Eunotia spp. (Bacillariophyceae) from Middle Eocene lake sediments and comments on the origin of the diatom raphe

Peter A. Siver and Alexander P. Wolfe

Abstract: Freshwater diatoms belonging to the genus *Eunotia* Ehrenberg 1837 are well preserved in Middle Eocene lake sediments from the Northwest Territories, Canada. Although two distinct valve morphologies are recognized, both have features that are entirely compatible with modern congeneric taxa, including dorsiventral valve morphology, striae spanning the valve face and extending onto the mantle, raphe structures on the mantle that extend distally onto the valve face, two helictoglossae per valve, and one apical rimoportula per valve. These findings establish that the genus *Eunotia*, and likely freshwater raphid diatoms as a whole, are more ancient than previously believed, dating back to at least 40 Ma. One of the observed morphotypes has a raphe spanning more than 80% of the valve length as well as a narrow hyaline area extending between proximal raphe endings and interrupting mantle striae. These features imply that the raphe system among certain ancient representatives of *Eunotia* was more developed relative to modern counterparts. The notion of progressive degeneration of the raphe within *Eunotia* is supported by several extant species. Collectively, these observations confirm molecular phylogenetic arguments that position *Eunotia* as a basal raphid diatom.

Key words: eocene, *Eunotia*, Eunotiaceae, diatom, raphe, rimoportula.

Résumé : Des Diatomées appartenant au genre *Eunotia* Ehrenberg furent découvertes parmi des sédiments lacustres datant de l'Éocène moyen, et provenant des Térritoires du Nord-ouest (Canada). On décrit deux morphotypes en détail, les deux possédant la gamme entière des caratères qui définissent le genre *Eunotia*: un plan valvaire dorsi-ventral, des stries présentes autant sur la face que sur la marge de chaque valve, le raphé traversant la marge ventrale avant d'aboutir sur la face, aux pôles de la valve, la présence de deux helictoglossae par valve, mais une seule rimoportule en position polaire interne. Ces Diatomées confirment la présence d'*Eunotia*, et donc des Diatomés raphidinées lacustres en general, à l'Écene moyen, datant d'au moins 40 Ma. Un des morphotypes étudiés possède un raphé fortement allongé (80 % de la longueur de sa valve), ainsi qu'un pseudoraphé prononcé sur la marge ventrale. Cette observation suggère la dégénération progressive du raphé chez *Eunotia*, une notion appuyée par plusieurs espèces actuelles de ce genre. La position phylogénétique basale d'*Eunotia* au sein des Diatomées raphidinées, postulée à priori par l'analyse moléculaire seule, est alors nouvellement confirmée par l'enregistrement fossile.

Mots clés : Éocène, *Eunotia*, Eunotiaceae, Diatomée, raphé, rimoportulae.

Introduction

Eunotia Ehrenberg 1837 is a large genus of predominantly freshwater diatoms that are especially successful in acidic habitats (Round et al. 1990; Krammer and Lange-Bertalot 1991). The genus belongs to the family Eunotiaceae Kützing 1844 within the subclass Eunotiophycidae Mann *in* Round et al. 1990. The subclass Eunotiophycidae is characterized by a reduced raphe system and the presence of rimoportulae and has historically included the genera *Actinella* Lewis 1864, *Desmogonium* Ehrenberg 1848 (combined with *Eunotia* by some authors), *Eunotia*, *Peronia* Brébisson & Arnott ex Kitton 1868, and *Semiorbis* Patrick 1966. More recently, three additional genera have been described and added to the Eunotiophycidae, each possessing amphoroid dorsiventral symmetry and raphe systems that are not integrated within the sternum: *Eunophora* Vyverman, Sabbe & Mann (Vyverman et al. 1998), *Amphorotia* Williams & Reid (Williams and Reid 2006*a*), and *Colliculoamphora* Williams & Reid (Williams and Reid 2006*b*). Although *Amphorotia* has a reduced raphe as in other eunotioid diatoms, *Eunophora* and *Colliculoamphora* have more complex raphe systems that include a central nodule between promixal raphe endings. The valve surfaces of *Eunophora* and *Colliculoamphora* are furthermore colliculate. Whereas a single polar rimoportula is present in several species of *Eunophora*, rimoportulae are altogether lacking in *Colliculoamphora*.

Eunotia is recognized on the basis of valve outline, raphe structure and position, and the presence of both helictoglossae and rimoportulae. Frustules of *Eunotia* are asymmetric about the apical axis, frequently forming a dorsiventral lunate valve outline. Each valve possesses raphe branches that extend from the ventral mantle, centrally, to the valve face near the apices, distally. Here, the raphe terminates in heli-

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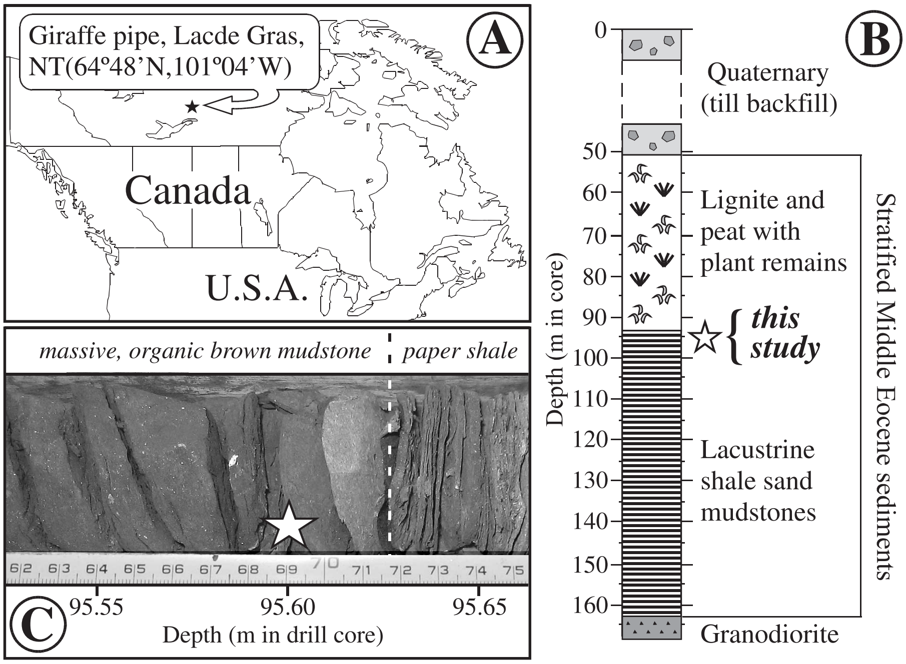
Fig. 1. (A) Location map of the Giraffe pipe kimberlite locality, (B) simplified core lithology, and (C) photograph of the sediment interval considered here.



ctoglossae internally and in external raphe fissures externally, which curve onto the valve face at each pole. Central nodules are lacking, whereas striae cross the valve face and extend onto both ventral and dorsal mantles. Most *Eunotia* have one rimoportula per valve situated at an apex, usually near the juncture of the valve face and mantle (Mayama and Kobayasi 1991; Williams and Reid 2006*a*).

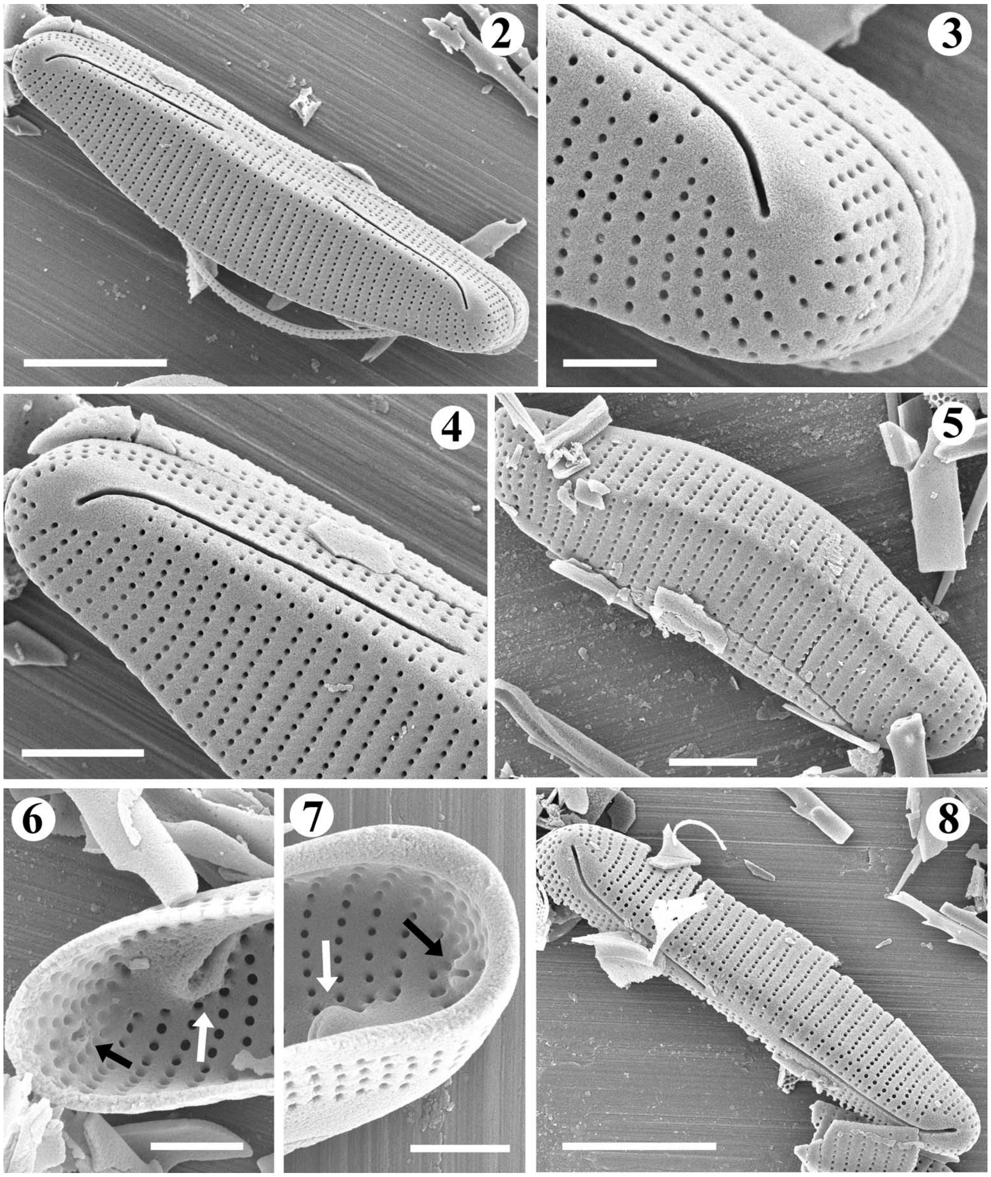
Although scattered occurrences of Late Cretaceous nonmarine diatoms have been reported (Chacón-Baca et al. 2002; Ambwani et al. 2003), the existing fossil record maintains that the majority of freshwater lineages arose between the Middle and Late Eocene and subsequently radiated rapidly and globally (Round et al. 1990; Krebs 1994; Sims et al. 2006). To this point, freshwater *Eunotia* are not known to occur prior to the Early Miocene (Bradbury et al. 1985). Two somewhat older extinct species, *Eunotia grovei* Desikachary & Sreelatha and *Eunotia marina* Schrader, have been described from marine sediments of Late Eocene to Early Oligocene age from New Zealand (Oamaru diatomite; Novitski and Kociolek 2005). Although there remains some question as to whether these diatoms originated in freshwater habitats and were subsequently transported to marine sediments, to date, they represent the oldest known representatives of *Eunotia*. Given the absence of diagnostic freshwater diatoms in these assemblages, Novitski and Kociolek (2005) contended that these early forms of *Eunotia* are indeed marine. Fossil *Colliculoamphora* are also present in the Oamaru deposit, whereas modern representatives inhabit warm marine environments (Williams and Reid 2006*b*). It is thus clear that Eunotiaceae includes several marine taxa, dating to at least the Late Eocene, despite representing a predominantly freshwater family of diatoms.

The importance of these issues lies in the relevance of *Eunotia* towards understanding the evolution of the raphe system in pennate diatoms as a whole, a topic that has been debated for over half a century (Berg 1948; Hustedt 1952; Kolbe 1956; Hasle 1973; Simonsen 1979; Mann 1984; Kociolek 2000; Mann et al. 2003; Sims et al. 2006). The primary question is whether the raphe morphology unique to the eunotioid genera represents a primitive state (or symplesiomorphy) possibly associated with the expansion of rimoportulae into the eunotioid raphe or alternately a derived state resulting from the progressive degeneration of a more complete "naviculoid" raphe system. Several recent molecular phylogenies (Mayama and Kuriyama 2002; Medlin and Kaczmarska 2004; Sorhannus 2004; Sims et al. 2006) partially or wholly support the first of these notions, namely that *Eunotia* belongs within the basal lineage of raphid pennate diatoms. To date, the fossil record has yielded few specimens that enable the testing of these phylogenetic hypotheses. In the present paper, we document definitive freshwater *Eunotia* from Middle Eocene sediments, thus extending the stratigraphic age of eunotioid diatoms by over 10 million years. These fossil diatoms have pronounced affinities with modern congeneric taxa. Comparative studies of these diatoms using scanning electron microscopy enable insights concerning the trajectory of raphe development.

Materials and methods

Diatom-containing sediment samples were identified in a drill core obtained from the Giraffe kimberlite locality (Fig. 1) situated in the Lac de Gras diamond field, Northwest Territories, Canada (Hamblin et al. 2003; Wolfe et al. 2006). The core was raised by BHP Billiton Diamonds Inc. (Kelowna, British Columbia) for assessment of the diamond grade in kimberlitic facies but was found to contain 67 m of stratified nonmarine sediments (mostly organic mudstone and shale) that accumulated in a relict lake that occupied the diatreme crater (maar) following eruption and kimberlite emplacement. The core was subsequently archived at the

Figs. 2–8. Valves of *Eunotia* morphotype ‘Giraffe 1’. **Fig. 2.** Valve depicting the position of the raphe along the ventral mantle, the hyaline region adjoining the proximal raphe endings, and evenly spaced, parallel striae. Scale bar = 5 µm. **Figs. 3 and 4.** Closeups of the poles of the specimen illustrated in Fig. 2. Distally, the raphe endings curve onto the valve face before terminating near the apices. Scales bars = 1 and 2 µm, respectively. **Fig. 5.** Specimen depicting the valve face and dorsal mantle. Note the continuity of striae between both parts of the valve. Scale bar = 5 µm. **Figs. 6 and 7.** Internal apical views of two different valves showing the position of helictoglossae along the mantle (white arrows) and rimoportula (black arrows) near the apices. Scale bars = 1 µm. **Fig. 8.** Ventral surface and valve face of a specimen for which the raphe extends more than 80% of the valve length. Scale bar = 2 µm.



Geological Survey of Canada in Calgary, where preliminary pollen and organic geochemical investigations have been undertaken (Hamblin et al. 2003). The age of kimberlite emplacement, from ^{87}Rb/^{87}Sr analyses of phlogopite, is 47.8 ± 1.4 Ma (Creaser et al. 2003), which provides a maximum age for lacustrine sedimentary sequence. Pollen assemblages further constrain these sediments to a Middle Eocene age (i.e., presence of *Pistillipollenites mcgregorii* Rouse) (Rouse 1977), implying that lake sedimentation closely followed the eruption (Hamblin et al. 2003). Likely owing to the crater’s steeply sloping morphometry, these organic sediments were not scoured by glacial erosion during the Quaternary but instead back-filled by a thick cover (~50 m) of glacial sediment that has served to entomb the material. Preservation is further enhanced by the absence of significant thermal or tectonic alteration since the eruptive event.

The current investigation is based on the 95.60 m level in the core. Since the core was drilled at a 47° angle, this corresponds to a vertical depth of ~70 m beneath the surface. This facies represents the terminal phase of the lake prior to becoming a peaty wetland, at which time waters were likely shallow and dystrophic (Siver and Wolfe 2005; Wolfe et al. 2006). Samples were processed by oxidation in 30% H_2O_2 followed by repeated centrifugation and rinsing. Aliquots of the cleaned slurry were air-dried onto heavy-duty aluminum foil, trimmed, and mounted to aluminum stubs with Apie-

Figs. 9–17. Valves of *Eunotia* morphotype 'Giraffe 2' (Figs. 9–13) and comparison with selected extant taxa (Figs. 14–17). **Fig. 9.** Valve showing the position of the raphe and associated hyaline regions. Scale bar = 10 μm. **Fig. 10.** Closeup of specimen in Fig. 9. Scale bar = 5 μm. **Fig. 11.** Internal valve view. Scale bar = 10 μm. **Figs. 12 and 13.** Magnifications of the poles of the specimen in Fig. 11. Note the well-developed helictoglossae (white arrows), the lack of rimoportula in Fig. 12, and the presence of single rimoportula in Fig. 13 (black arrow). Scale bars = 2 μm. **Figs. 14 and 15.** Valves of *Eunotia bidentula* W. Smith (Pilgrim Lake, New Jersey) (Fig. 14) and *Eunotia carolina* Patrick, 1958 (Singletary Lake, North Carolina,) (Fig. 15) showing raphe position along the ventral mantle and continuous striae between the proximal raphe endings on the mantle. Scale bars = 10 and 2 μm, respectively. **Fig. 16.** Internal view of the apex of *Eunotia croatana* (Catfish Lake, North Carolina). Note the advanced degeneration of raphe size (white arrow), diminished helictoglossa, and single apical rimoportula (black arrow). Scale bar = 1 μm. **Fig. 17.** Girdle view of the ventral surface of *Eunotia incisa* W. Smith ex Gregory (Pilgrim Lake). The raphe slits on this specimen fail to impinge onto the valve face, so that the entire raphe system can be observed in girdle view. Scale bar = 10 μm.

zon® wax. These were coated with a mixture of Au and Pd for 1 min in a Polaron model E sputter coater (Watford, Hertfordshire, UK.) prior to examination with a Leo 982 field emission scanning electron microscope (Jena, Germany). A minimum of 50 specimens of each *Eunotia* morphotype were examined as part of our investigation. Digested material is available from the authors for further examination and will eventually be placed in a public repository once the full range of taxa have been described.

Results

Two distinct morphotypes of *Eunotia* were observed in the 95.60 m section of the Giraffe pipe core. Preliminary light microscopic examinations of both H_2O_2-oxidized and untreated sediments from adjacent core levels also revealed the presence of these diatoms, although they are relatively uncommon. *Eunotia* do not appear in samples lower in the core, which reflect a deeper lake paleoenvironment in which the only diatom genus recorded to date is *Aulacoseira* Thwaites (Wolfe et al. 2006). The 95.60 m (and adjacent) core levels contain abundant chrysophyte scales, bristles, and cysts (Siver and Wolfe 2005) as well as siliceous testate protozoan plates and putative siliceous heliozoan remains. However, the two *Eunotia* morphotypes described below are the only diatoms present in this material. Ecologically, we infer a shallow lake or wetland with high concentrations of dissolved organic carbon and somewhat acidic waters.

Eunotia morphotype 'Giraffe 1' (Figs. 2–8)

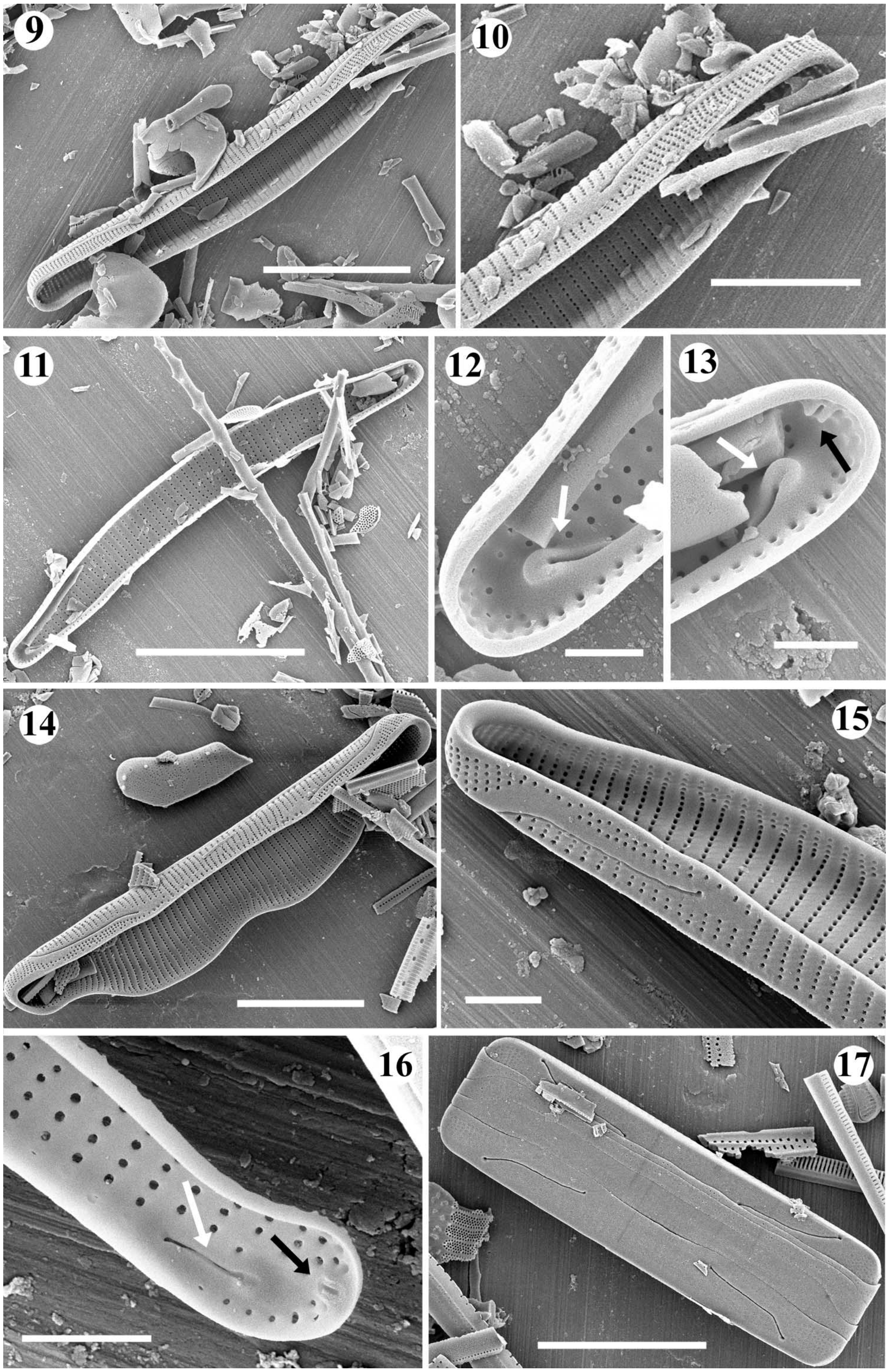
Valves of this diatom are small and dorsiventral with a straight ventral margin, a convex dorsal margin, and bluntly rounded apices. Valves range in size from 14 to 19 μm in length and from 2 to 3 μm in width and have 24–28 striae per 10 μm. The mantle is equally developed along both dorsal and ventral margins, forming a right-angle juncture with the valve face. Striae are largely parallel and evenly spaced over most the valve face, becoming slightly divergent towards the apices. Striae extend onto both dorsal and ventral mantles. Areolae are small, simple, circular, and evenly spaced except for interruptions at the face–mantle juncture and the proximal raphe endings. Closing plates were not observed on either external or internal valve surfaces. The portion of the raphe on the mantle is relatively straight, prior to curving onto the valve face near the apices (Figs. 2–4). The raphe system is well developed, spanning 70%–80% of total valve length (Figs. 2 and 8). The region between the proximal raphe endings, which represents 20%–25% of valve length, is distinctly hyaline (Figs. 2 and 8). Internally, each raphe branch terminates subapically along the mantle as a helictoglossa. A single rimoportula is present on only one apex either near the center (Fig. 6) or slightly towards the ventral surface (Fig. 7). The rimoportula is not stalked and opens externally as a simple pore.

Eunotia morphotype 'Giraffe 2' (Figs. 9–13)

Valves of this diatom are slender and lunate with a concave ventral margin, a convex dorsal margin, and rounded, slightly protracted apices. Valves range from 23 to 26 μm in length and from 3 to 3.5 μm in width and have 23–26 striae per 10 μm. The mantle is equally developed along both margins and forms a more or less right angle with the valve face. Striae are parallel and evenly spaced over the valve face, becoming slightly radiate near the apices, and extending onto the mantle. Striae density increases below the raphe near each apex (Fig. 10). Areolae are similar in structure and spacing to those on *Eunotia* morphotype 'Giraffe 1'. Each raphe branch spans ~25% of the valve length, terminating internally in well-developed helictoglossae (Figs. 12 and 13), and externally on the valve face near the apex. The raphe is surrounded by a siliceous hyaline zone that extends on the mantle well beyond the proximal raphe endings (Figs. 9 and 10). The portion of the ventral mantle between this hyaline zone is crossed with uninterrupted striae. A single unstalked rimoportula is positioned on the mantle closer to the dorsal margin on one of the apices (compare Figs. 12 and 13).

Discussion and conclusion

Our findings establish that freshwater representatives of *Eunotia* date to at least the Middle Eocene (i.e., 37.2–48.6 Ma), significantly older than the previous stratigraphic range of these diatoms, which extended no earlier than Early Miocene (cf. <23 Ma). Furthermore, since the morphology of these Eocene fossil forms is so similar to that of modern congeners, the origin of the genus is likely to be older yet. Thus, the defining morphological characters of the genus appear to have remained remarkably stable for at least ~40 Ma: Eocene *Eunotia* have a dorsiventral to lunate morphology, raphe branches on the mantle, distal raphe ends that terminate as helictoglossae, a single rimoportula per valve, and striae that cross the valve face, all of which are features clearly retained in modern counterparts (e.g., Figs. 14–17). Given the early stages of our work and the fact that we are observing individuals, not populations, formal descriptions



of either Giraffe pipe morphotype are premature at this time.

Hustedt (1952) proposed that the diatom raphe originated from araphid forms in the Middle Eocene. He hypothesized that raphe-bearing eunotioid and naviculoid diatoms evolved independently from an “ur-raphid” diatom morphologically comparable with *Peronia*. In *Peronia*, one valve has a fully developed raphe and rimoportulae at both apices, while the other valve has a vestigial raphe and single rimoportula at only one apex. In Hustedt’s (1952) original proposal, this vestigial raphe migrated from the valve face to the mantle, and a single rimoportula was retained, resulting in the eunotioid lineage of pennate diatoms. Although our findings do not disprove this evolutionary trajectory, they do indicate that the raphe of Eocene *Eunotia* was equally well developed as that of modern congeners, if not more so. For example, the protracted raphe observed in *Eunotia* morphotype ‘Giraffe 1’ is exceptional in two regards. First, it spans up to 80% of the length of the mantle, and second, it terminates centrally in a hyaline area spanning the region between proximal raphe endings and uninterrupted by mantle striae (Figs. 2 and 8). These features support the notion that some ancient representatives of *Eunotia* had more fully developed raphe systems relative to extant taxa and that, in these cases, the complexity of the raphe system has progressively diminished over time. In fact, one could argue that the hyaline region between the proximal raphe ends that lacks striae on *Eunotia* morphotype 'Giraffe 1' is a central nodule analogous to that found in *Eunophora* (Vyverman et al. 1998), in this sense recalling the central area in naviculoid genera.

Kolbe (1956) proposed that the raphe evolved by enlargement and expansion of terminal rimoportulae, an idea subsequently adopted by both Simonsen (1970) and Hasle (1973), perpetuated through considerations of the genera *Pseudohimantidium* Hustedt & Krasske and *Protoraphis* Simonsen. Both of these genera possess distinctive rows of four to nine apical rimoportulae that collectively form an external slit on the valve surface (Simonsen 1970; Gibson 1979). The original description of *Pseudohimantidium* already considered this row of rimoportulae as a possible precursor to the raphe system (Krasske 1941). Simonsen (1970) erected the family Protoraphidaceae to include both of these genera, despite the unconfirmed status of any actual evolutionary linkage between multiple apical rimoportulae and the raphe system. Later, Mann (1984) proposed that the raphe evolved from a *single* rimoportula at each pole of an ancestral araphid form. In this sequence, the rimoportula expanded initially towards the valve margin and then rotated back towards the valve center, prior to eventually merging with the sternum to create an integrated raphe system. In support of this model, Mann (1984) concluded that the araphid ancestor probably had two or more rimoportulae at each apex, given that the majority of eunotioid taxa retain at least one rimoportula per valve, in addition to the raphe. Here, the most important implication is that the eunotioid raphe system becomes an intermediate character state between early elongation of the rimoportula and full integration of the raphe and sternum (Sims et al. 2006). In diametric contrast, Kociolek (2000) noted that it was equally plausible that the earliest raphe system was fully developed, as in taxa such as *Peronia brasiliensis* Hustedt, and that remaining eunotioid diatoms retain various stages in the progressive degeneration of the raphe system. The molecular phylogenic data do not yet resolve these discrepant viewpoints because the *Eunotia* clade may occupy either derived or basal positions within the raphid diatoms, depending on the methods employed in data optimization and tree construction (Medlin and Kaczmarska 2004).

Our observations from the Giraffe pipe material further support the hypothesis that the raphe in *Eunotia* has shortened degeneratively over time and thus does not constitute an intermediate stage towards a more highly derived raphe system. This does not discredit Mann's (1984) proposed scenario of raphe evolution, since it may equally pertain to noneunotioid clades. However, the new specimens challenge the concept that *Eunotia* occupies an intermediate position in any such evolutionary sequence between the araphid and rapid diatoms. Instead, our findings suggest that early eunotioid diatoms had more fully developed raphe systems, much like early divergent representatives of the naviculoid and nitzschioid clades (Sims et al. 2006).

The notion of progressive degeneration of the *Eunotia* raphe is further compatible with observations of eunotioid taxa for which the raphe is reduced to the point where only a vestigial slit remains (Kociolek and Rhode 1998; Siver et al. 2006). These authors suggested that, in such cases, eunotioid taxa are evolving secondarily towards araphid forms. For example, *Eunotia* species with degenerated vestigial raphes include planktonic forms in which raphe branches range from a few micrometres in length (e.g., *Eunotia zazuminensis* (Cabejszekowna) Körner) to less than a micrometre (*Eunotia pseudofragilaria* Siver, Hamilton & Morales and *Eunotia croatana* Siver, Hamilton & Morales (Fig. 16)). In addition to raphe reduction, valves of these taxa are elongated and far less asymmetric about the apical axis than those of most *Eunotia*, thus producing overall morphologies similar to those of *Asterionella* Hassall and planktonic *Fragilaria* Lyngbye species (Siver et al. 2006). In contrast, some Middle Eocene *Eunotia* had highly developed raphes that extended almost the length of the valve (Figs. 2 and 8). Furthermore, the ventral margin of *Eunotia* morphotype 'Giraffe 1' is straight, so that the entire surface of the mantle could be in contact with the substratum during attachment or locomotion. Although some modern *Eunotia* also have straight ventral margins, the majority are lunate in valve outline with concave ventral surfaces, much as in *Eunotia* morphotype 'Giraffe 2'. In lunate forms, the evolutionary trend may have been towards a reduction of the raphe to those portions of the mantle near the apices that are in contact with underlying substrata. As some eunotioid diatoms migrated from the periphyton to the plankton, the raphe became functionally unnecessary, leading to further degeneration.

Beyond this focus on the raphe system of *Eunotia*, rimoportulae and areolae also merit brief consideration. Although the vast majority of eunotioid diatoms have one rimoportula per valve, a few have two or more per valve, whereas others lack these structures altogether (Vyverman et al. 1998; Williams and Reid 2006*a*, 2006*b*). The absence of rimoportulae in certain *Eunotia* and *Eunophora* species, and in all *Colliculoamphora*, has been considered a derived character state, although it remains uncertain whether the primitive state is one or two rimoportulae per valve (Vyverman et al. 1998). Our findings indicate that Middle Eocene *Eunotia* were characterized by a single rimoportula per valve (compare Figs. 12 and 13), supporting this as the primitive state for the genus, as initially proposed by Hustedt (1952). The position of rimoportulae in *Eunotia* specimens from the Giraffe pipe is remarkably similar to that in the majority of modern freshwater congeners, being situated near the juncture between valve face and mantle and slightly offset towards the dorsal valve margin. Interestingly, the rimoportulae of the fossil taxa *Eunotia grovei* and *Eunotia marina* are positioned entirely on the mantle close to the apex and opening externally along the ventral margin (Novitski and Kociolek 2005). This positioning may represent a difference between marine and freshwater *Eunotia*, although more study is clearly warranted.

Areolae on the valves of *Eunotia* were thought to lack either internal or external coverings (Round et al. 1990). It has subsequently been demonstrated that the external surfaces of areolae in many species are covered by flat, solid, disc-like volae (Mayama and Kobayasi 1991; Mayama 1993; Siver et al. 2006). Neither *Eunotia* morphotype from the Giraffe pipe material revealed the presence of such volae, suggesting this to be a primitive condition for the genus and that the presence of volae in modern forms represents a derived character. Preservation is unlikely a factor, given that volae are exquisitely preserved in valves of *Aulacoseira* from deeper stratigraphic units in the Giraffe pipe core (Wolfe et al. 2006).

In summary, our findings document freshwater members of the genus *Eunotia* in the Middle Eocene. These diatoms bear remarkable morphological similarities to extant representatives of the genus. Some of these ancient forms had more fully developed raphe systems, supporting the hypothesis that the eunotioid raphe has shortened (degenerated), and not lengthened, over time. We remain sanguine that the fossil record may yield even older diatoms in this clade. Given the preservational quality of specimens obtained from the Giraffe pipe's posteruptive maar sediments, and considering the age range of kimberlite emplacement in northern Canada (Heaman et al. 2003), this intriguing depositional environment should be explored more fully as a repository of ancient diatoms.

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