TROPICAL OCHROPHYTE ALGAE FROM THE EOCENE OF NORTHERN CANADA: A BIOGEOGRAPHIC RESPONSE TO PAST GLOBAL WARMING

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ABSTRACT

We report on exquisitely preserved specimens of freshwater siliceous algae belonging to the classes Synurophyceae (scaled chrysophytes) and Bacillariophyceae (diatoms) from middle Eocene lake sediments in Northern Canada. When considered in the context of closest extant relatives, these microfossils present unequivocal biogeographic and ecological affinities with warm-water ochrophyte assemblages. We have identified scales that are unambiguously assigned to *Mallomonas bangladeshica*, a chrysophyte now restricted to tropical lake ecosystems. The diatom genus *Actinella* is also well represented in these sediments, again with the most comparable extant congeners found in tropical to subtropical localities, particularly in the Southern Hemisphere. We surmise that fundamental biogeographic reorganizations among lacustrine algae took place during Eocene hothouse paleoclimates. In this light, future climate warming should be viewed as a potent vector for similar community shifts, with attendant limnological implications.

INTRODUCTION

The paleoclimatology of the Paleogene has received renewed interest because of possible analogy with anthropogenic climate warming. Indeed, enhanced greenhouse-gas loading appears to be a first-order explanation for anomalous warmth during the Paleogene, particularly at the Paleocene-Eocene boundary (55 Ma), and it persisted for at least 10 myr (Pagani et al., 2005; Zachos et al., 2008). At this time, latitudinal temperature gradients were greatly reduced, and the planetary cryosphere was vastly diminished or absent (Greenwood and Wing, 1995). These conditions are well exemplified by the presence of fossil conifer forests at polar latitudes in the Canadian Arctic (Greenwood and Basinger, 1994).

Paleogene greenhouse climates had fundamental consequences for ecosystems globally. Significant shifts in species diversity, community composition, and biogeographic range have been documented for a wide range of organisms, including fungi (Kalgutkar and McIntyre, 1991), pteridophytes (Brinkhuis et al., 2006), higher plants (Wing et al., 1995; 2005), mammals (Clyde and Gingerich, 1998), marine bivalves (Bice et al., 1996), and foraminifera (Kelly et al., 1988; Pak and Miller, 1992). By comparison, relatively little is known concerning Paleogene limnic organisms in general and siliceous ochrophyte algae in particular, in part because suitable sediments have been understudied. In this communication, we report on freshwater algae with pronounced tropical affinities from a small middle Eocene lake in northern Canada. This confirms that ecological responses to Paleogene hothouse climates included the unicellular algal groups that constituted the base of food chains in ancient lake ecosystems.

MATERIALS AND METHODS

The Giraffe Pipe locality (64°44′N, 109°45′W) is a kimberlite diatreme that has been infilled by a sequence of middle Eocene lacustrine and paludal sediments and subsequently covered by Neogene glacial deposits (Figs. 1A–B). The Giraffe Pipe is one of many kimberlites in the Lac de Gras field in the Northwest Territories of Canada, most of which have Cretaceous or Paleogene emplacement ages (Heaman et al., 2004). A 165 m drill core collared at 47° was obtained by BHP Billiton Diamonds Inc. in 1999 (core BHP 99-01) in order to assess the diamond potential of kimberlite underlying the maar sediments. This core contains 113.1 m of stratified organic sediment of middle Eocene age, including 44.8 m of peaty material underlain by 68.3 m of stratified lacustrine sediment, in many places finely laminated. Conversion of these core depths to their vertical equivalent implies stratigraphic thicknesses of 32.7 m for the peat and 51.1 m for lake sediments (Fig. 1C). Two air-fall tephra beds occur at the transition between lacustrine and paludal sedimentation, which marks the final infilling of the maar and incipient terrestrialization.

The age of this material is assessed in several ways. First, a $^{87}Rb/^{87}Sr$ model age from kimberlitic phlogopite is 47.8 ± 1.4 Ma (Creaser et al., 2004), providing a maximum age for lacustrine sedimentary sequence. Second, diameter-corrected (n = 2) and isothermal-plateau (n = 1) fission-track dates from the two tephra beds are highly coherent and statistically indistinguishable from 40 Ma (J. Westgate, personal communication, 2007). Third, pollen assemblages from both lacustrine and paludal facies include what are believed to represent diagnostic middle Eocene elements, including *Platycarya swasticoides* and *Pistillipollenites mcgregorii* (Rouse, 1977; Hamblin et al., 2003). We therefore envisage that, following phreatomagmatic kimberlite emplacement, a lake formed rapidly within the crater and persisted for ~7–8 myr before terrestrialization. The maar crater was then colonized by a forest dominated by *Metasequoia* Miki (Cupressaceae), as indicated by abundant mummified wood, needles, and resinite droplets. It is important to note that the protracted regional tectonic and thermal stability of the Slave Craton, into which the Giraffe Pipe was intruded, has resulted in near-zero diagenetic alteration of the fossil content, as testified by preservation at the cellular level (Wolfe et al., 2006). For this reason, the site has already provided a number of insights concerning early history of nonmarine ochrophyte algae (Siver and Wolfe, 2005a; 2005b; 2007).

The current investigation is based on samples from 98.44–116.32 m in the core (71.99–85.07 m vertical equivalent depth). This interval corresponds to depths between 2.41 m and 14.49 m below the transition from lake to forest paleoenvironments, immediately beneath the two tephra horizons (Fig. 1C). In a paleolimnological sense, the lake was at this time shallow and dystrophic. Scaled chrysophytes were prolific (Siver and Wolfe, 2005a; 2005b), and diatoms suggest an acidic lake-water chemistry (Siver and Wolfe, 2007). Siliceous sponge spicules and disarticulated testate protozoan (rhizopod) scales are also abundant in this portion of the core, which is entirely consistent with this paleoenvironmental interpretation. In a general sense, synurophytes are more common
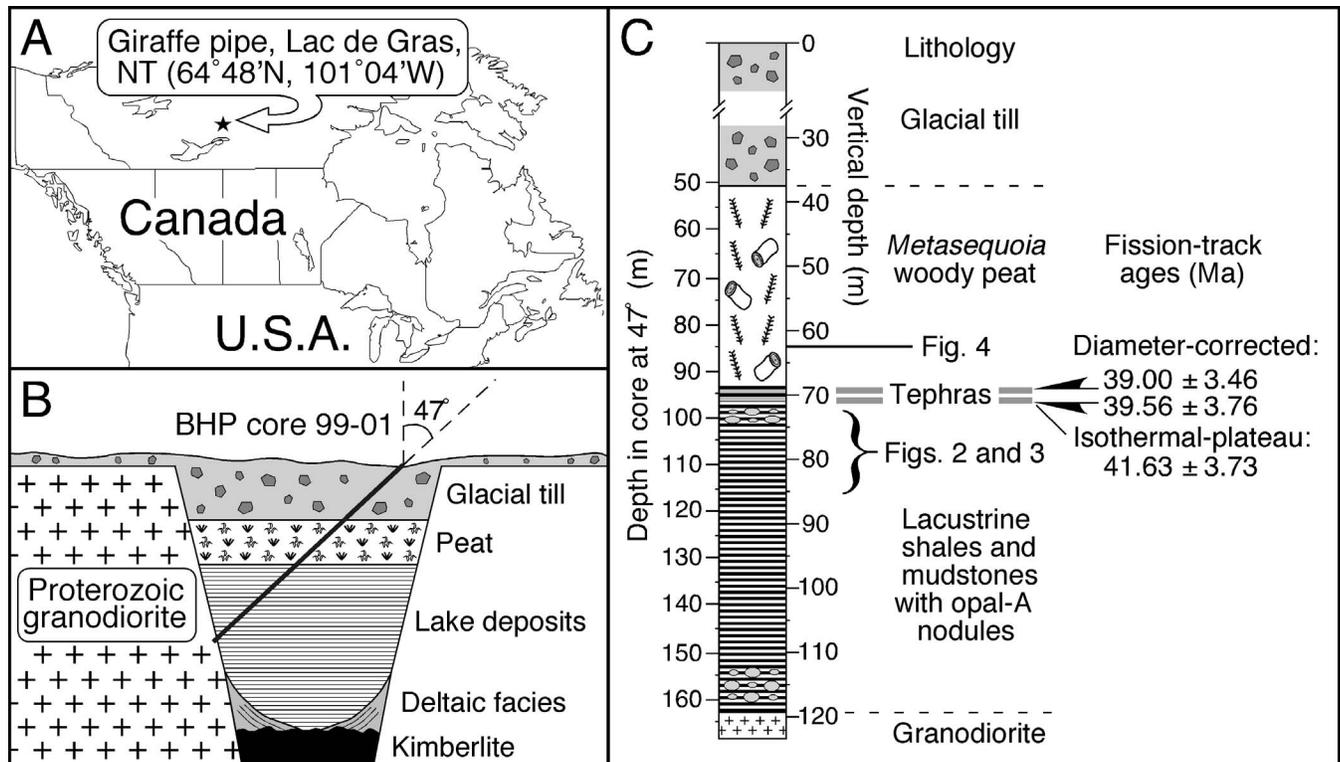
FIGURE 1—Location map and the Giraffe Pipe core. A) Location. B) Schematic stratigraphy. C) Lithostratigraphy and location of observations.

toward the top of this interval, whereas diatoms become more common lower in the section.

We conducted a detailed investigation using scanning electron microscopy (SEM) to fully explore the siliceous microflora of this interval. Small chips (~200 mg) of organic mudstone were first oxidized with 30% H_2O_2 overnight and then centrifuged and rinsed several times. Aliquots of cleaned slurry were air dried onto heavy-duty aluminum foil, trimmed, and mounted to aluminum stubs with Apiezon wax. These stubs were coated with an Au-Pd mixture for two minutes in a Polaron Model E sputter coater prior to examination with a Leo 982 field emission scanning electron microscope.

We compared specimens of a *Mallomonas* taxon found in Giraffe Pipe sediments with modern forms of *M. bangladeshica* illustrated in the literature and with a population we examined from a subtropical locality in South America (Siver and Vigna, 1996). An archived sample from a site within the delta region of the Paraná River originally collected by Siver and Vigna in 1994 containing *M. bangladeshica* was dried onto aluminum foil and prepared for SEM as noted above. The length, width, and diameter of the grapnel structure (see below) were measured for twenty scales each from Giraffe Pipe sediments and the South American locality using SEM. The analysis of variance routine in SPSS (SPSS Institute Inc., 1999) was used to test for potential differences in the morphometric characters.

All Giraffe Pipe sediment samples and collections from the Paraná River delta examined as part of this work are archived in Siver's laboratory. Splits of all Giraffe Pipe samples are also stored in Wolfe's laboratory. Samples containing *Actinella parva* from Lake Judd, Tasmania, are maintained by W. Vyverman (University of Gent).

OBSERVATIONS

Mallomonas bangladeshica (Takahashi & Hayakawa) Siver & Wolfe nov. comb. (Figs. 2A–F)—*Mallomonas bangladeshica* was originally described from Bangladesh as *Mallomonopsis peroneides* (*peronoides*) var. *bangladeshica* by Takahashi & Hayakawa (1979) and later transferred to

the species level within the genus *Mallomonopsis* by Wujek and Timpano (1984). Asmund and Kristiansen (1986) merged the genus *Mallomonopsis* with *Mallomonas*, but these authors incorrectly listed Wujek and Timpano as the taxonomic authorities for *Mallomonas bangladeshica*. Recognizing that the transfer to the species rank within the genus *Mallomonas* had not been made, Nicholls (1988) proposed the combination, but this was done in error according to the rules of the International Code of Botanical Nomenclature because reference to the proper page(s) within the original publication of Takahashi and Hayakawa (1979) was not made. Kristiansen and Preisig (2007) make a valid transfer to *Mallomonas* at the variety level, but not for the species designation. The lack of a formal designation for this chrysophyte mandates the following combination:

Mallomonas bangladeshica (Takahashi & Hayakawa) Siver & Wolfe comb. nov.

Basionym: *Mallomonopsis peronoides* var. *bangladeshica* Takahashi & Hayakawa (1979, p. 131, figs. 3–5 and 7–8).

Synonyms: *Mallomonopsis bangladeshica* (Takahashi & Hayakawa) Wujek & Timpano 1984; *Mallomonas peronoides* var. *bangladeshica* (Takahashi & Hayakawa) Kristiansen & Preisig 2007; *Mallomonas bangladeshica* (Takahashi & Hayakawa) Nicholls 1988 (invalid combination).

Scales belonging to the synurophyte *M. bangladeshica* are readily identified by the presence of a unique appendage that rises perpendicularly to the base plate near the scale's apex (Figs. 2A–B, E–F). This appendage takes the form of a grappling hook or lobate umbrella (Figs. 2E–F). Although this feature is present on most, but not all, scales sheathing the cell, it is viewed as diagnostic of this chrysophyte (Siver and Vigna, 1996; Kristiansen, 2002). Some scales with reduced or rudimentary grappling hooks are also typically found on the posterior half of the cell (Figs. 2C–D). In Giraffe Pipe specimens, there are no evident morphological differences with extant forms. We observed scales with well-formed and spectacularly preserved grapnel hooks (e.g., Fig. 2A) that are virtually identical to modern scales of *M. bangladeshica* (cf. Fig. 2B), as well as scales with less-developed appendages (e.g., Fig. 2C) that are found on the cell covering today (cf. Fig. 2D). In addition, the range in length
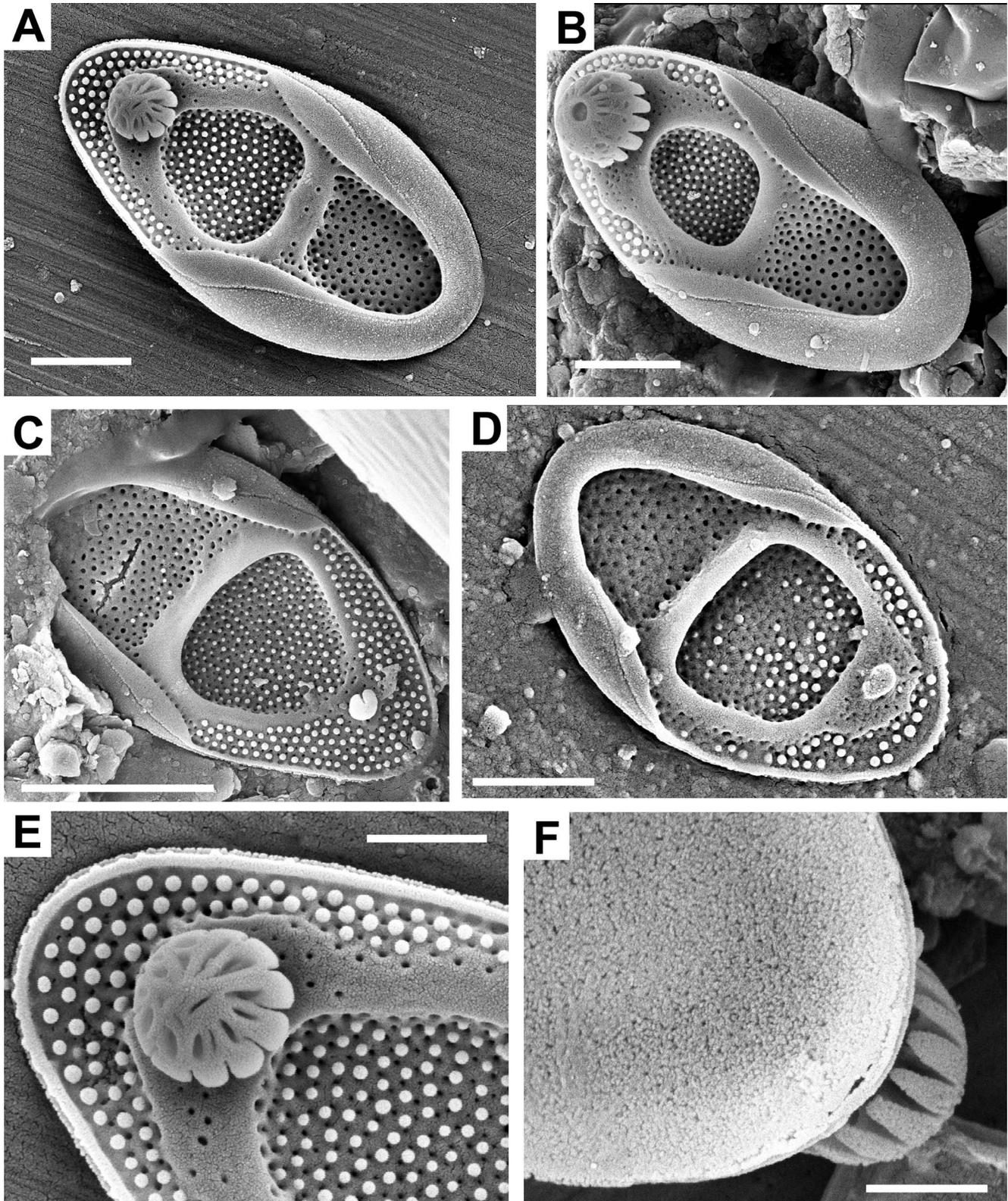
FIGURE 2—Fossil *Mallomonas bangladeshica* scales from Giraffe Pipe sediments (A, C, E–F) and modern forms from the Paraná River delta, Argentina (B, D). A–B) Whole scales, each with a posterior upturned rim, anterior thickened margin, large anterior depression, surface papillae, and a well-developed grappling hooklike structure. C–D) Whole scales similar to those depicted in A–B, except with small rudimentary and reduced grappling hooklike structures. E) Close-up of the grappling-hook structure as viewed from the top. F) A scale with a fully formed, grappling hooklike structure as viewed from the undersurface of the scale. Scale bars = 500 nm in E–F; 1 µm in A–B, D; and 2 µm in C.

(3.1–5.0 μm) and width (2.3–3.0 μm) of body scales and the diameter of the grapnel hook (650–850 nm) of Giraffe Pipe specimens were not significantly different from those observed for the living population of *M. bangladeshica* from South America examined as part of this study (length = 3.3–5.0 μm; width = 2.5–3 μm; diameter of grapnel hook = 600–900 nm) and within the limits reported in the literature by Asmund and Kristiansen (1986). We conclude that, from morphological and size perspectives, the scales found in Giraffe Pipe sediments are similar to and, in most respects, indistinguishable from those of modern specimens of *M. bangladeshica*.

Mallomonas bangladeshica has hitherto been documented only from warm regions and has been classified accordingly as endemic to the tropics (Cronberg, 1989; Kristiansen, 2002). Taxonomically, *M. bangladeshica* is placed within the series Peronoides (Asmund and Kristiansen, 1986), alongside *M. stella* Cronberg, *M. ceylanica* Dürrschmidt & Cronberg, and *M. peronoides* (Harris) Momeu & Péterfi. The former two taxa are also tropical, being reported from Africa and Asia, respectively, while the latter is more cosmopolitan but also restricted mostly to warm-region lakes (Siver and Vigna, 1996; Kristiansen, 2002). Our present observations (Figs. 2A, C, E–F) are the first fossil documentation of this chrysophyte lineage. The marked similarity between Giraffe Pipe and modern forms of *M. bangladeshica* mirror prior observations concerning additional chrysophyte genera from this deposit, collectively mandating prolonged evolutionary stasis within the synurophytes taken as a whole (Siver and Wolfe, 2005a; 2005b).

Actinella Lewis morphotype Giraffe 1 (Figs. 3A–D, G–H).—Abundant valves belonging to an undescribed diatom of the genus *Actinella* (hereafter: *Actinella* morphotype Giraffe 1) were found in the lower 2 m of the sediment section investigated here. *Actinella* is one of eight genera belonging to the Subclass Eunotiophycidae Mann *in* Round et al. (1990). Freshwater eunotioid diatoms are primarily distributed in acidic-to-dystrophic lake and wetland environments, where *Eunotia* is usually the most common genus (e.g., Patrick and Reimer, 1966; Krammer and Lange-Bertalot, 1991). The presence of *Actinella* in the Giraffe Pipe is thus ecologically consistent with our prior documentation of several morphotypes of *Eunotia* in the upper-lake facies of the core (Siver and Wolfe, 2007). Species of both *Eunotia* and *Actinella* possess a simple raphe positioned ventrally on each valve and terminating distally in distinct nodules near the apices (Round et al., 1990; Sabbe et al., 2001). Both genera have one or two simple rimoportulae per valve (Kociolek et al., 1997; Vyverman et al., 1998). Specimens from the Giraffe Pipe (Figs. 3A–D, G–H), however, can be reliably assigned to *Actinella* because the valves are highly heteropolar in valve view, the frustules are clavate in girdle view, and the raphe slits are of unequal lengths. The raphe of *Actinella* morphotype Giraffe 1 differs from *Eunotia* in that it lies entirely on the margin of the valve face and not on the mantle.

Specimens of *Actinella* morphotype Giraffe 1 are small, range in size from 11–35 μm × 1.8–2.8 μm, and have rounded head (Figs. 3G–H) and foot (Figs. 3C–D) poles. Although *Actinella* morphotype Giraffe 1 does not match exactly any modern species within the genus, it is most comparable to *Actinella parva* Vanhoutte & Sabbe (Figs. 3E–F), a species known only from the highlands of Tasmania (Sabbe et al., 2001). Like *Actinella* morphotype Giraffe 1, valves of *A. parva* are small, range in size from 11–31 μm × 1.5–2.3 μm (measured at the midpoint), and have similarly rounded head and foot poles. In addition, frustules of both taxa are clavate in girdle view, possess one rimoportula per valve that can be on either pole (Figs. 3D, G–H), have similar striae densities, and lack marginal spines. The position of the raphe and the size of the helictoglossae differ slightly between the two species, but otherwise their morphologies are similar.

Most extant *Actinella*, including all species with less complex head poles like *Actinella* morphotype Giraffe 1, are distributed in tropical and subtropical regions of the world, largely in the Southern Hemisphere (Kociolek et al., 1997; Metzeltin and Lange-Bertalot, 1998; Sabbe et al., 2001), with remarkable diversity in the Amazon basin (Kociolek et al.,

2001; Metzeltin and Lange-Bertalot, 2007) and tropical Africa (Kociolek and Rhode, 1998; Sabbe et al., 2001). Synthesis of the 58 taxa in *Actinella* recognized and reviewed by Kociolek et al. (2001), Sabbe et al. (2001), and Metzeltin and Lange-Bertalot (2007) reveals that 34 are South American, 11 are African, and 9 are Australasian endemics, with relatively few cosmopolitan or temperate representatives (4 taxa). The type species, *A. punctata* Lewis, clearly fits within this last category. *Actinella punctata* was originally described from a small, acidic water body in New Hampshire in the United States (Lewis, 1864). Furthermore, unlike congeneric taxa with strongly regionalized distributions, it has been documented in temperate North America, northern Europe, the southern United States, Papua New Guinea, and tropical South America (e.g., Woodhead and Tweed, 1957; Kociolek et al., 1997; Camburn and Charles, 2000; Gaiser and Johansen, 2000; Sabbe et al., 2001; Metzeltin and Lange-Bertalot, 2007). Besides *A. punctata*, which has a more complex morphology than *Actinella* morphotype Giraffe 1, other reports of *Actinella* taxa from temperate localities are rare, and the genus as a whole has been characterized as tropical (Round et al., 1990).

By comparison, the fossil record of *Actinella* is far more cryptic, with only three documented localities outside the current investigation, none of which is presently tropical. *Actinella penzhica* was described from Oligocene–late Eocene deposits on the Kamchatka Peninsula (Lupikina and Dolmatova, 1982), whereas *A. miocenica* was described from Miocene sediments in the Jilin Province of northeastern China (Li, 1988). *Actinella pliocenica* was originally described from the Pliocene of France (Héribaud, 1902) and subsequently reported as extant in Sierra Leone (Woodhead and Tweed, 1957). When this admittedly sparse fossil record is augmented by the documentation of *Actinella* morphotype Giraffe 1 from the middle Eocene of northern Canada, it is possible to hypothesize that *Actinella* was once more widely distributed at northern high latitudes than at present.

DISCUSSION AND CONCLUSIONS

The documentation of *Mallomonas bangladeshica* and *Actinella* morphotype Giraffe 1 can be integrated with the goal of refining the understanding of Cenozoic ochrophyte biogeography. The first observation is that these algae are morphologically very similar to their closest extant relatives. Indeed, earlier claims for protracted evolutionary stasis among both the scaled chrysophytes (Siver and Wolfe, 2005a) and the diatoms (Wolfe et al., 2006; Siver and Wolfe 2007) appear strongly supported by the taxa described here. We furthermore argue that it is not only the morphology of the siliceous components of these organisms that has remained conservative but also their general ecological characteristics. The envisaged paleoenvironment of the Giraffe Pipe during the terminal lacustrine phase (Fig. 1C) is one of a productive, shallow, acidic, and perhaps dystrophic body of water facing encroachment by terrestrial vegetation, including *Metasequoia* forest. We believe this situation to have been limnologically similar to the habitats in which closely related taxa currently thrive, as reviewed above. That the latter habitats occur primarily in subtropical-to-tropical parts of the world has considerable implications for the interpretation of Giraffe Pipe ochrophyte assemblages.

The abundance of *Metasequoia* megafossils (wood and needle litter; see Fig. 4) in Giraffe Pipe sediments immediately overlying the limnic facies provides some measure of paleoclimatic inference concerning the site at the time of deposition. Reproductive growth of *Metasequoia* has been circumscribed to a mean annual temperature range of 9–17°C, and mean annual precipitation regimes of 950–2040 mm (Mosbrugger et al., 2005; Liu et al., 2007). Given that the mean annual temperature and precipitation for Yellowknife, the closest meteorological station to the Giraffe Pipe locality, are −5.4°C and 267 mm, respectively, the middle Eocene climate of this region appears to have been at least 14°C warmer than present and approximately three times wetter. Under such conditions, the presence of ochrophyte algae with tropical ecological affinities appears less surprising, provided that adequate colonization vectors existed.
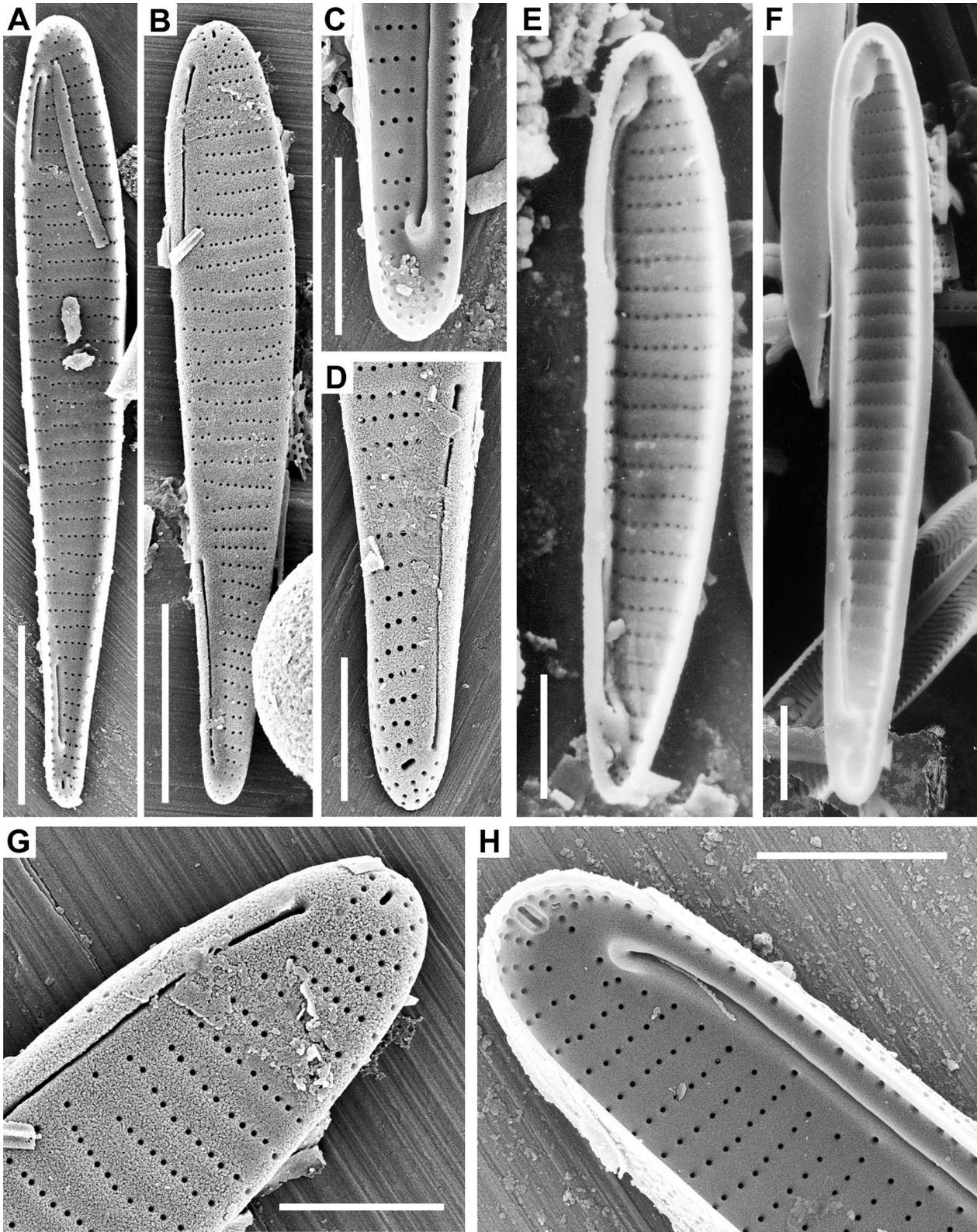
FIGURE 3—Valves of *Actinella* morphotype Giraffe 1 from Giraffe Pipe sediments (A–D, G–H) and the modern species, *A. parva*, from Lake Judd, Tasmania (E–F). A–B) Internal (A) and external (B) views of whole valves. Note the varying lengths of the raphe slits and their position along the ventral surface on the valve face. C–D) Internal (C) and external (D) views of the foot pole. Note the position of the helictoglossa (C) and the presence of a rimoportula on the valve (D). E–F) Internal views depicting overall valve shape, raphe structure, and the helictoglossae. G–H) Internal (G) and external (H) views of the head pole depicting the position of the helictoglossa and rimoportula. Scale bars = 2 μm in C–H; 5μm in A–B).
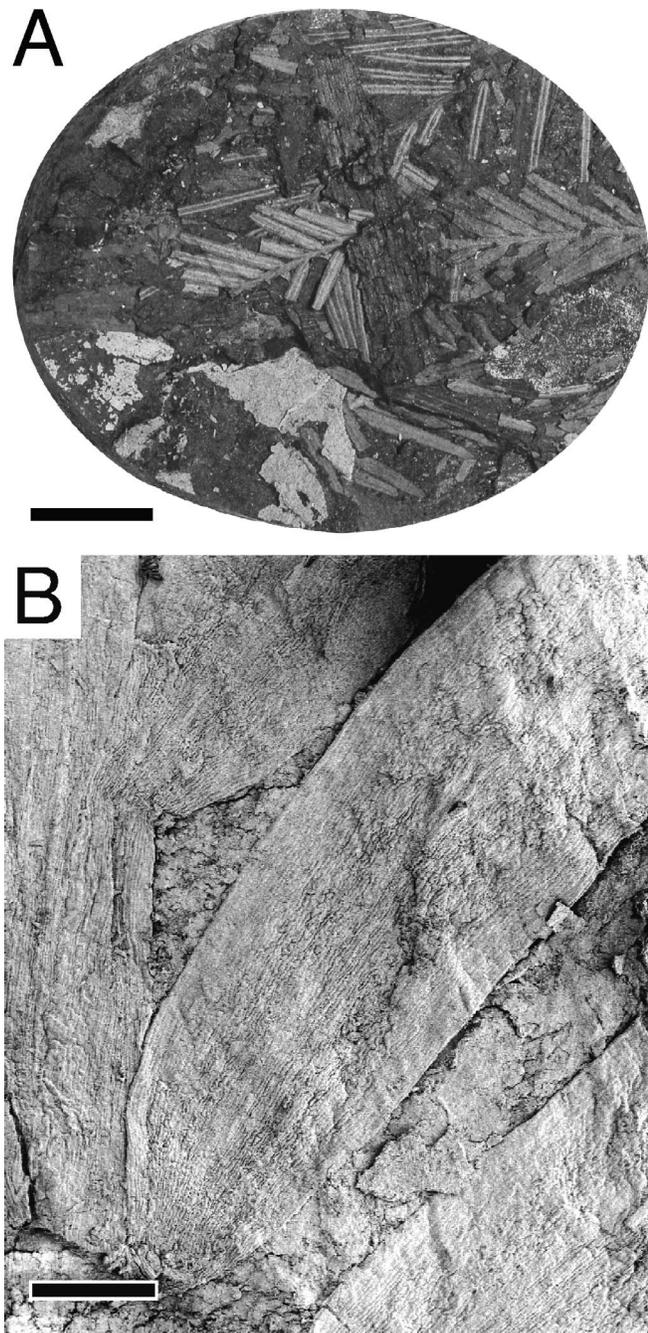
FIGURE 4—Examples of mummified *Metasequoia glyptostroboides* remains from Giraffe Pipe terrestrial sediments immediately overlying the lacustrine sequence. A) Litter dominated by *M. glyptostroboides* from a depth of 85 m in the core (62 m equivalent vertical depth; cf. Fig. 1). B) Higher magnification scanning electron micrograph of *Metasequoia* needles reveal their exceptional preservation. Scale bars = 1 cm in A, 500 μm in B.

In this sense, warmer summers and greatly extended ice-free seasons may have facilitated the colonization and survival of warm-water organisms in freshwaters throughout the Arctic, heightened by the presence of a more active hydrological cycle. Subsequently, as Cenozoic climates began to cool, warm-adapted lake organisms either perished or followed the retraction of warm climate belts toward the equator. It therefore seems plausible that the few modern taxa we surveyed that can be found in temperate regions (e.g., *Mallomonas peronoides*, *Actinella punctata*) are in fact relictual taxa from warmer climate intervals, having adapted to survival in colder climates. This may explain why there exist, within both

Mallomonas series Peronoides and *Actinella*, a handful of scattered distributional records from the temperate zone despite an overarching biogeographic affinity with warm climate zones.

These observations have several fundamental implications. First, ochrophyte algae are demonstrably responsive to climate. Eocene greenhouse climates allowed the survival of ochrophytes with warm-water affinities in northern Canada, far north of any known occurrence of related extant taxa. Second, as global climates continue to warm under increased anthropogenic greenhouse-gas forcing, we may predict that warm-water ochrophytes will undergo important range expansions. Indeed, there is already strong evidence that such processes have been initiated, given that chrysophytes and diatoms with boreal affinities are beginning to appear in the Arctic (Wolfe and Perren, 2001; Smol et al., 2005). We predict this trend to continue apace with current and future warming of the planet (Hansen et al., 2006). Third, because ochrophytes play important roles at the base of aquatic food chains, such ecological reorganizations are likely harbingers of more profound ecological changes at higher trophic levels.

ACKNOWLEDGMENTS

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