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Taxonomy and Distribution of Benthic Diatoms from Mono Lake, California, U.S.A.¹

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Abstract. The benthic diatom flora of Mono Lake is described from samples taken from three localities at depths of approximately 1, 5, and 10 meters on rock and sediment substrates. Relative abundances of 30 taxa were recorded from duplicate counts of 500 valves from each of 18 samples. Dominant taxa included Navicula crucialis, Nitzschia frustulum, N. latens, N. reimerii sp. nov., N. monoensis, sp. nov. and Anomoeoneis sphaerophora var. minor var. nov.; taxonomy, morphology, and distribution of these taxa are considered. Navicula crucialis, previously recorded from saline lakes in North Africa and highly variable in outline, was most abundant in sediment samples. Anomoeoneis sphaerophora var. minor, Nitzschia reimeri, and N. monoensis were most abundant in deeper waters whereas both N. latens and N. frustulum occurred most frequently in collections from shallow waters. Smaller individuals of N. latens were broader than larger specimens, and some N. frustulum cells resembled N. austriaca. Nitzschia monoensis has numerous girdle bands and prominent external distal raphe ends. Navicula crucialis, A. sphaerophora var. minor, and Nitzschia monoensis were observed with internal valves.

Mono Lake, located at the western edge of the Great Basin (Fig. 1), is a hypersaline (95 g/L in 1990) and alkaline (pH 10.0) (Herbst, unpublished data) remnant of Pleistocene Lake Russell. At a current surface elevation of 1,943 m, the lake has fluctuated considerably in the late Holocene (Stine, 1990). During the past 50 years, the lake has undergone a net decline of 14 m and a doubling of salinity, both attributable to diversion of tributary streams by the city of Los Angeles (National Academy of Sciences, 1987). The major ion content is dominated by sodium, with high anion concentrations of bicarbonate in addition to carbonate, chloride, and sulfate (Herbst, 1988).

The benthic environment is composed of sand and organic-rich mud sediments over much of the basin. Hard substrates occur as localized calcareous tufa formations, pumice and alluvial granite cobble, and gravel along the west, north, and south shores (Herbst, 1990).

The high salinity of Mono Lake restricts macrofaunal diversity to eight known benthic insects, all dipteran larvae (Herbst, 1988) and a single zooplankton species, *Artemia monica* Verrill. The dominant benthic insect is the alkali fly *Ephydra hians* Say (Ephydridae), a herbivore that grazes epilithic algae and epipelic microbial mats. Benthic algae from Mono Lake with which diatoms are known to occur include *Ctenocladus circinnatus* Borzi (Chlorophyceae)

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FIG. 1. Location of Mono Lake in relation to Pleistocene and present lakes of the Great Basin. Collection sites are indicated by dark circles. B, Black Point tufa shoal; D, DWP boat dock; L, Lee Vining tufa grove.

and several undetermined filamentous forms of Cyanobacteria, including species of Oscillatoria, Spirulina, and Lyngbya. Herbst & Bradley (1989) studied the growth response of mixed species of this benthic algal assemblage to varied salinity. Mono Lake benthic algae survived and grew within the range 50–150 g/L, though organic content and growth rates were reduced within the range 100–150 g/L. This study did not, however, attempt to correlate changes in species composition with salinity, or attempt to identify the pool of species used in the experimental inoculum.

Objectives of the present paper are to (1) identify the living benthic diatom taxa represented in Mono Lake, (2) describe diatom distributions with respect to depth zonation and substrate-type associations, and (3) provide an inventory of potential algal food resources for larvae and adults of the alkali fly. This information will help to provide a baseline of data for future ecological comparisons, to establish a basis for stratigraphic comparisons to fossil diatom assemblages in and around Mono Lake, and to provide a taxonomic guide for interpreting experimental studies of salinity on algal growth.

MATERIALS AND METHODS

Samples were collected using SCUBA from sediment and rock or tufa substrates from three localities in the lake, at Lee Vining tufa grove (LVTG), Black Point tufa shoal (BPTS), and DWP boat dock (DWP). Samples were taken at LVTG on 22 August 1990 at 5-m and 10-m depths and on 4 October 1990 at 15-cm and 1-m depths. Samples were taken at BPTS on 28 August 1990 at 5-m

	BPTS						
	l m		5 m		10 m		
	Sedi- ment	Rock	Sedi- ment	Rock	Sedi- ment	Rock	
Chaetoceros muelleri Lemm.						0.2	
Cyclotella bodanica Grun.							
C. cf. ocellata Pant.				Р	0.1		
Stephanodiscus spp.	Р		Р	Р	0.3	0.6	
S. carconensis Grun.							
S. excentricus Hust.							
Aulacoseira granulata (Ehrenb.) Grun.							
A. cf. solida (Grun. in V.H.)							
Melosira varians Agardh							
Fragilaria construens (Ehrenb.) Grun.							
F. pinnata Ehrenb.							
F. vaucheriae (Kütz.) Peters.							
Synedra acus Kütz							
Cocconeis placentula Ehrenb.				0.1		0.3	
Navicula crucialis (O. Müll.)	42.8	0.2	65.1	27.4	55.5	30.6	
N. radiosa var. tenella (Bréb. ex Kütz.) Grun.							
Neidium iridis (Ehrenb.) Cleve						Р	
Anomoeoneis costata (Kütz.) Hust.							
A. sphaerophora var.							
minor var. nov.	Р	Р	0.2	0.8	3.1	28.8	
Encyonema minutum (Hilse in Rabh.)							
D. G. Mann in Round et al.							
Amphora sp.							
Epithemia sp.							
Denticula sp.						0.4	
Rhopalodia gibba (Ehrenb.) O. Müll.							
Nitzschia frustulum (Kütz.) Grun.	25.3	62.9	30.4	60.1	34.2	20.4	
N. latens Hust.	31.9	36.9	3.4	10.4	2.7	7.2	
N. monoensis sp. nov.	Р	Р	0.9	1.0	4.1	11.3	
N. reimerii sp. nov.	Р		Р	0.2		0.2	
Nitzschia sp.							
Surirella nevadensis Hanna & Grant							

TABLE I

Mean relative abundances and distribution of diatom taxa in Mono Lake samples^a

^a P, present in random scan; not enumerated in determination of relative abundance.

and 10-m depths and on 3 October 1990 at 1-m depth. Samples at DWP were taken on 20 August 1990 at 1-m, 5-m, and 10-m depths. All collections were made by D.B.H. California Academy of Sciences Diatom Collection Accession Numbers for the samples are: 602407 (LVTG, 15 cm rock); 602408 (LVTG, 1 m rock); 602409 (LVTG, 5 m sediment); 602410 (LVTG, 5 m rock); 602411 (LVTG, 10 m sediment); 602412 (LVTG, 10 m rock); 602413 (BPTS, 1 m sediment); 602414 (BPTS, 1 m rock); 602415 (BPTS, 5 m sediment); 602416 (BPTS, 5 m rock); 602417 (BPTS, 10 m sediment); 602418 (BPTS, 10 m rock); 602419 (DWP, 1 m sediment); 602420 (DWP, 1 m rock); 602421 (DWP, 5 m sediment); 602422 (DWP, 5 m rock); 602423 (DWP, 10 m sediment); 602424 (DWP, 10 m rock).

LVTG					DWP							
			5 m		10 m		1 m		5 m		10 m	
15 cm Rock	l m Rock	Sedi- ment	Rock	Sedi- ment	Rock	Sedi- ment	Rock	Sedi- ment	Rock	Sedi- ment	Rock	
				0.1						Р	0.2	
										0.1		
					Р				Р	0.1		
		0.9		Р	0.3				0.1	0.2	0.6	
										Р		
				0.1						Р		
		0.2		0.1								
		0.2		0.2 P								
								Р		0.2		
								Р				
								Р				
				0.1	0.2	Р				0.2		
0.4	1.3	89.9	39.0	19.6	15.7	40.2	1.2	27.4	8.1	55.5	23.8	
	Р				р							
					r							
Р	Р	2.5	3.3	1.7	35.0	Р	Р	0.2	0.8	3.1	28.8	
								Р				
		_								P		
		Р				n	n			P	0.2	
7.0	57.0	4.0	49.0	4.9	147	100	P 55 0	00.0	179	Р 917	20.4	
4.U 02.6	57.9 40.8	4.0	42.0 10.4	4.3	14.7	12.2	00.U 43.8	22.0 10.9	11.0	21.7	20.4	
34.0	ч0.0 Р	0.8	4.1	70 7	11.5	40.2 P	ч0.0 Р	0.3	0.2	52.2	1.0	
Р	P	0.7	1.2	3.2	3.9	P	P	P.0.5	0.2	02.2	0.4	
-	-				0.0	-	-	-		0.2		
										Р		

TABLE I Continued

Material was cleaned by boiling in HNO₃, followed by a series of alternating rinses with distilled water, settling, and decanting to rid samples of oxidation by-products. Cleaned material was air-dried on coverglasses and mounted on microscope slides with Hyrax[®]. Light microscopic observations were made with a Reichart Polyvar microscope. To determine relative abundances of taxa, two counts of 500 complete valves were made from each of the 18 samples. Samples also were scanned in order to identify species not enumerated in the counts. Comments concerning relative abundances of taxa are based on the following definitions: present, found in scan of sample, not enumerated in count; rare, less than 1% relative abundance; frequent, 1–10% relative abundance; common, 11–25% relative abundance; abundant, >25% relative abundance.

For scanning electron microscopy (SEM), cleaned material was air-dried on



FIGS. 2-16. Figs. 2-10. Navicula crucialis, valve views. Fig. 6. Valve asymmetrical to longitudinal axis. Figs. 8, 9. Valves showing variation in central area. Figs. 11-16. Anomoeoneis sphae-

coverglasses, which in turn were mounted on aluminum stubs. Stubs bearing the material were sputter-coated with approximately 20 nm of gold-palladium and viewed with a Hitachi S-520 microscope at operating voltages of 10-20 kV.

RESULTS

A total of 30 morphologically distinct entities of diatoms, representing 18 genera, were found in the Mono Lake samples. The genus *Nitzschia* was represented by the greatest number of species (5), although the genera *Fragilaria* and *Stephanodiscus* each included the second largest number of taxa (3). The centric genera *Cyclotella* and *Aulacoseira* and the pennate genera *Navicula* and *Anomoeoneis* each were represented by two species. A complete listing of the taxa found in this study is included in Table I.

With regard to taxon distribution, the largest number of taxa represented in a single sample (19) occurred in the 10-m sediment sample from DWP. The smallest number of taxa represented in a sample (5) occurred in the 1-m rock sample from BPTS and in the 15-cm rock sample from LVTG. Average relative abundances of taxa in each collection is presented in Table I.

Forty percent of the total number of diatom taxa recorded during this investigation were identified in general scans only. Five species, including *Navicula crucialis*, *Nitzschia latens*, *N. monoensis*, *N. frustulum*, and *Anomoeoneis sphaerophora* var. *minor* were dominant, together comprising 95.3–100% relative abundance in the 18 samples. Comments follow on taxonomy, morphology, and distribution of these five species, as well as an additional species of *Nitzschia* that occurred consistently in the samples and is new to science.

Family Naviculaceae Kützing, 1844 Genus Navicula Bory de St. Vincent, 1822 Navicula crucialis (O. Müller) Frenguelli (Figs. 2–10, 17, 18)

Mono Lake specimens are 17–60 μ m long and 6.5–9.0 μ m broad. Valve shape is highly variable. Larger valves are bacilliform to linear-lanceolate and may be with or without protracted apices. Smaller valves are almost elliptical in outline. Valves may be asymmetrical to either the transverse or longitudinal axis. The central area is highly variable, ranging from cruciate to unilaterally expanded to striae being slightly shorter on one or both sides of the axial area. The narrow axial area contains a straight raphe. Striae are radiate, becoming parallel at the ends and number 16–18 in 10 μ m. Internal valves (Innenschalen) are formed.

(

rophora var. minor, valve views. Fig. 11. Innenschalen. Fig. 12. Valve asymmetrical to transapical axis. Fig. 15. Valve with acute poles. Light microscopy (LM); scale bar in Fig. 2 represents $10 \ \mu m$; all figures at same scale.



FIGS. 17–21. Figs. 17, 18. Navicula crucialis. Fig. 17. External valve view. Scale bar represents $10 \,\mu\text{m}$. Fig. 18. Internal valve view. Scale bar represents $5 \,\mu\text{m}$. Figs. 19–21. Anomoeoneis sphaerophora var. minor. Fig. 19. External valve view. Scale bar represents 3.75 μ m. Fig. 20. Internal valve

Variation in shape and central area morphology of this species has been noted earlier by Müller (1899) and Frenguelli (1929) in collections from North Africa. Mono Lake specimens resemble Hustedt's 1962 figure (fig. 1415, second illustration from left) of *N. subinflata* Grun. in Cleve, but do not match the description in Cleve (1893, p. 470) of the "central striae" being "stronger" or more prominent than others. *Navicula crucialis* differs from *N. subinflatoides* Hust. by the more slender, linear outline of the valves (*N. subinflatoides* is 10– 14 μ m broad; Hustedt, 1962). *Stauroneis legleri* Hust., a saltwater species, may be a synomym of *N. crucialis* (see Hustedt, 1962; Simonsen, 1987).

SEM reveals that distal raphe ends are deflected onto the valve mantle. Punctate striae are not in straight rows. Proximal raphe ends are curved in the same direction on the central nodule.

Navicula crucialis was recorded in all Mono Lake samples, ranging in relative abundance from rare to abundant. It was the most abundant species in five samples, including 1-m, 5-m and 10-m sediment, and 10-m rock samples from BPTS and the 5-m sediment sample from LVTG.

Genus Anomoeoneis Pfitzer, 1871 Anomoeoneis sphaerophora var. minor var. nov. (Figs. 11–16, 19–21; Fig. 14 illustrates the holotype)

Descriptio. Ambitu variabilis, valvae var. sphaerophora parvior subtiliter striatior. Longitudo 19-48 μ m. Latitudo 6.5-10 μ m. Striae 20-22 in 10 μ m.

Holotypus. CAS slide #216060.

Description. Valve outline variable, smaller and more finely striated than var. sphaerophora. Length 19-48 μ m, breadth 6.5-10 μ m. Striae 20-22 in 10 μ m.

Holotype. CAS slide #216060.

Type locality. Mono Lake, Lee Vining tufa grove, 10-m depth, rock scrape. Remarks. Variation in outline includes apices being narrowly rostrate, broadly rostrate, nearly acute or rounded, and margins being parallel or convex. The central area may be staurose or expanded unilaterally. Asymmetry may be to either the transapical or longitudinal axes. This variety resembles Müller's (1899)

view. Scale bar represents $3.75 \ \mu\text{m}$. Fig. 21. Internal valve view. Valve asymmetrical to longitudinal axis. Scale bar represents 2 μm . Scanning electron microscopy (SEM).

FIGS. 22-34. Figs. 22-24. Nitzschia frustulum. Figs. 25-28. N. latens. Figs. 29-32. N. reimerii sp. nov. Figs. 33-34. N. monoensis sp. nov. internal cells. LM; scale bar in Fig. 22 represents 10 μ m; all figures at same scale.

FIGS. 35-40. Fig. 35. Nitzschia frustulum, internal valve view. Cell shape similar to N. austriaca Hust. Scale bar represents 2 μ m. Fig. 36. N. frustulum, internal valve, cell terminus. Scale bar represents 1 μ m. Figs. 37, 38. N. latens, internal valve view. Scale bars each represent 2 μ m. Fig. 39. N. reimerii sp. nov. Internal valve view. Scale bar represents 10 μ m. Fig. 40. N. reimerii sp. nov. Internal view, cell terminus showing helictoglossa and enlarged terminal fibula. Scale bar represents 3 μ m. SEM.





A. sphaerophora var. güntherii and A. sphaerophora var. navicula (the latter is usually considered a synonym of the former; Hustedt, 1959; VanLandingham, 1967), but differs in the finer pattern of striation and narrower valves. Innenschalen are produced, a feature also recorded by Müller (1899) for his varieties of the species. Variation in the central area of A. sphaerophora was described earlier by McCall (1933).

Using SEM, puncta appear dash-like. The central nodule is raised internally and proximal raphe ends are deflected in the same direction. Pronounced helictoglossae are present at the poles. *Anomoeoneis sphaerophora* var. *minor* was observed in 13 samples, ranging in relative abundance from rare to abundant (two samples, 10-m rock at LVTG, 10-m rock at BPTS). Members of this taxon appear to prefer deeper waters.

> Family Bacillariaceae Ehrenberg, 1840 Genus Nitzschia Hassall, 1845 Nitzschia frustulum (Kütz.) Grun. (Figs. 22–24, 35, 36)

Mono Lake populations measure 8-32 μ m long and 3-4 μ m broad. Fibulae densities range from 11 to 13 in 10 μ m and striae number 22-24 in 10 μ m. Asymmetrical valves were abundant, some approaching the form of *N. austriaca* Hust. Krammer & Lange-Bertalot (1988) referred earlier to this phenomenon.

SEM revealed a N. austriaca-like cell showing robust fibulae and distinct helictoglossae.

Nitzschia frustulum was observed in all counts and was abundant in nine samples including all but one (10-m rock) sample from BPTS. Hustedt (1930), Laws (1988), and Wendker (1990a,b) characterized this species as a brackish water form, although it was categorized as cosmopolitan by Lowe (1974). Servant-Vildary (1984) recorded N. frustulum from saline lakes in Bolivia, and it was considered the dominant benthic diatom species in Mono Lake (National Academy of Sciences, 1987). This species was associated most often with rock substrates in shallow water.

Nitzschia latens Hust., 1949 (Figs. 25-28, 37, 38)

Valves measure 8-42 μ m in length and 4.0-5.5 μ m in breadth. Larger valves have parallel sides and protracted ends. Smaller valves are elliptical to almost round in outline. Fibulae number 10-21 in 10 μ m, are variable in size, and are spaced irregularly along the margin.

Nitzschia latens is distinguished from N. elliptica Hust. on the basis of length, breadth, and valve shape. According to Hustedt (1949), N. latens is 24–30 μ m long, 4.0–4.5 μ m wide, and has slightly protracted ends with straight or nearlystraight sides. N. elliptica, on the other hand, is shorter (13–22 μ m), but broader (5–6 μ m) than N. latens, and lacks protracted ends. Mono Lake samples contain specimens that resemble each of these two species, but also present are specimens that appear to form a morphological continuum between N. latens and N. elliptica. Simonsen (1987, p. 350) previously suggested a relationship between these two species. Noteworthy is the observation that smaller specimens tend to be at least as broad and sometimes broader than longer specimens. This condition was illustrated by Cholnoky (1966) for *N. elliptica* var. *alexandrina* Choln. (*sensu* Cholnoky, 1963, 1966, which appear to differ from the original concept of Cholnoky, 1958; see also Krammer & Lange-Bertalot, 1988), a taxon that, together with *N. etoshensis* Choln., may be close relatives or even possible synonyms of *N. latens*. The diatom described by Mason (1967) with nearly 50 striae per 10 μ m probably is *N. latens*.

SEM reveals striae to be parallel, with fine rows of circular puncta.

This species was recorded in all but one sample (10-m rock, LVTG). Relative abundance of N. *latens* ranged from rare to abundant, and this species was most abundant in four samples, including 15-cm rock sample at LVTG and 1-m and 5-m sediment and 5-m rock samples at DWP. This diatom occurred most frequently in shallow waters.

Nitzschia reimerii sp. nov.

(Figs. 29-32, 39, 40; Fig. 30 illustrates the holotype)

Descriptio. Valvae lateribus parallelis-leviter concavis, apicibus protractis capitatis, fibulis irregularium statuarum et spatiorum $6-8/10 \ \mu m$, striis $16-20 \ \mu m$ parallelis distincte punctatis, punctis $22/10 \ \mu m$. Latitudo $59-107 \ \mu m$. Latitudo $4-5 \ \mu m$.

Holotypus. CAS #216060.

Description. Valves with sides parallel or slightly concave, apices protracted, capitate. Fibulae of irregular size and spacing, 6-8 in 10 μ m. Striae 16-20 in 10 μ m, parallel and distinctly punctate. Puncta 22 in 10 μ m. Length 59-107 μ m, breadth 4-5 μ m.

Holotype. Slide CAS #216060.

Type locality. Mono Lake, Lee Vining tufa grove, 10-m depth, rock scrape. Etymology. Named for Dr. Charles W. Reimer, Curator Proprios, Academy of Natural Sciences of Philadelphia.

Remarks. This species resembles N. gessneri Hust. in valve outline, but N. gessneri is more narrow $(3-4 \ \mu m)$ and has finer densities of fibulae $(10-16 \ in 10 \ \mu m)$ and striae $(28-32 \ in 10 \ \mu m)$ (Hustedt, 1953). Nitzschia reimerii also resembles N. pertica Hohn & Hellerman in outline, but has finer striae $(24 \ in 10 \ \mu m \ in N. pertica)$ and coarser fibulae density $(9-12 \ in 10 \ \mu m \ in N. pertica)$ (Hohn & Hellerman, 1963). Another lanceolate Nitzschia species that resembles

FIGS. 41-46. Nitzschia monoensis sp. nov. Figs. 41-44. Valve views. Figs. 42, 43 are valves from the same frustule. Fig. 44. Arrow indicates large distal raphe end. Figs. 45, 46. Two frustules together showing physical relationships of raphe systems of each valve (arrows). LM; scale bar in Fig. 41 represents 10 μ m; all figures at same scale.

FIGS. 47–51. Nitzschia monoensis sp. nov. Figs. 47–49. External views. Fig. 47. Entire frustule. Scale bar represents $5 \,\mu$ m. Fig. 48. Frustule terminus showing distal raphe end (arrow) and numerous punctate girdle bands. Scale bar represents $3.75 \,\mu$ m. Fig. 49. Distal raphe end. Scale bar represents 1 μ m. Figs. 50, 51. Internal views. Fig. 50. Valve with numerous fibulae. Scale bar represents 10 μ m. Fig. 51. Fibulae taper away from raphe canal. Scale bar represents 2.5 μ m. SEM.





N. reimerii is N. fossilis (Grun.) Grun. in V.H., a smaller taxon [Krammer & Lange-Bertalot (1988) indicate that it is 30-85 μ m long] that has apices less attentuated than N. reimerii. Using SEM, fibulae appear robust, and at the ends of the valve they are elongated. This species was rare in two samples from BPTS, one sample from DWP, and rare to frequent in four samples from LVTG. Distribution of this species suggests a preference for deeper water.

Nitzschia monoensis sp. nov.

(Figs. 41-51; Figs. 42, 43 illustrate the holotype)

Descriptio. Valvae delicatae late lanceolate, raphe elevata diagonaliter in rustulum, poris externis terminalibus grandibus, fibulis 7–9/10 μ m, striis parallelis 42–46/10 μ m, pleuris numerosis punctatis. Longitudo 50–100 μ m. Latitudo 14–18 μ m.

Holotypus. CAS #216061.

Description. Valves delicate, broadly lanceolate. Raphe elevated, diagonal on the frustule, external terminal pores large, fibulae 7–9 in 10 μ m, striae parallel 42–46 in 10 μ m, pleurae numerous, punctate. Length 50–100 μ m, breadth 14–18 μ m.

Holotype. CAS slide #216061.

Type locality. Mono Lake, Lee Vining tufa grove, 5-m depth, rock scrape. Remarks. Using SEM, numerous punctate pleurae are revealed (Figs. 47, 48); external distal raphe ends are large (Figs. 48, 49). Internal costa extend across the valve surface to form fibulae. Costa are broadest near the raphe and taper across the valve face (Figs. 50, 51).

Presence of fibulae and the raphe system positioned diagonally on the frustule suggest placement of this species in *Nitzschia*. Within the genus, it may be part of the Epithemioideae-section (*sensu* Krammer & Lange-Bertalot, 1988) by virtue of the shape of the valve, large number of girdle bands and habitat (Krammer & Lange-Bertalot, 1988; Servant-Vildary, 1984). *Nitzschia monoen-sis* shares features of enlarged external distal raphe ends, lightly silicified valves and elevated raphe system with several genera considered by Paddock (1988), but differs by possessing true fibulae. Additional systematic studies will be necessary to determine the relationship between this Mono Lake endemic species, other species of *Nitzschia*, and those genera that bear elevated raphe systems.

Valves of this species are not well represented in the majority of Mono Lake samples, probably attributable to dissolution of valves in the highly alkaline conditions. This species does, however, form internal, bipartite, spore-like cells that were found to comprise over 70% of the cells counted in the 10-m sediment sample from LVTG. Ornamentation of the spore-like cells may be lacking or comprised of small pits or depressions on the "valve" (Figs. 33, 34). Costa-like striations also may be visible, but girdle bands are not known. Jones (1987) first described these cells and together with McLaughlin (1987) pondered their origin. We do not know if these cells represent a resistant stage in the life cycle of N. monoensis or are related to the Innenschalen produced by other species

as an apparent reaction to osmotic stress (e.g., Geitler, 1927). This diatom was found consistently in deep-water samples.

DISCUSSION

The number of diatom taxa (30) recorded during this investigation of the benthic flora of Mono Lake, although not a particularly large lake as compared to "typical" freshwater lakes, is significantly greater in terms of taxon richness than was recorded by previous investigators. Wornardt (1964, p. 2), for example, indicated that "no diatoms were found" from Mono Lake, although the National Academy of Sciences (1987) summary listed one species, *Nitzschia frustulum*, as the dominant diatom taxon. Mason (1967) reported two species of *Nitzschia* in the plankton, and Herbst (1988) earlier reported seven diatom taxa from Mono Lake. The lower species richness of Mono Lake may be attributed to the harsh chemical environment. The extreme nature of the lake's environment also is indicated by the large number of Innenschalen-producing species present and the frequency of aberrant valves observed, these being features described for diatoms from other saline environments (Frenguelli, 1929; Müller, 1899).

Heterogeneity is striking with regard to relative abundances of taxa within and between sites. Although some species appear to be best represented at a particular site, depth, or substrate type (e.g., N. monoensis and A. sphaerophora var. *minor* are best represented at greater depths), a pattern of dominance relative to these parameters is not apparent. The dominant taxa found during this study were identified earlier from some inland waters of high salt content or, in the case of newly described taxa, are closely related to species that occur in saline environments (Frenguelli, 1929; Müller, 1899; Servant-Vildary, 1984). In relation to the entire flora, published lists of benthic diatoms from saline lakes reveal that alkaline lakes of East Africa (Hecky & Kilham, 1973) and lower Grand Coulee lakes of Washington (Castenholz, 1960), lakes with diverse chemical characteristics from southern Bolivia (Servant-Vildary & Roux, 1990) and Saskatchewan (Hammer et al., 1983), and playa lakes from southern California (Busch & Kubly, 1980) share some species in common with the flora of Mono Lake. The chloride-dominated Great Salt Lake (Rushforth & Felix, 1982) and Solar Lake, Sinai (Ehrlich, 1978) harbor no species in common. Presence of some endemic taxa in Mono Lake indicates that the assemblage is distinctive. yet affinities with floras of other saline lakes, particularly alkaline systems, are indicated.

Presence of species in the Mono Lake flora that are more typical of freshwater environments (e.g., *Neidium iridis* and *Encyonema minutum*) are rare and probably of allochthonous origin. The nine centric taxa recorded from the lake also were rare in the benthic samples. Whether or not the planktonic species recorded from Mono Lake are residents or imported remains enigmatic.

The diatom flora of Mono Lake apparently has changed since the late Pleistocene. Solliday (1993) reports three diatom species from late Pleistocene sediments on Paoha Island (the largest of two islands in the lake) including A. costata, Surirella utahensis (Grun.) Hanna & Grant, and Cyclotella bodanica. These species are rare or absent from the Recent benthic flora. Wornardt (1964) reported five species from Late Pleistocene sediments of the Mono Lake basin, of which *A. costata* is reported here. Ecological changes in the Mono Lake basin related to fluctuations in water levels and effects of these fluctuations on the biota of the basin may be traceable with diatom remains. Using the Paoha Island deposit as a late Pleistocene baseline and the current study as a description of floristic composition relative to the Recent chemical milieu indicated by available data, paleolimnological reconstruction of the lakes' history may provide clues to the timing and degree of change in the diatom flora that, in turn, may be related to climatic change and/or human disturbance.

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