FRESHWATER DIATOM PALEONTOLOGY AND PALEOLIMNOLOGY OF THE LATE EOCENE FLORISSANT FORMATION, TELLER COUNTY, COLORADO

by

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A thesis submitted to the Faculty of the Graduate School of the University of Colorado in partial fulfillment of the requirement for the degree of Doctor of Philosophy Department of Geological Sciences 2011 This thesis entitled: Freshwater Diatom Paleontology and Paleolimnology of the Late Eocene Florissant Formation, Teller County, Colorado written by Mary Ellen Benson has been approved for the Department of Geological Sciences

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Freshwater Diatom Paleontology and Paleolimnology of the Late Eocene Florissant Formation,

Teller County, Colorado

Thesis directed by Associate Professor Dena M. Smith

The late Eocene Florissant lake shales are host to the most diverse early freshwater diatom flora known in the fossil record. These 34.05 ± 0.08 Ma deposits also yield well-preserved terrestrial and aquatic fossils that represent life during the approach to the final phase of cooling that followed the thermal maximum of the early middle Paleogene.

This study begins with a synthesis of the earliest (pre-Neogene) records of non-marine diatom genera from the Florissant and 8 other fossil localities. Nearly all pre-Neogene diatom genera are extant genera, and genus richness increased through time. Cumulative richness for the Florissant diatoms is 33 genera, 14 of which are first-time recorded occurrences. Florissant has 18 more genera than any of the 6 older floras examined.

The next component of the study is a detailed floristics assessment of the Florissant diatoms conducted at the Clare's Quarry site. A total of 20 freshwater diatom genera are described and imaged, 8 of which are first occurrences in the geologic record. Among these 20 genera, 4 new species and 2 new varieties are named. As many as 48 taxa show affinities for known modern species. In total, 55 taxa are described and illustrated.

The study concludes with an integrated examination of the paleolimnology of Florissant lake at Clare's Quarry from sedimentological characteristics of host lithologies, autecological preferences of the most similar modern diatom taxa (modern analogs), and the occurrences of associated macrofossils. Evidence is found in support of an anoxic hypolimnion and a deep bathymetry for the depocenter. The interpreted diatom paleoecology places this plankton-rich, open-water lake site within range of major stream outflow that introduced lake marginal and non-lake-dwelling diatoms, and plant and insect macrofossils into the lake. Slow suspension settling of diatoms, fine clays, and airfall tuffs characteristic of deep lake sedimentation is interrupted by fines of episodic distal turbidites.

This investigation demonstrates the power of integrating data from allied sub-disciplines to better characterize paleoenvironments and their inhabitants.

DEDICATION

I dedicate this manuscript to the person who had the most profoundly positive influence in my life through her independent spirit, her scholarly achievements, the strength and clarity of her convictions, her love of family and friends, her laughter, her sense of adventure, and her compassion for others; and who fostered and facilitated my love for learning: my mother, Frances Caroline Jilcott Benson.

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INTRODUCTION

Diatoms, being single-celled photosynthetic algae, are important indicators of chemical, physical, and biologic parameters of modern aquatic ecosystems throughout the world. Fossil freshwater diatoms are also used to interpret changes in water conditions in ancient lakes as old as Miocene. Fossil diatoms are especially useful tools in tracking changes in paleoclimate. Studying the rich assemblage at Florissant allows one to not only document the diversity and history of the diatom groups in deeper time, but it also provides an opportunity to gain a better understanding of the paleolimnology of Florissant lake. Florissant is a world-famous locality that has had much study of the generally terrestrial macrofossils that are so excellently preserved in the lake sediments, but there is still little that is actually known about the paleoenvironmental conditions within the lake, itself. This study will examine the diatom flora and then use that flora, along with abiotic lines of evidence, to better understand the ancient lake.

Project Objectives

The specific objectives of this research project are to re-examine the literature on the Florissant lake basin history, to identify the component taxa of the Florissant fossil diatom flora, to place this flora into a geochronologic context and compare it with known freshwater diatom floras from this early time period, to describe and image each Florissant diatom taxon, to determine what possible habitats the diatoms might represent, to relate the diatom occurrences to the different host lithologies, and to integrate the lithologic and stratigraphic evidence with all the paleoecologic indicators to describe the paleolimnological parameters for the Clare's Quarry site.

Organization of the Dissertation

Four over-riding questions posed by the research objectives are addressed in Chapters 1 through 4. Note that the manuscripts for Chapters 2 through 4 are composed and formatted according to requirements for publication in peer-reviewed publications, as indicated. The principal questions, the ways they are addressed in each corresponding chapter, and their significance in the broader context are discussed below.

Chapter 1.

What new interpretations about the history of the Florissant lake basin can be discerned from a re-examination of the published literature?

This chapter presents a synthesis of the major conclusions of historically published literature on the Florissant paleo-valley and lake system; and, on the basis of the integration of these data, considers alternative views from those commonly presented in the current literature. For example, this new examination uncovers the possibility that the Florissant paleo-lake could have had an extensive areal extent and duration that would exceed the estimates that are now in publication. This opens up the opportunity for the Florissant Formation to become an even more significant fossil site that contains a wider array of habitats and covers a time period in which evolutionary changes among like taxa might be recorded.

Chapter 2.

How does the Florissant fossil diatom flora compare with other early non-marine diatom assemblages?

This chapter provides a synthesis of the Florissant fossil diatom genera and the flora of 8 additional localities that cumulatively represent the complete record of published taxa from the earliest appearance of non-marine diatoms in late Cretaceous through late Oligocene. The results demonstrate the greater genus-richness of the Florissant diatom flora in the context of the other known early floras. Although the record suggests a general increase in diatom diversity during the Eocene epoch, it is recognized that optimal conditions for preservation may have played the more important role in this fossil record. Nevertheless, diatom taxa from these Eocene sites are contributing a large number of new taxa for study and comparison with those from other sites. The Florissant and other Eocene localities are extending the geologic ranges of many extant freshwater diatom lineages by millions of years.

Publication: Has been through pre-review process for *Micropaleontology*.

Chapter 3.

How diverse is the Florissant fossil diatom flora? What taxa are represented, and what are their morphological characteristics? Of the taxa present in Florissant lake sediments, which are extant; which have only been recorded in other fossil sites; and which have never before been described?

This chapter is an illustrated descriptive account of each diatom taxon identified to genus, species, or variety (wherever possible) from the Florissant flora preserved at the Clare's Quarry site. The taxa are presented in systematic order. Comparisons with known taxa are provided, and new taxa are named. This study provides to the diatom community the first described and illustrated account of the taxa observed at the Florissant locality. These data will now be available for researchers world-wide to compare with taxa from modern and ancient floras. This work also provides irrefutable evidence for the often-cited assessment that these 34 million year-old Florissant diatoms have affinities to modern taxa.

Publication: To be submitted for publication in *Bibliotheca Diatomologica*.

Chapter 4.

What do the Florissant fossil diatoms in combination with their respective host lithologies indicate about the nature of the paleo-lake and its catchment area?

This chapter examines and integrates the lithology and stratigraphy data with ecological information from the fossil diatoms and the occurrences of associated macrofossils to characterize the paleolimnological parameters of Florissant lake at the Clare's Quarry site. This study demonstrates the value of using an integrated approach to addressing questions that have both biotic and abiotic implications. The findings that include deep lake bathymetry, anoxic hypolimnion, slow sedimentation rate, encroachment of terrestrial mud deposits, airfall origin of tuffs, and the range of habitats that bordered the lake are strengthened by multiple lines of evidence. This approach, applied to other Florissant sites could provide a set of stratigraphic

sections whose paleolimnological parameters have been determined. This will create a patchwork of data points that can be used to more fully interpret the history of the lake system.

Publication: In preparation for submittal for publication in *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*.

Future Directions for Research

My future research on the Florissant Formation will be concerned with obtaining data to address additional aspects of the history of the paleo-lake. The following topics are of particular interest to me.

Diatom floristics of the "middle shale"

Future investigations of the "middle shale" unit of the Florissant Formation at several sites within the Florissant Fossil Beds National Monument would allow comparisons of lithology, stratigraphy, mineralogy of any airfall tuffs, and the diatom flora with those aspects of the "lower shale" at Clare's Quarry. Of particular interest are the "Original" Scudder site on the northwest end of Big Stump Hill and the MacGinitie-3 site north of Lower Twin Rocks Road.

Preliminary examination of samples from the section at the Original Scudder site reveals species of the genus *Aulacoseira* that have not yet been recognized at Clare's Quarry. These are abundant in particular intervals. Excellent SEM images attest to this. A detailed floristics account of the diatom flora at this site would potentially shed further light on paleolimnological

parameters of this portion of the lake. More broadly, such a study would further inform paleodiatomists of the early occurrence of additional species of *Aulacoseira* and add to our understanding of this long-ranging freshwater lineage.

The importance of a new study of the MacGinitie-3 site is based on the controversial observation in archived slides from that site of the diatom genus *Stephanodiscus*, along with a range of additional species that have not been documented elsewhere in the Florissant sections. A thorough new examination of the diatoms in this site would help to resolve the mystery surrounding this set of archival slides. Of greater significance, should the genus *Stephanodiscus* be confirmed from the efforts of a new study at Florissant, it would revolutionize the current belief that this genus did not evolve until latest Miocene or Pliocene time (Krebs, 1994). Such a first-occurrence of this genus would extend the fossil record for *Stephanodiscus* by nearly 29 million years.

Revisiting the stratigraphy of the Florissant Formation

A renewed field effort to examine the exposures throughout the entire region, both within and beyond the Monument boundary, could potentially answer questions about the stratigraphic order of the "lower," "middle," and "upper shale" units and could confirm the structural and stratigraphic relationships among these units and with the granite and Wall Mountain Tuff. The incorporation of seismic and gravity surveys and water-well logs would enhance the likelihood of defining the geometry of the basin and tracking the volcanic and tectonic influences on the history of the lacustrine system. Perhaps evidence for a local vent for the pyroclastics in the Florissant beds will be discovered. Potential parallels could be evaluated between the Florissant lake basin and other areas of late Eocene to middle Oligocene magmatism that are associated with extensional tectonics in the Wet Mountains region of Colorado (Klein et al., 2010). Such work could potentially provide a more accurate perspective on how Tertiary continental lake basins in volcanically and tectonically active areas evolved in the southern Rocky Mountain region.

High resolution analysis of diatom microlaminae

It has become evident during the current study that, while the "paper shale" on outcrop that can be split to within <1/3 mm thickness is generally interpreted as couplets containing a single discrete diatomite lamina, it has been shown in petrographic thin section that these diatomite laminae are not homogeneous in their microscopic architecture. A high-resolution study of the diatom-rich microlaminae of the fossiliferous laminated shales is needed to clarify the depositional relationships among the various diatom taxa, the diatoms and the detrital clay/ash, the sapropel, and the macrofossils in the Clare's Quarry section. This could show whether or not the diatoms were deposited in discrete microlaminae that reflect planktic seasonal blooms or in lenticular or disrupted microlaminae that reflect mixing with clays prior to settling to the lake floor. The relative thickness of the more discrete bloom laminae could indicate seasonal events, and the chronological order of diatom taxa occurrences could suggest successional trends.

Although caution must be exercised when using taphonomic assemblages to represent living diatom populations, insights gained through this type of inquiry could further our understanding of trends suggestive of the life habits of these ancient relatives of modern diatoms. More could be revealed about the potential relationship of diatoms and the preservation of leaves and insects in the Florissant locality that could potentially be more broadly applied to other Tertiary lacustrine fossil deposits. This could advance our perspectives on the many factors that play a role in fossil taphonomy. CHAPTER 1

LITERATURE SYNTHESIS OF THE FLORISSANT ANCIENT LAKE

SETTING

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Background

The late Eocene Florissant Formation in central Colorado is a world-famous fossil deposit that has been extensively studied over the past century. Previous investigators have assembled a body of knowledge that continues to be cited by subsequent workers. The following is a review of this seminal literature particular to the lake origin, maximum original areal extent, stratigraphy, age, volcanic source for tuffs, duration as a lake, type of lake and bathymetry, paleoclimate and topography, paleo-elevation, tectonic history of the basin, and hypotheses as to the processes of fossil preservation.

The purpose of this review is to present published interpretations about the general features and development of the Florissant lake basin to provide the reader with a general overview of the regional setting; and, where appropriate, to offer alternative perspectives, which have also been integrated into the discussion of Chapter 4.

Florissant fossil Lagerstätte: geological significance and location

The late Eocene Florissant Formation is a world-famous fossil Lagerstätte ("motherlode") that contains extremely well-preserved paleobotanical and fossil insect and invertebrate assemblages from lacustrine facies, and mammal fossils from the associated fluvial deposits. The importance of this deposit is in, not only the extraordinary fossil preservation, but also its unique position in geologic time at the terminus of a long period of transition from the warm global climates of the Paleocene/Eocene thermal maximum (Prothero, 1994; Zachos et al., 2001).

The Florissant Formation is known from a relatively small area in the vicinity of the town of Florissant in Teller County, Colorado (Figure 1), west of Colorado Springs.



Figure 1. Location of Florissant, Colorado (small rectangle).

The Florissant Formation extends northwest and south of the town of Florissant (Figure 2). Principal fossil sites are located within the Florissant Fossil Beds National Monument, established in 1969, which is to the south of Florissant on County Highway 1. The detailed paleontologic and paleolimnological studies featured in Chapters 2, 3, and 4 of this dissertation were conducted at the "Florissant Fossil Quarry" (referred to in this study as Clare's Quarry), a privately-owned commercial operation that is located just south of the town of Florissant and west of County Highway 1 (Figure 2).



Figure 2. Location map of the Clare's Quarry study site showing the maximum estimated present-day subsurface extent of the Florissant Formation and the boundary of the Florissant Fossil Beds National Monument.

Florissant paleo-lake setting from previous studies

Origin of the lacustrine basin

The Florissant paleo-lake system is interpreted as having formed as a consequence of the damming of a southward flowing fluvial drainage by lahars that flowed from volcanic terrane on the south and west (Evanoff et al., 2001). The lithology of the damming material consisted of both fine volcanic lahars and coarse volcanic rubble generated by periodic eruptions of the Guffey volcano that is part of the Thirty-nine Mile volcanic field southwest of the modern areal extent of the Florissant Formation (Meyer, 2003; Epis and Chapin, 1974).

Areal extent

Early efforts to define the areal extent of the Florissant Formation have resulted in generalized maps that exaggerate the area of actual surface exposure. The principal example of this that persists in the literature is the geologic map by Wobus and Epis (1978) (Figure 2) that shows the entire area within the topographic valley trend as Florissant Formation. It is demonstrated by Niesen (1969) and Evanoff et al. (1992) that, in fact, Quaternary alluvium and gravels cover most of the area mapped by Wobus and Epis (1978) as Florissant Formation. The more detailed mapping of Niesen (1969) and Evanoff et al. (1992) demonstrates that the lake deposits are exposed only in ridge and hill slopes, trenches, and roadcuts. Subsurface data have not been exploited to identify the formation's extent. Although it is shown by Evanoff et al. (1992) that the Florissant lahar mudstone and fluvial sand unit is the topographically lowest of

exposures in the valley floor within the National Monument, the extent of the lacustrine beds has not been determined.

There are conflicting views among investigators as to the paleo-lake size and geometry and, consequently, the original position and nature of the shoreline. While some believe the lake was limited to the present-day topographic trend (Evanoff et al., 2001; Meyer, 2003), others conclude that the lake area was larger than present-day topography would suggest (MacGinitie, 1953; McLeroy and Anderson, 1966). Meyer 's (2003) estimates for the areal extent of the paleo-lake of approximately 30 km² (18.6 mi.²) uses the generalized dimensions (1.5 km wide and 20 km long) indicated by the Wobus and Epis (1978) map. Meyer (2003) further states that the present-day outcrop area of the Florissant Formation indicates that there has been minimal structural change in this area since the Eocene. MacGinitie (1953, p. 4) states, "The present outline of the (Florissant) beds is due to complex faulting and subsequent erosion, and does not represent, in any sense, an old lake margin."

It is reasonable to conclude, therefore, that the original areal extent of the lake paleobasin is unknown; and that, as a result, much information about the original topography and the nature of the catchment area is unknown.

Stratigraphy

Exposures of Florissant lake deposits within the Florissant Fossil Beds National Monument and surrounding area have been informally assigned to three units on the basis of outcrop characteristics. These units are referred to as the "lower shale," "middle shale," and "upper shale" (Evanoff et al., 2001), each being recognized in separate exposures that do not show unambiguous contacts with the other units. These units are, therefore, separated from each other both stratigraphically and geographically. All three units contain finely laminated shales referred to as "paper shales", blocky shales, and mudstones that alternate with volcanic tuff beds. The finely laminated "paper shales" are described as couplets of submillimeter thick sheets of diatomite, tuff, and smectite clay (Weilbacher, 1963; McLeroy and Anderson, 1966; and O'Brien et al., 2002).

Reference to these unique exposures by names that indicate vertical (therefore, implying chronologic) order suggests a certain depositional history that would benefit from further work to identify marker horizons. Seismic surveys would be helpful in delineating the basin fill and in searching for lithologic horizons to correlate.

Late Eocene age

A mean radiometric age of 34.05 ± 0.08 Ma for the Florissant Formation was determined with 40 Ar/ 39 Ar single-crystal sanidine laser-fusion analysis from four tuffs from the "upper shale" and one tuff from the "middle shale" from locations within the Monument (McIntosh and Chapin, 2004). Additionally, mammal teeth and bones from brontotheres and *Mesohippus* recovered from the fluvial deposits that underlie the middle shale are consistent with the North American Mammal Age (NALMA) of Chadronian (Worley, 2004; Prothero, 2004) that places it in the late Eocene. This has been further corroborated by additional mammal fossils recovered in the Florissant Formation (Lloyd et al., 2008).

Source of the volcanic units in the Florissant Formation

According to McIntosh and Chapin (2004), the source of the radiometrically dated volcanic tuffs in the "upper shale" and "middle shale" of the Florissant Formation is unknown for two principal reasons: there is neither a geochronologic nor a mineralogic match. The 34.05 Ma mean age of the Florissant tuffs is inconsistent with any of the dated ignimbrites in the region. The mean radiometric age for the Guffey andesites is 36.1 Ma; and the Thirty-nine Mile Andesites are 35-36.5 Ma (McIntosh and Chapin, 2004). These ages pre-date the Florissant radiometric age by at least 1 million years.

Compositionally, the Florissant tuffs from the "middle" and "upper shales" that were radiometrically dated in the McIntosh and Chapin (2004) study are inconsistent with the Guffey andesites and the ignimbrites of the Thirty-nine Mile volcanics. The feldspar phenocrysts of the Florissant tuffs are dominantly plagioclase and those of the Guffey/Thirty-nine mile field are dominantly sanidine (McIntosh and Chapin, 2004). The work by McIntosh and Chapin (2004) shows that the source for the intraformational Florissant tuffs is not likely to be the Guffey/Thirtynine mile field, but is yet, undetermined.

Duration of the lake

An estimate of 2,500 –5,000 years for the duration of the lake was made by McLeroy and Anderson (1966) on the basis of observations from "middle shale" sites in the Florissant Formation. This estimated duration period was determined by counting the diatomaceous (white) laminae in petrographic thin sections and attributing each to an annual diatom bloom. An exact count of each diatomaceous lamina would require the careful collection and preparation of thin sections throughout the entire exposure of middle shale to account for the inclusion of frequent but non-uniform additions of pyroclastic material and non-bedded mudstone units that pervade the middle shale section; and, furthermore, the careful examination of each lamina is necessary to exclude ash laminae that are also light-colored. Although it is true that this level of intensive analysis was done in the study by McLeroy and Anderson (1966), it is uncertain as to the amount of vertical section that was examined in this way. Their approach would, however, provide a reasonable assessment of duration for the unknown portion of the middle shale examined. It can only be surmised that the counts were then extrapolated to the overall thickness of the middle shale, providing an approximation of the minimum duration of the middle shale where the thicknesses had been measured. As for the duration of a potentially larger lake system, such estimates can only be deduced from broader-ranging data.

Alternative estimates for the duration of the lake are based on the 35-36.5 Ma radiometric age of the lower member of the Thirty-nine mile Andesite (McIntosh and Chapin, 2004) that is credited with having dammed the drainage to form the lake (Epis and Chapin, 1974). This breccia complex of predominantly fragmental intermediate to mafic rocks covers approximately 2,600 km² to an average depth of 150 m and possibly also assisted in forming the Antero lake basin (Epis and Chapin, 1974). If the initial development of the Florissant lake occurred at 35-36.5 Ma, the earliest lake sediments would have been deposited as much as one million years before the origin of the dated tuffs from the "middle shale" and the "upper shale" Florissant units.

This would extend the life of the entire lake system, now represented only by the preserved and exposed Florissant beds, to at least one million years, and possibly to as much as 2.45 million years of duration.

Type of lake and bathymetry

Samples from five exposures of "middle shale" and "lower shale" of the Florissant Formation were petrographically examined by McLeroy and Anderson (1966). These deposits were interpreted as being characteristic of a lake that was permanently stratified with no mixing of top and bottom waters on the basis of the preservation of laminations, the absence of evidence of scour or bottom turbulence, and the exclusion of benthic organisms (McLeroy and Anderson, 1966). The absence of benthos, the presence of pyrite, and the excellent fossil leaf and insect preservation attest to the likelihood that the hypolimnion was consistently anoxic and, therefore, inhospitable to bottom feeders and infauna (McLeroy and Anderson, 1966). Permanent stratification would occur as a result of either lack of turbulent mixing or density instabilities that are insufficient to mix vertically adjacent water masses (Cohen, 2003). It was recognized by McLeroy and Anderson (1966), that many modern subtropical lakes experience some overturn despite the apparent minimal seasonal temperature fluctuations. As an alternative to thermal stratification, McLeroy and Anderson (1966) attributed the lack of mixing in Florissant paleolake to chemical stratification that resulted in denser bottom waters due to increased salinity in the hypolimnion (monolimnion) compared with less saline waters of the epilimnion (mixolimnion). The mechanism for this proposed increase in bottom-water salinity was the release of salts from the substrate, referred to as endogenic meromixis (Cohen, 2003). This increase in total concentration of dissolved ions can include cations of sodium, potassium, calcium, and magnesium; and anions of chloride, carbonic acid, carbon dioxide, and sulfate (Cohen, 2003). In open-basin lakes, the outflow rate would keep the solute concentrations in equilibrium (Cohen, 2003). A build-up of these ions in the bottom-waters would be more likely

to occur in closed-basin lakes, and such concentrations would result in the precipitation of evaporate minerals (Cohen, 2003).

In this examination of the Florissant lake sediments at Clare's Quarry, the lake is interpreted as sufficiently deep to have a basinal (profundal) floor that remained below storm wave base. This is indicated by the following features: the apparent lateral continuity of bedding thickness, absence of erosional contacts, lack of disruption of finely laminated beds, and excellent preservation of fossils. These same observations are evidence that the lake, if it overturned at all, experienced only incomplete seasonal or annual mixing in the upper water column, never overturning the waters of the hypolimnion. This is further shown by the secondary evidence of pyrite nodules and framboids in the sediments that indicate anoxic bottom-water conditions. The anoxia would be compatible with the high organic influx into the lake whose respiration would have depleted the oxygen and elevated the levels of carbon dioxide in the bottom-waters. The findings of this study do not support the hypothesis of the permanent chemical stratification proposed by (McLeroy and Anderson, 1966), as there is no mineralogic evidence for concentrations of mineral salts in the bottom-waters of the Florissant paleo-lake at Clare's Quarry. Alternatively, if the Florissant paleo-lake were a very deep lake and permanently stratified, temperature-driven density stratification mechanisms could have played a role in the isolation of the hypolimnion and the consequent anoxia. An example of a deep subtropical meromictic lake that maintains a temperature-driven density stratification is Lake Tanganyika (Plisnier et al. 1999). In Lake Tanganyika, the mechanical energy from wind is insufficient to overcome temperature-driven density stratification, and a permanent thermocline exists that prevents mixing below about 100-200 meters (Plisnier et al. 1999).
Paleoclimate, topography, and elevation

On the basis of terrestrial paleobotanical evidence principally from the "middle shale," Florissant lake has been interpreted as a high-elevation, low-relief intermontane lake (Gregory and Chase, 1994; Evanoff et al., 2001) with a warm temperate to subtropical climate (Meyer 2003; Leopold and Clay-Poole, 2001). Paleo mean annual temperature has been estimated using the CLAMP method (Wolfe, 1995) as 12.8 ± 1.5 °C, with a mean annual precipitation of 72 ± 31 cm with 57 ± 16 cm during the growing season (Gregory and McIntosh, 1996). The NLR (nearest living relative) method gives an estimate of mean annual temperature as no lower than 17.5°C (4-6.8° warmer than the CLAMP method) (Leopold and Clay-Poole, 2001). Integrated leaf and pollen records suggest that the area experienced moderate summer rainfall and mild, dry winters (Leopold and Clay-Poole, 2001).

Estimates of elevation for the vegetated slopes surrounding the paleo-valley include those of MacGinitie (1953) (based on nearest modern relatives to the fossil flora of the "middle shale") that range from 300 to 900 meters. More recent studies are based on lapse rates with temperature decreases of 1°C per 1,000 meters of elevation gain. These estimates using the lapse rates established for the fossil flora produce a range from 1,900 to more than 4,100 meters (Meyer, 2003) for the paleo-elevation of Florissant.

Tectonic history of the modern Florissant valley

The tectonic history of the present-day Florissant valley is not well-known, and questions of the stratigraphic relationships among the three informal lacustrine units ("lower shale,"

"middle shale," and "upper shale") of Evanoff et al. (2001) are largely unanswered. Faults have been delineated by several workers (MacGinitie, 1953; Niesen, 1969; and Evanoff et al., 1992). Two important questions about the tectonic history are relevant to this study: (1) was there faulting in the Florissant lake valley prior to and during the deposition of the lake shales; and (2) was there post-depositional normal faulting that created a patchwork of lake sediment remnants preserved in grabens?

The Florissant lake valley was interpreted by MacGinitie (1953) to have undergone syndepositional faulting. The following data were interpreted as supporting this view. MacGinitie (1953) showed a complexly faulted Florissant valley with a series of high-angle normal faults that formed grabens that were filled with preserved Florissant sediments. He envisioned these sediments as in-filled synclines within the grabens, to which he attributed the dips and structural relationships that he observed in the field. MacGinitie (1953) shows moderate to high-angle dips on basal breccias, lake beds, and the overlying rhyolites in areas within and proximal to the valley. He interprets the timing of major tectonic deformation to have been subsequent to the extrusion of the Thirtynine Mile volcanic units and earlier than the eruption of the trachyte that overlies the Florissant lake beds and caps the hills just southwest of the town of Florissant. This timing would be concurrent with the deposition of the lake sediments.

Evidence for post-depositional faulting includes many additional lines of evidence. McIntosh and Chapin (2004) document the mid to late Eocene period of volcanism in the central Colorado volcanic field as being from 32 to 38 Ma. This was followed during the Neogene by block faulting and erosion in the region, which resulted in the scattered nature of modern outcrops of units of similar age and composition (Steven, 1975; Epis and Chapin, 1974).

Geologic mapping by early investigators in the area has confirmed faulting within the modern Florissant valley. Most recently, the geologic map of the Florissant Fossil Beds National Monument by Evanoff et al. (1992) shows five north to south trending inferred fault traces along the western flank of the modern Florissant valley. Additionally, three more are variously oriented near the southern end of the Monument on the east and west sides of the valley center and in the vicinity of Lower Twin Rocks Road. No offset is noted in the field along these possible faults.

Niesen (1969) mapped the geology of the modern Florissant valley designating the relatively few scattered Florissant Formation outcrops along flanking hillsides and exposures that emerge in the valley floor from beneath the more extensive Quaternary cover. Niesen showed the approximate location of three high-angle normal faults that transect the area and can be interpreted to form an eastward tilted graben that preserved the Florissant Formation in its present topographic configuration (See discussion of Hanneman et al. (1996) seismic data below). On Niesen's 1969 map, two (F-1 and F-2) faults run generally north to south on the east side of the valley and have down to the west offsets. The third fault (F-3) is northwest to southeast trending in the area to the west of the modern valley and has a down to the northeast offset; it is inferred where it intersects the drainage at the southern end of the mapped extent of the valley just south of where the Thirtynine Mile Lower Andesite becomes prominent at the surface. None of these faults is represented on the Evanoff et al. (1992) map; however, when Wobus and Epis compiled data for their 1978 USGS geologic map of the area, they incorporated

Niesen's F-3 fault as an inferred fault without showing any offset relationship. Regionally, this fault is on trend with the Pulver Gulch-Rocky Gulch Fault to the northwest and parallels four additional northwest to southeast trending faults that transect the Thirtynine Mile volcanic field to the southwest (Wobus and Epis, 1978). Although Wobus and Epis (1978) did not incorporate Niesen's F-1 and F-2 faults into their map, these two faults are on trend with a normal fault that is south of the mapped termination of the Florissant Formation within the valley. This normal fault also has a down to the west offset and forms the east flank of Wrights Reservoir at the upper end of the northeast flowing arm of Fourmile Creek (Wobus and Epis, 1978).

From field observations, MacGinitie (1953) concluded that the present areal extent of the Florissant Formation is only a fragment of the original deposit, with no way of knowing how extensive this lake system might have been; he observed no thinning of the beds toward the margins of the modern mapped areal extent; and he speculated that the Florissant beds may have covered a very much larger area, observing that their present outline is a result of late Tertiary faulting in the region.

Further support for tectonic readjustment within the modern Florissant valley is provided by shallow seismic refraction and reflection surveys conducted over several areas within Florissant Fossil Beds National Monument by Whitehall Geogroup, Inc. and discussed in Hanneman et al. (1996). The seismic survey differentiated valley-fill sediments from Pike's Peak Granite at the basement and in surface exposures. Across the portion of the main Florissant valley in which Grape Creek trends north-south, a refraction line from the Petrified Forest area on the west of County Highway 1 shows that the Tertiary fill thickens toward Grape Creek to the east side of the valley (Hanneman et al. (1996). Analysis of reflection data from the southwestern part of the Monument, also on the west side of the main valley, indicates that the thickness of the Florissant Formation increases in the direction of Grape Creek to the east of the main valley (Hanneman et al., 1996). In the southeastern area of the Monument in the vicinity of Lower Twin Rocks Road, refraction data show that a Tertiary paleovalley exists south of the eastern fork of the Grape Creek drainage; and once again, the sediments indicate a wedge-shaped valley fill that thickens from east to west, in contrast to the surveys that cross the main Florissant valley. The published image of this seismic line (Hanneman et al., 1996) was examined, and a thickness estimate of the valley-fill sediments of from 45 m on the thinner east side to 90 m on the thicker west side was calculated (Tien Grauch, pers. comm.). And lastly, reflection data from the Barksdale Campground area northeast of Lower Twin Rocks Road suggest that a Tertiary paleovalley is situated to the east of the northeast trending portion of the Grape Creek stream valley (Hanneman et al. (1996). The placement of Niesen's (1969) F-1 and F-2 faults is coincident with the location of the thickness trends observed in the seismic data. For example, the F-2 fault that is interpreted as down to the west allows for the asymmetric preservation of infilled sediment in a wedge shape having the thick side adjacent to the up-thrown granite wall on the steep east flank of the Florissant valley. Also, on the east side of the valley across from the Petrified Forest is an active spring in granite grus surrounded by quaking aspens situated along the fault trace of Niesen's F-2.

Examination of the groundwater source in the modern Florissant basin points to fracture systems in the granitic bedrock as the primary aquifer (Mast, 2007). Several seeps and springs within the Florissant Fossil Beds National Monument are fed by groundwater that is delivered to the surface through fractures in the granite. An example of one in the Monument is described

above on the east side of the valley from the Petrified Forest. From recent compilations of water well data along the present-day valley immediately south of the Monument boundary, it is evident that domestic well-water is being produced from a system of fractures that cut both granite and the valley-fill shales that exist at depth (George Whitney, pers. comm., 2011). Furthermore, the juxtaposition of granite overlying shale in some of these wells gives additional strength to the likelihood of faults with measurable displacement. The virtual separation of two parts of the mapped extent of the lake beds to the south of the Monument boundary by a drainage divide consisting of granite further suggests tectonic adjustment.

On the basis of these field observations of faulting, fracturing, and the abrupt thickness changes shown from seismic data, it is reasonable to agree with MacGinitie (1953), McLeroy and Anderson (1966), and Niesen (1969) that tectonic activity within the Florissant valley has resulted in the preservation of only remnants of the original Florissant Formation; and, therefore, much of the footprint and sedimentary record of the original lake basin is missing.

Explanations for extraordinary fossil preservation

McLeroy & Anderson (1966) were among the first to describe sedimentary and stratigraphic evidence from the Florissant lake beds that points to the common contributing factors for excellent macrofossil preservation: minimal transport distance, early burial, burial in extremely fine sediments, accumulation in an anoxic setting, and lack of disturbance by physical or biological agents. These observations strongly support deposition in a relatively deep-water position within an isolated hypolimnion.

Additional observations of the exquisite nature of the fossil leaf and insect preservation at the fossil sites have led to other taphonomic hypotheses. The most recent concept invokes bacterial and planktic diatom biofilm as trapping agents for leaves and insects. They are envisioned as floating mats that are coated by the mucus and protected from degradation prior to sinking into an anoxic hypolimnion where they are preserved as fossils (Harding and Chant, 2000, O'Brien et al., 2002, and O'Brien et al., 2008). Such a hypothesis offers a process by which the leaves and insects could have been captured and delivered intact to the anoxic depths before burial. The absence of diatoms in other well-preserved fossil leaf and insect deposits has not been addressed by proponents of this method. The likelihood of diatoms, bacteria, and other algae in the periphyton along the lake shores and shallows of streams being in close proximity with deciduous leaves that are released in the fall suggest a greater potential opportunity for them to create cohesive leaf clusters. High resolution analysis is needed that maps the diatom flora in the diatomite microlaminae, the associated detrital clays, and the plant leaves to establish a better understanding of the nature of their relationships. The seasonality of the diatom blooms needs to be established as it relates to the timing of leaf accumulation.

Conclusions

This body of data offers reasons to consider that the areal extent of the original Florissant lake system could have well-exceeded that of the present-day outline of the Florissant Formation. Field relationships and structural, seismic, and water-well log data attest to the tectonic instability of the region, giving credence to the proposal that the known limits of the Florissant Formation represent only a remnant of the original fluvio-lacustrine system, now preserved in late Tertiary down-dropped fault blocks. Future studies on the paleolimnology of the larger Florissant lake system would benefit from additional examination of these data.

While the lower andesite of the Thirtynine Mile volcanic field is credited with being the probable damming structure at the southern end of the fluvial drainage that created the lake, the geochronology and volcanic mineralogy of the tuffs within the Florissant Formation support the conclusion that the intraformational pyroclastic deposits are not from the Guffey/Thirtynine Mile volcanic field, as formerly proposed, and that the source is unknown. Additional support for this conclusion is provided for the Clare's Quarry tuffs in Chapter 4.

The radiometric age of the tuffs interpreted as the dam at the outflow of the lake provides a new sense for the possible duration of the lake system that extends it from the previous estimates of 2,500 to 5,000 years for the "middle shale" to from 1 to 2.45 million years.

The biofilm macrofossil preservation model needs further examination to address some of the unresolved relationship issues as to the timing and proximity of leaf accumulation and planktic and benthic diatom blooms.

It is acknowledged that, as is common in geologic and paleontological studies, much evidence is missing and can never be recovered. Although this review may not provide conclusive new data, it provides background for the discussion of the Florissant paleolimnology in Chapter 4. Furthermore, it offers a survey of the data already in the literature that may open the door to new approaches in the quest for fresh clues to the history of this lake system, the basin dynamics, and the relationships to regional periods of volcanic and tectonic activity.

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CHAPTER 2

Pre-Neogene (>23.8 Ma) biochronology of non-marine diatoms, with an account of the late Eocene flora of the Florissant Formation, central Colorado, USA

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ABSTRACT

Recent studies of the non-marine diatom assemblages from Eocene deposits in North America extend the fossil record of several extant freshwater diatom lineages. While the findings of these studies agree with the previously predicted timing of origin for major morphological diatom groups, these accounts increase the number of first-occurring genera from that of the former fossil record of non-marine diatoms. Among the recently-studied sites discussed here are the early and middle Eocene deposits in Canada, dated respectively at 52 and >42 Ma, that provide the first published evidence of an early pulse in the post-Cretaceous radiation of freshwater diatoms. In addition, a survey of previously reported fossil diatoms from the 34 Ma lake sediments of the Florissant Formation in central Colorado, supplemented by additional taxa from the current examination of that flora, has resulted in the first-known occurrences of many extant diatom genera. In total, the Florissant Formation contains the most diverse (genus-rich) early freshwater diatom flora on record, which suggests a second pulse in freshwater diatom radiation during pre-Neogene time that contributed to the rich taxonomic diversity of today.

An overview of the pre-Neogene non-marine diatom biochronology from published records and from recent original work is presented. Central to this contribution are two geologic range charts that synthesize these data. With utilization of the geologic range charts, the pre-Neogene non-marine (fresh and brackish water) diatom floras from the 9 published localities, supplemented by the latest findings from the Florissant Formation and other Eocene sites, are easily compared in composition and taxon-richness at the genus level and higher. Cumulatively, the Florissant fossil diatom investigations yield a total of 33 freshwater diatom genera. This number exceeds by 20 genera all other known non-marine diatom-bearing Eocene and older deposits. The Florissant diatom flora consists of taxa with decidedly modern affinities, has superior diversity (taxon-richness), and yields the first-reported occurrence in the geologic record of 14 freshwater genera.

From the 9 featured pre-Neogene (>23.8 Ma) sites, genera of centric, araphid, biraphid, and monoraphid morphologic groups are represented. Although the first occurrences in these deposits must be treated as apparent first occurrences due to the innate incompleteness of the fossil record, such occurrences confirm that species of many of the modern non-marine diatom genera had evolved prior to the end of the Eocene (33.7 Ma).

It is anticipated that this synthesis of the pre-Neogene non-marine diatom floras will provide to the greater research community necessary paleontological data for interpreting the true geologic ranges of several diatom lineages. Perhaps such data will generate insights to diatom phylogenetics that may lead to a greater understanding of their evolutionary histories. Further research could potentially relate changes in diatom forms to global events that include climate shifts.

INTRODUCTION

Organization

Central to this study on the early biochronology of non-marine diatoms are two geologic range chart illustrations that synthesize the generic lists of diatom occurrences from the 9 published pre-Neogene localities throughout the world. The discussion presents the rationale for the study, a review of the diatom fossil record, a paleoclimate context for trends in diatom diversity, major taphonomic processes that influence completeness of record, and the potential future use of fossil data in diatom phylogenetic research. This section is followed by a detailed review of the published pre-Neogene non-marine diatom floras that includes the locality descriptions, age, nature of each deposit, methods, and taphonomic constraints affecting the quality of the samples for each locality. The age data provided in the original descriptions of each site are re-evaluated in the context of revisions to Cenozoic epoch boundaries and updated radiometric age assignments. The significance of these findings to our understanding of early non-marine diatom biochronology is summarized.

The Impetus for this Investigation

The course of late Mesozoic through Cenozoic radiation, evolution, and extinction of non-marine diatom lineages is not well-established due in great measure to the sparseness of the geologic record. The late Eocene Florissant freshwater diatoms presently under investigation in central Colorado, along with early and middle Eocene freshwater floras from additional sites in North America, are greatly advancing our knowledge of early Cenozoic non-marine diatom taxa and potentially will foster interpretations of the evolution and extinction of species in the context of global events.

In support of an apparent response by diatom floras to large-scale processes is the coincident timing of observed increases in marine diatom species (Spencer-Cervato, 1999); species turnover (Barron and Baldaulf, 1995), and variability in size range of frustules (Finkel et al., 2005) with global climate change (Miller et al., 2009). Similarly, freshwater diatom diversity shows parallels in timing with increases in marine diatom diversity observed for the Neogene floras (Krebs, 1994). This study suggests paracontemporaneity of increases in the number of non-marine genera during the Paleogene with the rise in marine diatom species diversity that initiated in early and middle Eocene and built through late Miocene (Spencer-Cervato, 1999).

Global processes, such as climate change, that impacted nutrient availability in marine settings (Finkel et al., 2005), could have had a collateral effect on aquatic continental settings.

The geologic range chart is a graphic synthesis in which first-occurring freshwater diatom taxa from the late Eocene Florissant Formation are shown within the context of the known record of pre-Neogene freshwater diatoms. It is a goal of this study, that these data, shown within a geochronologic framework, will promote greater discussion about the potential interplay between the course of freshwater diatom evolution and coincident global events.

THE STATE OF THE ART OF DIATOM BIOCHRONOLOGY

The Geologic Significance of Diatoms

Diatoms are microscopic, single-celled, photosynthesizing, golden-brown algae that live in marine, brackish, and freshwater systems. They also inhabit soils and live on a variety of substrates that are exposed to light and moisture or moist air. Modern diatoms are abundant and widely distributed within an array of aquatic habitats throughout the world and show great sensitivity to ecological variation (Barron, 1997). On the whole, diatoms are key agents of global biotic productivity that fluctuates in response to global climate change (Scherer et al., 2007; Barron and Baldauf, 1995). Diatoms form bipartite, siliceous cell walls (frustules) that may be preserved in sediments for millions of years. They are useful in biostratigraphic, paleoenvironmental, and evolutionary research due to their rapid rate of evolution, complex morphology, and wide global distribution (Harwood and Nikolaev, 1995; Bradbury, 1999).

Diatom Biochronology

The siliceous exoskeletons of marine diatoms have been found as fossils in rocks as old as early Jurassic (~190 Ma) (Rothpletz, 1896; 1900); yet, the earliest documented freshwater diatoms are from deposits only as old as early Cretaceous (~140 Ma) (Harwood and Nikolaev, 1995; Harwood et al., 2007).

The marine diatom record for the last 110 million years is well-established due to deepsea drilling and is utilized in studies of evolution, paleobiogeography, and paleoceanography (Yanagisawa and Akiba, 1990; Yanagisawa, 1996). Although the geologic record provides no direct evidence to show that marine diatoms existed before early Jurassic, estimates based on the rate of evolution of ribosomal genes suggest that diatoms originated near the Permian-Triassic boundary (~240 Ma) (Kooistra et al., 2003). The combination of fossil morphological data with molecular genetic sequencing data suggests a more conservative age estimate of between late Triassic (~221 Ma) and early Jurassic (~190 Ma) for the earliest diatoms (Julius, 2007). More recent molecular results from Brown and Sorhannus (2010) indicate that the diatom lineage evolved sometime near the Devonian-Carboniferous boundary (~354 Ma). When comparing the fossil record with genetic data, it must be kept in mind that genetic speciation will have occurred before sufficient morphological differences are recognized that would distinguish separate lineages (Philippe et al., 1994). Also, much of the early history of marine diatoms may have been lost to the dissolution of silica in seawater or by the absence of a biomineralized structure (hard cell wall) in the early forms (Harwood, 1999). Regardless of the uncertainties surrounding the timing of diatom origins, the fossil record provides evidence that marine diatoms began to radiate by the early Cretaceous (~140 Ma) (Harwood and Nikolaev, 1995; Harwood et al., 2004). Primarily on the basis of marine diatoms, it has been estimated that, during Cretaceous through Paleogene time, diatom genera were evolving at the rapid rate of 1.63 genera/m.y., with an extinction rate of 1.29 genera/m.y. (Strelnikova, 1990). This rate increased during Neogene time with a new genus evolving every 100,000 to 300,000 years (Barron and Baldauf, 1995). A study by Theriot et al. (2006) in Quaternary lake deposits demonstrates that new diatom species could have evolved in as little as 4,000 years. Such a rapid rate of evolution of species would provide markers for tracing these changes in ancient continental deposits.

In contrast to the rich marine diatom fossil record, non-marine diatoms from geologic deposits older than Neogene are relatively rare throughout the world, generally occurring sparsely in South Korea, Mexico, India, Canada, and the western United States. In general, the pre-Neogene sites that are described in the literature contain relatively few taxa, with assemblages ranging from 3 to 12 genera. It is uncertain as to whether this paucity of fossil non-marine diatoms in pre-Neogene deposits is a result of limitations on silica frustule preservation in original depositional settings, the diagenetic remineralization of opaline frustules into amorphous non-skeletal biogenic silica or into opal-CT or quartz in older continental sediments, or the lack of preservation of representative diatom-bearing geologic units. However, on the basis of the molecular data of the diatom lineage, it is not likely that such a delay in the appearance of fossil forms was due to the actual timing of the evolution of frustule-bearing freshwater diatoms. In the early pre-Neogene, there are few unambiguously non-marine diatom-bearing Cretaceous or subsequent Paleogene sites on record. Published reports of localities from the Paleogene-Neogene boundary and younger describe more taxon-rich floras. Paleocene records are not

known; however, the Eocene epoch is proving to be a time of transition in which diversity in taxa underwent major increases.

Factors that Influence the Continental Diatom Fossil Record

Broad influences of climate and tectonic stability produce the environmental settings that are optimal for continental diatoms to flourish and evolve (Bradbury, 1999). Secondly, environmental conditions in the post-mortem setting will determine the preservation of the diatom frustules (Stoermer and Smol, 1999).

Diatom Diversity in the Context of Global Climate Change

Although caution must be used when drawing parallels between the timing of diversity events of non-marine diatoms and those of marine diatoms, it is interesting to note that the nonmarine record assembled in this study shows major increases in the number of genera at times broadly coincident with peaks in the diversity of marine diatoms. Two such increases in nonmarine diatom diversity correspond with the marine diversity peaks that occurred in middle Eocene (50-45 Ma) (Sims et al., 2006) and late Eocene to early Oligocene (38-22 Ma) (Strelnikova, 1990). These increases in marine diatom diversity are turnover events that are associated with global cooling (Barron and Baldauf, 1995; Scherer et al., 2007).

It has been proposed by Scherer et al. (2007) and Barron and Baldauf (1995) that times of rapid evolutionary turnover in marine diatom species coincide with periods of major rapid cooling at high latitudes or major reorganization of ocean surface-water circulation due to changes in continental positions. A proposed explanation for this rapid turnover is that cold ocean waters suppress competition from calcareous plankton such as coccolithophorids (Scherer et al., 2007), enabling marine diatoms to flourish. The high rate of extinction and rise of new species of marine diatoms was accompanied by a greater provincialism in the high latitude marine diatom assemblages (Barron, 1997).

On a smaller scale than that of the marine turnover trends, continental (non-marine) diatom species evolution and extinction during the Neogene are linked to variability in climate (Starratt, 2007) and tectonically dynamic settings that promote geologic stability of lake basins in which endemic forms evolve (Bradbury, 1999). An example from Neogene deposits demonstrates speciation in the freshwater diatom assemblages at Tule Lake, California, that track gradual cooling and drying trends across the Pliocene-Pleistocene boundary (Bradbury, 1991; 1992). Similarly, examples of the impact of warming trends on freshwater diatom speciation are also known. A late Quaternary example suggestive of climatic influence on freshwater diatom evolution is provided by the morphological shift of *Stephanodiscus niagarae* Ehrenberg to an endemic species *S. yellowstonensis* Theriot and Stoermer in Yellowstone Lake, Wyoming, over the period from 13.7 to 10.0 Ka that corresponds with a shift to a warmer climate (Theriot et al., 2006).

The middle and late Eocene continental deposits that yield the bulk of the freshwater diatom fossil data are partial records of the initial 25 million year period of gradual global cooling from warm, tropical climates of the early Eocene thermal maximum "hot-house" conditions to the "ice-house" conditions that brought about polar ice sheets in Oligocene and Miocene time and eventually resulted in our modern global climate (Zachos et al, 2001; Miller et al., 1987). The ~50 Ma middle Eocene freshwater deposits of Canada were not only contemporaneous with a time of marine diatom turn-over, as shown by Barron and Baldauf (1989; 1995), but also exhibit an increased number of freshwater taxa over those recorded from the late Cretaceous. Furthermore, the 34 Ma late Eocene Florissant freshwater deposits of this study correspond with an interval within a global relative cooling peak that endured for approximately 2.5 million years at the end of the Eocene and the beginning of the Oligocene epoch (Zachos et al, 2001; Miller et al., 1987). This Eocene-Oligocene cooling peak not only corresponds with a diversity explosion in the marine realm, as described by Barron and Baldauf (1989; 1995), but the contemporaneous Florissant Formation doubles the number of new freshwater diatom genera relative to the early and middle Eocene tally. The Florissant diatom flora contains the terminal record of the freshwater forms that evolved during the most extreme cooling period that followed the early Eocene thermal maximum. The Florissant flora, therefore, populates a unique position along the pathway of major phylogenetic advances that drove the freshwater diatom species expansion that was to follow in the Neogene.

One might consider that aspects of the Eocene continental setting might have provided optimal conditions that allowed for the expansion of freshwater diatom species in North America. Perhaps the development of isolated interior lakes in western North America as a result of late Cretaceous-early Tertiary Laramide and post-Laramide orogenic activity that continued in the Rocky Mountains until earliest Oligocene (Tweto, 1975), the contribution of volcanic silica and limiting nutrients, and the accompanying gradual global cooling provided the conditions conducive to rapid diatom speciation that resulted in species provincialism in the Florissant and other Eocene lake systems. Repeated periods of geologically- or biologicallydriven dispersal of these presumed endemics into new niches as climates cooled may have promoted further speciation.

<u>Taphonomy</u>

As the fossil record is the key component used to assemble a framework for the diatom biochronology in this discussion, investigators must be mindful of the imperfect nature of the fossil record of continental diatoms, and acknowledge the taphonomic processes that impact the type and quality of preservation that, when favorable, result in the occurrence of fossil sites. The completeness of the geologic record of non-marine diatoms is, therefore, not only dependent upon the timing of continental diatom evolution and the preservation of diatom-bearing sedimentary deposits, but it also requires optimal conditions for the preservation of the silica that is the principal component of the cell wall (frustule) of diatoms.

The diatom frustule is sensitive to the concentration of dissolved silica, pH, and temperature of the water in both the water column of the lake and in the substrate pore-fluids after burial. The frustules, composed of hydrated silicon dioxide (opal-A), tend to be relatively stable in subaqueous environments that remain silica-rich and have a pH of <9 (Stoermer and Smol, 1999). Conversely, frustule dissolution will occur in environments that are deficient in dissolved silica and/or are highly alkaline.

Once the frustules have been incorporated into the bottom sediments, prolonged exposure to geothermal heat of >35°C in regions of high heat-flow or during burial to 500-600 meters can result in the transformation of opal-A to opal-CT (porcellanite) and eventually to quartz (chert) (Hein et al., 1978). Such mineral transformation alters the structure of the frustule (Williams et al., 1985). In extreme cases, the frustule appears only as a relict image or is completely obliterated in a groundmass of amorphous biogenic silica (Mustoe, 2005). Even when the frustule remains relatively intact, if the host sediments become silicified, the matrix cannot be disaggregated to free the frustules. A similar difficulty occurs in deposits where diatoms are encased in phosphatic coprolites. In both cases, the examination of diatoms is limited to crosssectional views in petrographic thin section and to scanning electron microscopy.

Another low-grade diagenetic process that renders the diatom-bearing host-rock shales of volcanic terranes resistant to disaggregation is the redistribution of both the biotic amorphous diatom silica and the abiotic amorphous silica derived from the alteration of volcanic ash to smectite clays. This process is one of adsorption of the dissolved silica by the clays in high-silica waters (Williams et al., 1985). The adsorbed silica is better-ordered opal-CT and acts to bind the clay grains, locking the diatoms into the matrix. Freshwater fossil diatoms encased in limestone; however, have an advantage of being capable of release from the matrix by dissolving the host-rock in dilute hydrochloric acid (Lohman and Andrews, 1968).

As detailed taxonomic analysis is required to provide useful data on fossil diatoms, the deposits that have undergone the least amount of alteration will yield the most reliable data. The pre-Neogene floras described here are variously limited by the factors outlined above. For each flora surveyed in this study, the taphonomic conditions of the sample material are noted, and wherever provided by the original author, the sample preparation method is included.

Diatom Paleontology and Phylogenetic Research

As well as the on-going debate among diatomists over unresolved questions of the timing and controls of diatom evolution, there remains uncertainty as to the genetic relationships among many diatom clades (Sims et al., 2006; Julius, 2007; Harwood et al., 2007). Although marine diatom records pre-date those of continental diatoms, there is controversy over whether diatoms that inhabit brackish water and freshwater environments evolved from marine taxa as the rising seas invaded land masses over geologic time, or whether fresh or brackish water forms gave rise to marine taxa. Many researchers believe that these concepts are not mutually exclusive and find evidence supportive of both potential scenarios.

Most of our understanding of diatom biochronology in "deep time" is based upon the marine fossil record, which is extensive for late Mesozoic and Cenozoic eras. Modern diatom taxonomic and ecologic studies greatly contribute to the growing knowledge of fossil diatom systematics and paleoecology. Morphologic data are coupled with molecular sequencing data to develop hypotheses about relationships among lineages (phylogenetics). This research leads to the development of hypotheses about evolution (Julius, 2007). Approximately 24,098 diatom species are currently described (Julius, 2007), and new modern taxa are continually being added. Diatom systematics is a work-in-progress, with a pressing need for revisions that incorporate genetic data for many modern taxa.

While in pursuit of an accurate perspective on early (pre-Neogene) biochronology of nonmarine diatoms, investigators must balance the ever-changing trends in the systematics of modern taxa with the depauperate nature of the fossil record. Despite the difficulty of obtaining paleontological data on pre-Neogene continental deposits, continued progress in this direction is necessary to provide morphological data on fossil taxa within a temporal context in order to strengthen phylogenetic interpretations.

Geologic Framework for Diatom Biochronology

Any chronologic record is built upon a time-frame. The accuracy of that time-frame and the consistency with which it is used in the literature impact the reliability of the interpretations made from such an assembly of data. Therefore, it is imperative that accuracy and consistency in reference to periods of geologic time be attempted in any discussion of biochronology at the geologic scale. Standardized Cenozoic epochs and epoch subdivisions have undergone revision in the literature over time, as additional fossil discoveries and refinements in radiometric dating of volcanic materials and in magnetostratigraphy occurred. Much of the early paleontological fieldwork in western North America was done by vertebrate researchers who developed and used a system of biochronology referred to as the North American Land Mammal Ages (NALMA) (Wood et al., 1941). Many field descriptions show age assignments to this system, which was revised by Woodburne (1987) and later by Prothero (1995). This system continues to be relevant when used in concert with radiometric ages as presented for the North American western interior in Smith et al. (2008). For these reasons, it is important when reviewing fossil literature published several decades ago to determine the currency of the age data.

For the sake of accuracy and consistency, the references to Cenozoic epochs and their subdivisions in this literature review are qualified as to their most reliable age assignments. The Cenozoic epoch boundaries and subdivisions by Berggren et al. (1995) were adopted as the standard reference for the "1998 Geologic Time Scale" by the Geological Society of America. The epoch boundary delineations of Berggren et al. (1995) are applied to the units discussed in this review: Eocene epoch (54.8-33.7 Ma); with the principal subdivisions as follows: early Eocene (=Ypresian stage) (54.8-49.0 Ma), early middle Eocene (=Lutetian stage) (49.0-41.3 Ma), late middle Eocene (=Bartonian stage) (41.3-37.0 Ma), and late Eocene (=Priabonian stage)

(37.0-33.7 Ma). Although the NALMAs show a slight overlap at the upper and lower epoch boundaries, the Eocene NALM ages follow from oldest to youngest in this order: Wasatchian (upper 4 biozones) and Bridgerian (lower biozone = Br-1) in early Eocene; Bridgerian (upper 2 biozones = Br-2 and Br-3), Uintan (all biozones), and Duchesnean (all biozones) in middle Eocene; and Chadronian (all biozones but top of uppermost) in late Eocene (Prothero, 1995).

PRE-NEOGENE NON-MARINE DIATOM FLORAS

Geologic and Taxonomic Record of Pre-Neogene Non-marine Diatom Floras

The following is a brief account of the published reports and unpublished new findings of fossil non-marine diatoms from known pre-Neogene deposits. The documented pre-Neogene non-marine diatom sites are in South Korea, India, Mexico, Canada, and the United States. Data from the published records for some of the North American localities were supplemented upon examination of slides reposited in the California Academy of Sciences in San Francisco. The published data are further augmented by the results of a new study of the fossil diatoms from the Clare's Quarry site in the late Eocene Florissant Formation of Colorado (Benson and Kociolek, in review). The summaries presented here include the age, location, type of matrix, method of sample preparation, list of diatom taxa, and paleoecologic interpretation, where provided by the original reference. The order of taxa listed throughout the text and Tables follow the classification of freshwater diatoms presented in Round et al. (1990). Many of the earliest deposits are profoundly altered by taphonomic or diagenetic processes that limit diatom identification of the few occurring taxa to thin section or SEM. For this reason, matrix and

method of preparation are included to emphasize the difficulty of obtaining detailed taxonomic and quantitative assemblage data from these ancient deposits.

All the featured deposits, but for those in the early Cretaceous Myogok Formation in South Korea, contain extant freshwater diatom genera and species that have strong affinities to modern species. The Korean taxa are included in the summaries for the purpose of completeness; however, because the focus of this examination is on fossil assemblages that have an affinity to modern freshwater taxa, the Korean deposit is not included in the taxonomic comparisons.

The North American fossil freshwater diatom localities discussed here are shown in Figure 1. The Deccan Traps sites in India are featured in Figure 2.



Figure 1. Locations of pre-Neogene non-marine diatom deposits in North America discussed in this review.



Figure 2. Locations of late Cretaceous non-marine diatom deposits in India.

A synthesis of the freshwater diatom genera occurring in the 8 North American sites and those cumulatively from the Deccan Traps sites in India is presented in the annotated geologic range chart in Table 1., which illustrates the currently known pre-Neogene freshwater diatom biochronology. Table 1. Annotated pre-Neogene freshwater diatom biochronology chart. This geologic range chart for late Cretaceous (columns on right) through Paleogene (mid-left columns) shows genus ranges with first record of occurrences appearing at the far right end of each colored bar. Genera with first-occurrences in the late Cretaceous are tracked with the blue bars, those in the early Eocene with pink bars, those in the middle Eocene with orange bars, those in the late Eocene with yellow bars, and those in the Oligocene with green bars. The annotations (initials) in each column show the sources of these observations, and the Key to Abbreviations gives literature citations for each.

Annotated Geologic Range Chart of Late Cretaceous through Paleogene Freshwater Diatoms - from Published Fossil Sites										
	0.00	"L Olig - E Mioc"	Oligocene	Late Eocene	Middle Eocene	Middle Eocene	Middle Eocene	Early Eocene	Late Cretaceous	Late Cretaceous
	Age		(~30 Ma)	(~34 Ma)	(>42 Ma)	(~45 Ma)	(~48 Ma)	(~52 Ma)	(>65 Ma)	(70 Ma)
		Canvon Ferry	Pittsburg Bluff	Florissant	Giraffe Pipe	Dewey	Wagon Bed	Horsefly	DeccanTraps	Huepac
	Locality	Montana	Oregon	Colorado	NWTer, Canada	Idaho	Wyoming	Brit Col., Canada	India	Son Mexico
Family	Genue	montana	oregon	00101000	innini, vanada	Mario	Wyonang	Dife.col., canada	inaia	oon, mexico
r anny	Cyclotella				AW&PS					
Stephanodiscaceae	Puncticulata				AW&PS				-	
	Discostella				AW&PS					
Melosiraceae	Melosira	VL	MK&	KL: ES			L&A	PB	1	BC&: CB&
Paraliaceae	Ellerbeckia			ES						
Aulacoseiraceae	Aulacoseira			ES; SS; MB&PK	AW&	PB; MB		PK; MB	KA&	
	Eoseira							AW&ME (ng)		
Orthoseiraceae	Orthoseira			KL; ET; MB&PK SS						
Anaulaceae	Anaulus						L&A (ns)			
Fragilariaceae	Fragilaria	VL	MK&	KL; FR&DW ES; MB&PK	AW&PS	PK	L&A (ns)			BC&; CB&
	Staurosirella	VL		ES	AW&PS					
	Staurosira	VL		MB&PK	AW&PS					
	Pseudostaurosira	VL								
	Fragilariaforma			ES	AW&PS					
	Diatoma			KL; FR&DW ES; MB&PK		PK		PB; PK; MB		
	Renadra				•	1		PN		
	Ambistria	VL		KL, FRADIV, ES, SS, WIDAPK			18A (na ne)			
Tabellariaceae	Tabellaria			KI		PK: MB		PK · MB		BC&CB&
	Tetracyclus	VI	MK&	KL · ES· SS· MB&PK		PK		PR	1	Dod, obd
	Oxyneis	VL	WINCO	112, 20, 00, MBai 10	AW&PS: PS&				-	
Eunotiaceae	Eunotia		MK&	KL: ES: SS: MB&PK	PS&AW: AW&PS	PK: MB		PB		
	Actinella				PS&AW PS&				-	
Anomoeoneidaceae	Anomoeoneis						L&A (ns)			
Cymbellaceae	Rhoicosphenia			KL						
	Cymbella	VL	MK&	KL; FR&DW						
Gomphonemataceae	Gomphonema	VL	MK&	KL; ES; SS; MB&PK						
	Gomphoneis			KL; FR&DW		PK				
	Gomphopleura		MK&							
Achnanthaceae	Achnanthes	VL		KL; FR&DW						
Cocconeidaceae	Cocconeis	VL	MK&							
A chnanthidiaceae	Acnnanthidium			ES; MP; MB&PK						
	Planothidium			ES; MP; MB&PK					RS&	
	Platessa			MD2: MD2DK						
	Diadosmis			SS: MRADK					+	
Amphinleuraceae	Frustulia			KL: MB&PK	1	PK MB		PK		
Pinnulariaceae	Pinnularia	VL	MK&	KL: ES: SS: MB&PK	AW&PS	1 10, 1010	L&A		-	
Naviculaceae	Adlafia			MB&PK						
	Navicula	VL		KL; ES; MB&PK			L&A			
Stauroneidaceae	Stauroneis	VL		ME; MB&PK			L&A			
Catenulaceae	Amphora			KL						BC&; CB&
Bacillariaceae	Nitzschia			KL; ES; MB&PK			L&A		RS&	
Rhopalodiaceae	Epithemia			ES						
	Rhopalodia			ES						
Surirellaceae	Surirella	VL								
(Uncertain)	Nupela				AW&PS PS&				<u> </u>	
Kanada Abbasadaka 🗧	 ••••••••••••••••••••••••••••••••••••	 					0K - 0-ll Kh	tale to materia at Oating 1		
Key to Abbreviations- References: VL = Van Landingham, 1970; MK& = McKnight et al., 1995; KL = Kenneth Lohman, in notes at National Museum of Natural History; GK = Gallard Markeviations, in notes at California Academy of Sciences; ES = Eugene										

Stoemer In: Meyer, 2003; SS = Sarah Spaulding, personal comm.; MB = Mary Ellen Benson, this study; PK = Pat Kociolek, this study; MB&PK = Pat

This geologic range chart illustrates the timing of first-occurrences of reported freshwater taxa that have modern affinities for the period prior to Neogene. A comparison of the assemblages from the nine featured localities shows the 7 earliest-occurring and longest-ranging freshwater diatom genera from the late Cretaceous (shown in blue bars), an increase of 6 genera in the early Eocene (shown in pink bars), a surge of 16 additional genera in middle Eocene (shown in orange bars), and the subsequent increase of 14 genera at the late Eocene Florissant site (shown in yellow bars). The two sites chosen to represent the Oligocene add 4 more genera (shown in green); however, this number understates the diversity that follows in late Oligocene and Miocene deposits, especially in western North America (Bradbury and Krebs, 1995). This chart demonstrates the importance of the Florissant site as a unique record of the taxa that had evolved by late Eocene time in the interior lakes of western North America. The following paragraphs provide an account of the information that contributed to this presentation of the early fossil freshwater diatom biochronology.

Early Cretaceous Non-marine Diatoms of South Korea

The earliest non-marine diatoms are recognized from the (140-130 Ma) early Cretaceous Myogok Formation in the Jasong synthem (Valanginian-Hauterivian) of South Korea (Chang et al., 2003; and Harwood et al., 2004; 2007). The deposit is interpreted as representing sedimentation in tectonically active intermontane grabens. The taxa include the following genera: *Calyptosporium, Cypellachaetes, Pseudopyxilla*, and *Hyalotrochus* (Harwood et al., 2007). The diatoms are relatively well-preserved resting spores and are morphologically dissimilar to the taxa observed in other non-marine deposits of pre-Neogene age. For this

reason, this site is not included in the comparison chart of Table 1. These taxa have greater affinity to the marine diatoms from early Cretaceous deposits of Antarctica (Gersonde and Harwood, 1990; Harwood and Gersonde, 1990) and Australia (Nikolaev and Harwood, 1997; Nikolaev et al., 2001) than to other known pre-Neogene freshwater diatom floras (Harwood et al., 2007).

Late Cretaceous Non-marine Diatoms of Mexico

The next earliest flora is the (70 Ma) late Cretaceous non-marine diatoms from the Tarahumara Formation, near Huepac, Sonora, in northern Mexico (Chacon-Baca et al., 2002; and Beraldi-Campesi et al., 2004). According to the authors, these diatoms range in habitat from freshwater lacustrine to brackish and are preserved in carbonaceous cherts associated with stromatolites. In addition to the diatoms, there are other algal microfossils, pollen grains, plant and fungal spores, fungal filaments, crustaceans, and organs of vascular plants that are interpreted as belonging to freshwater systems (Beraldi-Campesi et al., 2004). Only basic shapes of frustules and filamentous colonies are seen in the prepared petrographic thin-sections. The forms described from these beds are observed to have affinities for the following four extant genera: *Melosira*, *Fragilaria*, *Tabellaria*, and *Amphora* (Chacon-Baca et al., 2002; and Beraldi-Campesi et al., 2004). Of these four genera, only *Tabellaria* is an exclusively freshwater form (Round and Sims, 1981).

Late Cretaceous Freshwater Diatoms of India

The next earliest confirmed freshwater diatoms are reported from three sites within the late Cretaceous (>65 Ma) Deccan intertrappean beds (Maastrichtian) of India. The Mohgaon-Kalan fossil locality is located 0.5 km west of the village (22° 1'N; 79° 11'E), in the Chhindwara District of Madhya Pradesh (Ambwani et al., 2003). The material is described by the author as buff-colored diatomaceous chert collected from an excavated water well from a section composed primarily of red and green silty clays, sandstones, marls, laminated clays and shales with marls and limestones in thin fossiliferous sedimentary beds between basaltic flows that dammed drainages to form lakes. Also reported are pollen, palynomorphs, egg shells of dinosaurian and avian affinities, and freshwater pelecypods. Because of the resistive nature of the chert matrix, the method of examination of the diatoms was via petrographic thin sections and SEM imaging methods. *Aulacoseira* sp. was the only diatom taxon identified (Ambwani et al., 2003).

A second locality is in the Lameta Formation (slightly older Maastrichtian), 13 km northeast of Warora, Pisdura, Chandrapur District, Maharashtra (Ambwani et al., 2003). The sample material in which the diatoms were found was poorly phosphatized dinosaurian coprolites; therefore, petrographic thin sections and SEM imaging were used to examine the single taxon of *Aulacoseira* sp. (Ambwani et al., 2003).

A third study was conducted on the Deccan lacustrine intertrappean sediments near the village of Naskal, Andhra Pradesh, India (Singh et al., 2007). Diatoms were recovered from within the rhizopod (*Thecamoeba*) cysts at Lucknow and examined by Eugene Stoermer (one of the authors of the referenced article). The diatom-bearing cysts occur in carbonaceous shale, along with unidentifiable leaf remains and other microfossils. Preparation methods included

crushing the sample to ~5mm pieces, treatment with dilute nitric acid, heating, and rinsing to oxidize and remove all soluble organic matter. This was followed by mixing the residue with polyvinyl alcohol, spreading onto cover slips, drying, and mounting onto slides with Canada balsam. Of the diatoms observed, all were pennate forms encased in the cysts, so detailed aspects of their morphology were poorly visible. Only the following two taxa were identifiable to genus: *Nitzschia* and *Planothidium* (Singh et al., 2007).

Early Eocene Freshwater Diatoms of British Columbia, Canada

The richly fossiliferous early Eocene (~52 Ma) lake deposits of Horsefly, British Columbia, Canada, have yielded freshwater diatoms (Wolfe and Edlund, 2005). Although reported as early middle Eocene by the original authors, Wolfe and Edlund (2005) give a numerical age range of 44-52 Ma for the Horsefly lake beds, indicating that it crosses the boundary from early Eocene-middle Eocene (Berggren et al., 1995). This age range is based upon the following: palynological evidence (Rouse et al., 1971), paleoichthyological data (Wilson, 1977), and paleomagnetic (Symons and Wellings, 1989) correlations to radiometrically dated sequences (Hills and Baadsgaard, 1967). Although the Horsefly deposit, itself, has not been radiometrically dated, more recent studies of stratigraphically correlative fossil fish and plant deposits place the age between ~50.5-52.0 Ma (Barton and Wilson, 2005). One such site is Quilchena in which sanidine from tephras from within the fossil beds have been dated at an 40 Ar/³⁹Ar age of 51.5 ± 0.4 Ma (Villeneuve and Mathewes, 2005). Although the exact timing of the appearance of the diatoms studied in the Horsefly samples cannot be determined from this information, the maximum age assignment of 52 Ma (early Eocene) is used for the Horsefly deposit in this study.

Two sites are described as the lower varved section exposed immediately upstream from Hobson's Horsefly Mine in the H2 sequence of Wilson and Barton (1996) and a correlative exposure 15 km to the SE (Black Creek Road fossil locality) (Wolfe and Edlund, 2005). The field descriptions state that samples were taken from a 33.5 cm thick section of 767 varved couplets of white (summer) diatomaceous laminae separated by dark (winter) pyrite-rich clays interbedded with 31 discrete beds of tuff or ash-rich graded turbidites. Preservation and abundance are described as "remarkable for material of this age." The authors report that wellpreserved centric diatoms were present in 20% of the white laminae; and primarily highly fragmented araphid pennate diatoms (Fragilariaceae), constituting a diatom hash, were observed in 80% of the white laminae. Almost all centric and pennate diatoms were said to be fractured due to compaction or microtectonics, and extraction of intact specimens from the sediment matrix was only rarely achieved (Wolfe and Edlund, 2005). Diatom identifications were made via petrographic thin sections after the sample material was stabilized with epoxy, and by SEM imaging of broken surfaces. A new species of a new genus was described: *Eoseira wilsonii* Wolfe & Edlund n. gen., n. sp. E. wilsonii is viewed as an ancient form within the centric family Aulacoseiraceae to which the genus Aulacoseira belongs. Eoseira is not known from any other fossil locality and is one of the few described freshwater diatom genera that is now extinct (Wolfe and Edlund, 2005).

J.P. Bradbury's USGS Locality Record of the Horsefly deposit (reposited at California Academy of Sciences) includes a handwritten note indicating the presence of the following
genera: "Diatoma hiemale, Melosira?, Tetracyclus lacustris, and Eunotia?" along with Chrysophyte cysts.

For this study, examinations were made in 2007 of one of Bradbury's prepared biological slides [#16VI81-3(3)] of Horsefly material that was collected by M.V.H. Wilson (06-16-81) and reposited at the California Academy of Sciences. The slide in the CAS database is identified as Accession #701462, Slide #1021059. The following 5 genera were recognized: *Aulacoseira*, *Frustulia*, *Meridion*, *Diatoma*, and *Tabellaria*. This brings the total to-date genera observed from Horsefly to 8. Refer to Plate 1. (Figure 7) for an image of *Diatoma* sp. from this study.

Middle Eocene Freshwater Diatoms of Wyoming

A diverse freshwater diatom flora was recovered from the middle Eocene (~48 Ma) (Smith et al., 2008) Wagon Bed Formation, Beaver Divide, Fremont County, Wyoming, by Lohman and Andrews (1968). The diatom locality is referred to as the "Beaver Divide escarpment" (SE1/4 SE1/4 sec 24, T 32N, R 95 W) (USGS diatom loc. 5416, same as USGS Cenozoic loc. 20031). The diatom-bearing material was in reworked slump blocks of cherty limestone of the Eocene Wagon Bed Formation that were incorporated into the Beaver Divide Conglomerate Member of the Oligocene White River Formation. Diatoms were found entombed in the limestone-filled interiors of calcareous freshwater mollusks that had escaped silicification, resulting in their relatively higher quality of preservation than diatoms in the original source formation (W1/2 SE1/4 SE1/4 sec 5, T 32N, R 84 W) (USGS diatom loc. 5422) (Lohman and Andrews, 1968). Both the diatom flora and the host gastropod limestone found at the studied site were interpreted by Lohman and Andrews (1968) to be of the Wagon Bed Formation because, although completely replaced by silica at other localities, the same diatom flora and the same fauna in the gastropod-bearing limestone are known within the Wagon Bed Formation elsewhere, and neither has been found anywhere in the Oligocene White River Formation.

A discrepancy regarding the age of the Wagon Bed Formation is perpetuated in the modern literature by the fact that the Lohman and Andrews (1968) published account reports that the formation was of "late Eocene" age despite the fact that these original authors also state that the source material for the diatoms was of "Uintan" NALM age, which is of middle Eocene age (Prothero, 1995). The middle Eocene age for the Wagon Bed Formation is further supported by revisions to the Eocene-Oligocene stratigraphy in the Beaver Divide area (Emry, 1974) that demonstrate a substantial hiatus represented by an erosional unconformity between the Wagon Bed units and the overlying Oligocene White River Formation. Further evidence that places the age of the Wagon Bed Formation located on the southern rim of the Wind River basin well within the middle Eocene are K/Ar ages ranging from 45.5-46.0 Ma from the upper volcaniclastic facies (Pekarek et al., 1974) and an 40 Ar/ 39 Ar age of 47.7 ± 0.12 Ma from sanidine in the white lignitic tuff within the fluvial-lacustrine facies (Smith et al., 2008) that is likely to be the facies that contained the diatom-bearing gastropod limestone. It is for these reasons that this study accepts the age of 48 Ma for the Wagon Bed diatoms, which places them in the early middle Eocene.

The diatoms in the Wagon Bed Formation examined by Lohman and Andrews (1968) were recovered following dissolution of the limestone. As many as 9 freshwater diatom genera were identified. Of these, *Ambistria* was named as a new genus. The remaining 8 genera observed from this material are these: *Melosira*, *Anaulus*, *Fragilaria*, *Navicula*, *Anomoeoneis*,

Pinnularia, Stauroneis, and *Nitzschia*. Twenty-seven new species were described. Seven other species identified were only known from younger Cenozoic deposits. The genus *Anaulus* is present in marine deposits of the late Cretaceous (Campanian) of western Siberia (Strelnikova, 1975). *Melosira* is identified in late Cretaceous (Campanian) of western Siberia (Strelnikova, 1975), but also from fresh-to-brackish water habitats of the late Cretaceous (Maastrichtian) in Mexico (Chacon-Baca et al., 2002; Bernaldi-Campesi et al., 2004).

Middle Eocene Freshwater Diatoms of Idaho

Fossil freshwater diatoms have been recovered from the middle Eocene (~45 Ma) lake deposits of the Dewey beds, Challis volcanics, Valley County, Idaho (Axelrod, 1998). These beds also contain a rich macrobotanical forest flora referred to as the Thunder Mountain flora that is described as middle Eocene by Axelrod (1998). The informally named Dewey beds are volcaniclastic sedimentary rocks that were deposited in the Thunder Mountain caldera following cessation of the eruptive phases. The age of the lake beds is confined to the period between 46.3 Ma, which is the age of the underlying Sunnyside Rhyolite, and 43 Ma, which is the age of the unconformably overlying Lookout Mountain Latite (Leonard and Marvin, 1984; and Adams, 1985). For this review, the age of the Dewey bed diatoms is considered to be approximately 45 Ma.

The locality is near the Dewey Mine, in the Rainbow Peak USGS 7 ¹/₂ minute quadrangle, in the Thunder Mountain mining district (unpublished notes of J.P. Bradbury, USGS, reposited at the California Academy of Sciences). The CAS database description states that the samples were collected by B.F. Leonard in 1986, from "a roadcut at 7,680 feet elevation, 0.3 miles northeast of the mine, 0.3 miles upgrade from a cookhouse and 0.1 miles east-southeast of a spring." As described by Axelrod (1998), the shales are diatomaceous and contain fine-grained bentonitic layers that have expanded and broken the strata into small (3-7 cm long) blocks and chips. The diatomaceous lake beds are 3-4 m thick. They are associated with paleomacroflora of *Equisetum* and *Typha*, along with fine sediments and lignite suggestive of a lake shore setting (Axelrod, 1998). According to J.P. Bradbury, USGS (as noted in Axelrod, 1998), this material contains only a single diatom species identified as *Aulacoseira* cf. *A. hibschii*.

For this study, examinations were conducted in 2007 on 2 prepared biological slides from the Dewey beds material reposited at the California Academy of Sciences. The slide identified in the CAS database as Accession #702135, Slide #1028080 contained unknown centrics including the genus *Aulacoseira*. A second slide identified as CAS Accession #702136, Slide #1028081 contained unknown centrics and the following 8 genera: *Aulacoseira, Eunotia, Frustulia, Tabellaria, Diatoma, Tetracyclus*, possibly *Fragilaria*, and possibly *Gomphoneis*. Refer to Plate 1. (Figures 3 through 6) for images of specimens of some of the genera observed in this study.

Middle Eocene Freshwater Diatoms of Northwest Territories, Canada

Fossil freshwater diatoms occur in the middle Eocene (>42 Ma) lake beds that overlie the (~48 Ma) Giraffe Pipe kimberlitic diatreme, Slave Province, Northwest Territories, Canada (Wolfe et al., 2006; Siver and Wolfe, 2007; Wolfe and Siver, 2009; and Siver et al., 2010). The locality is described as being in the Lac de Gras kimberlite region, ~300 km northeast of Yellowknife, NWT; 64° 44' N, 109° 45' W. The Giraffe Pipe is one of several kimberlites

within the Ekati Mine property that are assigned a Rb-Sr phlogopite model age of 47.8 ±1.4 Ma, indicating emplacement in early middle Eocene (Creaser, et al., 2004). As detailed by the referenced diatom investigators above, the diatoms were obtained from samples collected from a 47° angled drill core that penetrated a ~120 m (thickness corrected) portion of the crater-fill sediments before laterally intersecting Proterozoic granodiorite external to the crater wall. From top to base, the core (thickness corrected) contained ~37 m of Quaternary glacial till, 33 m of terrestrial woody peat, two air-fall tephra beds (that provide the upper-limit age for the lake sediments), 51 m of stratified lake shale and mudstone, and ~5 m of granodiorite before reaching total depth. This evidence indicates that, following the eruptive stages of the kimberlite intrusion, the depression filled with meteoric water to form a small closed-basin lake with an estimated diameter of 250-400 m, which filled with fine lake sediments to later become topped by terrestrial sediments (Wolfe and Siver, 2009), and was eventually eroded and covered with Quaternary glacial material. The lake shales and mudstones are described as both massive and fissile, splitting along bedding planes; and are either laminated or mottled with nodular opal-A (Wolfe and Siver, 2009).

Although the anticipated Giraffe kimberlite was not encountered during this core drilling endeavor, and the total thickness of the crater-fill sediments was not reached; age constraints on the diatoms from the lake sediment core are provided by the overlying air-fall tephra beds with fission track dates (39 to 42 Ma) that average ~40 Ma (Wolfe and Siver, 2009) and by collateral palynological evidence that shows the post-eruptive crater-fill from the core to be of middle Eocene age (Hamblin et al., 2003). For these reasons, the age of these diatoms for this review is conservatively placed at >42 Ma to correspond with the age of the oldest overlying tephra.

From the Wolfe et al. (2006) study, centric diatom soft-parts (chloroplast remnants, organelles), as well as intact frustules, were seen. Associated microfossils are said to include colonial chlorophytes and scaled chrysophytes. The single genus described in this study is *Aulacoseira* with affinities to the extant *A. alpigena* and *A. lirata* (Wolfe et al., 2006). The authors discuss their method of sample preparation for viewing diatom cells in the matrix with light microscopy by embedding with resin and grinding to thin sections ~ 30 μ m thick. These were examined at 1000 x under oil immersion using differential interference contrast optics. Additionally, fresh fractures perpendicular to the bedding plane were examined with a field emission scanning electron microscope (FEI SEM). Transmission electron microscopy (TEM) was also employed: small sediment granules (~5 mm³) were embedded unstained in low-viscosity resin, sectioned to ~50 nm, and examined with a field emission TEM.

Continued research on the middle Eocene Giraffe Pipe lake sediments has generated additional diatom taxa. The sample material was prepared for viewing the diatoms via both SEM and the standard light microscopy methods. The genus *Eunotia*, collected from massive organic mudstone from the terminal lake phase deposits just below the tephra-bearing contact with the peaty paludal facies, was described by Siver and Wolfe (2007). Further work on samples from a 25 m thick portion of the lake bed facies represented in the approximate middle of the core has resulted in the first-appearance of the following: three centric diatom genera of the Stephanodiscaceae family (*Cyclotella*, *Discostella*, and *Puncticulata*); four pennates of the Fragilariaceae family (*Cysneis*) (Wolfe and Siver, 2009; Siver et al., 2010). The genus *Actinella* was reported from this site (Siver and Wolfe, 2009; Siver et al., 2010). Two

additional genera (*Nupela*) (Siver et al., 2010) and (*Pinnularia*) (A.P. Wolfe and P.A. Siver, personal communication, 2010) are also observed at Giraffe Pipe. Collectively, so far, this locality has yielded a total of 13 genera, 9 of which are first-occurrences.

Late Eocene Freshwater Diatoms of Colorado

The late Eocene Florissant Formation is a world-famous fossil Lagerstätte ("motherlode") that contains extremely well-preserved paleobotanical, fossil insect, and fossil vertebrate assemblages from lacustrine and associated fluvial deposits. Three lake bed shales designated "upper," "middle," and "lower" by Evanoff et al. (2001) alternate with and are finely interbedded with mudstones, coarse volcanic tuffs, and volcanic ash. Sanidine crystals in the "upper shale" tuffs and "middle shale" cap rock provide an average ⁴⁰Ar/³⁹Ar radiometric age of 34.05 ± 0.08 Ma (McIntosh and Chapin, 2004). The Florissant Formation is isolated to a relatively small area in the vicinity of the town of Florissant in Teller County, Colorado (Figure 3).



Figure 3. Location map of Florissant, Colorado (small rectangle).

Present-day exposures of the Florissant Formation are limited to scattered roadcuts into the subsurface and slopes of hills and ridges that roughly flank the present-day creek drainages northwest and south of the town of Florissant (Figure 4). Principal fossil sites are located within the Florissant Fossil Beds National Monument to the south of Florissant on County Highway 1; however, this area is closed to private collecting, and permits must be obtained from the National Park Service for approved research only. Additional collecting by workers in the early part of the 20th Century was done in areas now outside the Monument, but most of these are closed to the public. The only publicly accessible collecting locality is the privately-owned commercial Florissant Fossil Quarry (referred to in this study as Clare's Quarry) at which a fee is charged for restricted collecting. Clare's Quarry is located just south of the town of Florissant and west of County Highway 1 (Figure 4).



Figure 4. Location map of Florissant study area showing the outline of the Florissant Fossil Beds National Monument, the Clare's Quarry fossil site (black triangle), and the "Petrified Forest" fossil locality. Three additional fossil sites are MacGinitie-3 (MG3, black diamond), Princeton 1880 (PRN, black bull's-eye), and US 24 roadcut (RDC, white bull's-eye). The two unmarked roads that extend eastward from County Highway 1 are Upper Twin Rocks Road (north) and Lower Twin Rocks Road (south).

Fossil diatoms have been noted in the lake sediments of the Florissant Formation from early records (MacGinitie, 1953; Lohman, 1960; McLeroy and Anderson, 1966; Lohman and Andrews, 1968) and later studies (O'Brien et al., 2002; 2008); yet, no one prior to the current investigators has published taxonomic descriptions and images that document the composition of these diatom assemblages. The following accounts demonstrate both the early interest in the diatoms at Florissant and the more recent effort to characterize the diatom flora.

Many localities within the Florissant Formation have been examined for diatoms. Sample voucher material collected by early investigators, diatom slides, and descriptions of stratigraphic sections from the Florissant Formation are reposited at the National Museum of Natural History (the Smithsonian Institute) (NMNH) in Washington, D.C. and at the California Academy of Sciences (CAS) in San Francisco.

The earliest published taxonomic reference to Florissant fossil diatoms is a brief statement characterizing the assemblage as highly diverse (Lohman, 1960). Subsequently, Lohman reported that a minimum of 30 diatom species were recognized from the Florissant Formation (Lohman and Andrews, 1968), but no taxonomic lists or descriptions were published by Lohman. No records of Florissant diatom taxa were found in Lohman's career files that are archived at the U.S. Geological Survey in Denver. In 2010-11, however, an exhaustive search by Ms. Linda Hollenberg, Museum Specialist/Assistant Collections Manager in the Department of Botany at the National Museum of Natural History, recovered Lohman's hand-written taxonomic lists of diatoms observed in slides from 3 sites in the Florissant Formation from 1940, 1957, and 1965.

The recovered unpublished lists from Lohman's work on record at NMNH include the following information. Lohman examined 3 slides (#2106, 2107, and 2108) from sample 2993 collected by H.D. MacGinitie in 1937, from a locality described as "1 ¹/₂ mile southwest of town (of Florissant)," which corresponds with the general area historically referred to as the "Petrified Forest," which is approximately central within the National Monument boundary and just west of County Highway 1 (Figure 4). This area contains strata that are considered by Evanoff et al. (2001) to be the "middle shale" informal member. In these slides, Lohman identified these 18 diatom genera: Melosira, Melosira roeseana Rabenhorst (=Orthoseira according to Round et al., 1990), Fragilaria, Diatoma, Synedra, Tabellaria, Tetracyclus, Eunotia, Rhoicosphenia, Gomphonema, Gomphoneis, Achnanthes, Frustulia, Pinnularia, Caloneis (=Pinnularia according to Round et al., 1990), Navicula, possibly Amphora, and Nitzschia. The NMNH records show that Lohman also examined slide #3024 from sample 4417 that he collected in 1957 (F5-4) described as "1/4 inch thick blue black laminated fairly soft shale, 5 ft. stratigraphically below #4416," from the Princeton 1880 locality (locality #5 on MacGinitie's 1953 map) also in the "middle shale" of Evanoff et al. (2001) in which he identified the genera Tetracyclus and Melosira.

Among the voucher samples and slides in this archival collection at CAS are 2 slides (Accession #40220, Slide #345080 and Slide #345083) and material collected by H.D. MacGinitie on an uncertain date, from site number 3 that is north of the road cut on Lower Twin Rocks Road (MacGinitie, 1953) and is in the "middle shale". Records in the CAS database show that the genus *Stephanodiscus* was identified by Galina Khursevich in the two slides from the MacGinitie-3 site. Also, in the CAS archived collection, there is a sample collected by H.D. MacGinitie in 1937, from the location in the "middle shale" historically referred to as the "Petrified Forest in the vicinity of the Big Stump." Included also in the CAS archived collection is a set of 12 slides from samples collected by W.S. Burbank and K.E. Lohman in 1950, that were taken from a stratigraphic section whose location is generally consistent with the site referred to as the "Petrified Forest." A second set attributed to K.E. Lohman was collected in 1957, and contains 5 slides from samples from an uncertain locality referred to only as "Florissant lake beds" assumed to be "middle shale." One additional slide and sample collected by Lohman in 1957, was obtained from an unspecified outcrop along Lower Twin Rocks Road. Another single slide from a sample that was probably taken from a Lower Twin Rocks Road exposure was collected by C.A. McLeroy and R.Y. Anderson on an unrecorded date. As well as can be determined from the descriptions provided, these sample sites are now within the boundary of the Florissant Fossil Beds National Monument and are most likely to have been collected from the "middle shale" of Evanoff et al. (2001).

Three of the slides from the CAS archival collections referenced above were examined in the current investigation on the "middle shale." Two from Lohman's 1957 collection are these: Accession #601857, Slide #375003; and Accession #601858, Slide #375005. The third CAS slide is from the MacGinitie-3 site: Accession #40220, Slide #345080. Additionally, for this study, new slides were prepared from several samples collected in 2006 and 2007 from the "middle shale" at three sites in the Florissant Fossil Beds National Monument. Two of these sites were formerly collected by Scudder within the area of the old "Petrified Forest," and the third is a re-visit to the MacGinitie-3 site north of Lower Twin Rocks Road.

The findings of this diatom assemblage assessment of the "middle shale" sites in total are as follows. The diatom genus recognized as *Stephanodiscus* was only observed in the CAS archived slide #345080 prepared by G. Hanna from material collected from the MacGinitie-3 site. It is important to note that concern has been expressed by the CAS staff regarding possible contamination of slides prepared by Hanna due to the lab procedures that were followed. Adding to the cautionary position regarding the occurrence of *Stephanodiscus* in the Florissant flora is the fact that this genus does not appear in the NMNH unpublished taxonomic lists of Lohman, it is not observed in the 2 Lohman 1957 CAS slides examined in this study, it is not found in slides from the newly sampled Petrified Forest sites, nor was it seen in slides made from the re-sampled MacGinitie-3 site. In addition to the suspicious occurrences of Stephanodiscus in the CAS Hanna slide #345080 from the MacGinitie-3 site, the following genera were identified in that slide: several species of Aulacoseira (derived from Melosira), Fragilaria, Diatoma, Synedra, Tetracyclus, Eunotia, Navicula, Gomphonema, Achnanthoid genera, Planothidium, and *Pinnularia*. These taxa, at least at the genus level, are consistent with those found in the other reports; yet, at the species level, many of those seen in this slide have not yet been documented elsewhere in the Florissant samples. From the Lohman 1957 collection, the slides identified as Accession #601857, Slide #375003 and Accession #601858, Slide #375005 contained mostly Aulacoseira; but Planothidium was also observed in Slide #375003 (shown in Plate 1., Figures 1 and 2). Many of the same genera were represented also in the slides made recently from the other "middle shale" sites of the old Petrified Forest area in this study. Overall, this examination of all the available records of previous work and from the current examination of samples from the "middle shale" sites at Florissant has produced a list of these 17 genera: Aulacoseira,

Orthoseira, Fragilaria, Diatoma, Synedra, Tabellaria, Tetracyclus, Eunotia, Rhoicosphenia, Gomphonema, Gomphoneis, Achnanthes, Frustulia, Pinnularia, Navicula, possibly Amphora, and Nitzschia. The presence of the genus Stephanodiscus has not been verified by this investigation; therefore, is not included in the current list of genera in the Florissant fossil diatom flora. Of these genera, the following 6 are reported for the first time in the geologic record: Orthoseira, Synedra, Rhoicosphenia, Cymbella, Gomphonema, and Achnanthes (Tables 1 and 2).

"Lower shale" (Evanoff et al., 2001) sites of the Florissant Formation include these two: a locality on US 24 east of the town of Florissant examined by Lohman in 1957; and the exposure at the Florissant Fossil Quarry (Clare's Quarry site), the private fossil quarry just south of the town of Florissant (Figure 4). An overview of the fossil diatom flora from the "lower shale" sites is presented, beginning with the unpublished taxonomic lists by Lohman from the NMNH records. The material examined included two samples collected by Lohman in 1957, from a locality described as the "0.4 mile east of town (of Florissant) on south side of US 24, center W¹/₂ NE¹/₄ SW¹/₄ sec. 1, T13S, R71W, Lake George 7¹/₂ min. quad." Lohman identified in the "lower shale" 11 of the 18 genera noted above from the "middle shale" sites and 2 additional genera. From sample 4429 described as "gray, light weight tuffaceous shale from top of exposure," slide #3579, Lohman identified these genera: Melosira, Diatoma, Meridion, Tetracyclus, and Navicula. From sample 4428 described as "massive gray-brown mudstone, 4 ft. stratigraphically below top," slide #3578, Lohman identified these 13 genera: Melosira, Fragilaria, Diatoma, Meridion, Tetracyclus, Eunotia, Rhoicosphenia, Cymbella, Gomphonema, Achnanthes, Frustulia, Pinnularia, and Navicula. This list adds 2 genera (Meridion and *Cymbella*) to the taxa he recorded from the "middle shale" sites. These 5 genera from the

"middle shale" sites, *Orthoseira*, *Synedra*, *Tabellaria*, *Amphora*, and *Nitzschia*, were not noted by Lohman in these samples from the "lower shale" roadcut site. The following discussion focuses on the published and recent investigations in the "lower shale" at Clare's Quarry.

Two published accounts reference Florissant fossil diatoms in the "lower shale" at Clare's Quarry. These two studies provide taxonomic lists that confirm the occurrence of a total of 22 genera (Round and Williams *In* Harding and Chant, 2000; and Stoermer *In* Meyer, 2003) from the Clare's Quarry. In the current independent investigation, a detailed sampling of the Clare's Quarry site has yielded an additional 8 genera, bringing the total to-date number of genera to 30. Of the total 30 genera from these three studies at Clare's Quarry, 13 are first-time occurrences in the fossil record. Details of these studies at Clare's Quarry are provided in the following three paragraphs.

From the "lower shale" at the Clare's Quarry site, 6 diatom genera were identified by Frank Round and David Williams, as reported by Harding and Chant (2000). Although the samples were described as "vertically continuous blocks of laminated lacustrine sediment" from the quarry exposure, no reference was given as to the stratigraphic position of individual samples. Samples were made into polished thin sections for examination with SEM and into petrographic thin sections for viewing with a petrographic microscope. Freshly split bedding surfaces that contained macrofossils were examined for diatoms with backscattered and secondary electron microscopy. Energy dispersive X-ray spectroscopy was also used for element analysis. The following is the list of genera reported: *Synedra, Diatoma, Achnanthes, Fragilaria, Gomphoneis,* and *Cymbella.* The assemblages were found to consist almost exclusively of pennate diatoms, dominated (>85%) by one species of *Synedra.* Second in abundance was *Diatoma* sp. Specimens of *Achnanthes* sp. and *Fragilaria* sp. were uncommon, and rarer were *Gomphoneis* sp. and *Cymbella* sp. (Harding and Chant, 2000).

A preliminary examination of samples from Clare's Quarry by Eugene Stoermer, cited by Meyer (2003), indicated that taxa with affinities for 19 modern freshwater diatom genera were observed. No reference as to collection methods or stratigraphic position was recorded (Eugene Stoermer, personal communication, 2006). Sample preparation included the standard hydrogen peroxide method (Stoermer et al., 1995) followed by placing a beaker of rinsed sample in distilled water into an oven set to 100° C over night (Sarah Spaulding, personal communication, 2006). The genera observed by Stoermer are listed: *Aulacoseira, Synedra, Achnanthidium, Planothidium, Diatoma, Melosira, Navicula, Eunotia, Gomphonema, Pinnularia, Meridion, Nitzschia, Fragilaria, Staurosirella, Fragilariaforma, Ellerbeckia, Epithemia, Rhopalodia, and Tetracyclus.* This report adds 16 genera to the number observed by Round and Williams. Stoermer stated that other possibly extinct forms were also observed. *Aulacoseira* and *Synedra* were the most abundant genera in these samples (Meyer, 2003).

The current investigation at the Clare's Quarry site has resulted in the identification of a minimum of 20 freshwater genera and 1 allochthonous specimen of a marine genus. The samples were collected from a 5 meter-thick stratigraphically-controlled vertically-continuous section of interbedded laminated shale, volcanic tuff, and homogeneous mudstone. Several genera include multiple species. The descriptions and images of these taxa are provided in a separate manuscript that is in preparation. An initial goal to quantify relative abundances of taxa was not possible at this site due to challenges to sample disaggregation posed by the indurated state of the matrix. To address this challenge, several preparation methods, modified from Green

(2001), were used. These included the standard hydrogen peroxide method, sodium hexametaphosphate with sodium carbonate method, and treatment with sulfuric acid. In the end, complete matrix disaggregation was not achieved, and mechanical crushing was the preferred method, as it was believed to yield a more representative taxonomic sample than the other methods attempted. This method was augmented with SEM imagery. The list of freshwater genera observed in this independent study include the following: Aulacoseira, Orthoseira, Fragilaria, Staurosira, Diatoma, Synedra, Tetracyclus, Eunotia, Gomphonema, Achnanthidium, Planothidium, Platessa, Psammothidium, Diadesmis, Frustulia, Pinnularia, Adlafia, Navicula, Stauroneis, and Nitzschia. This list adds 9 genera to those observed by Round and Williams and Stoermer in the studies referenced above. Although the qualitative relative abundance of taxa varied among sample intervals, the overall vastly most abundant genera were Synedra, Diatoma, and Aulacoseira. Planothidium, Platessa, Navicula, and Gomphonema genera were uncommon. The genera Fragilaria, Staurosira and Tetracyclus were very uncommon, yet they were morphologically diverse. The remaining genera were rare to very rare. From the three abovenoted studies, a total of 30 freshwater genera are recorded from the Florissant Formation at the Clare's Quarry locality. This study adds 5 genera to the cumulative 8 first-occurring non-marine genera listed above in the accounts of Round and Williams and Stoermer. The following 13 Florissant diatom genera are the earliest occurrences in the freshwater fossil record from the "lower shale": Ellerbeckia, Orthoseira, Synedra, Cymbella, Gomphonema, Achnanthes, Achnanthidium, Platessa, Psammothidium, Diadesmis, Adlafia, Epithemia, and Rhopalodia. Additionally, a marine diatom genus, Actinoptychus, (confirmed by David Harwood, personal communication) was present only as a single fragmented specimen in a single sample; and it

constitutes an anomalous occurrence, thought to have been transported by wind or avian transit. This genus is not discussed further here as it is not a freshwater form, and the first appearance of *Actinoptychus* is in marine deposits of late Cretaceous (Campanian) age in western Siberia (Strelnikova, 1975).

In addition to the 30 genera observed in the "lower shale" at Clare's Quarry, the identification by Lohman of *Rhoicosphenia* in the lower shale of the US 24 roadcut increased the total number of genera to 31. The additional two genera (*Tabellaria* and *Amphora*) observed by Lohman in the middle shale sites bring the total number of Florissant fossil diatom genera to 33. Of these, the number of first-occurring freshwater diatom genera discovered in the Florissant Formation is 14. The results of this comprehensive review of the record, along with additional original work are provided in a simple set of taxonomic lists that tally the occurrences of the 33 genera, now documented, for the Florissant fossil diatom flora (Figure 5). The composited generic list from the Florissant diatom investigations is shown in Table 1., where it can be visually compared with the generic lists for the other pre-Neogene deposits herein reviewed.

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Totals 17 13 20 22 33	Totals	17	13	20	22	33	14

Figure 5. Chart of 33 diatom genera that represent the Florissant fossil diatom flora, their occurrences according to location, and those that are first-time occurrences in the geologic record. (Location symbols are keyed to map in Figure 4: MG3 is MacGinitie-3, PRN is

Princeton 1880, PET is undifferentiated Petrified Forest, and RDC is the US 24 roadcut east of Florissant.)

Oligocene Freshwater Diatoms of Oregon

Nine genera of freshwater diatoms have been recovered from an early Oligocene (29.83 Ma) pyroclastic debris flow that was deposited in a shallow-marine forearc basin in the Pittsburg Bluff Formation in northwestern Oregon (McKnight et al., 1995). The identified genera include *Melosira*, *Cocconeis*, *Cymbella*, *Eunotia*, *Fragilaria*, *Gomphonema*, *Gomphopleura*, *Pinnularia*, and *Tetracyclus*. At the time, these findings extended the geologic range of the genus *Gomphonema* by approximately 15 Ma, as it was previously thought to have evolved in the Miocene (Kociolek and Stoermer, 1993).

Oligocene to Miocene Freshwater Diatoms of Montana

A freshwater diatom flora was described from the Canyon Ferry, Montana, paleobotanical fossil locality of approximately late Oligocene to early Miocene age (Van Landingham, 1970). The locality is about 12 miles N-NW of Townsend, Montana, on the west bank of Canyon Ferry Reservoir. The diatomaceous layers occur in the uppermost unit (the volcanic ash and tuff unit) of the four units of the Oligocene complex. This unit has a thickness of 800 ft. and is conformably overlain by Miocene sediments consisting mainly of sand, gravel, and clay with a thickness of approximately 500 ft. The boundary between the Miocene and Oligocene is described as poorly defined and transitional (Van Landingham, 1970). Because the material was unconsolidated, biological slides were made using a conventional slurry method. The taxonomic list includes a total of 15 genera. Van Landingham (1970) characterizes the flora as being dominated by *Melosira distans* (65%) and *M. granulata* (22%). Species of *Fragilaria* were reported to occur as follows: *Fragilaria lapponica* (revised to genus *Staurosirella* Williams & Round) (4%), *F. construens var. venter* (revised to genus *Staurosira* Ehrenberg) (2%), and *F. brevistriata* (revised to genus *Pseudostaurosira* Williams & Round) and *F. virescens* (~1%). Additional genera are *Achnanthes*, *Cocconeis*, *Cymbella*, *Gomphonema*, *Navicula*, *Pinnularia*, *Stauroneis*, *Surirella*, *Synedra*, and *Tetracyclus* (Van Landingham, 1970).

SUMMARY OF OBSERVATIONS

Graphic Synthesis of the Early Fossil Freshwater Diatom Record

The data in the geologic range chart of pre-Neogene non-marine diatom families and genera (Table 1.) have been extracted to create a simplified generic range chart (Table 2.). This chart identifies first-occurrences of genera through time, as indicated by the fossil record. These patterns in the fossil record show the latest time of first-occurrence; but, due to the potential for missing fossil data, they may not reflect true evolutionary trends of these major freshwater diatom lineages.

Perspectives on the Geologic Range Charts

The geologic range chart in Table 2. should be used with the understanding that, as a geologic record, it is inherently incomplete. A lesson learned from the literature is that, with the increased number of sampled sites, the timing of first-occurrences has gotten pushed farther

back. For example, prior to the year 2000, the pre-Neogene freshwater diatom published record was limited to 4 of the 9 localities discussed here, restricting the earliest first-occurrences to middle Eocene, and reducing the total number of observed genera from the current 47 to only 26. It would be a mistake, therefore, to assume that this chart contains sufficient information upon which to fully test the phylogenetic hypotheses. Potential inconsistencies between the fossil record and predictions from the genetic phylogenies should be evaluated in the context of the spotty nature of the fossil data and the inescapable variability in the paleohabitats sampled.

Although care has been taken in this study to use fossil localities that have relatively well-documented radiometric ages, the fossil literature is often inexact as to the age of the diatom-bearing deposits being reported, especially where no associated datable volcanic material is available. As discussed previously, even where age is provided, both marine and freshwater literature show inconsistency in age assignments relative to the Cenozoic epochs. It is, therefore, important to show numerical ages based on the actual radiometric dates, where possible. As more reviews of diatom first-occurrences take place, it will be increasingly important for the specific diatom-bearing intervals to be stratigraphically refined and for age data to be updated and integrated into the literature.

Table 2. Simplified pre-Neogene freshwater diatom biochronology chart. This geologic range chart for late Cretaceous (base) through Paleogene (top) time shows occurrences (black dots) for the 47 genera of freshwater diatoms with modern affinities from the nine fossil localities featured in this study. The three major morphological groups (centrics, araphids, and raphids) are labeled across the top. Ages of the localities are indicated by dashed horizontal lines. The dotted vertical bars (maximum reported ranges) are artificially terminated in early Miocene in this chart, but all these genera with the exception of *Eoseira* are modern and would extend into the Holocene.



Timing of the Expansion of Major Diatom Groups

In terms of large-scale trends in the evolution of diatoms, it is generally agreed that centric diatoms graded into araphid pennates, and araphid pennates graded into the raphe-bearing pennate diatoms, which are a natural group (Alverson and Theriot, 2005). Furthermore, SSU rRNA sequences and preliminary molecular clock calculations of Sorhannus (2007) predict that early representatives of modern araphid diatoms had evolved by the early Cretaceous (~ 100 Ma), and that raphid taxa had evolved by the late Cretaceous (~ 75 Ma).

The results of the current study support these general trends (Table 2.). The record shows the occurrence of 2 centric genera, 2 araphid genera, and 3 raphid genera in the 2 late Cretaceous non-marine deposits of record. Many more genera of these major groups appear in the Paleogene sites. All the genera that occur in these 9 Late Cretaceous through Paleogene sites show strong taxonomic affinities to modern taxa. Some examples of these taxa are shown in Plate 1.

Table 2. shows that at least as many as 2 non-marine centric genera had evolved by late Cretaceous; and, with the addition of 7 genera from Paleogene sites, it confirms that at least as many as 9 centric genera had evolved prior to the beginning of the Neogene.

The prediction by Sorhannus (2007) that araphid diatoms had evolved by the early Cretaceous (~ 100 Ma) was not tested in this study, as no freshwater fossil records were available for the time period prior to late Cretaceous. Nevertheless, 2 araphid genera are documented from the 2 late Cretaceous sites. An additional 10 araphid genera were observed from the Paleogene sites. This would indicate that at least as many as 12 freshwater araphid genera had evolved prior to the beginning of the Neogene. Sorhannus' (2007) assertion that raphid taxa had evolved by the late Cretaceous (~ 75 Ma) is supported by the observation of 3 freshwater raphid genera from the 2 deposits of late Cretaceous age in this study. A tally of the earliest occurrences of raphid genera shows that, from the 1 early Eocene and 3 middle Eocene sites of record, 9 additional raphid genera were recorded, totaling 12 raphid taxa prior to the late Eocene Florissant site that provided 11 more raphid genera, bringing the total to 23 raphid genera. A minimum of 3 more raphid genera appear in the remaining Paleogene sites featured in the chart. In sum, at least as many as 26 modern freshwater raphid genera had evolved prior to the beginning of the Neogene.

This study agrees with the view that all three major modern freshwater diatom groups had evolved prior to late Cretaceous. The occurrences of these major groups as early as the late Cretaceous strongly indicate that the earliest and most primitive forms of these taxa first appeared prior to the time interval for which freshwater fossil data have been recovered and published.

Advances in Freshwater Diatom Biochronology at the Genus Level

Wolfe and Edlund (2005) have described in the early Eocene Horsefly lake deposits of British Columbia, Canada, the now-extinct new genus *Eoseira* that is believed to be an ancient link between *Aulacoseira* and older centric diatoms. Wolfe and Siver (2009), in middle Eocene Giraffe Pipe lake sediments from the Northwest Territories, Canada, have pushed back the range for 3 genera in the Stephanodiscaceae family of non-marine diatoms. Among these is *Cyclotella*, whose previously-accepted time of origin was 20 million years later in the Miocene (Krebs, 1994; Krebs et al., 1987). Also at the Giraffe site, Wolfe and Siver (2009) and Siver and Wolfe (2007) have extended the currently published freshwater fossil record of the genus *Eunotia* by more than 25 million years from the formerly posted record of origination in middle Miocene (15 Ma) (Bradbury et al., 1985). Extending this record, the previously unpublished observations presented in this study show occurrences of *Eunotia* in both the early Eocene Horsefly beds of British Columbia and the middle Eocene Dewey beds of Idaho that substantially pre-date the *Eunotia* occurrence in middle Eocene Giraffe site. Further work by Siver et al. (2010) in the middle Eocene of the Northwest Territories extends the record of the genus *Actinella* by about 6 million years from the former first-occurrence in deposits ranging from late Eocene to Oligocene age. The first-ever fossils of the extant genera *Nupela* and *Oxyneis* were recovered from the Giraffe site in the Northwest Territories (Siver et al., 2010).

Previously published accounts of the diatoms from the late Eocene Florissant lake deposits of central Colorado, aided by the current investigation, provide a rich new flora that extends the geologic range of as many as 14 extant freshwater genera. The Florissant diatom flora is exceptional because it is the earliest highly diverse freshwater flora known, with species representing as many as 33 modern genera. The 14 geologically first-appearing genera include *Ellerbeckia*, *Orthoseira*, *Rhoicosphenia*, *Achnanthidium*, *Platessa*, *Psammothidium*, *Diadesmis*, *Adlafia*, *Epithemia*, and *Rhopalodia* that were not formerly reported prior to the Neogene. The first-occurrences of *Synedra* and *Achnanthes* are pushed back by 10 million years from the Oligocene-Miocene deposits at the Canyon Ferry locality in Montana (Van Landingham, 1970). The first-occurrences of *Cymbella* and *Gomphonema* are pushed back by 4 million years from the middle Oligocene Pittsburg Bluff locality in Oregon (McKnight et al., 1995). The remaining Florissant genera provide a continuation of the record of 17 earlier recognized genera.

Implications of this Study for Freshwater Diatom Biochronology

Despite the caveats regarding the incompleteness of the fossil record, this range chart of pre-Neogene freshwater diatom sites provides concrete morphologic evidence based on the presence, rather than the absence, of taxa that reflect, in part, the sequence and timing of phylogenetic changes that mark the early establishment of modern freshwater diatom populations in North America. It has been shown that, although the mechanisms at play may not be fully understood, these floral changes are temporally somewhat coincident with increases in taxonomic diversity observed in the marine diatom realm that are linked to global cooling events. In the following paragraphs, first-occurrences of genera shown in this study are discussed in relation to some of the predicted lineage relationships of Sorhannus (2004), Sims et al. (2006), Siver and Wolfe (2007), and Brown and Sorhannus (2010). Also briefly mentioned are the possible influences of human history and habitat on the current fossil record.

Although the singular species of the araphid genus *Synedra* observed at Florissant is a freshwater taxon, as substantiated by collateral macrofossil data, the genus *Synedra* also contains species that are associated with marine or marginally marine and brackish water environments. Previous to this study, first-reports of the marine species of *Synedra* are from early Oligocene (Barron and Baldauf, 1995). Not only the earlier first-occurrence of the non-marine form, but also the presence of *Synedra* as a dominant taxon in the Florissant lake sediments potentially signals an early tolerance for a freshwater habitat for this genus that began at least as early as the late Eocene.

The araphid *Fragilaria*-like forms of the family of Fragilariaceae are reported from as early as late Cretaceous in fresh to brackish water deposits of Mexico (Chacon-Baca et al., 2002; Bernaldi-Campesi et al., 2004). These limited Cretaceous occurrences were followed in the Paleogene by what appear to be surges in the freshwater Fragilariaceae diversity in the middle Eocene sites of North America and in the late Eocene flora of Florissant that correspond with increased diversity in Fragilariaceae genera in the marine realm (Sims et al., 2006). Whether such diversity increases are real or an artifact of the limited number of fossil sites, there is in the Florissant substantial morphological variability observed in the Fragilariaceae taxa, especially among the Staurosiroid forms.

On the basis of the more recent work of Brown and Sorhannus (2010) that pushes back the origins of diatoms to the Carboniferous -Permian boundary, all the evidence mounted in the current study reflects only the most recent portion of the evolutionary history of diatoms.

The addition to the fossil record of the genus *Adlafia* in the late Eocene Florissant is possibly due to the fact that earlier workers did not distinguish it from species of the genus *Navicula* (Round et al., 1990).

On an ecological note, the late Eocene Florissant flora uniquely yields the first-identified centric *Orthoseira* specimens and diminutive species of the raphid genus *Diadesmis*, both of whose modern relatives occupy moist aerophytic niches. The timing of first-occurrences of these genera in the Florissant deposits may be attributed to a general lack of preservation of sediments from these marginal habitats in older fossil sites.

Future Directions

The challenges to discovering the earliest vestiges of freshwater diatom forms will be met through the continued search for diatom-bearing deposits that pre-date the current freshwater fossil record. This will require the efforts of a large body of investigators to pool their energies globally in such a search.

Continued work on known pre-Neogene floras will be necessary to further populate and amend the current biochronology. In this pursuit, the compelling task at hand for the freshwater paleodiatomist is to describe and document the taxa from even the most difficult of rock matrices in an effort to close the gaps in the early record. Continued high-resolution species-level analysis of the late Eocene Florissant diatom flora at the Clare's Quarry site and other stratigraphic sections within the Florissant Fossil Beds National Monument will help to more fully characterize the resident taxa and their ecological associations. Such intensive floristic work at Florissant has the potential to uncover subtle species shifts through time that can be evaluated in the context of changes or stability in the depositional setting.

We will look forward to further advancements from the species-level taxonomic work that continues in the early and middle Eocene sites of Canada by Siver, Wolfe, Edlund, and colleagues and anticipate the growing set of phylogenetic implications emerging from such work. With more study of freshwater diatom-rich Eocene sites and the future discovery of additional floras in earlier pre-Neogene deposits, a clearer sense of the timing of the evolution of ancestral forms will emerge. With a more accurate biochronology as a framework, future workers can better evaluate possible links between diatom evolution and the complex processes that drive or reflect global change.

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Figure 1. *Aulacoseira* sp., valve view. Light microscopy image of specimen from the "middle shale" of the late Eocene Florissant Formation, Teller County, Colorado. Collected from the Lohman 1957 section, Lower Twin Rocks Road. California Academy of Sciences Accession #601857, Slide #375003. (Scale bar = $10 \mu m$.)

Figure 2. *Planothidium* sp., valve view. Light microscopy image of specimen from the "middle shale" of the late Eocene Florissant Formation, Teller County, Colorado. Collected from the Lohman 1957 section, Lower Twin Rocks Road. California Academy of Sciences Accession #601857, Slide #375003. (Scale bar = $10 \mu m$.)

Figure 3. Undetermined centric, valve view. Light microscopy image of specimen from the middle Eocene Dewey beds, Valley County, Idaho. Collected by Leonard in 1986. Thunder Mountain mining district. California Academy of Sciences Accession #702135, Slide #1028081. (Scale bar = $10 \mu m$.)

Figure 4. *Eunotia* sp. 1, valve view. Light microscopy image of specimen from the middle Eocene Dewey beds, Valley County, Idaho. Collected by Leonard in 1986. Thunder Mountain mining district. California Academy of Sciences Accession #702135, Slide #1028081. (Scale bar = $10 \mu m$.)

Figure 5. *Eunotia* sp. 2, valve view. Light microscopy image of specimen from the middle Eocene Dewey beds, Valley County, Idaho. Collected by Leonard in 1986. Thunder Mountain mining district. California Academy of Sciences Accession #702135, Slide #1028081. (Scale bar = $10 \mu m$.)

Figure 6. *Frustulia* sp., valve view. Light microscopy image of specimen from the middle Eocene Dewey beds, Valley County, Idaho. Collected by Leonard in 1986. Thunder Mountain mining district. California Academy of Sciences Accession #702135, Slide #1028081. (Scale bar = $10 \mu m$.)

Figure 7. *Diatoma* sp., valve view. Light microscopy image of specimen from the early Eocene Horsefly beds, British Columbia, Canada. Collected by Wilson in 1981. California Academy of Sciences Accession #701462, Slide #1021059. (Scale bar = $10 \mu m$.)



CHAPTER 3

FRESHWATER DIATOM FLORISTICS OF THE LATE EOCENE FLORISSANT FORMATION, CLARE'S QUARRY SITE, CENTRAL COLORADO, USA

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Summary/Abstract

The late Eocene diatom flora from the lacustrine deposits of the Florissant Formation in Teller County, Colorado, is typical of the ancient community of Aulacoseira-pennate genera (Fragilaria) of Krebs (1994) that is characteristic of temperate freshwater lakes of the Paleogene of western North America. The current study centers on the diatom taxa in samples from a measured stratigraphic section exposed at the Clare's Quarry site near the small town of Florissant. Diatom taxa are documented through the systematic descriptions and illustrations presented here. The fossil diatom flora of this locality includes a minimum total of 21 genera from 14 families. All but 3 of the families are represented by a single genus. The most diverse family is *Fragilariaceae* with 4 genera. Eight of the total 21 genera are first occurrences within the geologic record. Although the diatom frustules are relatively well-preserved in this site, processing challenges inherent with indurated shales and mudstones have rendered results that highlight the appearance of variously identifiable individuals rather than providing a quantitative assemblage assessment. This study is a survey of taxa using light microscopy and scanning electron microscopy. These findings are organized according to the classification of freshwater diatoms (modified from Round et al., 1990; and Kingston, 2003). The discussion contains descriptions and image plates of 4 new species, 2 new varieties of known species, 2 nominate

varieties of known species, 8 numbered species that are similar to known species but that have insufficient data to confidently assign to either a known species or to propose a new species name; 38 morphotypes for this site that are identifiable only to genus, and 1 morphotype that is of an uncertain affiliation within the centric group.

Introduction

Background

For more than the past one hundred and thirty years, the Florissant area of central Colorado has been known as a location for giant petrified Sequoia tree stumps and exquisitely preserved plant leaf, pollen, insect, spider, mollusk, fish, shorebird, and mammal fossils contained in the lacustrine and associated fluvial deposits of late Eocene age (Meyer, 2003). The area that includes the majority of this fossil Lagerstätte was preserved in 1969, by the U.S. National Park Service as the Florissant Fossil Beds National Monument. The lake bed shales are interbedded with mudstones, volcanic ash, and coarse volcanic tuffs that contain sanidine crystals that provide an average 40 Ar/ 39 Ar radiometric age of 34.05 ± 0.08 Ma (McIntosh and Chapin, 2004). The understanding of the lake history is based upon the interpretation that the lacustrine system formed as a result of lahars that dammed the fluvial drainage (Evanoff et al., 2001). A series of three lake deposits, designated "lower," "middle," and "upper" shales are recognized within the Florissant paleobasin (Evanoff et al., 2001).

Among the algal microflora that inhabited the Florissant lake system are freshwater diatoms (division Bacillariophyta and classes Coscinodiscophyceae, Fragilariaophyceae, and Bacillariophyceae). Fossil diatoms at Florissant were recognized in early investigations (MacGinitie, 1953) as contributors to the laminated nature of the lake beds. Pioneering studies that relate diatoms to sedimentation processes were conducted by Weilbacher (1963) and McLeroy and Anderson (1966) and form the basis for many of our current interpretations about the paleolimnology of the ancient lake. Studies that associate diatom and bacterial biofilm with macrofossil preservation are more recent contributions (Harding and Chant, 2000; O'Brien et al., 2002; O'Brien et al., 2008). Florissant diatoms in a set of samples from the Florissant Fossil Quarry (Clare's Quarry) were identified to genus level, and interpretations about their autecology were made by Frank Round and David Williams as noted in Harding and Chant (2000). A second set of samples from the same site was examined by Eugene Stoermer from which a list of 19 modern genera for which the fossil diatoms showed morphologic affinity was noted in Meyer (2003). A contribution of the current research is an illustrated floristics assessment of representatives of the unusually diverse Florissant fossil diatom flora from the field site referred to as Clare's Quarry.

Rationale for Study

The freshwater diatom fossil record is deficient in tracing the course of diversification from the early forms of the Cretaceous period that are reported in Chang et al. (2003), Harwood et al. (2004, 2007), Chacon-Baca et al. (2002), Beraldi-Campesi et al. (2004), Ambwani et al. (2003), and Singh et al. (2007) to those of decidedly modern affinity that begin to appear in the early and middle Eocene deposits (Lohman and Andrews, 1968; Wolfe and Edlund, 2005; Bradbury *In* Axelrod, 1998; Wolfe et al., 2006; Siver and Wolfe, 2007; Wolfe and Siver, 2009) and that dominate the flora of this late Eocene Florissant locality. The Florissant diatom flora is a representation of diversification of genera and species that is unprecedented in the early fossil record. This investigation demonstrates that the Florissant diatom flora is the most diverse (genus rich) early freshwater diatom flora known. Additionally, with few exceptions such as the middle Eocene Giraffe Pipe locality in Northwest Territories of Canada (Wolfe et al., 2006; Siver and Wolfe, 2007; Wolfe and Siver, 2009; and Siver et al., 2010), Cretaceous and Eocene freshwater diatom deposits are so altered by diagenesis or other taphonomic processes that researchers are generally limited to thin section imagery of only single taxa. Despite the taphonomic damage and processing difficulties inherent with these indurated shales at Florissant, with extreme diligence, a relatively representative survey of the diatom flora was possible. For this reason, and the geologic significance of this highly diverse flora, the Florissant deposit is a uniquely favorable locality for accessing the record of the many late Eocene first-occurring modern taxa.

Location

The study area is south of the town of Florissant in Teller County, Colorado. The town of Florissant is reached via U.S. Highway 24, and is 38 miles west of Colorado Springs, which is 70 miles south of Denver (Text Figure 1.).



Text Figure 1. Location map for Florissant study area west of Colorado Springs.

The site of this investigation is the Florissant Fossil Quarry (referred to here as Clare's Quarry) that is located just south of the town of Florissant and north of the Florissant Fossil Beds National Monument (Text Figure 2.).



Text Figure 2. Location of Clare's Quarry site in relationship to the town of Florissant and the Florissant Fossil Beds National Monument.

The Clare's Quarry site is a stratigraphic section of the "lower shale" of the Florissant Formation (Evanoff et al., 2001) within a small, privately-owned, commercial fossil quarry on the east-facing wall of a forested knoll west of County Road 1, less than 0.2 miles south of the town of Florissant and less than 0.4 miles north of the Florissant Fossil Beds National Monument. The quarry is within the U.S. Geological Survey Lake George 7.5 minute topographic series quadrangle map in the SE ¹/₄, SE ¹/₄, Section 2, T13S, R71W; at 38° 56.605' N, 105° 17.459' W. Samples were collected from a 5-meter thick stratigraphic section whose base is at an elevation of 8,272 feet (2,521.3 meters). A detailed description of the host rock and implications about the depositional setting of the Florissant Formation at Clare's Quarry are being prepared in a separate manuscript. Text Figure 3. shows the stratigraphic section with the host lithology types and the samples illustrated in this study.



Text Figure 3. Clare's Quarry stratigraphic section showing lithologic units and position of samples for diatom specimens that are illustrated in the image plates. Letters indicate shale/mud cycles.

Materials and Methods

Collection Methods

Field collection at the Clare's Quarry site was done on June 15, 2005 and July 14, 2006. The bedding at the exposure is flat-lying from north to south and dips into the hillside ~2° to N27°W. The quarry face had been frequently cut during the past decade by the owners using heavy equipment in fossil retrieval operations. A stratigraphic section on the east-facing quarry wall was measured (Text Figure 3.). Before collecting samples, surfaces were swept clean. Hammer and chisel were used to break into the rock to obtain fresh material. Stratigraphically contiguous samples were removed from the total section of 4.91 meters. Each sample was placed into a labeled plastic zip-lock bag and sealed. The measured stratigraphic position relative to the "zero" marker horizon was marked on each bag. The section was photographed with the scale in place to document the sample positions relative to the lithologic units. Samples were further cleaned with pressurized air and distilled water, and detailed descriptions were completed.

Preservation and Taphonomic Considerations

At this study site, the diatoms are relatively well-preserved as to their mineral constituency and microstructural integrity; although, under SEM, etching of frustule surfaces is indicated in some samples. It is reasonable to assume, therefore, that some amount of the cell wall silica may have been lost or re-ordered, in some cases possibly contributing to a weakening of frustule walls. It is unclear whether valve disarticulation and girdle band detachment are due to natural causes during sedimentation and burial or to preparation methods. The natural process

of compaction has resulted in plastic deformation of elongate diatom forms such as *Diatoma* and *Synedra* and differential elastic and brittle collapse of cylindrical frustules of *Aulacoseira*. The probable diagenetic redistribution of amorphous silica of both biogenic origin and from devitrification of volcanic glass and partial alteration of feldspars to clays has resulted in an indurated shale and mudstone matrix that resists disaggregation. As an anthropogenic overprint, the decision to crush the samples to make the slurry for slide preparation resulted in the fragmentation of a large number of frustules. Secondary breakage occurred from splitting the matrix and sputter-coating the SEM stubs.

In the end, this floristics study represents neither intact living diatom populations (life assemblages or biocoenoses), nor death assemblages (thanatocoenoses) (Schäfer, 1972). It is, rather, the product of a systematically conducted survey of a taphonomic diatom assemblage (taphocoenosis) (Stoermer and Smol, 1999) that represents portions of the living population that occupied various niches within and peripheral to the lake in which their frustules were deposited. The taxon list is a record of the uncommon to rare sightings of whole and greater than half frustules or valves surviving the destructive processing methods previously described. For this reason, caution must be observed with regard to size ranges of the individuals recorded in this study, as it reflects only the frustules that remained relatively intact after preparation. Although accurate for those individuals, it does not fully represent the potential size range of the taxa present in the assemblage. The floral composition presented here has been generated from both light microscopy and scanning electron microscopy (SEM). The individual diatoms observed under light microscopy represent the group of taxa that were structurally sound enough to survive the rigors of burial and the destructive processing techniques; and, as well, they were

within a particular size range that allowed for some whole or greater than half valves to survive such conditions. On the other hand, SEM images are from completely non-directed searches on prepared stubs from samples selected for their known richness or diversity. The SEM survey results are somewhat less restricted by structural soundness and size range of the frustule, but are biased in favor of sample intervals that reflect greater diatom concentrations and greater diversity of taxa.

Sample Preparation

Field samples were examined and described as to lithology, sedimentary features, stratigraphic contacts, and macrofossil content. Subsamples were selected and prepared under a binocular microscope to isolate the fresh interior portion of the rock. Each subsample was cleaned with pressurized air, then washed in distilled water, and freeze-dried in the lab. Experimentation with matrix disaggregation using the following three chemical methods prescribed in Green (2001) modified by George Breit, USGS (personal communication), and augmented with timed motorized shaker and sonication. These methods are (1) heating in 30% hydrogen peroxide, cooling, and applying hydrochloric acid; (2) heating in sodium hexametaphosphate; and (3) heating in sulfuric acid. None of these tested methods resulted in matrix disaggregation. For these methods in total, a range of 48-84% of the initial 1 gram sample volume remained intact after extended test times. In the end, the diatom light microscope slides were prepared using three methods: slurries from sonication of whole rock chips in distilled water air-dried on cover slips using Battarbee chamber method (Battarbee, 1973) and permanently mounted on glass slides using Naphrax or Zrax mounting medium; mechanical crushing and pulverization of whole rock chips with mortar and pestle in distilled water

rendering a slurry for direct application onto cover slips that were heat-dried on a hot plate and permanently mounted; and slurries drawn from the hydrogen peroxide and the sodium hexametaphosphate preparations for direct application onto cover slips that were heat-dried on a hot plate and permanently mounted. Scanning electron microscopy samples were prepared as follows: freshly broken samples were cleaned with pressurized air; fresh, untreated chips and residual treated chips from each of the chemical methods were mounted on stubs with doublesided black tape; stubs for low-vacuum imagery were sputter-coated with gold and palladium, and those for field emission or ionic beam imagery were not coated.

Data Analysis

The diatom slides were examined and digitally photographed under 1000x magnification with Olympus Vanox and Olympus BX 51 light microscopes. Scanning electron microscopy was performed with JEOL Tungsten JSM-5800 low vacuum instrument at the US Geological Survey in Denver; and FE JEOL JSM-7401-F field emission and FEI Nova 600-I focused electron beam instruments at the Nanomaterials Characterization Facility at the University of Colorado. Strictly quantitative methods were not attempted due to the high degree of valve fragmentation resulting from destructive processing methods necessitated by the lack of matrix disaggregation.

Specimen Repository

All specimens featured in this study are reposited at the University of Colorado Natural History Museum in Boulder. Clare's Quarry site has the UCM Locality #2005015. The specimens are catalogue numbered from UCM #40917 through #41045, as detailed in the upcoming discussion.

Results

<u>Taxonomy</u>

The taxa of the Florissant fossil diatom flora are presented in the order of the classification of freshwater diatoms modified from Round, Crawford, & Mann (1990); and Kingston (2003). Representative diatom taxa of the following 14 modern families are observed in this investigation at the Clare's Quarry site: *Aulacoseiraceae* Crawford, *Orthoseiraceae* Crawford, *Heliopeltaceae* H.L. Smith, *Fragilariaceae* Greville, *Tabellariaceae* Kützing, *Eunotiaceae* Kützing, *Gomphonemataceae* Kützing, *Achnanthidiaceae* D.G. Mann, *Diadesmidaceae* D.G. Mann, *Amphipleuraceae* Grunow, *Pinnulariaceae* D.G. Mann, *Naviculaceae* Kützing, *Stauroneidaceae* D.G. Mann, and *Bacillariaceae* Ehrenberg.

These are the 21 genera that are identified in this study: *Aulacoseira* G.H.K. Thwaites, *Orthoseira* G.H.K. Thwaites, *Actinoptychus* C.G. Ehrenberg, *Fragilaria* H.C. Lyngbye, *Staurosira* C.G. Ehrenberg, *Diatoma* Bory de St.-Vincent, *Synedra* C.G. Ehrenberg, *Tetracyclus* J. Ralfs, *Eunotia* C.G. Ehrenberg, *Gomphonema* C.G. Ehrenberg, *Achnanthidium* Kützing, *Planothidium* Round et Bukhtiyarova, *Platessa* Lange-Bertalot, *Psammothidium* Bukhtiyarova et Round, *Diadesmis* Kützing, *Frustulia* C.A. Agardh; Rabenhorst, *Pinnularia* C.G. Ehrenberg, *Adlafia* Moser, Lange-Bertalot et Metzeltin, *Navicula* Bory de St.-Vincent, *Stauroneis* Ehrenberg, and *Nitzschia* Hassall. All of these genera live in modern aquatic and associated settings, and the taxa observed in this study show extreme affinity to modern species.

The taxonomic descriptions and illustrations that follow include 4 newly described species, 2 new varieties, 2 nominate varieties of previously known species, 8 numbered species

for this site that are similar to known species but that have insufficient data to confidently to propose a new species name or assign them to a known species, and (in the style of Siver and Wolfe, 2007) 38 numbered morphotypes for this site from specimens that are identifiable only to genus, as well as one centric morphotype whose genus is unresolvable.

<u>Taphonomy</u>

In SEM, the diatom frustules show various degrees of destruction including plastic deformation and brittle collapse attributed in part to compaction during burial. Despite the damaged condition of most specimens and the partial occlusion of frustules by residual matrix in the samples, light microscopy provided relatively good images of the uncommonly whole and nearly-whole specimens that allowed identification to genus, and in some cases, to species level. The SEM imagery made it possible to distinguish finer features that allowed for greater certainty as to genus and, in some cases, to species or variety level.

Note that size ranges provided in the following descriptions are intended to show only the range of what was observed in this study and is not intended to limit the range of the taxon described.

--Species List

---Class Coscinodiscophyceae

Aulacoseira G.H.K. Thwaites 1848

Aulacoseira clarensis sp. nov.

Plate 1, Figures 1-7; Plate 2, Figures 1-6.

Syntypes

UCM #s 40917 – 40926 Figured Specimens UCM #40927

Description

Morphology: centric frustule; tapering cylindrical valve in girdle view; valve height greater than diameter; moderately tall collum; valve face flat in smaller end of size range, but one face of joined sibling pairs shows slight convex-up face in larger valve size range; valve face interior areolae are evenly distributed and covered with round to irregular velar plates; mantle exterior areolae small, evenly-spaced, narrow elliptical to rectangular in shape; rounded elliptical velar plates cover areolae on mantle interior; at least 1 supporting strut below areolae is seen from mantle exterior; rows of mantle areolae straight or slightly spiral to the left away from linking spines (sinistrorse); robust linking spines are flat spatulate (broadly anvil- or spade-shaped) at ends, robust stems of linking spines extend from mantle rim and become profoundly flattened spatulate (broadly anvil- or spade-shaped) ends that display apiculate tips in some individuals; linking spines may bear silica granules; at least one row of areolae enters the stem of each linking spine and becomes a single slit before terminating; separation valves not identified; ringleiste solid, moderately thick, and very shallow; one or more (probably two) rimoportulae positioned over the 3 areolar rows nearest to the ringleiste are distinguished best in SEM; simple rimoportula shape is subapically elongate oval with aperture slit slanted to right or to left toward ringleiste; pervalvar rows of fine nodes (milling) along outer rim of collum; translucent copulae sometimes observed in SEM over frustules or entire filaments; wide variability in height to diameter ratio among individuals; this variability is also observed between sibling frustules of filaments.

Dimensions: Diameter: 2.5-13.0 μm (in girdle view, measured at valve face)
Height: 6-21 μm
Rows of areolae/10 μm: 20-30
Areolae/10 μm: 16-18
Mantle height/valve diameter ratio: 1.6-2.4

Comments

Taphonomic Effects: in girdle view, valves become increasingly flared from valve face toward and into the collum due to compressional failure in a direction perpendicular to the mantle surface (compaction direction that corresponds generally with the interpreted bedding plane of the host rock). Compressional fractures in mantle, visible only in SEM, may run subparallel or transverse to pervalvar axis. The flattening is less pronounced at the narrower, structurally more stable valve face terminus where the linking spines are often still interlocked with a sibling valve. The measured girdle-view diameter at the valve face is used as the valve diameter for these differentially flattened specimens. As the two valve faces, held together by the still interdigitated linking spines, form a structurally sound entity after taphonomic collapse and removal of the mantle wall, individuals in valve view are also somewhat commonly observed in both SEM and LM. Orientation/Habit/Associations: frustules typically lie in girdle view, often in groups of tangential, parallel-oriented filaments forming a series of compacted monospecific layers or layers with other elongate taxa such as *Synedra* and *Diatoma*. Specimens in some samples are observed as single frustules or valves of disarticulated filaments that show random lateral orientation and lie among other randomly-oriented individuals of *Synedra* and *Diatoma*, as well as less common *Gomphonema*, *Navicula*, *Tetracyclus*, *Achnanthidium*, *Planothidium*, *Psammothidium*, *Fragilaria*, *Staurosira*, *Eunotia*, *Pinnularia*, and *Stauroneis*. This species occurs ubiquitously in the laminated shales of this site, but with the exception of a thick interval that is dominated by *Synedra* and *Diatoma* in which it is noticeably absent. *A. clarensis* sp. nov. is best illustrated from samples CQ2-1-03, CQ1-11-12, CQ1-12-13, and CQ1-13-14.

Most Similar Published Species: A. *italica* (Ehrenberg) Simonsen emend. R.M. Crawford, Y.E. Likoshway & R. Jahn.

Reference: (Crawford et al., 2003)

Morphology: "Valves united by broadly anvil- or spade-shaped linking spines that vary in length among sibling valve pairs. A single row (rarely two) of areolae run up into the stem of the spine which may bear a number of granules. Separation spines of the same length as linking spines but tapering to a fine point are formed very rarely. Areolae are subcircular, or more usually, angustelliptic to fine slits and arranged in sinistrorse, spiralling rows. Velum a spongiform plate covering the inner aperture of the areola and suspended by 3 or 4 supports from the sides of the areola. Valve face more or less covered by randomly arranged areolae or areolae absent. Rimoportulae one or more, usually two, per valve, visible with difficulty in the LM and positioned 4-5 areolae distant from the ringleist. Outer aperture of rimoportula not distinguishable in SEM from areolae; inside aperture terminates a straight tube lying flat against the valve surface and oriented transverse to the areolar rows. Ringleist solid, narrow and shallow. This species forms resting spores." (Crawford et al., 2003)

Dimensions: Diameter: 3-32 μm (Krammer and Lange-Bertalot, 1991) Height: 8-20 μm (Krammer and Lange-Bertalot, 1991) Rows of areolae/10 μm: 18-25 (Crawford et al., 2003) Areolae/10 μm: 10-20 (Crawford et al., 2003)

Ecology: "not well known but clearly differs from the planktonic species in occurring with species of the genera *Gomphonema*, *Rhopalodia*, *Epithemia*, *Cymbella*, *Encyonema*, *Eunotia*, *Pinnularia*, *Neidium*, *Synedra*, *Surirella* and *Stauroneis*; all of them essentially benthic and characteristic of a very different environment from the open water plankton of *A. ambigua* and *A. granulata* (Ehrenberg) Simonsen for example." (Crawford et al., 2003) Geologic range of *A. italica*: middle Eocene to modern. The earliest described was (as *Meloseira italica*) in the middle Eocene Wagon Bed Formation in Wyoming (Lohman & Andrews, 1968). [Original published age for the host deposit of the Wagon Bed Formation was "late Eocene;" however, updated radiometric dating of associated volcanics (Smith et al., 2008) confirms an age of 47-49 Ma, placing it in early to middle Eocene.] Modern occurrences, while they do exist, may not be as common as in the fossil record (Crawford et al., 2003).

New Species Diagnosis

The new species is designated on the basis of the following characteristics: greater density of areolae rows per 10 μ m when compared with *A. italica*, being more similar in striae density to *Melosira italica* var. *multistriata* Patrick (Patrick, 1940); the closer proximity of the rimoportulae to the ringleiste; and the distinctive rimoportula that, as seen from valve interior, is a simple labiate structure with a diagonally-slitted aperture, rather than the flat transverse tube with an apically-oriented straight-slitted aperture as with *A. italica* (Crawford et al., 2003). The location and shape of the one or two rimoportulae are similar to that of *A. ambigua* (Grunow) Simonsen, but this new species is distinguished from *A. ambigua* primarily on the basis of the solid ringleiste (rather than hollow) and sinistrorse (rather than dextrorse) mantle striae (Potopova et al., 2008).

A distinguishing feature of this fossil species at this site is the hour-glass shape of joined sets of sibling valves in girdle view. Although this is a taphonomic distortion due to differential collapse of the valves toward the frustule center (as seen in SEM) and is interpreted as an artifact of the burial process rather than an original shape, it is suggestive of relatively weak walls of the mantle, ringleiste, and collum, as opposed to other species of *Aulacoseira* observed elsewhere in the Florissant deposits. It is uncertain as to whether the less-well silicified walls are a species characteristic, an environmentally-induced phenomenon (Stoermer et al., 1985; Stoermer and Julius, 2003), or if partial dissolution of the frustule of this taxon might have occurred in the water column prior to burial.

Etymology

The name recognizes the uniqueness of this species to the Florissant Formation and its particularly common occurrence at the Clare's Quarry site. It bears the epithet of the family who owns the quarry.

Aulacoseira sp. 1, [aff. *A. distans* (Ehrenberg) Simonsen] Plate 3, Figures 1-6.

Figured Specimens

UCM #40928

Description

Morphology: centric frustule; large regularly-spaced round areolae on valve face; linking spines surround valve face in valve view; deep ringleiste with possibly one or two rimoportulae on the interior surface of the ringleiste.

Dimensions: Diameter: ~8 µm

Height: not observed

Rows of areolae/10 μ m: not observed

Height/diameter ratios: not observed

Comments

Taphonomic Effects: undetermined; taxon observed only in valve view under LM.

Orientation/Habit/Associations: rarely seen, occurring with *Orthoseira*, *Diadesmis*, *Synedra*, *Frustulia*, *Pinnularia*, *Gomphonema*, *Achnanthes*, *Fragilaria*, *Navicula*, and a rare undetermined centric. Sample CQ1-8-09.

Most similar published species: A. distans (Ehrenberg) Simonsen

References: (Krammer, 1991a); (Crawford and Likhoshway, 1999); (Potapova et al., 2008). Description: "cylindrical valves; rows of areolae straight, parallel or almost parallel to the pervalvar axis; spines are small, situated at the end of each pervalvar costae. The ringleiste is thick, solid and deep. There are several rimoportulae situated near the ringleiste. They are not visible from the outside of the valve, but open inside as short tubes." (Potapova et al., 2008). "Has distinct heterovalvy, separation valves have no spines, areolae over whole valve face, spines on the mantle edge are usually positioned between rows of areolae on the mantle which are in more or less straight rows, deep thick ringleist with numerous rimoportulae against its inner side" [Crawford and Likhoshway, 1999, upon re-examination of original material of *Aulacoseira distans* (Ehrenberg) Simonsen].

Dimensions: Diameter: 4-20 (35?) µm (Crawford and Likhoshway, 1999)

Height: 3.5-10.0 µm (Krammer and Lange-Bertalot 1991a);

8-10 μm (Crawford & Likhoshway, 1999)

The following accounts were provided in Potapova et al. (2008): Mantle Height to Diameter Ratio: always <1, usually ranges 0.3-0.8;

Rows of Areolae per 10 µm: 11-15; Areolae per 10 µm along pervalvar axis: 13-17.

Ecology: "small species like *A. distans* are rarely found in the phytoplankton of larger lakes and are more usually reported from the bottom sediments of smaller, soft/acid-water lakes." (Florin, 1981; Camburn & Kingston, 1986; Haworth, 1988; Siver & Kling, 1997).

Geologic range of *A. distans*: "abundant in many fossil freshwater samples and unlikely to be found as a modern form" (Krammer, 1991a; Crawford and Likhoshway, 1999).

Aulacoseira morphotype 'Clare's 1'

Plate 4, Figure 1.

Figured Specimens

UCM #40929

Description

Morphology: centric frustule, straight-sided cylindrical valve in girdle view; valve height greater than diameter; moderately wide collum; evenly spaced, nearly straight rows of round areolae; shallow ringleiste at interior of mantle-collum contact.

Dimensions: Diameter: 6 µm

Height: 15.5 µm

Rows of areolae/10 μ m: est. 20/10 μ m

General height/diameter ratios: ~3:1

<u>Comments</u>

Taphonomic Effects: intact valves rare; distinguished only in girdle view under LM.

Orientation/Habit/Associations: occurs as individuals in association with *A. clarensis* sp. nov. at this site. Sample CQ2-1-03.

Aulacoseira morphotype 'Clare's 2'

Plate 4, Figure 2.

Figured Specimens

UCM #40930

Description

Morphology: centric frustule, cylindrical girdle view, mantle areolae partially covered by a copula, irregular to rounded mantle areolae; rows of mantle areolae show a dextrorse curvature, small linking spines emerge from mostly single pervalvar costae;

Dimensions: Diameter: est. 13.5 -15.0 µm

Height: 12.5 µm

Rows of mantle areolae/10 μ m: est. 24

Areolae in pervalvar direction/10 μm: est. 22 General height/diameter ratios: 0.83 - 0.93

Comments

Taphonomic Effects: sibling valve crushed; linking spines show much breakage; taxon observed only in external girdle view with SEM.

Orientation/Habit/Associations: rarely seen, occurring with *A. clarensis* sp. nov., *Synedra*, *Diatoma*, *Tetracyclus*, *Fragilaria*, *Achnanthidium*, *Planothidium*, *Psammothidium*, and *Staurosira*. Sample CQ1-13-14.

Aulacoseira morphotype 'Clare's 3'

Plate 4, Figure 3.

Figured Specimens

UCM #40931

Description

Morphology: centric frustule, valve face areolae, robust stems of linking spines; slit-like extensions of pervalvar areolae rows at base of linking spines.

Dimensions: Diameter: est. 4-5 µm

Height: not observed

Rows of areolae/10 μ m: not observed

General height/diameter ratios: not observed

Comments

Taphonomic Effects: breakage of attached sibling valve; taxon observed only at angle to girdle and valve view with SEM.

Orientation/Habit/Associations: single specimen observed and only in SEM, occurring with *Aulacoseira clarensis* sp. nov., and the suite that are found in Sample CQ1-13-14.

Orthoseira G.H.K. Thwaites 1848

Orthoseira roeseana (Rabenhorst) O'Meara

Plate 5, Figures 1-15; Plate 6, Figure 1.

Figured Specimens

UCM #40932 - 40935

Description

Morphology: centric frustule, cylindrical in girdle view, valve diameter slightly greater than height; three large processes (carinoportulae) in a broad hyaline area at center of valve face with well-developed collars to the exterior; valve face dense with rows of coarse round areolae radiating from central hyaline area; valve costae become rib-like and terminate in short bladelike marginal spines; on the mantle margin, the spines originate from single pervalvar costae, from two costae that converge, or as detached costae from a marginally branched set; from the base of the spines, the curved and branched costae create the appearance of anastomosing striae toward the mid-mantle; between mantle costae, irregularly pervalvar rows of coarse areolae become finer towards the unornamented distal mantle; copulae are split and ligulate, exposing rows of mantle areolae that extend beneath; mantle height/valve diameter ratio <1.

Dimensions: Diameter: 13-17 µm

Height: est. 11-16 μm Rows of mantle areolae/10 μm: 10-18 Mantle areolae/10 μm: est. 20 Height/diameter ratios: est. 0.85-0.94

Comments

Taphonomic Effects: although only fragments of frustules in girdle view are most often observed at this site, they are somewhat common in some samples. Their characteristic large size, coarse anastomosing areolar rows on the mantle fragments, the radial coarse areolae rows on valve face, and blade-like spines are readily recognized as this genus. Orientation/Habit/Associations: few seen as entire valves under LM; most commonly as large fragments of mantle in LM; only a single, partly-occluded specimen observed in SEM. Samples CQ1-8-09, CQ1-12-13, and CQ1-27-35.

Species assignment: O. roeseana (Rabenhorst) O'Meara.

References: (Poulíčková and Hašler, 2007; Krammer & Lange-Bertalot, 1991a; Hustedt, 1930; Houk, 1993; Spaulding & Kociolek, 1998)

Description: centric frustule, cylindrical valve in girdle view, generally valve width greater than mantle height, flat valve face with radial rows of areolae and 1-4 (mostly 3) carinoportulae in central hyaline area, blade-like pervalvar marginal spines.

Dimensions: Diameter: 8-70 µm

Length: 6-13 µm

Note on strong subspecific affinity to Houk's (1993) *O. roeseana* ("*epidendron*" group) described as follows: "relatively deep valve mantle with longitudinal rows of distinct pori, occasionally dichotomising towards the cingulum. A regular ring of mostly long, simply tapered or spatulated, sometimes forked spines occur at the valve margin. The spines have short ribs at the valve mantle and valve face margin. Between these ribs there are distinct shallow depressions with rows of pori. On the valve face the single radial rows of puncta are continuous from the depressions towards the center, however, the central part is almost without pori but with 2-7 carinoportulae. The aforementioned circular patches on the valve margin (in other forms) were not observed. The cingulum is composed of several, mostly 3-5, relatively wide, areolated
open and closed bands. The cell size fluctuates over a wide range in diameter (6-40 μm) and length (15-38 μm)." (Houk, 1993, p. 388-395)

Ecology: "*Orthoseira* species are found almost exclusively in subaerial habitats, particularly in bryophyte communities growing on alkaline substrata and are rarely found in lakes or high-order streams." (Stoermer and Julius, 2003); "recorded from Hungarian and American caves" (Kol, 1964; St. Clair & Rushforth, 1976); "as a photobiont from lichens" (Lakatos et al., 2004); and "mostly found among wet mosses or on soil attached to roots of some higher plants, or as a mat on dripping stones or rocks" (Houk, 1993). Living populations of *Orthoseira roeseana* (Rabenhorst) O'Meara are observed at well-illuminated sites outside limestone caves and at their entrances in the Czech Republic (Poulíčková and Hašler, 2007).

Geologic Range of genus *Orthoseira*: unknown in the fossil record as freshwater taxon prior to this occurrence. Many modern species of this genus exist.

Actinoptychus C.G. Ehrenberg 1841, 1843

Actinoptychus sp. 1, [aff. A. senarius Ehrenberg (= A. undulatus)] Plate 7, Figures 1-3

Figured Specimens

Description

Morphology: centric frustule, valve face densely punctate and sectored into estimated six sectors that are alternately raised and depressed; areolar striae somewhat radial from center of valve face, especially so on raised sector; a single, round rimoportula on exterior of raised sector near margin of valve face; row of marginal nodes or short spines just above mantle; distinct, finely ribbed mantle at valve face margin. Species not observed in girdle view, so height/diameter ratios cannot be determined at this site.

Dimensions: Diameter: est. 24 µm

Height: not observed Rows of mantle areolae/10 µm: not observed General height/diameter ratio: not observed

Comments

Taphonomic Effects: only a single, incomplete valve in valve view under LM is identified in this investigation.

Orientation/Habit/Associations: seen only as a single valve fragment in LM in Sample CQ1-10-11.

Most similar published species: A. senarius Ehrenberg [= A. undulatus]

Reference: (Round et al., 1990).

Description: centric frustules, discoid, solitary; valve face sectored into 6 sectors that are alternately elevated or depressed; central area plain or granulate; valve areolae in radiate striae; external tubes of rimoportulae prominent, usually located at distal points on radii of elevated sectors; thickened rim around valve margin; spines on mantle margin, growths, or siliceous ridges, and the edge is produced into a smooth flange; copulae plain, split, and wide.

Ecology: *A. senarius* Ehrenberg seems to be restricted in its paleogeographic distribution due to its preference for brackish water environments: this species is known from brackish marginal marine Paleocene and early Eocene deposits (Van Eetvelde and Dupuis, 2004).

Geologic range of genus *Actinoptychus*: unknown in the fossil record from freshwater lake deposits prior to this occurrence; known from as early as late Cretaceous marine shelf deposits of the Moreno Shale of California (Harwood and Nikolaev, 1995). *A. senarius* is recorded from Paleocene brackish marginal marine deposits in the Dieppe-Hampshire sub-basin of the North Sea Basin in the UK and France, and in the late Paleocene and early Eocene of the Paris Basin, France (Van Eetvelde and Dupuis, 2004).

Undetermined Centric

Centric morphotype 'Clare's 1'

Plate 8, Figures 1-6

Figured Specimens

UCM #40937

Description

Morphology: centric frustule, round in valve view; fine marginal striae that grade into distinctly areolated striae that converge into center of valve face; robust spines are suggested along margin.

Dimensions: Diameter: est. 20 µm

Height: undetermined Valve Face Rows of Areolae/10 µm: est. 22 Mantle Striae/10 µm: undetermined

Comments

Taphonomic Effects: substantial breakage of frustule and partially obscured by attached matrix; view skewed, so measurements are approximate.

Orientation/Habit/Associations: extremely rare, as only one single observation at this site. Associated with these genera *Synedra*, *Aulacoseira*, *Planothidium*, *Gomphonema*, *Diatoma* in Sample 1-10. ---Class Fragilariophyceae

Fragilaria H.C. Lyngbye 1819

Fragilaria vaucheriae var. lohmans var. nov.

Plate 9, Figures 1-8; Plate 10, Figures 1-7

Syntypes

UCM #s 40938-40951

Description

Morphology: araphid pennate, ovate-elliptical, fusiform, elliptical lanceolate to linear elliptical frustules; rectangular in girdle view; broadly or acutely rounded apices; slightly inflated hemispheric fascia sometimes extends beyond center point on valve face; narrow sternum; uniseriate lineolate valvar striae are parallel to very slightly radiate and extend onto mantle; striae offset at sternum by one-third to one-half width of costae; lineolae within each stria shorten from rectangular to round toward sternum; apical pore field of porelli in parallel rows discernable only in SEM; no linking spines observed, no labiate process evident from exterior, and internal views obstructed; several girdle bands uniserially punctate along margin; although generally symmetrical, some individuals (especially of the more ovate forms) show slight apical and transapical asymmetry, and a few have a tear-drop shape; length/width ratio is widely variable.

Dimensions: Width: 2.5-3.5 µm

Length: 6.5-36.0 µm Valve face striae/10 µm: 16-20 Length/width ratio: 2.6-10.3

Comments

Taphonomic Effects: survived burial and lab preparations relatively well. Girdle bands somewhat separated from valves and compressed. Elongate individuals tend to show more breakage.

Orientation/Habit/Associations: found as singles, often in a group, but not seen in ribbon-like filaments. Commonly associated with *Aulacoseira clarensis* sp. nov., *Synedra*, *Diatoma*, *Staurosira*, and *Gomphonema*. Samples CQ1-11-12 and CQ1-13-14.

Most similar published species: *F. vaucheriae* (Kützing) Petersen var. *vaucheriae*. References: (Patrick & Reimer, 1966; and Krammer & Lange-Bertalot, 1991a) Description: (from Patrick and Reimer, 1966) "Frustules usually in short or fairly long chains, occasionally occurring singly. Valve linear to linear-lanceolate; narrowed toward the rostrate, rounded apices. Pseudoraphe narrow. Central area usually on only one side of the valve. Striae parallel or slightly radiate, occasionally slightly shortened opposite the central area."

Dimensions: (from Patrick & Reimer, 1966)

Breadth: 2-4 μm Length: 10-40 μm Valve face striae/10 µm: 12-16

Length/width ratio: 5-10

Dimensions: (from Krammer & Lange-Bertalot, 1991a)

Breadth: 4-5 μm Length: not stated Valve face striae/10 μm: 9-14 Length/width ratio: undetermined

Ecology: *F. vaucheriae* is a modern freshwater species and seems to prefer cool water (Patrick and Reimer, 1966); often it is abundant in eutrophic reservoirs (Hoagland and Peterson, 1990).

Geologic range of genus *Fragilaria*: an extant genus whose earliest recorded occurrences are from the late Cretaceous (70 Ma) Tarahumara Formation in Sonora, Mexico, (Chacon-Baca et al., 2002; Bernaldi-Campesi et al., 2004).

New Variety Diagnosis

Fragilaria vaucheriae var. *lohmans* var. nov. is distinguished from the nominate variety by the following characteristics: the frustule shape ranges from ovate to fusiform and elliptical-lanceolate to linear-lanceolate; length and width ranges are smaller; apices range from broadly rounded to cuneate, rather than rostrate; greater density of striae on valve face; and the fascia varies from unilateral to nearly fully bilateral in some individuals.

Etymology

The name recognizes the pioneering work on fossil diatoms done by Kenneth E. Lohman of the U.S.G.S. from the 1950s and 1960s in which the earliest collections were made at Florissant and other Tertiary sites in the western U.S.

Staurosira C.G. Ehrenberg 1843; P. Petit ex Pelletan 1889
Staurosira morphotype 'Clare's 1' [aff. S. construens var. venter (Ehrenberg) Hamilton;
S. venter (Ehrenberg) Cleve & Möller]

Plate 11, Figures 1-3; Plate 13, Figures 1-3.

Figured Specimens

UCM #40952 - 40957

Description

Morphology: araphid pennate frustule; broadly elliptical to fusiform or clavate in valve view with broadly rounded to round cuneate apices; rectangular in girdle view; broad to narrow axial area; uniseriate striae with round to transapically elongate oval puncta; short striae extend onto mantle; marginal linking spines originate from costae, are solid at base, and project outwards from valve face and then re-curve back toward valve; imperforate cingulum has multiple elements; apical pore fields not observed. Dimensions: Width: 2.75-3.50 μm Length: 4.0-7.5 μm Valve face striae/10 μm: 14-20 Length/width ratio: 1.45-2.14

Comments

Taphonomic Effects: relatively good frustule survivability from destructive slide preparation methods.

Orientation/Habit/Associations: occur in chains or singly; associated with *Aulacoseira*, and diverse pennate taxa. Samples CQ1-13-14.

Most similar published species: Staurosira construens var. venter (Ehrenberg) Hamilton;

Staurosira venter (Ehrenberg) Cleve & Möller

References: Patrick & Reimer (1966); Morales (2006b)

Description: round to elliptical and rhomboidal valve shape; variable size, shape, and striae density; sternum generally narrow and lanceolate, but width variable; valvocopula wider than other girdle elements; distinguished from *Staurosirella pinnata* by its finer striae; intermediate in size, shape, and striae density between *S. construens* and *S. construens* var. *pumila*.

Dimensions: (from Patrick & Reimer, 1966)

Width: 3-6 µm

Length: 5-9 μm

Valve face striae/10 μ m: 14-16, variable

Length/width ratio: 1.50-1.67

Dimensions: (from Morales, 2006b)

Width: variable Length: variable Valve face striae/10 µm: 14-19, variable Length/width ratio: variable

Ecology for variety: (Patrick & Reimer, 1966) this variety prefers water of fairly low nutrient content (oligotrophic to mesotrophic).

Ecology for genus: taxa from this genus are a common component of shallow water floras in rivers and lakes. (Kingston, 2003)

Geologic Range of genus *Staurosira*: a modern genus whose earliest recorded occurrence is by Wolfe & Siver (2009) in the middle Eocene Giraffe Pipe lacustrine deposits of Northwest Territories, Canada.

Discussion

The presence or absence of spines in *Staurosira* and *Staurosirella* species complexes is unsettled among investigators (Morales & Manoylov, 2006); and, according to Paull et al. (2008, p. 222),

neither spine shape nor presence of a hollow/solid core within a spine is a reliable character for distinguishing among *Staurosira venter* and *Staurosirella pinnata*.

Staurosira morphotype 'Clare's 2' [aff. *S. incerta* Morales] Plate 12, Figures 1-2, & 4; Plate 13, Figures 4-8.

Figured Specimens

UCM #40958 - 40966

Description

Morphology: valves generally isopolar, araphid pennate frustule; centrally-expanded, elongate elliptical to rhombic and lanceolate in valve view with cuneate to rostrate apices; or may be heteropolar with respect to apical axis; rectangular to wedge-shaped in girdle view; narrow, elliptical to lanceolate axial area; narrow, uniseriate striae with apically elongate elliptical to rectangular areolae; broad costae; striae extend onto rounded mantle; internally, striae areolae covered by vola; imperforate cingulum; apical pore field on valve.

Dimensions: Width: 3.0-3.5 µm

Length: 10-14 µm Valve face striae/10 µm: 13-14 Length/width ratio: 3.33-4.00

Comments

Taphonomic Effects: relatively good survivability from destructive slide preparation methods.

Orientation/Habit/Associations: occur in chains or singly; associated with *Aulacoseira*, and diverse pennate taxa. Samples CQ1-13-14.

Most similar published species: Staurosira incerta Morales

Reference: Morales (2006c)

Description: "frustules rectangular in girdle view forming chains by means of marginal spines; valves isopolar with rostrate apices; central sternum narrow and lanceolate; striae are parallel or slightly radial toward the poles; striae of slit-like areolae that bear delicate vola; spines are hollow, spatulate and located on costae; apical pore fields well-developed and located on the valve mantle; no rimoportulae are present; several non-areolate bands compose cingulum; valvocopula is much wider than other elements; valvocopula is closed and has fimbriae that attach to the costae a the valve interior."

Dimensions: Width: 4-6 µm

Length: 8-17 µm Valve face striae/10 µm: 13-16 Length/width ratio: 2.0-2.8

Ecology of species S. incerta: alkaliphilous and oligotraphentic (Morales, 2006c).

Staurosira morphotype 'Clare's 3'

Plate 12, Figure 3.

Figured Specimens

UCM #40967

Description

Morphology: araphid pennate frustule; elliptical valve with round cuneate apices; narrow, uniseriate striae with apically elongate elliptical to rectangular areolae; broad costae; striae extend onto rounded mantle; no spines observed; wide imperforate valvocopula; apical pore field positioned on valve face at poles.

Dimensions: Width: 3 µm

Length: 10 µm Valve face striae/10 µm: 12-14 Length/width ratio: 3.33

Comments

Taphonomic Effects: relatively good survivability from destructive slide preparation methods.

Orientation/Habit/Associations: occur in chains or singly; associated with *Aulacoseira*, and diverse pennate taxa. Samples CQ1-13-14.

Diatoma Bory de St.-Vincent 1824

Diatoma tenuis Agardh

Plate 14, Figures 1-5.

Figured Specimens

UCM #40968 - 40971

Description

Morphology: araphid, linear frustule with broadly rounded apices; regularly-spaced transapical internally-raised costae visible from exterior as hyaline areas; fine uniseriate transapical valvar striae of round puncta are slightly off-set at sternum and extend onto mantle where they become deflected away from bases of costae; narrow sternum extends length of valve connecting apical pore fields; polar striae radiate from axial area; radial rows of poroids form valvar apical pore field; no apical spines observed; internal lateral valvar labiate structure in polar region; two rows of poroids on valvocopula, two rows of transapically elongated poroids on each of multiple ligulate cingulum bands.

Dimensions: Width: 5 µm

Length: > 60 μ m; no complete valves observed Striae/10 μ m: 7/2 μ m; est. 35/10 μ m Costae/10 μm: 6 Striae/2 Costae: 7 Areolae/10 μm: est. 75 Length/width ratio: est. ~ 12.0

Comments

Taphonomic Effects: because of their elongated linear valve shape, individuals in LM are fragmented during the destructive slide preparation; often seen in matted masses along with other elongate genera; SEM views commonly show plastic flexure of frustules in layers among other diatoms and matrix grains.

Orientation/Habit/Associations: extremely common in most laminated shale samples. Associated with *Synedra* in CQ1-17-19; and elsewhere often with *Synedra*, *Aulacoseira*, *Gomphonema*, and *monoraphids*; figures illustrate specimens in samples CQ1-13-14 and CQ2-0-04.

Species Assignment: D. tenuis Agardh

References: Morales and Potapova (2000) NAWQA for name validation; abbreviated description, dimensions, and ecology below from Williams (1985).

Description: valves linear with slightly sub-capitate pole; striae indistinct in LM; primary and secondary transapical ribs evident; in SEM, a small discrete internally-raised sternum extends the length of valve connecting apical pore fields; uniseriate areolated valvar striae extend onto mantle; usually one labiate process per valve situated within a single pole; pore fields indistinct

in LM; girdle region visible but bands not differentiated in LM; a tiny lip at external portion of valve mantle adjacent to valvocopula; a few spine stubs scattered at tips of pore fields; the valvocopula has twin rows of poroids, one row each for pars interior and pars exterior; valvocopula band is open; four or more ligulate cingulum bands are observed, each with two rows of poroids.

Dimensions: Width: 2-5 µm

Length: 20-120 µm Striae/10 µm: 16-20 Costae/10 µm: 6-10 Length/width ratio: 10-24

Ecology: Williams (1985) states that this species generally ranges from freshwater to brackish. According to Moss (1981), upper size range specimens of *D. tenuis* (11.2-72.9 μ m) are confined to planktic habitats, while those in the lower size range (18.2-48.8 μ m) are confined to the periphyton. Additionally, Moss (1981) states that, during the autumn neither *Diatoma* nor *Synedra* formed planktic populations, but these species did grow and reproduce in the periphyton.

Geologic range of genus *Diatoma*: a modern genus whose earliest reported occurrence is in material collected by M.V.H. Wilson from the early Eocene Horsefly lake deposits of British Columbia, Canada, recorded as *Diatoma hiemale* by J.P. Bradbury in notes with the diatom herbarium collection at California Academy of Sciences (CAS). Also, *Diatoma tenuis* was

recognized from the Horsefly material by Benson and Kociolek for this study in a slide identified as CAS Accession #701462, Slide #1021059.

Synedra C. G. Ehrenberg 1830

Synedra sp. 1 [aff. S. ulna (Nitzsch) Ehrenberg; S. acus Kützing] Plate 15, Figures 1-5.

Figured Specimens

UCM #40972 -40976

Description

Morphology: araphid pennate, linear lanceolate isopolar frustules gradually tapering to acutely rounded cuneate apices; central area slightly swollen with hemispheric fascia extending semibilaterally; parallel transapical striae aligned or slightly off-set at a straight and narrow sternum; uniseriate striae of lineolate to elliptical areolae terminating in round areolae at sternum; apical pore fields observed on mantle in SEM, but indistinguishable in LM; imagery of apical interior insufficient to determine presence of labiate processes that are diagnostic of this genus; valvocopula has a single row of poroids; other cingulum elements also have a row of poroids. Dimensions: Width: 4-6 µm (range observed for complete individuals)

Length: 74-88 µm (range observed for complete individuals)

Valve face striae/10 µm: 16-19

Length/width ratio: 14.67-18.50 (range observed for complete individuals)

Most similar published species 1: Synedra ulna Nitzsch, Synedra ulna (Nitzsch) Ehrenberg Reference: Morales, Hamsher & Mantell (2007) NAWQA.

Synedra ulna Nitzsch:

Description 1. (original description by Nitzsch 1817, translated from Latin by Karin C. Ponader): narrow, very long, linear with acute apices; it exceeds all related species in length in relationship to width.

Synedra ulna (Nitzsch) Ehrenberg:

Description 1. (description of Hustedt, 1959): linear to lanceolate (linear in girdle view) with narrow ends.

Description 2. (description of Patrick & Reimer, 1966): apices can be rostrate and either broadly or sharply rounded; the axial area is narrow and expands at the center of valve leaving a commonly square or rectangular central area devoid of striae; striae are parallel throughout the valve.

Dimensions: (from Hustedt, 1959)

Width: 5-9 μm Length: 50-350 μm Valve face striae/10 μm: 8-12 Length/width ratio: 10.0-38.9 Most similar published species 2: Synedra acus Kützing:

Description 1: (original description by Kützing 1844): long and narrow valves, fine-structured and an even tapering of its apices.

Description 2: (description of DeToni, 1892): valves narrowly lanceolate almost fusiform with apices that can range from rostrate to capitate; central sternum narrow; central area oblong or square.

Dimensions: (from Hustedt, 1959)

Width: 5-6 μm Length: 100-300 μm Valve face striae/10 μm: 12-14 Length/width ratio: 20-50

Genus Assignment:

Due to obscured features in these specimens, the only distinction observed between individuals of this genus and those of *Fragilaria* cf. *F. vaucheriae* is the extended length of the *Synedra* frustule.

Comments

Taphonomic Effects: *in situ* specimens as seen in SEM show that frustules are both fractured and flexed from burial compaction; their needle-like shape, the taphonomic structural damage, and the mechanical crushing during slide preparation result in few entire specimens; most of the groundmass in the majority of slides is a *Synedra*-rich hash.

Orientation/Habit/Associations: one of the three most abundant genera observed in the laminated shales of the Clare's Quarry locality; often found in clusters or matted layers sometimes with frustules aligned in parallel and other times randomly oriented; *Synedra* layers are often equally populated with either *Diatoma tenuis* and/or *Aulacoseira clarensis* sp. nov.

Ecology 1: planktic *Synedra* species can be abundant in oligotrophic, mesotrophic, and eutrophic lakes; whereas benthic species can be common in rivers (Kingston, 2003, p. 616, citing several authors).

Geologic range of genus *Synedra*: occurs in modern environments and is unknown in the fossil record prior to this occurrence in late Eocene.

Tetracyclus J. Ralfs 1843

Tetracyclus sp. 1 [aff. *T. polygibbum* (Pantocsek) Jousé]

Plate 16, Figures 1, 4, 5; Plate 17, Figure 3.

Figured Specimens

UCM #40977 - 40980

Description

Morphology: araphid pennate, slightly heteropolar frustule; elongate elliptical valve shape with broadly rounded apices; and rectangular in girdle view. The valve exterior is described: axial area indiscernible on valve exterior; two light-toned transapical shadows indicate internal primary costae (transapical ribs); small round areolae on valve face somewhat aligned along margin but are increasingly scattered toward sternum and do not form distinct transapical rows or striae. Internally, the sternum has diffuse borders; primary ribs extend completely across midregion of valve face, whereas each polar region has a marginal secondary rib that does not reach the sternum and is often curved toward mid-region of valve; between primary ribs and lateral to the sternum are straight, linear, transapical depressions (or ghost striae) that generally contain areolae. In both internal and external valve views, apical surfaces contain porelli forming densely-spaced radiating striae; mantle is tall and smoothly rounded; apical and central striae irregularly extend from valve face onto mantle. Cingulum consists of a valvocopula with a septum and open ligulate primary copulae that contain septa. A series of pervalvar parallel bars line the interior of each copula and are formed as extensions of pores on the obscured pars interior of each band. No pleura are observed. Total cingulum elements in a sequence is as many as nine girdle bands. Among the specimens placed into this group, a single, transapicallyoriented labiate process is observed in one hemisphere within the mid-region of the interior valve face.

Dimensions: Width: 6-10 µm

Length: 15-19 µm

Mantle height (as seen in SEM): est. 2.8 µm

Valve face striae/10 µm: est. 20 Striae between 2 costae: 8-10 Costae/10 µm: 2-4 Length/width ratio: 1.9-2.5

Comments

Taphonomic Effects: individuals of this genus tend to survive the taphonomic processes relatively well, owing to their compact shape, thick cell wall, and the increased structural integrity provided by the costae.

Orientation/Habit/Associations: Found in valve view and as separated septa in association with a variety of other pennate diatoms including *Synedra*, *Diatoma*, and the centric *Aulacoseira*. Sample CQ1-13-14.

Ecology for genus: "the species of this genus are usually found in shallow water and seem to prefer cold water" (Patrick & Reimer, 1966)

Geologic range of genus *Tetracyclus*: early Eocene to modern. *T. lacustris* was recognized by Platt Bradbury (archival notes at California Academy of Sciences) from the early Eocene Horsefly deposit in British Columbia, Canada.

Most Similar Published Species

Tetracyclus polygibbum (Pantocsek) Jousé

Reference: the following description and dimensions are from Williams (1996).

Description: valve shape gently elliptical; apices broadly rounded; robust primary transapical ribs and seldom secondary or tertiary ribs; sternum is central, linear and slightly raised, one to two (maximum of three) labiate structures that vary in location from valve face to the mantle-valve juncture, apical pore fields are absent, and there is no information about the cingulum.

Dimensions: Width: 7.5-10.0 µm

Length: 20-45 µm Valve face striae/10 µm: 15-25 Striae between 2 costae: 8-10 Costae/10 µm: 1-3 Length/width ratio: 2.7-4.5

Tetracyclus sp. 2 [aff. T. ellipticus (Ehrenberg) Grunow]

Plate 17, Figures 1, 2.

Figured Specimens

UCM #40981 - 40982

Description

Morphology: araphid pennate, isopolar frustule; circum-elliptical valve shape with broadly rounded apices; rectangular in girdle view; faint narrow linear sternum; fine transapical striae; at least one primary costa and possibly secondary costae in polar areas; at least one labiate structure lateral to sternum in mid-region of valve face interior.

Dimensions: Width: 7.0-8.5 µm

Length: 11-12 µm Valve face striae/10 µm: est. 20 Striae between 2 costae: undetermined Costae/10 µm: 3 Length/width ratio: 1.41-1.57

Comments

Taphonomic Effects: individuals of this species tend to survive the taphonomic processes relatively well, owing to their compact shape, thick cell wall, and the increased structural integrity provided by the costae. Only light microscope views, so unable to match valve views with girdle views for further description.

Orientation/Habit/Associations: Found in valve view and as separated septa in association with a variety of other pennate diatoms including *Synedra*, *Diatoma*, and the centric *Aulacoseira*. Samples CQ1-10-11 and CQ1-12-13.

Most Similar Published Species 1: Tetracyclus elliptica (Ehrenberg) Grunow var. elliptica

Reference: description and dimensions that follow are from Patrick & Reimer (1966).

Description: "frustules in girdle view rectangular, with intercalary bands and septa. Valve elliptical to elliptical-lanceolate. Pseudoraphe narrow, often indistinct. Costae varying in length, some extending across the valve, others marginal. Fine punctate striae between the costae. This taxon is distinguished by its shape."

Dimensions: Width: 16-32 µm

Length: 30-50 µm Striae/10 µm: 20-24 Costae/10 µm: 2-4 (Calculated Length/width ratio: 1.56-1.88)

Most Similar Published Species 2: *Tetracyclus ellipticus* (Ehrenberg) Grunow var. *ellipticus* Reference: description and dimensions are from Williams (1996).

Description: "valves gently elliptical (almost circular in some valves) with broadly rounded poles; transapical ribs robust, primary, rarely secondary or tertiary; striae more or less parallel; sternum central, linear, slightly raised; pore fields greatly reduced at polar mantle, but evident; 1-2 (maximum 3) rimoportulae present, located either on valve face or (less frequently) at mantle/face junction; cingulum consisting of 3 distinct components: all bands open, ligulate. Valvocopula attaching by crenelated lip overlaying ribs; pars interior consisting of 2-4 (5) distinct rows of poroids (which coalesce internally), ligula absent; septum extending from pars interior with small pore penetrating pole of band. Primary copulae number no more than *ca*. 10

elements, each having pronounced advalvar ligula. Secondary copulae of 4 elements; pore area and septum absent, but pars interior consisting of 1-3 rows of poroids. Pleura not observed."

Dimensions: Width: 25-40 µm

Length: 30-45 µm Striae between costae: 5-10 Costae/10 µm: (2) 3-4

(Calculated Length/width ratio: 1.13-1.20)

Geologic range of species *Tetracyclus ellipticus* (Ehrenberg) Grunow: found in Miocene Clarkia Formation in Idaho (Bradbury et al., 1985); the recorded range of this species is from Oligocene to Quaternary (Li, 1982); but it has never been reported from deposits as old as those in this study (late Eocene).

Tetracyclus sp. 3 [aff. T. lata (Hustedt) D.M. Williams]

Plate 17, Figures 4-6.

Figured Specimens

UCM #40983

Description

Morphology: araphid pennate, isopolar frustule; elliptic-fusiform valve shape; broadly cuneate apices; robust primary and secondary costae, narrow, faint sternum; fine transapical striae; at least one labiate structure lateral to sternum in mid-region of valve face interior.

Dimensions: Width: 10.0-10.5 µm

Length: 19-22 µm Valve face striae/10 µm: est. 30 Striae between 2 costae: 6-7 Costae/10 µm: 2-3 Length/width ratio: 1.9-2.1

Comments

Taphonomic Effects: individuals of this species tend to survive the taphonomic processes relatively well, owing to their compact shape, thick cell wall, and the increased structural integrity provided by the costae. Only light microscope views, so unable to match valve views with girdle views for further description.

Orientation/Habit/Associations: Found in valve view and as separated septa in association with a variety of other pennate diatoms including *Synedra*, *Diatoma*, and the centric *Aulacoseira*. Samples CQ1-13-14.

<u>Most Similar Published Species</u>: *Tetracyclus lata* (Hustedt) D.M. Williams Reference 1: description and dimensions that follow are from Williams (1996). Description: linear to lanceolate valve shape; central linear faint sternum; robust primary costae and seldom secondary or tertiary costae; labiate structures occur on the valve face or mantle and usually are 2, but range from 1-3, with a maximum of 6; cingulum is unknown.

Dimensions: Width: 2-25 µm

Length: 40-75 µm Valve face striae/10 µm: undetermined Striae between 2 costae: 8-10 Costae/10 µm: 2-4 (Calculated Length/width ratio: 3-20)

Tetracyclus sp. 4 [aff. *T. rhombus* (Ehrenberg) Ralfs in A. Pritchard] Plate 17, Figures 7 & 8.

Figured Specimens

UCM #40984

Description

Morphology: araphid pennate, isopolar frustule; lanceolate-fusiform valve shape; broadly cuneate apices; sternum indistinct; robust primary costae and two sets of secondary costae; fine transapical striae; at least one labiate structure lateral to sternum in mid-region of valve face interior.

Dimensions: Width: 11.0 µm

Length: 26.5 µm Valve face striae/10 µm: undetermined Striae between 2 costae: undetermined Costae/10 µm: 3 Length/width ratio: 2.41

Comments

Taphonomic Effects: individuals of this species tend to survive the taphonomic processes relatively well, owing to their compact shape, thick cell wall, and the increased structural integrity provided by the costae. Only light microscope views, so unable to match valve views with girdle views for further description.

Orientation/Habit/Associations: Found in valve view and as separated septa in association with a variety of other pennate diatoms including *Synedra*, *Diatoma*, and the centric *Aulacoseira*. Samples CQ1-13-14.

Most Similar Published Species: *Tetracyclus rhombus* (Ehrenberg) Ralfs in A. Pritchard Reference: description and dimensions that follow are from Williams (1996). Description: linear-lanceolate valves; central, linear faint sternum; robust primary costae, seldom secondary or tertiary costae; apical pore fields are possibly absent; labiate structures occur on the valve face and mantle and usually are 2, but range from 1-3, with a maximum of 6; mantle possesses an external ridge; cingulum is undescribed.

Dimensions: Width: 30-40 µm

Length: 30-65 µm Valve face striae/10 µm: 15-20 Striae between 2 costae: 8-10 Costae/10 µm: 2-3 (Calculated Length/width ratio: 1.0-1.6)

Geologic range of the species *Tetracyclus rhombus* (Ehrenberg) Ralfs in A. Pritchard: known from the Miocene Latah Formation, Spokane, Washington (Williams, 1996).

Tetracyclus sp. 5 [aff. *T. lancea* (Ehrenberg) M. Peragallo in Heribaud] Plate 17, Figure 9.

Figured Specimens

UCM #40985

Description

Morphology: araphid pennate, isopolar frustule; linear-lanceolate valve; cuneate apices; central, linear narrow sternum; robust primary costae; fine transapical striae; at least one labiate structure lateral to sternum in mid-region of valve face interior.

Dimensions: Width: 9.5-12.0 µm

Length: 30.0-35.0 µm Valve face striae/10 µm: est. 30 Striae between 2 costae: 8-10 Costae/10 µm: 3 Length/width ratio: 2.92-3.16

Comments

Taphonomic Effects: individuals of this species tend to survive the taphonomic processes relatively well, owing to their compact shape, thick cell wall, and the increased structural integrity provided by the costae. Only light microscope views, so unable to match valve views with girdle views for further description.

Orientation/Habit/Associations: Found in valve view and as separated septa in association with a variety of other pennate diatoms including *Synedra*, *Diatoma*, and the centric *Aulacoseira*. Samples CQ1-12-13.

Most Similar Published Species: *Tetracyclus lancea* (Ehrenberg) M. Peragallo in Heribaud Reference: description and dimensions that follow are from Williams (1996).

Description: linear-lanceolate valves; central, linear sternum; robust primary costae, seldom secondary or tertiary costae; labiate structures occur on the valve face and usually range from 1-3, but can be 4; an apical pore field is either absent or greatly reduced; the cingulum has 4 components with all bands open and ligulate; pars interior has 2-4 rows poroids coalescing as a bar internally; septum extends from pars interior with a series of small pores penetrating the band; pars exterior is plain; primary copulae consist of 10-12 bands with advalvar ligula; secondary copulae consist of approximately 4 bands without a ligula pore; a single pleural band is present; the mantle has an external ridge; occasional small stubble spines are positioned at the mantle-valve face border.

Dimensions: Width: 15-25 µm

Length: 60-140 µm Valve face striae/10 µm: 5-8 Striae between 2 costae: Costae/10 µm: 3-4 (Calculated Length/width ratio: 4.0-5.6)

Tetracyclus morphotype 'Clare's 1'

Plate 16, Figure 2.

Figured Specimens

UCM #40986

<u>Description</u>: interior of polar region of a copula with septum showing porelli penetrating the exterior and into the rim. Sample CQ1-13-14.

Tetracyclus morphotype 'Clare's 2'

Plate 16, Figure 3.

Figured Specimens

UCM #40987

<u>Description</u>: polar puncta on valve extending onto mantle that has a distinct mantle step (below the linear depression that parallels mantle rim) that is characteristic of this genus but not observed in other individuals examined at this site. Sample CQ1-13-14.

---Class Bacillariophyceae

Eunotia C. G. Ehrenberg 1837

Eunotia morphotype 'Clare's 1'

Plate 18, Figures 1-4.

Figured Specimens

UCM #40988 - 40990

Description

Morphology: biraphid pennate, asymmetrical to apical axis, elongate slightly-arcuate valve shape with slightly convex dorsal margin and a straight ventral margin; rounded asymmetrical cuneate apices; a broad, nearly straight sternum; transapical uniseriate striae of round puncta; striae extend over a steep-sided dorsal mantle; distal raphe ends are positioned near apical sternum margin and curve away from sternum. Ultrastructures not observable in these specimens. In SEM, observe valvocopula with two rows of advalvar poroids; and several cingulum elements, each with double rows of poroids.

Dimensions: Width: est. 3.5-4.0 µm

Length: est. 40.0 µm Valve face striae/10 µm: 22-24 Length/width ratio: 10.0-11.4

Comments

Taphonomic Effects: commonly incomplete frustules due to mechanical damage in processing.

Orientation/Habit/Associations: uncommon; usually seen in valve view in LM; associated with a variety of pennates and *Aulacoseira* in samples CQ1-11-12 and CQ1-13-14.

Ecology of genus: among the modern species, a wide variety of conditions are tolerated from aerophytic habitats to flowing or still waters; and from alkaline to circumneutral pH to highly acidic (Kingston, 2003).

Geologic range of genus *Eunotia*: occurs in modern environments; earliest occurrence is in the early Eocene Horsefly lake deposits of British Columbia, Canada, as recorded by J.P. Bradbury in notes with diatom herbarium collection at California Academy of Sciences (CAS). Also, species of *Eunotia* were observed for this study from the middle Eocene Dewey beds of Idaho, by Kociolek and Benson in the slide identified as CAS Accession #702136, Slide #1028081 from material reposited at California Academy of Sciences. The Dewey beds are lake deposits within the Challis volcanics in the area of the Thunder Mountain mining district described in Axelrod (1998).

Gomphonema C. G. Ehrenberg 1832

Gomphonema morphotype 'Clare's 1'

Plate 19, Figures 1-5.

Figured Specimens

UCM #40991 - 40995

Description

Morphology: biraphid pennate, elongate, heteropolar frustule; clavate in valve view; wedgeshaped in girdle view; poles broadly rounded; astigmate; broad sternum; uniseriate, generally lineolate striae on valve face extend onto tall mantle; broadly-spaced striae are sigmoidal and radial near central area and become parallel toward apices; although most puncta within the striae are lineolate and elongated in a subapical direction becoming shortened as they approach the sternum, the final punctum of each of the 12 striae in central region is a round unoccluded poroid; away from the central area and parallel to the sternum, the final punctum of each stria is a loculate pore that is occluded by a single reniform vola that leaves a crescent-shaped slit convex to sternum. An interrupted stauros is present at the central area of the valve face where it is partially bisected in one hemisphere by a shortened stria of a few round poroids entering from the valve margin; a split apical pore field with rows of small round poroids is present at foot pole of each valve; raphe proximal ends simple, and distal ends straight at terminus. Cingulum elements number three or more and indicate a row of poroids.

Dimensions: Width: est. 6-7 µm

Length: 30-32 μm Valve face striae/10 μm: 9-11 Lineolae/10 μm: 11/2 μm; so, est. 55/10 μm Length/width ratio: 4.6-5.0

Comments
Taphonomic Effects: somewhat intact after burial and lab preparations. Brittle fracture of valves, separation of cingulum, and destruction of ribs between lineolae within striae are somewhat common, as observed in SEM.

Orientation/Habit/Associations: found as single associated with *Synedra*, *Tetracyclus*, *Aulacoseira*, and *Diatoma* in samples CQ1-13-14 and CQ2-1-03.

Ecology of genus *Gomphonema*: modern species are found in nearly every habitat type in circumneutral lakes and streams (Kociolek & Spaulding, 2003).

Geologic range of genus *Gomphonema*: a modern genus with no reported occurrence earlier than this late Eocene deposit.

Gomphonema morphotype 'Clare's 2' Plate 20, Figures 1-3; Plate 21, Figure 3.

Figured Specimens

UCM #40996 - 40997

Description

Morphology: biraphid pennate, elongate, heteropolar frustule; wedge-shaped girdle view; coarsely outlined striae visible on mantle; narrow fascia indicated by apically lineate hyaline area in central area; cingulum elements number three or more and show a row of poroids at head pole; apical pore fields delimited at foot pole.

Dimensions: Width: undetermined Length: 43 µm Mantle striae/10 µm: 8-9 Length/width ratio: undetermined

Comments

Taphonomic Effects: somewhat intact after burial and lab preparations.

Orientation/Habit/Associations: found as single associated with Synedra, Tetracyclus,

Aulacoseira, and Diatoma in samples CQ1-13-14.

Gomphonema morphotype 'Clare's 3'

Plate 20, Figures 4, 5.

Figured Specimens

UCM #40998

Description

Morphology: biraphid pennate, naviculoid to slightly heteropolar lanceolate frustule; narrow sternum; coarse striae slightly radiate in central area, becoming more parallel toward poles; asymmetrical fascia with an interrupted stauros in central area; possible stigma near sternum on narrow side of fascia; apical pore fields delimited at foot pole.

Dimensions: Width: 4 µm

Length: 21-22 μm Valve face striae/10 μm: 9-12 Length/width ratio: 5.25-5.50

Comments

Taphonomic Effects: somewhat intact after burial and lab preparations.

Orientation/Habit/Associations: found as single associated with other pennates in sample CQ1-

18-20.

Gomphonema morphotype 'Clare's 4' [aff. G. lindsayi Kociolek,

Spaulding, Sabbe et Vyverman]

Plate 20, Figure 6.

Figured Specimens

Description

Morphology: biraphid pennate, heteropolar frustule; clavate in valve view; wedge-shaped in girdle view; poles broadly rounded; astigmate; flat to slightly concave valve face; uniseriate striae of loculate crescent-shaped lineolae converging toward axial area; proximal raphe ends simple, slightly expanded and separated by an extremely narrow area; distal raphe ends are slightly deflected in same direction and extend onto tall mantle; raphe bisects well-defined apical pore field on mantle at foot pole; fine, densely-spaced loculate lineolate striae prominent along valve margin and on mantle of head pole; cingulum appears closed at head pole; a single row of poroids ornaments the advalvar margin of the valvocopula.

Dimensions: Width in middle: undetermined

Length: 31 µm Valve face striae/10 µm: 7-8 Length/width ratio: undetermined

Comments

Taphonomic Effects: recognized only in SEM; relatively intact after burial; brittle fracture of cingulum; damage to head pole.

Orientation/Habit/Associations: solitary, commonly associated with *Synedra* and *Aulacoseira*. Sample CQ1-13-14.

<u>Most similar published species</u>: *G. lindsayi* Kociolek, Spaulding, Sabbe et Vyverman Reference: Kociolek, Spaulding, Sabbe, and Vyverman (2004).

Description: valves lanceolate-clavate with poles rounded; raphe straight, lateral, with external proximal ends small, positioned close together; internal proximal ends broadly recurved; axial area narrow at poles, expanded towards center; stigma lacking; striae lineate, parallel to radiate at poles; apical pore field distinct at foot pole; valves have slit-like or C-shaped areolae; proximal raphe endings slightly dilated; distal endings curved in same direction and extend onto mantle; apical pore field positioned on mantle; striae at head pole appear more closely spaced on mantle. Is comparable to *G. lowei* Kociolek, Spaulding, Sabbe et Vyverman (with 6-7 striae per 10 μ m), but has finer striae (9-13 per 10 μ m).

Dimensions: Width: 4-8 µm

Length: 16.0-35.5 μm Valve face striae/10 μm: 9-13 Length/width ratio: 4.00-4.44

Ecology: brown-water habitats in Tasmania, Australia. Collected by J.P. Bradbury in 1984 and 1985 as part of a paleolimnology study (Bradbury, 1986).

Distinction from G. lowei and G. lindsayi: G. morphotype 'Clare's 4' has 7-8 striae per 10 µm.

Gomphonema morphotype 'Clare's 5'

Plate 21, Figures 1, 2.

Figured Specimens

UCM #41000

Description

Morphology: biraphid, broadly clavate, heteropolar frustule; broadly-rounded cuneate apices; filiform raphe; medium width sternum; possibly unilateral fascia; uniseriate lineolate striae are slightly radial in central region and become more parallel toward poles; proximal raphe ends not discernable in this specimen; distal raphe ends are hooked; distal raphe end at foot pole bisects apical pore field.

Dimensions: Width: est. 4 µm

Length: est. 18 µm Valve face striae/10 µm: est. 13 Lineolae/10 µm: est. 16 Length/width ratio: est. 4.5

Comments

Taphonomic Effects: frustule impacted by partial brittle collapse, as seen in SEM.

Orientation/Habit/Associations: Occurs in association with wide variety of pennates and *Aulacoseira* in samples CQ1-11-12.

Gomphonema morphotype 'Clare's 6'

Plate 21, Figure 4.

Figured Specimens

UCM #41001

Description

Morphology: biraphid, wedge-shaped girdle view of heteropolar frustule; broadly-rounded head pole; slightly cuneate foot pole; biseriate areolate striae of small round puncta that extend onto tall mantle; perforated cingulum open at head pole.

Dimensions: Width: undetermined

Length: est. 32 µm

Mantle striae/10 µm: est. 10

Length/width ratio: undetermined

Comments

Taphonomic Effects: frustule impacted by partial brittle collapse, as seen in SEM.

Orientation/Habit/Associations: Occurs in association with wide variety of pennates and *Aulacoseira* in samples CQ1-13-14.

Gomphonema morphotype 'Clare's 7'

Plate 22, Figures 1, 2, 3, 4.

Figured Specimens

UCM #41002 - 41003

Description

Morphology: biraphid, naviculoid to slightly heteropolar, broadly lanceolate frustule; narrowly cuneate apices; narrow sternum; no fascia present; internal central nodule in central area and canal-like internal nature of striae; internal proximal raphe ends are slightly unidirectionally curved; uniseriate lineolate striae are radial to sinusoidal in central region and become straight and parallel toward apices; cuneate apex with a simple distal raphe end and apical poroids may be the head pole; interpreted as foot pole, distal raphe end is hooked and bisects valvar apical pore field.

Dimensions: Width: est. 15-16 μm Length: est. 44-46 μm Valve face striae/10 μm: 12-15 Lineolae/10 μm: est. 24 Length/width ratio: 2.93-2.88

<u>Comments</u>

Taphonomic Effects: frustule impacted by partial brittle collapse in SEM.

Orientation/Habit/Associations: only two individuals recognized in this deposit, as only in SEM are polar regions characterized. Occurs in association with wide variety of pennates and *Aulacoseira* in sample CQ1-13-14.

Achnanthidium Kützing 1844

Achnanthidium morphotype 'Clare's 1'

Plate 23, Figures 1, 2, 3, 4.

Figured Specimens

UCM #41004 - 41006

Description

Morphology: monoraphid (heterovalvar) pennate, lineate lanceolate frustule with rounded to slightly rostrate apices; uniseriate striae that are parallel to slightly radiating; rounded, elliptical to lineolate areolae; filiform raphe deflected to opposite sides poleward; distinct central area only on raphid valve; simple proximal raphe ends; distal raphe ends indistinct in observed specimens. Dimensions: Width: est. 5.0-6.5 μm

Length: est. 18-19 μm Valve face striae/10 μm: 20-22 Length/width ratio: 2.9-3.6

Comments

Taphonomic Effects: commonly incomplete frustules due to mechanical damage in processing.

Orientation/Habit/Associations: uncommon; usually seen in valve view in LM; associated with a variety of pennates and *Aulacoseira* in samples CQ1-13-14.

Ecology for the genus *Achnanthidium*: usually a stipitate habitat (attached to substrate by a mucilaginous stalk) (Kingston, 2003); thriving in moving water and in rapids (Peterson & Hoagland, 1990; Peterson & Stevenson, 1992), and in wave zones of lakes (Brown, 1973; Kingston, 1980); tend to be in flowing, turbulent, oxygenated waters (Cholnoky, 1968). Living populations of *A. minutissimum* Kützing Czarnecki have also been observed in well-illuminated sites outside limestone caves and at their entrances (Poulíčková and Hašler, 2007).

Geologic range of genus *Achnanthidium:* a modern genus whose earliest recorded occurrence is from the late Eocene of this deposit.

Planothidium Round & Bukhtiyarova 1996

Planothidium morphotype 'Clare's 1'

Plate 24, Figure 1.

Figured Specimens

UCM #41007

Description

Morphology: monoraphid (heterovalvar) pennate, lineate lanceolate frustule with rounded to cuneate apex; multiseriate striae that are parallel to slightly radiating; distinct horseshoe-shaped marginal sinus in central area only on araphid valve.

Dimensions: Width: est. 4 µm

Length: undetermined Valve face striae/10 µm: 5/2 µm, est. 25/10 µm Length/width ratio: undetermined

Comments

Taphonomic Effects: only a single fragmentary specimen observed.

Orientation/Habit/Associations: uncertain; in sample CQ1-11-12.

Ecology for the genus *Planothidium*: adnate on sand and pebbles, more common in alkaline waters (Bukhtiyarova & Round, 1996). Living populations of *P. lanceolatum* (Brébisson)

Lange-Bertalot have been observed in well-illuminated sites outside limestone caves and at their entrances (Poulíčková and Hašler, 2007).

Geologic range of genus *Planothidium*: a modern genus whose earliest recorded occurrence is cited by Singh et al. (2007) from the late Cretaceous Deccan traps of India.

Planothidium morphotype 'Clare's 2'

Plate 24, Figure 2.

Figured Specimens

UCM #41008

Description

Morphology: monoraphid (heterovalvar) pennate, lineate lanceolate frustule with rounded apices; striae are parallel to slightly radiating poleward; relatively wide lanceolate sternum, distinct horseshoe-shaped marginal sinus in central area only on araphid valve.

Dimensions: Width: 3 µm

Length: 13 µm Valve face striae/10 µm: 23 Length/width ratio: 4.33

Comments

Taphonomic Effects: valves sometimes split apart. Orientation/Habit/Associations: uncommon; usually seen in valve view in LM; associated with a variety of pennates and *Aulacoseira* in samples CQ1-13-14.

Planothidium morphotype 'Clare's 3'

Plate 24, Figures 3 & 4.

Figured Specimens

UCM #41009

Description

Morphology: monoraphid (heterovalvar) pennate, lineate lanceolate to elliptical frustule with rounded cuneate apices; striae are parallel to slightly radiating poleward; raphid valve has a stauros interrupted by a single shortened stria, a filiform raphe, and simple proximal and distal raphe ends. Araphid valve has a narrow lanceolate sternum and a distinct horseshoe-shaped marginal sinus in central area.

Dimensions: Width: 4.5 µm

Length: 12 µm Valve face striae/10 µm: 20 Length/width ratio: 2.67

Comments

Taphonomic Effects: valves sometimes split apart, many broken.

Orientation/Habit/Associations: uncommon; usually seen in valve view in LM; associated with a variety of pennates and *Aulacoseira* in samples CQ1-13-14.

Planothidium morphotype 'Clare's 4'

Plate 24, Figures 5, 6, & 7.

Figured Specimens

UCM #41010

Description

Morphology: monoraphid (heterovalvar) pennate, lineate lanceolate frustule with rounded cuneate apices; striae are parallel to slightly radiating poleward; raphid valve has a bilateral rectangular stauros, a filiform raphe, and simple proximal and distal raphe ends. Araphid valve has a narrow lanceolate sternum and a unilateral central area, as the marginal sinus.

Dimensions: Width: 5 µm

Length: 18 µm

Valve face striae/10 μ m: 9/5 μ m; est. 18/10 μ m

Length/width ratio: 3.6

Comments

Taphonomic Effects: valves often broken.

Orientation/Habit/Associations: uncommon; usually seen in valve view in LM; associated with a variety of pennates such as *Diatoma*, *Fragilaria*, *Gomphonema*, *Navicula*, and *Tetracyclus* in sample CQ1-18-20.

Platessa Lange-Bertalot 2004

Platessa florissantia sp. nov.

Plate 25, Figures 1-4.

Syntypes

UCM #s 41011 – 41014

Description

Morphology: monoraphid (heterovalvar) pennate, short elliptical to elongate-elliptical frustule with rounded to round cuneate apices; narrow, imperforate cingulum; parallel to slightly radiating uniseriate striae may become biseriate poleward; uniseriate areolae are apically elongated, whereas biseriate areolae are small and round; mantle areolae in a single row align with but are separated from the valvar striae. The raphid valve is flat to slightly concave; has a straight filiform raphe that ends both proximally and distally in a simple, straight, slightly expanded fissure on the valve exterior; the position of the distal raphe ending is either at the valve face-mantle juncture or is valvar to this juncture; and has a nearly symmetrical stauros that may be interrupted only by one or two very short striae from the valve margin. Characteristics of the araphid valve have not been described here, as such data are inconclusive in these samples.

Dimensions: Width: 3.5-5.0 µm

Length: 8.0-11.5 µm Valve face striae/10 µm: 20-22 Length/width ratio: 2.3

Comments

Taphonomic Effects: valve separation and cingulum detachment common; due to the very small size of frustules, only specimens observed in SEM can be described with necessary detail to distinguish this genus from *Achnanthidium* and related taxa.

Orientation/Habit/Associations: with a variety of pennates and *Aulacoseira* in samples CQ1-11-12 and CQ1-13-14.

<u>Most similar published species 1</u>: *Platessa conspicua* (A. Mayer) Lange-Bertalot, formerly *Achnanthes conspicua* A. Mayer. References: descriptions below are from Krammer and Lange-Bertalot

(2004), as translated in Morales (2006a).

Description of genus: the genus *Platessa* is distinguished from other genera that have been split from *Achnanthes* sensu lato in that it has a flatter valve shape; there is a slight concavity to the raphe valve and convexity to the araphid valve, which is the opposite of *Psammothidium*; externally, the distal and proximal raphe ends are straight, unlike those of *Planothidium*; although the areolae are generally arranged in biseriate rows, they show a tendency to become single rows; the areolae tend to be stretched apically, rather than transapically, as in

Achnanthidium.

Description of species: *P. conspicua* has elliptical to linear-elliptical valves with broadly rounded ends; raphe valve has a narrow axial area and a hyaline area crossing the central area that looks as if one stria has been omitted. This hyaline area is not obviously thickened. The rapheless valve is similar, except that the axial area is more broadly lanceolate.

Dimensions: Width: $4-6(7.5) \mu m$

Length: 7-16 (20) µm Valve face striae/10 µm: 11-16 (Calculated length/width ratio: 1.75-2.67)

Most similar published species 2: Achnanthes conspicua A. Mayer

Reference: descriptions from Mayer, 1919, as described in Morales (2002).

Description: valves broadly elliptical with acute or rounded apices; striae on raphe valve parallel in central region to strongly radiate toward apices; central region has a narrow clear area on both sides of central nodule; pseudoraphe valves have slightly radial striae, which in larger specimens are slightly more separated in the central region; central sternum is lanceolate with expanded region at center of valve; externally, proximal ends of raphe are not widened and end directly opposite each other, and distal raphe ends terminate at valve face/mantle junction and do not bend; striae on raphe valves have 2-5 rows of areolae; and striae on pseudoraphe valves have 2 or more rows of areolae.

Dimensions: (from Mayer, 1919)

Width: 5.5 µm

Length: 10-12 µm

Valve face striae/10 µm: 13-14

(Calculated length/width ratio: 1.82-2.18)

Dimensions: for North American populations (from Morales, 2002)

Width: 3.5-5.5 µm

Length: 3.5-13 µm

Valve face striae/10 µm: 13-16

(Calculated length/width ratio: 1.00-2.36)

Ecology for the species Achnanthes conspicua: found in oligotrophic to eutrophic waters,

especially those with low alkalinity and middle to high electrolytes (Krammer & Lange-Bertalot,

2004).

Geologic range of genus *Platessa*: a modern genus whose origins are derived from revisions of the genus *Achnanthes*, whose earliest recorded occurrence is reported by Frank Round and David Williams *In* Harding & Chant (2000) in this late Eocene deposit.

New Species Diagnosis

Platessa florissantia sp. nov. is distinguished from the genus type species *P. bavarica* Lange-Bertalot & G. Hofmann (Krammer and Lange-Bertalot,

2004) by the following characters: its entire and perfectly elliptical valve outline; wider copulae; a distinct, imperforate rim of silica at the valve face-mantle juncture; a wider stauros on the raphid valve, the greater tendency for uniseriate than biseriate striae, a narrower lanceolate sternum on the araphid valve. *Platessa florissantia* sp. nov. is distinguished from *Platessa conspicua* (A. Mayer) Lange-Bertalot by the tendency to have mostly uniseriate tending toward biseriate striae, rather than 3 or more rows of areolae per stria, and the greater density of striae of 20-22 per 10 μm compared with 11-16 per 10 μm in *P. conspicua*.

Etymology

The name refers to the geologic formation of Florissant and its place name from the town of that name in Colorado in which this species is first described.

Platessa morphotype 'Clare's 1'

Plate 25, Figure 5.

UCM #41015

Description

Morphology: monoraphid (heterovalvar) pennate, elongate elliptical, slightly convex araphid valve with rounded apices; uniseriate striae that are parallel to slightly radiating; areolae apically elongated; a single row of mantle areolae; a narrow lanceolate sternum and a unilateral central area on this araphid valve.

Dimensions: Width: est. 4.5 µm

Length: 10 µm Valve face striae/10 µm: 18 Length/width ratio: 2.22

Comments

Taphonomic Effects: only a single specimen observed and in SEM.

Orientation/Habit/Associations: in sample CQ1-11-12.

Psammothidium Bukhtiyarova & Round 1996

Psammothidium morphotype 'Clare's 1'

Plate 26, Figures 1 & 2.

Figured Specimens

UCM #41016

Description

Morphology: monoraphid (heterovalvar) pennate, elongate elliptical, slightly convex araphid valve with rounded apices; uniseriate striae that are parallel to slightly radiating; areolae apically elongated; a single row of mantle areolae; a narrow lanceolate sternum and a unilateral central area on this araphid valve.

Dimensions: Width: 7 μm Length: 13.5 μm Valve face striae/10 μm: 26 Length/width ratio: 1.93

Comments

Taphonomic Effects: only a single specimen observed and in SEM.

Orientation/Habit/Associations: associated with a variety of pennates and *Aulacoseira* in sample CQ2-1-03.

Ecology for the genus *Psammothidium*: most species of the modern genera are restricted to acidic waters (Flower & Jones, 1989; Bukhtiyarova & Round, 1996).

Geologic range of genus *Psammothidium*: a modern genus whose existence is derived from revisions of the genus *Achnanthes*. The earliest recorded occurrence of *Achnanthes* is reported by Frank Round and David Williams *In* Harding & Chant (2000) in this late Eocene deposit.

Diadesmis Kützing 1844

Diadesmis morphotype 'Clare's 1'

Plate 27, Figure 1.

Figured Specimens

UCM #41017

Description

Morphology: biraphid pennate, naviculoid frustule with broadly rounded to rounded cuneate apex; flat valve face with sparse, occluded, elongate puncta separated by transapical ribs; silica ridge at valve face and mantle juncture; and shallow mantle with a single row of poroids.

Dimensions: Width: undetermined

Length: undetermined

Valve face striae/10 µm: undetermined

Length/width ratio:undetermined

Comments

Taphonomic Effects: commonly incomplete frustules due to mechanical damage in processing.

Orientation/Habit/Associations: uncommon; usually seen in mudstones of samples CQ1-27-35.

Ecology for the genus *Diadesmis*: typically aerophytic and tends to be associated with mosses and attached to damp rocks; often in waters of low conductance and slightly low pH (Kociolek & Spaulding, 2003). *Diadesmis* is almost restricted to subaerial habitats like damp moss or rock; the following species are observed at well-illuminated sites outside limestone caves and at their entrances: *D. aerophila* (Krasske) D.G. Mann, *D. contenta* (Grunow ex Van Heurck) D.G. Mann, and *Diadesmis gallica* W. Smith (Poulíčková and Hašler, 2007).

Geologic range of genus *Diadesmis*: occurs in modern environments; earliest recorded occurrence is in this late Eocene deposit.

Diadesmis morphotype 'Clare's 2' Plate 27, Figure 2.

UCM #41018

Description

Morphology: biraphid pennate, naviculoid frustule with rounded cuneate apex; centrally expanded frustule with rounded cuneate apex; a filiform raphe bisects sternum ridge; simple proximal raphe ends are widely spaced; rounded bilateral fascia; and dense, slightly radial rows of puncta.

Dimensions: Width: est. 3 µm

Length: est. 13 µm Valve face striae/10 µm: est. 32-34 Length/width ratio: est. 4.33

Comments

Taphonomic Effects: commonly incomplete frustules due to mechanical damage in processing.

Orientation/Habit/Associations: uncommon; usually seen in mudstone of sample CQ2-2-05.

Diadesmis morphotype 'Clare's 3'

Plate 27, Figure 3.

UCM #41019

Description

Morphology: valve view of fragment showing central area with rounded bilateral fascia and widely spaced simple proximal raphe ends; slightly expanded central area of rectangular-shaped portion in valve view; dense, parallel to slightly radial rows of puncta.

Dimensions: Width: est. 4 µm

Length: est. undetermined Valve face striae/10 µm: est. 26 Length/width ratio: undetermined

Comments

Taphonomic Effects: commonly incomplete frustules due to mechanical damage in processing.

Orientation/Habit/Associations: uncommon; usually seen in mudstone of sample CQ1-10-11.

Diadesmis morphotype 'Clare's 4'

Plate 27, Figure 4.

Figured Specimens

Description

Morphology: girdle view of incomplete frustule showing rectangular shape; shallow mantle and mantle poroids, hyaline thickness of broad fascia in central area, and cingular elements.

Dimensions: Width: undetermined

Length: undetermined Striae or poroids on mantle/10 µm: 27 Length/width ratio: undetermined

Comments

Taphonomic Effects: commonly incomplete frustules due to mechanical damage in processing.

Orientation/Habit/Associations: uncommon; usually seen in mudstone of sample CQ1-10-11.

Diadesmis morphotype 'Clare's 5'

Plate 27, Figures 5-6.

Figured Specimens

UCM #41021

Description

Morphology: polar fragment showing rounded cuneate pole with a straight raphe within a broad axial area bordered by short straight striae and a silica ridge at valve face and mantle juncture; simple distal raphe ending; two opposing crescent-shaped hyaline areas lateral at pole.

Dimensions: Width: undetermined

Length: undetermined Striae or poroids on mantle/10 µm: 26 Length/width ratio: undetermined

Comments

Taphonomic Effects: commonly incomplete frustules due to mechanical damage in processing.

Orientation/Habit/Associations: uncommon; usually seen in mudstone of sample CQ2-2-05.

Note Regarding Uncommon Crescent Feature: the two opposing crescent-shaped hyaline areas lateral at pole observed in this specimen. Similar features are observed at both poles in SEM internal views of modern specimens of *Diadesmis aerophila* (Krasske) D.G. Mann from caves in central Moravia in the Czech Republic (Poulíčková and Hašler, 2007).

Diadesmis morphotype 'Clare's 6'

Plate 28, Figures 1-2.

UCM #41022 - 41023

Description

Morphology: greater-than-half valve fragment with broadly rounded to cuneate apex; narrowly separated proximal raphe ends on rounded bilateral fascia; raphe bisects thick, broad sternum; parallel to slightly radial elongate puncta are separated by transapical ribs; silica ridge at valve face and mantle juncture.

Dimensions: Width: est. 3 µm

Length: est. 20-22 µm Valve striae/10 µm: 26 Length/width ratio: est. 6.67-7.33

Comments

Taphonomic Effects: commonly incomplete frustules due to mechanical damage in processing.

Orientation/Habit/Associations: uncommon; usually seen in mudstone of sample CQ2-0-04.

Diadesmis morphotype 'Clare's 7'

Plate 28, Figure 3.

UCM #41024

Description

Morphology: small, biraphid pennate, linear elliptical frustule with rounded apices; straight raphe within broad, lanceolate sternum; distinct round, bilateral central area (central nodule); fine, parallel valvar striae whose density is unresolvable in LM.

Dimensions: Width: 2.5 µm

Length: 11 µm Valve striae/10 µm: undetermined Length/width ratio: 4.4

Comments

Taphonomic Effects: commonly incomplete frustules due to mechanical damage in processing.

Orientation/Habit/Associations: uncommon; usually seen in mudstone of sample CQ1-12-13.

Diadesmis morphotype 'Clare's 8'

Plate 28, Figure 4.

UCM #41025

Description

Morphology: small, biraphid pennate, lineate rectangular frustule with rounded apices; straight raphe within medium-width sternum; distinct round, bilateral central area (central nodule); fine, parallel valvar striae. Dimensions: Width: 2.5 µm

Length: 12 μm Valve striae/10 μm: 32 Length/width ratio: 4.8

Comments

Taphonomic Effects: commonly incomplete frustules due to mechanical damage in processing.

Orientation/Habit/Associations: uncommon; usually seen in mudstone of sample CQ1-8-09.

Frustulia C.A. Agardh 1824; Rabenhorst 1853

Frustulia rhomboides var. coloradensis var. nov.

Plate 29, Figures 1-5.

Syntypes

UCM #s 41026-41028

Description

Morphology: biraphid, rhombic lanceolate frustule with rounded cuneate apices; a straight, filiform raphe within a broad sternum terminates in a tip formed at juncture of two axial ribs at distal raphe end (porto crayon); dense, parallel to slightly radiate, uniseriate striae of small round puncta form a cross-pattern due to the relatively uniform spacing of puncta in apical and transapical directions; fascia absent; externally, slightly transapically expanded proximal raphe ends are widely separated by an elongate central nodule; internally, the proximal raphe ends are slightly deflected and the central nodule is eccentric, being slightly expanded on one side; externally, distal raphe ends are "T-shaped"; an irregular row of poroids parallels raphe along both sides of axial area.

Dimensions: Width: 20 µm

Length: est. 78 µm Transverse striae/10 µm: 30-31 Longitudinal striae/10 µm: est. 36 Length/width ratio: est. 3.9

Comments

Taphonomic Effects: because of their large size and elongated shape, individuals in LM are fragmented during the destructive slide preparation.

Orientation/Habit/Associations: very uncommon; associated with a wide variety of pennate taxa and the genus *Aulacoseira* in sample CQ1-13-14 and with *Diadesmis* in CQ1-10-11.

Most Similar Published Species: F. rhomboides var. amphipleuroides (Grunow) Cleve

Reference: Patrick & Reimer, 1966

Description: this variety differs from the nominate variety in that the siliceous ribs enclosing the raphe are slightly eccentric and bent a little; and also the central nodule is elongate.

Dimensions: Width: 15-30

Length: 70-160 μm Transverse striae/10 μm: 22-24 Longitudinal striae/10 μm: 18-24 Length/width ratio: 4.67-5.33

Ecology of *Frustulia rhomboides* var. *amphipleuroides* : (from Patrick & Reimer, 1966) found in slightly acid water of low mineral content.

Geologic range of genus *Frustulia*: a modern genus whose earliest occurrence has been observed in early and middle Eocene by Kociolek and Benson for this study in slides reposited at the California Academy of Sciences from the Horsefly lake deposits in British Columbia, Canada, (CAS Accession #701462, Slide #1021059) and the Dewey beds in Idaho, (CAS Accession #702136, Slide #1028081), respectively.

New Variety Diagnosis:

This new variety *Frustulia rhomboides* var. *coloradensis* var. nov. is distinguished from *F. rhomboides* var. *amphipleuroides* by its greater density of transverse and longitudinal striae and from the nominate variety both by its greater density of striae and by its eccentric elongated central nodule.

Etymology:

The name recognizes the state of Colorado in which this species is found.

Pinnularia C.G. Ehrenberg 1843

Pinnularia morphotype 'Clare's 1'

Plate 30, Figure 1.

Figured Specimens

UCM #41029

Description

Morphology: biraphid, linear frustule with broadly rounded apices; filiform raphe with distal ends deflected and simple proximal ends slightly unilaterally deflected to opposite side from distal raphe end deflections; very closely-spaced proximal raphe ends; parallel biseriate alveolate striae of round puncta, each stria having a single areola nearest the wide axial area; a broad stauros fascia in central area.

Dimensions: Width: est. 7 µm

Length: 42 µm Striae/10 µm: 8-9 Length/width ratio: est. 6

Comments

Taphonomic Effects: because of their large size and elongated shape, individuals in LM are fragmented during the destructive slide preparation.

Orientation/Habit/Associations: uncommon; sometimes associated with *Diatoma*; observed in samples CQ1-11-12.

Ecology of this genus: often abundant in low conductance, slightly acidic freshwaters (Kociolek & Spaulding, 2003).

Geologic range of genus *Pinnularia*: a modern genus whose earliest reported occurrence is by Lohman & Andrews (1968) in the 47-49 Ma. middle Eocene Wagon Bed Formation in Wyoming.

Pinnularia morphotype 'Clare's 2' Plate 30, Figure 2.

Figured Specimens

UCM #41030

Description

Morphology: biraphid, linear frustule with broadly rounded apex; raphe with distal ends deflected and simple proximal ends slightly unilaterally deflected to opposite side from distal raphe end deflections; coarse outlines of alveoli are radial near central area and parallel toward pole.

Dimensions: Width: est. 7 µm

Length: undetermined

Striae/10 µm: 6-7

Length/width ratio: undetermined

Comments

Taphonomic Effects: because of their large size and elongated shape, individuals in LM are fragmented during the destructive slide preparation.

Orientation/Habit/Associations: uncommon; observed in sample CQ1-10-11.

Pinnularia morphotype 'Clare's 3'

Plate 30, Figure 3.

Figured Specimens

UCM #41031

Description

Morphology: biraphid, linear frustule with broadly rounded apex; raphe with distal ends

deflected; coarse alveoli radiate away from poles.

Dimensions: Width: est. 5 µm

Length: undetermined

Striae/10 µm: est. 10

Length/width ratio: undetermined

Comments
Taphonomic Effects: because of their large size and elongated shape, individuals in LM are fragmented during the destructive slide preparation.

Orientation/Habit/Associations: uncommon; observed in sample CQ1-10-11.

Pinnularia morphotype 'Clare's 4'

Plate 30, Figure 4.

Figured Specimens

UCM #41032

Description

Morphology: biraphid, linear frustule with broadly-rounded to slightly subcapitate apex; raphe with distal ends deflected around terminal nodule at apex; coarse alveoli radiate away from central area, become parallel mid-poleward, and then radiate away from poles at apex; a fascia partially visible in central area.

Dimensions: Width: est. 3.5 µm

Length: est. 30 µm Striae/10 µm: 17 Length/width ratio: est. 8.57

<u>Comments</u>

Taphonomic Effects: because of their large size and elongated shape, individuals in LM are fragmented during the destructive slide preparation.

Orientation/Habit/Associations: uncommon; observed in sample CQ1-10-11.

Pinnularia morphotype 'Clare's 5'

Plate 30, Figure 5.

Figured Specimens

UCM #41033

Description

Morphology: biraphid, linear frustule fragment of central area showing multiseriate alveoli converging on central area around a lanceolate rhombic bilateral fascia; proximal raphe ends are unilaterally deflected.

Dimensions: Width: est. 9 µm

Length: undetermined Striae/10 µm: 9-10 Length/width ratio: undetermined

Comments

Taphonomic Effects: because of their large size and elongated shape, individuals in LM are fragmented during the destructive slide preparation.

Orientation/Habit/Associations: uncommon; observed in sample CQ1-10-11.

Adlafia Moser, Lange-Bertalot et Metzeltin 1998

Adlafia tellerii sp. nov.

Plate 31, Figures 1-7.

<u>Syntypes</u>

UCM #s 41034-41041

Description

Morphology: biraphid pennate, naviculoid, linear elliptical to lanceolate frustule shape; broadly rounded apices; striae radial to sinusoidal in central region, become nearly parallel away from center, after which a shortened stria on each side of the sternum marks a reversal in angle of striae (abruptly convergent) that continues polewards; striae are uniseriate with round puncta; striae extend along height of tall mantle; straight filamentous raphe to valve margin where deflection prominent; proximal raphe ends simple and slightly expanded; distal raphe ends unilaterally deflected onto apical mantle in a curve that well-exceeds 90 degrees; short curved striae continue on mantle on both sides of raphe, terminating against a hyaline ridge that follows the raphe curve. Cingulum elements often missing; when present, valvocopula has a transverse row of poroids on both advalvar and abvalvar margins. <25 μ m length; organic occlusions on areolae not differentiated in this fossil material.

Dimensions: Width in middle: est. 4.5-6.0 µm

Length: est. 15-22 µm Frustule height: est. 3-4 µm Valve face striae/10 µm: 16-18 Areolae/10 µm: est. 24 Length/width ratio: 3.33-3.67

Comments

Taphonomic Effects: relatively intact after burial, but for some areas of dissolution (corrosion) of valve mantle margin and associated cingulum elements on some individuals, as observed in SEM.

Orientation/Habit/Associations: solitary, sometimes associated with *Fragilaria*. Observed only in SEM and only in Sample CQ1-11-12.

Most similar published species: Adlafia muscora (Kociolek et Reviers) Moser, Lange-Bertalot et Metzeltin.

References: Kociolek & Spaulding, 2003; Morales, 2003 - 8th NAWQA; the following description is taken from Moser, Lange-Bertalot & Metzeltin, 1998, *In* Morales & Le, 2005. Description: naviculoid, linear to linear-lanceolate frustule shape; rostrate to subcapitate apices; areolae round and occluded by a porous vola which lies at the outer periphery of each individual areola. In Morales (2003), this areolae covering is described as "a persistent extracellular organic coating that remains on modern specimens after acid digestion". Uniseriate radial striae. Raphe is simple filiform with external distal ends strongly deflected in the same direction; external proximal ends may be undeflected or slightly unilaterally deflected in direction opposite distal end deflection. Internally, distal raphe ends have a relatively small raised lip-like termination (helictoglossa); internally, proximal raphe ends are conspicuously unilaterally bent in opposite direction from distal ends. Girdle bands closed with two rows of poroids present on the valvocopula.

Dimensions: Width: (not specified)

Length: $<25 \,\mu m$

Valve face striae/10 µm: (not specified)

Length/width ratio: (not specified)

Ecology: aerophytic habitats, especially around mosses; some species found in oligotrophic lakes (Kociolek & Spaulding, 2003).

Next most similar published species: *Adlafia suchlandtii* (Hustedt) Lange-Bertalot. Reference: from Moser, Lange-Bertalot & Metzeltin, 1998, *In* Lange-Bertalot, 2001. Description: valves linear; apices almost indistinctly protracted, cuneately narrowed with obtusely rounded ends.

Dimensions: Width: 2.5-3.0 μm (type material); 2.0-3.5 μm (other) Length: 12-15 μm (type material); 11-20 μm (other) Valve face striae/10 μm: 26-28 Length/width ratio: 4.8-5.0 (type); 5.5-5.7 (other)

Ecology for species: in various waters, predominantly associated with oligosaprobic conditions; locally frequent on intermittently wet bryophytes; aerophilous.

Geologic range of genus *Adlafia*: an extant genus not previously recognized in the fossil record prior to this late Eocene occurrence.

New Species Diagnosis:

This new form is assigned to the genus *Adlafia* rather than the genus *Placoneis* on the basis of its less than 25 μ m length.

Adlafia tellerii sp. nov. is distinguished from the genus type species *A. muscora* and from *A. suchlandtii* by its broadly rounded apices. The absence of the areolar vola described by Morales (2003) has little diagnostic relevance in fossil forms, as such organic material would not be expected to survive natural deterioration brought about by taphonomic processes.

Etymology

The name recognizes the location in which not only this new species is found, but in which the earliest record of the genus *Adlafia* is reported. It bears the epithet of the Colorado county of Teller in which this study was conducted.

Navicula Bory de St.-Vincent 1822

Navicula eomenisculus sp. nov.

Plate 32, Figures 1-3.

Syntypes

UCM #41042 - 41043

Description

Morphology: biraphid, naviculoid frustule; broadly lanceolate valves; symmetrical in apical and transapical planes; poles gradually tapering toward acutely rounded, cuneate apices; moderately narrow axial area containing a ridge in which the raphe lies; filamentous raphe with simple proximal and distal raphe ends; astigmate; small central nodule; striae uniseriate with slit-like areolae (lineolae); striae straight parallel in apical regions becoming slightly radiating and sinusoidal in center; 3-4 shorter striae on each side of central area.

Selected Dimensions:

Width in middle: 12-14 µm

Length: 30-34 µm Striae/10 µm: 12-13 at center, 15 toward apices Lineolae/10 µm: 24-30 Length/width ratio: 2.43-2.50

Comments

Taphonomic Effects: despite their larger size, frustules of this species tend to have survived the taphonomic and lab processes relatively well.

Orientation/Habit/Associations: Found as singles in valve view in association with a variety of other pennate diatoms including *Synedra*, *Diatoma*, and the diminutive monoraphid forms, as well as the centric *Aulacoseira*. Samples CQ1-13-14 and CQ1-32-50.

Most similar published species: Navicula menisculus Schumann.

References: Morales (2001); Lange-Bertalot (2001); Krammer & Lange-Bertalot (2008, reprinted from 1997 & 1999); Pantocsek (1902).

Description 1 (from Morales, 2001): broadly lanceolate with frequently perfectly cuneate ends; axial area is narrow, striae are very conspicuous; lineolae are often visible during routine analyses; striae are radiate and sometimes somewhat curved at the central portion of the valve due to the fact that the raphe lies on a depression (ridge) that runs along the axial area of the valve. The striae are slightly radiate to parallel at the valve ends. Although this taxon may

occasionally have a short stria flanked by smaller ones at one side of the central area, the reverse is usually true; i.e., a smaller stria is surrounded by two longer ones.

Dimensions: (none given)

Description 2 (from Lange-Bertalot (2001): valves, considerably uniform in outlines, broadly lanceolate tapering to the cuneate ends, not protracted, simply rounded acutely to somewhat obtusely; raphe moderately lateral, central pores distinct, slightly deflected to the secondary side; axial area moderately narrow, almost linear; central area relatively small, circular to rhombic; striae moderately radiate becoming parallel to somewhat indistinctly convergent at the ends; lineolae comparatively coarse.

Dimensions: from Lange-Bertalot (2001):

Width: 11.0-12.5 μm Length: 32-50 μm Striae/10 μm: 8.5-9.5 Lineolae/10 μm: 24-25 Length/width ratio: 2.9-4.0

Description 3 (from Krammer & Lange-Bertalot (2008, reprinted from 1997 & 1999): valves broadly lanceolate.

Dimensions: Width: 7.5-12.0 µm

Length: 15-50 µm Striae/10 µm: 8-12 Lineolae/10 µm: 25-30 Length/width ratio: 2.00-4.17 Description 4 (from Pantocsek, 1902): valves lanceolate, subrostrate poles, straight raphe, central nodule inflated, striae radiate.

Dimensions: Width: 9-11 µm

Length: 27-29 µm

Striae/10 µm: 10

(Calculated length/width ratio: 2.64-3.00)

Ecology of *N. menisculus* from Lange-Bertalot (2001): meso- to moderately eutrophic, chalkrich and hence well-buffered freshwater lakes, intolerant to saprobity levels higher than oligo- to β -meso-saprobic.

Geologic range of the genus *Navicula*: earliest recorded occurrence of this modern genus is in middle Eocene Wagon Bed Formation of Wyoming by Lohman and Andrews (1968).

New Species Diagnosis

The new species is designated on the basis of the following characteristics that distinguish it from *N. menisculus* Schumann: greater density of striae of 12-13 per 10 μ m in center and 15 per 10 μ m toward poles; the slighter angle of radiation of the central area striae; the more gradual tapering along valve margin toward acutely rounded, cuneate apices, that results in more sharply angled poles; and the 2.5:1 length/width ratio of the valve that gives it a more centrally expanded shape.

Etymology

The name recognizes the close similarity of the new species with *N. menisculus* Schumann, and the Eocene epoch in which the new species makes its first appearance in the fossil record.

Stauroneis C.G. Ehrenberg 1843

Stauroneis morphotype 'Clare's 1'

Plate 33, Figures 1-3.

Figured Specimens

UCM #41044

Description

Morphology: biraphid, lanceolate elliptical frustule with narrowly rounded cuneate apices; a narrow rectangular bilateral stauros fascia (central nodule) in central area; parallel uniseriate striae of small round puncta, becoming slightly radial toward pole; narrow axial area; straight simple distal raphe end; simple proximal raphe end; and pseudoseptum evident at valve apex interior.

Dimensions: Width: 16.5 μm Length: est. 60 μm Striae/10 μm: 18-19

Comments

Taphonomic Effects: because of their large size and elongated linear valve shape, individuals in LM are fragmented during the destructive slide preparation.

Orientation/Habit/Associations: very uncommon; found in sample CQ2-1-03.

Ecology of genus *Stauroneis*: both benthic and planktic habitats of lakes and streams (Kociolek & Spaulding, 2003).

Geologic range of genus *Stauroneis*: a modern genus whose earliest reported occurrence is by Lohman & Andrews (1968) in the 47-49 Ma. middle Eocene Wagon Bed Formation in Wyoming.

Nitzschia Hassall 1845

Nitzschia morphotype 'Clare's 1'

Plate 34, Figures 1-2.

Figured Specimens

Description

Morphology: raphid keeled, fragmentary lineate elliptical frustule with rounded apices; transapical striae; a fibulate raphe system and keel on right lateral of valve, and hyaline areas of fibulae prominent.

Dimensions: Width: est. 6.5-7.0 µm

Length: undetermined

Striae/10 µm: 20-21

Length/width ratio: undetermined.

Comments

Taphonomic Effects: because of their elongated linear valve shape, individuals in LM are fragmented during the destructive slide preparation.

Orientation/Habit/Associations: very uncommon; found in sample CQ1-10-11.

Ecology of genus *Nitzschia*: many freshwater species are epipelic in microhabitat; this genus also contains planktic, epilithic, and epiphytic species (Lowe, 2003).

Geologic range of genus *Nitzschia*: a modern genus whose earliest reported occurrence is by Singh et al. (2007) in the late Cretaceous Deccan Traps of India.

Discussion

Of the 21 diatom genera identified in the Clare's Quarry site in the Florissant Formation, three are clearly dominant within the flora in the laminated shale units. This is the result of the intentional effort to isolate slide source material to the light-colored fine diatomite laminae of the laminated shale facies. These most abundant taxa are species of the genera Synedra, Diatoma, and Aulacoseira, which are elongate in frustule morphology. Among these, the Aulacoseira forms filamentous colonies. Their modern species are capable of living in the plankton of lakes, although they are not exclusive to planktonic habitats. Synedra and Diatoma occur in the Florissant flora as monospecific genera. The specimens of *Synedra* are similar to *S. ulna* and *S.* acus, but are not conspecific to any known species. The individuals of *Diatoma* are assessed to be conspecific with the modern *D. tenuis*. The clearly dominant species of *Aulacoseira* at Clare's Quarry is A. clarensis sp. nov., which is closely similar to A. italica, a form known mostly from fossil deposits. Uncommonly, taxa that have affinities for A. distans, A. granulata, and possibly A. valida are also noted. All other taxa observed are uncommon to rare in abundance. Tetracyclus, Gomphonema, Achnanthidium, and Navicula are uncommon. The genera Fragilaria and Staurosira are very uncommon, but morphologically diverse; and the remaining genera are rare.

Of major significance is the fact that this flora contains the geologically earliest recognized occurrence of the following 8 genera: *Orthoseira*, *Synedra*, *Gomphonema*, *Achnanthidium*, *Platessa*, *Psammothidium*, *Diadesmis*, and *Adlafia*. Additionally, the isolated occurrence of *Actinoptychus*, although assumed to be allochthonous in origin, signifies its firstreported occurrence in freshwater deposits; however, its range as a marine taxon extends back to late Cretaceous (Strelnikova, 1975).

The 12 freshwater genera that were reported in the fossil record prior to the late Eocene of this deposit include the following: *Aulacoseira, Fragilaria, Staurosira, Diatoma, Tetracyclus, Eunotia, Planothidium, Frustulia, Pinnularia, Navicula, Stauroneis,* and *Nitzschia*. As discussed in the body of this report, *Fragilaria* was first reported from late Cretaceous continental deposits of Mexico; *Aulacoseira, Planothidium,* and *Nitzschia* were first observed from late Cretaceous continental deposits of India; and the remaining genera were first reported in early and middle Eocene lake deposits from British Columbia and Northwest Territories, Canada, and Wyoming and Idaho, USA. A review of the pre-Neogene non-marine diatom biochronology that includes a graphic synthesis and compares the flora from these deposits is in preparation in a separate manuscript.

The ecologic implications of the Florissant fossil diatom flora are in keeping with modern inland lakes that contain not only lake-dwelling taxa, but residents of a wide array of environments that border the lake, such as littoral benthics, riverine, and aerophytic species (Spaulding and McKnight, 1999). A forthcoming manuscript is in preparation that discusses the diatom ecology in the context of the sedimentology of this deposit to better define the processes at play in this lake environment.

This new account of the Florissant fossil diatom flora provides the clear evidence that supports the view that freshwater diatoms representing a minimum of 21 modern genera and several modern species had evolved prior to the existence of the 34 million year age of the Florissant lake system. Specifically, this record fills an informational gap about the phylogenetic progression of freshwater diatoms between early and middle Eocene floras of Canada, middle Eocene floras of Wyoming and Idaho, and the diverse and well-documented Neogene floras from other sites in western North America.

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(PLATES with figure captions on preceding page)

Figure 1. *Aulacoseira clarensis* sp. nov., SEM, showing girdle view of sibling valves joined by linking spines. Representative valve width at sibling juncture. Valve apparent diameter expanded due to flattening at less heavily silicified ringleiste and collum. Rimoportula seen on mantle interior adjacent to ringleiste. Sample CQ2-1-03. Syntype UCM #40917.

Figure 2. *Aulacoseira clarensis* sp. nov., SEM, enlargement of rimoportula of specimen shown in Figure 1. Orientation of slit is to the left toward the ringleiste. Sample CQ2-1-03. Syntype UCM #40917.

Figure 3. *Aulacoseira clarensis* sp. nov., SEM, detail of rimoportula of a different individual. Orientation of slit is to the right toward the ringleiste. Note the solid, moderately thick, shallow ringleiste. Sample CQ1-12-13. Syntype UCM #40918.

Figure 4. *Aulacoseira clarensis* sp. nov., SEM, girdle view of exposed linking valve of frustule showing subtle sinistrorse spiraling of areolar rows on mantle exterior. Spatulate linking spines interlock sibling valves. Sample CQ1-13-14. Syntype UCM #40919.

Figure 5. *Aulacoseira clarensis* sp. nov., SEM, flat, broadly spatulate linking spines with apiculate tips. Spines are rimmed with granules. One or more areolar rows enter the stem of each spine. Sample CQ1-13-14. Syntype UCM #40920.

Figure 6. *Aulacoseira clarensis* sp. nov., SEM, rows of elliptical to rounded rectangular areolae on exterior of valve mantle. Within the areolae, tiny struts are visible that support the velar plates in the interior of valve. Sample CQ1-13-14. Syntype UCM #40921.

Figure 7. *Aulacoseira clarensis* sp. nov., SEM, view of thick-based linking spines with heavily silicified stems; two spines interlocking with spatulate terminae seen on right. One or more areolar rows enter the stem of each spine. Sample CQ1-13-14. Syntype UCM #40922.



Figure 1. *Aulacoseira clarensis* sp. nov., SEM, gently concave interior of valve face with dense areolae covered by subcircular velar plates. Broadly spatulate linking spines with granules and apiculate tips along girdle on left and right. Sample CQ1-13-14. Syntype UCM #40923.

Figure 2. *Aulacoseira clarensis* sp. nov., SEM, detail of specimen shown in Figure 1. Dense coverage of areolae on interior of valve face and velar plates that are positioned over the areolae. Sample CQ1-13-14. Syntype UCM #40923.

Figure 3. *Aulacoseira clarensis* sp. nov., SEM, external translucent sheathing copula covering frustule; shown at sibling juncture with underlying linking spines and mantle areolae faintly visible. Sample CQ1-13-14. Syntype UCM #40924.

Figure 4. *Aulacoseira clarensis* sp. nov., LM, two images of same individuals in girdle view at different focal lengths. One complete frustule in center joined at each end to sibling valves. Right image illustrates the prevailing "hour-glass" frustular girdle view profile; the wide, plain colli of the frustule; the darkened lateral dimples in the valve walls pervalvar from the colli indicate the shallow depth of the ringleiste. Left image shows linking spines at sibling juncture; small, evenly-spaced, elliptical to rectangular mantle areolae; and gentle sinistrorse spiraling of areolar rows on mantle exterior. Although no conclusive rimoportulae are observed, a slight hyaline feature adjacent to the ringleiste in the left image is suggestive of a rimoportula, as seen in SEM images in Plate 1. Sample CQ1-13-14. Syntype UCM #40925.

Figure 5. *Aulacoseira clarensis* sp. nov., LM, two images of same individuals in valve view at different focal lengths. Both images show dense coverage of areolae on valve face and linking spines along the girth. Lowermost spines rimming the lower image illustrate the broadly spatulate-anvil shape. Sample CQ1-13-14. Syntype UCM #40926.

Figure 6. *Aulacoseira clarensis* sp. nov., LM, linking spines extending from a fragment of valve mantle. A single intact spine shows the broadly spatulate-anvil shape. Sample CQ1-13-14. Figured Specimen UCM #40927.



Figure 1-6. *Aulacoseira* sp. 1, LM, six images of same individual in valve view at different focal lengths. Valve covered with large round areolae, linking spines marginal to valve face; Fig. 4-6 deep, solid ringleiste with one or two possible rimoportulae on the interior surface of the ringleiste. Sample CQ1-8-09. Figured Specimen UCM #40928.



Plate 4-Aulacoseira morphotypes "Clare's 1, 2, & 3"

Figure 1. *Aulacoseira* morphotype "Clare's 1", LM, two images of same individuals in girdle view at different focal lengths. Both images show the less common straight valvar girdle view profile and a very wide collum. Left image is a view of exterior of mantle with evenly spaced, nearly straight rows of round areolae. Right image is an interior view with darkened indications of a shallow ringleiste at mantle-collum contact and mottled texture of velar plates on interior mantle wall. Sample CQ2-1-03. Figured Specimen UCM #40929.

Figure 2. *Aulacoseira* morphotype "Clare's 2", SEM, uncollapsed centric valve in girdle view with dextrorse spiraling of areolar rows on mantle exterior partially obscured by sheathing copula, lying adjacent to the typical *A. clarensis* sp. nov. collapsed (hour-glass) morphotype. Sample CQ1-13-14. Figured Specimen UCM #40930.

Figure 3. *Aulacoseira* morphotype "Clare's 3", SEM, separation valve with thick based, conical separation spines at ends of pervalvar costae. Elongate mantle areolae at outer stem of spines. Valve face areolae visible. Sample CQ1-13-14. Figured Specimen UCM #40931.



Plate 5-Orthoseira roeseana (Rabenhorst) O'Meara

Figure 1-3. *Orthoseira roeseana*, LM, three images of same individual in girdle view at different focal lengths. Narrow collum visible; areolar striae on mantle anastomosing both toward and away from spines, blade-like spines marginal to valve face; Fig. 2-3 ring-like suggestions of velar plates over areolae in valve interior. Sample CQ1-12-13. Figured Specimen UCM #40932.

Figure 4-9. *Orthoseira roeseana*, LM, six images of same individual in valve view at different focal lengths. Three rimmed carinoportulae in central area; radial valve face striae of coarse round areolae. Sample CQ1-8-09. Figured Specimen UCM #40933.

Figure 10-15. *Orthoseira roeseana*, LM, six images of same individual in girdle view at different focal lengths. Cingulum visible in 12-15; copulae split and ligulate, exposing rows of mantle areolae that extend beneath; robust anastomosing areolar striae on mantle, becoming finer toward collum; blade-like spines marginal to valve face. Sample CQ1-12-13. Figured Specimen UCM #40934.


Figure 1. *Orthoseira roeseana*, SEM, relict blade-like spines on mantle along valve face margin. Spines are extensions of mantle costae and valve face costae, but for occasional spine bases that originate as separate costae around which mantle costae curve or branch, creating the appearance of anastomosing striae toward the spines. Sample CQ1-27-35. Figured Specimen UCM #40935.



Plate 7-Actinoptychus sp. 1

Figure 1-3. *Actinoptychus* sp. 1, LM, three images of same individual in valve view at different focal lengths. Valve fragment is sectored into six sectors that alternate in high and low relief. Valve face has radiating large round areolae and nodes and spines are suggested along margin in Figs. 2 & 3; Fig. 1 suggests a rimoportula on the marginal area of the raised sector. Sample CQ1-10-11. Figured Specimen UCM #40936.



Plate 8-Undetermined Centric

Figure 1-6. Centric morphotype 'Clare's 1', LM, fragmented valve view of same individual in six images at different focal lengths. Figs. 1 & 2 show large round valve face. Figs. 2 & 3 reveal fine marginal striae that seem to grade into distinctly areolated striae that converge into the center of the valve face, as observed in Figs. 4-6. Robust marginal spines are suggested on the left margin in Figs. 4-6. Sample CQ1-9-10. Figured Specimen UCM #40937.



Figure 1. *Fragilaria vaucheriae* var. *lohmans* var. nov., SEM, whole lanceolate frustule with valves apart, bilateral fascia (central area), diminution of lineolae length to rounded puncta toward sternum. Sample CQ1-13-14. Syntype UCM #40938.

Figure 2. *Fragilaria vaucheriae* var. *lohmans* var. nov., SEM, whole ovate frustule with valves apart, bilateral fascia (central area), diminution of lineolae length to rounded puncta toward sternum. Sample CQ1-13-14. Syntype UCM #40939.

Figure 3. *Fragilaria vaucheriae* var. *lohmans* var. nov., SEM, partly crushed whole lanceolate frustule with bilateral fascia and apical pore field on left. Sample CQ1-13-14. Syntype UCM #40940.

Figure 4. *Fragilaria vaucheriae* var. *lohmans* var. nov., SEM, surface with group of frustules showing a range of morphotypes. (Light horizontal streaks across image are artifacts of SEM.) Sample CQ1-11-12. Syntype UCM #40941.

Figure 5. *Fragilaria vaucheriae* var. *lohmans* var. nov., SEM, enlarged view of frustule apices from image in Figure 3, showing apical pore fields. (Light horizontal streaks across image are artifacts of SEM.) Sample CQ1-11-12. Syntype UCM #40941.

Figure 6. *Fragilaria vaucheriae* var. *lohmans* var. nov., SEM, elongate frustule with completely bilateral fascia. Such forms are easily confused with *Synedra* sp. Distinguished from *Synedra* sp. by its less-well-delimited fascia boundaries, more pronounced offset of striae, and lineolae size diminution towards sternum. (Light horizontal streaks across image are artifacts of SEM.) Sample CQ1-11-12. Syntype UCM #40942.

Figure 7. *Fragilaria vaucheriae* var. *lohmans* var. nov., SEM, internal valve view showing transapical striae, bilateral fascia, and girdle bands. Sample CQ1-11-12. Syntype UCM #40943.

Figure 8. *Fragilaria vaucheriae* var. *lohmans* var. nov., SEM, fusiform valve showing a slightly inflated unilateral fascia with dark areas of phantom striae. Sample CQ1-11-12. Syntype UCM #40944.



Figure 1. *Fragilaria vaucheriae* var. *lohmans* var. nov., LM, lanceolate frustule with valves apart; slightly bilateral fascia (central area); striae parallel. Sample CQ1-13-14. Syntype UCM #40945.

Figure 2. *Fragilaria vaucheriae* var. *lohmans* var. nov., LM, lanceolate frustule with valves apart; slightly bilateral fascia (central area); striae parallel. Sample CQ1-13-14. Syntype UCM #40946.

Figure 3. *Fragilaria vaucheriae* var. *lohmans* var. nov., LM, lanceolate to clavate frustule with apicular and transapical asymmetry; strongly bilateral fascia (central area); striae parallel to slightly radial from sternum. Sample CQ1-13-14. Syntype UCM #40947.

Figure 4. *Fragilaria vaucheriae* var. *lohmans* var. nov., LM, elliptic-lanceolate frustule with valves apart; unilateral fascia (central area); striae parallel to slightly radial from sternum. Sample CQ1-13-14. Syntype UCM #40948.

Figure 5. *Fragilaria vaucheriae* var. *lohmans* var. nov., LM, lanceolate frustule with valves apart; strongly bilateral fascia (central area); striae parallel to slightly radial from sternum; apices missing or obscured. Sample CQ1-13-14. Syntype UCM #40949.

Figure 6. *Fragilaria vaucheriae* var. *lohmans* var. nov., LM, elliptic-lanceolate frustule with valves apart; apically and transapically asymmetrical; unilateral fascia (central area); striae somewhat radial from sternum. Sample CQ1-13-14. Syntype UCM #40950.

Figure 7. *Fragilaria vaucheriae* var. *lohmans* var. nov., LM, elliptic-ovate frustule with transapical asymmetry; unilateral fascia (central area); striae parallel to slightly radial from sternum; sternum shows curvature adjacent to fascia. Sample CQ1-13-14. Syntype UCM #40951.



Plate 11-Staurosira morphotype 'Clare's 1'

Figure 1. *Staurosira* morphotype 'Clare's 1', SEM, valve view at angle of elliptical frustule shows medium-width elliptical axial area; short uniseriate striae of transapically elongate elliptical areolae; narrow striae and broad costae show slight off-set across axial area; marginal spines on costae project outward away from valve, then are re-curved back toward valve at termina; round broken bases of spines are solid, rather than hollow. Sample CQ1-13-14. Figured Specimen UCM #40952.

Figure 2. *Staurosira* morphotype 'Clare's 1', SEM, valve view at angle of clavate frustule shows narrow axial area; narrow uniseriate striae of round areolae show slight off-set laterally; costae broad; marginal spines on costae project outward away from valve, then are abruptly re-curved back toward valve at termina; round broken bases of spines are solid, rather than hollow. Sample CQ1-13-14. Figured Specimen UCM #40953.

Figure 3. *Staurosira* morphotype 'Clare's 1', SEM, girdle view of elongate elliptical or lanceolate frustule shows steep-sided mantle; cingulum elements are indistinctly discernable; round areolae of narrow valvar striae extend onto mantle; marginal spines on broad costae. Sample CQ1-13-14. Figured Specimen UCM #40954.



Plate 12-Staurosira morphotypes 'Clare's 2 & 3'

Figure 1. *Staurosira* morphotype 'Clare's 2', SEM, three-quarters valve view of centrallyexpanded lanceolate frustule with rostrate apices shows medium-width elliptical axial area; narrow uniseriate striae of apically-elongate elliptical to rectangular areolae; broad costae; striae and costae show slight off-set across axial area; apical pore field barely discernable on mantle; no marginal spines present. Sample CQ1-13-14. Figured Specimen UCM #40958.

Figure 2. *Staurosira* morphotype 'Clare's 2', SEM, three-quarters valve view of centrallyexpanded lanceolate frustule with rostrate apices shows side of girdle area; medium-width elliptical axial area; narrow uniseriate striae of apically-elongate elliptical to rectangular areolae; broad costae; striae and costae show slight off-set across axial area; apical pore field barely discernable on mantle; no marginal spines present. Sample CQ1-13-14. Figured Specimen UCM #40959.

Figure 3. *Staurosira* morphotype 'Clare's 3', SEM, broken valve view of centrally-expanded lanceolate frustule with rounded cuneate apices shows side of girdle area and part of valve face; part of valvar axial area exposed; narrow uniseriate striae of apically-elongate elliptical to rectangular areolae; broad costae; apical pore field discernable on valve face at pole; no marginal spines present; wide valvocopula on valve to the right. Sample CQ1-13-14. Figured Specimen UCM #40967.

Figure 4. *Staurosira* morphotype 'Clare's 2', SEM, interior of broken centrally-expanded lanceolate frustule with rostrate apices shows internal view of uniseriate striae with minute volae barely discernable. Sample CQ1-13-14. Figured Specimen UCM #40960.





5 um

Plate 13-Staurosira morphotypes 'Clare's 1 & 2'

Figure 1. *Staurosira* morphotype 'Clare's 1', LM, valve view of broadly elliptical frustule with broadly rounded apices; narrow, parallel to slightly radial striae separated by broad costae that are slightly off-set across axial area. Sample CQ1-13-14. Figured Specimen UCM #40955.

Figure 2. *Staurosira* morphotype 'Clare's 1', LM, valve view of elongate elliptical frustule with broadly rounded apices; narrow elliptical axial area; narrow, parallel to slightly radial striae separated by broad costae that are slightly off-set across axial area. Sample CQ1-13-14. Figured Specimen UCM #40956.

Figure 3. *Staurosira* morphotype 'Clare's 1', LM, valve view of fusiform frustule with cuneate apices; narrow elliptical axial area; narrow, parallel to slightly radial striae separated by broad costae that are slightly off-set across axial area. Sample CQ1-13-14. Figured Specimen UCM #40957.

Figure 4. *Staurosira* morphotype 'Clare's 2', LM, valve view (on left) and wedge-shaped girdle view (on right) of lanceolate frustule with rostrate apices; narrow lanceolate axial area; narrow, parallel to slightly radial striae separated by broad costae that are slightly off-set across axial area. Sample CQ1-13-14. Figured Specimen UCM #40961 (left) and Figured Specimen UCM #40962 (right).

Figure 5. *Staurosira* morphotype 'Clare's 2', LM, valve view of rhombic lanceolate frustule with cuneate apices; narrow lanceolate axial area; narrow, parallel to slightly radial striae separated by broad costae that are slightly off-set across axial area. Sample CQ1-13-14. Figured Specimen UCM #40963.

Figure 6. *Staurosira* morphotype 'Clare's 2', LM, valve view of clavate frustule with one pole broadly rounded rostrate and the other, narrowly rostrate; narrow lanceolate axial area; narrow, parallel to slightly radial striae separated by broad costae that are slightly off-set across axial area. Sample CQ1-13-14. Figured Specimen UCM #40964.

Figure 7. *Staurosira* morphotype 'Clare's 2', LM, valve view of centrally-expanded lanceolate frustule with rostrate apices; elliptical axial area; narrow, parallel to slightly radial striae separated by broad costae that are slightly off-set across axial area. Sample CQ1-13-14. Figured Specimen UCM #40965.

Figure 8. *Staurosira* morphotype 'Clare's 2', LM, valve view of elongate, centrally-expanded lanceolate frustule with rostrate apices; narrow axial area; narrow, parallel to slightly radial striae separated by broad costae that are slightly off-set across axial area. Sample CQ1-13-14. Figured Specimen UCM #40966.



Figure 1-2. *Diatoma tenuis*, SEM, part of frustule in external valve view showing parallel striae, transapical costae, and straight narrow sternum. Fig. 2 is close-up view of Fig. 1, showing slightly off-set uniseriate striae of small round puncta, sternum, and costae. Sample CQ1-13-14. Figured Specimen UCM #40968.

Figure 3. *Diatoma tenuis*, SEM, external view of broadly rounded apex with radial striae and extended sternum beyond terminal costa, and distinct apical pore field. Sample CQ1-13-14. Figured Specimen UCM #40969.

Figure 4. *Diatoma tenuis*, LM, valve view of broadly rounded apex revealing terminal costae, radial apical striae, extended sternum, and single transapical labiate structure on left lateral. Sample CQ2-0-04. Figured Specimen UCM #40970.

Figure 5. *Diatoma tenuis*, SEM, external valve view showing slightly off-set striae at sternum on valve face, perforated valvocopula, and partially-attached perforated cinguli. Striae separated by costae extend onto mantle, as seen on left valve. Sample CQ1-13-14. Figured Specimen UCM #40971.



Figure 1. *Synedra* sp. 1, SEM, complete frustule in valve view showing partially bilateral fascia. Sample CQ1-13-14. Figured Specimen UCM #40972.

Figure 2. *Synedra* sp. 1, SEM, apical pore field on mantle. Sample CQ1-13-14. Figured Specimen UCM #40973.

Figure 3. *Synedra* sp. 1, SEM, girdle view of perforated cingulum. Sample CQ1-13-14. Figured Specimen UCM #40974.

Figure 4. *Synedra* sp. 1, SEM, frustule in valve view with valves separated. Sample CQ1-11-12. Figured Specimen UCM #40975.

Figure 5. *Synedra* sp. 1, LM, valve view showing narrow sternum and very slight off-set of parallel striae. Sample CQ1-13-14. Figured Specimen UCM #40976.



Figure 1. *Tetracyclus* sp. 1 [aff. *T. polygibbum* (Pantocsek) Jousé], SEM, valve view showing slight heteropolar frustule, radial puncta at poles, axial area indiscernible on valve exterior, and 2 light transapical shadows indicating internal primary costae (ribs). Areolae on valve face midsection are increasingly scattered toward sternum rather than aligned in transapical rows. Sample CQ1-13-14. Figured Specimen UCM #40977.

Figure 2. *Tetracyclus* morphotype 'Clare's 1', SEM, interior of polar region of a copula with septum showing porelli penetrating the exterior and into the rim. Sample CQ1-13-14. Figured Specimen UCM #40986.

Figure 3. *Tetracyclus* morphotype 'Clare's 2', SEM, polar puncta on valve extending onto mantle. This taxon has a distinct mantle step (below the linear depression that parallels mantle rim) that is characteristic of this genus but not observed in the individuals shown in Figures 1, 2, 4 and 5. Sample CQ1-13-14. Figured Specimen UCM #40987.

Figure 4. *Tetracyclus* sp. 1 [aff. *T. polygibbum* (Pantocsek) Jousé], SEM, frustule interior with internal views of valve and cingulum that show two primary costae (transapical ribs), one secondary costa, a wide irregular sternum, distinct shallow apunctate (ghost) striae between the mid-section costae, dense radiating polar puncta, and a broken valvocopula lined with pervalvar rows of pores and an abvalvar septum in cross-section, a minimum of six alternating primary copulae lined with pervalvar rows of pores, and pervalvar-oriented pores on each ligula. Sample CQ1-13-14. Figured Specimen UCM #40978.

Figure 5. *Tetracyclus* sp. 1 [aff. *T. polygibbum* (Pantocsek) Jousé], SEM, girdle view showing extensions of valve puncta onto the rounded, steep valvar mantle (note that the rows of puncta along costae are shortened); and the valvocopula and eight additional cingulum elements, each with uniseriate rows of slit-like puncta on the advalvar band margin and pore areas on the ligulae. Sample CQ1-13-14. Figured Specimen UCM #40979.



Figure 1. *Tetracyclus* sp. 2 [aff. *T. ellipticus* (Ehrenberg) Grunow], LM, valve view showing broadly elliptical shape; at least one primary costa and two others (may be primary or secondary). Sample CQ1-10-11. Figured Specimen UCM #40981.

Figure 2. *Tetracyclus* sp. 2 [aff. *T. ellipticus* (Ehrenberg) Grunow], LM, valve view showing elliptical shape with broadly rounded apices; primary costae and one or more labiate structures lateral to sternum in mid-region on valve face. Sample CQ1-12-13. Figured Specimen UCM #40982.

Figure 3. *Tetracyclus* sp. 1 [aff. *T. polygibbum* (Pantocsek) Jousé], LM, elongate elliptical valve showing at least two robust costae; fine transapical striae are discernable. Sample CQ1-10-11. Figured Specimen UCM #40980.

Figure 4-6. *Tetracyclus* sp. 3 [aff. *T. lata* (Hustedt) D.M. Williams], LM, three valve views at different focal lengths showing in Figure 4 three primary costae and two sets of secondary costae; the surface areolae in fine transapical striae; central, linear, narrow, slightly raised sternum; labiate structure right lateral to sternum in mid-region on valve face. Figure 5 shows distinct primary and secondary costae. Figure 6 shows a single open septum. These three images are at same scale. Sample CQ1-13-14. Figured Specimen UCM #40983.

Figure 7-8. *Tetracyclus* sp. 4 [aff. *T. rhombus* (Ehrenberg) Ralfs in A. Pritchard], LM, two valve views at different focal lengths showing in Figure 7 four primary costae and one or two sets of secondary costae, and at least one labiate structure lateral to the sternum in the mid-region on the valve face. Figure 8 shows the septum. These two images are at same scale. Sample CQ1-13-14. Figured Specimen UCM #40984.

Figure 9. *Tetracyclus* sp. 5 [aff. *T. lancea* (Ehrenberg) M. Peragallo in Heribaud], LM, large lanceolate-fusiform in valve view showing six primary costae and a narrow, linear sternum. Sample CQ1-12-13. Figured Specimen UCM #40985.



Figure 1-2. *Eunotia* morphotype 'Clare's 1', SEM, frustule in external valve view showing multiple perforated cingula and parallel to radial valve face striae that extend over steep-sided mantle. Fig. 2 is detailed view of apex of Fig. 1, showing uniseriate striae of small round puncta and double rows of poroids on cingulum elements. Sample CQ1-11-12. Figured Specimen UCM #40988.

Figure 3. *Eunotia* morphotype 'Clare's 1', LM, valve view of asymmetrically cuneate apex with distinct distal raphe, areolate striae, and broad sternum. Sample CQ1-13-14. Figured Specimen UCM #40989.

Figure 4. *Eunotia* morphotype 'Clare's 1', LM, valve view of asymmetrically cuneate apex with distinct distal raphe, areolate striae, and broad sternum. Sample CQ1-13-14. Figured Specimen UCM #40990.



Plate 19-Gomphonema morphotype 'Clare's 1'

Figure 1. *Gomphonema* morphotype 'Clare's 1', SEM, whole clavate frustule in valve view showing lineolate striae converging toward axial area in central area and parallel to radial toward poles, simple proximal raphe ends, partially obscured interrupted astigmate stauros in central area, straight simple distal raphe ends, and apical pore field at foot pole. Sample CQ1-13-14. Figured Specimen UCM #40991.

Figure 2. *Gomphonema* morphotype 'Clare's 1', SEM, valve view showing lineolate striae reduced in length as converge toward axial area to become a round areola at final position adjacent to sternum in central area; poleward from central area, the final areolae nearest sternum are crescent-shaped (convex toward sternum) with reniform volae; simple proximal raphe ends are closely spaced, and an interrupted astigmate stauros forms central area. Filiform raphe bisects sternum. Sample CQ1-13-14. Figured Specimen UCM #40992.

Figure 3. *Gomphonema* morphotype 'Clare's 1', SEM, internal valve view of fragment exposing coarsely cut striae beneath surface lineolae; typical of several *Gomphonema* species. Sample CQ1-13-14. Figured Specimen UCM #40993.

Figure 4. *Gomphonema* morphotype 'Clare's 1', SEM, external surface of foot poles of frustule with straight distal raphe end that bisects sternum and extends through apical pore field; poleward striae are lineolate; and cingula are partially attached. Sample CQ2-1-03. Figured Specimen UCM #40994.

Figure 5. *Gomphonema* morphotype 'Clare's 1', SEM, external surface of foot pole of frustule with straight distal raphe end that bisects sternum and extends through apical pore field; poleward striae are lineolate with final lineolae nearest sternum crescent-shaped; and cingula are partially attached. Sample CQ1-13-14. Figured Specimen UCM #40995.



Figure 1-3. *Gomphonema* morphotype 'Clare's 2', LM, whole frustule in girdle view (same individual at three focal lengths); coarse internal nature of striae along mantle; thickened hyaline area at fascia; distinct borders of apical pore field at foot pole; perforated cingulum. Sample CQ1-13-14. Figured Specimen UCM #40996.

Figure 4-5. *Gomphonema* morphotype 'Clare's 3', LM, whole frustule in valve view (same individual at two focal lengths). Fig. 4 shows possible stigma on left side of stauros; radiating striae near central area that become parallel toward poles; straight raphe with simple proximal and distal ends. Fig. 5 is same individual as in Fig. 4, but different focus allows borders of apical pore field at foot pole to become visible. Sample CQ1-18-20. Figured Specimen UCM #40998.

Figure 6. *Gomphonema* morphotype 'Clare's 4', SEM, whole wedge-shaped frustule in girdle view with valve face visible at low angle showing slightly concave valve face (depressed along sternum); extremely closely-separated simple proximal raphe ends in central area; uniseriate valve face striae of partially-occluded small reniform lineolae that extend onto tall mantle; distal raphe ends are unilaterally deflected and extend onto apical mantle; prominent apical pore field on mantle at foot pole bisected by raphe end; closely-spaced loculate reniform lineolae on head pole mantle; cingulum appears closed at head pole; single row of poroids adorns the advalvar margin of the valvocopula. Sample CQ1-13-14. Figured Specimen UCM #40999.

10 um 5 um 10 um

Figure 1-2. *Gomphonema* morphotype 'Clare's 5', SEM, Fig. 1 is whole clavate frustule in valve view showing lineolate striae converging toward axial area; simple proximal raphe ends; interrupted stauros in central area; and unilaterally hooked distal raphe ends at poles. Fig. 2 is close-up of individual in Fig. 1 and shows apical pore field bisected by hooked distal raphe end at foot pole. Sample CQ1-11-12. Figured Specimen UCM #41000.

Figure 3. *Gomphonema* morphotype 'Clare's 2?', LM, internal valve view of partial valve showing foot pole with hooked distal raphe end bisecting radial rows of poroids that compose the apical pore field. Sample CQ1-13-14. Figured Specimen UCM #40997.

Figure 4. *Gomphonema* morphotype 'Clare's 6', SEM, damaged clavate frustule in girdle view showing biseriate striae of small round puncta. Perforated cingulum elements visible at head pole. Sample CQ1-13-14. Figured Specimen UCM #41001.



Figures 1-2. *Gomphonema* morphotype 'Clare's 7', SEM, greater-than-half frustule showing interior and exterior of valves. Fig. 1 shows internal central nodule in central area and canal-like internal nature of striae; internal proximal raphe ends are slightly unidirectionally curved; uniseriate lineolate striae are radial to sinusoidal in central region and become straight and parallel toward apices. Figure 2 is an enlarged view of cuneate apex with a simple distal raphe end and apical poroids. Sample CQ1-13-14. Figured Specimen UCM #41002.

Figure 3-4. *Gomphonema* morphotype 'Clare's 7', SEM, Fig. 3 is three-quarter frustule showing internal and external views of lineolate striae, striated central area, and cuneate apex. Fig. 4 is close-up of lineolate striae and valvar apical pore field that is bisected by a deflected distal raphe. Sample CQ1-13-14. Figured Specimen UCM #41003.


Plate 23-Achnanthidium morphotype 'Clare's 1'

Figure 1. *Achnanthidium* morphotype 'Clare's 1', SEM, nearly whole frustule showing raphid valve view with parallel to slightly radiating uniseriate striae, round to elliptical areolae; filiform raphe appears deflected to opposite sides toward poles; distinct central area; simple proximal raphe ends; distal raphe ends are indistinct in this specimen. Sample CQ1-13-14. Figured Specimen UCM #41004.

Figure 2. *Achnanthidium* morphotype 'Clare's 1', SEM, nearly whole frustule showing araphid valve view with parallel to slightly radiating uniseriate striae; elliptical to lineate areolae; narrow- to medium-width sternum. Sample CQ1-13-14. Figured Specimen UCM #41005.

Figure 3-4. *Achnanthidium* morphotype 'Clare's 1', LM, three-quarter frustule shown at different focal lengths with parallel to slightly radiating striae and a rounded apex. Fig. 3 shows the raphid valve with an interrupted stauros in the central area and simple proximal raphe ends of a straight filiform raphe. Fig. 4. shows the araphid valve with a diminished central area. Sample CQ1-13-14. Figured Specimen UCM #41006.



Plate 24-Planothidium morphotypes 'Clare's 1 - 4'

Figure 1. *Planothidium* morphotype 'Clare's 1', SEM, central area of internal view of araphid valve with a horseshoe-shaped marginal sinus on right and a lanceolate-shaped sternum that abruptly narrows poleward away from central area. Coarseness of striae suggests that they are multiseriate. Sample CQ1-11-12. Figured Specimen UCM #41007.

Figure 2. *Planothidium* morphotype 'Clare's 2', LM, frustule with valves separated; striae are parallel to slightly radiating; the araphid valve is to the right with a wide lanceolate sternum, and a horseshoe-shaped marginal sinus is on right side of central area. Sample CQ1-13-14. Figured Specimen UCM #41008.

Figures 3-4. *Planothidium* morphotype 'Clare's 3', LM, of the same individual. Fig. 3 shows the raphid valve with a stauros interrupted by a single stria on left in the central area, and simple proximal raphe ends of a straight filiform raphe. Fig. 4. shows the araphid valve with a horseshoe-shaped marginal sinus on right central area and no central area on left. Sample CQ1-13-14. Figured Specimen UCM #41009.

Figures 5, 6, & 7. *Planothidium* morphotype 'Clare's 4', LM, of the same individual. Fig. 5 is the raphid valve with a bilateral rectangular stauros in central area. Fig. 6 shows the central convexity of the raphid valve as the focal length changed. Fig. 7 is the araphid valve with a unilateral central area representing the marginal sinus. Sample CQ1-18-20. Figured Specimen UCM #41010.



Figure 1. *Platessa florissantia* sp. nov., SEM, elliptical frustule showing slightly concave raphid valve at angle; imperforate cingulum partially detached; straight filiform raphe; proximal and distal raphe ends are simple and slightly expanded; uniseriate striae of apically elongated areolae parallel to slightly radiating; single row of mantle areolae; stauros distinct. Sample CQ1-13-14. Syntype UCM #41011.

Figure 2. *Platessa florissantia* sp. nov., SEM, elliptical frustule showing slightly concave raphid valve at angle; underlying araphid valve offset to side; straight filiform raphe; proximal and distal raphe ends are simple and slightly expanded; uniseriate striae of apically elongated areolae parallel to slightly radiating; single row of mantle areolae; stauros distinct. Sample CQ1-11-12. Syntype UCM #41012.

Figure 3. *Platessa florissantia* sp. nov., SEM, elliptical frustule showing slightly concave raphid valve at angle; imperforate cingulum partially detached; straight filiform raphe; proximal and distal raphe ends are simple and slightly expanded; uniseriate striae of apically elongated areolae in central region become biseriate with smaller round areolae toward poles; striae parallel to slightly radiating; stauros distinct. Sample CQ1-13-14. Syntype UCM #41013.

Figure 4. *Platessa florissantia* sp. nov., SEM, elliptical frustule showing flat raphid valve face; cingulum partially detached; straight filiform raphe; proximal and distal raphe ends are simple and slightly expanded; uniseriate striae of apically elongated areolae; striae parallel to slightly radiating; single row of mantle areolae discernable; stauros distinct; many of exterior areolae and raphe are thinly occluded. Sample CQ1-13-14. Syntype UCM #41014.

Figure 5. *Platessa* morphotype 'Clare's 1', SEM, elliptical frustule showing slightly convex araphid valve face; underlying raphid valve offset to side; uniseriate striae of apically elongated areolae; striae parallel to slightly radiating; single row of mantle areolae discernable; unilateral central area. Sample CQ1-11-12. Figured Specimen UCM #41015.





Figure 1. *Psammothidium* morphotype 'Clare's 1', SEM, elliptical frustule with rounded apices showing uniseriate striae parallel to slightly radiating; transapically expanded areolae that are partially occluded on exterior and exterior by cribria. Raphid valve (broken portion on lower left) is slightly convex and has a single row of mantle areolae. Araphid valve interior has narrow lanceolate sternum and a unilateral central area. Sample CQ2-1-03. Figured Specimen UCM #41016.

Figure 2. *Psammothidium* morphotype 'Clare's 1', SEM, detailed view of lower apex of individual in Fig. 1, showing external and internal details of mantle areolae, cribria covering the transapically elongated areolae within the uniseriate striae. Sample CQ2-1-03. Figured Specimen UCM #41016.





Figure 1. *Diadesmis* morphotype 'Clare's 1', SEM, mostly obscured frustule showing flat valve face with sparse, occluded, elongate puncta separated by transapical ribs; broadly rounded to cuneate apex; silica ridge at valve face and mantle juncture; and shallow mantle with a single row of poroids. Sample CQ1-27-35. Figured Specimen UCM #41017.

Figure 2. *Diadesmis* morphotype 'Clare's 2', LM, valve view showing centrally expanded frustule with rounded cuneate apex; a filiform raphe bisects sternum ridge; simple proximal raphe ends are widely spaced; rounded bilateral fascia; and dense, slightly radial rows of puncta. Sample CQ2-2-05. Figured Specimen UCM #41018.

Figure 3. *Diadesmis* morphotype 'Clare's 3', LM, valve view of fragment showing central area with rounded bilateral fascia and widely spaced simple proximal raphe ends. Sample CQ1-10-11. Figured Specimen UCM #41019.

Figure 4. *Diadesmis* morphotype 'Clare's 4', LM, frustule of rectangular shape in girdle view showing shallow mantle and mantle poroids, hyaline thickness of broad fascia in central area, and cingular elements. Sample CQ1-10-11. Figured Specimen UCM #41020.

Figure 5-6. *Diadesmis* morphotype 'Clare's 5', LM, polar fragment of same individual at two focal lengths showing rounded cuneate pole with a straight raphe within a broad axial area bordered by short straight striae and a silica ridge at valve face and mantle juncture; simple distal raphe ending; two opposing crescent-shaped hyaline areas lateral at pole. Sample CQ2-2-05. Figured Specimen UCM #41021.



Plate 28-Diadesmis morphotype 'Clare's 6, 7, & 8'

Figure 1. *Diadesmis* morphotype 'Clare's 6', LM, greater-than-half valve fragment with external valve view; broadly rounded to cuneate apex; narrowly separated proximal raphe ends on rounded bilateral fascia; raphe bisects thick, broad sternum; parallel to slightly radial elongate puncta are separated by transapical ribs; silica ridge at valve face and mantle juncture. Sample CQ2-0-04. Figured Specimen UCM #41022.

Figure 2. *Diadesmis* morphotype 'Clare's 6', LM, greater-than-half valve fragment with internal valve view; broadly rounded to cuneate apex; narrowly separated proximal raphe ends on rounded bilateral fascia; raphe bisects thick, broad sternum; parallel to slightly radial elongate puncta are separated by transapical ribs; silica ridge at valve face and mantle juncture. Sample CQ2-0-04. Figured Specimen UCM #41023.

Figure 3. *Diadesmis* morphotype 'Clare's 7', LM; small, whole, linear elliptical frustule in valve view with rounded apices; straight raphe within a prominent medium-width lanceolate sternum; round, bilateral central area (central nodule) distinct; fine parallel valvar striae unresolvable in LM. Sample CQ1-12-13. Figured Specimen UCM #41024.

Figure 4. *Diadesmis* morphotype 'Clare's 8', LM, small, whole, linear rectangular frustule in valve view; straight raphe within a prominent medium-width sternum; round, bilateral central area (central nodule) distinct; parallel valvar striae discernable. Sample CQ1-8-09. Figured Specimen UCM #41025.



Figure 1-3. *Frustulia rhomboides* var. *coloradensis* var. nov., SEM, Fig. 1 is rhomboid lanceolate frustule in external valve view showing rounded cuneate poles; straight, filiform raphe within a broad, apically perforated sternum; dense, parallel, uniseriate striae of small round puncta form a cross-pattern due to the uniform spacing of puncta in apical and transapical directions; fascia absent; proximal raphe ends widely separated. Fig. 2 shows "T-shaped" distal raphe end. Fig. 3 features widely-spaced proximal raphe ends that are slightly transapically expanded; an irregular row of poroids parallels raphe along both sides of axial area. Sample CQ1-13-14. Syntype UCM #41026.

Figure 4. *Frustulia rhomboides* var. *coloradensis* var. nov., LM, internal structure of valve apex showing tip formed at juncture of two axial ribs at distal raphe end (porto crayon); cross-pattern of apically and transapically aligned puncta. Sample CQ1-13-14. Syntype UCM #41027.

Figure 5. *Frustulia rhomboides* var. *coloradensis* var. nov., LM, interior of valve face showing eccentric central nodule where proximal raphe ends in a slight deflection. Sample CQ1-10-11. Syntype UCM #41028.



Figures 1. *Pinnularia* morphotype 'Clare's 1', SEM, external valve view showing a broad stauros fascia in central area; parallel biseriate alveoli of small round puncta; filiform raphe with closely-spaced simple proximal ends with slight deflection and an oppositely deflected hooked distal end. Sample CQ1-11-12. Figured Specimen UCM #41029.

Figure 2. *Pinnularia* morphotype 'Clare's 2', LM, polar fragment of valve showing broad outlines of alveoli and a hooked distal raphe end. Sample CQ1-10-11. Figured Specimen UCM #41030.

Figure 3. *Pinnularia* morphotype 'Clare's 3', LM, apical fragment of valve showing closely-spaced outlines of alveoli and a hooked distal raphe end. Sample CQ1-10-11. Figured Specimen UCM #41031.

Figure 4. *Pinnularia* morphotype 'Clare's 4', LM, greater-than-half valve fragment showing broad fascia extending to valve margin on one side of central area; central alveoli converge on central area, mid-way poleward alveoli are parallel, and polar alveoli diverge away from apex around a hyaline apical nodule. Sample CQ1-10-11. Figured Specimen UCM #41032.

Figure 5. *Pinnularia* morphotype 'Clare's 5', LM, valve view of central area fragment showing multiseriate striae alveoli converging on central area around a lanceolate rhombic bilateral fascia; proximal raphe ends are unilaterally deflected. Sample CQ1-10-11. Figured Specimen UCM #41033.





Figure 1. *Adlafia tellerii* sp. nov., SEM, whole frustule in valve and girdle view showing uniseriate striae of round areole converging toward axial area; proximal raphe ends simple, slightly expanded; distinct central area; tall mantle; distal raphe ends are unidirectionally deflected, broadly curving to base of mantle to nearly 180 degrees and bisecting area of densely-spaced rows of porelli at apices; cingulum not visible. Sample CQ1-11-12. Syntype UCM #41034.

Figure 2. *Adlafia tellerii* sp. nov., SEM, whole frustule in girdle and valve view showing uniseriate striae of round areole converging toward axial area; proximal raphe ends simple, slightly expanded; distinct central area; tall mantle; distal raphe ends are unidirectionally deflected, broadly curving to base of mantle to nearly 180 degrees and bisecting area of densely-spaced rows of porelli at apices; only apical cingulum elements visible. Sample CQ1-11-12. Syntype UCM #41035.

Figure 3. *Adlafia tellerii* sp. nov., SEM, whole frustule in girdle and valve view showing uniseriate striae of round areole converging toward axial area; proximal raphe ends simple, slightly expanded; distinct central area; tall mantle; distal raphe ends are unidirectionally deflected, broadly curving to base of mantle to nearly 180 degrees and bisecting area of densely-spaced rows of porelli at apices; cingulum broken, but visible. Sample CQ1-11-12. Syntype UCM #41036.

Figure 4. *Adlafia tellerii* sp. nov., SEM, two whole frustules in girdle and valve view showing uniseriate striae of round areole converging toward axial area; proximal raphe ends simple, slightly expanded; distinct central area; tall mantle; distal raphe ends are unidirectionally deflected, broadly curving to base of mantle to nearly 180 degrees and bisecting area of densely-spaced rows of porelli at apices; on lowermost frustule, cingulum shows both advalvar and abvalvar marginal uniseriate rows of puncta. Sample CQ1-11-12. Syntypes UCM #41037 (top) and UCM #41038 (bottom).

Figure 5. *Adlafia tellerii* sp. nov., SEM, two whole frustules in girdle and valve view showing uniseriate striae of round areole converging toward axial area; proximal raphe ends simple, slightly expanded; distinct central area; tall mantle; distal raphe ends are unidirectionally deflected, broadly curving to base of mantle to nearly 180 degrees and bisecting area of densely-spaced rows of porelli at apices; on uppermost frustule, cingulum folded between valves. Sample CQ1-11-12. Syntypes UCM #41039 (top) and UCM #41040 (bottom).

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Figure 1. *Navicula eomenisculus* sp. nov., LM, central area of valve face showing slightly radiating to sinusoidal striae in central region; and external proximal raphe ends are simple without curvature. Raised axial region is moderately narrow, but prominent, and is bisected by the raphe. Sample CQ1-13-14. Syntype UCM #41042.

Figure 2-3. *Navicula eomenisculus* sp. nov., LM, whole valve view showing two different focal lengths. Fig. 2 features the gradual tapering of the valve toward sharply angled poles; acutely rounded, cuneate apices; the "ridge" that forms the axial area and the straight raphe; striae slightly curve to radiate away from central area, but become straight and parallel toward apices. Fig. 3 shows a central nodule as thickened hyaline area and lineolae forming the striae. Sample CQ1-32-50. Syntype UCM #41043.

10 um



Figures 1-3. *Stauroneis* morphotype 'Clare's 1', LM, greater-than-half frustule fragment in valve view. Fig. 1 shows a narrow bilateral stauros fascia in central area; and parallel to radial uniseriate striae of small round puncta. Fig. 2 features narrowly cuneate apex with straight simple distal raphe end. Fig. 3 reveals the pseudoseptum at apex. Sample CQ2-1-03. Figured Specimen UCM #41044.







Figures 1-2. *Nitzschia* morphotype 'Clare's 1', LM, polar fragment in valve view showing transapical striae, raphe and keel on right lateral, and fibulate hyaline areas prominent. Sample CQ1-10-11. Figured Specimen UCM #41045.



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Aulacoseira morphotype 'Clare's 2'

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Orthoseira roeseana (Rabenhorst) O'Meara

Actinoptychus sp. 1

Undetermined Centric morphotype 'Clare's 1'

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Stauroneis morphotype 'Clare's 1'

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Achnanthidium

A. morphotype 'Clare's 1'

Actinoptychus

A. sp. 1

Adlafia

A. tellerii sp. nov.

Aulacoseira

A. clarensis sp. nov.

A. sp. 1 – [aff. A. distans (Ehrenberg) Simonsen]

A. morphotype 'Clare's 1'

A. morphotype 'Clare's 2'

A. morphotype 'Clare's 3'

Diadesmis

D. morphotype 'Clare's 1'

D. morphotype 'Clare's 2'

D. morphotype 'Clare's 3'

D. morphotype 'Clare's 4'

D. morphotype 'Clare's 5'

D. morphotype 'Clare's 6'

D. morphotype 'Clare's 7'

D. morphotype 'Clare's 8'

Diatoma

D. tenuis Agardh

Eunotia

E. morphotype 'Clare's 1'

Fragilaria

F. vaucheriae var. lohmans var. nov.

Frustulia

F. rhomboides var. coloradensis var. nov.

Gomphonema

- G. morphotype 'Clare's 1'
- G. morphotype 'Clare's 2'
- *G.* morphotype 'Clare's 3'
- *G.* morphotype 'Clare's 4'
- *G.* morphotype 'Clare's 5'
- G. morphotype 'Clare's 6'
- *G.* morphotype 'Clare's 7'

Navicula

N. eomenisculus sp. nov.

Nitzschia

N. morphotype 'Clare's 1'

Orthoseira

O. roeseana (Rabenhorst) O'Meara

Planothidium

- P. morphotype 'Clare's 1'
- *P.* morphotype 'Clare's 2'
- P. morphotype 'Clare's 3'
- P. morphotype 'Clare's 4'

Pinnularia

- *P.* morphotype 'Clare's 1'
- *P.* morphotype 'Clare's 2'
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- *P.* morphotype 'Clare's 5'

Psammothidium

P. morphotype 'Clare's 1'

Stauroneis

S. morphotype 'Clare's 1'

Staurosira

- *S.* morphotype 'Clare's 1'
- *S.* morphotype 'Clare's 2'
- *S.* morphotype 'Clare's 3'

Synedra

S. morphotype 'Clare's 1'

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- *T.* morphotype 'Clare's 2'

Undetermined Centric

Centric morphotype 'Clare's 1'

CHAPTER 4

Paleolimnology from diatom paleoecology and sedimentology for the late Eocene Florissant Formation, Clare's Quarry, Teller County, Colorado, USA

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Abstract

The late Eocene Florissant Formation in central Colorado has been recognized for nearly a century as a richly productive and diverse fossil Lagerstätte containing giant tree stumps, plants, diatoms, insects, other invertebrates, fish, and birds from the lacustrine facies and mammal remains from the fluvial facies. The current investigation focuses on the Clare's Quarry site where biotic and abiotic evidence are assessed to reveal insights into the lake character and the processes of deposition that resulted in the accumulation and preservation of the fossil-bearing host rock.

The sedimentary and stratigraphic record shows that the study site was positioned within a deep-water lake setting in which bottom-waters remained isolated and anoxic for long periods. During times with low rates of sedimentation that are interpreted as "normal lake deposition," the primary process of deposition was suspension settling of fine terrestrial clays from the outflow of streams; diatoms that bloomed in the epilimnion; diatoms transported from lake margin and stream environments; leaves and insects from marginal terrestrial habitats; and airfall volcanic ash and granular tuff. These normal lake sedimentation periods were episodically interrupted by rapidly deposited, suspension-settled fine clays from the distal regions of mud-dominated subaqueous lake marginal deposits that prograded into and retreated from the lake at intervals.

The fossil diatom flora consists of 3 dominant genera whose modern relatives live, at various seasons and at various times in their life cycle, in the planktic zone of the epilimnion of lakes, in the bottom sediments, or in the periphyton along the shallows of lakes and streams. A wide array of additional diatom taxa from lake margin, stream, bog or wetland habitats are represented in the rare fraction observed in these sediments. The diatom taxa provide support for the lake depth and range of habitats that are interpreted as peripheral to the ancient lake.
Keywords: Eocene, diatoms, lacustrine, paleolimnology, Florissant, Lagerstätte

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1. Introduction

The late Eocene Florissant fossil Lagerstätte locality in central Colorado is a unique source of paleontological data for terrestrial and aquatic flora and fauna preserved in lacustrine and fluvial sediments. Despite the wealth of research findings generated over the past century,

the understanding of the processes that controlled biologic productivity and deposition of sediments within the aquatic habitats of the lake and lake margin remains incomplete.

The current study focuses on the physical and chemical parameters of the aquatic habitats and the sedimentary processes that resulted in the accumulation and preservation of the lake deposits. This effort relies primarily on the integration of data from fossil diatoms (microscopic algae) and associated macrofossils with evidence from the lithologic character, stratigraphic relationships, and diagenetic mineralogy of the host-rock at the study site. The site selected for this study is Clare's Quarry because of its excellent stratigraphic exposure and its purported diverse diatom flora (Meyer, 2003).

The following sections set the framework for this paleolimnological investigation by providing an overview of the Florissant deposit, the lake origin, age, location, paleoclimate, and paleotopographic setting. These parameters influence the physical and chemical processes and affect the biologic productivity in the lake. The role that diatoms potentially play in the assessment of the paleolimnology is reviewed as context for this discussion.

1.1 Geological setting

1.1.1 Florissant fossil Lagerstätte: description, significance, age, and location

The late Eocene Florissant Formation is a world-famous fossil Lagerstätte that contains extremely well-preserved paleobotanical and fossil insect and invertebrate assemblages from lacustrine facies, and mammal fossils from the associated fluvial deposits. The lake is interpreted as a lahar-dammed fluvial drainage in which fossils accumulated in the fine sediments (Evanoff et al., 2001). The importance of this deposit is in, not only the extraordinary fossil preservation, but also its unique position in geologic time at the terminus of a long period of transition from the warm global climates of the Paleocene/Eocene thermal maximum (Prothero, 1994; Zachos, 2001). Three lake bed shales designated "upper," "middle," and "lower" by Evanoff et al. (2001) alternate with and are finely interbedded with mudstones, coarse volcanic tuffs, and volcanic ash. Sanidine crystals in the "upper shale" tuffs and "middle shale" cap rock provide a mean ⁴⁰Ar/³⁹Ar radiometric age of 34.05 ± 0.08 Ma (McIntosh and Chapin, 2004). The Florissant Formation is known from a relatively small area in the vicinity of the town of Florissant in Teller County, Colorado (Figure 1).



Figure 1. Location of Florissant, Colorado (small rectangle).

Exposures of the Florissant Formation are limited to scattered roadcuts that penetrate the subsurface and to slopes of hills and ridges that roughly flank the present-day creek drainages northwest and south of the town of Florissant (Figure 2). Principal fossil sites are located within the Florissant Fossil Beds National Monument, established in 1969, which is to the south of Florissant on County Highway 1; however, this area is closed to private collecting. The only publicly accessible collecting locality is the privately-owned commercial Florissant Fossil Quarry (referred to in this study as Clare's Quarry) that is the site of this study and is located just south of the town of Florissant and west of County Highway 1 (Figure 2).



Figure 2. Location map of the Clare's Quarry study site showing the maximum estimated present-day subsurface extent of the Florissant Formation and the boundary of the Florissant Fossil Beds National Monument.

The Clare's Quarry study site is an approximately 5 meter thick stratigraphic section consisting of these four primary lithologies: diatomaceous laminated shales ("paper shales"), brown mudstones, a single grey conchoidal mudstone, and coarse to fine-grained volcanic tuffs. Fourteen sequences of shale and mudstone were recognized and alphabetically assigned letter designations of AA through M from top to base. The Clare's Quarry section is considered by Evanoff et al. (2001) to represent the "lower shale" of the Florissant Formation.

1.1.2 Florissant paleoclimate, topography, and elevation inferred from paleobotany

On the basis of terrestrial paleobotanical evidence, the Florissant paleo-lake has been interpreted as a high-elevation, low-relief intermontane lake (Gregory and Chase, 1994; Evanoff et al., 2001) with a warm temperate to subtropical climate (Meyer, 2003; Leopold and Clay-Poole, 2001). Paleo mean annual temperature (MAT) estimated from leaf morphology using the CLAMP method (Wolfe, 1995) was found to be 12.8 ± 1.5 °C. The NLR (nearest living relative) method provides an estimate of MAT as no lower than 17.5°C (4-6.8°C warmer than the CLAMP method) (Leopold and Clay-Poole, 2001). Boyle et al. (2008) used a weightedaveraging partial least squares regression (WAPLS) to estimate mean annual temperature using higher-level taxa in modern forest plots and determined temperature estimates of 12.5-18.1°C for Florissant. These results are consistent with a warm temperate lowland or subtropical to tropical highland climate, and they encompass the previous estimates from leaf morphology and NLR methods. The WAPLS study implies a possibility for infrequent air-temperature freezing at the lowest end of the genus-level MAT estimate range of $14.5 \pm 2.2°$ C for Florissant, but states that it marks the lower bounds of plausibility for the paleotemperture (Boyle et al., 2008). As MAT must be <8-10°C for an ice cover to form on a lake (Kalff, 2002), the lowest end of the range for MAT estimates from all methods is well above this temperature. On the basis of these temperature estimates, it is unlikely that Florissant lake would have experienced any period of ice-over.

Estimates of paleo-elevation for the vegetated slopes surrounding the paleo-valley from MacGinitie (1953) (using nearest modern relatives to the fossil flora) range from 300 to 900 m. Studies based on lapse rates with temperature decreases of 1°C per 1,000 meters of elevation gain produce a range from 1,900 to > 4,100 m (Meyer, 2003) for the paleo-elevation of Florissant. If the genus-based WAPLS estimate of 14.7°C is used for MAT with previous leaf morphology estimates of late Eocene sea-level temperature, an estimate for Florissant paleo-elevation would fall within the range of ~1,600- 2,800 m (Boyle et al., 2008).

A mean annual precipitation of 72 ± 31 cm with 57 ± 16 cm during the growing season is estimated from leaf morphology (Gregory and McIntosh, 1996). Meyer (2003) gives a range of 50-80 cm of annual rainfall with most of it occurring during the growing season in the late spring and early summer and a distinct dry season. Integrated leaf and pollen records suggest that the area experienced moderate summer rainfall and mild, dry winters (Leopold and Clay-Poole, 2001).

1.2 Fossil diatoms in lake studies

1.2.1 Diatoms as indicators of paleolimnology

As diatoms are photosynthesizing algae, they require light in their aquatic environments. Modern diatoms live in waters ranging from marine to fresh, standing to flowing, and in wet soils and moist air that surrounds and sustains bryophyte communities (Stoermer and Smol, 1999). Many taxa live in habitats that are within the photic zone of freshwater lakes and streams. Limiting nutrients include nitrogen and phosphorus, and soluble silica must be available in the water for metabolic function and for the production of a hard cell structure (frustule) (Round et al., 1990). Diatoms occupy planktic habitats in lakes and streams, and benthic habitats in littoral zones of lakes and stream margins. Planktic diatom communities develop best in water depths no shallower than approximately 1.8 m (Bradbury and Winter, 1976; Haworth, 1979). Depending upon the light penetration through the seasons, benthic diatom communities thrive in water depths that range from 3 to 9 m (Stone and Fritz, 2004). One of the more specialized benthic habitats includes moss-covered rocks and tree bark in splash zones of fluvial systems in which aerophytic diatoms thrive in the moist air (Patrick and Reimer, 1966).

Diatom frustules, as sedimentary particles, in deep lakes can include taxa from the planktic epilimnion of the lake, planktic taxa from in-flowing streams, and benthic taxa that thrive in the littoral zones of the lake and margins of streams (Stevenson and Smol, 2003). The flattest, most central part of a lake basin will contain a sediment record that integrates indicators from across the lake (Stevenson and Smol, 2003). Contributions from higher reaches of the water-shed can be found as allochthonous frustules in the lake sedimentary record.

Paleolimnologists use diatoms recorded in the sediments as proxies for physical (temperature, light, and turbulence) and chemical (pH, dissolved organic carbon, nutrients, and

salinity) conditions (Battarbee et al., 2001). These parameters are reflected in diatom assemblage compositions. Although biological controls are important also, such factors are difficult to identify with any certainty from the sediment record (Battarbee et al., 2001).

1.2.2 Diatom taphonomy in paleolimnology

The accuracy of any survey of fossil diatom taxonomic diversity or any interpretation of paleolimnology that is based on diatoms is dependent upon the accumulation and preservation of forms that are representative of the living population. The number and types of individuals per volume of sediment will be impacted by the habitats represented, the seasonal bloom cycle, the availability of nutrients, physical transport within the lake, ingestion and redeposition by consuming organisms, sedimentary reworking of the substrate, and post mortem destructive mechanisms such as breakage and dissolution.

Just as diatom productivity is dependent upon the availability of nutrients and dissolved silica in the water, the preservation of diatom frustules in the rock record of a lake is largely influenced by the chemistry of the water column and the pore waters of the substrate. Much paleolimnology research has found that diatom data from lake sediments are a reliable indicator of the living population (Battarbee, 1979, 1981; Haworth, 1980). Other studies, however, indicate that post-mortem dissolution of diatom frustules is so prevalent in lake waters that the diatoms present in the sediments are not representative of the living population in the epilimnion

in either quantity or taxonomic composition, as some taxa are more prone to dissolution than are others (Battarbee et al., 2005).

Although no direct evidence of frustule dissolution was encountered in the current study at Clare's Quarry, this investigation recognizes that the taxa in the sediments may not be fully representative of the populations of diatoms that lived in the ancient lake waters. This work is, rather, an analysis based on information that can be obtained from those taxa that are present, as they must represent portions of the ancient living populations that occupied various niches within and peripheral to the lake in which their frustules were deposited. Caution is used when interpreting aspects of the paleolimnology that singly rely on the diatom data; and collateral sedimentary evidence is viewed as more reliable support for general conclusions made in this study.

2. Goals of study

The purpose of this study is to examine the paleontologic and sedimentary evidence at the Clare's Quarry site for new clues to the paleolimnology of the Florissant lake system. This includes the identification and analysis of evidence that points to lake and lake marginal habitats, lake bathymetry, chemical and physical parameters of the lake, and processes of deposition of the lake sediments. A unique contribution of this study over previous works is the incorporation of the diatom paleontology and paleoecology as collateral evidence for the lake setting that contributed to this fossil Lagerstätte. Furthermore, this study is built on a stratigraphic and

lithologic framework that allows for the observation of patterns among diverse types of data that can lead to interpretations of relationships among the biotic and abiotic components.

3. Methods

3.1 Sample collection

A total of 74 contiguous lithologic samples of non-uniform volume were collected from the measured stratigraphic section at Clare's Quarry (Figure 3.). Among these were 45 samples from the 14 designated shale facies (AA-M) of this study, 25 from the 11 recognized brown mudstone facies (A-M), 1 composite sample from the single grey conchoidal mudstone facies (C mudstone), and 3 from the 2 thickest discrete volcanic tuff facies. The samples were examined with a binocular microscope and described as to lithology, sedimentary features, stratigraphic contacts, and macrofossil content.

3.1.1 Diatom sample preparation

For diatom studies, subsamples of non-uniform size were selected from the 45 shale and 25 mudstone facies and prepared under a binocular microscope to isolate the fresh interior portion of the rock. Each subsample was cleaned with pressurized air, then washed in distilled water, and freeze-dried in the lab.

Diatom light microscope slides were prepared using either of two chemical methods or two mechanical methods. The two chemical preparation methods were guided by procedures set forth by Green (2001) and modified by G. Breit (pers. com., 2009). Secondary subsamples (1 gram dry mass each) were processed by one of these two methods: (1) heating in 30% hydrogen peroxide, cooling, and applying hydrochloric acid; or (2) heating in sodium hexametaphosphate. Slurries were drawn from the rinsed hydrogen peroxide and the rinsed sodium hexametaphosphate preparations for direct application onto cover slips that were heat-dried on a hot plate and permanently mounted. The mechanical preparation methods included these: (1) Battarbee chamber settling method (Battarbee, 1973) of slurries from sonication of crushed sheet-thin chip secondary subsamples (~2.5 mm each) in distilled water that were air-dried on cover slips and permanently mounted on glass slides; or (2) mechanical crushing and pulverization of sheet-thin chip secondary subsamples (~2.5 mm each) with mortar and pestle in distilled water rendering a slurry for direct application onto cover slips that were heat-dried on a hot plate and permanently mounted. All permanent mounts of cover slips onto glass slides were made using Naphrax or Zrax mounting medium.

Scanning electron microscopy samples (~2.5 mm diameter) consisted of either freshly broken samples or residual treated chips from each of the two chemical methods described above that were cleaned with pressurized air and mounted on stubs with double-sided black tape. Stubs for low-vacuum imagery were sputter-coated with gold and palladium, and those for field emission or ionic beam imagery were not coated.

3.1.2 Lithologic sample preparation

Thirty-four subsamples were selected for petrographic examination from the 26 principal volcanic tuff beds from the study site, most having laminated shales in direct contact with the tuffs. The goal was to examine the tuffs for textural and mineralogic properties, but also to determine the constituents of the diatomaceous shale laminae. Friability and splitting along bedding planes were serious concerns during preparation. To remedy this prior to sawing, where necessary, the subsamples were injected with blue epoxy. Then, the blocks were cut, labeled, and carefully packaged for shipment to a commercial vendor for thin section preparation.

3.2 Microscopy

3.2.1 Diatom identification

Light microscope slides were viewed using an Olympus BX 51 light microscope with 100x objective and camera system; and a JEOL JSM-5800 low vacuum SEM at the US Geological Survey in Denver, and FE JEOL JSM-7401-F field emission and FEI Nova 600-I focused ionic beam instruments at the Nanomaterials Characterization Facility at the University of Colorado. Strictly quantitative methods were not attempted due to the high degree of valve fragmentation resulting from destructive processing methods necessitated by the lack of matrix disaggregation.

3.2.2 Stratigraphic survey of diatom genera

For a relative sense of the distribution of diatom genera primarily within the shale units through the stratigraphic section, a timed survey was conducted using an Olympus BX 51 light microscope with a 100x objective. Estimates were made of the relative frequencies of occurrence of 18 of the 21 genera that were recognized in Benson and Kociolek (in review, see also Chapter 3). Additionally, the *Achnanthidium-Platessa-Psammothidium* genera were lumped into the single group "Achnanthoid" because of the difficulty of differentiating these diminutive forms in the light microscope. Ninety minute surveys along specific slide transects were done on a total of 29 slides (22 of shale and 7 of mudstone). Raw counts were recorded for specimens that ranged from fragments (< 10% to \geq 50%) to the rare whole frustule. The decision whether or not to count the specimen was determined only by the examiner's certainty as to genus. The visual estimates for these three dominant genera were guided by the American Geologic Institute Data Sheet - visual comparison charts for estimating percentage composition (Terry and Chilingar, 1955).

3.2.3 Petrography of lithologic units

Of the 35 petrographic thin sections of principal tuffs and their affixed laminated shales, selected samples were examined using a Zeiss Petrographic microscope with ProRes C5 camera and software; and an Olympus BX 51 light microscope with 10x, 40x, and 100x objectives and camera system.

The four primary lithologies constituting the stratigraphic section at Clare's Quarry are diatomaceous laminites ("paper shales"), brown mudstones, grey conchoidal mudstones, and coarse to fine-grained volcanic tuff. Owing to the difficulty of optically identifying clay-sized minerals derived from the alteration or weathering of volcanic particles, representative samples of each of the four primary lithologies were analyzed using x-ray diffraction and interpreted with the RockJock program (Eberl, 2003) by George Breit at the U.S. Geological Survey.

Samples of a nodule within the tuffs of the L shale and the surrounding matrix were analyzed by x-ray diffraction to determine what authigenic minerals had formed in the lake.

3.4 SEM with electron dispersive spectroscopy for mineral identification

Euhedral mineral crystals within pumice blebs in the tuffs were identified with electron dispersive spectroscopy (EDS) analysis under scanning electron microscopy with the JEOL JSM-5800 low vacuum SEM at the U.S. Geological Survey.

4. Results of investigation

The results of the lithologic and stratigraphic analysis include descriptions, mineral content from x-ray diffraction, secondary minerals, mudstone to shale ratios, and descriptions

and origin of volcanic components. The findings from the diatom paleontological examination are the diatom floral components, stratigraphic distribution, relationships of taxa to lithology, and paleoautecological assessment. The associated fossils are described and displayed in stratigraphic relationship to the diatom and sedimentary data. These results are graphically presented in Figure 3 in which the lithologic units are shown in stratigraphic sequence creating a framework for comparing the occurrences of laminated shales, mudstones, and tuffs; nodules; diatoms, and associated fossils. Each of these categories of findings is detailed in the following paragraphs.

Figure 3. Annotated lithologic log of the stratigraphic section at the Clare's Quarry study site showing lithologic units, sample numbers (red = x-ray diffraction), trends in mud to shale ratio, the position and general distribution of altered pyrite nodules, and the general occurrence of fossil diatoms and associated macro-fossils, as identified by symbol keys above each column.



The stratigraphic section at Clare's Quarry consists of 4.91 meters of quarry wall that exposes tuffaceous laminated shales, brown mudstones, grey mudstones, and coarse to mediumgrained volcanic tuffs (Figure 3). The "cap-rock tuff" is at the top of the section and the "big tuff" is in the lower half. The shale and mudstone units alternate, and these alternating pairs are assigned letter designations AA through M. These names for the tuffs and letters for the shales and mudstones are used throughout this and all discussions and figures that refer to the units in stratigraphic position.

The stratigraphic section at the study site and examples of its lithologic types are shown in greater detail in Figure 4. Subhorizontal beds dip approximately 2 degrees to the northwest (Figure 4. A). The coarse volcanic cap-rock tuff caps the exposure (Figure 4. B and C). The units that underlie the cap-rock tuff include the following: a series of alternating buff-colored diatomaceous laminated shales with tuffs (Figure 4. D, F, H); brown blocky mudstones (Figure 4. L); grey conchoidal mudstone (Figure 4. E); and medium to fine grained volcanic tuffs (Figure 4. G). These beds are laterally continuous over the approximately 30 m (98.43 ft) length of the exposure, each having a consistent thickness and lithology along the north to south oriented quarry face. Such flat-lying beds, with undisturbed contacts, suggest that deposition took place on surfaces that were bathymetrically flat and distal from tectonic perturbations; that the setting was protected from lake tidal, storm wave, and fluvial erosion; and that the sediments remained free from biotic disturbance. Sharp contacts between principal lithologic units are readily observed in outcrop and are present between micro-scale units in thin-section. Each principal lithologic type is individually described.

Figure 4. A. Study site at Clare's Quarry (scale bar = 2.5 meters); B. a coarse volcanic tuff caprock in the exposure (scale bar = 50 cm); C. coarse lithic and crystalline texture of "caprock tuff" (scale bar = 10 mm); D. "B shale:" interbedded laminated shale and tuff (scale bar = 5 mm); E. "C mudstone:" grey conchoidally fractured mudstone (scale bar = 5 cm); F. "F shale:" interbedded laminated shale and tuff (scale bar = 1 cm); G. the "big tuff." 16 cm thick coarse and fine tuff (scale bar = 5 cm) ; H. "H shale:" interbedded laminated shale and tuff (scale bar = 1 cm); G. the "big tuff." 16 cm thick coarse and fine tuff (scale bar = 5 cm) ; H. "H shale:" interbedded laminated shale and tuff (scale bar = 1 cm); I. fossilized tree stem in the middle of the "H shale" (scale bar = 5 cm); J. euhedral crystal of albite plagioclase feldspar found in pumice bleb shown in K (scale bar = 1 mm); K. pumice bleb showing compaction loading into underlying laminated shales in the middle of the "H shale" (scale bar = 1 mm); L. "M mudstone:" brown blocky, massive mudstone (scale bar = 2.5 cm); M. nodule of jarosite after pyrite with goethite in a tuff unit of the "L shale" (scale bar = 1 cm).



The laminated shales (also called "paper shales") are a complex of finely alternating diatomite laminae with very thin beds or laminae of detrital brown clay in the shales of the lowermost one-quarter of the section (K through M shales) or with very thin beds or laminae of volcanically-derived grey clay in the shales of the uppermost three-quarters of the section (A through J shales). These shale-clay couplets are intermittently interlaminated with volcanic tuff that widely ranges in grain size and thickness. The up-section replacement of the brown detrital clay component by the grey tuffaceous clay within the laminated shales corresponds with changes in the diatom and other fossil assemblages that are discussed in a later section. The diatom laminae primarily consist of individual < 1 mm (.20 -.33 mm) thick, diatom-rich, amorphous silica layers that conform to the surfaces upon which they accumulated. Where they are formed on flat, even surfaces, they are flat and relatively uniform in thickness. Where they overlie the irregularities of underlying less-plastic volcanic tuff grains, they show geopetal infilling; and where they are overlain by more dense volcanic tuff grains, they reflect settling and compaction irregularities. There is no indication of disruption of the laminae by the tuff grains, as they were deposited on these extremely fine laminae, as there is no appreciable reduction in thickness, but for the minor irregularities from overlying grains settling followed by compaction into the underlying surface. This strongly suggests that the underlying laminites were somewhat soft to elastic when the overlying tuffs were deposited. Then, compaction after burial resulted in further accommodation of the harder, more dense volcanic grains by the more plastic diatomaceous laminae. Had these diatom-rich laminae been in a more liquid state, such as that of a siliceous ooze, they could not have been preserved as discrete laminae. After exposure, the

laminites split apart easily, giving rise to the term "paper shale". As the laminites split apart, they free the very thin tuff beds that are incorporated. These interbedded tuffs within the laminated shales, as observed both in outcrop and thin section, consist of fine clay- to coarse sand-sized material interpreted as intermittent air-fall and reworked fines from suspension settling from terrestrial input events. Pumice, euhedral to subhedral mineral crystals, and lithic grains and alteration products constitute these intercalated tuffs. Graded bedding within the tuff units varies from normally graded (fining upward) to reverse grading followed by normal (coarsening upward, then fining upward). Upon removal from outcrop, there is a strong tendency for the diatom laminae immediately adjacent to the tuff beds to remain affixed to the tuff beds, whether above or below them due to the compaction-induced microscopic interdigitation at their contacts.

Discrete volcanic tuff deposits also form thin to thick beds that constitute a primary lithology type at Clare's Quarry. Laminated shale forms bounding and minor internal laminae within these units. Petrographically, the discrete tuff beds consist of medium to coarse, subhedral to euhedral, phenocrysts of primarily plagioclase, sanidine, biotite, and other mafic minerals. These phenocrysts show only partial alteration while retaining their original textural positions. There is no evidence of detrital grains or matrix, and textures show no evidence of reworking. The grains include partially hydrolyzed glass shards, juvenile lithoclasts (or wall-rock xenoliths), and pumice blebs with preserved flow-textures containing euhedral albite and biotite phenocrysts. Occasionally, perfectly intact diatom frustules are observed interstitial to the coarse phenocrysts. The volcanic units are described in greater detail in section *4.1.4*.

Two types of mudstone units are observed in the Clare's Quarry section and, because of the different implications as to their origin, they are discussed separately. The brown mudstone units are discrete beds that range from 6 to 31 cm thick and consist of medium brown, earthy, indurated micaceous clay. These mudstones show fining upward just below the contact with the overlying shale/tuff bed. In concert with this fining upward trend, each mudstone exhibits a waxy texture in the upper part, relative to the more silty and earthy nature of the main portion. The exposed mudstone beds tend to have an irregular blocky fracture for the most part, but exhibit a subconchoidal fracture toward the fining upward top. Scattered fine plant debris is also sometimes observed in the mudstone. A single find of a relatively intact fossil leaf that does not conform to the bedding orientation, as indicated by the horizontal bed boundaries, suggests rapid burial. No internal bedding orientation or parting surfaces are observed in the mudstone, although some wispy lineations are suggested. Apparent from base to near the top is the subhorizontal organization of fine platey mineral grains such as mica. No indication of bioturbation either by infauna or plant growth is evident.

The second type of mudstone occurs in only one exposed bed in the Clare's Quarry section. It is a massive grey conchoidally fractured mudstone that forms a 85 cm thick unit that exhibits pillow-like structures in outcrop. It has sharp lower and upper contacts with the laminated shales. It separates the underlying C shale from the overlying B shale. The contact of this grey mudstone with the underlying C shale is the "zero marker" (Figure 3) of Meyer (personal communication, 2005). The unit exhibits variations among the fine clay-sized constituents. No evidence of bioturbation is observed, and no signs of graded bedding are found. Organic debris is absent from this unit.

4.1.1 Mineral content of units from x-ray diffraction analysis

X-ray diffraction results (Figure 5-A through C) show that all primary lithologies are dominantly composed of smectite, a weathering product of the volcanic terrane, ranging from 34 to 47 weight % (wt.%) among them. The second most abundant constituent in all, except for the thick tuff bed (CQ15) (Figure 5-B), was glass/amorphous silica, ranging from 39 to 42 wt.% in the diatomaceous laminites; 39 wt.% in the grey conchoidal mudstone; and 17 wt.% in the brown mudstones.

Figure 5. X-ray diffraction charts showing mineralogic composition in weight percent for selected samples of the primary lithology types at Clare's Quarry: chart A is laminated shales, chart B is volcanic tuffs, and chart C is mudstones.



Common to the two types of volcanic tuffs (Figure 5-B) is the depauperate amount of crystalline quartz of less than 0.5 wt.%. Except for this low amount of crystalline quartz and the shared high content of smectite, they show variability in composition. After smectite at 37 wt.%, the next most abundant minerals in the thick tuff bed (CQ15) were plagioclase at 23 wt.%, anorthoclase at 17 wt.%, glass/amorphous silica at 14 wt.%, and potassium feldspar at 9 wt.%. After smectite at 42 wt.%, the next most abundant minerals in the frothy tuff of L shale (CQ46) was glass/amorphous silica at 35 wt./%, halloysite/kaolinite at 10 wt.%, and illite/mica at 8 wt.%. The high glass/amorphous silica content in the frothy tuff of L shale (CQ46) was visually suggested by the dominance of pumice in the sample. Coupled with the absence of plagioclase, the presence of halloysite in the frothy tuff implies weathering in an intense leaching environment (Moore & Reynolds, 1997).

It is reasonable that the diatomaceous laminites (CQ14, CQ2-SP3, and CQ25) (Figure 5-A) have high glass/amorphous silica content ranging from 39 to 42 wt.%, as the diatom frustules are opal and would appear to have the signature of amorphous silica. These dia-laminites have very high smectite at from 34 to 47 wt.%. They have a range of from 3 to 6 wt.% of crystalline quartz. Their total feldspar contents are in the range of from 6 wt.% (CQ2-SP3), to 11 wt.% (CQ25), to 17 wt.% (CQ14). The higher feldspar composition is suggested in CQ25 and CQ14 because of the porcellanitic weathering texture, especially in CQ14 which has greater anorthoclase. Sample CQ2-SP3, with much less feldspar and higher goethite, splits more readily along bedding planes and is more typical of the term "paper shale." CQ25 is unique among the dia-laminites in that it has 10 wt.% illite/mica. The brown mudstones (CQ-35 and CQ13sp) (Figure 5-C) are very similar in mineralogy. They are high in smectite at 35 and 39 wt.%, respectively; glass/amorphous silica is 17 wt.% for each. They each are relatively high in crystalline quartz at 13 and 10 wt.%, respectively; but CQ35 has 30 wt.% total feldspars and CQ13sp has 22 wt.%. Another difference is that CQ35 has 5 wt.% illite/mica and CQ13sp has 12 wt.%.

The grey conchoidal mudstone (CQ-SX2-4) (Figure 5-C) contains 40 wt.% smectite, 39 wt.% glass/amorphous silica, and 20 wt.% total feldspars. The much higher glass/amorphous silica content of this grey conchoidal mudstone of 39 wt.% contrasts with the 17 wt.% of the brown mudstone, and, along with its pillow-like textures, strongly suggest a high content of volcanic glass (ash).

4.1.2 Secondary minerals and textures after pyrite

At Clare's Quarry, convincing indirect evidence of pyrite in the Florissant lake beds is observed in two forms. These are (1) replacement minerals after pyrite nodules in tuff beds and (2) external molds after framboidal pyrite as grains within the shale beds, as observed in SEM. Nodules and flat concentrations of oxidized iron are found in the tuff beds associated with the laminated shales. One of the nodules from a tuff from the L shale was shown by x-ray diffraction analysis to consist of the minerals jarosite (a secondary sulfate) at the core and goethite (iron oxide) at the rim. Jarosite is a replacement mineral after sulfides, and among them, commonly, pyrite (Deer et al., 1992). The presence of jarosite in the nodule indicates the former presence of crystalline pyrite in nodular concentrations.

4.1.3 Terrestrial mudstone to lake shale ratio sequences

The stratigraphic section exhibits cyclical changes in the sediment contribution over time (Figure 3). This is reflected in the repetition of sequences composed of units of laminated tuffaceous shales that are abruptly overlain by units of brown massive mudstones. The mudstone to shale ratios within these sequences show four sets of sequences that reveal, from base to top, one full and one partial cycle. Upon close examination, many fine details build on these gross features to reveal important clues about the depositional and diagenetic setting.

One can determine from the gross pattern (Figure 3) that there is an increase in the mudstone to shale thickness ratio ("mudding up") and a decrease in this ratio ("mudding down"). A complete mudstone:shale cycle is defined here as a mudding up sequence followed by a mudding down sequence. These patterns are illustrated in Figure 3 in which Sequence 1 (a mudding up sequence) followed by Sequence 2 (a mudding down sequence) together form a single mudstone:shale cycle.

A further look at the progression of these mudstone:shale cycles up-section at Clare's Quarry shows that the second cycle begins with Sequence 3 (a second mudding up sequence) that was interrupted early by the 16 cm thick pyroclastic airfall tuff ("big tuff" of G). It does not appear that the deposition of the big tuff had any disruptive effect on the mudding up sequence as the mudding up sequence continues with the C shale (Sequence 4). This 4^{th} sequence was interrupted early by the 85 cm thick C mudstone (a grey, massive, conchoidally fractured, pillow-textured, volcanic glass-rich, airfall deposit). It appears that the mudding down sequence was skipped, but the mudstone:shale ratios were re-set at a very low mudstone:shale ratio as it began again with Sequence 4. (Note that the thickness of the big tuff unit has been omitted from the mudstone:shale ratio calculations.) The next sequence is incomplete, but begins with the Unit AA shale and is interrupted by a >50 cm thick very coarse crystalline, plagioclase-rich airfall tuff referred to as the cap-rock tuff. (Note that, again, neither the C ash-rich mudstone nor the cap-rock tuff thicknesses was used in calculating mudstone:shale ratios.)

4.1.4 Volcanogenic components

Ver Straeten (2007) observed that volcanogenic sediments in the ancient Florissant lake beds are of three basic types: simple, coarse-to fine-grained, normally graded beds, of probable airfall origin; medium to coarse pumiceous beds of airfall or riverine input; and mixed volcanogenic/detrital sediment of riverine origin.

In the current study at Clare's Quarry, samples of the caprock tuff of unit AA and the big tuff of unit G, along with a number of thinner tuffs interbedded with the shale units, were petrographically examined. The samples are compositionally uniform, regardless of their thickness and grain size. They consist of euhedral and marginally altered crystals of plagioclasedominated feldspars, and minor sanidine, biotite, hornblende, and quartz; marginally devitrified glass shards, partially corroded pumice grains; and juvenile lithic grains that are rich in plagioclase and mafic phenocrysts. Texturally, the caprock tuff of unit AA is non-sorted and non-graded, the grains are supported in a glass-altered matrix that is devoid of detrital material. The big tuff of the G unit shows compositional consistency with the caprock tuff, but has greater variety in texture.

The big tuff consists of a series of 6 subunits characterized as follows: (1) a basal pumice bed of altered glass shards and glassy FeO2-rich micro-lapilli with accretionary rims, and lined and filled vugs; (2) a set of two beds of medium to fine-grained particles each overlying a thin layer of grey ash, the lower one appears to fine-upward into the central grey ash layer and is followed by a coarsening upward bed; the granular portions contain partially altered glass shards, marginally altered plagioclase crystals, juvenile lithic grains with plagioclase phenocrysts, probable sanidine, and possibly amorphous silica; (3) a medium to coarse grained somewhat reverse-graded unit with increasing altered ash showing shrinkage cracks as a soft matrix toward the top; and contains marginally altered crystals of plagioclase, juvenile lithic grains with plagioclase and mafic phenocrysts, accretionary micro-lapilli, and lined and filled vugs; (4) a medium to coarse granular bed with non-sorted particles overlying a white clay that overlies a thin grey ash layer; composition of grains is the same as in 3; (5) a fine to medium granular bed that is somewhat sorted, but shows no size grading; the finer material includes a groundmass of altered ash; the grains are crystals of rim-altered plagioclase, FeO₂-rich micro-lapilli with accretionary rims with lined and filled vugs, and altered "ghost" juvenile lithic grains that have left the more stable plagioclase phenocrysts floating in the clay; (6) a set of fine, medium, and coarse granular beds separated by 3 thin grey ash layers that seem to contain the coarsest of the

grains; a large portion of the larger grains appear white (as in the pumice) in hand specimen; and in thin section, they show a similar texture and composition as that detailed in 5.

Additionally, isolated pumice blebs that are encased between the shale laminae in the H shale were examined and found to contain euhedral crystals of a slightly calcic albite, as identified by electron dispersive spectroscopy analysis (EDS), and euhedral biotite crystals in a matrix of linear vesicular pumice.

4.1.5 Volcanic source of tuffs

The dominance of plagioclase feldspar phenocrysts relative to those of sanidine and quartz is important in determining the volcanic source for the tuffs at Clare's Quarry and in the Florissant deposits, in general (McIntosh and Chapin, 2004). As described above, the two thicker volcanic tuff units at Clare's Quarry show an intermediate mineralogic composition with dominantly plagioclase phenocrysts and a lower sanidine and quartz content. In contrast, the phenocrysts in tuffs of the Guffey andesites of the Thirty-nine Mile field are dominantly sanidine and quartz (McIntosh and Chapin, 2004).

4.2 Paleontology

4.2.1 Clare's Quarry fossil diatom flora

The diverse fossil diatom flora from Clare's Quarry consists of a minimum total of 21 genera from 14 families, all of which are extant in modern lake and associated environments (Benson and Kociolek, In Review). Differences between the fossil diatom flora in this study and the modern taxa are principally at the species level, although several modern species are also represented in the Clare's Quarry flora. The taxonomic list of the Clare's Quarry diatom flora is constructed in the systematic order as modified from Round et al. (1990) (Figure 6).
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Figure 6. Diatom taxa observed at Clare's Quarry, shown according to systematic order.

4.2.1.1 Diatoms in a stratigraphic context

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The stratigraphic distribution of 18 diatom genera plus the "Achnanthoid" group in the shales and mudstones are determined from estimates of relative frequencies and are shown in Figures 7 and 8. The taxa occurring at an estimated average of $\geq 1\%$ are shown in relative percent (blue); whereas, those at < 1% are shown in counts (red). Consistently, the three most common genera are *Synedra*, *Diatoma tenuis*, and *Aulacoseira clarensis*.



Figure 7. Estimated relative percent of diatom genera for laminated shales (A & B through F Shales). Genera are listed from left to right in order of decreasing relative abundance

Figure 8. Estimated relative percent of diatom genera for laminated shales (G through I Shales and K through M Shales); and an average of five mudstone units. (Genera are listed from left to right in order of decreasing relative abundance.)



At the Clare's Quarry site, fossil diatom frustules were observed primarily from the laminated shales in which the dominant diatom genera were *Synedra*, *Diatoma*, and *Aulacoseira*. Uncommon to rare within these shales were species of the genera *Fragilaria*, *Staurosira*, *Tetracyclus*, *Eunotia*, *Gomphonema*, *Planothidium*, *Frustulia*, *Pinnularia*, *Adlafia*, *Navicula*, *Stauroneis*, and *Nitzschia*, and the Achnanthoid group. *Orthoseira* was extremely rare. Diatom frustules were also present, but rare, in the brown mudstones and included the genera typical of the shales, along with an increased occurrence of *Orthoseira* and the appearance of *Diadesmis*. Additionally, in petrographic thin section, diatoms typical of the laminated shales, especially *Aulacoseira*, were observed interstitially among the coarse grains of some of the tuff units. Each assemblage is discussed according to host lithofacies.

Three principal diatom assemblages are distinguished within the laminated shales (Figures 7 and 8) on the basis of relative dominance of the 3 most abundant and widespread genera. Laminated shales of the lithofacies sequences M through G are characterized by the dominance of the genera *Synedra* and *Diatoma tenuis*, with the virtual absence of *Aulacoseira*. The assemblage of the laminated shales of lithofacies sequences F through C is also dominated by *Synedra*, but the second most dominant genus varies between *Diatoma tenuis* and *Aulacoseira*. The third assemblage is recognized in the laminated shales of lithofacies sequences B through A and contains both *Synedra* and *Aulacoseira* as co-dominant genera, with the virtual absence of *Diatoma tenuis*. The uncommon and rare genera in all 3 of the laminated shale assemblages are similar and include the Achnanthoid group, and the genera *Planothidium*,

Navicula, Tetracyclus, Fragilaria, Staurosira, Gomphonema, very rare Orthoseira, and very rare Stauroneis.

The diatom assemblage observed in the brown mudstones (Figure 8-G) includes the following distribution as to the relative frequency. The matrix grains dominated the slurry, which produced very few diatoms. Those observed, however, were clearly dominated by *Synedra* and less so by *Diatoma tenuis*. Frequent among the less common were the genus *Orthoseira* and the Achnanthoid group. Rare were *Navicula* and *Aulacoseira*. Very rare were *Pinnularia, Tetracyclus, Diadesmis, Staurosira*, and *Gomphonema*. Extremely rare were *Fragilaria, Eunotia, Nitzschia, Frustulia*, and *Planothidium*. Only a single fragment of *Actinoptychus* was found in any of the Florissant material, and that specimen was from the brown mudstone facies.

Although the grey conchoidal mudstone of sequence C was also surveyed in the same way for diatoms, it contained only a trace that consisted of 3 fragments of *Synedra*, 1 fragment of *Diatoma tenuis*, 2 >half frustules of *Diadesmis*, and 1 fragment of *Orthoseira*.

In summary, this survey shows a dominance of 3 genera (*Aulacoseira*, *Synedra*, and *Diatoma*) over the remaining 15 genera and 1 group recognized. The significance of the diatom generic distributions within these units is discussed in a later section.

4.2.1.3 Diatom bloom occurrences as laminae in the paper shales

An examination of the diatomite laminae in petrographic thin section reveals that the laminated shales consist of somewhat laterally continuous microlaminae in which diatom taxa show distinct patterns of distribution. As an example of these patterns of taxonomic groupings, photomicrographs from the richly diatomaceous sample CQ1-13-14 of the F shale unit are shown in Figure 9. In this sample, mono-generic microlaminae of *Aulacoseira* (Figure 9-B) alternate with nearly bi-generic microlaminae of *Synedra* and *Diatoma tenuis* (Figure 9-A); and these alternate with mixed microlaminae of *Aulacoseira*, *Synedra*, and *Diatoma tenuis* (Figure 9-C). Interspersed between these groupings are microlaminae with various amounts of a light-colored (flocculated?) clay or ash matrix that has incorporated a sparse array of additional benthic diatoms such as *Tetracyclus* (Figure 9-D) and genera of the *Fragilariaceae* family (Figure 9-E) along with *Aulacoseira*, *Synedra*, and *Diatoma tenuis*. At intervals between the diatom laminae, a dark golden brown organic fabric is encountered that contains probable benthic diatoms including *Tetracyclus* and others of undetermined affinity (Figure 9-F).

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Figure 9. Photomicrographs from sample CQ1-13-14 of the F shale featuring taxonomic groupings of diatoms in somewhat continuous microlaminae: A. *Synedra* and *Diatoma tenuis*; B. *Aulacoseira*; C. a mixed assemblage of *Synedra*, *Diatoma*, and *Aulacoseira*; D. *Synedra*, *Diatoma*, and *Aulacoseira* with the added presence of other benthic pennates in a slightly opaque matrix; E. shows the mixture of all the diatom taxa in areas with and without the matrix of D.; and F. organic material containing diatoms such as probable benthic *Tetracyclus* and others of undetermined affinity. (Scale bars represent 10 µm except in F., which is 20 µm.)

As all the genera observed in the diatom flora at Clare's Quarry are extant genera, and the taxa observed in this study include or show extreme affinity to modern species; it is reasonable to approximate the habitat preferences and tolerances of the fossil forms by referring to those of their nearest modern species; or, generally to those of the same genus or family (Round and Bukhtiyarova, 1996a, b; and Round, 1997). As a result, the diatom habitats interpreted for the Florissant flora are inferred on the basis of autecological parameters at the family, genus, or species levels for the modern analogs (Figure 10).

Diatom Morphological	Family	Genus	Analog Species	Life Habit	рН	Sali nity	Opt. Temp	Turbu lence	Nutri ents
Group									
Centrics	Aulacoseiraceae	Aulacoseira	italica	Т	nu -ak	F, B		hi	
			distans	т	ас		~cold, 11-12°C	hi	0
	Orthoseiraceae	Orthoseira	roeseana	Ba	ak				
	Heliopeltaceae	Actinoptychus		Р		B, M			
Araphid Pennates	Fragilariaceae	Fragilaria	vaucheriae	Ρ, Β	ak	F	cool	lo	E
		Staurosira	construens	В	nu -ak	F, B			0, M
		Diatoma	tenuis	Ρ, Β	ak	F, B			
		Synedra	ulna	Ρ, Β	nu -ak	F, B			0 - E
	Tabellariaceae	Tetracyclus		В			cold		
Raphid Pennates	Eunotiaceae	Eunotia		B, Ba	ak -ac			lo - hi	O - E
	Gomphonemataceae	Gomphonema		Ρ, Β	ak -ac			lo - hi	
Monoraphid Pennates	Achnanthidiaceae	Achnanthidium	minutissima	В	ak	F		hi	
		Planothidium		В	ak				
		Platessa	A. conspicua	В	lo ak				O - E
		Psammothidium		В	ac				
Biraphid Pennates	Diadesmidaceae	Diadesmis		Ba	~ac	F			0
	Amphipleuraceae	Frustulia		B, Ba	~ac	F			
	Pinnulariaceae	Pinnularia		B, Ba	~ac	F			
	Naviculaceae	Adlafia		Ba					
		Navicula	menisculus	В	~ak	F		lo	M, E
	Stauroneidaceae	Stauroneis		P, Ba	ak				
Keeled Pennates	Bacillariaceae	Nitzschia		P, B, Ba	ak			lo	

Figure 10. Diatom taxa from Clare's Quarry with inferred autecological parameters for modern analog taxa. Life habits are T = tychoplanktic, P = planktic, B = benthic, Ba = benthic aerophytic. pH is nu = neutral, ac = low, or ak = high. Salinities are F = fresh, B = brackish, M = marine. Nutrient levels are O = oligotrophic, M = mesotrophic, E = eutrophic.

Each genus observed at the study site is discussed in terms of the habitat preferences that are provided in the cited literature, the source for the data in Figure 10. Any omissions in types of information are due entirely to the limitations of the information available in the references surveyed. For this reason, it should be understood that this review, whose results are illustrated in Figure 10., is not presented as a complete account and is not intended to limit sub-habitats for diatom genera to those data provided here. It is but a guide to the array of sub-habitats represented in the fossil taxa for Florissant lake. The genera are arranged according to the systematic order of Round et al. (1990). They are later discussed in terms of their occurrences relative to the host lithologies and associated fossils.

4.2.1.4.1 Aulacoseira

One of the three most abundant diatom genera observed at the Clare's Quarry site is *Aulacoseira clarensis* sp. nov., which is most similar to the modern and fossil species *A. italica* (Ehrenberg) Simonsen emend. R.M. Crawford, Y.E. Likoshway and R. Jahn.

The genus *Aulacoseira* is tychoplanktic, growing mostly in the plankton, but having the capacity to survive burial in sediments (Stoermer and Julius, 2003). The ecologic parameters of the species *A. italica*, as the modern analog for the new fossil species *A. clarensis*, have been characterized by Crawford et al. (2003) as "not well known." This species is said to occupy a clearly different habitat from that of the open-water planktic species of *A. ambigua* and *A. granulata* (Ehrenberg) Simonsen in that it occurs with benthic species that include the genera

Gomphonema, *Eunotia*, *Pinnularia*, *Synedra*, and *Stauroneis* (Crawford et al., 2003). Species of *Aulacoseira* may exist in several different forms due to silica limitation in which heavily structured or thinly structured valves may convey ecological meaning (Stoermer et al., 1985). Suggestive of an at least part-time residence in the planktic setting, however, is the observation of Lund (1954) that turbulence is important in keeping the subspecies *subarctica* of *A. italica* in suspension. Hustedt (1957) noted that *Aulacoseira italica* is oligohalobous and alkaliphilous. Gasse (1986) found a dominance of *A. italica* var. *bacilligera* in Lake Tana, Africa, in which the waters range in pH from 7.5-8.4. *Aulacoseira italica* var. *tenuissima* from Lake Lovojärvi, South Finland, thrives in a pH range of 7.0-7.5 (Simola et al., 1990), placing it well within the range of a circumneutral pH. This range of circumneutral to moderately alkaline for *Melosira italica* (*Aulacoseira italica*) is confirmed, and a designation of fresh to brackish water is noted by Rymer et al. (1988).

Less common at the study site are specimens of a species of *Aulacoseira* that has affinity to the fossil species *A. distans* (Ehrenberg) Simonsen. *A. distans* is characterized as rarely found in the phytoplankton of larger lakes and is more usually reported from the bottom sediments of smaller, soft/acid-water lakes (Florin, 1981; Camburn and Kingston, 1986; Haworth, 1988; Siver and Kling, 1997). Moos et al. (2005) concluded that *A. distans* should be classified as a tychoplanktic species; and that, as such, it prefers shallow water, but exists over a wide range of depths. Weckstrom et al. (1997) determined that most varieties of *A. distans* have an optimum temperature range of 10.89 to 12.15°C. *A. distans* is among the species associated with slightly acidic, oligotrophic conditions found in relatively cold climates (Leira, 2005). Because of the requirement of wind circulation to maintain the suspension of the heavily silicified frustules of

this species within the epilimnion, the occurrence of *A. distans* in great abundance would indicate high wind speeds, suggesting a lake setting with open exposure or high elevation (Liu and Shi, 1989).

4.2.1.4.2 Orthoseira

Orthoseira species are found almost exclusively in subaerial habitats, particularly in bryophyte communities growing on alkaline substrata and are rarely found in lakes or high-order streams (Patrick and Reimer, 1966; Stoermer and Julius, 2003). *O. roeseana* is found in association with lichen in tropical cloud forests (Lakatos et al., 2004); and in shallow, illuminated entrances of limestone caves (Poulickova and Hasler, 2007).

4.2.1.4.3 Actinoptychus

Actinoptychus senarius Ehrenberg is restricted to brackish and brackish marginal marine environments (Van Eetvelde and Dupuis, 2004).

4.2.1.4.4 Fragilaria

The genera of the family Fragilariophyceae are part of the spring periphyton community of rivers that can respond, with rapid growth, to small additions of organic and inorganic nutrients (Perrin et al., 1987). Taxa live in the periphyton, epipsammon, epiphyton, epipelon, epidendron, haptobenthon, and plankton (Kingston, 2003). Degree of environmental disturbance and nutrient availability can influence their habitat preference (Kuhn et al., 1981). Certain planktonic populations in large lakes can selectively develop either offshore (Stoermer and Yang, 1970) or nearshore (Stoermer, 1968). This family includes the following genera that are found in the study site: *Fragilaria*, *Staurosira*, *Diatoma*, and *Synedra*.

The genus *Fragilaria* includes species that thrive as phytoplankton in lakes (Kingston, 2003). A species identified in the fossil site of this study is *F. vaucheriae* that is found in streams in the Arctic where it occurs among mixed periphyton communities on rocks in streams with reduced current flow (Ki et al., 2009). *F. vaucheriae* is often abundant in eutrophic modern reservoirs (Hoagland and Peterson, 1990) and prefers fresh water that has a cool temperature (Patrick and Reimer, 1966). *F. vaucheriae* is reported from benthic habitats in moderately alkaline waters ranging in pH from 8.0 - 9.4 (Castenholz, 1960).

4.2.1.4.5 Staurosira

The genus *Staurosira* includes the former *Fragilaria construens and F. elliptica*. *Staurosira* species are a common component of shallow water floras in rivers and lakes (Kingston, 2003). Specimens of *Staurosira* from the study site most closely resemble these two species: *S. construens* var. *venter* (Ehrenberg) Hamilton, which prefers water with a fairly low nutrient content (oligotrophic or mesotrophic) (Patrick and Reimer, 1966); and *S. incerta* Morales, which is alkaliphilous and oligotraphentic (favoring nutrient-poor conditions) (Morales, 2006). Gasse (1986) reports that *S. construens* occurs under a wide range of conditions, but it is mostly found in fresh waters with medium pH. Rymer et al. (1988) show that *S. construens* var. *venter* can live in waters with a pH ranging from circumneutral to moderately alkaline and in fresh to brackish waters.

4.2.1.4.6 Diatoma

The araphid pennate genus *Diatoma* occurs in the Clare's Quarry site as a single species with an elongate morphology that is identified as *Diatoma tenuis* Agardh.

Diatoma tenuis has a high tolerance for Na, SO, and conductivity of the water (Potapova and Charles, 2003). Williams (1985) states that *D. tenuis* generally ranges in habitat from fresh to brackish water. According to Moss (1981), *D. elongatum* (synonomous with *D. tenuis*) forms planktic colonies in the spring and not in the autumn; yet, they live and reproduce in the periphyton of the same lakes during both spring and autumn. *D. tenuis* occupies both epiphytic and planktic habitats (Krammer and Lange-Bertalot, 2004). *D. elongatum* (*D. tenuis*) is reported from benthic habitats in moderately alkaline waters ranging in pH from 8.0 - 9.4 (Castenholz, 1960).

4.2.1.4.7 Synedra

A single species of the araphid pennate genus *Synedra* is one of the three most abundant taxa recognized at the study site and is most similar to the two modern species *Synedra ulna* (Nitzsch) Ehrenberg and *Synedra acus* Kützing.

The genus *Synedra* includes species that thrive as phytoplankton in lakes and can be very abundant in oligotrophic, mesotrophic, and eutrophic lakes during different seasons (Kingston, 2003). Species of *Synedra* that co-occur with *Diatoma tenuis* form planktic colonies in lakes in the spring but not in autumn; whereas, they are abundant in the periphyton of these same lakes in both spring and autumn (Moss, 1981). Benthic *Synedra* populations can also be major components of river communities (Main, 1988). A designation of fresh to brackish water and a pH range of circumneutral to moderately alkaline are reported for *S. ulna* by Rymer et al. (1988). *S.ulna* and *S. acus* are both found in moderately alkaline lake settings with pH ranging from 8.0 - 9.4 (Castenholz, 1960).

4.2.1.4.8 Tetracyclus

Tetracyclus is not well known from modern floras, being most frequently found in fossil deposits (Kingston, 2003). Specimens from the study site closely resemble the following modern species: *T. polygibbum* (Pantocsek) Jousé, *T. elliptica* (Ehrenberg), *T. lat*a (Hustedt) D.M. Williams, *T. rhombus* (Ehrenberg) Ralfs in A. Pritchard, and *T. lancea* (Ehrenberg) M. Peragallo in Heribaud. A general ecology of the genus indicates that species of *Tetracyclus* are usually found in shallow water and seem to prefer cold water (Patrick and Reimer, 1966).

4.2.1.4.9 Eunotia

Eunotia are benthic diatoms with cells that may grow singly, in filaments, or at the ends of short stalks, attached to a variety of substratum types (Kociolek and Spaulding, 2003). Within the genus *Eunotia*, species show a range of tolerance for nutrient concentrations and organic contaminants. Some species are restricted to oligotrophic waters, others prefer eutrophic waters, and others prefer habitats of high sulfate levels (Kociolek and Spaulding, 2003). Species are found in a wide variety of habitats from aerophytic to flowing or still waters and conditions from alkaline to circumneutral pH to highly acidic (Kingston, 2003). The genus is most diverse in softwater or acid-water habitats (Patrick and Reimer, 1966; Krammer and Lange-Bertalot, 1991). Some species live in the tops of sphagnum plants (Patrick and Reimer, 1966).

4.2.1.4.10 Gomphonema

Species of *Gomphonema* produce long, mucilaginous stalks, with the cells growing upward from the point of attachment of the stalk. The colonies form thick, mucilaginous masses attached to surfaces along the shores of lakes, rivers, and streams (Kociolek and Spaulding, 2003). Some forms have been characterized as lake inhabitants, whereas others are considered to be rheophils (living in high-flow streams). At times, some taxa are found in the plankton of lakes. Cells may grow individually or form massive benthic colonies that blanket any available substrate, some being epiphytes (Patrick and Reimer, 1966). Some are cosmopolitan, while others are restricted to specific regions (Kociolek and Spaulding, 2003); many are found across a wide range of pH levels. Freshwater monoraphid diatoms are benthic in habit, living attached to substrata in shallow to mid-depth habitats of lakes and rivers (Stoermer, 1980). Many are specialized for life as epiphytes, and others frequently occur attached to sand and rocks (Kingston, 2003). Taxa live primarily as unicells, either on short stalks (*Achnanthidium*), or adnate to the substratum (*Psammothidium*, *Planothidium*, and *Platessa*). In the latter habit, the raphe valve is against the substratum, potentially allowing the cell to move to new locations (Kingston, 2003).

Achnanthidium species are haptobenthic unicells on short stalks, common on a wide range of substrata including plants and rocks; have a stipitate habit and are found in turbulent, well-oxygenated water; taxa are held above the dense prostrate masses of other taxa on stalks, where they can take advantage of more rapid replenishment of the host of chemical constituents flowing past (Kingston, 2003). They thrive in moving water and rapids (Peterson and Hoagland, 1990) and in wave zones of lakes (Brown, 1973). Small cells like *A. minutissimum* are physiologically more active than larger diatom cells, due partly to their large surface to volume ratios (Kingston, 2003). *Achnanthidium minutissima* tolerates alkaline waters (Potapova and Charles, 2003; Castenholz, 1960).

4.2.1.4.12 Planothidium

The genus *Planothidium* is a benthic adnate form attached to sand or pebbles, and is more common in alkaline waters (Bukhtiyarova and Round, 1996).

4.2.1.4.13 Platessa (formerly Achnanthes conspicua Mayer)

The new fossil species *Platessa florissantia* sp. nov. described from this study site is most similar to the modern species *Achnanthes conspicua* Mayer from which the genus *Platessa* was derived. *Achnanthes conspicua* is found in oligotrophic to eutrophic waters, especially those with low alkalinity and middle to high electrolytes (Krammer and Lange-Bertalot, 2004).

4.2.1.4.14 Psammothidium

The genus *Psammothidium* is an adnate benthic, most abundant on sand, and prefers soft/acidic waters (Flower and Jones, 1989; Bukhtiyarova and Round, 1996).

4.2.1.4.15 Diadesmis

The genus *Diadesmis* is characteristically aerophytic and tends to grow in association with mosses and attached to damp rocks. It occurs across North America, often in waters of low conductance and slight acidity (Kociolek and Spaulding, 2003). This genus may be found in oligotrophic waters (Patrick and Reimer, 1966).

4.2.1.4.16 Frustulia

Frustulia occurs in benthic habitats singly or in mucilaginous tubes. Species are found across North America, and they are often abundant in slightly acid waters that are high in dissolved organic carbon and low in conductance (Patrick and Reimer, 1966; Kociolek and Spaulding, 2003). Frustulia is also found growing on the tops of sphagnum plants (Patrick and Reimer, 1966).

4.2.1.4.17 Pinnularia

Pinnularia is often abundant in low conductance, slightly acidic freshwaters (Kociolek and Spaulding, 2003). Also, some species are benthic aerophytic, being associated with lichen (Lakatos et al., 2004).

4.2.1.4.18 Adlafia

Specimens of the genus *Adlafia* were recognized at the study site and were described as a new species *Adlafia tellerii* sp. nov. This new fossil species is most similar to two modern species *A. muscora* (Kociolek et Reviers) Moser, Lange-Bertalot et Metzeltin, which lives in aerophytic habitats, especially around mosses (Moser, Lange-Bertalot and Metzeltin, 1998). The fossil species *A. tellerii* is also quite similar to *A. suchlandtii* (Hustedt) Lange-Bertalot, which is found in various waters, and is also aerophytic, and predominantly associated with intermittently wet bryophytes (Moser, Lange-Bertalot and Metzeltin, 1998).

The genus *Navicula* is a large taxonomic group that has a broad distribution in nearly every freshwater habitat across North America (Kociolek and Spaulding, 2003). Some prefer low current conditions of streams or lakes. More specifically, however, the specimens from this study are described as the new species *Navicula eomenisculus* sp. nov., which is most similar to the modern species *N. menisculus* Schumann. *N. menisculus* prefers mesotrophic to moderately eutrophic conditions in chalk-rich, well-buffered freshwater lakes (Lange-Bertalot, 2001). This species tends to be benthic (Hoagland et al., 1982).

4.2.1.4.20 Stauroneis

Species of the genus *Stauroneis* range from benthic to planktic habitats of lakes and streams (Kociolek and Spaulding, 2003). Some species prefer alkaline waters. Also, some species are aerophytic, being associated with lichen (Lakatos et al., 2004).

4.2.1.4.21 Nitzschia

Most species of *Nitzschia* are epipelic in microhabitat, but the genus also contains planktic, epilithic, and epiphytic species (Lowe, 2003). Epipelic habitats are most abundant in slow-moving streams or in lentic environments such as lakes, ponds, and wetlands. Diatoms from this group can also be found in quiet pools of swift streams where slower current velocities allow fine sediments to fall from suspension (Lowe, 2003). These species contain endocellular symbiotic cyanobacteria and can therefore fix nitrogen; they usually occur singly, but may form stellate colonies or live in mucilage tubes (Lowe, 2003). Some species live endophytically in sphagnum leaves (Patrick and Reimer, 1966). Species of *Nitzschia* are reported from benthic habitats in moderately alkaline waters ranging in pH from 8.0 - 9.4(Castenholz, 1960).

4.2.2 Associated fossils in stratigraphic context

Previously reported fossils from Clare's Quarry are leaves from the genera *Cedrelospermum* (an extinct genus in the elm family), *Fagopsis* (an extinct genus of the beech family), *Chamaecyparis* (false cedar), and *Sequoia* (redwood) (Meyer et al., 2004). The common insects are ants, beetles, and crane flies (Meyer et al., 2004). A complete, extremely well-preserved shorebird, a probable relative of the modern plover (Order *Charadriiformes*, Family *Charadriidae*) (Meyer, 2003), was found in 1997 by a quarry owner from a bed that approximately corresponds to the L mudstone of this study (Cole Anderson, pers. comm., 2011). A fossil fish was recovered from the contact between the H shale and the overlying H mudstone (Nancy Clare Anderson, pers. comm., 2005). Diatoms were observed in the shales (Harding and Chant, 2000; O'Brien et al., 2002: O'Brien et al., 2008; Meyer, 2003) at Clare's Quarry.

In the current study, the macrofossil occurrences observed are described and reported in stratigraphic and lithologic context and are shown in Figure 3. Plant fossils observed include leaves and leaf fragments found in the shale units: *Sequoia*, in the L shale; *Chamaecyparis*, in

AA and H shales; other conifer, in H shale; broadleaf trees, in AA, C, H, and L shales. The leaves and leaf fragments in the mudstone units are fewer, but include these: *Typha*, in the B mudstone; and broadleaf trees, in the L mudstone. Additionally, a fossilized tree stem with a diameter of >5 cm was observed in the approximate center of the H shale (Figure 4. I).

Incomplete or whole individual insects were occasionally recovered from the AA, H, J, K, L, and M shales; and from the K mudstone. Rare spider specimens were found in the AA and M shales.

Ostracod specimens (~0.7 mm in length) identified as the species *Cypris florissantensis* are reported from several Florissant localities (Meyer, 2003). Specimens resembling this species were observed in the laminated shales and on surfaces of ash in tuff beds at Clare's Quarry. More commonly, there are specimens of a bean-shaped type of ostracod (possibly related to the genus *Candona*) that is extremely tiny and widely observed on fine-grained laminae in many units at Clare's Quarry. The small bean-shaped ostracods in Clare's Quarry appear to be external molds, but some of the larger specimens of *Cypris* appear to have some of shelly material remaining. The ostracods are exclusive to either laminated shales or ash beds, and are not observed in the mudstones.

Mollusks present at Clare's Quarry include rare *Planorbis*-like aquatic gastropods that are often associated with tuffs above the G Shale, and are interpreted by Wagner et al. (2004) to suggest a deeper lake habitat in the uppermost part of the exposure.

From a paleobotanical census study by Wagner et al. (2004), a comparison of leaves found at Clare's Quarry with those from the "middle shale" shows that there is a higher representation of *Chamaecyparis* and a lower occurrence of *Fagopsis* at Clare's Quarry. Both *Fagopsis* and *Chamaecyparis* are indicative of valley-bottom vegetation (Meyer, 2003). Additionally, it was observed by the Wagner team that *Typha* (cattails), an aquatic macrophyte that occupies locally shallow and marshy areas near the shoreline of freshwater bodies (Meyer, 2003) was concentrated in distinct layers at Clare's Quarry (Wagner et al., 2004).

5. Discussion

5.1 Depositional, volcanic, and secondary processes

5.1.1 Episodic inflow of terrestrially-derived mud into the deep lake basin

Potential controls on the mudstone:shale depositional trends include climate, volcanism, and tectonism, as primary drivers. A complete mudstone:shale cycle likely represents the progradation and retreat of lake marginal mud deposits (lacustrine pro-delta) that mirrors gradual shifts in precipitation, availability of terrestrial mud, topography of the catchment area, or basin bathymetry.

With only the abbreviated view at Clare's Quarry, relative to the larger depositional record, it cannot be determined with certainty whether or how major pyroclastic events might be related to the processes that controlled the mudstone:shale cycles. It might be anticipated, however, that, with increased frequency of the more intense volcanic activity (as demonstrated by the big tuff of G, the C mudstone ash deposit, and the cap-rock tuff of AA), increased local

rainfall, increased volume of volcanically-derived soils, volcanically induced earth tremors dislodging slope cover, and topographic readjustment that increased gradient of terrain could have led to an increased mud supply into the basin. Although the deposition of the big G tuff (Sequence 3) seems to have had little direct impact on the mudstone:shale ratio, immediate changes in the diatom flora directly following this event suggest an environmental response within the lake. The increased volcanism that resulted in the C mudstone ash deposit (Sequence 4) is coincident with the skipped mudding down (mud retreat) sequence and, rather, re-sets the mudstone:shale ratio to a very low number. This suggests a restoration of deeper water or a cessation of processes that drive the mud entry into the lake. Independent diatom and other fossil data coincident with the interruption of the mudding up sequences (Sequences 3 and 4) would tend to favor a possible up-section increase in lake bathymetry.

The terrestrial mud supply was never sufficient to entirely fill, in any single deposit or in any mudding up cycle, the portion of the basin represented at Clare's Quarry, as the deep lake bathymetry remained viable after each mud event. Evidence for this is the observation that the laminated shale deposits were consistently restored.

5.1.2 Airfall origin of the volcanic tuffs

Textural features and mineralogic composition of the caprock tuff and the big tuff of G are consistent with airfall tuffs. The compositional indicators for airfall tuffs are the presence of euhedral plagioclase, biotite, and probable hornblende crystals, juvenile magmatic grains, accretionary micro-lapilli or spherical shards, and fine cuspate glass shards (Cas and Wright,

1987). In terms of alteration, the following is recognized: relict glass shards show *in situ* devitrification, juvenile lithic matrix show *in situ* diagenetic alteration leaving behind the lath-shaped feldspar phenocrysts in their original random orientations; and the plagioclase crystals are in a relatively fresh condition. Furthermore, there is no evidence of reworking such as wear or breakage. Any grain-size or grain-density sorting is rather imperfect and can be explained best by airfall processes rather than water-lain deposition. In some units, there is apparent graded bedding which might be interpreted as reverse graded as often as normal graded bedding. Finally, on the basis of textural relationships within the coarse tuffs, the clay component is a product of *in situ* alteration of the glass shards or airfall volcanic dust, and it contains no aspects of detrital origin. There are no coarse detrital components in any of the samples examined. Furthermore, the units are compositionally consistent with each other. This mineralogic composition and textural character is typical of the direct delivery of pyroclastic material from an eruptive volcanic event into the lake (Königer and Stollhofen, 2001; and Ed DeWitt, pers. comm., 2010).

A study of the preservation potential of airfall tuffs in an ancient deep lake in the tectonically-controlled Saar-Nahe Basin in Germany shows that tuffs that accumulate in offshore lacustrine settings have a high preservation potential. The contributing factors to the tuff preservation include the availability of accommodation space during lake-level rise; the virtual absence of wave reworking or fluvially-generated currents; the slow sedimentation rates of the non-pyroclastic sediment; and the absence of bioturbation in an anaerobic lake bottom (Königer and Stollhofen, 2001). The Saar-Nahe tuff deposits exhibit sharp and planar contacts, planar lamination, (multiple) graded bedding, and laterally constant thickness. Those tuffs alternate

with black laminated shales that signify the maximum flooding stage of the lake (when it was deepest). These characteristics are also observed in the Clare's Quarry tuffs.

5.1.3 Source of the tuffs

The source of the airfall tuffs in Clare's Quarry is undetermined. Petrography of the caprock of the AA sequence and the big tuff of the G sequence and x-ray diffraction of the G tuff showed that the dominantly plagioclase phenocrysts and lower sanidine and quartz content distinguish these tuffs from those of the Guffey/Thirtynine Mile field, according to the mineralogy of McIntosh and Chapin (2004). This distinction of the Clare's Quarry tuffs is consistent with the findings of McIntosh and Chapin (2004) for the radiometrically dated tuffs from the "middle shale" and "upper shale" of the Florissant Formation.

5.1.4 Secondary mineralogic processes

5.1.4.1 Pyrite and jarosite formation

The precipitation of pyrite in a sedimentary setting takes place under reducing conditions that are created in anoxic aqueous environments (Goldhaber and Kaplan, 1975) or in waters with high concentrations of organic matter (Cohen, 2003). The formation of nodular and framboidal pyrite occurs during the early stages of diagenesis and indicates oxygen deficiency in the sediments (Wignall and Newton, 1998). Early diagenetic pyrite nodules in tuffs and framboids within the laminated shales of Clare's Quarry favor anoxia in the sediments of the lake, contributing to the excellent preservation of macrofossils. This is further evidence of a deep lake depositional setting at the study site.

The later-stage alteration of pyrite to jarosite signals a time when groundwaters became very acidic (pH of 2-4) and oxidizing, which facilitated the alteration of the mineral from a sulfide to a sulfate (Brophy and Sheridan, 1965). As the timing of the replacement of the pyrite nodules by jarosite is undetermined, it could have occurred with post-depositional changes in lake water or groundwater chemistry or with subsequent exposure and weathering.

5.1.4.2 Smectite clay formation

As illustrated by x-ray diffraction, smectite is the dominant clay mineral in the Clare's Quarry section. Smectite clay is a product of weathering and alteration of volcanic glass and silicate minerals in volcanic terranes (Moore and Reynolds, 1997). It is also formed as a precipitate in pore spaces of permeable rocks in weathering conditions associated with very slow movement of water in environments ranging from swampy lowlands to arid and semiarid regions (Berner, 1971).

The chances for alteration and preservation of an ash-fall deposit depends upon the environment in which it falls; therefore, the types of clays that are the alteration products can indicate aspects of the environment in which it fell (Moore and Reynolds, 1997). This is especially true in subaqueous environments of deposition, as water is necessary for the leaching away of ions that are freed in the alteration reactions. The alteration mineral kaolinite can result

from ash falling into the highly acidic aqueous environment of a coal swamp; smectite indicates that silica-rich ash fell into a mildly alkaline aqueous environment; and zeolites or zeolite with k-spar indicate ash-fall in a highly alkaline setting such as a playa lake (Moore & Reynolds, 1997). The dominance of smectite in the absence of kaolinite in the Clare's Quarry section suggests that the airfall volcanic ash may have accumulated in a mildly alkaline lake basin. The absence of zeolites and carbonates in the sediments, however, rules out a highly alkaline setting for the deep basin.

The percentage of smectite in the all the lithologies at Clare's Quarry far exceeds the estimated amount that would have been derived from the alteration of the ash within the lake (G. Breit, pers. comm., 2011). It is probable, therefore, that a large portion of the smectite was of detrital origin.

5.2 Paleontology and habitat recognition

5.2.1 Correlation of diatom genera with lithologies

Diatoms from the light-colored submillimeter laminae in the shales contain 3 dominant genera (*Synedra, Diatoma tenuis*, and *Aulacoseira*). The modern equivalent species of the genera *Synedra, Diatoma tenuis*, and *Aulacoseira* can occupy the planktic habitat of open-water deep mid-latitude lakes during periods of their life cycles and produce seasonal or annual blooms. As well, they thrive during other seasons in either a dormant state in the sediments, as with *Aulacoseira*, or as blooms in the benthic periphyton of streams and lakes during other

seasons, as with *Synedra* and *Diatoma tenuis*. The grey or brown organic clay portion of the couplets within the laminated shales contain mixtures of diatoms that include not only *Synedra*, *Diatoma tenuis*, and *Aulacoseira*, but also the less common non-planktic taxa.

The lack of matrix among the frustules of *Aulacoseira*, *Synedra*, and *Diatoma tenuis* in the pure diatomite laminae of the shales strongly suggest that they were from planktic blooms (Figure 9. A, B, and C). It is likely that the diatoms in the mixed clay laminae (Figure 9. D, E, and F) were brought into the lake during periods (possibly seasons) of higher runoff that delivered individuals from the distant stream and lake margin habitats.

While diatoms are rarely observed in the brown mudstones, those that are present suggest a diverse assemblage that could have lived in the planktic zone, in shallow lacustrine or fluvial habitats, on moss-covered rocks along tributaries, or in wetlands. Such an assemblage supports the interpretation that these mudstones were distal deposits of lacustrine turbidites from storm events. In such deposits, shallow-water, littoral, and riverine diatoms were transported as allochthonous particles into the deeper lake basin.

5.2.2 Diatom paleoecology and habitats

The autecological assessment of the modern analogs for the fossil diatom taxa from Clare's Quarry (Figure 10), in conjunction with the genus distribution surveys (Figures 7 and 8), illustrates that the fossil diatom genera are most representative of tychoplanktic/planktic habitats of lake surface waters that were dominantly circumneutral to mildly alkaline, as represented by the modern taxa *Aulacoseira italica, Synedra ulna,* and *Diatoma tenuis*. Although represented by less frequently appearing taxa, a diverse array of benthic habitats is indicated that includes marginal lake and stream settings that range in pH from mildly acidic to mildly alkaline and offer a wide range of substrate surfaces for attachment.

Observe that the planktic habitats that sustain populations of *Aulacoseira, Synedra*, and *Diatoma tenuis* are the photic regions of the open-water epilimnion of deep lakes where water circulation is available for buoyancy during planktic habitation. The photic zone of lakes tends to become more alkaline as phytoplankton (diatoms and other algae) consumes carbon dioxide; whereas, the hypolimnion receiving substantial amounts of organic matter tends to become acidic with the concentration of carbon dioxide and carbonic acid (Patrick and Reimer, 1966). Thus, the biotic activity influences the properties of the diatom habitat zones. As only the photic zone is the region of diatom growth, the pH indicated by the diatoms reflects only that of the photic zone portion of the lake epilimnion and littoral margins, and not necessarily that of the deeper lake.

The array of habitats inferred for the Clare's Quarry diatom flora is synthesized into these four ecological settings in which only relative depth is implied (Figures 11 and 12): mildly acidic lake and lake margin conditions, circumneutral to mildly alkaline lake and lake margin conditions, swift-flowing rivers, and slow-flowing streams. The primary life zones within these environments include the epilimnion of a deep lake and swift-flowing rivers, littoral/shallow water from lake and stream margins, aerophytic zones from peat bogs or from moss-covered rocks in splash zones of rivers. The species of many genera show a variation in pH tolerances and nutrient requirements and are found in several habitats; whereas, others are more restricted in habitat preferences. Some are exclusively planktic or benthic; whereas, others can live as either.

The modern diatom genera that thrive in each sub-habitat within the four ecological settings are indicated in Figures 11 and 12. The tychoplanktic Aulacoseira distans prefers mildly acidic conditions, as do the following benthic taxa: Psammothidium, Frustulia, Pinnularia, Diadesmis; and Eunotia tolerates a wide range of pH. Preferring circumneutral to mildly alkaline lake surface waters are the tychoplanktic taxon Aulacoseira italica and the sometimes planktic taxa Synedra ulna, Diatoma tenuis, Fragilaria vaucheriae, Stauroneis, Nitzschia, and Gomphonema. Benthic taxa that thrive in circumneutral to mildly alkaline lake margins include Fragilaria vaucheriae, Diatoma tenuis, Nitzschia, Gomphonema, Staurosira construens, Achnanthidium minutissima, Planothidium, Platessa conspicua, Navicula menisculus, Orthoseira roeseana, Stauroneis, and Eunotia. Benthic diatoms that live in the shallow turbulent zones bordering high-flow rivers or streams include Achnanthidium and Gomphonema, while Nitzschia and Eunotia prefer quiet pools away from the fast water flow. The benthic species of Gomphonema, Staurosira, Eunotia, Stauroneis, and Nitzschia can live in shallow water zones of slow-flowing streams. Aerophytic benthic diatoms such as Orthoseira roeseana (that prefers higher pH), Eunotia, Diadesmis (that prefers lower pH), Frustulia, *Pinnularia*, Adlafia, Stauroneis, and Nitzschia can be found attached to moss-covered rocks in splash-zones, associated with other bryophytes near pools along the banks of streams, in the sphagnum moss of peat bogs, and in shallow alkaline settings. No pH data is provided for the benthic *Tetracyclus* or the aerophytic benthic *Adlafia*, so they are included in both lake environment depictions. Diatoms that prefer water with low conductivity are *Diadesmis*,

Frustulia, and *Pinnularia*; while *Diatoma tenuis* has a higher tolerance for conductivity, showing a preference for increased sodium and sulfate in the environment. *Achnanthidium minutissima* thrives well in turbulent, well-oxygenated waters in fast-flowing streams. Nutrient requirements differ among genera, as well, with *Fragilaria vaucheriae* and *Navicula menisculus* commonly found in eutrophic waters; and *Diadesmis* and *Aulacoseira distans* thriving best in oligotrophic waters. *Synedra ulna, Eunotia,* and *Platessa conspicua* can tolerate a range of nutrient levels from high to low. *Frustulia* tolerates habitats with high organic carbon content.



Figure 11. Proposed environmental settings and sub-habitats likely to be inhabited by these diatom genera from the Florissant diatom flora showing A. mildly acidic conditions in the photic zone, and B. circumneutral to mildly alkaline conditions in the photic zone. (Scale is relative.)



Figure 12. Proposed environmental settings and sub-habitats likely to be inhabited by these diatom genera from the Florissant diatom flora showing A. a swift-flowing river, and B. a slow-flowing stream. (Scale is relative).

The four ecological settings featured here are common within the watershed of most inland balanced or over-filled lakes (Bohacs et al., 2000) and reflect subtle changes tied to seasonal precipitation, storm events, and basin geometry adjustments that result in lake waterlevel fluctuations over time. Although the sub-habitats from a circumneutral to mildly alkaline lake and swift-flowing streams are overwhelmingly better represented in the diatom record at the study site, to some degree, all of these habitats supplied diatom frustules that were delivered into the deep lake setting at a position distal from the point of inflow of rivers or major streams, where they are now recovered from the lake sediments.

The habitats suggested by the diatom data are corroborated in other Florissant sites by the ecological range of terrestrial plant leaf and pollen, and insect taxa from moist riparian and drier slopes, along with bryophytes from stream-side and aquatic macrophytes from wetlands (Meyer, 2003). We propose that the diatom genera within the Clare's Quarry fossil flora originated from the habitats shown in Figures 11 and 12 and, accordingly, that those habitats were part of the larger Florissant paleo-lake system, despite the fact that several of these habitats have left no sedimentary record in the preserved portions of the deposits that now define the Florissant Formation.

5.2.3 Diatom seasonality

Considerations as to the seasonality of diatom blooms in the late Eocene Florissant lake, located in the mid-latitudes with a warm-temperate to subtropical climate, are guided by modern diatom bloom cycles, interpretations of fossil sites of similar age, and interpretations of
microlaminae within the rock record at the study site. The bloom cycles of planktic diatoms can be affected by local conditions such as climate, insolation determined by geographic latitude, and the introduction of fluvial input and volcaniclastic material into the lake system. As a general guide, modern lakes in middle and high latitudes have diatom blooms that occur during early spring to early summer, sometimes with a less pronounced second maximum in autumn; whereas, modern tropical and subtropical (lower latitude) lakes have winter diatom blooms (Zolitschka, 1990).

From the fossil record, an example of a high latitude lake that existed during the globally warm early Eocene is represented at Horsefly, British Columbia, Canada. The study of the fossil diatoms suggests the summer as the primary bloom season. Samples are described as varved couplets of white (summer) diatomaceous laminae separated by dark (winter) pyrite-rich clays that are interbedded with discrete beds of tuff or ash-rich graded turbidites (Wolfe and Edlund, 2005).

The opposite is shown for the middle latitude subtropical Eocene lake site of Eckfeld Maar, Germany. In this example, the late middle Eocene diatomaceous laminites consist of light-colored laminae, largely composed of diatoms and clay minerals, that alternate with darkcolored laminae of mixed origin (mineral and plant detritus and green algae) (Mingram, 1998). In this site, diatom blooms seemed to coincide with the time of quiet sedimentation during the drier winter season (Mingram, 1998).

The paleobotanical interpretations of Meyer (2003) and Gregory and McIntosh (1996) for the Florissant paleoflora indicate wetter spring and summer growing seasons followed by drier periods in fall and winter. If a pattern of drier winter blooms, similar to that at Eckfeld Maar, dominated the productive cycles of the Florissant fossil diatoms, the close association between the diatom-bearing units and the occurrence of abundant well-preserved leaf fossils could be explained as the result of seasonally co-occurring autumn-winter processes. Secondly, the sedimentary evidence that indicates extremely slow rates of deposition for the shale containing the diatom microlaminae and the low volume of associated detrital material is consistent with deposition during periods of low rainfall, such as the drier autumn or winter.

Contrary to the sedimentary suggestion of Florissant primary tychoplanktic/planktic diatom production occurring in the autumn or winter are studies by Lund (1954) and Moss (1981 First, the Lund (1954) study shows that the tychoplanktic *Aulacoseira italica*, the modern analog for the fossil species *A. clarensis*, blooms in the spring. Populations of *Melosira italica* (*A. italica*), spend the summer in the lake sediments and rise to the epilimnion in autumn where they persist over the winter as plankton; yet, growth does not begin until spring when blooms are triggered by increases in light and temperature. So, the presence of *Aulacoseira* frustules in the sediments may give a mixed seasonal signal, with some representing bloom periods and others, non-growth periods. The second study by Moss (1981) on the modern *Diatoma tenuis* and modern analog species of *Synedra* shows that these taxa produce planktic blooms in the spring.

Evidence of seasonal progression of the tychoplanktic *Aulacoseira* and planktic *Synedra* and *Diatoma tenuis* are identifiable as discrete microlaminae in the sedimentary record at the Clare's Quarry site. Microlaminae observed in petrographic thin-section photomicrographs (Figure 9.) of the F shale (Figure 3.) are interpreted as spring blooms and non-growth accumulations of the fossil taxa. The matrix-free microlaminae containing only *Aulacoseira* (Figure 9. B) represent discrete spring blooms of *Aulacoseira*. Matrix-free microlaminae

containing mixed *Aulacoseira*, *Synedra*, and *Diatoma tenuis* (Figure 9. C) represent transitional periods of *Aulacoseira* growth co-occurring with spring blooms of the planktic *Synedra* and *Diatoma tenuis*. Microlaminae with clay matrix and mixed taxa of planktics and benthics (Figure 9. D and E) represent periods of allochthonous input of clay and diatoms from the lake, stream, and marginal environments. Such discrete microlaminae of taxa strongly suggest a seasonal progression of the 3 tychoplanktic/planktic taxa in the F shale unit at the Clare's Quarry site. Additional work is needed to fully characterize these successions as to their order and periodicity; and to survey additional diatomaceous shale units within the section.

To reconcile the potential contradiction between the sedimentary record that indicates slow sedimentation rates for the diatom laminae (suggestive of autumn or winter frustule accumulation) and the spring diatom blooms shown from the studies of modern tychoplanktic (Lund, 1954) and planktic (Moss, 1981), the following is proposed. The sedimentation rate for the diatomaceous shales in the deep lake setting of Clare's Quarry was consistently slow throughout the seasons, with the depocenter being sufficiently far offshore from the fluvial input of sediments. Exceptions to the slow rate of sedimentation occurred during the cyclical deposition of discrete mudstone units that represent the rapid influx of terrestrial mud and are devoid of diatomaceous laminae.

5.2.4 Relationships among diatoms, associated fossils, and lithofacies

As diatoms are present primarily in the laminated shales, and the leaf and insect fossils are generally found in the laminated shales, they show a gross coincidence (Figure 3). The especially rich leaf and insect/spider-bearing units of the H, J, K, L, and M shales tend to be dominated by *Synedra* and *Diatoma tenuis* specimens and appear to be deficient in *Aulacoseira*. Within this group of *Synedra* and *Diatoma tenuis* dominated shale intervals, there are also the apparent increase in the conifer leaf specimens, the occurrence of a tree stem, and the discovery of a bird specimen and a fish fossil. It is observed that *Aulacoseira* specimens are more prevalent in the laminated shale intervals that have no insects, and are coincident with units that contain mollusks (especially gastropods). The increase in *Orthoseira* and *Diadesmis* (aerophytic benthics) specimens occurs in the B mudstone and is coincident with the observation of the macrophyte *Typha*, found only in the B mudstone.

The virtual absence of diatoms and other fossils in the grey conchoidal mudstone is consistent with the diagnosis of this unit as an airfall deposit of volcanic ash.

From the brown mudstone, the rare bird specimen in its excellent condition of preservation with beak, bones, eye, and feathers in place shows that no scavenging and no destruction by transport occurred after death. The preservation of this bird called for rapid sinking of its carcass into the anaerobic hypolimnion of the lake, extremely rapid burial by the fine muds that encased it, and compaction that flattened its three dimensional form. This set of processes was possible because of the rapid influx of the muds that formed the host L mudstone unit. Further evidence for a rapid rate of sedimentation in a quiet setting is the leaf fossil mentioned earlier that cut across the horizontal bedding direction. Diatoms are less abundant in these mudstones than in the laminated shales, but are of the same genus composition with the added presence of the aerophytic bryophyte-dwelling *Diadesmis* and *Orthoseira*, suggesting input from the splash zones of streams and other moist habitats outside the lake.

5.2.5 Diatom contribution to macrofossil preservation: the biofilm model revisited

The biofilm model of Harding and Chant (2000), O'Brien et al. (2002), and O'Brien et al. (2008) is a concept that, if viable, could explain how large quantities of leaf and insect remains underwent only minimal apparent deterioration before burial; however, this concept requires that planktic diatom blooms occurred penecontemporaneously with the entry of the leaves and insects into the lake. As angiosperms dominate the fossil flora at Florissant (Meyer, 2003), they are likely to have shed their mature leaves in autumn. The seasonality of the tychoplanktic/planktic diatom blooms in this fossil site is interpreted as having followed the pattern of modern midlatitude lakes, with all three dominant genera, *Aulacoseira, Synedra*, and *Diatoma tenuis* having produced spring, rather than autumn, blooms (Lund, 1954; Moss, 1981).

The potential is doubtful for the dominant tychoplanktic/planktic diatoms of the fossil species *Aulacoseira clarensis, Synedra, or Diatoma tenuis* at Clare's Quarry to have acted as binding agents for leaf mats in the epilimnion during autumn (when the leaves would have been accumulating) for the following reason. The modern analogs for these three taxa bloom in the spring: *Aulacoseira italica* (Lund, 1954); and *Synedra* and *Diatoma tenuis* (Moss, 1981). So, the timing of the growth periods of the 3 dominant tychoplanktic/planktic diatom taxa is not contemporaneous with the delivery of mature leaves to the lake surface in autumn.

An alternative model explaining the proximity of the leaf fossils with diatom laminae is based upon the observations by Moss (1981) that, although the modern *Diatoma tenuis* and modern analog species of *Synedra* produce planktic blooms in the spring, they also produce

autumn blooms in benthic habitats of the periphyton of lake and stream margins. If, in fact, the leaves were bound by bacteria- and benthic diatom-generated biofilm associated with *Diatoma tenuis* and *Synedra* of the periphyton during autumn, this would support a localized matting process along the shallows of the lake and streams and would require the rafting of the leaf clusters into the open-waters of the lake in the spring or summer, during the periods of higher rainfall. This interpretation is suggested by the presence of what appear to be probable benthic diatom taxa associated with the organic matter in the photomicrograph of the F shale at Clare's Quarry (Figure 9. F).

5.3 Proposed lake history: paleolimnological interpretation for the Clare's Quarry section of the Florissant Formation

From this assessment of the nature of the sediments, their boundary relationships, and the distribution of diatoms and other fossil material, the following lake history at the Clare's Quarry site is proposed.

The high-elevation lake region, surrounded by low relief topography, experienced a warm temperate to subtropical climate with no period of ice-over on the lake. As evidenced by the excellent preservation of leaf and insect fossils and the undisturbed laminated nature of the shales, the lake was deep enough for its floor to have consistently escaped circulation from wind, normal waves, storm waves, and seasonal or annual overturn. Only incomplete seasonal or annual mixing that did not reach the basin bottom waters probably occurred. Perhaps temperature-driven density stratification created a stable cell within the hypolimnion, and the

relatively cool waters slowed organic decay by any resident aerobic bacteria. The confinement of bottom-waters set up anoxia in the lower water column and in the substrate as oxygen became depleted through respiration of the settling organic material. These anoxic conditions prevented habitation in the hypolimnion and its substrate by aerobic life forms, leaving detritus and sediments undisturbed. Pyrite nodules and framboids formed in the anoxic substrate.

Sedimentation onto the deep basin floor from the pelagic region of the lake occurred at a relatively slow rate and consisted of the suspension settling of particles from these sources: (1) autochthonous tychoplanktic and planktic lacustrine diatoms; (2) allochthonous planktic and benthic diatoms from flowing stream habitats, benthic diatoms and ostracods from stream and lake marginal habitats, minor amounts of organic detrital clay from the terrestrial setting; and (3) periodic airfall ash. In addition, the deep lake sedimentation included pyroclastically-loaded individual and clusters of terrestrial plant leaves and insects that were suspended in the epilimnion. Within the basin, laminated shales were laid down, and pulses of pyroclastic material made the volumetrically largest contribution and was deposited at a much higher sedimentation rate than the laminated shales.

On the quiet basin floor, diatom frustules accumulated in microlaminae, along with extremely small amounts of ash/clay airfall and stream-delivered fine detrital material, forming couplets. In the early period of deposition, the clays within the couplets were organic-rich and brown; but, later, became primarily a non-organic grey ash/clay. From the planktic environments of the lake and streams, monospecific microlaminae of *Synedra* frustules alternated with microlaminae of *Synedra* and *Diatoma tenuis*, and allochthonous clay-rich microlaminae of mixed taxa of less common pennate benthics from the shallow stream margins or littoral zone. These diatomite microlaminae alternated with microlaminae of organic matter. The occurrences of these taxonomic groupings are interpreted as follows. The *Synedra*-dominated microlaminae, whether alone, or with *Diatoma tenuis*, represent seasonal blooms of these planktic taxa from both lake and stream habitats. The mixed-taxa microlaminae represent stream runoff with an assortment of lake and stream planktics and stream benthics, along with small quantities of fine clay.

Although the depositional center for the laminated shales was relatively deep and undisturbed, and, therefore, distal from points of inflow of any fluvial system that drained areas of high to medium stream flow, the diatom assemblages reflect contributions from the upper reaches of streams and terrestrial settings that were transported into the lake. The habitats suggested by the diatom data are corroborated by the range of terrestrial plant and insect taxa from moist riparian and drier slopes, along with bryophytes from stream-side and aquatic macrophytes from wetlands.

Episodically, this deep lake setting received discrete, high-volume deposits of fine clay particles that were delivered to the lake from the bordering terrestrial environments. These particles arrived on the lake floor through suspension settling from mud deposits that entered upslope regions of the lake, possibly as underflows from turbidity currents originating from flood events from rivers. These fine clay-sized particles were widely dispersed as suspended plumes over the deep lake where they were rapidly deposited into the deep basin of this slightly acidic freshwater lake, quietly covering the flat-lying laminated shales without disruption on even the finest scale. The initial phase of mud particles consisted of platey minerals such as clay and micas that settled as flat-lying grains to form the blocky texture of the mudstones. This was followed by the final phase of the mud deposition characterized by a notable fining upward of the clay particles that produced a smooth and almost waxy texture at the top of each mudstone bed. This process produced moderately thick tabular units of massive, brown mudstone (with sharp, but non-erosional, upper and lower contacts) that alternate with the laminated shale units. The mineralogy of these brown mudstones (Figure 5-C) is high in the feldspars, amorphous silica, and smectite clay and fine granular quartz and mica derived from weathering of the surrounding volcanogenic terrain. The concentration of diatoms within these mudstone units is very low; however, the taxa that appear are consistent with those observed in the laminated shales of the basin floor deposits, but for the added presence of two genera (Diadesmis and Orthoseira) that are aerophytic in habitat, living attached to moss on rocks and logs in splash zones and in intermittently wet areas along the margins of streams. On the basis of the texture, mineralogic content, lateral continuity, thickness, sharp stratigraphic contacts, macrofossil content, and diatom content, the origin of these deposits is consistent with suspension settling of fine particles into the deep interior of the lake at a position distal from a possible mud delta front.

The relative periodicity of these intermittent mud deposit events is suggested by the mudstone to shale ratio of sequences that show progressive increases and decreases in mudstone to shale thicknesses. It is hypothesized that these fluctuations represent variations in pro-delta progradation into and retreat from the lake. These mud encroachments and retreats were interrupted by resurgences of volcanic activity that produced high volumes of pyroclastic airfall material that fell into the lake. As these volcanic events increased in frequency, the lake level

may have deepened as evidenced by the increased presence of the tychoplanktic diatom species of *Aulacoseira* in the epilimnion. *Aulacoseira* frustules from seasonal blooms accumulated on the basin floor as monospecific microlaminae. Alternating with *Aulacoseira* were microlaminae of the sometimes planktic *Synedra* and *Diatoma tenuis*. Aquatic clams and gastropods from offshore habitats were captured in the pyroclastics and were preserved in the bottom sediments.

The final depositional event recorded in the section at the study site was the coarse airfall tuff of the caprock deposited in the lake basin to a thickness that exceeded 50 cm.

6. Conclusions

An integration of paleoecological data from the diatom flora and associated macrofossils with sedimentary evidence and volcanic petrology has enriched the paleolimnology assessment of the ancient Florissant lake basin at the Clare's Quarry site. A summary chart is provided of the conclusions based on information obtained from this study (Figure 13).

Figure 13. Chart of interpretations about the Florissant paleo-lake from the sedimentary and paleontological data at Clare's Quarry.

Conclusions about the Paleo-lake from the Sediments and Paleontology at Clare's Quarry		
Interpretations	Evidence	
Nature of Lake at Depo-site	Sedimentary	Biological
deep, at least below storm wave base and below photic zone	undisturbed bedding	dominated by open-water planktic diatom taxa; absence of infauna
low-energy setting	clay-sized detrital grains; laminated beds; sharp, non-erosional conacts	biologic grains of micron-scale; planar organic matter (leaves); low mechanical damage
suspension-settling deposition	fine, platey detrital grains	microlaminae of diatoms
distal from stream deposition	clay-sized detrital grains; non-erosional contacts	dominantly lake planktic diatoms
anoxic bottom water	pyrite nodules & framboids	absence of infauna; presence of organic matter; good leaf & bird preservation
pH range: mildly acidic to mildly alkaline	smectite alteration, absence of mineral precipitates	range of diatom pH tolerances
received fine & coarse grn air-fall pyroclastics	fresh nature of phenocrysts, shards, pumice, & juvenile clasts; in-situ textures; absence if detrital matrix; sharp, non-erosional contacts; consistency of composition among beds	entrapped planktic diatoms between pyroclastic grains
received fines from distal marginal turbidites of terrestrial origin	discrete massive mud beds with fining-upward tops	low abundance of diatoms from wide- ranging habitats that include moss- dwelling taxa
episodic encroachment and retreat of lake margin terrestrial mud source	mud to shale ratios gradually increase and decrease	fluctuations in diatom taxa correlate with lithology
depo-site maintained a deep bathymetry	laminated shale deposition resumed after each mud incursion	increase in open-water planktic diatom taxa; continued absence of infauna
peripheral array of stream and littoral habitats	such smectite-rich sediments point to a highly weathered catchment area	diversity of non-planktic diatoms and riparian & littoral plant species

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The typical sediment accumulation style within this deep lake habitat was one in which extremely slow sedimentation of diatom frustules; fine and medium-grained pyroclastics; and leaves, insects, and plant debris accumulated in an undisturbed anoxic setting where they formed laminated shales. Bottom-water anoxia was maintained by incomplete mixing due to depth and oxygen depletion through organic matter respiration. Coarse pyroclastics from an undetermined volcanic source episodically fell into the lake and sank to form discrete tuff beds. This set of processes characterized the deep-water basin deposition. This normal lake sedimentation was punctuated by processes from outside the lake that abruptly delivered homogeneous terrestrial muds to the basin floor. The repetition of units of laminated shales alternating with massive brown mudstones at the study site represents the convergence of two different sediment regimes. Thus, the depositional model is one in which periodic sudden influxes of mud were deposited onto the lake margin, at some distance from the study site. Each of these mud incursion events was followed by suspension settling of the dispersed finer fraction from the water column onto the distal deep water lake basin floor.

The calculated mudstone to shale ratios suggest "mudding-up/mudding-down" sequences that compose cycles reflecting progradation and retreat of suspension settled fines at the distal periphery of a mud-encroached lake margin. These progressive increases in the volume of mudstone to laminated shale are probably in response to climatically induced increasedprecipitation events; abruptly increased topographic slope and stream gradient; increased availability of volumes of mud to be mobilized down slopes, and/or agitation of the ground (from earthquake or tremor) to loosen the mud on unstable slopes.

The diatom frustules and associated fossils accumulated in a deep lacustrine setting distal from the point of inflow of major streams. While perhaps only a partial record of the original populations, the modern analogs for the fossil diatoms indicate habitats from four major environments: mildly acidic lake conditions, circumneutral to mildly alkaline lake conditions, swift-flowing river settings, and slow-flowing stream settings. The life zones within these environments and the modern diatoms that occupy them include the planktic and benthic habitats. Planktic habitats include the following: (1) mildly acidic lake surface waters (Aulacoseira distans); and (2) circumneutral to mildly alkaline lake surface waters (Aulacoseira italica, Synedra ulna, Diatoma tenuis, Stauroneis, Fragilaria vaucheriae, Nitzschia, and Gomphonema). Benthic habitats include these: (1) mildly acidic lake margins (Psammothidium, Frustulia, Pinnularia, Diadesmis, and Eunotia); (2) circumneutral to mildly alkaline lake margins (Fragilaria vaucheriae, Diatoma tenuis, Nitzschia, Gomphonema, Staurosira construens, Achnanthidium minutissima, Planothidium, Platessa conspicua, Navicula menisculus, Orthoseira roeseana, Stauroneis, and Eunotia); (3) shallow water turbid zones bordering high-flow rivers or streams (Achnanthidium and Gomphonema); (4) quiet pools away from the fast stream flow (*Nitzschia and Eunotia*); (5) shallow water zones of slow-flowing streams (Gomphonema, Staurosira, Eunotia, Stauroneis, and Nitzschia); and (6) very rarely, terrestrial (aerophytic) benthics attached to moss-covered rocks in splash-zones and associated with other bryophytes near pools along the banks of streams, in the sphagnum moss of peat bogs (*Diadesmis* prefers lower pH), and in alkaline settings (*Orthoseira* prefers higher pH). Overall, the habitats best represented in the Florissant deposits at Clare's Quarry are the planktic zones of circumneutral to mildly alkaline lake surface waters.

The assessment of the fossil diatom taxa followed by their autecological implications for the seasonality of planktic and benthic blooms illuminates a possible alternative explanation for the proximal relationship of diatoms with leaf and insect fossils. This alternative model pairs the fossil leaves and insects with the autumn blooms of benthic diatoms within the periphyton of lake and stream margins, as opposed to the spring blooms of planktic diatoms of the open-water lake. This finding is contrary to the implied role of the diatom in the biofilm macrofossil preservation model (Harding and Chant, 2000; O'Brien et al., 2002; and O'Brien et al., 2008) that calls upon planktic blooms in the spring as binding agents for the leaf and insect fossils.

This investigation at Clare's Quarry is unique in that it is the only Florissant study that characterizes the diatom assemblages and the first to do so in the context of the sedimentary data. Furthermore, biotic and abiotic evidence is presented in chronological order that allows tracking of changes in the lake processes over time. A stratigraphic sequence of lithologic units is described, providing a standard section for Clare's Quarry, which can be compared with other sections and potentially used for future correlation of pyroclastic beds. In addition, this study is exceptional in its use of diatoms to interpret paleolimnology in such an ancient lake. While this study at Clare's Quarry finds consistency with previously published interpretations of a deep lake bathymetry and anoxic bottom-waters for sites in the "middle shale," it also describes processes of deposition and diatom habitat parameters that expand our perspectives on the lake as a multi-faceted and dynamic ecosystem. The utilization of multiple lines of evidence strengthens our interpretations of the specific site while expanding our thinking about the larger lake system.

The observations brought forth in this study add perspective to the geometry and history of the lake whose sediments host this important fossil Lagerstätte. These new data refine our

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understanding of the geologic processes that impacted the aquatic habitat and created the sediment reservoir which preserved this unique paleontological record.

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SUMMARY

This investigation of the late Eocene freshwater diatom flora from the Florissant Formation has expanded the biochronology of non-marine diatoms by extending the geologic ranges of 14 genera by several million years. These findings shore up the observations of many diatom investigators that non-marine diatoms must have originated long before their first fossil records would suggest. This study is the first diatom floristics survey ever completed at the Florissant locality and, thereby, characterizes these taxa in detail. With the recognition of 33 extant diatom genera, the locality is credited with being the most diverse early freshwater diatom flora yet recorded. Four new species and 2 new varieties were identified and described.

The Florissant diatoms are the oldest fossil diatoms to be used with their modern analog taxa to help determine the conditions of a lacustrine paleoenvironment. This study is unique in that diatom data was used in concert with the sedimentary evidence to probe the mysteries of the lake basin and its history. A particularly useful outcome is the evidence for the peripheral lake margin habitats that shows that the entire lake system was not restricted to a deep basin. The diatoms, along with sedimentary evidence, reflect episodic influxes of terrestrial fine sediments that attest to major events that may have been driven by fluxes in paleoclimate or tectonic and volcanic activity.

This work has further stimulated curiosity about regional tectonic- and climatecontrolled events that influenced the depositional history of the Florissant lake system and the diagenetic processes that affected the lake sediments. The integration of diatom fossils with abiotic evidence has provided insights into the general paleolimnology of the ancient lake.

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