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FRESHWATER DIATOMS

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DIATOMEAS DE AGUA DULCE

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INTRODUCCION

Aparentemente durante el Oligoceno las diatomeas invaden los habitats dulceacuícolas en escala masiva. Aunque hay algunas en el Eoceno, no es común encontrarlas en rocas continentales tempranas de éste período.

No obstante, que las especies de diatomeas tienen una gran proliferación en agua dulce y aún en habitats terrestres, es poco conocida su evolución post-eocénica, lo cual trae como consecuencia que en la actualidad no sea posible subdividir las rocás continentales del Terciario con base a las diatomeas fósiles.

Esto será posible en un futuro, si se hace un esfuerzo de conocer su ecología y sistemática, y si la colección de diatomeas en rocas del Terciario son descritas con propiedad y bien documentadas.

La bioestratigrafía de las diatomeas de agua dulce puede proveer una valiosa información para aclarar los medios ambientes de depósito del Terciario en el NW de América y además dar un importante conocimiento de la evolución y significado ecológico de estos organismos.

La paleoecología o más específicamente, la paleolimnología (estudio de sistemas lacustres antiguos) puede ser un importante aspecto de la historia geológica del Terciario y Cuaternario; el es-

tudio de las diatomeas ha provisto información detallada acerca de los niveles de agua antiguos, salinidad y contenido de nutrientes de sistemas lacustres pasados. Esta información paleolimnológica puede ser relacionada con el estudio de climas del pasado, tectonismo o actividad biológica en ecosistemas terrestres. La aplicación de esta información paleoecológica, indirectamente ayuda a la búsqueda de recursos minerales, esto es siempre una necesidad para estudios puramente bioestratigráficos, pues la ecología juega un papel muy importante en la distribución espacial y temporal de los organismos.

La paleoecología también juega un papel crítico en estudios modernos ambientales que pretenden determinar el impacto de la civilización tecnológica sobre el ambiente. Esto se está convirtiendo en una creciente e importante preocupación de las industrias de explotación minera.

El impacto ambiental que producen estudios de un ecosistema acuático en un período de dos o tres años aún esta lejos de convencer a muchas personas de que la verdadera línea de base ha sido establecida. Desafortunadamente tales trabajos superficiales causan retraso o cancelación de otras exploraciones y proyectos valiosos.

Gran cantidad de registros ecológicos están disponibles en los sedimentos de lagos existentes. El contenido de diatomeas y polen en esos sedimentos pueden ser analizados para elaborar un registro ambiental básico local que refleje tendencias y tasas de cambio.

BIOLOGIA, MORFOLOGIA Y TAXONOMIA DE BACILLARIOPHYCEAE

La siguiente sección es traducida de Ruth Patrick,1959, Capitulo 7, Bacillariophyceae,p.p. 171-189 in Fresh-water. Biology (2a. ed) editada por Edmondson W.T., John Wiley & Sons, Inc. 1248 pp.

Bacillariophyceae o diatomeas, son algas unicelulares, usualmente microscópicas, que se caracterizan por tener una pared celular de sílice. Esta pared consiste de dos valvas, que son superficies más o menos planas unidas por una banda o cinturón. El grosor de esta pared celular puede variar grandemente; desde muy delgado en ciertas especies típicas del plancton a bastante gruesas en ciertas especies bentónicas del ártico y zonas templadas. La clasificación está basada en la ornamentación que presentan en la pared de sílice.

En algunos casos las características empleadas en taxonomía pueden ser vistas en preparaciones frescas con objetivos secos (sin aceite) pero la identificación crítica, usualmente implica que se lave el material y sea observado con un objetivo de aceite de inmersión. El lavado se lleva a cabo hirviendo el material con ácido nítrico o sulfúrico el cual se añade un agente oxidante (dicromato de potasio), se lava varias veces con agua destilada y para separar las frústulas de la muestra, se deja reposar ésta y posteriormente se decanta. Una pequeña cantidad es entonces transferida a un vidrio de reloj para secarla y posteriormente montarla en un medio altamente refractivo tal como el Hyrax o euparol.

Los diatomeas pueden vivir solas o formando colonias o fila-

mentos. Todas secretan una sustancia mucilaginosa que cubre casi toda la pared de sílice; la cantidad y distribución de ésta varía grandemente, por ejemplo, gracias a ésta sustancia las células se pueden adherir unas con otras formando colonias o filamentos y en otras especies va a permitir que se adhieran a un cierto sustrato.

Cada diatomea contiene un núcleo. La división celular vegetativa es acompañada de mitosis y el núcleo reproductivo es formado por meiosis. Los cromosomas son facilmente definibles, pero debido a su gran número son algunas veces difíciles de contar.

Los cloroplastos pueden ser pocos o numerosos, y variar grandemente en tamaño y forma. Los pigmentos que han sido identificados son: clorofila alfa y c; B y E carotenos, fucoxantinas, neufucoxantinas A y B; diatoxantinas y diadinoxantinas. La abundancia de los carotenoides es la que da ese color café oro a las diatomeas.

Los productos almacenados son generalmente grasas y aceites muy diferentes a los de las algas, las cuales almacenan varios tipos de carbohidratos.

La reproducción es comunmente vegetativa. La formación de auxosporas parece indicar en muchos casos un tipo de reproducción sexual, esta ha sido reconocida en muchos géneros (Patrick, 1954). La ocurrencia de la reproducción sexual comparada con la división celular vegetativa ordinaria resulta relativamente rara.

DISTRIBUCION

Las diatomeas están ampliamente distribuidas en aguas dulces y

marinas, también son encontradas en fangos húmedos y sobre plantas húmedas tales como Sphangnum (Patrick, 1948). Aunque hay muchas especies tolerantes a variaciones en las condiciones ambientales, muchas son bastante específicas en sus requerimentos. Por ejemplo, ciertas especies pueden resistir una concentración definida de sustancias disueltas tales como los cloruros.

La abundancia relativa de las especies de diatomeas ha sido muy útil para indicar el tipo de agua en la cual habitan. Los ecólogos las han usado para indicar el grado de contaminación de un cuerpo de agua y otras variaciones en las condiciones ecológicas; los paleontólogos pueden averiguar por núcleos sedimentarios si un lago profundo o un estanque somero existió en tiempos pasados, su temperatura y las características químicas del agua. En determinadas condiciones ambientales pueden hacerse una estimación más confiable si se emplea un patrón de especie en lugar de tomar solo en cuenta las especies indicadoras.

Es mucho más dificil establecer de una forma precisa a los géneros que a las especies; y solo pocas generalizaciones pueden hacerse acerca de un tipo de ambiente ecológico en el cual algunos géneros tienen un mejor desarrollo. Frecuentemente muchas especies del género Eunotia y Frustulia son encontrados en aguas con un contenido bajo en calcio y magnesio y con un pH por abajo del 7; sin embargo, ciertas especies de estos géneros prefieren un rango de pH de 5 a 6.

Otros géneros contienen especies las cuales parecen evitar

aguas ácidas y con bajas concentraciones de calcio y magnesio. Esta son: Mastogloia, Diploneis, Amphipleura, Cyrosigna, Denticula, Ephitemia y Rhopalodia. Otros géneros tales como Cylondrotheca y muchas especies de Nitzschia parecen preferir aguas con un contenido iónico bastante alto, esas aguas pueden ser duras como las del Oeste de la parte central de Estados Unidos o bien pueden ser más o menos salobres.

La temperatura es otro factor ambiental que parece efectuar la distribución de las diatomeas. Ciertos géneros tales como Tetracyclus y Amphicampa son usualmente encontrados en regiones montañosas frías. Frecuentemente los géneros Diatoma y Ceratoneis son encontrados en regiones templadas frías y en regiones templadas meridionales. Las especies de tales géneros tienen su máximo desarrollo en invierno y al principio de la primavera, o al final del otoño si la temperatura del agua es cálida durante los meses de verano.

CLASIFICACION

El sistema generalmente aceptado de clasificación de diatomeas, es aquel publicado por Schütt en 1896; el dividió a las diatomeas en dos grupos principales, los cuales Hustedt (1930) los refiere como Ventrales y Pennales. Recientemente Hendey (1937) propone un sistema de clasificación el cual parece mucho más lógico y natural. Como se verá abajo, la clasificación reconoce un orden y varios subordenes de igual posición. Estudios posteriores indican que estos subordenes pueden ser elevados a nivel de Orden.

Clasificación según Handey (1937) con algunas modificaciones y adiciones.

División Chrysophyta
Clase Bacillariophyceae
Orden Bacillariales

1. Suborden Discineae
1. Familia Cascinodiscaceae
1.1 Subfamilia Melosiroideae
Género Melosira
1.2. Subfamilia Cascinodiscoideae
Género Coscinodiscus, Cyclotella, Stephanodiscus

2. Suborden Biddulphineae
I. Familia Biddulphiaceae
I.1. Subfamilia Biddulphioideae
Género Biddulphia
I.2. Subfamilia Terpsinioideae
Género Terpsinoe, Hydrocera
II. Familia Chaetoceraceae
II.1. Subfamilia Chaetoceroideae
Género Chaetoceros

3. Suborden Saloniineae
I. Familia Rhizosolenioideae
Género Rhizosolenia, Attheya

4. Suborden Araphidineae
I. Familia Fragilariaceae
I.1. Subfamilia Tabellarioideae
Género Tetracyclus, Tabellaria
I.2. Subfamilia Meridionoideae
Género Meridion, Diatoma
I.3. Subfamilia Fragillarioideae
Género Asterionella, Ceratoneis, Centronella, Fragilaria, Opephora, Synedra, Amphicampa

5. Suborden Raphidioidineae
I. Familia Eunotiaceae
I.1. Subfamilia Peronioidae
Género Peronia
I.2. Subfamilia Eunotioideae
Género Eunotia, Actinella

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6. Suborden Monoraphidineae
I. Familia Achnanthaceae
I.1. Subfamilia Cocconeioideae
Género Cocconeis
I.2. Subfamilia Achnanthes, Rhoicosphenia, Eucocconeis

7. Suborden Biraphidineae

I. Familia Naviculaceae

I.1. Subfamilia Naviculoideae

Género Amphipleura, Anomoeneis, Brebissonia, Caloneis. Diatomella, Diploneis, Frustulia, Gyrosigma, Mastogloia, Navicula, Neidium, Pinnularia, Stauroneis

I.2. Subfamilia Amphiproroideae

Género Amphiprora

II. Familia Gomphonemaceae

II.1 Subfamilia Gomphonemoideae

Género Gomphonema, Gomphoneis

III. Familia Cymbellaceae

III.1 Subfamilia Cymbelloideae

Género Cymbella, Amphora

IV. Familia Epithemiaceae

IV.1 Subfamilia Epithemioideae

Género Epithemia, Denticula

IV.2 Subfamilia Rhopalodioideae

Género Rhopalodia

V. Familia Nitzschiaceae

V.1. Subfamilia Nitzschioideae

Género Nitzschia, Cylindrotheca, Bacillaria, Hantzschia

VI. Familia Surirellaceae

VI.1 Subfamilia Surirelloideae

Género Surirella, Cymatopleura, Campylodiscus

PALEOLIMNOLOGY OF LAKE TEXCOCO, MEXICO. EVIDENCE FROM DIATOMS[1]

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ABSTRACT

A 46-m core from the lacustrine sediments beneath Mexico City was analyzed to establish a stratigraphic sequence of diatom assemblages for use in interpreting the climatic and limnologic history of ancient Lake Texcoco.

Diatoms were found in nearly every 20-cm sample interval, and several major zones were established. Planktonic and benthonic–epiphytic assemblages alternate throughout the core, both of fresh- and brackish-water types. The alternations reflect the fact that the coring site is marginal to the main basin of the lake, and limnologic conditions change as water levels rise and fall.

A freshwater planktonic assemblage dominated by *Stephanodiscus niagarae* in deeper parts of the core indicates that a large, cool, and possibly deep lake existed about 100,000 years ago, either because of pluvial or because of tectonic factors. This is replaced (depth 35 to 30 m) by a freshwater benthonic–epiphytic assemblage characterized by *Denticula elegans* and other marsh diatoms. The marshes were probably maintained by springs from the shore when the lake was reduced to saline pools in the center of the basin.

As water levels rose again (core depths 30 to 5 m), brackish water flooded the marshes, and brackish benthonic diatoms (such as *Anomoeoneis costata, Campylodiscus clypeus,* and *Nitzschia frustulum*) replaced the earlier floras. These were periodically replaced by brackish planktonic diatoms (as *Cyclotella striata* and *Cyclotella quillensis*) when the lake was deeper, but the earlier freshwater planktonic flora never recurred. The same brackish planktonic and benthonic diatoms that prevailed for several tens of thousands of years are found today confined to the brackish pools of Lake Texcoco that are remnants of the former larger lake. The long interval of fluctuating brackish floras probably represents Wisconsin time.

The last 10,000 years of the lake's history is marked by a return of the marsh flora, suggesting a climate drier than that of Wisconsin time. A marked climatic change, however, is not necessary to explain this last change in the diatom flora, and it seems likely that the pluvial climate inferred for the southwestern United States had less effect at the latitude of Mexico City (19° 30′) than farther north.

INTRODUCTION

This paleolimnologic study of Lake Texcoco, Mexico, began in 1968 when I was a postdoctoral fellow at Yale University under the advisement of E. S. Deevey and G. E. Hutchinson. It was partly supported by a grant from the American Philosophical Society. The project was continued at the Limnological Research Center of the University of Minnesota where I was a National Science Foundation postdoctoral fellow under H. E. Wright. The enthusiasm and support of these individuals have greatly facilitated this work. In addition, I wish to acknowledge the kind help of P. B. Sears, of L. Zevaert, who provided material for study, and of Prof. J. L. Lorenzo and his colleagues at the Instituto Nacional de Antropologia e Historia in Mexico City, who have shared with me many of their insights about the environmental history of the Basin of Mexico.

GEOLOGIC SETTING

The general sequence of events that led to the formation of the Basin of Mexico has been traced (Mooser et al. 1956; Mooser 1963). The basin began as a graben in the Tertiary trans-Mexico volcanic belt, bounded on the east and west by two fault zones and their associated volcanoes, Sierra de Las Cruces and the Sierra Nevada, the latter containing the famous volcanoes Popocatepetl and Iztaccihuatl. The faults and volcanoes have been active

[1] Contribution 92, Limnological Research Center, University of Minnesota.

throughout the Tertiary, progressively covering the Cretaceous basement; particularly massive extrusions of acidic lava and probable sinking of the graben floor occurred in the Miocene and Pliocene, defining a valley whose integrated river system drained to the south (Figueroa et al. 1968). The northern limits of the valley are defined by lower mountains produced by faulting and volcanism in the region of Pachuca. The valley was closed in the late Pliocene when basaltic volcanic activity from centers located in the southern part of the basin (the massive Chichinautzin lavas and Sierra Ajusco) dammed the valley. The basin thus formed was rapidly sedimented with clastic and pyroclastic material to a thickness of 800 m (Figueroa et al. 1968), and the regional drainage converged to the lowest part, where a lake has persisted until modern times.

LIMNOLOGIC SETTING

Today the Basin of Mexico is a plain (elevation about 2,236 m) surrounded on the east, south, and west by high mountains (3,000–6,000 m). It was a closed hydrographic system before being artificially drained in 1900, and precipitation in the mountains and runoff from summer rains drained into a chain of lakes that nearly traversed it from north to south (Fig. 1). After the rainy season (May–October) the lakes were frequently joined into a single sheet of water (elevation 2,242 m), which during the dry winter months was separated into a number of subbasins, some artificially contained by dikes. The principal ones and their elevation relative to Lake Texcoco listed from north to south are [elevations from Zeevaert (1952) and Bonaparte et al. (ca. 1900)]:

Zumpango	+6 m;
Xaltocan	+3 m;
San Cristobal	+3 m;
Texcoco	0 m;
Mexico	+0.85 m;
Xochimilco	+3.5 m;
Chalco	+3.5 m.

Lake Texcoco is the lowest in the series and the most saline, both because of evaporation and because thermal springs flow into it (Mooser 1963). The Mexico subbasin, artificially contained by Aztec dikes to the west of Lake Texcoco, was maintained by freshwater from Chalco, Xochimilco, and numerous springs from Chapultepec, southwest of Mexico City. It drained into Lake Texcoco during times of water surplus through an organized system of canals and gates. In similar fashion Lake Chalco was separated from Lake Xochimilco. Because of the abundance of freshwater in the southern part of the basin, Chalco, Xochimilco, and Mexico were extensively used for *chinampa* farming (Deevey 1957).

The draining of the Basin of Mexico and the growth of Mexico City have created some engineering problems. The early dikes, especially that of Netzahuacoyotl (ca. 1450 A.D.), were built to prevent seasonal floods of saline water from entering the highly productive *chinampa* farms southwest of the capital. Flooding continued in colonial times, and the need for effective sewage disposal for the city that was rapidly growing onto the plain of Lake Texcoco demanded that the lakes be systematically drained. The first efforts began in the 17th century, and the work was finally completed in 1945 with the Tequisquiac tunnel, which has reduced the surface area of Lake Texcoco to a rainy-season area of only 200 km^2 (Mooser 1963).

As the drainage of the lakes was effected, and more and more water was pumped from aquifers of sands and silts beneath the lake plain, Mexico City began to sink into the highly bentonitic clays that underlie it. This problem is especially serious where heavy buildings are constructed in the metropolitan areas. Dr. L. Zeevaert has for many years conducted studies of the mechanical nature of the lake sediments of the basin, principally beneath Mexico City, to seek competent strata for the placement of foundation pilings. He has taken numerous cores of

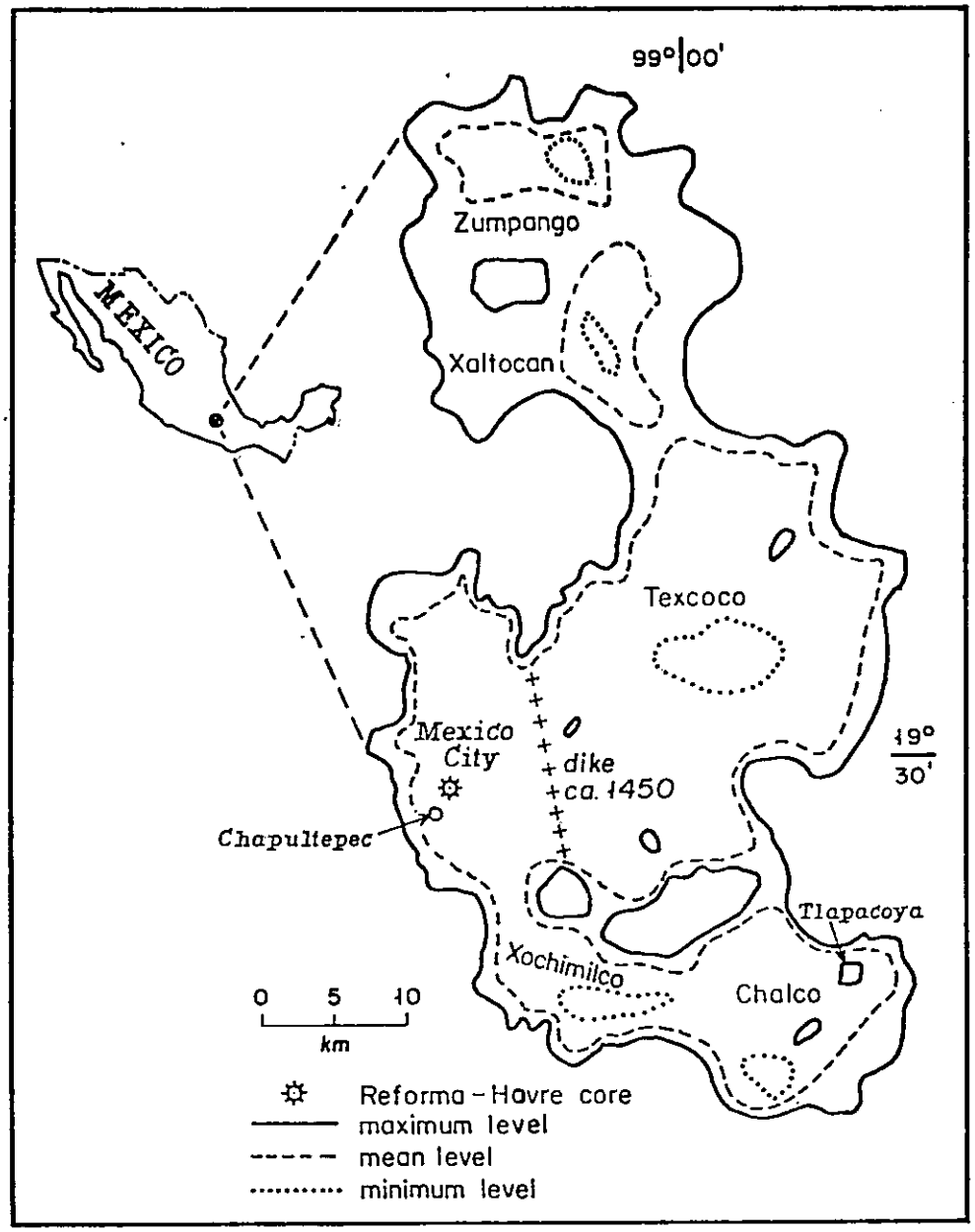


FIG. 1 Index map showing lakes in the Basin of Mexico. Adapted in part from J. L. Lorenzo (*in* Mooser et al. 1956).

the sediments with a simple Shelby tube sampler that is forced into the lake sediments by a mechanized coring rig. In resistant material a jar hammer is used. Cores about 10-cm diam and 2 m long are taken in this fashion and their sedimentology, mechanical properties, and water content are studied. Through this work Zeevaert (1952, 1953) has compiled a detailed stratigraphy of the Basin of Mexico to depths of about 70 m. He has been most interested and cooperative with respect to ancillary scientific studies on his cores and has provided both Sears' and

Clisby (1955) and me (Bradbury 1970*b*) with samples.

LACUSTRINE STRATIGRAPHY

The Pleistocene stratigraphy in the Basin of Mexico was first studied in detail by Bryan (1948). He worked with the exposures of soils, tuffs, and alluvium on the margins of the basin and divided them into units of the following names, characters, and ages:

Noche Buena—soils and alluvium, with pottery shards; Pre-Classic, Classic, and Post-Classic.

Toltolzingo—dark brown soils, alluvium, some eolian material.

Barrilaco—caliche-pedocal; Altithermal 4,500–7,500 B.P.

Becerra—alluvium-pedalfer, *Elephas, Equus, Bison* etc.; Cochrane-Mankato.

Morales—caliche-pedocal; Wisconsin interstadial.

Tacubaya—yellow-brown alluvium-pedalfer; Tazewell-Cary.

Tarango—acidic volcanic tuff, water-deposited; Plio-Pleistocene?

Bryan (1948) assumed that these formations or their equivalents exist in the lacustrine deposits in the center of the basin, and Zeevaert (1952, 1953) correlated Bryan's strata with the alternating layers of lacustrine clays, silts, and sands underneath Mexico City. Lithology is used as the basis for correlation of the coarser units, whereas lake clays are thought to be contemporaneous with soil formation and reduced alluviation. Deposits high in calcium carbonate are considered equivalents of the caliches on the basin margins.

Foreman (1955) more carefully analyzed the sediments beneath Mexico City, and, although he did not use the formational names of Bryan and Zeevaert, he showed their correlation to his findings. His stratigraphy is generalized into seven zones, but despite the complete lithologic description, they do not have diagnostic characteristics. This seems to be a result of high variability of the sediments and the predominance of ash and weathered ash in them.

Bryan's names applied to the stratigraphy beneath Mexico City are useful in speaking about the section. Considering the effects of erosion and the occurrence of hiatuses in the marginal alluvium and soils, as compared to the more complete depositional record in the central part of this closed basin, temporal equivalents can only be sporadic. In addition, correlations based on concepts such as pedalfers = clays, pedocals = caliches (which in several cases are high concentrations of ostracod carapaces) seem to be simplistic representations of complicated and distinctive environments. Mooser et al. (1956) pointed out that it is still adventurous to identify the upper limit of the Tarango formation beneath Mexico City. For now, despite the usefulness of Bryan's formations, the lacustrine deposits of the Basin of Mexico should be characterized in their own right and not equated with the marginal deposits.

FOSSIL STUDIES

Major advances in characterizing these deposits have come from fossil studies, and foremost of these is the pollen-stratigraphic work of Sears (1952) and Sears and Clisby (1955). These were preceded by an exploratory study by Deevey (1944).

Sears and Clisby studied two of Zeevaert's cores to depths of more than 70 m. They attempted paleoclimatic interpretation, but satisfactory pollen zonation is not possible because the percentage frequencies of the major taxa are quite variable throughout the core. In addition, pollen in the coarser sediments is scarce and poorly preserved. Pollen abundance correlates with clay zones and is used in environmental reconstruction. Maxima in the amount of oak, fir, and alder pollen as opposed to pine pollen are considered to represent warm-moist periods.

Foreman (1955) noted the presence of ostracods, sponge spicules, and diatoms; he divides the latter into elongate and circular groups but does not use any of these fossils for stratigraphic zonation.

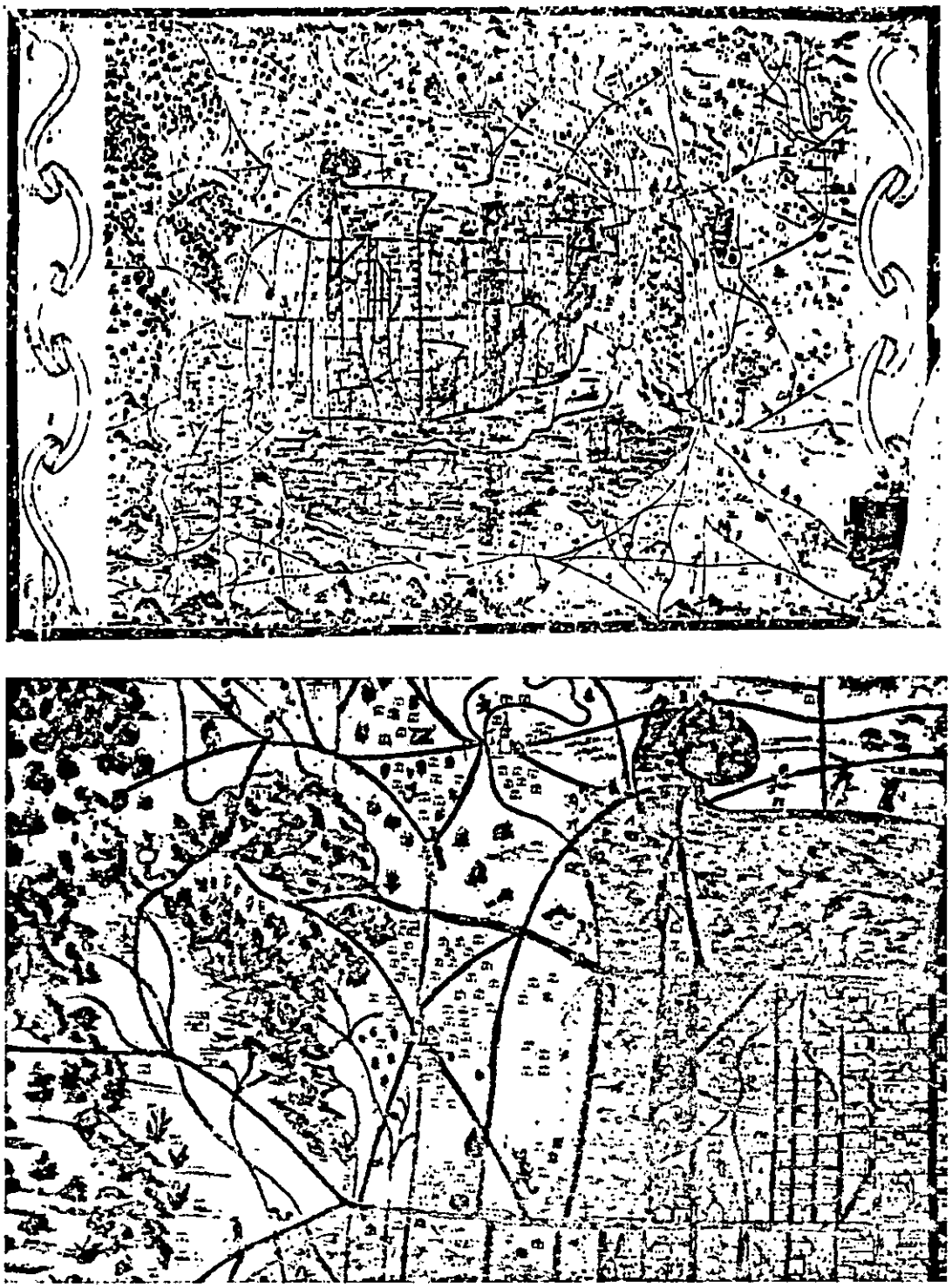


FIG. 2. Alonzo de Santa Cruz map showing the Basin of Mexico in 1550 A.D. (from Linne 1948). Upper panel—general map of the Basin of Mexico. Lower panel—enlarged central section of the map showing probable location of core P 366-2 near upper hunter in canoe.

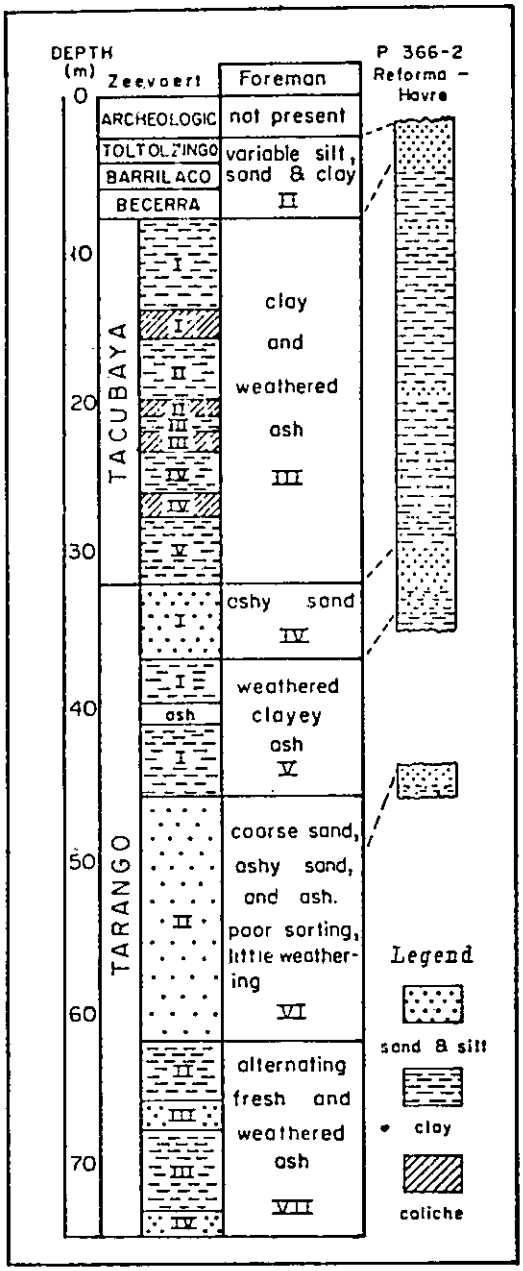


FIG. 3. Correlation of core P 366-2 with the stratigraphic divisions of Zeevaert (1952) and Foreman (1955). Difference in depths results from the marginal position of P 366-2 relative to their sections.

Earlier studies of diatoms from the Pleistocene sediments of Lake Texcoco include the taxonomic work of Ehrenberg (1869) and Lozano (1917); P. Conger used diatoms of the Becerra formation to interpret the environment of deposition of human and mammoth remains in the study of Tepexpan Man by de Terra et al. (1949).

DIATOM STUDIES

The present work represents the first attempt to produce a diatom stratigraphy in the Basin of Mexico. The coring site was at the intersection of Paseo de la Reforma and Calle Havre, about 4 km S 70° W from the center of Mexico City (the Zocalo) and about 2 km N 60° E of Chapultepec Hill (Fig. 1). The core (P 366-2), taken by Zeevaert in May 1967 in connection with the construction of a large hotel at this site, was similar to those studied by Foreman and Sears and Clisby in 1955 and to the many described by Zeevaert (1952, 1953). It was initially 50 m long, but after Zeevaert's mechanical analysis of some sections only the upper 35 m were well represented, although there were a few samples from 44 to 46 m available for study.

The coring site is shown in Fig. 2, a reproduction of the 1550 Alonzo de Santa Cruz map of the Basin of Mexico (from Linne 1948). The spot cannot be precisely indicated, but it is probably very near the canoeist shown hunting water birds with a spear at the top (west) of the map. Chapultepec Hill is behind and to the left of the hunter.

The Alonzo de Santa Cruz map shows the lacustrine environment of the Basin of Mexico before any attempts were made to drain the lakes and therefore represents a more or less normal state of affairs, although the activities of man (dikes, canals, hunting, fishing, and so forth) had clearly modified the environment. What is important here is to notice the abundance of aquatic vegetation, the apparent shallowness of the lakes, the placement of Netzahuaçoyotl's dike separating Lake Mexico from saline Lake Texcoco to the east, and the presence of springs or other sources of water at Chapultepec Hill.

The coring site is clearly marginal relative to the main basin of Lake Texcoco,

and Zeevaert's work shows that the formations beneath Mexico City dip basinward and so are found at greater depths to the northeast. The amount of dip is about 2 m/km.

SEDIMENTOLOGY AND CORRELATION

The strata found in the P 366-2 core can be correlated with those of Zeevaert and Foreman only by lithology, because the depths are not equivalent. The variability of lithology makes this difficult, but the sedimentologic descriptions and analyses of Zeevaert (unpublished but on file) indicate that the upper units of his "Tarango" formation are represented, as is the "Tacubaya" formation. These sediments are difficult to subdivide, and the likelihood of lateral variation toward the basin margin further complicates correlation. Nonetheless, they can be differentiated from the overlying "Becerra," "Barrilaco," and "Toltolzingo" formations. The probable correlation is shown in Fig. 3, but I must stress that I do not feel these names are justly applied to the deposits beneath Mexico City.

A detailed sedimentologic study has not been made of core P 366-2. The sediments are generally similar to those of the cores carefully described by Foreman (1955), being predominantly fine sands, silts, weathered ash and some clay, and occasional unweathered ash. They are diagrammatically characterized in Fig. 4 and compared with Zeevaert's (unpublished) water-content analyses. Fossils are abundant; siliceous phytoliths, sponge spicules, and diatoms are common, as are calcareous ostracod carapaces. Snails are less common but found in certain zones, especially the coarser ones. Pollen is generally abundant in the finer sediments, particularly the clays and weathered ash, and occasionally seeds and fish bones are found. The locations of high concentrations of ostracod carapaces and of fish fossils are indicated in Fig. 4. The fish have been identified by R. R. Miller and C. Barbour. In some zones the sediments are penetrated by root holes, suggesting emergent vegetation in a shallow lake.

Diatom Ecology

Diatoms were examined at 20-cm intervals where possible throughout the core. There were 400 diatoms distributed in 12 to 60 taxa counted from each sample; 204 taxa were identified and their frequency of occurrence calculated. Of those, 88 had abundancies of at least 2%, and their frequencies are plotted in Fig. 4. The species that had similar depth distributions were arranged in assemblage groups to facilitate discussion of the limnological variation against time; these groups are identified ecologically at the top of the figure. Each species plotted is numbered consecutively to help the reader locate its frequency silhouette when it is mentioned in the text. An alphabetical listing of all species found is given in Table 1, with information about their ecology and modern distribution.

Ideally, fossil diatoms that have similar frequency distributions with depth constitute fossil assemblages that reflect past ecological associations. In practice the effects of reworking and transportation of diatom frustules can obscure the internal ecological coherence of fossil associations, especially in shallow lakes, and it is not always possible to interpret successfully every element in a fossil assemblage. On the whole, however, the species of the diatom assemblage groups do reflect uniform ecology, within the rather broad limits of diatom autecology. Some latitude in ecological uniformity results from the juxtaposition of similar but not identical distributions (in the interests of saving space).

Groups I–VI are dominantly freshwater diatoms, the vast majority being benthonic species preferring somewhat alkaline water and tolerant of small amounts of salt. Group I has two species, *Nitzschia tryblionella* (1) and *N. hungarica* (3), that Cholnoky (1968) refers to as brackish-water species, but Hustedt (1930) records

→

FIG. 4.

TABLE 1. *List of diatoms found in the Reforma-Havre (P 366-2) core*

	Ecological characteristics*			Occurrence in Mexico†					
	S	pH	IC	1	2	3	4	5	6
Achnanthes exigua Grun.	F	8	O_2						
A. hauckiana Grun.									
A. hungarica (Grun.) Grun.									
A. lanceolata (Breb.) Grun.	F	7.2–7.5	O_2						
A. marginatula Grun.									
A. minutissima Kutz.	F	8	O_2						
Amphiprora alata Kutz.									
Amphora acutiuscula Kutz.									
A. coffaeiformis salina (W. Sm.) A. Cl.	B	8+							
A. macilenta Greg.									
A. ovalis Kutz.	F–B	8.2				×		×	
A. ovalis pediculus Kutz.	F	8.0–8.2							
A. veneta Kutz.	F–B	8.0–8.5				×	×	×	×
Anomoeoneis costata (Kutz.) Hust.	B	9–10	Na_2CO_3	×	×				
A. sphaerophora (Ehr.) Pfitz.	F–B	8.5					×		
A. sphaerophora sculpta O. Mull.				×	×				
Caloneis bacillum (Grun.) Cl.	F	8							×
C. lewisii inflata (Schultze) Patr.	F–B	A							
C. limosa (Kutz.) Patr.									
C. oregonica (Ehr.) Patr.	B–M	A						×	
C. permagna (J. W. Bail.) Cl.									
C. ventricosa subundulata (Grun.) Patr.									
Campylodiscus clypeus Ehr.	B	8.6–8.7							
C. noricus Ehr.									
Chactoceras Ehr.	B–M	A		×					
Cocconeis diminuta Pant.	F	8							
C. placentula Ehr.	F	8+				×		×	
C. thumensis A. Mayer	F	8							
Cyclotella comensis Grun.									
C. kutzingiana Thwaites	F	8							
C. meneghiniana laevissima (v. Goor) Hust.	F–B	8		×		×			
C. quillensis Bailey	B	>7							
C. striata (Kutz.) Grun.	B–M	6.9–8.6	SS	×		×		×	
Cyclotella sp. cf. *C. stylorum* Brightwell	F	A							
Cymatopleura solea (Breb.) Wm. Sm.									
Cymbella cistula (Hemp.) Grun.	F	6–9	O_2						
C. cistula maculata (Kutz.) v. Heurck									
C. helvetica Kutz.									
C. mexicana (Ehr.) Cl.	B	A				×		×	
C. pusilla Grun.	B	7–8							
C. ruttneri Hust.									
C. triangulatum (Ehr.) Cl.	F	8							
C. turgida (Greg.) Cl.									
C. ventricosa Kutz.									
Denticula elegans Kutz.	F	8						×	

* Ecological characteristics provided for the species plotted in Fig. 4. S = salinity and F = freshwater, B = brackish water, M = marine water. pH = recorded pH and A = alkaline water, a = acidic. IC = indicator characteristics and SS = stable salinity, Ae = aerophil, W = warm water, E = eutrophic, het = heterotroph, O = oligotrophic. This information is largely from Cholnoky (1968), Patrick and Reimer (1966), Hustedt (1930), and Bright (in prep.).

† 1 = Texcoco (10,000); 2 = Tlaxcala (3,500); 3 = Chalco (2,140); 4 = Tlaxcala (1,130); 5 = Xochimilco (690); 6 = Zumpango (200). Numbers in parentheses represent conductivity in μmho/cm.

TABLE 1. Continued

	Ecological characteristics*			Occurrence in Mexico†					
	S	pH	IC	1	2	3	4	5	6
Diatoma hiemale (Roth) Heib.									
Diploneis elliptica (Kutz.) Cl.									
D. oblongella (Naeg. ex Kutz.) Ross	F–B	8+							
D. parma Cl.									
D. pseudovalis Hust.									
D. puella (Schum.) Cl.									
D. smithii (Breb. ex Wm. Sm.) Cl.									
Epithemia hyndmanni Wm. Sm.	F	7.5–8							
E. intermedia Fricke									
E. sorex Kutz.									
E. turgida (Ehr.) Kutz.	F	8.2						×	
E. zebra (Ehr.) Kutz.	F–B	8.2–8.5				×		×	×
Eunotia curvata (Kutz.) Lagerest.									
E. diodon Ehr.									
E. flexuosa Breb. ex Kutz.									
E. glacialis Meist.									
E. incisa Wm. Sm. ex Greg.									
E. maior (Wm. Sm.) Rabh.	F	~7.0							
E. pectinalis (O. F. Mull) Rabh.									
E. serra diadacma (Ehr.) Patr.									
Fragilaria brevistriata (Grun.)	F	7.5–7.8	O_2			×		×	
F. capuchina Desm.									
F. construens venter (Ehr.) Grun.	F	7.7–7.8	O_2			×			
F. leptostauron dubia (Grun.) Hust.									
F. pinnata Ehr.	F	7.6–7.7	O_2			×		×	
F. vaucheriae (Kutz.) Peters									
Frustulia rhomboides amphipleuroides (Grun.) Cl.									
Gomphonema accuminatum coronata (Ehr.) Wm. Sm.									
G. angustatum (Kutz.) Rabh.	F	7.5–7.7							
G. dubraviscense Pant.									
G. gracile Ehr.	F	7.2–7.4							×
G. lanceolatum insignis (Greg.) Cl.	F	8						×	×
G. longiceps subclavata Grun.				×					
G. parvulum Kutz.	F	7–9	O_2 lack	×		×		×	×
G. sphaerophorum Ehr.									
G. tergestinum (Grun.) Fricke									
G. ventricosum Greg.									
Gyrosigma obtusatum (Sulliv. & Wormley) Boyer									
G. spencerі (Quek.) Griff. & Henfr.									
Hantzschia amphioxys (Ehr.) Grun.	F–B	7.8–8.0	Ae					×	
Mastogloia smithii lacustris Grun.									
Melosira granulata (Ehr.) Ralfs.	F	7.9–8.2	W–E					×	
M. italica (Ehr.) Kutz.	F	8							×
M. varians Ag.									
Navicula accomoda Hust.									
N. acceptata Hust.									
N. agrestis Hust.									
N. anglica subsalsa (Grun.) Cl.									
N. capitata hungarica (Grun.) Ross	F	8				×			

TABLE 1. Continued

	Ecological characteristics*			Occurrence in Mexico†					
	S	pH	IC	1	2	3	4	5	6
N. cari Ehr.									
N. cincta (Ehr.) Ralfs				×	×				
N. circumtexta Meist. ex Hust.									
N. coconeiformis Greg. ex Grev.									
N. consentanea Hust.									
N. cryptocephala Kutz.	F	8					×		
N. cuspidata (Kutz.) Kutz.	F–B	8.3–8.6		×			×		
N. cuspidata ambigua (Ehr.) Cl.									
N. cuspidata heribaudi Pergallo	F–B	8.3–8.6							
N. exigua Greg. ex Grun.	F	7.5–8.0							
N. festiva Krasske									
N. fragilarioides Krasske	F								
N. graciloides A. Mayer									
N. gregaria Donk.									
N. grimmei Krasske									
N. holophila (Grun.) Cl.	B	A			×		×		
N. huefleri Grun.									
N. huefleri leptocephala (Breb. ex Grun.) Patr.									
N. laevissima Kutz.									
N. lagerheimi Cl.	F	7.8							
N. lanceolata (Ag.) Kutz.									
N. minima Grun.	F	7.5–8.0	O_2 lack						
N. minuscula Grun.								×	
N. muralis Grun.									
N. oblonga Kutz.	F–B	A							
N. peregrina (Ehr.) Kutz.									
N. protracta Grun.									
N. pseudoscutiformis Hust.									
N. pupula rectangularis (Greg.) Grun.	F	8						×	×
N. pygmaea Kutz.	B	A		×					
N. radiosa Kutz.									
N. rhynchocephala Kutz.	F	7.3–7.6							×
N. rhynchocephala germainii (Wallace) Patr.									
N. salinarum Grun.									
N. semen Ehr. emend. Donk.									
N. seminuloides Hust.									
N. subhamulata Grun.									
N. submuralis Hust.									
N. texana Patr.	F	A							
N. tripunctata (O. F. Mull.) Bory	F–B								
Neidium affine (Ehr.) Pfitz.									
N. iridis (Ehr.) Cl.	F	6							
Nitzschia acuta Hantz.									
N. amphibia Grun.	F	8.5	O_2 lack			×		×	×
N. amphibioides Hust.									
N. angustata (Wm. Sm.) Grun.									
N. capitellata Hust.									
N. clausii Hantz.									
N. communis Rabh.	F	8	N_2 het			×	×		
N. confinis Hust.									
N. denticula Grun.	F	8.2–8.5							
N. dissipata (Kutz.) Grun.									
N. epithemioides Grun.	B	9–10							
N. filiformis (Wm. Sm.) Hust.									
N. fonticola Grun.									
N. frustulum Kutz.	B	7–10	O_2 lack	×	×	×	×	×	×

TABLE 1. Continued

	Ecological characteristics*			Occurrence in Mexico†					
	S	pH	IC	1	2	3	4	5	6
N. ganderscheimiensis Krasske									
N. gracilis Hantz.									
N. hantzschiana Rabh.									
N. hungarica Grun.	F–B	7–9	O_2 lack	×					
N. kutzingiana Hilse	F	7.5–7.8							
N. linearis Wm. Sm.	F	7.8							
N. microcephala Grun.	F	8.3–8.5	N_3 het						
N. obtusa Wm. Sm.									
N. palea (Kutz.) Wm. Sm.	F	6–9	O_2 lack		×	×	×	×	×
N. palea tenuirostris Grun.									
N. paleacea Grun.	F	7.8–8.2	E						
Nitzschia sp. aff. *N. punctata* (Wm. Sm.) Grun.									
N. stagnorum Rabh.									
N. subtilis Kutz.	F	a	N_2 het						
N. tarda Hust.									
N. tryblionella Hantz.	F–B		Cl^-						
N. tryblionella victoriae Grun.									
N. vitrea Norman									
N. vivax Wm. Sm.									
Pinnularia acrosphaeria Wm. Sm.									
P. appendiculata (Ag.) Cl.									
P. bogotensis (Grun.) Cl.									
P. borealis Ehr.	F–B	6	Ac			×			
P. braunii (Grun.) Cl.									
P. braunii amphicephala (A. Mayer) Hust.									
P. divergentissima (Grun.) Cl.									
P. globiceps Greg.									
P. maior (Kutz.) Rabh.	F	6						×	
P. microstauron (Ehr.) Cl.	F	6–b	O_2 lack						
Pleurosigma delicatulum Wm. Sm.									
Rhoicosphenia curvata (Kutz.) Grun.	F	A	O_2					×	
Rhopalodia gibba (Ehr.) O. Mull.	F	7.8						×	×
R. gibberula margaritifera Rabh.	F	A	CO_3, SO_4						
R. gibberula protracta Grun.	F–B	A	W–O		×		×		
Scoliopleura peisonis Grun.									
Stauroneis acuta Wm. Sm.									
S. anceps Ehr.									
S. kriegeri Patr.	F	5.5–8							
S. lapponica A. Cl.									
S. legleri Hust.	B	A							
S. phoenicentron (Nitz.) Ehr.	F–B	6.8							
S. smithii Grun.									
Stephanodiscus niagarae Ehr.									
Surirella angustata Kutz.									
S. ovalis Breb.									
S. ovata pinnata Wm. Sm.									
S. peisonis Pant.	B	A	Na_2CO_3						
S. striatula Turpin	B–M	A							
S. tenera Greg.	F	7.6							
Synedra acus Kutz.									
S. rumpens familiaris (Kutz.) Hust.									
S. rumpens scotica Grun.									
S. socia Wallace									
S. ulna (Nitz.) Ehr.	F					×			×

both as not uncommon in freshwater. Group II does not appear ecologically distinct from group I. Group III consists of three species of *Fragilaria* that inhabit shallow standing water with *p*H slightly under 8. Group IV together with group III form the dominants in several zones of the core. Group IV contains all freshwater benthonic species, *Cocconeis placentula* (21) being an epiphyte; these species frequently inhabit marshes with water of *p*H 8 or higher. Group V is a large group composed of minor elements of the freshwater benthonic flora; generally their *p*H requirements are alkaline. Group VI, although it has a distinctive distribution in the core, is also composed of alkaline freshwater benthonic species. This group, characterized by *Amphora ovalis* (56), may be somewhat less tolerant of salinity variations (Hutchinson et al. 1956).

Group VII contains benthonic and planktonic species of anomalous ecology; for example, *Anomoeoneis sphaerophora* (60), *Melosira italica* (61), and *Nitzschia communis* (63) are all freshwater species, while *Stauroneis legleri* (62) and *Nitzschia epithemioides* (64) are brackish-water species. This may result from reworking and the introduction of dead frustules from other habitats, or possibly some of the species have a wider ecologic amplitude than previously suspected.

Group VIII is composed largely of benthonic brackish-water species. The presence of *Amphora coffaeiformis salina* (66), *Navicula halophila* (65), and *Cymbella pusilla* (68) suggest very saline conditions (Hustedt 1930).

Group IX is composed of a single species, *Nitzschia frustulum* (70); it is a brackish-water species (Cholnoky 1968), but it is found in a wide range of environments and appears to be tolerant of fluctuating conditions. Some of its variability may be the result of misidentification or confusion with similar species, but reliable systematists have reported it in freshwater environments (e.g., Patrick et al. 1967).

Group X contains brackish benthonic diatoms, two of which, *Anomoeoneis costata* (72) and *Surirella peisonis* (74), live in water with high concentrations of sodium carbonate (Cholnoky 1968).

Group XI is composed of brackish-water planktonic diatoms that do not tolerate variations in salinity. It is dominated by *Cyclotella striata* (79) and *Chaetoceras* sp. (77) although locally *Cyclotella quillensis* (80) and *Cyclotella* sp. cf. *C. stylorum* (81) are important. Most authors recognize the close relationship between *C. stylorum*, *C. quillensis*, and *C. striata* (Boyer 1927; Hustedt 1962) and their distribution throughout the core suggests that they are variations of the same thing, possibly ecotypes. The same possibly holds true for *Cyclotella meneghiniana laevissima* (78) (Hustedt 1962).

Group XII contains alkaline freshwater diatoms, the most abundant being *Melosira granulata* (83), a planktonic form. The rest are either epiphytic or benthic species.

A brief survey of the diatoms in modern lacustrine environments in the Basin of Mexico and nearby areas was made to serve as an ecological framework for interpreting the diatoms in the core. Samples were collected from the lakes and ponds identified in Table 1. About 50% of the common species from the core were also common elements of these aquatic environments. Of the species in the freshwater environments (Tlaxcala 1,130, Chalco, Xochimilco, and Zumpango) 82% belonged to the freshwater groups I–VII from the core, and 47% of the species in Lake Texcoco and the saline Tlaxcala pond were found in the brackish-water groups VIII–XI. This was a small sample, and little definitive ecologic information can be gained from it, but it indicates that a substantial fraction of the common diatom flora of ancient Lake Texcoco can be found today in the Basin of Mexico, and that the paleoecologist need not seek vastly different environments from those existing today to explain many of the floristic changes in the Pleistocene sediments of the basin.

TABLE 2. *The zones delineated in the core and their dominant diatoms (see also Fig. 4)*

Zone and depth	Diatoms	Group	Ecology
1. 2–3 m	*DENTICULA ELEGANS* (22)	IV	Epiphytic and benthonic diatoms characteristic of freshwater of high pH; most tolerate low salinity.
	Cocconeis placentula (21)	IV	
	Nitzschia amphibia (23)	IV	
	Rhopalodia gibberula margaritifera (24)	IV	
	Navicula cryptocephala (20)	IV	
	Fragilaria brevistriata (19)	III	
	Amphora veneta (8)	II	
	Amphora ovalis (56)	VI	
2. 3–4 m	*FRAGILARIA BREVISTRIATA* (19)	III	*Fragilaria* spp. are commonly found in shallow standing water and are tolerant of a wide range of salinity; the remaining species are found in brackish-water benthonic and planktonic environments.
	Fragilaria construens venter (17)	III	
	Anomoeoneis costata (72)	X	
	Campylodiscus clypeus (73)	X	
	Surirella peisonis (74)	X	
	Nitzschia frustulum (70)	IX	
	Anomoeoneis sphaerophora (60)	VIII	
	Chaetoceras sp. (77)	XI	
3. 4–11 m	*NITZSCHIA FRUSTULUM* (70)	IX	All forms are characteristic of brackish water; *C. striata* and *Chaetoceras* sp. are planktonic, the others benthonic.
	Campylodiscus clypeus (73)	X	
	Anomoeoneis costata (72)	X	
	Rhopalodia gibberula protracta (71)	X	
	Navicula halophila (65)	VIII	
	Chaetoceras sp. (77)	XI	
	Cyclotella striata (79)	XI	
4. 11–14 m	*CYCLOTELLA STRIATA* (79)	XI	Flora similar to the preceding zone, but it shows a dominance of planktonic species *C. striata* and *Chaetoceras* sp.
	Chaetoceras sp. (77)	XI	
	Nitzschia frustulum (70)	IX	
	Nitzschia communis (63)	VIII	
	Anomoeoneis costata (72)	X	
	Campylodiscus clypeus (73)	X	
	Rhopalodia gibberula protracta (71)	X	
5. 14–16 m	*AMPHORA OVALIS* (56)	VI	Flora is similar to the last two zones, but presence of *A. ovalis*, *F. construens venter*, and *E. zebra* suggests fresher water than the preceding floras.
	Epithemia zebra (59)	VI	
	Fragilaria construens venter (17)	III	
	Nitzschia frustulum (70)	IX	
	Campylodiscus clypeus (73)	X	
	Anomoeoneis costata (72)	X	
	Rhopalodia gibberula protracta (71)	X	
	Surirella peisonis (74)	X	
	Cocconeis diminuta (75)	X	
	Chaetoceras sp. (77)	XI	
	Cyclotella striata (79)	XI	
6. 16–19 m	*CYCLOTELLA STRIATA* (79)	XI	Dominance of brackish planktonic (*C. striata* and *Chaetoceras* sp.), the remainder being brackish benthonic.
	Chaetoceras sp. (77)	XI	
	Anomoeoneis costata (72)	X	
	Campylodiscus clypeus (73)	X	
	Nitzschia frustulum (70)	XI	
	Navicula halophila (65)	VIII	
7. 19–20 m	*NAVICULA HALOPHILA* (65)	VIII	Brackish-benthonic diatoms dominate.
	Cyclotella striata (79)	XI	
	Nitzschia frustulum (70)	IX	
8. 20–23 m	*CYCLOTELLA QUILLENSIS* (80)	XI	Brackish planktonic dominate; presence of *F. construens venter* suggests presence of fresh-water nearby.
	Cyclotella striata (79)	XI	
	Cyclotella sp. cf. *C. stylorum* (81)	XI	
	Anomoeoneis costata (72)	X	
	Cocconeis diminuta (75)	X	
	Fragilaria construens venter (17)	III	
9. 23–25.10 m	*FRAGILARIA BREVISTRIATA* (19)	III	Many diatoms from the freshwater groups plus the *Fragilaria* spp. indicate shallow, fresh, alkaline water.
	Fragilaria construens venter (17)	III	
	Fragilaria pinnata (18)	III	
	Rhopalodia gibba (15)	II	
	Nitzschia amphibia (23)	IV	
	Cocconeis placentula (21)	IV	
	Cyclotella striata (79)	XI	
10. 25.10–27 m	*NAVICULA HALOPHILA* (65)	VIII	Brackish-benthonic diatoms dominate.
	Nitzschia frustulum (70)	IX	
	Anomoeoneis costata (72)	X	
	Cyclotella striata (79)	XI	
	Cyclotella meneghiniana laevissima (78)	XI	
	Chaetoceras sp. (77)	XI	

TABLE 2. Continued

Zone and depth	Diatoms	Group	Ecology
11. 27– 27.75 m	*CYCLOTELLA* SP. CF. *C. STYLORUM* (81)	XI	*Cyclotella* dominates, and the remaining flora is from brackish-benthonic habitats; possibly this zone is a subzone of the following one.
	Campylodiscus clypeus (73)	X	
	Anomoeoneis costata (72)	X	
	Rhopalodia gibberula protracta (71)	X	
12. 27.75– 29.50 m	*CAMPYLODISCUS CLYPEUS* (73)	X	Brackish-benthonic diatoms dominate.
	Anomoeoneis costata (72)	X	
	Rhopalodia gibberula protracta (71)	X	
	Cocconeis diminuta (75)	X	
	Surirella peisonis (74)	X	
	Cymbella mexicana (76)	X	
	Cyclotella striata (79)	XI	
13. 29.50– 33.50 m	*DENTICULA ELEGANS* (22)	IV	Freshwater, alkaline benthonic and epiphytic diatoms; many other spp. from groups I–V.
	Cocconeis placentula (21)	IV	
	Rhopalodia gibberula margaritifera (24)	IV	
	Nitzschia amphibia (23)	IV	
	Navicula cryptocephala (20)	IV	
	Nitzschia frustulum (70)	IX	
14. 33.50– 35 m	*MELOSIRA GRANULATA* (83)	XII	Planktonic and shallow, freshwater diatoms from alkaline, warm, eutrophic lakes.
	Cyclotella sp. (81)	XI	
	Fragilaria brevistriata (19)	III	
15. 35 m–?	STEPHANODISCUS NIAGARAE		Cool planktonic freshwater diatom, characteristic of deep, north-temperate lakes:
	[This zone has been determined from the core Bellas Artes 80, which was originally studied by Sears and Clisby (1955) and Foreman (1955). Only scattered samples of this core exist, and the extent of this zone is unknown.]		
44–46 m	*DENTICULA ELEGANS* (22)		
	Cocconeis placentula (21)	IV	Freshwater, alkaline benthonic diatoms; *H. amphioxys* is an aerophilic species.
	Nitzschia amphibia (23)	IV	
	R. gibberula margaritifera (24)	IV	
	Hantzschia amphioxys (25)	IV	
	Rhopalodia gibba (15)	V	
		II	
	(The limits of this zone are not fixed because it is separated from the other zones by several meters of sediments that may contain more than one diatom assemblage. For this reason it is not numbered.)		

In addition to the zones listed above, a diatom assemblage was noted in a sample from ≃70 m in the Bellas Artes 80 core. Its equivalent probably exists beneath the depth reached by P 366-2. This zone, like the one at 35 m, is dominated by *Stephanodiscus niagarae*.

Diatom Zonation

Distinctive assemblages of diatoms were used to delineate 15 zones in the core (Table 2). They have been numbered in Fig. 4 and labeled with the name of the diatom considered most characteristic of each zone.

A discussion of the paleolimnology of Lake Texcoco must be preceded by a consideration of the mechanics of lacustrine change in this shallow lake and how the marginal diatom floras are affected. As those of many lakes in semiarid regions with periodic rainfall, its level and salinity fluctuate widely from season to season, sometimes in response to single storms. In 1629 the waters of Lake Texcoco rose 8 m and submerged a town for 5 consecutive years (Bonaparte et al., ca. 1900). Such floods impose markedly differing habitats to which the algae rapidly adjust. During periods of meager rainfall the lakes evaporate and the water level retreats from the shore to leave mudflats and saline pools. In the center of the basin a shallow saline lake can remain.

This simplified picture of lake-level fluctuation is complicated by the fact that the area around Lake Texcoco, especially in the area of the coring site and to the southwest, has long been known for the abundance of perennial freshwater seeps and springs, whose water supported the prosperous *chinampa* agriculture in this part of the basin (Coe 1964). Thus, during the low-water stages it appears that

the marginal, marshy, freshwater environments supported by the springs extended basinward and were repeatedly invaded by transitory floods of saline water from the central basin of Lake Texcoco. Reduced spring flow, to be expected during long dry periods, can add another variable to this picture.

The validity of this scheme is supported by historic documentation of floods that plagued the marginal marshland *chinampa* agriculture of the area. For example, the King of Texcoco, Netzahuacoyotl, built a dike in 1450 to prevent the saline waters of the main basin from entering the western subbasin of the lake (Fig. 1).

The diatoms from the Pleistocene sediments of Lake Texcoco belong to four broad ecological groups: brackish benthonic, brackish planktonic, freshwater benthonic-epiphytic, and freshwater planktonic. These groups and the lacustrine environments that produced them are shown in Fig. 5, arranged in an idealized climatic sequence. Actually, the changes between freshwater marsh, shallow saline water, and deep saline water can occur rapidly and can be reversed. The freshwater planktonic diatoms represent more stable lacustrine environments.

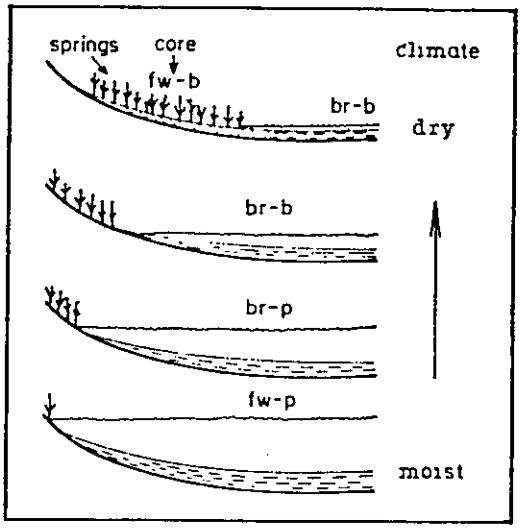


FIG. 5. Schematic representation of the four distinct lacustrine environments of Lake Texcoco suggested by diatom analysis of core P 366-2. At the highest levels (bottom sketch), when the lake may have overflowed, freshwater-planktonic (fw-p) diatoms occurred. Decrease in the water level and increased salinities produces brackish-planktonic diatoms (br-p). As water levels continue to drop brackish-benthonic diatoms (br-b) flourish in shallow, saline water. During the lowest lake levels, spring-fed freshwater marshes extend basinward from the margins of the lake. Associated with the marshes are freshwater-benthonic (fw-b) diatoms, and brackish-benthonic forms are present in the remnant saline pools in the center of the basin. These assemblages can be tentatively related to a climatic change from moist to dry.

Paleolimnology

The earliest recorded diatom assemblage comes from a depth of about 70 m in the Bellas Artes 80 core studied by Foreman (1955) and Sears and Clisby (1955). It is not shown in Fig. 4. It is dominated by *Stephanodiscus niagarae*, a freshwater-planktonic diatom, indicating that a large, possibly deep, cool lake existed at that time. The salinity of the lake was low and constant, and the lake probably had an outlet. More than 20 m of sediment may separate this zone from the next known assemblage; it is not known what limnologic conditions they represent.

The lowest diatom assemblage from core P 366-2 (44–45 m, Fig. 4) is unnumbered because it is separated from the overlying sediments by 9 m. It consists of marsh diatoms, principally *Denticula elegans* (22), and indicates that at that time the lake was very shallow. It is not known whether the disappearance of the earlier large cool lake conditions resulted from drainage or from desiccation.

This marshy environment ultimately was followed by a return of the large lake, as shown by zone 15 which is dominated by *S. niagarae*, but these conditions were short-lived and it evolved into a shallower, more eutrophic and possibly warmer lake characterized by a *M. granulata* (83) assemblage (zone 14). Zone 13 shows another return of marsh diatoms dominated by *D. elegans* (22). Probably this time the lake level fell by desiccation, and only saline brines and salt flats occurred in the

central portions of the basin, where the minimum lake levels have been recorded in modern times (Fig. 1). This is suggested by the succeeding zones (12 to 3) which have predominantly brackish-water diatoms.

With the return of moister climate the lake began to fill, and floods of saline water extended toward the margins of the lake basin. Variable water depths are suggested by the alternation of brackish-benthonic and brackish-planktonic assemblages (zones 12, 11, and 10), followed in zone 9 by a slight increase in *Fragilaria* spp. (group III) and other diatoms in groups II, IV, and V, which indicate a brief period of shallower but fresher water. The brackish lake continued to dominate, however. Zones 8, 6, and 4 reflect deeper brackish water supporting brackish-planktonic diatoms as *C. quillensis* (80) and *C. striata* (79), and zones 7, 5, and 3 reflect shallower water with brackish-benthonic diatoms.

The artificial zone boundaries (zones 11 to 3) obscure the complex variations the lake underwent during the long period represented. A somewhat better idea can be gained by following the fluctuations of the frequency curves of the diatoms in groups VIII–XI. Both the brackish-planktonic diatoms of group XI and the very saline-benthonic diatoms of group VIII increase rapidly to high levels and then fall suddenly. Group IX, containing only the diatom *N. frustulum* (70), is important throughout this interval, but even with its wide tolerance its abundance is highly variable. The same is true to a lesser extent for those forms of group X.

A note of caution may be introduced here regarding the frequency distribution of *Cyclotella* sp. cf. *C. stylorum* (81). Its highly erratic distribution at depths of 23 and 27 m may be the result of reworking from lacustrine deposits left by the shrinking lake after zone 14. Here it is associated with *M. granulata* (83), and the same association can be found in a fossil diatomite surrounding the shores of Lake Amatitlan in Guatemala. These associations, incidentally, suggest that the *Cyclotella* sp. in question is not ecologically related to *C. stylorum*, a marine species (Hustedt 1962), even though they are similar morphologically, but shares the alkaline, warm, eutrophic habitat of planktonic *M. granulata*. Its anomalous associations with group X diatoms at 27 m and with *C. striata* (79) at 23 m, plus the fact that at these levels it is mostly in a broken condition, support the conclusion that its appearance results from reworking. The question cannot be settled, however, until adequate taxonomic work is done with this species. This problem does not significantly alter the paleolimnologic history presented in the preceding paragraph.

Above zone 3, the sequence indicates that lake levels fell, and freshwater marsh conditions again extended basinward. In zone 2 the *Fragilaria* spp. (17, 18, 19) indicate shallow standing water of slightly alkaline *p*H. In zone 1, the occurrence of *D. elegans* (22) with *Hantzschia amphioxys* (25), an aerophilic diatom, suggests that the water level may have been even shallower.

In general, the coarser-textured parts of the core, as indicated by low values in Zeevaert's water-content curves (Fig. 4), contain diatom floras that belong either to the freshwater benthonic groups I–VII or to the very saline benthonic group VIII, while the finer sediments correlate in most instances with planktonic diatoms (group XI and XII) or with brackish-benthonic diatoms of groups IX and X. Coarser sediments would be expected in either shallow-water environment, whether fresh or saline, while a deeper lake would favor the accumulation of fine sediment. The coarser sediments also frequently have root holes, which, however, are not confined to these materials. There is a limited negative correspondence between the number of species found in each sample (Fig. 4) and Zeevaert's water-content curve.

These observations, although not all quantified, offer additional paleolimnologic information. The freshwater marshes

can be expected to contain more habitats and hence more species, and the presence of root holes helps to substantiate their existence. Coarser sediment would tend to accumulate in these marshes if they drained slowly basinward.

Correlations

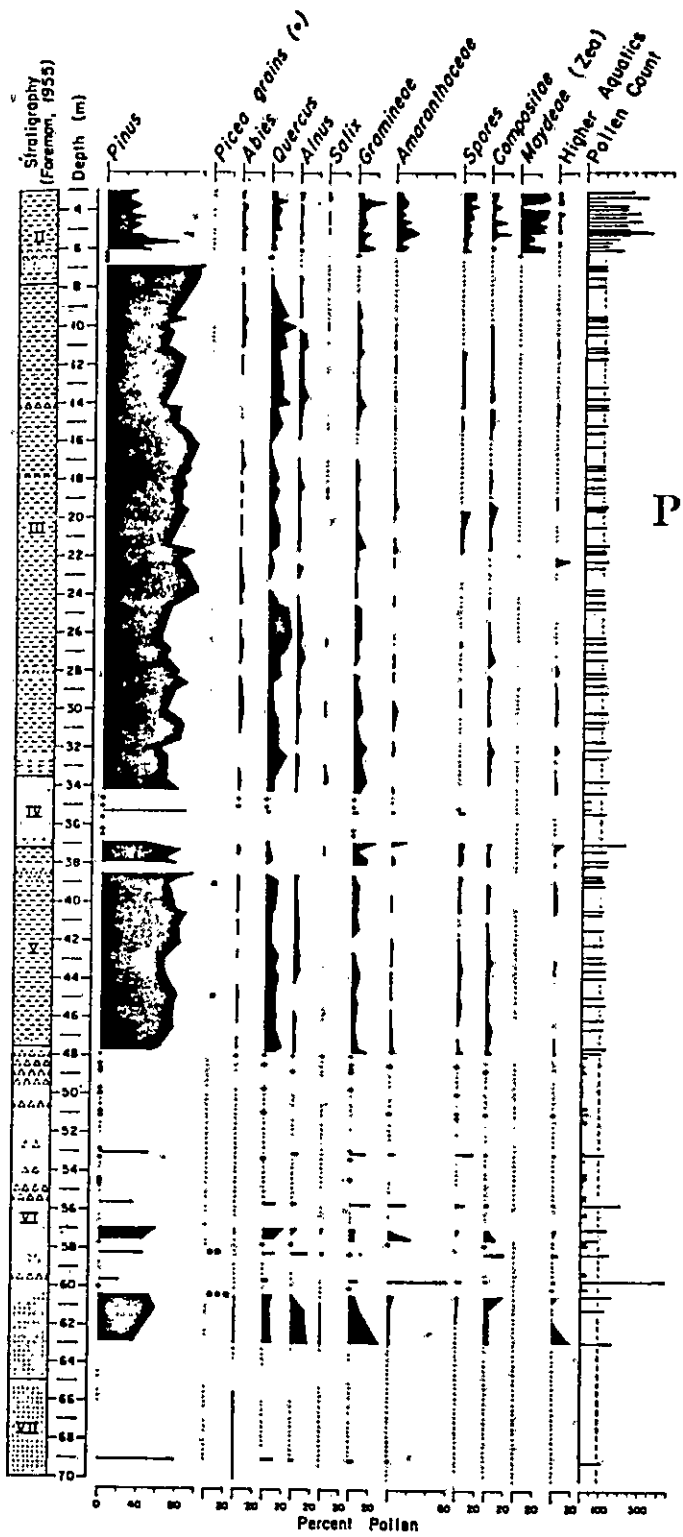
Until additional cores are studied, the question of intrabasin correlation of the diatom zones cannot be definitively answered. Zeevaert's (1952, 1953) work shows good correlation of his sedimentologic zones from core to core, and I suspect that the diatom stratigraphy presented will hold underneath all of Mexico City. Probably toward the center of the basin, where limnologic conditions were frequently very saline, the freshwater marsh zones will not be present. The *Stephanodiscus* zone (about 35+ m) has been found more than 23 km to the northeast in wells of the saline evaporation plant, Sosa Texcoco, and there is some evidence that the brackish-planktonic diatom zones have similar distributions. The diatoms found associated with the skeletal remains of Tepexpan Man (P. Conger *in* de Terra et al. 1949) might fit in any number of zones beneath zone 2, and a longer profile is required on the northeast side of the basin before correlations can be made. Zones 1 and 2 do seem to have local extent around Mexico City and have turned up in excavations for the new subway there.

To the southeast and into the basins of Xochimilco and Chalco, zones 1 and 2 may be expected to increase in thickness, since these *chinampa* areas are supplied by an abundance of freshwater springs. A diatomite containing a dominance of *Fragilaria* spp. occurs at a depth of 1.75 m at Culhuacan in the Xochimilco basin (a sample studied from Sears' 1952 study), and at Tlapacoya (Fig. 1) the same species and *D. elegans* are found in sediments that date from 24,000 years B.P. (Bradbury 1970*a*). *Fragilaria* and *Denticula* alternate throughout the upper 6 m of the Tlapacoya sections, but below this, in sediments dated at 24,000 to 35,000 years B.P. (Mooser 1967), diatoms of group X are common: *Campylodiscus clypeus*, *A. costata*, and *N. frustulum* (Bradbury 1970*a*). The radiocarbon dates on core P 366-2 (Fig. 4) place the boundary between zones 2 and 3 at a considerably later date than this (assuming that the change found at Tlapacoya is the same kind of transition), so we are faced here with the likelihood that some of these zones have a considerable time transgression. This is what might be expected in Lake Chalco, which is not only separate from and higher than Lake Texcoco but also has an ample supply of freshwater.

Another possibility exists that the glacial substages that White (1962) established for the volcano Iztaccihuatl may be embraced by the ages of core P 366-2. It is conceivable that the last three planktonic diatom zones (zones 8, 6, and 4) relate to glacial advances on the sides of this volcano, but these zones do not reflect particularly dramatic climatic changes because they all consist of brackish-planktonic diatoms. On the other hand, marked changes in precipitation and temperature may not be needed to extend the glaciers now existing on Popocatepetl and Iztaccihuatl to lower elevations (White 1954). Probably the stratigraphy of Lake Chalco is more sensitive to the glacial fluctuations on these peaks, and correlation must wait until they are studied in greater detail. The age of the planktonic peaks in core P 366-2 is 30,000 years or more according to the radiocarbon dates, and therefore they appear rather early for White's (1962) tentative correlations of his glacial advances with the Rocky Mountain sequence.

Diatom, pollen, and chemical studies by Hutchinson et al. (1956) on cores from Lake Patzcuaro in Michoacan show a marked dry period beginning at depths

FIG. 6. →



POLLEN DIAGRAM MADERO CORE MEXICO CITY, MEXICO

Percentages of total pollen
(Clisby & Sears 1955)

Explanation

Weathered ash and clay

Fresh ash

Ostracod marl

Sand and silt

No pollen

Pollen types in counts less than 90

around 6 m, and it is reasonable that this dry period should be correlated with the falling lake levels in the Basin of Mexico indicated by zones 1 and 2. The Patzcuaro material was not dated, and it was only tentatively correlated with Sears' (1952) archaeologic sequences, which implies that the dry period was much later (say about 2,300 years B.P.) than the transition in Lake Texcoco (about 6,000–10,000 years B.P.). Further studies in both lakes are needed for conclusions about regional correlation.

Of all possibilities for correlation, Sears and Clisby's (1955) pollen studies in similar cores from the sediments of Lake Texcoco should prove the most rewarding. Unfortunately, obvious correlations for most stratigraphic levels have not been found, although one would expect that the pollen types labeled as moisture indicators (*Alnus*, *Quercus*, and *Abies*) would correspond to peaks in planktonic diatoms. All that can be said for the time being is that both parameters are highly variable and that until pollen and diatoms are studied from the same core the matter will remain unsolved. All in all, the pollen from these sediments shows a somewhat monotonous stratigraphic distribution when it is plotted as percentages of total pollen rather than relative proportions of arboreal pollen alone (Fig. 6). On this basis, the most evident break in Sears and Clisby's (1955) counts is found in the upper 6 m, where Gramineae, Amaranthaceae, Compositae, and *Zea* become very abundant as opposed to arboreal pollen. This corresponds rather well to the boundary between zones 3 and 2, suggesting a lowering of lake levels. This change in the pollen stratigraphy seems clearly to be the handiwork of agricultural man in the Basin of Mexico (Clisby and Sears 1955).

Most of Sears' (1952) pollen work in archaeologic horizons of the basin involves sediments younger than those of core P 366-2, but some of his deeper profiles (Chimalhuacan and Chapingo) may cover the same time as the upper levels of this core. His dry phase, zone D, may correspond to some part of diatom zones 2 or 1 of this study. Sears' zone C, representing a wet interval presumably corresponding to the Zacatenco high beach level (2,242 m) of 3,500 years ago, is too young to be covered within the time span of core P 366-2. At any rate, it appears that the elevation of this coring site was somewhat higher than the 2,242-m level, so the marshes that existed there at that time may not have been flooded then.

Limnologic changes that appear in the Basin of Mexico since about 6,000 years B.P., particularly in marginal areas of the basin, are not necessarily solely the result of natural climatic or hydrologic changes, because from this time on agricultural man played an increasingly important role in the area. It is not too presumptive to speculate that early agriculturalists took advantage of the favorable conditions on the spring-fed shores of Lake Texcoco and possibly initiated primitive systems for farming those marshes that provided land dry enough for planting and water shallow enough for growth. An attractive model for such a system is the ridged fields (Parsons and Denevan 1967) that pre-Columbian agriculturalists used in many parts of Mexico and Central and South America. These consist of mounds or ridges of earth built above the shallow-water levels of flooded, low ground. The ridges provide rich, aerated soil next to abundant water that offers excellent conditions for farming and at the same time provides a certain amount of protein in the form of fish, turtles, water-fowl, and so forth. The construction of a ridged field requires nothing more complicated than a digging stick to heap the marsh sediments above water level, but even a primitive system of ridges and canals and possibly dikes would vastly alter a natural limnologic environment.

The diatom evidence from Lake Texcoco cannot prove these speculations independently. The abundance of *Zea* pollen at equivalent levels in Sears and Clisby's (1955) cores is supporting evidence, and

the likelihood that the remarkable *chinampa* agricultural system evolved from the similar but more primitive ridged field system seems logical. Archaeological evidence to test these ideas might be obtained near Mexico City or in the remaining *chinampa* areas to the southwest. Possibly some of it is covered by the Recent basalt flows from Xitle and other volcanic centers.

Although the diatoms from core P 366-2 may be only suggestive with respect to the questions of early man and agriculture in the Basin of Mexico, they offer much more positive information on earlier geologic questions. Mooser et al. (1956) discussed the difficulties in assigning maximum ages to the lake deposits and to the formation of the basin, although these features are generally considered to be Plio-Pleistocene. This problem rests on the identification of the Tarango formation beneath Mexico City. Where the Tarango formation is developed on the margins of the basin it predates the basaltic eruptions that are thought to have blocked the south-draining valley to form the Basin of Mexico. Previous volcanic rocks were nonbasaltic. Thus the Tarango formation should be an alluvial deposit free of basaltic components. The presence of deep strata within this formation containing abundant remains of S. *niagarae*, a freshwater-planktonic diatom characteristic of large, cool temperate lakes in North America, clearly suggests that these deposits are not entirely alluvial. Also, Foreman (1955) found basalt fragments at similar depths in the same formation.

Fish fossils (Fig. 4) from core P 366-2 have been identified by R. R. Miller and C. D. Barbour (personal communication) as *Chirostoma humboldtianum*, belonging chiefly to the Lerma drainage basin. The present fish fauna of the Basin of Mexico is entirely of Lerma affinities (Arellano 1953; Meek 1904). The earliest fish fossil from the core occurs at a depth of 35 m; it indicates that at least since perhaps 100,000 years B.P. the Basin of Mexico sometimes contained a large lake, which evidently drained northward to the Lerma system.

The planktonic diatoms and fish fossils from these deep levels support the contention of Mooser et al. (1956) that the formation currently identified as Tarango beneath Mexico City (Zeevaert 1952, 1953) is not the same thing as Bryan's (1948) Tarango formation on the margins of the basin. This change considerably lessens the inferred age of these sediments as Pliocene (Zeevaert 1953), but it appears that they represent more time than the Wisconsin alone (Sears and Clisby 1955).

Perhaps the most important conclusion that can be drawn from the diatom stratigraphy of these deposits is that climatic changes known to have occurred in more northerly latitudes do not seem to have been reflected in this region of Mexico. Admittedly, lakes are sometimes not such sensitive climatic indicators as we might wish, but the remarkable persistence of many diatom species throughout this long time and their common distribution in the basin today clearly suggest that truly pluvial climates did not reach this area. If anything, the relatively small frequencies of planktonic diatoms in the upper part of the core suggest that the lake was shallow and that the climate was therefore arid during the late Pleistocene. This is in agreement with the implications from the late Pleistocene–early post-Pleistocene vertebrate faunas of the Tehuacan Valley 200 km east-southeast of Lake Texcoco. Today the Tehuacan Valley has a hot, semitropical thorn-scrub forest and a small-mammal fauna characterized by the cotton rat (*Sigmodon*) and the kangaroo rat (*Dipodomys*). The fauna of the late Pleistocene and early post-Pleistocene in this area lacks these animals entirely but has high percentages of small mammals that characterize the arid and seasonally cooler interior plains of northern Mexico. If this kind of environment prevailed in the Tehuacan Valley area (Flannery 1967), it seems reasonable to suppose that the nearby Basin of Mexico was also drier at that time than it is today.

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PALEOECOLOGY OF THE UPPER MIOCENE HUALAPAI LIMESTONE MEMBER OF THE MUDDY CREEK FORMATION, NORTHWESTERN ARIZONA

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ABSTRACT

Diatoms and ostracodes in the Upper Miocene Hualapai Limestone Member of the Muddy Creek Formation indicate that this deposit, often regarded as a fresh-water limestone, formed in a brackish-water environment. The fossils, particularly the diatoms, have marine affinities and suggest that the saline nature of the Hualapai basin may have resulted from marine influence. Similar associations of diatoms and ostracodes are well known in modern estuaries or brackish-water lagoons. It is hypothesized that the Gulf of California may have extended northward to the Lake Mead area in late Miocene time to provide a marine coastal environment for the deposition of the Hualapai Limestone Member, and for the massive salt deposits in the Muddy Creek Formation.

INTRODUCTION

The presence of well-preserved diatoms and ostracodes in the Hualapai Limestone Member of the Muddy Creek Formation near Lake Mead, northwestern Arizona (Fig. 1), provides information about the origin of this deposit that relates to the late Tertiary tectonic history of the Basin and Range province. The purpose of this paper is to review the ecology of the modern counterparts of the fossils in the Hualapai Member and to tentatively reconstruct the depositional environment of this unit.

The Hualapai Limestone Member of the Muddy Creek Formation was deposited about 8 m.y. (million years) ago in a topographic depression at the base of the Grand Wash Cliffs south of Lake Mead, Arizona (Blair, 1978). The dominant lithology is fine-grained, white-to-buff-colored limestone that locally contains thin beds and concretions of opaline chert. Siltstones, claystones, and mudstones, sometimes gypsiferous, are found in the lower part of the member, and they presumably grade into the dominantly clastic sedimentary rocks of the lower part of the Muddy Creek Formation. The Hualapai is generally unfossiliferous, although locally limestone molds of ostracodes are common, and well-preserved ostracodes occur in the gysiferous siltsones and claystones near the base of the member. Diatoms are also found in the basal gypsiferous rocks, and in addition they occur on and within the nodules of opaline silica (Blair, 1978).

Both the diatoms and ostracodes appear to be widely distributed in the Hualapai Limestone Member. The sample locality (Fig. 1) is where the best preserved specimens in the area are found. A systematic search of this unit would probably reveal other localities where paleoecologic studies could be made.

The mode of diatom preservation is interesting. The best preserved diatom frustules are found within powdery siliceous coatings on the surface of the opaline nodules. Within the outer part of the nodules, the diatoms are loosely cemented by reprecipitated silica, yet on freshly broken, weathered, or HF-etched surfaces, many species are well enough preserved that they can still be identified. Towards the center of the opaline nodules the diatoms appear only as ghosts completely engulfed by and filled with silica. No diatoms appear in the center of the nodules; apparently they have been completely dissolved and reprecipitated to produce cristobalite and chert.

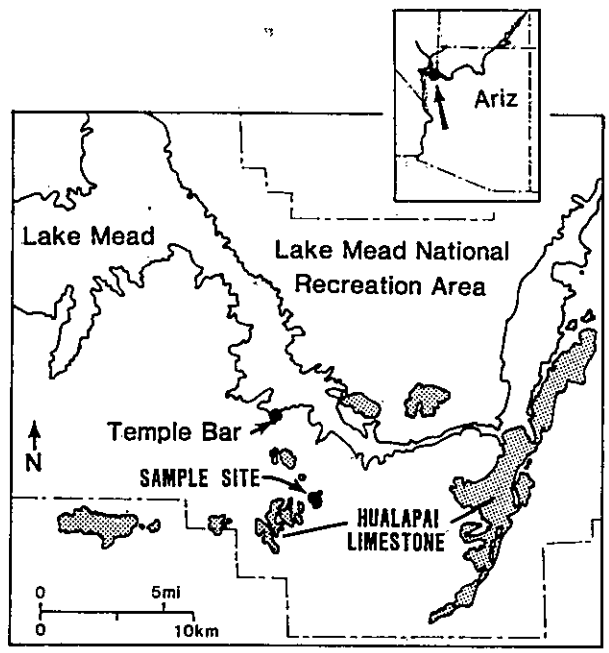

Figure 1.—Index map showing the Lake Mead area, outcrops of the Hualapai Limestone Member of the Muddy Creek Formation (patterned), and the sample site. Modified from Blair (1978).

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DEPOSITIONAL ENVIRONMENT OF THE HUALAPAI LIMESTONE MEMBER

The diatoms and ostracodes in the Hualapai Limestone Member augment the paleoenvironmental interpretation of this deposit as deduced from sedimentological, mineralogical, and geological studies of the limestone and its associated opaline cherts (Blair, 1978, and Blair and others, 1979). The ecological interpretation based on the diatoms can be equated directly with that of modern occurrences of these algae because the forms in the Hualapai are morphologically very close or identical to modern species. Therefore, although they are of late Miocene age, it is probable that the diatoms lived in environments very similar to the modern habitats where they are presently found. Not only are the diatoms essentially modern in appearance, but also the fossil diatom assemblage suggests a biological association that commonly occurs today in coastal environments. This correspondence of species and associations strengthens the paleoecological interpretation from fossils. Even though the ostracode species are extinct, they also provide important paleoecological information because they belong to a modern genus with well-known ecological requirements.

OSTRACODE STUDIES

Two species of ostracodes occur in the Hualapai Limestone Member: *Cyprideis lockerti* (Stephenson, 1935), and *Cyprideis stephensoni* Sandberg, 1964 (R. M. Forester, oral communication, 1979). *C. lockerti* and *C. stephensoni* occur together in Miocene brackish water deposits of Louisiana (Sandberg, 1964a).

Modern members of the genus *Cyprideis* have their major development in low-salinity (brackish = 5 - 30‰ total dissolved solids) marginal marine water bodies, and as a group they are tolerant of a wide range of salinities (Sandberg and Plusquellec, 1974). It is therefore reasonable to suspect that this was also true of the *Cyprideis* species from the Hualapai Member. In addition, these ostracodes occur in tremendous numbers locally in the limestone, suggesting that rapidly varying environment parameters, such as salinity, had excluded less tolerant ostracode species of true fresh-water or normal marine habitats. In modern brackish-water environments it is not uncommon to find one or another *Cyprideis* species as being overwhelmingly dominant in the ostracode community (Sandberg and Plusquellec, 1974). Although the genus *Cyprideis* can dominate in inland brackish-water environments, the absence of typical inland saline water ostracodes such as *Limnocythere* spp. lends some support to a marginal marine (lagoon or estuary) environment.

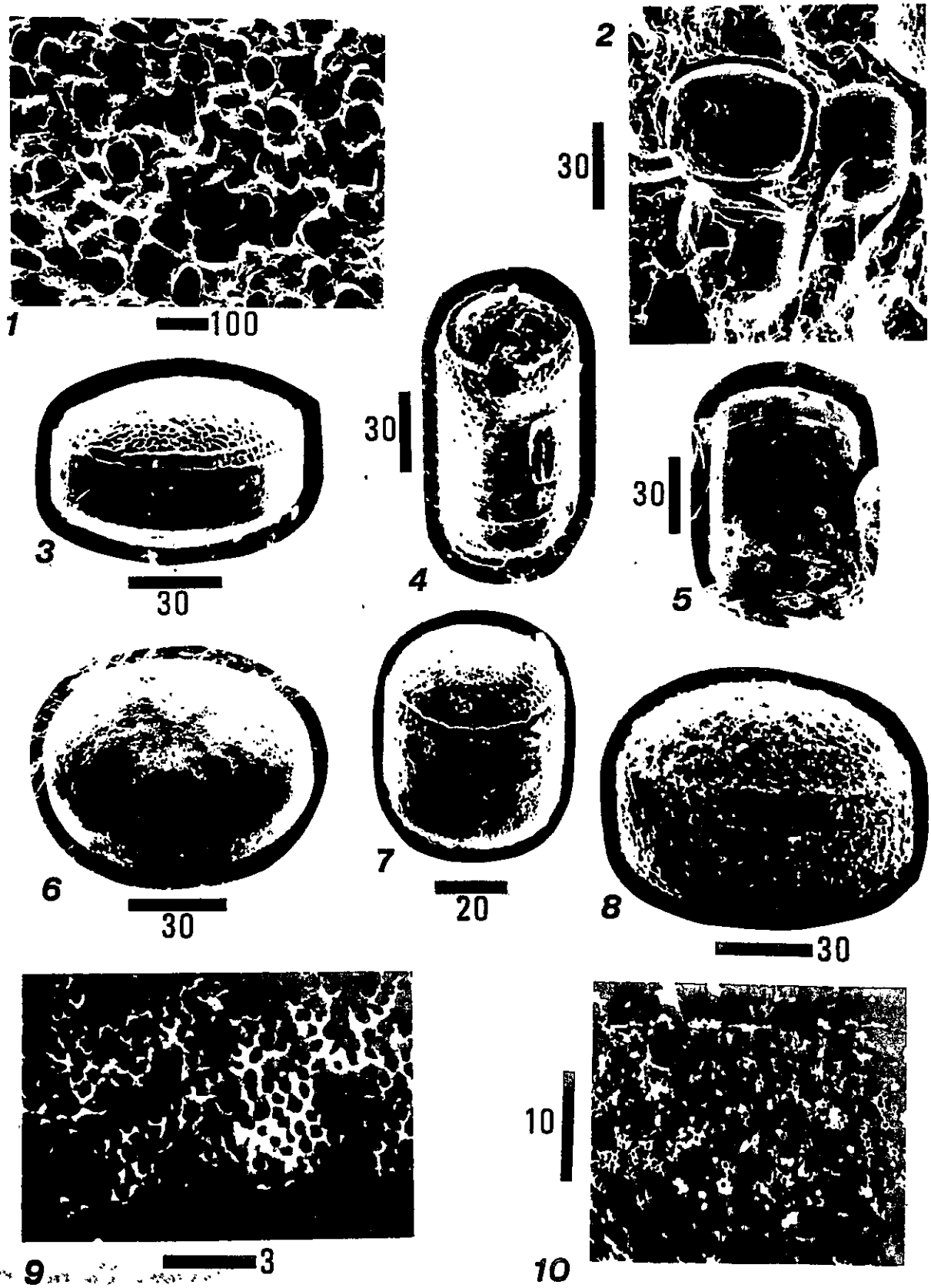
The work of Vesper (1975) on the relationship of carapace modes and salinity for the species *Cyprideis torosa* (Jones, 1850) indicates that the more highly noded forms are found in less saline water (below 10‰), whereas the smooth-shelled forms characterize more saline water. Noded individuals of the *Cyprideis* species of the Hualapai Limestone Member are very rare, and if this ecophenotypic characteristic applies to other species of the genus including extinct ones as Sandberg (1964b) suggests, it would indicate that the salinity of the water in which the Hualapai Limestone was deposited seldom dropped below 15‰ and probably seldom exceeded 25‰.

DIATOM STUDIES

In the simplest ecological classification of diatoms based on salinity, three habitats are recognized (marine, brackish, and fresh water) that reflect the optimal salinity for a diatom's growth. The system has been extended into hypersaline waters and variously subdivided (Kolbe, 1932, Hustedt, 1953). Regardless of the number of divisions of the salinity spectrum, this classification is somewhat rigid, for it does not take into account the salinity tolerance of diatom species. Simonsen (1962) introduced the concept of salinity tolerance to account for the distribution and association of diatoms with regard to salinity, and it has been modified and expanded by Ehrlich (1975). According to this classification there are species with limited tolerance to salinity variation (stenohaline) and species which tolerate large fluctuations in salinity (euryhaline). The brackish water habitat is almost entirely populated with euryhaline diatoms: those that grow well over a wide range of salinity. It is interesting to note, nevertheless, that there are two groups of euryhaline diatoms. Those that have their optimal growth in marine water (salinity 35‰) but which easily tolerate both higher and lower salinity, and those that live predominantly in fresh water (salinity below 5‰) but which readily adapt to higher salinities. Thus a brackish-water habitat can be populated either by euryhaline fresh-water diatoms, or by euryhaline marine diatoms. In general, brackish-water environments near the coast have proportionally greater numbers of marine euryhaline diatoms, whereas saline lakes, ponds, and springs far inland contain largely fresh-water euryhaline species. Presumably, this reflects the difficulty of transporting marine euryhaline diatoms far inland, although chemical differences between diluted seawater and inland salt lakes may also be important in controlling the distribution of these two groups.

The diatom flora of the Hualapai Limestone Member (Fig. 2–8) contains a larger representation of both marine and continental euryhaline species. The euryhaline marine species of the genus *Melosira (Melosira moniliformis* and *Melosira nummuloides)* dominate the flora, but locally euryhaline continental species, such as *Navicula halophila, Amphora coffaeiformis,* and *Entomoneis paludosa* are very

Figure 2.—Scanning electron photomicrographs of diatoms from the Hualapai Limestone Member of the Muddy Creek Formation. 1, massive development of *Melosira nummuloides* (Dillw.) Ag.; 2–5 and 7, *Melosira nummuloides*; 6 and 8, *Melosira dubia* Ktz.?; 9, an enlargement of 6; 10, an enlargement of 8. Scales in micrometers.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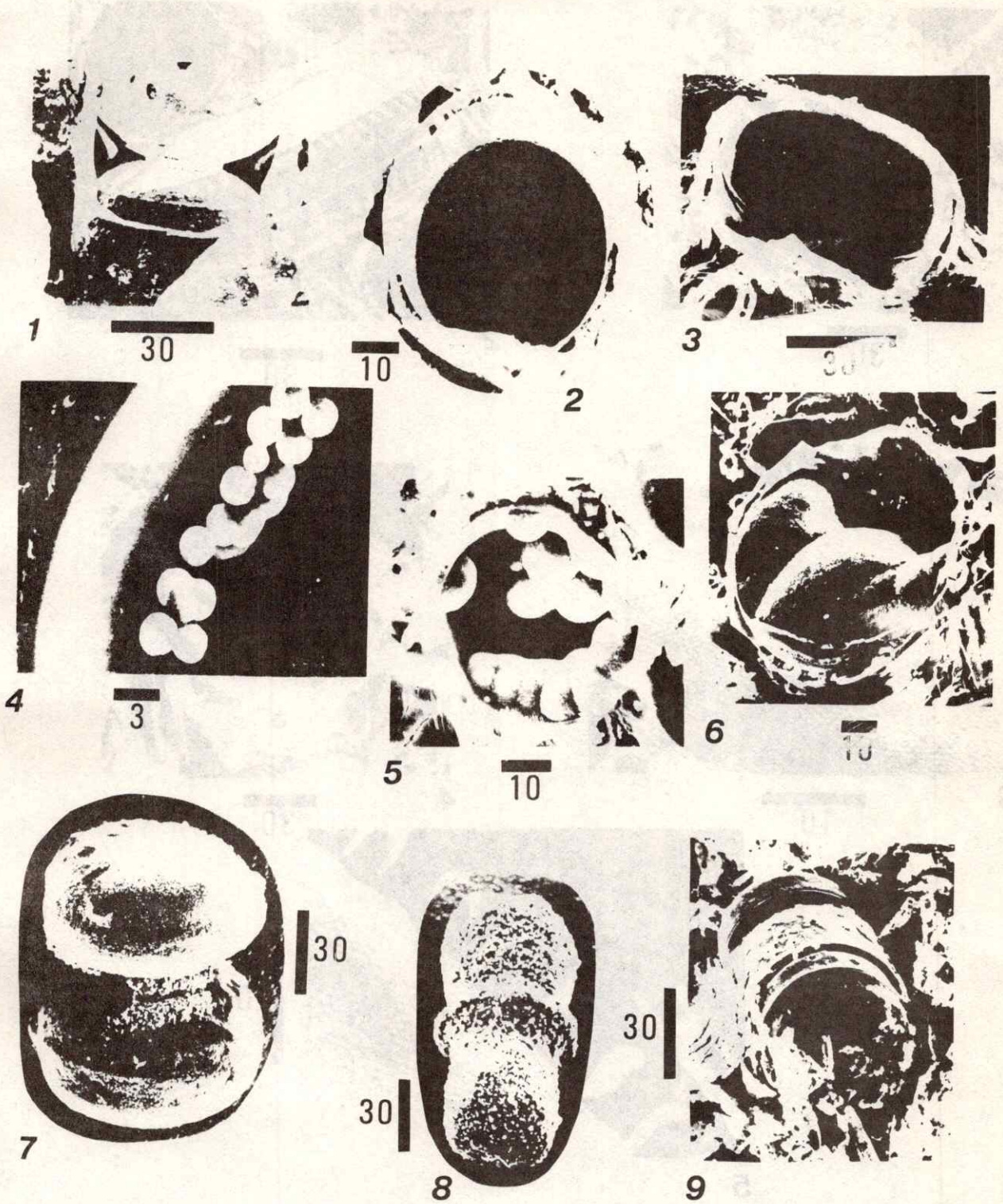

Figure 3.—1, Two cells of *Melosira nummuloides*, showing attachment area; 2, interior view of *Melosira moniliformis* (Mull.) Ag.?; 3, 7, and 9, internal cast of *Melosira moniliformis*; 4, 5, and 6, reprecipitated silica (Lepispheres) progressively filling the interior of *Melosira* cells; 8, internal cast of *Melosira juergensi* Ag. Scales in micrometers.

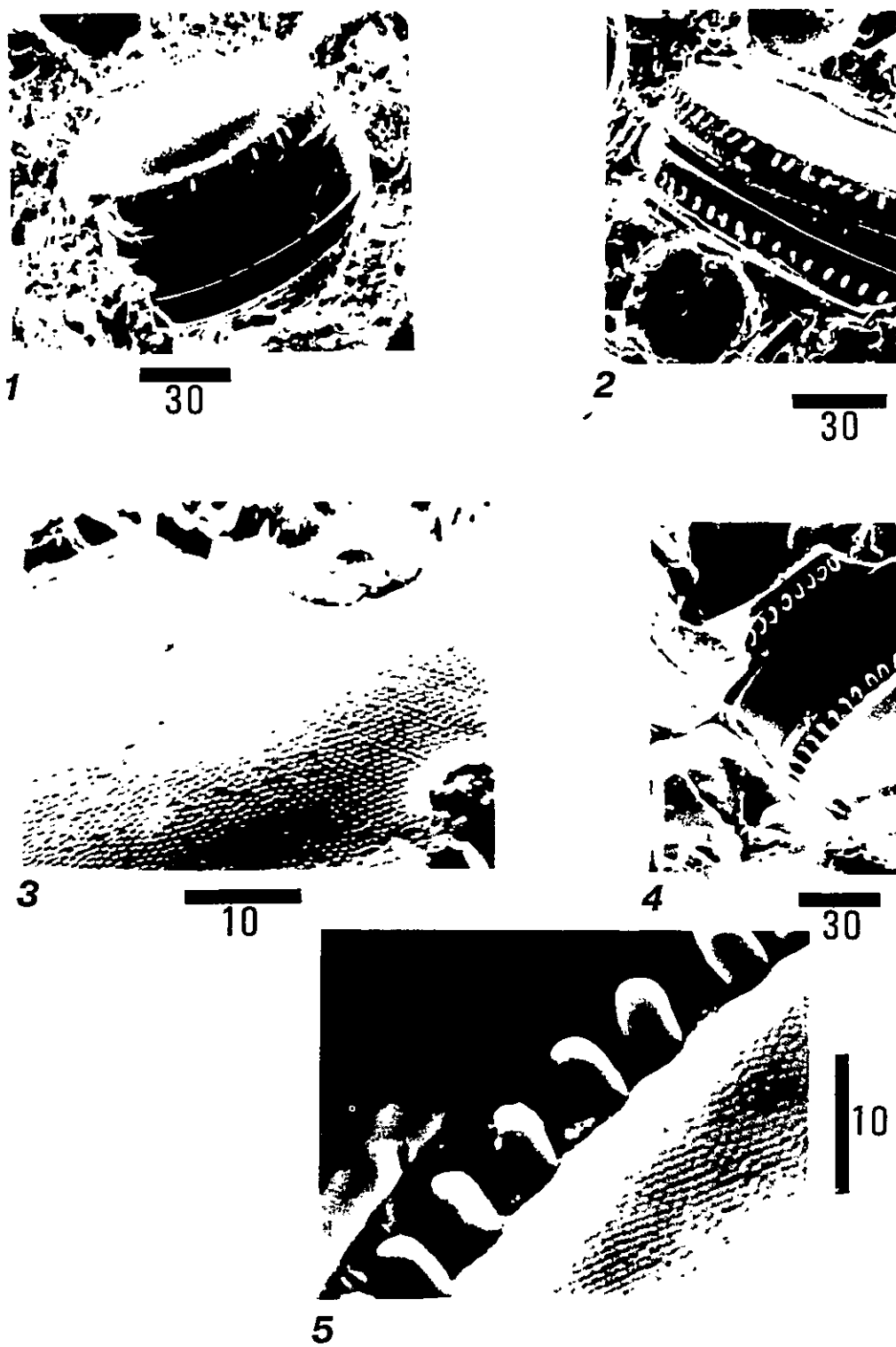

Figure 4.—1–5, internal surface of *Coscinodiscus* sp. or *Actinocyclus* sp. Note the presence of labiate processes in 1, 2, 4, and 5, apparently filled or mantled with reprecipitated silica. Scales in micrometers.


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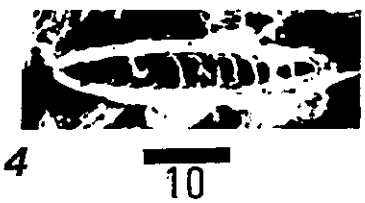
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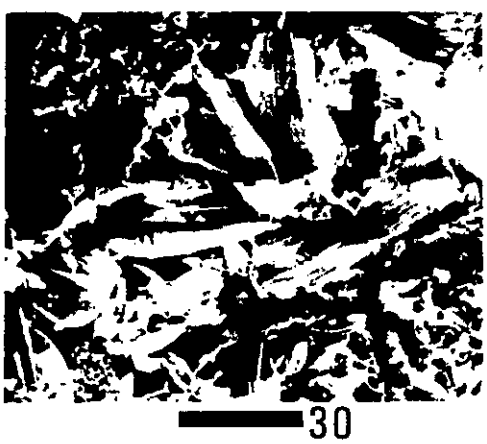
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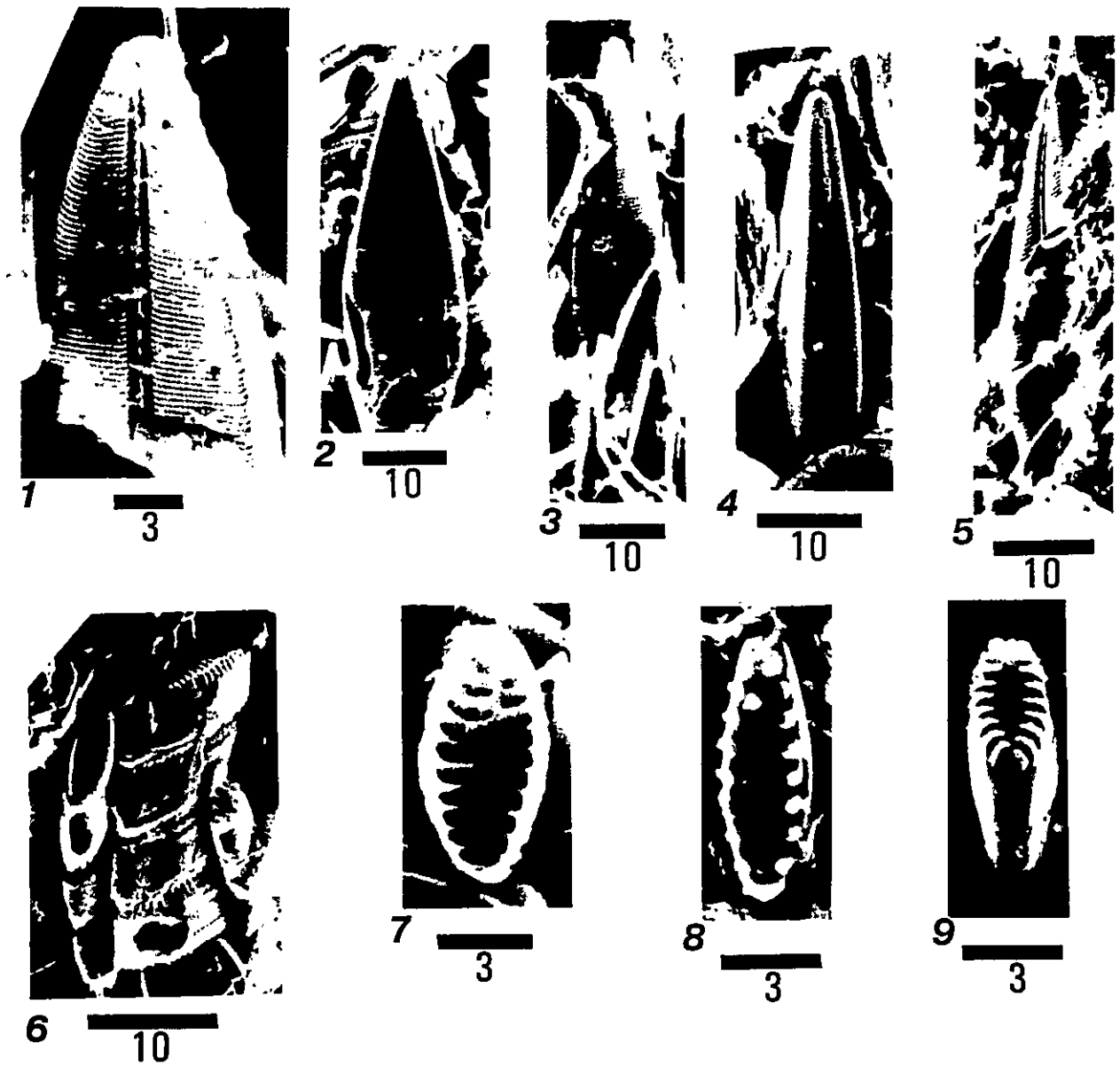

Figure 6.—1–5, *Navicula halophila* (Grun.) Cl.; 6, 8, and 9, *Fragilaria brevistriata* Grun.; 7, *Fragilaria construens* v. *venter* (Ehr.) Grun. Scales in micrometers.

common. The euryhaline marine species of *Melosira*, including the less abundant species, *Melosira juergensi* and *Melosira dubia* are most commonly found today in coastal marine environments, typically estuaries or brackish coastal lagoons, where they live attached to submerged or emergent aquatic plants or to rock surfaces near shore (Cholnoky, 1968; Round, 1971). The same ecology and habitat apply to the other euryhaline marine species, such as *Amphora arcus* v. *sulcata* and *Amphora hyalina* (Cholnoky, 1961; Griffen, 1966; and Hustedt, 1955). The continental euryhaline species live in similar benthonic habitats (Cholnoky, 1968).

The only diatoms associated with the opaline cherts in the Hualapai Limestone Member characteristic of freshwater environments are *Fragilaria construens* v. *venter*, and *Fragilaria brevistriata*. Both these species tolerate some fluctuations in alkalinity and salinity, and are commonly found in slightly saline environments. For example, they

Figure 5.—1 and 2, *Nitzschia*? sp.; 3, *Anomoeoneis costata* (Ktz.) Hust.; 4, *Denticula* sp.; 5 and 6, *Cymbella pusilla* Grun.; 7 and 8, *Entomoneis paludosa* (W. Sm.) Reim. Scales in micrometers.

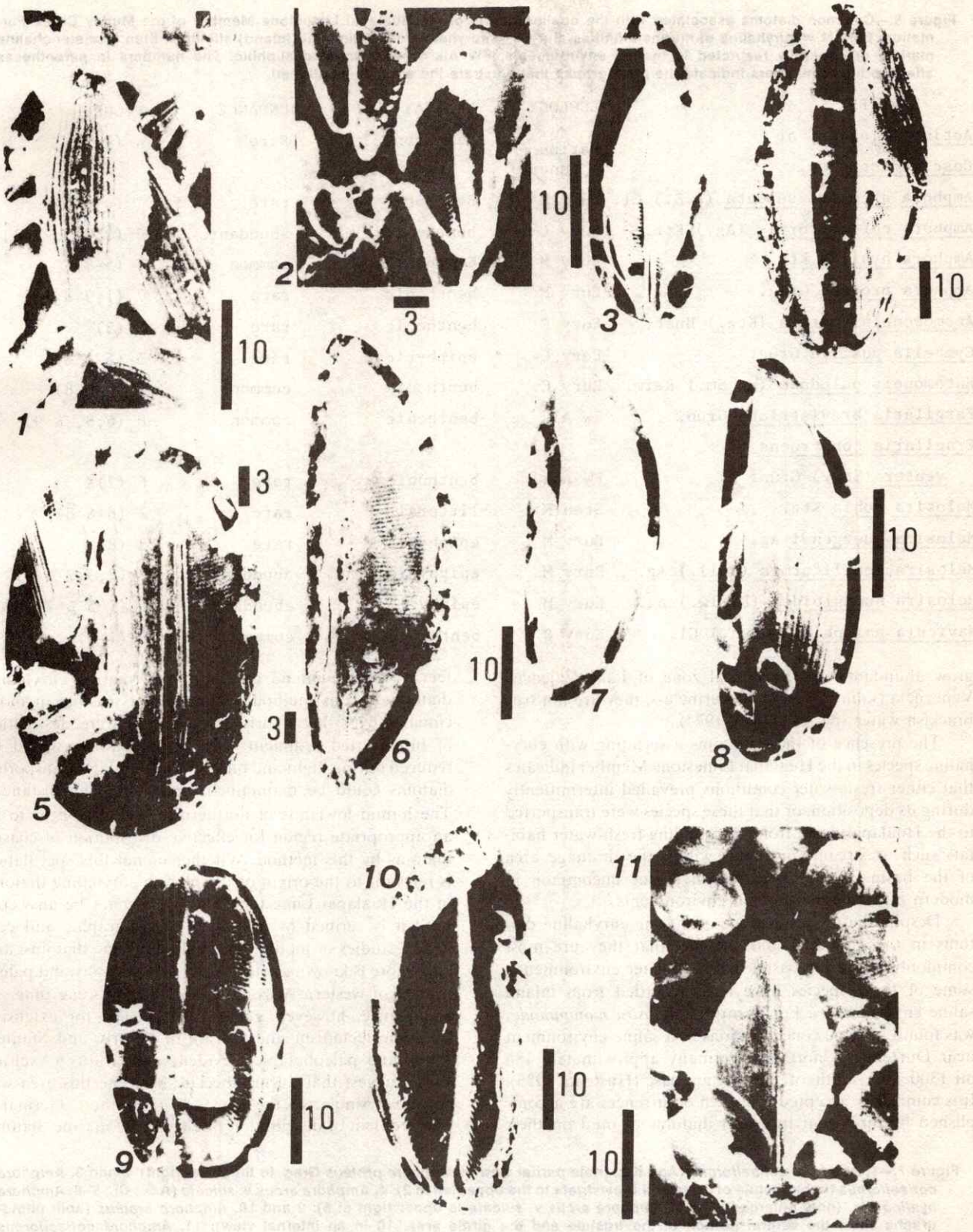

Figure 8.—Common diatoms associated with the opaline cherts of the Hualapai Limestone Member of the Muddy Creek Formation. Eury M = euryhaline of marine affinities, Eury C = euryhaline of continental (inland) affinities, Sten M = stenohaline marine, or generally restricted to marine environments, FW Alk = fresh water alkaliphilic. The numbers in parentheses after the figure numbers indicate the photographs that illustrate the species mentioned.

SPECIES	ECOLOGY	HABITAT	ABUNDANCE	FIGURE
Actinocyclus sp. or Coscinodiscus sp.	Marine genera	planktonic?	Rare	4 (1-5)
Amphora arcus v. sulcata (A.S.) Cl.	Eury M	Benthonic	rare	7 (4 & 5)
Amphora coffaeiformis (Ag.) Ktz.	Eury C	benthonic	abundant	7 (1,2,3, & 11)
Amphora hyalina Ktz.	Eury M	benthonic	common	7 (5-8)
Amphora proteus Greg.	Eury M	benthonic	rare	7 (1,9 & 10)
Anomoeoneis costata (Ktz.) Hust.	Eury C	benthonic	rare	5 (3)
Cymbella pusilla Grun.	Eury C	epiphytic	rare	5 (5 & 6)
Entomoneis paludosa (W. Sm.) Reim.	Eury C	benthonic	common	5 (7 & 8)
Fargilaria brevistriata Grun.	FW Alk	benthonic	common	6 (6,8, & 9)
Fragilaria construens v. venter (Ehr.) Grun.	FW Alk	benthonic	rare	6 (7)
Melosira dubia Ktz.	Sten M	littoral	rare	2 (6 & 8)
Melosira juergensi Ag.	Eury M	epiphytic	rare	3 (8)
Melosira moniliformis (Mull.) Ag.	Eury M	epiphytic	abundant	3 (2,3,7 & 9)
Melosira nummuloides (Dillw.) Ag.	Eury M	epiphytic	abundant	2 (1-5 & 7); 3 (1)
Navicula halophila (Grun.) Cl.	Eury C	benthonic	common	6 (1-5)

grow abundantly in the littoral zone of Lake Valencia, Venezuela (salinity 1.3‰). Nevertheless, they are not true brackish water species (Lowe, 1974).

The presence of these diatoms associating with euryhaline species in the Hualapai Limestone Member indicates that either fresh-water conditions prevailed intermittently during its deposition, or that these species were transported to the Hualapai basin from surrounding fresh-water habitats such as streams or ponds within the drainage area of the basin. Such transportation is not uncommon in modern estuarine or lagoonal environments.

Despite the preponderance of marine euryhaline diatoms in the Hualapai and the fact that they are most commonly found in coastal brackish-water environments, some of these species have been recorded from inland saline environments. For example, *Melosira nummuloides* was found in large concentrations in a saline environment near Durrenberg, northern Germany approximately 186 mi (300 km) south of the Baltic coast (Hustedt, 1925). It is commonly accepted that such occurrences are accomplished by birds that transport diatoms in mud on their feet. Extensive inland distribution of marine euryhaline diatoms by this method would appear feasible in moist climates over flat, poorly-drained land were desiccation of bird-carried sediment with living diatoms would be reduced during flight and on stopovers, and the transported diatoms could be maintained alive over long distances. The humid lowlands of northern Germany appear to be an appropriate region for effective distribution of coastal diatoms by this method. Whether or not this speculation is relevant to the origin of the marine euryhaline diatoms in the Hualapai Limestone Member cannot be answered until it is verified by additional biogeographic and ecological studies of modern euryhaline marine diatoms, and until more is known about the paleotopography and paleoclimate of western Arizona during late Miocene time. At first glance, however, geological evidence for extensive Cenozoic tectonism and volcanism (Eberly and Stanley, 1978), and paleobotanical evidence for aridity (Axelrod, 1937) suggest that during the late Miocene this area was not at all similar to the lowlands of northern Germany. The problem of distribution of euryhaline marine diatoms

Figure 7.—1, *Amphora coffaeiformis* (Ag.) Ktz. (note partial view of *Amphora proteus* Greg. to the lower right); 2 and 3, *Amphora coffaeiformis* (note frustule of *Fragilaria brevistriata* to the upper left in 2); 4, *Amphora arcus* v. *sulcata* (A.S.) Cl.; 5–8, *Amphora hyalina* Ktz. (note enlarged view of *Amphora arcus* v. *sulcata* to upper right of 5); 9 and 10, *Amphora proteus* (both photographs show the ventral portion of the frustule and the girdle area; 10 in an internal view); 11, *Amphora coffaeiformis* Scales in micrometers.

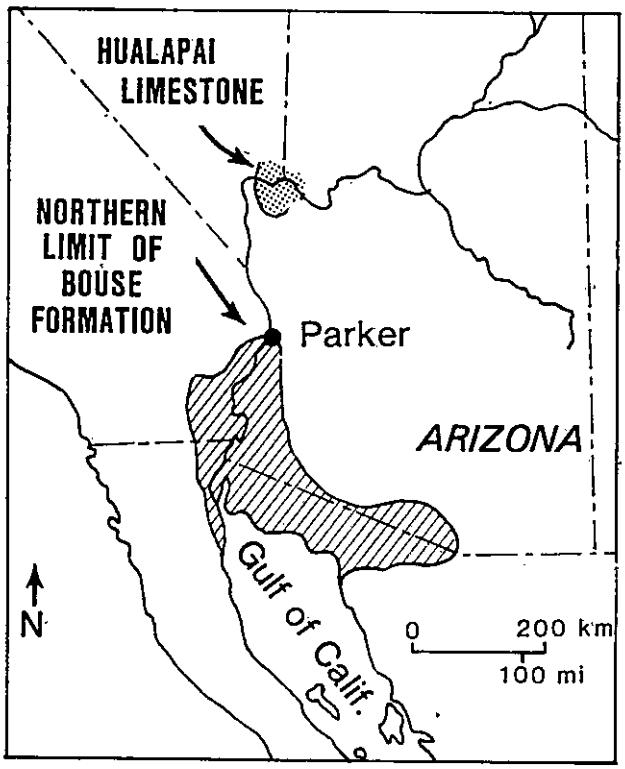

Figure 9.—Index map showing the northern limit of the Bouse Formation (in outcrop) and the location of the Hualapai Limestone Member of the Muddy Creek Formation. Modified from Blair (1978).

to inland saline environments is clearly facilitated by a close proximity of the sea, and it seems logical that nearby coastal environments are even more necessary in rugged, arid landscapes.

STRATIGRAPHIC EVIDENCE

Lithostratigraphic evidence as well as paleoecology of the Hualapai Limestone Member also suggests marine influence during the deposition of the Muddy Creek Formation. Massive halite deposits in the Muddy Creek Formation are reported in the subsurface of the Hualapai Valley (Peirce, 1972), the Detrital Valley (Longwell, 1963), and north of Lake Mead in the Virgin Valley (Mannion, 1963). The authors who have described these deposits ascribed them to nonmarine evaporite environments which have concentrated halite dissolved from Paleozoic evaporite deposits on the Colorado Plateau. The salt deposits are pure, and range from nearly 1000 ft (300 m) to more than 4,000 ft (1,200 m) in thickness. Marine evaporites of this magnitude are well-known, but clear-cut examples of equally thick lacustrine evaporites are not. For example, although the trona-halite beds of the Wilkins Peak Member in the Green River Formation occur throughout more than 3,280 ft (1,000 m) of section, individually they are not more than 260 ft (80 m) thick. They are separated by similar or greater thicknesses of clastic and carbonate sediments and contain a wide variety of unusual evaporite minerals (Bradley and Eugster, 1969). The diverse mineralogical nature of lacustrine evaporites appear to be a common characteristic of these deposits (Picard and High, 1972). Mineralogical homogeneity on the other hand often characterizes marine evaporites because the bitterns in sea water are minor compared to the dissolved amounts of sodium chloride: calcium sulfate, and calcium carbonate.

Clearly these comments are not offered as proof that the Muddy Creek Formation was deposited under the influence of a marine environment. There are several specific, if somewhat contrived, scenarios of exclusively continental deposition that could account for the distinctive paleontologic, litholigic, mineralogic, and geochemical characteristics of this formation. It seems simpler, however, to believe that a marine embayment, similar to that which produced the Pliocene Bouse Formation (Fig. 9), somewhat later extended northward to the Lake Mead area in late Miocene time to partially influence the deposition of the Muddy Creek Formation. The tectonic processes to accomplish this do not seem complicated or unusual to this part of country during late Miocene time (Eberly and Stanley, 1978).

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