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CENTRIC DIATOMS OF LAKE TAHOE

Albert D. Mahood1,2, Robert D. Thomson1,3, and Charles R. Goldman1

Abstract.—An understanding of the mechanisms of phytoplankton species interaction is dependent on a precise knowledge of what species exist within the community. The centric diatoms of Lake Tahoe, California–Nevada, which are often the dominant component of the phytoplankton community, are presented in both light and scanning electron microscopy (SEM) photographs. Specific attention has been given to initial cell forms of Cyclotella stelligera Cleve and Gruenow and C. comta (Ehrenberg) Kützing through the aid of the SEM.

Lake Tahoe, formed by a graben fault, is a remarkably unproductive subalpine environment. Currently under the influence of rapid urbanization as a year-round resort area, it is beginning to show signs of the earliest stages of eutrophication (Goldman 1974).

As was the case with most of the biological sciences, the early interest in taxonomy characterized the beginning stages of limnology. With the development of new techniques for measuring biological processes (such as photosynthesis and respiration) in lakes, emphasis on taxonomy declined and studies of community metabolism became a major thrust in limnological research. The study of the limnology of Lake Tahoe during the past 20 years has stressed primary productivity, response to nutrients by algae, and water chemistry of the lake and its tributaries. With further advances in the study of lake processes, it became apparent that an understanding of the mechanisms of phytoplankton species interaction with one another and with their chemical-physical environment is prerequisite to the understanding of dynamic processes in the lake. Thus, aquatic biologists have returned by necessity to research at the species level that requires a renewed interest in taxonomic work. Periodically the phytoplankton community of Lake Tahoe is dominated by diatoms. The large number of diatoms and their role as water quality indicators have stimulated an increasing emphasis on taxonomic studies of diatoms in an ongoing limnological research program at Lake Tahoe, conducted by the Tahoe Research Group of the University of California, Davis. Although diatoms continue to be the most common dominants of Lake Tahoe, recent research shows that a few species other than diatoms (particularly small, spheroid green or yellow-green algae) have become significant contributors to the phytoplankton community (Tilzer and Goldman 1978). This may have resulted, in part, from a drastic change in the grazing zooplankton population caused by the introduction of the opossum shrimp, Mysis relicta (Goldman et al. 1979).

This paper is presented to establish an accurate, practical reference to the centric diatoms of Lake Tahoe. Species identification was established and verified in this study through collaborative identification of specimens by authorities in diatom taxonomy. To assist future investigators, the original individually mounted slides of verified species are deposited at the Department of Geology, California Academy of Sciences, San Francisco, and an additional set of slides and reference material is stored at the Division of Environmental Studies, University of California, Davis.

Materials and Methods

Phytoplankton samples were collected in van Dorn samplers as described by Goldman (1974). Periphyton samples were collected

from artificial substrates made of Pyrex glass cylinders (Goldman 1974) or from the natural rock substrates found in the lake.

The cleaning and mounting of fossil as well as recent diatom material has been extensively discussed by Van Heurck (1896), Mea-
kin (1939), Hendey (1964), Patrick and Reimer (1966), Lohman (1972), and Mandra et al. (1973). The techniques that were most appropriate for the relatively small species of *Cyclotella* and *Melosira* were variations of those procedures developed by Hanna (1930),
Figs. 18-21. Cyclotella spp.: 18, *C. ocellata* (SEM), external view of partially decomposed valve (scale = 1 μm); 19, *C. antiqua*, external valve view (scale = 10 μm); 20, same, external valve view, partially cleaned valve (scale = 1 μm); 21, same, internal view (scale = 1 μm).

Meakin (1939), Lohman (1972), and Van der Werff (1955). The Van der Werff technique, using a succession of treatments with hydrogen peroxide, potassium permanganate, and oxalic acid, proved to be the least destructive.

Light microscope (LM) observations and photographs were taken with an Olympus
IMT, using Kodak High Contrast Copy film. Scanning electron microscopy (SEM) observations and photographs were taken with a Cambridge S-180.

**Systematics**

Classification of the higher taxa of centric diatoms follows the scheme set forth by Patrick and Reimer (1966). Classification of individual species follows the systems proposed by Van Landingham (1967, 1969).

- **Division**: Bacillariophyta
- **Class**: Bacillariophyceae
- **Order**: Eupodiscaceae
- **Family**: Coscinodiscaceae
- **Genera**: Melosira Agardh
  - *Cyclotella* Kützing
  - *Stephanodiscus* Ehrenberg

**Cyclotella antiqua** W. Smith

Figs. 6,7,19-21

References: Hustedt 1930: 102, Fig. 75; Cleve-Euler 1951:43, Fig. 51; Schmidt 1900: Pl. 224, Fig. 45. California Academy of Sciences No. 60944.

The cells are cylindrical, valves slightly concave. The diameter varies from 15–23 μm. Because of the broadly rounded marginal zone (Figs. 19,20), the margin appears narrow, approximately one-third the radius. This species is characterized by the 5–8 conical depressions in the central zone, filled with irregularly arranged areolae. The apex of the cone is directed toward the central area. The valve is covered by fine radiating punctae (Figs. 19,20).

Distinguishing characteristics: 5–8 conical depressions in the central zone.

Distribution in Lake Tahoe: infrequent.


**Cyclotella contorta** (Ehr.) Kützing

Figs. 9–12, 22–30

Reference: Hustedt 1930: 99, Fig. 69. CAS No. 61078.

The cells are cylindrical with concentrically undulating valves. The valves are concave or convex. Species from Lake Tahoe vary from 15–40 μm in diameter. The marginal striae form a zone approximately half the radius. At the margin of the valve, the alveolae (Figs. 24,25) appear as short darkened striae under the light microscope (Fig. 12). The areolae of the central area are radiating or irregular (Figs. 22,23). This species clearly displays 2–3 well-defined labiate processes set out by shortened marginal striae. The labiate processes are not as well developed in the initial cell form as they are in the valve of later developed cells (Figs. 27,30).

Distinguishing characteristics: isolated punctae and shortened dark marginal substructures.

Distribution in Lake Tahoe: common.

Ecology: alkaliphilous, oligohalobus (indifferent), mesosoprobic, euplanktonic (Lowe 1974), eutrophic (Van der Werff 1957).

**Cyclotella ocellata** Pantocsek

Figs. 4,5,8,18

References: Pantocsek 1902: Pl. 15, Fig. 318; Hustedt 1930: 100, Fig. 68; Schmidt 1906: Pl. 206, Figs. 8,9; Cleve-Euler 1951: Figs. 64s–v. CAS No. 60946.

Cells cylindrical, always found singly. Valve surface flat to slightly concave. Valve diameters from 8–11 μm. The marginal striae are irregular, 15 in 10 μm. The marginal striae zone is slightly less than half the radius in width. The central area is usually found with three distinct, symmetrically distributed areolae, although specimens with 4–5 areolae have been observed. Cleve-Euler (1951) has suggested that *C. ocellata* be included within the species *C. kutzingiana* (Thwaites) Chauvin as the variety *planetophora*. *C. ocellata* has not been found in sufficiently large numbers to give more definitive diameters or structural variations.

Distinguishing characteristics: Large punctae in the central area symmetrically arranged.

Distribution in Lake Tahoe: infrequent.

Ecology: alkaliphilous, oligohalobus (indifferent), periphytic (Lowe 1974).

**Cyclotella stelligera** Cleve and Grunow

Figs. 1–3,13–17

References: Hustedt 1930: 100, Fig. 65; Cleve-Euler 1951: 43, Fig. 52. CAS No. 60947.

The single cylindrical cells are concentrically undulated, with the marginal striae zone one-third the radius. Ornamentation of the marginal zone is composed of
Figs. 22–25. *Cyclorella comta*: 22, external view of convex valve, irregular central area, two isolated labiate pores within the marginal striae; 23, external view concave valve; 24, internal view, concave valve, two labia across from one another; 25, internal view of concave valve, radial alveolae pattern. Scale = 10 μm. SEM.
prominent alveolate striae, 10-12 in 10 μm. These striae are composed of small areolae (Figs. 13, 16). The central area is composed of a single large areola surrounded by a stellate arrangement of 5-6 areolae, although the stellate arrangement may vary considerably.

Figs. 26-30 Cyclotella comta (SEM): 26, external view of whole cell (scale = 10 μm); 27, detail of labiate pore of vegetative cell (Fig. 23) (scale = 1 μm); 28, external view of initial cell (scale = 10 μm); 29, internal view of initial cell (scale = 10 μm); 30, detail of labiate area of initial cell (Fig. 28) (scale = 1 μm).
The presence of the central areola clearly separates this species from *C. glomerata* Bachmann. Ornamentation of the initial cell form is characterized by marginal striations similar to those of normal vegetative cells, although the central area of the initial cell is

more irregularly arranged (Fig. 15). The initial cell is spherically developed and can be distinguished from the flat or slightly convex vegetative cells (Figs. 14,17). *C. stelligera* from Lake Tahoe vary from 3–11 μm in diameter.

Distinguishing characteristics: stellate arrangement of the central areolae with a central areola.

Distribution in Lake Tahoe: frequent.


*Melosira distans* var. *alpigena* Grunow

Figs. 39,48

The cells are cylindrical, with the valve mantles parallel. The poroid ornamentation of the valve is parallel to the pervalvar axis. The margin of the valve is furnished with relatively short spatulate spines (Fig. 48) that mesh with the adjacent cell.

Distinguishing characteristics: The mantle is shorter than *M. italica* (Ehr.) Kützing and more heavily silicified (Stoermer and Yang 1969).

Distribution in Lake Tahoe: rare.

Ecology: acidophilous, eutrophic, oligosaprobic (Van der Werff 1957), periphytic (Lowe 1974).

*Melosira granulata* (Ehr.) Ralfs

Fig. 40

Reference: Hustedt 1930: 87, Fig. 44

The cells are cylindrical, valve mantle parallel, valve face flat, with poorly developed pseudosulcus. The ornamentation of the valve is variable. The valve margin is furnished with a corona of irregular spines with longer spines overlapping the next cell in the colony. In a few cells observed, spines often extended the length of the mantle of the next cell. Alveolae are arranged obliquely along the pervalvar axis. So few individuals of the species were found in the samples that no reasonable estimate of the species size could be made. Hustedt (1930) found the range to be 5–21 μm in diameter and 5–18 μm in mantle height.

Distinguishing characteristics: irregular, long marginal spines.

Distribution in Lake Tahoe: rare in plankton, common in Emerald Bay periphyton.


*Melosira italica* (Ehr.) Kützing

Figs. 31–38,46,47

References: Hustedt 1930: 92, Fig. 52; Cleve-Euler 1951: 26, Fig. 16c. CAS No. 60949.

The cells are cylindrical, valve mantle parallel, valve face flat, with an extremely small pseudosulcus. Under the light microscope the pseudosulcus appears deeply incised, forming a right angle with the mantle. The sulcus extends about half the radius of the lumen (Fig. 47). The valve surface is irregularly alveolate. The margin of the valve is furnished with a corona of small spines that mesh with the corresponding structures of the adjacent cell (Fig. 46). Ornamentation of the valve mantle is composed of a linear to spiral arrangement of circular to elongate alveolae (Figs. 36,38,46). The valve mantle varies, 6–17.5 μm in length, and the valve diameter varies from 6.5–18 μm.

Distinguishing characteristics: corona with regular denticulate structures and lacking the pronounced spine of *M. granulata*. *M. italica* can be distinguished from *M. ambiguа* (Grun.) O. Müller by the extremely small pseudosulcus.

Distribution in Lake Tahoe: common.


*Melosira undulata* (Ehr.) Kützing

Fig. 41

Reference: Hustedt 1927: 243, Fig. 102.

The cells are cylindrical, valve mantle parallel, with a flat valve face forming a very small pseudosulcus. The mantle ornamentation is composed of parallel fine punctae arranged along the pervalvar axis. Conspicuous mucous pores form a ring one-fourth to one-third the distance between the valve and the girdle edge. Although the external mantle walls are parallel, the inner surface of the wall is clearly undulated (Fig. 41). The undu-
lation is seen as a varying thickness of the wall, with the thickest portion about two-thirds below the valve face. Hustedt (1927) found this species to have a diameter of 16–18 μm and a mantle height of 20–35 μm. *M. varians* C. A. Agardh appears to be sim-

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*Figs. 42–45. Melosira varians, girdle views. Scale = 10 μm. LM.*
ilar, although the thickening is much reduced and lacks the mantle ornamentation of *M. undulata*.

Distinguishing characteristics: large size and distinctive parallel punctae.

Distribution in Lake Tahoe: infrequent in plankton.

Figs. 50-55. *Stephanodiscus* spp.: 50, valve view; 51, 52, same, left side focused on margin, right side focused on central area; 53, same, three-fourths view of convex valve; 54, same, girdle view of recently divided cell; 55, *S. carco-nensis*, valve view, left side focused on central area, right side focused on margin.

*Melosira varians* C. A. Agardh
Figs. 42-45, 49

References: Hustedt 1930: 85, Fig. 41; Cleve-Euler 1951: 29, Fig. 20. CAS No. 60050.

The cells are cylindrical, valve mantle parallel, valve face flat with a very inconspicuous pseudosulcus. The much-reduced pseudosulcus gives the appearance of a ho-
mogenous wall thickness. The ornamentation of the valve face and the irregular fine punctae of the mantle can only be resolved with difficulty, using the light microscope. The valve diameter varies from 13–29 \( \mu m \).

Distinguishing characteristics: rectangular shape in girdle view and the lack of visible ornamentation.

Distribution in Lake Tahoe: infrequent.


**Stephanodiscus alpinus** Hustedt

Figs. 50-54,56-58

References: Hustedt 1930: 110, Fig. 86; Cleve-Euler 1951, 53, Figs. 70c.f. CAS No. 60951.

The cells are cylindrical with concentrically undulating valves. The valve face is concave or convex, 10–29 \( \mu m \) in diameter (Figs. 56,58). The strong radial striae are separated by a very narrow hyaline rib, with 8–11 ribs in 10 \( \mu m \) at the margin. The marginal striae are composed of three rows of fine areolae, 18–20 areolae in 10 \( \mu m \) (Fig. 56) to about one-third the radius, where they become either bipunctate or unipunctate to the center of the valve. The marginal striae have a zigzag appearance under the light microscope (Figs. 51,52). The marginal spines are located at the junction of the hyaline rib and the mantle, with one spine per rib. Strutted processes are irregularly arranged on the mantle just below the marginal spines. The mantle (Figs. 56,58) is finely punctate up to the radial striaions, without the separating hyaline area as reported by Stoermer and Yang (1969).

A comparison of the major morphological structures were made between the species originally designated as **Stephanodiscus astraea** var. *minutula* (Kutz.) Grunow from Lake Tahoe material and **Stephanodiscus alpinus** Hustedt and Ruttner from Grundsee (Mahood 1978). The measurements taken on Lake Tahoe material compared more closely to the samples and descriptions of *S. alpinus* by Stoermer and Yang (1969) and Huber-Pesalozzi (1942). An extensive discussion of the *S. astraea* var. *minutula*–*S. alpinus* question by Theriot and Stoermer (1982) substantially agrees with our findings. In our examination of Hustedt’s slide number 7, from the H. E. Sovereign collection (Mahood 1978), it appears that, when the diameter of the *Stephanodiscus* has a range of 10–17 \( \mu m \), there is one spine at the end of each rib and the central area is irregular. When the diameter is 19–45 \( \mu m \) the arrangement of the spines is irregular and the central area is radial. When *Stephanodiscus* from Lake Tahoe and *S. alpinus* from Hustedt’s slide number 10 from the Sovereign collection were compared to the smaller *Stephanodiscus* on Hustedt’s slide 7, we concluded that in each case the measurements match the description for *S. alpinus*.

Distinguishing characteristics: strong radial striaations and marginal spines at the end of each rib.

Distribution in Lake Tahoe: common.


**Stephanodiscus caronensis** Grunow

Fig. 55

References: DeToni 1894; Schmidt 1901: Pl. 228, Figs. 5–6,9–10. CAS No. 60952.

The cells are disk shaped, approximately 49 \( \mu m \) in diameter. There are 15 striae in 10 \( \mu m \) at the margin, with 5–7 striae between thickened hyaline ribs. The central area is granular. The marginal areolae extend toward the central area to form hyaline riblike structures. The spines are submarginal.

This species is typically thought to be a fossil form. However, Elmore (1921) reported this species in the living state from Devil’s Lake, North Dakota. It is also reported alive in Biwa Lake, Japan (Skvortzow 1936). It is difficult to justify the inclusion of *S. caronensis* in the Lake Tahoe algal community on the basis of the collection of a single valve, and its presence is simply noted.

Distinguishing characteristics: very pronounced hyaline ribs and granular central area.

Distribution in Lake Tahoe: very rare.

**DISCUSSION**

Light microscopy and scanning electron microscopy photographs are presented to aid
Figs. 56–58. *Stephanodiscus alpinus*: 56, external view of concave valve showing spines at margin of each rib; 57, internal view of valve, strutted processes beneath spines, convex; 58, external view of convex valve. Scale = 10 μm. SEM.
in the identification of some difficult species. It is not our intent to rely on SEM as a means of species identification, but rather as a technique that can assist the light microscopist in pragmatic investigations involving some of the more important species.

The denticulate structure of Melosira italica are seen as sharp, well-defined spines, whereas the corona of M. distans var. alpigena can be seen as spulate ended spines (Figs. 46,48). The coronal structures of M. distans var. alpigena are extremely difficult to resolve even under optimum conditions of light microscopy. In this case the SEM photographs may assist the investigator in a more accurate separation of these species in initial investigations of the community.

The very small forms of Cyclotella stelligera range from 3.5–10 μm in diameter and present the light microscopist with a most difficult task. The characteristics of C. stelligera, a stellate central area and central areola, are only positively verified under optimum conditions. For original positive identification within a community, C. stelligera must be cleared and mounted in Hyrax or other appropriate high refractive index medium. The SEM photographs of this species (Fig. 14–15,17) have given additional and confirming information, especially regarding the silicified axiospore or initial cell (Anonymous 1975).

Of particular importance are the SEM photographs of the initial cell forms of both Cyclotella stelligera (Figs. 14–15,17) and C. comta (Figs. 28–29). In light microscopy the initial cell of C. stelligera does not resolve well, making identification based on the stellate central area almost impossible. Since the initial cell is almost spherical, the problem is further complicated by depth of field. The SEM photograph of C. stelligera (Fig. 17) shows the imperfectly formed central area while clearly showing the development of the alveolate striae.

The SEM photographs of the initial cell form of C. comta (Figs. 28–30) may offer a partial solution to the continuing discussion of C. comta–C. bodanica complex in that the initial cell of C. comta resembles C. bodanica in the length of the marginal striae. From the SEM photographs the apparent difference, length of striae, between the two may be due to the spherical shape (Fig. 28), poor development of the striae (Fig. 30), and the accompanying difficulties with depth of field when the initial cell is viewed with the light microscope. The characteristics, marginal striae half the radius, of C. comta are seen in the vegetative cell (Figs. 22–27) but not in the initial cell forms. The evidence seems to indicate that C. comta is the acceptable identification for the morphological characteristics ascribed to C. comta in Hustedt (1930).

To ensure consistent and accurate identification of species treated in this paper, individual centered, mounted specimens were verified by the following diatom taxonomists: G. Collins and B. McFarland, United States Environmental Protection Agency, Cincinnati, Ohio; S. Van Landingham, Cincinnati, Ohio; C. L. Christensen, Iowa Academy of Sciences, Waterloo, Iowa; E. F. Stoeermer, University of Michigan, Ann Arbor, Michigan; R. Firth, Seaforth, England.

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