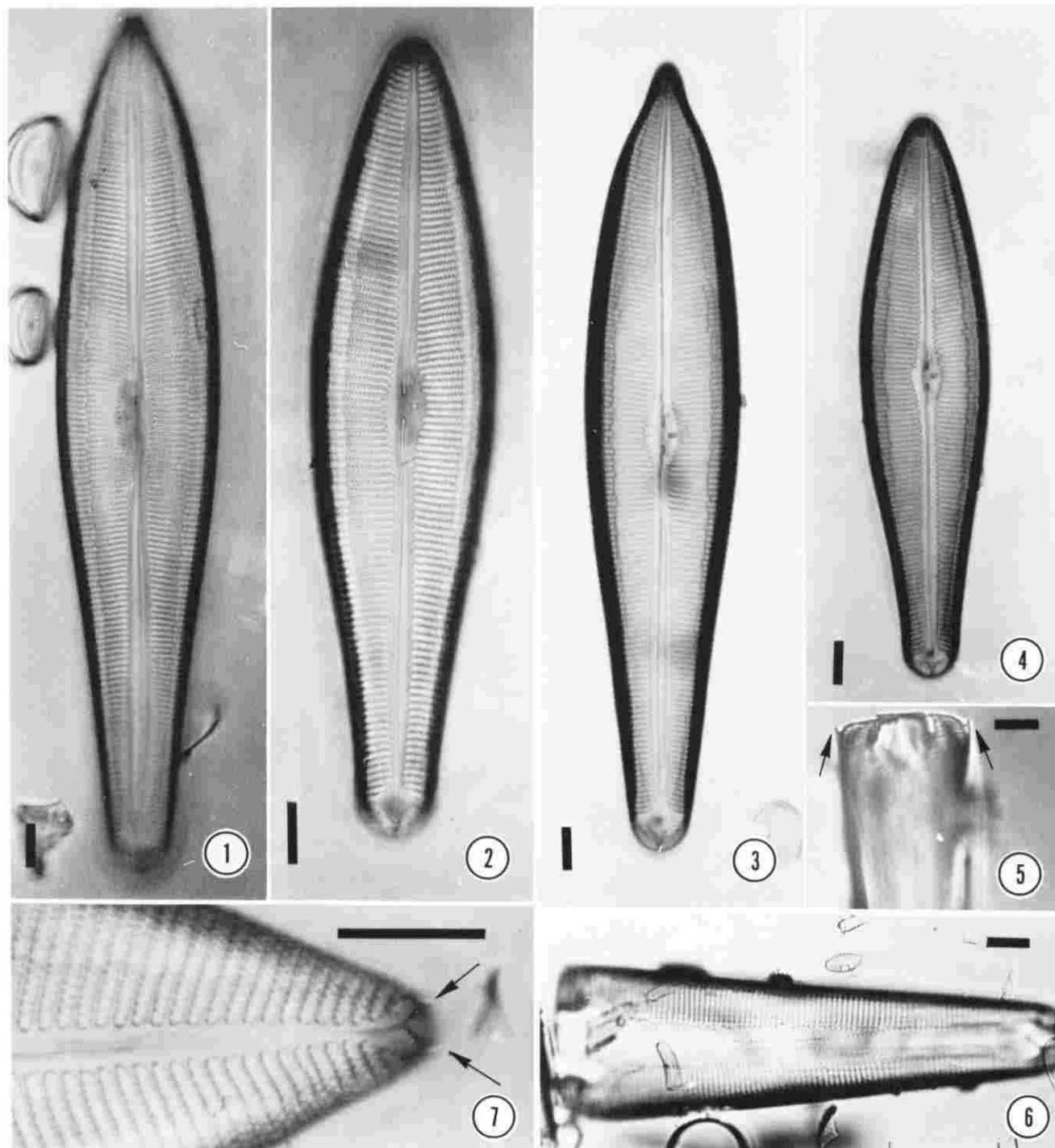
The headpole of each valve has two spines which are detectable in girdle (Fig. 5) and valve (Fig. 7) view. The spines are ca. 0.5–1.0  $\mu\text{m}$  in length and project distally in the valvar plane (Figs. 7, 9). The terminal raphe fissure curves between the spines and extends onto the valve mantle (Fig. 9). Striae of the headpole mantle are composed of areolae similar to those on the valve face and radiate uninterrupted about the valve apex (Fig. 9).

At the footpole, pores dissimilar in appearance to the areolae form a bilobed apical pore field (APF) (Fig. 11). The APF extends from the valve face onto the valve mantle and terminates at the girdle band (Fig. 11). The terminal raphe fissure at the footpole curves between the lobes of the APF (Fig. 11). Porelli of the APF are shown to be true pores that taper as they pass through the frustule (Figs. 13, 14).

Internal structure is dominated by a broad siliceous axial plate. The axial plate is broadest at mid-valve and tapers towards the poles (Fig. 15). The plate expands laterally from the axial area, lying beneath a considerable portion of each stria (Fig. 16). The plate then joins costae (Fig. 17) to form chambers situated between the interior valve surface and axial plate (Fig. 18). In the central area the axial plate is penetrated by both the proximal raphe ends and stigma. There is usually one stigma, but two may be present. The stigma appears rounded externally (Fig. 19), but as a slightly raised slit internally (Fig. 20). The proximal raphe ends appear straight and slightly enlarged externally (Fig. 19) but curve back towards the poles internally (Fig. 20). Both the stigma and raphe ends are positioned on the internally raised central nodule (Figs. 15, 20). The raphe penetrates the axial plate through the axial area (Fig. 15) and terminates in helictoglossae at both the headpole (Fig. 21) and footpole (Fig. 22). Both terminal raphe fissures extend externally beyond the helictoglossae without penetrating the valve (Fig. 23). The filamentous raphe has asymmetrical parts to the central costa and is of the key and slot type (Fig. 24). A small pseudoseptum is present at the headpole (Fig. 21).

#### DISCUSSION

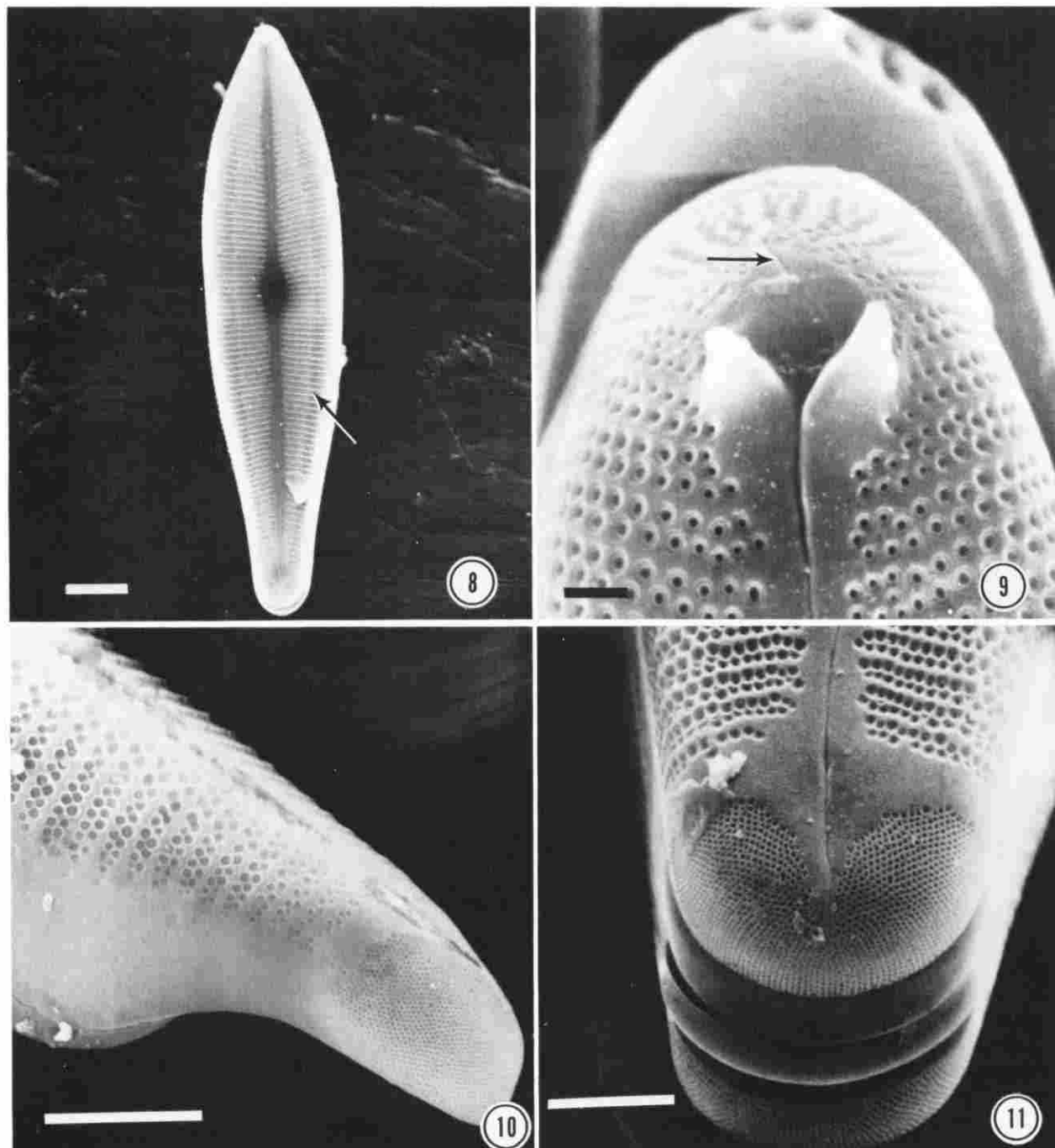
Morphological features observed in *G. mammilla* agree in general with the description presented by Patrick and Reimer (1975) including valve shape,



FIGS. 1-7. *Gomphoneis mammilla*. LM. All scale bars = 10  $\mu$ m. FIGS. 1-4. Valve views. Specimens show lanceolate to elliptical-lanceolate valve shape, submarginal longitudinal lines and striae composed of two rows of puncta. Also evident are the isolated stigma and filamentous raphe. Figures 1, 3 illustrate subrostrate headpoles, Figures 2, 4 illustrate broadly rounded headpoles. FIG. 5. Girdle view of headpole, illustrating apical spines (arrows). FIG. 6. Girdle view, with striae and isolated areolae on valve mantle and a single row of areolae on the girdle band. FIG. 7. Valve view of headpole, illustrating apical spines (arrows).

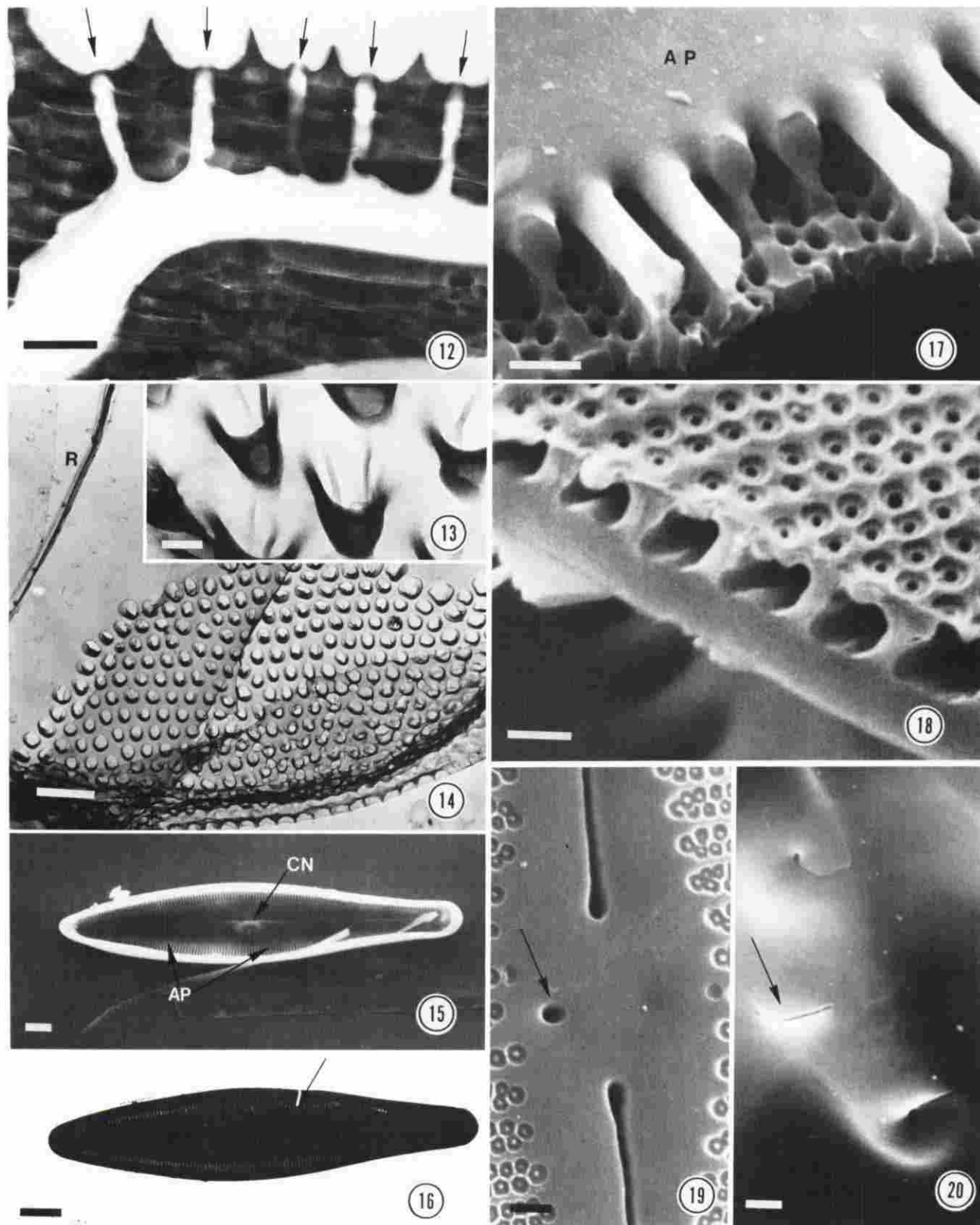
number of striae in 10  $\mu$ m, raphe structure and number and position of stigmata. Ultrastructural observations revealed that the raphe is of the key and lock type described by Krammer (1982a), who has ob-

served this type of raphe in closely related genera (such as *Gomphonema*). Differences with respect to other characteristics were, however, noted. Length and breadth dimensions observed in the present

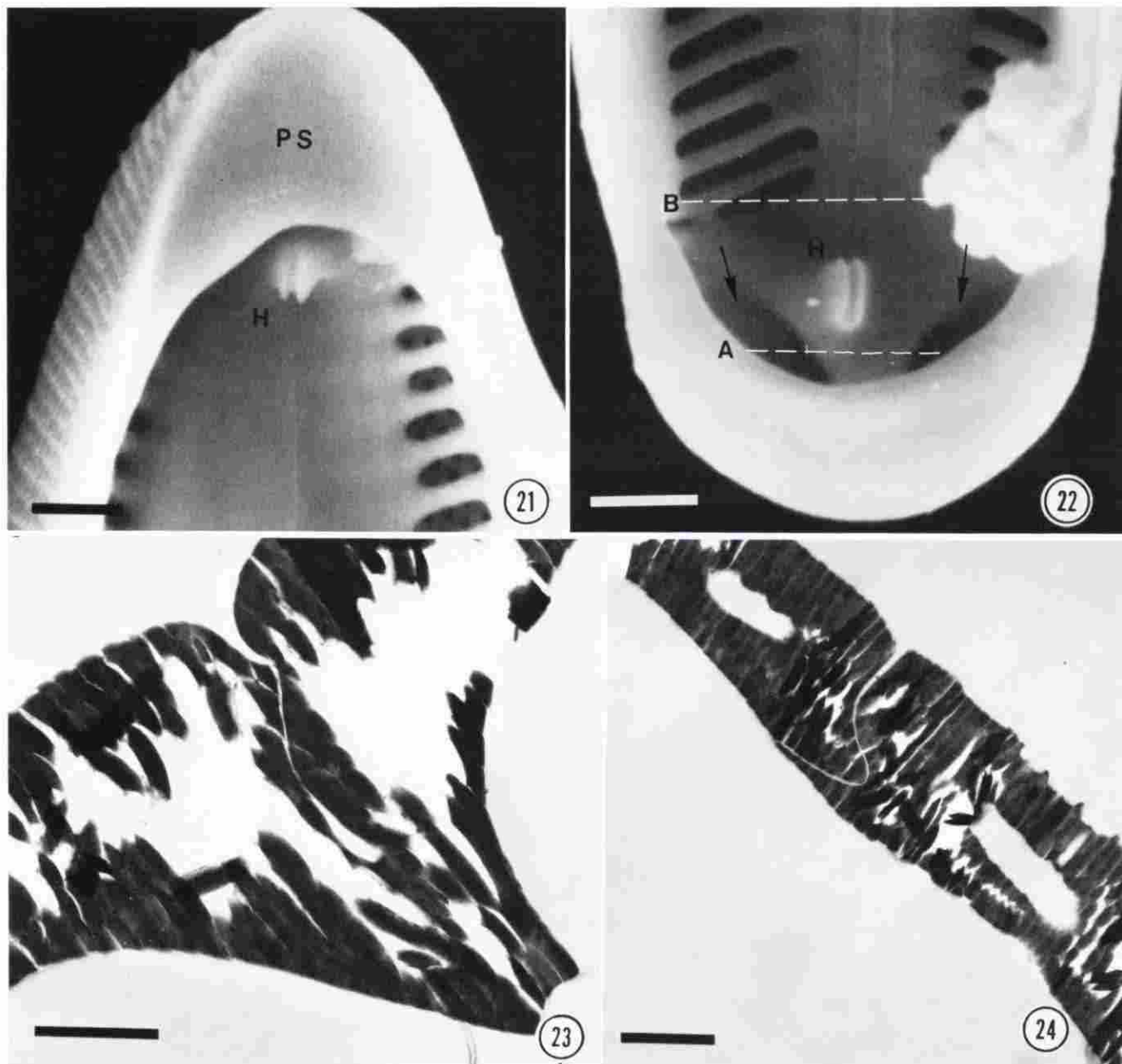


FIGS. 8–11. *Gomphoneis mammilla*. SEM. FIG. 8. External view of valve. Note longitudinal line (arrow). Scale bar = 10  $\mu\text{m}$ . FIG. 9. External valve view of headpole showing apical spines and terminal fissure of raphe (arrow). Scale bar = 1  $\mu\text{m}$ . FIG. 10. Oblique external view of footpole and lower portion of valve showing one lobe of APF and striae with isolated areolae on mantle. Scale bar = 5  $\mu\text{m}$ . FIG. 11. External view of footpole showing bilobed APF and curved terminal raphe fissure. Scale bar = 5  $\mu\text{m}$ .

FIGS. 12–20. *Gomphoneis mammilla*. FIG. 12. TEM. Transapical section near footpole, areolae with elevated rims (arrows) are located in depressions on valve exterior. Scale bar = 0.5  $\mu\text{m}$ . FIGS. 13, 14. TEM. Carbon replicas of APF. FIG. 13. Tapered porelli of the APF. Scale bar = 0.1  $\mu\text{m}$ . FIG. 14. One of two lobes of APF with raphe (R) nearby. Scale bar = 1  $\mu\text{m}$ . FIG. 15. SEM. Valve interior, illustrating



axial plate (AP) and central nodule (CN). Scale bar = 10  $\mu\text{m}$ . FIG. 16. TEM. Valve view illustrating position of axial plate (arrow). Scale bar = 10  $\mu\text{m}$ . FIGS. 17-20. SEM. FIG. 17. Internal view of broken valve at mid-valve showing costae joined to axial plate (AP). Scale bar = 1  $\mu\text{m}$ . FIG. 18. External view of broken valve at mid-valve near the margin showing chambers formed by axial plate, costae and basal siliceous layer. Scale bar = 1  $\mu\text{m}$ . FIG. 19. External view of central area showing enlarged proximal raphe ends and stigma (arrow). Scale bar = 1  $\mu\text{m}$ . FIG. 20. Internal view of central area showing proximal raphe ends of slit-like stigma (arrow). Scale bar = 1  $\mu\text{m}$ .



FIGS. 21–24. *Gomphoneis mammilla*. FIG. 21. SEM. Internal view of headpole showing pseudoseptum (PS) and helictoglossa (H). Scale bar = 2.5  $\mu$ m. FIG. 22. SEM. Internal view of footpole showing helictoglossa (H). The two lobes of the APF are also visible. Dashed lines indicate approximate areas where thin sections for Fig. 23 (A) and Fig. 24 (B) were made. Scale bar = 2.5  $\mu$ m. FIGS. 23–24. TEM-thin sections. FIG. 23. Footpole immediately distal to helictoglossa illustrating distal raphe end does not penetrate completely through the valve. Scale bar = 1  $\mu$ m. FIG. 24. Footpole just proximal to helictoglossa, showing key and slot raphe with complete penetration through the valve. Scale bar = 1  $\mu$ m.

study are greater than those reported by Patrick and Reimer (1975). Apical spines at the headpole have not been reported previously; their possible function is not known. Differences between forms of the same population with respect to outline of the headpole suggest the possibility of two discrete taxa. A broadly rounded specimen was illustrated by Patrick and Reimer (1975) while Ehrenberg (1854) and Grunow (in van Heurck 1880) have illustrated subrostrate specimens. Further taxonomic studies are war-

ranted to determine if intermediate forms can be found or if the two forms should be separated.

Depressions of the striae and external areolar morphology in *G. mammilla* produce a pitted valve exterior which is similar in appearance to that of *Didymosphenia geminata* (Lyngb.) M. Schm. (Dawson 1973). Internally, areolae of *G. mammilla* differ in structure from those of closely related genera. For example, Mann (1982) has discussed the flap-like volate occlusions of some species of *Gomphonema* and

*Didymosphenia*, and hymenate occlusions of *Rhoicosphenia*. Unlike these types, there are no perforated plates or obstructions associated with the areolae of *G. mammilla*. Areolar structure observed in *G. mammilla* most closely resembles that of *Gomphonema olivaceum* and *G. quadripunctatum*, which also possess unobstructed puncta (Dawson 1974).

The axial plate may be the most significant structural and taxonomic characteristic observed in this study. It is responsible for producing the effect of longitudinal lines in *G. mammilla*. Previous reports on the nature of longitudinal lines in the genus *Gomphoneis* have varied. Hustedt (1935) illustrated two lines on either side of the axial area, similar to the longitudinal lines in some *Pinnularia* taxa, in his interpretation of this characteristic in *G. mammilla*. Patrick and Reimer (1975) termed the structure responsible for producing longitudinal lines in *Gomphoneis* as being "septum-like." Lange-Bertalot (1978) suggested the lines are produced by thread-like structures. Recently Krammer (1982b) has observed the internal structure responsible for longitudinal lines in "*Gomphonema (Gomphoneis) transylvanicum*," and noted they were produced by closed alveoli in the valve mantle. The difference in density of silica produced by the underlying axial plate along a portion of each stria forms the image of a single longitudinal line on either side of the axial area in *G. mammilla*. The axial plate cannot be termed a septum because it is derived from the valve proper rather than the girdle bands (Ross et al. 1979). Ours is the first ultrastructural description of the axial plate in the genus *Gomphoneis* and in the Gomphonemaceae sensu Patrick and Reimer (1975), although similar structures have been observed in *Caloneis* (Kolbe and Götz 1943, Walker et al. 1979, Edgar 1980), *Pinnularia* (Pickett-Heaps et al. 1979, Jackson 1980) and *Cyclotella* (Lowe 1975).

Ultrastructural observations on *G. mammilla* allow discussion on the validity of *Gomphoneis* as a taxon and the relationship of doubly-punctate *Gomphonema* taxa and related forms to *Gomphoneis*. Separation of *Gomphoneis* and *Gomphonema* receives some support from the present study. Generic characteristics described by Cleve (1894), including doubly-punctate striae and longitudinal lines, have been observed in *G. mammilla*. Based on our observations of this taxon, characteristics that might help define the genus include longitudinal lines formed by an axial plate, presence of isolated stigmata instead of simple pores, apical spines and a pseudoseptum at the head-pole and recurved internal proximal raphe ends. Although these have been observed in other *Gomphoneis* species, (personal observations) a complete inventory of all *Gomphoneis* taxa must be made to determine the usefulness of the proposed characteristics.

Exceptions to the generic characteristics described by Cleve (1894) appear to exist, as with *Gomphonema cantalicum* Brun and Hérib., which is re-

ported to have longitudinal lines, an isolated stigma and recurved proximal raphe ends but striae composed of a single row of puncta (Cleve 1894, Schmidt 1899). Variability in the number of rows of puncta comprising the striae demonstrated in some *Gomphonema* species (Lange-Bertalot 1980, Drum 1969, Drum and Hopkins 1966, Hustedt 1945, Krammer 1982b) could suggest similar variability in *Gomphoneis*, and thus *Gomphonema cantalicum* might, as suggested by Schmidt (1899), be more closely allied to *Gomphoneis*.

Our results shed some doubt on the affinity between *Gomphonema transylvanicum* Pant. and *Gomphoneis mammilla*. Basic differences between the two with respect to construction of the longitudinal line and other valvar components suggest these taxa are not closely related. Observations on other *Gomphoneis* species are necessary to determine if *Gomphonema transylvanicum*, as proposed by Krammer (1982b), is properly placed in the genus *Gomphoneis*.

In addition to the characteristic of striae composed of double rows of simple puncta, Dawson (1974) transferred *Gomphonema quadripunctatum* and *G. olivaceum* to *Gomphoneis* because both of these *Gomphonema* taxa also possessed APF porelli similar to striae punctae, lacked curvature of the terminal raphe fissures and had a pseudoseptum at the head-pole. Except for the presence of a pseudoseptum and similar construction of the puncta, none of the other features have been observed in *G. mammilla*. Since these species lack an axial plate (and therefore lack longitudinal lines) they cannot be classified in the genus *Gomphoneis* as we envision it. We feel that the two taxa examined by Dawson (1974) constitute a natural group within *Gomphonema*.

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## LIFE HISTORIES OF *BLIDINGIA MINIMA* (CHLOROPHYCEAE), ESPECIALLY SEXUAL REPRODUCTION<sup>1</sup>

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### ABSTRACT

*Blidingia minima* (Näg. ex Kütz.) Kylin from Muroran, Hokkaido, Japan, has been shown to exhibit four patterns of life history in culture. Sexual reproduction, reported fully for the first time in the genus, occurs in two of them. I. An isomorphic-heteromorphic complex in which erect, tubular sporophytes alternate with dioecious gametophytes of the same forms, with the irregular production by both phases of discoid or pulvinate (pincushion-like) microthalli capable of both sexual and asexual reproduction. II. An alternation of heteromorphic phases in which an erect, tubular sporophyte alternated irregularly with a gametophytic microthallus. III. An asexual alternation of heteromorphic phases in which an erect, tubular frond alternates irregularly with a microthallus by means of quadriflagellate zoospores. IV. An asexual, monophasic life cycle in which erect, tubular fronds are perpetuated by quadriflagellate zoospores. The first pattern occurred in spring populations from one of three sites. The second occurred in populations from two sites. The third and

fourth occurred in all populations tested. The life history of *Blidingia minima* from Muroran is similar to that of *Kornmannia zostericola* from Muroran.

**Key index words:** asexual reproduction; *Blidingia minima*; Chlorophyceae; life history; prostrate microthallus; sexual reproduction

The genus *Blidingia* was proposed by Kylin in 1947 to accommodate *Enteromorpha minima* Nägeli ex Kützinger after culture experiments by Bliding (1938) and himself showed that the following features distinguished it from *Enteromorpha*: 1) Quadriflagellate zoospores lacking eyespots are the only reproductive cells produced; 2) During germination, all of the cytoplasm of the settled zoospore migrates into a germination tube and is walled off from the empty spore; 3) The germling produces prostrate branches which form an initially monostromatic disc that becomes distromatic in the center and gives rise to an erect, tubular frond with many initial cells.

The life history of *Blidingia* species from various localities has been investigated: *B. minima* (as *Enteromorpha nana* var. *minima*) from Muroran, Japan (Ya-

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