

Heteropolar eunotioid diatoms (Bacillariophyceae) were common in the North American Arctic during the middle Eocene

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ABSTRACT – Eunotioid diatoms that express asymmetry in both the apical and transapical axes, forming heteropolar valves, are generally placed in the genus *Actinella*. The degree of heteropolarity varies between species, ranging from subtle differences between poles to highly differentiated head poles bearing an apical protuberance. *Actinella* species with less difference between the poles and lacking an apical protuberance are gradational with *Eunotia*. With over 100 known species reported globally, primarily in the tropics, only *Actinella punctata* Lewis, 1864 is currently known from North America. As part of a biotic survey and inventory project focused on the middle Eocene Giraffe crater locality near the Arctic Circle in northern Canada, we have uncovered a wealth of eunotioid diatoms including at least five heteropolar species attributed to *Actinella*, three of which are described formally herein as *A. hickeyi* sp. nov., *A. goodwinii* sp. nov. and *A. kimberlitica* sp. nov.. These diatoms all lack apical protuberances and bear resemblance to modern heteropolar counterparts within *Eunotia*. The objectives of this contribution are to report the findings from the Giraffe locality relative to modern and fossil eunotiophycid taxa, discuss the use of heteropolarity as a distinguishing character for the genus *Actinella*, and consider the palaeoclimatic and biogeographical implications of these observations.

KEYWORDS: *Actinella*, *Eocene*, *Eunotia*, *Eunotiophycidae*, *non-marine diatoms*

INTRODUCTION

The subclass Eunotiophycidae of the class Bacillariophyceae (diatoms) represents a relatively small assemblage of taxa that are unique in possessing short raphe (often referred to as rudimentary) but lacking central nodules, yet are the only raphe-bearing diatoms having rimoportulae (Patrick & Reimer, 1966; Round *et al.*, 1990). The rimoportula is a primitive structure found on many centric and araphid diatoms, but is lacking on the vast majority of raphid diatoms with the exception of the Eunotiophycidae. Currently, there are eight genera recognized within the Eunotiophycidae: *Actinella* Lewis, *Eunotia* Ehrenberg, *Desmogonium* Ehrenberg (not recognized by some authors), *Eunophora* Vyverman, Sabbe & Mann, *Peronia* de Brébisson & Arnott ex Kitton, *Semiorbis* Patrick, *Amphorotia* Williams & Reid and *Perinotia* Metzeltin & Lange-Bertalot (Sabbe *et al.*, 2001; Williams & Reid, 2006; Wetzel *et al.*, 2012). These genera are distinguished on the basis of symmetry about the transapical axis, structure of the striae and position of the raphe either on the face of the valve (*Peronia*) or primarily on the valve mantle (all other genera). All of the genera, except for *Peronia*, are asymmetrical about the apical axis. Two of the genera, *Actinella* and *Peronia*, are also asymmetrical about the transapical axis, yielding heteropolar apices referred to as the head (larger or wider end) and foot poles (Sabbe *et al.*, 2001; Melo *et al.*, 2010). The heteropolar nature of the valve is the key feature separating *Actinella* from the other genera that also have the raphe situated largely on or close to the mantle (Sabbe *et al.*, 2001; Ripple & Kociolek, 2013).

Two additional genera are noteworthy. Taylor *et al.* (2014) recently proposed the genus *Actinellopsis* Taylor, Karthick &

Kociolek and separated it from *Actinella* based primarily on the position of the raphe being situated on the valve face along the margin. We question whether this character is sufficient to establish a new genus and, at this time, we are reluctant to consider *Actinellopsis* as more than a proposed taxon. We do agree with Taylor *et al.* (2014) that the structure of the raphe on *Actinellopsis murphyi* Taylor, Karthick & Kociolek bears resemblance to the raphe on *Actinella giraffensis* Siver, Wolfe & Edlund (Siver *et al.*, 2010). *Bicudoa* Wetzel, Lange-Bertalot & Ector is a recently described genus lacking a raphe, helicoglossae and rimoportulae that may represent a highly derived eunotiophycid diatom (Wetzel *et al.*, 2012).

Actinella punctata Lewis, the generic type, was first described by Lewis (1864) from Saco Pond, a small, shallow, waterbody situated in the mountains of New Hampshire, USA. Today, the pond is acidic, dilute, low in nutrients, and harbours most, if not all, of the intriguing diatoms originally illustrated by Lewis (1864, 1865) over 150 years ago (Siver & Camfield, 2007). There are now close to 100 described species of *Actinella* (Ripple & Kociolek, 2013), but interestingly *A. punctata* remains the only species that has been observed in modern collections from North American localities (Siver & Hamilton, 2011). This large and characteristic taxon is widespread along the east coast of North America, and has also been reported from midwestern and western localities on the continent, as well as other regions in the world (Kociolek *et al.*, 1997; Ripple & Kociolek, 2013). A limited number of other heteropolar Eunotiophycidae species, currently classified under *Eunotia*, have also been reported from North American waterbodies. These include *Eunotia rhomboidea* Hustedt, *Eunotia faba* (Ehrenberg) Grunow in van Heurck, and

Table 1. Vertical depths of eleven studied samples from Giraffe Lake core and the presence of *Actinella* species in each sample.

Number	Sample	Vertical depth (m)	Species present
1	14-3-100	109.64	<i>A. hickeyi</i>
2	14-2-22	110.36	<i>A. hickeyi</i>
3	14-2-32	110.46	<i>A. hickeyi</i>
4	14-2-56	110.70	<i>A. kimberlitica</i> , <i>A. hickeyi</i>
5	14-2-107	111.21	<i>A. kimberlitica</i>
6	15-1-65	116.79	<i>A. kimberlitica</i> , <i>A. goodwinii</i>
7	15-1-100	117.14	<i>A. kimberlitica</i> , <i>A. goodwinii</i>
8	15-1-131	117.45	<i>A. kimberlitica</i> , <i>A. goodwinii</i> , <i>A. sp. 2</i>
9	16-3-23	117.87	<i>A. hickeyi</i> , <i>A. goodwinii</i> , <i>A. sp. 1</i> , <i>A. sp. 2</i>
10	16-3-42	118.06	<i>A. goodwinii</i> , <i>A. sp. 1</i>
11	16-3-81	118.45	<i>A. goodwinii</i>

Eunotia papilioforma Furey, Lowe & Johansen, each bearing slightly club-shaped and heteropolar valves. Sabbe *et al.* (2001) noted that valves of *E. rhomboidea* could be isopolar or heteropolar and noted that placement in *Eunotia* requires further study. Furey (2011) clearly stated that valve shape and position of the helictoglossae in *E. papilioforma* are asymmetrical to the transapical axis, but still placed the taxon in *Eunotia* despite also noting that *Actinella* species are distinguished from *Eunotia* by heteropolar valve shape. Placement of *E. papilioforma* under *Eunotia*, rather than *Actinella*, given their distinguishing criteria, is unclear and this taxon may more appropriately belong in *Actinella*. Regardless of the generic assignment of *E. rhomboidea* and *E. papilioforma*, it is clear based on the hundreds of diatom studies performed throughout North America over the last century that heteropolar Eunotiophycidae species are extremely rare. A similar case has been made globally (see Sabbe *et al.*, 2001).

The Giraffe fossil locality (64°48'N, 110°04'W) is a kimberlite diatreme crater that formed following phreatomagmatic volcanism, subsequently infilled with a sequence of Eocene lacustrine and then paludal sediments, and was later entombed with Neogene glacial deposits (Wolfe *et al.*, 2006; Siver & Wolfe, 2009). A 165 m long drilled core was retrieved from the crater by BHP Billiton Inc. during diamond exploration and later archived at the Canadian Geological Survey (Calgary). The core contains over 40 m of terrestrial sediment atop 65 m of lacustrine mudstone of middle Eocene age (Wolfe *et al.*, 2006; Siver & Wolfe, 2009). Both the terrestrial (Doria *et al.*, 2011) and lacustrine (Siver & Wolfe, 2005; Wolfe *et al.*, 2006) deposits contain abundant fossil remains with extraordinary preservation, including numerous freshwater diatoms among other siliceous microfossils (Wolfe & Siver, 2009; Siver *et al.*, 2010). As part of a biotic survey and inventory project focused on the lacustrine mudstones we have uncovered a wealth of Eunotiophycidae diatoms, mostly contained within a 16 m section of the core, and representing species of *Eunotia* and *Actinella*. Of special interest is the presence in this single fossil locality of five or more species each exhibiting a heteropolar condition and that are most appropriately classified as *Actinella*. The purpose of this contribution is to report our findings to date and formally describe three of the species.

MATERIALS AND METHODS

Mudstone chips (50–100 mg) from eleven sections of the Giraffe core spanning 8.81 m (Table 1) were oxidized using 30% H₂O₂

under low heat for a minimum of an hour, rinsed with distilled water, and the resulting slurries stored in glass vials. This procedure results in separation of many siliceous microfossils from the mudstone matrix. In addition, small fragments of mudstone, each containing many embedded microfossils, remain within each preparation. Aliquots of each slurry were air dried on to pieces of heavy duty aluminum foil and directly on to circular glass coverslips. The aluminum foil samples were trimmed, attached to aluminum stubs with Apiezon® wax, and coated with a mixture of gold and palladium for 2 min with a Polaron Model E sputter coater. Samples were examined with a Leo 982 field emission or an FEI Nova scanning electron microscope (SEM). The coverslips were mounted on to glass slides with Naphrax and examined with a Leica DMR or an Olympus BX51 light microscope (LM). A minimum of 20 specimens for each species were used for morphometric analysis.

Each sample from the Giraffe core is identified with a three-part number (Table 1). The first number represents the core box. Deeper sections of the core correspond to larger box numbers. Each box contains three 1.5 m core lengths, identified as channels 1, 2 and 3. The second number represents the channel. The third number indicates the length in centimetres measured down from the top of a core length. For example, sample 14-3-100 represents a sample taken from 100 cm down along the core length in channel 3 from box 14.

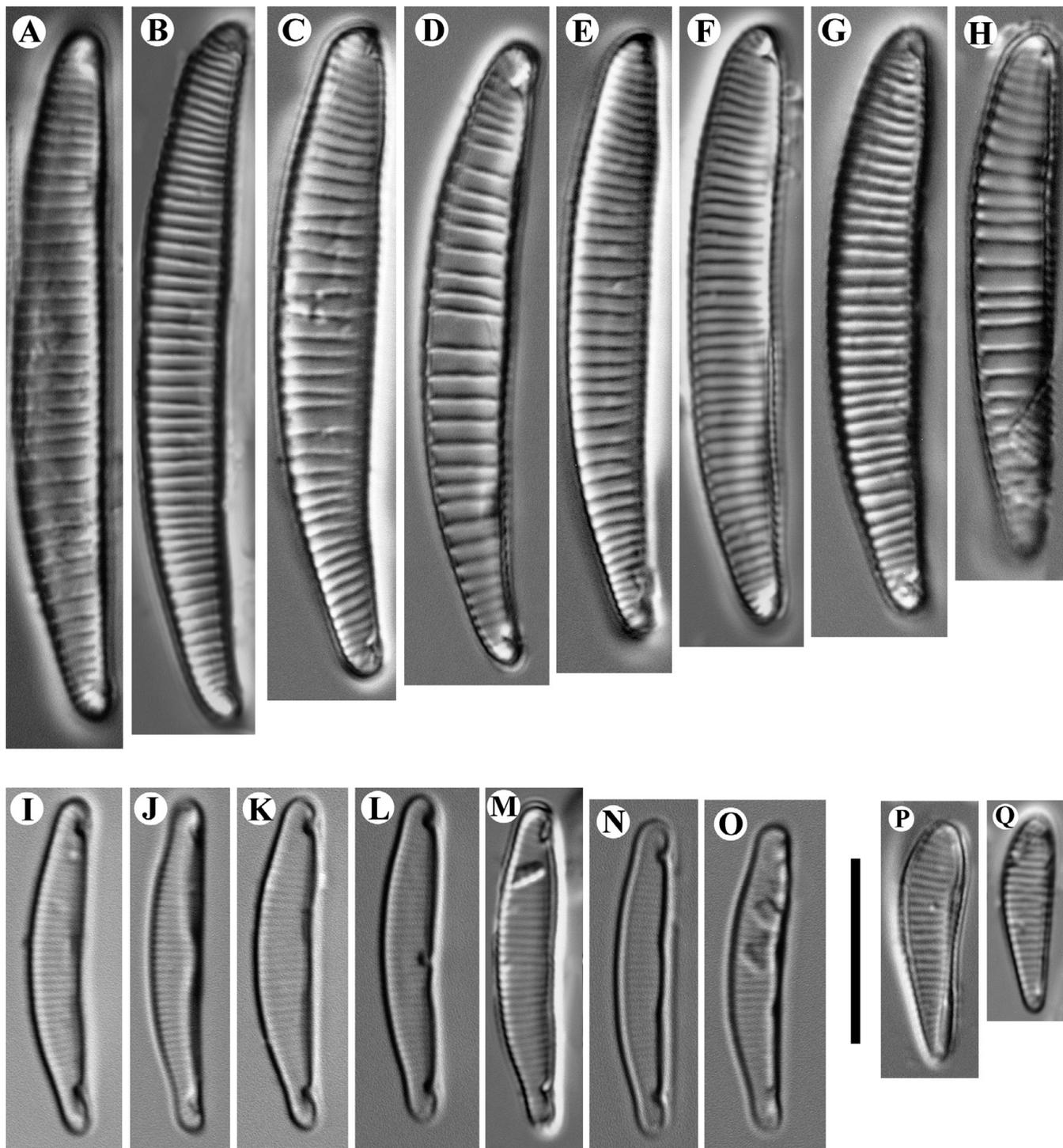
RESULTS

Eunotiophycidae specimens from the Giraffe locality represent at least five, and probably six, different species with heteropolar valves (Pls 1–6). One of these species, *Actinella giraffensis*, has been previously described (Siver *et al.*, 2010), and we now have examined a sufficient range of specimens to describe three additional species formally. Remains of two more species have also been uncovered, but since we have examined a limited number of specimens to date, only preliminary observations are given herein.

SYSTEMATIC PALAEOONTOLOGY

Actinella hickeyi Siver, Bishop, Wolfe & Lott sp. nov.
(Pl. 1, figs A–H; Pl. 3, figs A–F; Pl. 4, figs A–D)

Derivation of name. The epithet is in honour of the late Professor Leo Hickey, Yale University, an extraordinary



Explanation of Plate 1. figs A–H. Light micrographs of *Actinella hickeyi* sp. nov.; figs I–O. *A. kimberlitica* sp. nov.; figs P–Q. *A.* sp. 2. Note the heteropolar nature of the valve for all three taxa, the widely spaced striae for *A. hickeyi*, and the incised nature of the helictoglossa for *A. kimberlitica*. Fig. B is the holotype specimen for *Actinella hickeyi* and fig. M the holotype specimen for *A. kimberlitica*. Scale bar 10 μm.

palaeobotanist and friend who was keenly interested in the Giraffe locality.

Holotype. Here designated as the specimen circled on the glass slide marked ‘Giraffe 16-3-23 C’ and deposited at the Canadian

Museum of Nature, CANA 94961. The holotype is illustrated in Plate 1, fig. B.

Type material. Material from section 16-3-23 of the Giraffe core collected by A. P. Wolfe & P. A. Siver.

Description. Specimens of *Actinella hickeyi* have a slight dorsi-ventral design, are asymmetrical with respect to the transapical axis, and have rounded head and foot poles (Pl. 1, figs A–H; Pl. 3, figs A–C). Valves have a slight convex dorsal margin and a straight ventral margin; they range in size from 27–40 $\mu\text{m} \times$ 4–6 μm . The foot pole is often bent slightly towards the ventral side of the valve (Pl. 3, figs A–D). The striae are parallel with the transapical axis, widely and often unevenly spaced in the middle of the valve, have a range of 8–13 in 10 μm , and become more closely and evenly spaced at the poles (Pl. 1, figs A–H; Pl. 3, figs A–C). The striae on the valve face are aligned with the striae on the dorsal mantle, but not with those on the ventral mantle. There is a series of short and closely spaced striae between the raphe slits and the lower edge of the mantle (Pl. 3, fig. E). The areolae are small, circular, evenly spaced pores that lack coverings (Pl. 3, figs D and F). Internally, the areolae are often recessed within a linear depression (Pl. 3, fig. B; Pl. 4, fig. A).

The raphe slits range in length from 5–7 μm and are situated on the mantle (Pl. 3, fig. E). The distal raphe fissure usually terminates on the mantle (Pl. 3, fig. E), or a short distance up on to the valve face (Pl. 3, figs D and F). Both the distal and proximal raphe fissures end as large circular pores (Pl. 3, figs D–F), and internally the distal end of the raphe terminates as a well-formed helictoglossa (Pl. 4, figs B–D). There is one rimoportula per valve positioned on the ventral mantle between the helictoglossa and the apex (Pl. 3, fig. E; Pl. 4, figs C–D). The rimoportula can be found on either the foot (Pl. 4, fig. C) or head (Pl. 4, fig. D) pole, and typically on opposite ends of valves from the same frustule (Pl. 3, fig. C, arrows). On each apex, the lower margin of the mantle is thickened and extended inward forming a shallow pseudosepta (Pl. 4, figs A–D). There are typically three open girdle bands per frustule, each with two to three rows of pores. The pole-end of the valvocopula is thickened and extends past the valve apex (Pl. 3, fig. E).

Remarks. *Actinella hickeyi* sp. nov. was found in four sections, spanning over 8 m of the core (Table 1). These sections were largely dominated with other eunotioid diatoms, chrysophyte cysts and numerous species of *Mallomonas*, especially a species resembling *M. lichenensis* Conrad and *M. porifera* Siver & Wolfe.

Actinella goodwinii Siver, Bishop, Wolfe & Lott sp. nov.
(Pl. 2, figs A–I; Pl. 5, figs A–F)

Derivation of name. The epithet is in honour of Professor Richard Hale Goodwin from Connecticut College, a botanist and pioneer in land conservation, and his wife of over 70 years, Esther.

Holotype. Here designated as the specimen circled on the glass slide marked ‘Giraffe 16-3-23 D’ and deposited at the Canadian Museum of Nature, CANA 94962. The holotype is illustrated in Plate 2, fig. F.

Type material. Material from section 16-3-23 of the Giraffe core collected by A. P. Wolfe & P. A. Siver.

Description. Specimens of *Actinella goodwinii* are strongly dorsi-ventral with a slight concave ventral margin, a convex dorsal margin with two undulations, and protruding apices (Pl. 2, figs A–I;

Pl. 5, figs A–E). One apex, the foot pole, is narrower, slightly sub-capitate and extended further than the other apex, or head pole, yielding a heteropolar condition. The undulations, especially the one towards the foot pole, are less pronounced on smaller valves. Valves range in size from 16–36 $\mu\text{m} \times$ 4.4–6.5 μm . The mantle is wide and forms a right angle with the valve face (Pl. 5, figs A–D) except around the foot pole where it is slightly wider, angled outward and extended past the valve face (Pl. 5, fig. A, arrow). This difference in the width and angle of the mantle between each pole often yields a slight rhomboidal shape in girdle view, more pronounced on the foot pole end of the frustule (Pl. 5, fig. D).

The striae are evenly spaced, parallel over most of the valve, become slightly radiate around the apices, and range from 16 to 20 in 10 μm (Pls 2 and 5). The striae on the valve face align roughly with those on the mantle; however, there are often additional shorter striae on the mantle (Pl. 5, figs A and D). There is a series of short and more closely spaced striae between the raphe slits and the lower edge of the mantle (Pl. 5, figs C–D). The areolae are very small, circular, evenly spaced pores that lack coverings on both the external and internal surfaces (Pl. 5). The raphe slits are short, terminated on each end with small pores, and are positioned on the mantle (Pl. 5, figs B–D). The proximal end of the raphe is situated about one-third of the distance from the valve face, traverses up to the valve margin, and terminates a short distance on to the valve face (Pl. 5, figs B–D). Internally, the distal ends of the raphe slits terminate as small helictoglossae along the ventral margin (Pl. 5, figs E–F). The helictoglossa on the foot pole terminates further from the apex than the one on the head pole. There is one rimoportula per valve positioned on the foot pole apex slightly towards the dorsal margin (Pl. 5, figs E–F, arrows). The lower margin of the mantle is thickened around each apex, especially around the foot pole where it is extended inward forming a shallow pseudoseptum (Pl. 5, fig. F). There are three to four wide, open and wavy girdle bands per frustule, each with well-developed striae.

Remarks. *Actinella goodwinii* was found in six closely spaced sections spanning 1.6 m of the core (Table 1). These sections were largely dominated with scaled chrysophyte remains, including especially high numbers of a species resembling *Mallomonas lichenensis*, *M. porifera* and chrysophyte cysts, other eunotioid diatoms, the diatom *Oxyneis apporrecta* Siver, Wolfe & Edlund, and euglyphids.

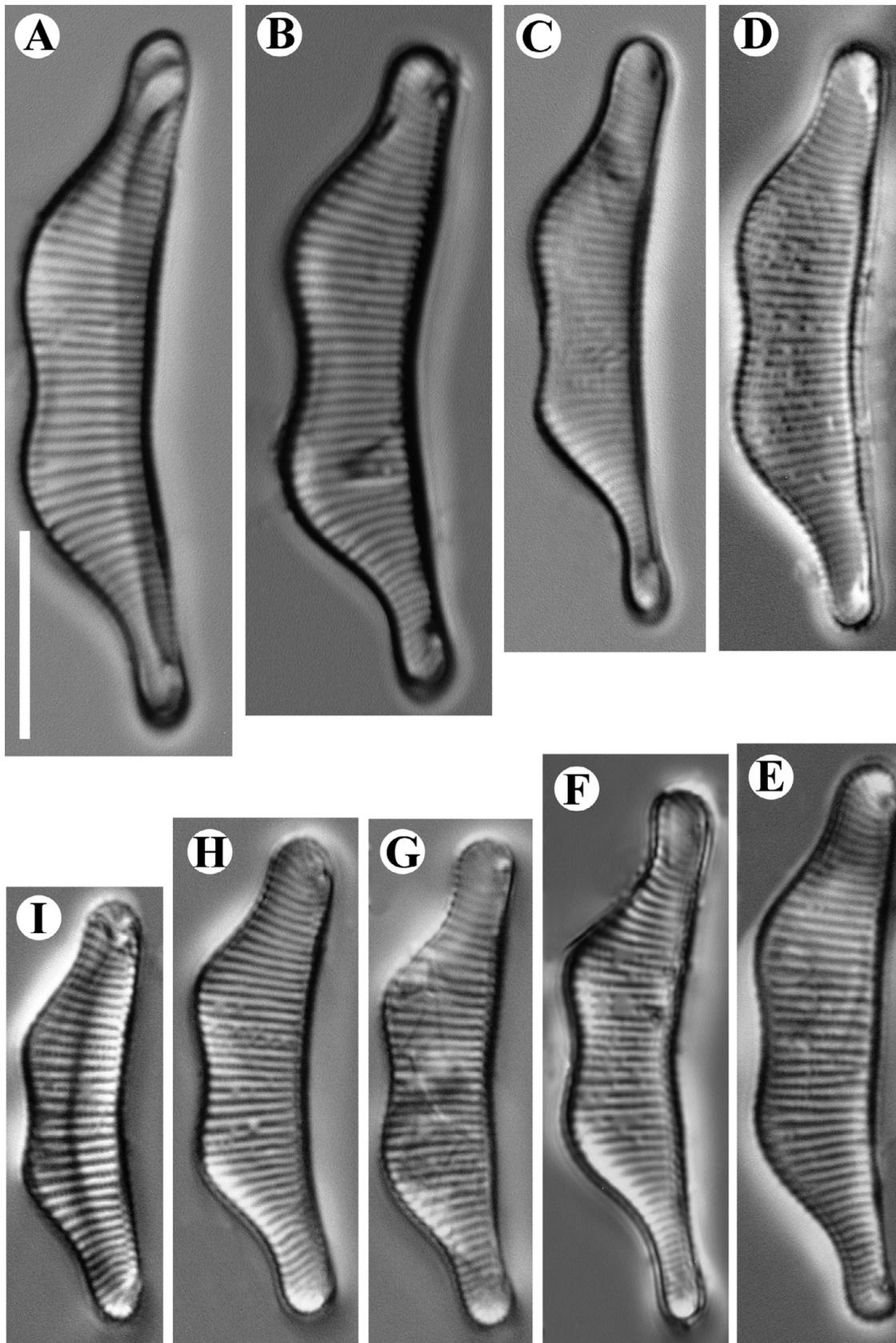
Actinella kimberlitica Siver, Bishop, Wolfe & Lott sp. nov.
(Pl. 1, figs I–O; Pl. 6, figs A–C)

Derivation of name. The epithet refers to the kimberlite intrusion giving rise to the Giraffe maar.

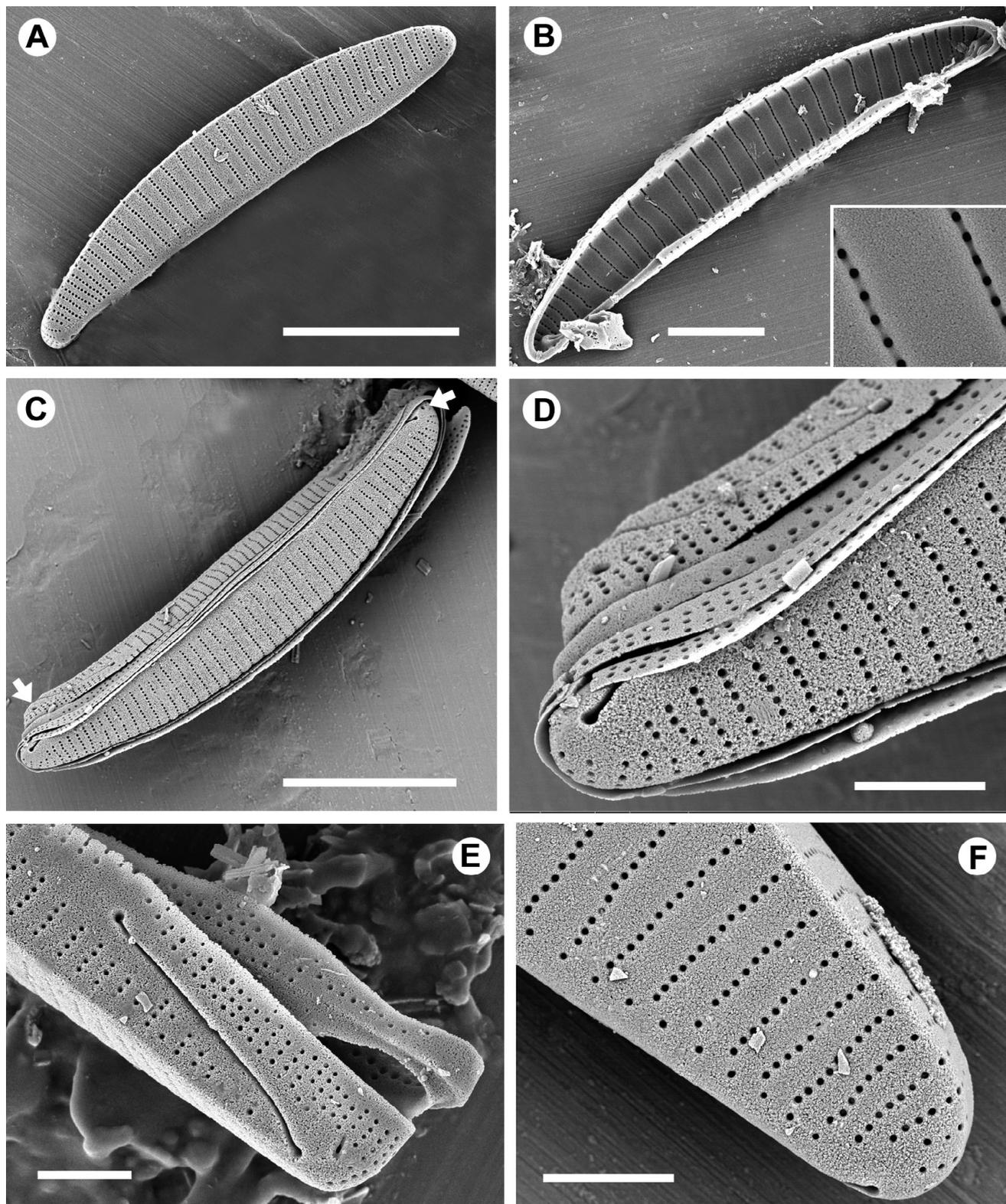
Holotype. Here designated as the specimen circled on the glass slide marked ‘GP 15-1-131 Siver E’ and deposited at the Canadian Museum of Nature, CANA 94963. The holotype is illustrated in Plate 1, fig. M.

Type material. Material from section 15-1-131 of the Giraffe core collected by A. P. Wolfe & P. A. Siver.

Description. Valves are small, narrow, linear with a slight dorsi-ventral design, asymmetrical with respect to the transapical axis, and range in size from 14–19 $\mu\text{m} \times$ 2–3 μm (Pl. 1, figs I–O; Pl.

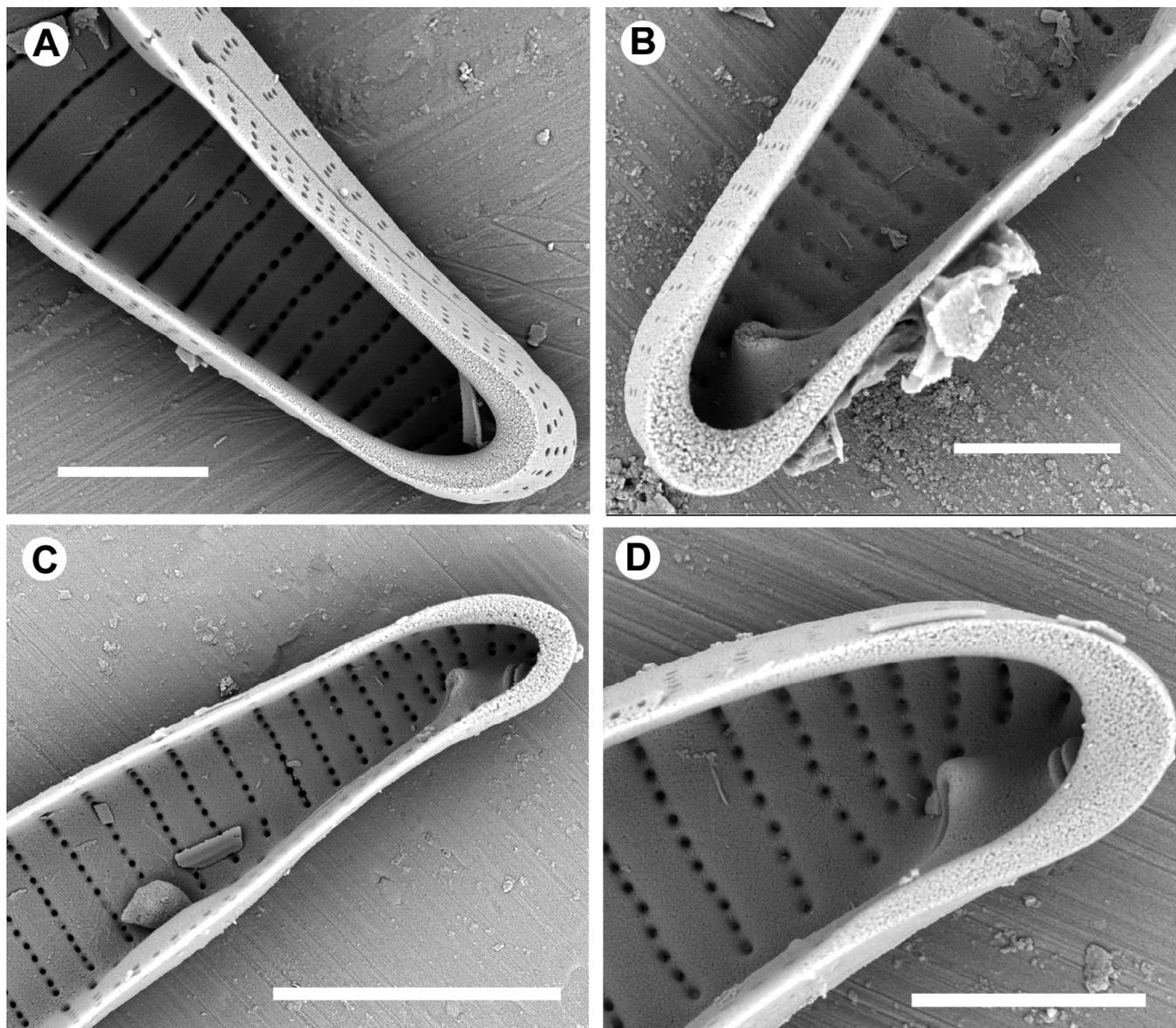


Explanation of Plate 2. Light micrographs of *Actinella goodwinii* sp. nov., depicting a size diminution series. Note the extended and narrower foot pole and even distribution of striae. Fig. F is the holotype specimen. Scale bar 10 μ m.



Explanation of Plate 3. Scanning electron micrographs of *Actinella hickeyi* sp. nov.: **figs A–B.** External and internal views depicting the distribution of striae and heteropolar nature of the valve. Insert in B shows the arrangement of areolae within shallow linear depressions on the internal surface.

fig. C. Whole frustule showing the positions of rimoportulae on opposite ends of each valve (arrows). **fig. D.** Close-up of the foot pole of the specimen in C showing details of the copulae. Note the terminal pore on the distal raphe fissure. **fig. E.** Raphe slit positioned completely on the mantle. Note the large pores on both the distal and proximal ends of the raphe, the series of small closely spaced striae below the raphe, the rimoportula, and the thickened and extended end of the valvocopula. **fig. F.** Close-up of a head pole depicting the distal raphe fissure terminating close to the apex near the margin. Scale bars 10 μm (A and C), 5 μm (B) and 2 μm (D–F).



Explanation of Plate 4. Scanning electron micrographs of *Actinella hickeyi* sp. nov., depicting internal structure: **figs A–C**, the foot pole; **fig. D**, the head pole. Note the well-developed helictoglossae that often extend halfway across the valve face, the location of the rimoportulae closer to the ventral surface near the apex, and the shallow pseudoseptum. Scale bars 5 μm (C) and 2 μm (A–B, D).

6, figs A–C). The dorsal margin is slightly convex, the ventral margin is straight and the apices are rounded. The foot pole is narrower and extends further relative to the helictoglossa than the head pole (Pl. 1, figs I–O; Pl. 6, figs A–B, arrows). There is a narrow, but distinct, axial area aligned along the ventral valve margin that connects the distal raphe ends (Pl. 6, fig. A). The striae are closely and evenly spaced across the entire valve, parallel with the transapical axis, and range in density from 22–26 per 10 μm . The areolae are small, circular, evenly spaced pores that lack coverings (Pl. 6; figs A–C).

The raphe slits are situated on the mantle and gradually bend up on to and terminate on the valve face (Pl. 6, figs A–B). Externally, the distal and proximal raphe fissures terminate

as small pores. Internally, the distal end of the raphe terminates as a well-formed helictoglossa bent slightly towards the dorsal margin, yielding an incision-like appearance when viewed with a light microscope (Pl. 1, figs I–O). There is one rimoportula per valve apically positioned on the foot pole (Pl. 6, fig. C, arrow).

Remarks. *Actinella kimberlitica* was found in five sections spanning almost 7 m of the core (Table 1). These sections were largely dominated with scaled chrysophyte remains, including a species resembling *Mallomonas lichenensis* and *M. porifera*, chrysophyte cysts, numerous other eunotioid diatoms, the diatom *Oxyneis apporrecta*, and euglyphids.

Additional *Actinella* taxa

Specimens of two additional heteropolar forms representing *Actinella* were recovered from the Giraffe locality, including a long slender diatom designated provisionally as *Actinella* sp. 1 (Pl. 6, figs D–F), and a small club-shaped form designated as *Actinella* sp. 2 (Pl. 1, figs P–Q). We note their presence in the core, but elect not to officially describe them at this time until additional specimens can be investigated to establish their full range of characters. However, the presence of these additional taxa provides an expanded perspective of the full diversity of eunotiophycid diatoms from the deposit.

Actinella sp. 1. Specimens of this taxon ranged between 50 and 55 μm in length, and have heteropolar valves that taper gradually from about 5 μm wide at the head pole to 3 μm wide at the foot pole (Pl. 6, fig. D). A slight bend in valve shape occurs along the dorsal margin closer to the foot pole, and both apices are rounded. The mantle forms a right angle with the valve face except around the foot pole where it is angled outward and extended past the valve face (compare Pl. 6, figs E and F). There is a distinct axial area aligned along the ventral valve margin that connects the distal raphe ends (Pl. 6, figs D and F, white arrows). Striae are closely and evenly spaced, parallel with the transapical axis and composed of tiny areolae that lack occlusions at least on the external surface. Striae are continuous on to the mantle, and become radially aligned around the apices (Pl. 6, figs E and F). The raphe is straight, runs diagonally along the mantle to the valve margin, and bends sharply up onto and terminates midway on the valve face. The raphe on the head pole is more sharply angled onto the valve face and the distal fissure terminates closer to the apex than on the foot pole (compare Pl. 6, figs E and F). Each distal fissure is surrounded by a well-developed hyaline region. Although we have not yet been able to examine internal structure, we believe this taxon has at least one rimoportula situated on the foot pole (Pl. 6, fig. F, black arrow). Based on limited observations, frustules are slightly clavate in girdle view (not shown). The overall valve morphology and the structure of the raphe appear to distinguish this taxon from all other described *Actinella* species.

Actinella sp. 2. Valves are small, range in length from 10–14 μm to 2.5–3.5 μm , and are distinctly club-shaped with a wide head pole and narrow foot pole (Pl. 1, figs P–Q). Apices are rounded, and the striae are closely spaced and parallel with the transapical axis. It is possible that these specimens represent very small valves of *Actinella giraffensis* (Siver *et al.*, 2010); however, since we have not found similar-shaped valves of this size in material containing numerous specimens of the later taxon, it likely represents a new species.

DISCUSSION

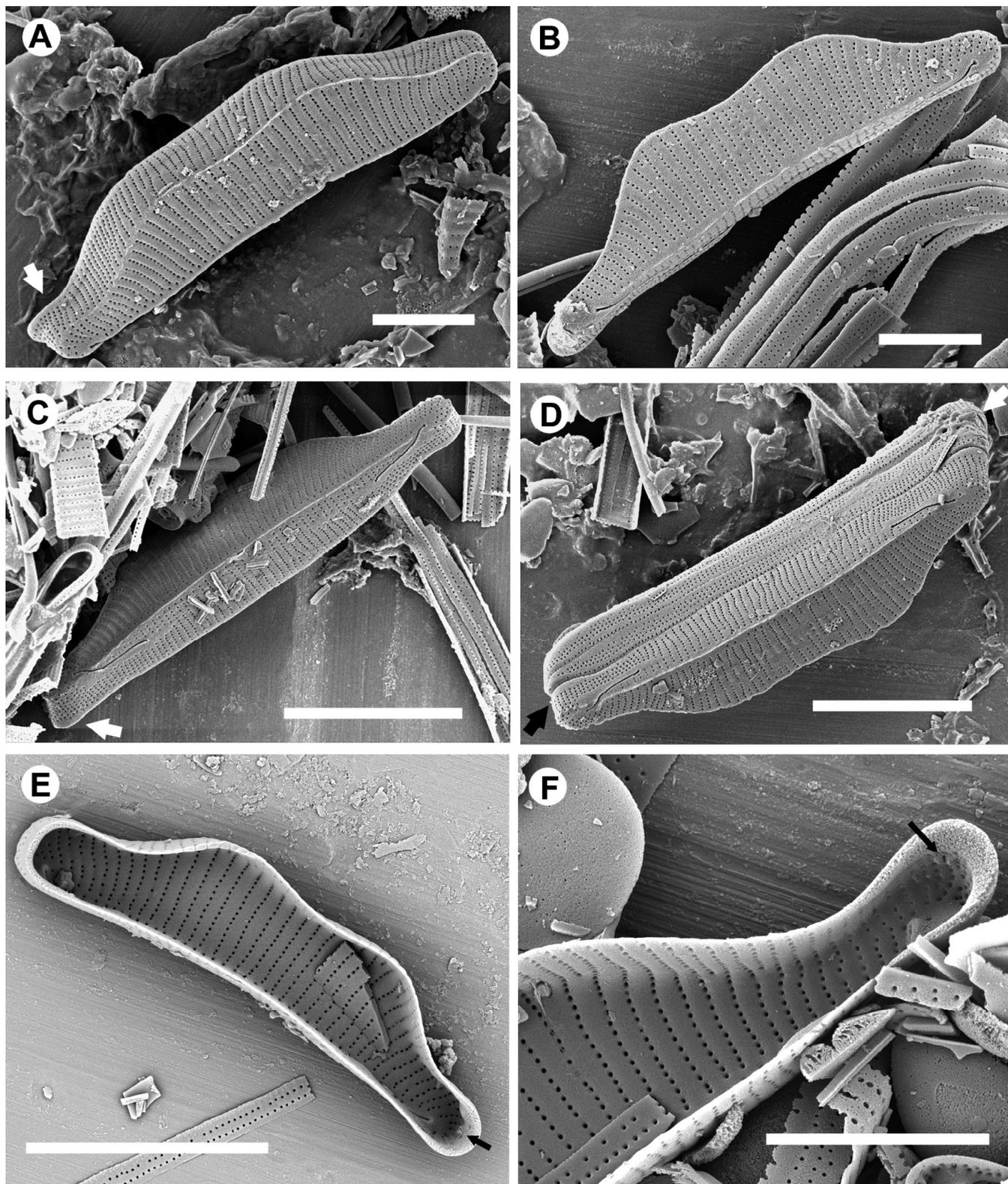
The position and reduced nature of the raphe, presence of rimoportulae, and features of the striae, areolae and helicoglossae are similar for *Actinella* and *Eunotia*, and both genera are, without doubt, evolutionarily closely related (Round *et al.*, 1990; Kociolek, 2000). The primary, and to date perhaps only valid, character separating *Actinella* from *Eunotia* is the heteropolar shape of the valve (Round *et al.*, 1990; Sabbe *et al.*, 2001; Melo *et al.*, 2010; Ripple & Kociolek, 2013). By definition, valves of *Eunotia* are symmetrical to the transapical axis (*Eunotia rhomboidea* and a few related taxa being the exceptions, as stated previously),

while those of *Actinella* are not, yielding the heteropolar condition. As noted by Sabbe *et al.* (2001), heteropolarity is the obligatory character for inclusion in *Actinella*, and this is the primary criterion on which we ascribe the new species from the Giraffe pipe as belonging to *Actinella*. In our opinion, given the current definitions of both genera, the new species are best classified as *Actinella*.

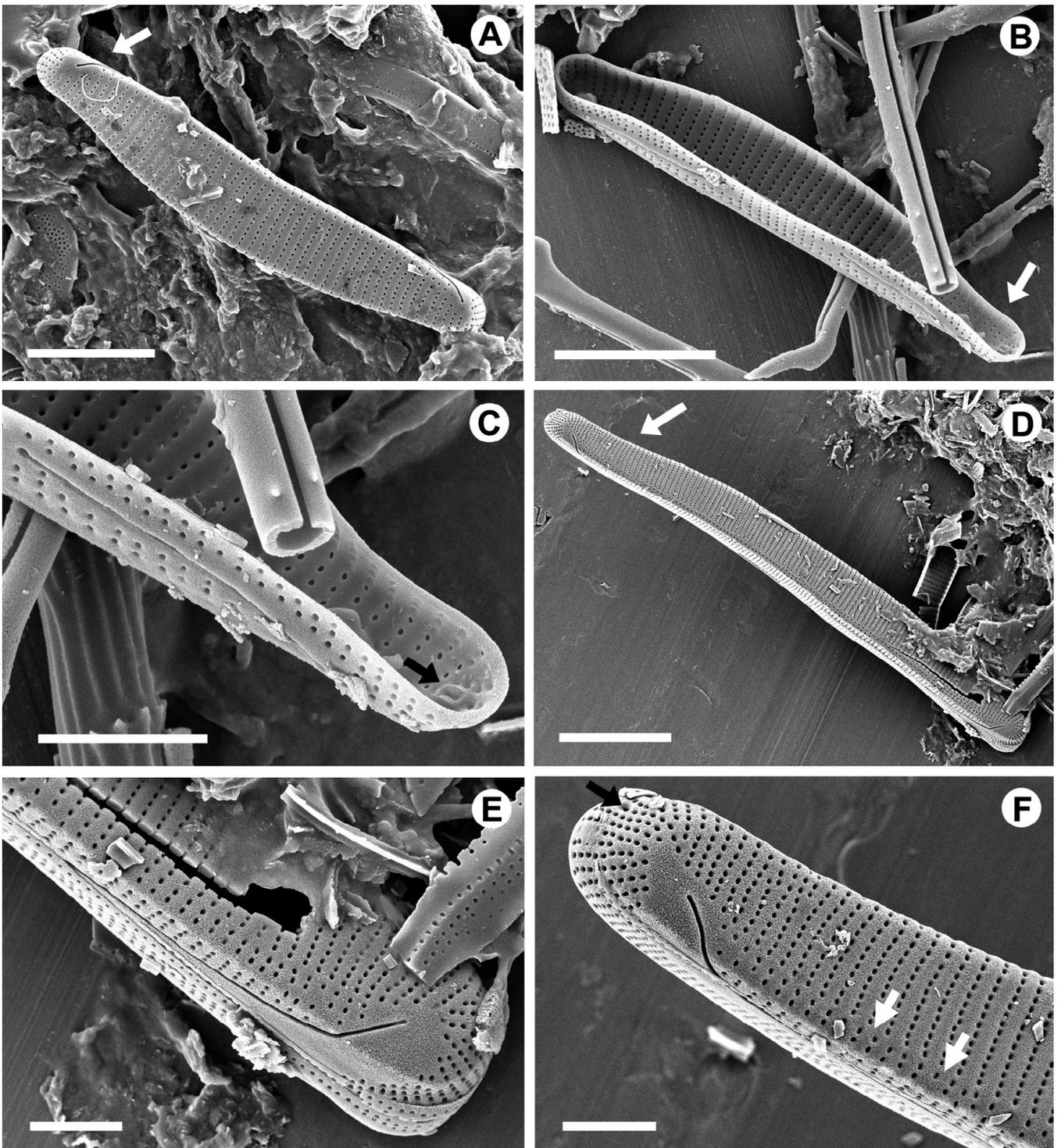
Although all *Actinella* species are heteropolar in valve view, polarity in girdle view remains an open question. Many *Actinella* species are also heteropolar in girdle view forming clavate or wedge-shaped frustules (Sabbe *et al.*, 2001; Siver *et al.*, 2010). However, a few species have been noted to be rectangular or linear in girdle view, and sometimes narrower in the middle of the frustule (Lewis, 1864; Patrick & Reimer, 1966; Metzeltin & Lange-Bertalot, 1998). Also, as noted by Sabbe *et al.* (2001), polarity in girdle view is not always given in original descriptions and this character needs to be determined for many *Actinella* species before a thorough study can be made for the genus. Although we believe frustules of *Actinella hickeyi* are indeed slightly clavate in girdle view based on observations of a few specimens with light microscopy, whole frustules have proven difficult to find and we have not been able to examine this character thoroughly with SEM despite observing hundreds of isolated valves.

Based on our current observations, *Actinella goodwinii* is also heteropolar in girdle view (i.e. clavate), with a somewhat wider and rectangular-shaped head pole, and a slightly rhomboidal-shaped and narrower foot pole. This morphology is consistent with the different shapes found at each valve pole, and the rhomboidal-shape of the foot pole is reminiscent of that observed on some *Eunotia* taxa, particularly *Eunotia rhomboidea* Hustedt. Valves of *Eunotia rhomboidea* can be isopolar or heteropolar in valve view and, as noted by Sabbe *et al.* (2001, p. 337), ‘heteropolarity in *Eunotia* cells is the exception rather than the rule’. Since valves of *A. goodwinii* are always heteropolar in valve view, this taxon is best described as *Actinella*.

The degree of heteropolarity found in *Actinella* species ranges from very slight to extreme. Many species of *Actinella*, such as *A. punctata* Lewis and *A. guianensis* Grunow, produce valves with uniquely shaped and highly inflated head poles relative to the foot pole. This difference is taken to extremes in taxa such as *A. mylaertii* Sabbe & Vyverman and *A. comperei* Sabbe, Vanhoutte & Vyverman, where the foot pole is more or less reduced to a narrow point with a width of less than 2 μm (Sabbe *et al.*, 2000; 2001). However, there are a fair number of *Actinella* species that bear only a slight heteropolarity and at first glance could be mistaken for *Eunotia*. For example, *Actinella indistincta* Vyverman & Bergey, *A. pararobusta* Metzeltin & Lange-Bertalot, *A. parva* Vanhoutte & Sabbe and *A. pareunotioides* Metzeltin & Lange-Bertalot display limited heteropolarity in valve view, possess valves that lack inflated poles, and are ‘*Eunotia*-like’. In fact, some species were initially described as *Eunotia*, only later being transferred to *Actinella* based on the heteropolar nature of the valve (Metzeltin & Lange-Bertalot, 2007). Other species, such as *A. gessneri* Hustedt and *A. siolii* Hustedt, have very inflated head and foot poles and display only slight heteropolarity in the transapical axis. Still, other species were initially described belonging to *Asterionella* Hassall, only later discovered to possess reduced raphes, and transferred to *Actinella* (Kociolek & Rhode, 1998). Metzeltin & Lange-Bertalot (2007) described *A.*



Explanation of Plate 5. Scanning electron micrographs of *Actinella goodwinii*. **figs A–C.** Valves depicting the valve face (A–B), dorsal mantle (A) and ventral mantle (C). Note the deep width of the mantle, the small raphe slits positioned on the upper part of the mantle, and the outward-angled foot pole (arrow on A). **fig. D.** Whole frustule depicting both the valve and ventral girdle view. Note the slight rhomboidal shape in girdle view at the foot pole (arrow). **fig. E.** Internal view of a valve. Note the apical position of the rimoportula (arrow). **fig. F.** Close-up of the foot pole showing the small helictoglossa, position of the rimoportula (arrow), and the thickened portion of the mantle forming the shallow pseudoseptum around the apex. Scale bars 10 μ m (C–E) and 5 μ m (A–B, F).



Explanation of Plate 6. figs A–C. Scanning electron micrographs of *Actinella kimberlitica* sp. nov.: **A**, external and **B**, internal views showing the arrangement of striae and position of the raphe slits. The foot poles are depicted with arrows; **C**, close-up of the foot pole of the specimen in **B** showing the raphe and terminal position of the rimoportula (arrow). **figs D–F.** Scanning electron micrographs of *A. sp. 1*: **D**, specimen depicting the long, slender and tapering nature of the valve. Note the bending of the valve on the foot pole (arrow); **E–F**, close-ups of the head (**E**) and foot (**F**) poles of the specimen in **D**. Note the bending of the distal raphe fissure up on to the valve face and the hyaline zone surrounding the distal end of the raphe. In **F**, black arrow indicates the rimoportula, while the white arrows denote the position of the axial area along the ventral margin. Scale bars 10 μ m (**D**), 5 μ m (**A–B**) and 2 μ m (**C, E–F**).

rionegrensis Metzeltin & Lange-Bertalot as being commonly isopolar with a rare number of valves displaying a slight heteropolarity. These authors further expressed difficulty in assigning this taxon to a given genus. Since heteropolarity is rare and not the norm for *A. rionegrensis*, it may best be placed in *Eunotia* or *Desmogonium* (see Sabbe *et al.*, 2001). We view the degree of heteropolarity expressed in *A. hickeyi* and *A. goodwinii* to be slight, but clearly distinct, present on all valves, and within the range expressed by numerous species currently included in *Actinella*.

Should the heteropolar character be used to distinguish between the genera *Actinella* and *Eunotia*? This question, reviewed by Sabbe *et al.* (2001), has a rather long history, with some authors (e.g. Cholnoky, 1954; Metzeltin & Lange-Bertalot, 1998) arguing for placement of *Actinella* at the subgeneric rank under *Eunotia*, and thus demoting the use of heteropolarity as a distinguishing character at the generic level. In fact, Metzeltin & Lange-Bertalot (1998) described a distinctly heteropolar taxon as *Eunotia falcifera* Metzeltin & Lange-Bertalot, and further placed it in the proposed subgenus *Cultria* under the genus *Eunotia*. *Cultria* was to accommodate heteropolar species with head poles that are more or less rounded and lack an apical protuberance. However, Metzeltin & Lange-Bertalot (2007) later retracted this position and transferred *Cultria*, along with *E. falcifera*, to *Actinella*. As already noted, many *Actinella* species are morphologically closely allied with *Eunotia* counterparts, such as *A. aotearoaia* Lowe, Biggs & Francoeur, *A. parva*, *A. indistincta*, *A. eunotioides* Hustedt, *A. robusta* Hustedt, *A. peronioides* Hustedt, and the Giraffe taxa described in this paper and earlier by Siver *et al.* (2010).

Heteropolarity is likely an adaptation for attachment, either directly on to a substrate, through formation of a mucilaginous stalk (e.g. *Actinella aotearoaia*), or to each other to form a colony (Sabbe *et al.*, 2001). In fact, in his original description of *Actinella*, Lewis (1864) recorded stellate colonies of *A. punctata*, with cells connected to each other by their foot poles. One of us (PAS) has observed such colonies of *A. punctata* in plankton samples from Lewis' type locality, Saco Pond. If a heteropolar shape facilitates attachment, and if attachment would prove beneficial for survival, then one possible scenario is that the heteropolar condition evolved multiple times within *Eunotia*, yielding a suite of species now classified as *Actinella*. Such a hypothesis would explain why some *Actinella* taxa have morphologically similar counterparts in *Eunotia*. As discussed below, we certainly recognize this possibility with respect to the relationship between *Actinella goodwinii* and *Eunotia bidentula* W. Smith. If this scenario is proven correct, *Actinella* would represent a polyphyletic genus in need of re-evaluation.

Combining *Actinella giraffensis* (Siver *et al.*, 2010) with the results of this study, there are now at least five, and probably six, *Actinella* species known from the Giraffe locality. This finding is especially intriguing from three points of view. First, there are more *Actinella* species in this single Eocene locality than known today from all of North America and Europe (Siver & Wolfe, 2009; Ripple & Kocielek, 2013). In addition, a review of the literature for *Eunotia* shows that heteropolar specimens are extremely rare (Sabbe *et al.*, 2001), making the range of heteropolar eunotiophycid taxa in the Giraffe material even more impressive and unique. Second, the high-latitude geographical location

of the Giraffe locality is far removed from the modern centres of biodiversity for *Actinella* in the Southern Hemisphere (Kocielek *et al.*, 2001; Sabbe *et al.*, 2001), which is especially pronounced in low pH brown-water (humic) ecosystems of the tropics (Melo *et al.*, 2010). These observations support the hypothesis proposed by Siver & Wolfe (2009) that this genus was historically much more widespread than at present in the Northern Hemisphere. This hypothesis is further supported by the fact that the only other known fossil finds for *Actinella* are from the Northern Hemisphere, having being uncovered from eastern Russia (*Actinella penzhica*; Lupikina & Dolmatova, 1984), France (*Actinella pliocenica*; Héribaude, 1902), and the northern Province of Jiling in China (*Actinella miocenica*; Li, 1988). Third, it is equally intriguing that these Eocene taxa lack highly heteropolar *Actinella* species and ones with apical protuberances, as well as more elaborately shaped *Eunotia* taxa similar to ones found today especially in South America (Metzeltin & Lange-Bertalot, 1998; 2007). It is tempting to suggest that the Eocene may represent a time period where *Actinella* was beginning to diverge from *Eunotia* by evolving a heteropolar condition more adapted for an attached life style, and prior to the time where both genera began to develop more elaborate valve morphologies. Future molecular phylogenetic studies will undoubtedly help elucidate the evolutionary histories of these two closely related genera and determine their generic validity.

The morphological structure of *Actinella goodwinii* is similar to *Eunotia bidentula* (Siver & Hamilton, 2011), and it is possible that the two taxa shared a common ancestor. The overall valve shape, structure of the raphe, striae pattern and wide girdle bands are very similar in both species (Siver & Hamilton, 2011). In addition, Siver & Hamilton (2011) illustrated a similar apical structure for *E. bidentula* as found on *A. goodwinii*, and the base of the mantle around the apices is thickened on both taxa. However, the consistent heteropolar nature of *Actinella goodwinii* specimens clearly distinguish it from the modern *E. bidentula*. In addition, valves of *A. goodwinii* have a slight, but clearly discernable, concave ventral surface and frustules with foot poles that are slightly rhomboid in girdle view. The ventral surface on *E. bidentula* specimens is straight and the frustules rectangular in girdle view. *Eunotia bidentula* specimens are also larger, have more pronounced capitate apices, and have a longer raphe. Lastly, the distal raphe fissure terminates at the valve margin on *E. bidentula* (Siver & Hamilton, 2011), whereas on *A. goodwinii* specimens it bends up and extends on to the valve face. In our opinion, the slight modifications on *A. goodwinii* that yield its heteropolar nature and reduced raphe structure may be the result of adaptation to an attached life style.

Actinella goodwinii also bears some resemblance to *Eunotia camelus* Ehrenberg, *E. cameliopsis* Metzeltin & Lange-Bertalot, *E. schneideri* Metzeltin & Lange-Bertalot and *E. diodon* Ehrenberg, but can be distinguished from each based on the heteropolar nature of the frustules, differences in valve morphology and raphe structure. Specimens of *E. camelus* and *E. cameliopsis* have concave ventral margins and two undulations along the dorsal margin similar to *A. goodwinii*. However, on larger specimens of both *E. camelus* and *E. cameliopsis* the number of dorsal undulations increases and becomes less distinct. In addition, the distal raphe end of *E. camelus* encircles the apex, and specimens of *E. cameliopsis* possess widely spaced striae. Relative to

A. goodwinii, valves of *E. schneideri* have less-defined dorsal undulations and a straight ventral margin, whereas valves of *E. diodon* have wider apices and a different raphe structure.

The overall structure of *A. hickeyi* is unique among *Actinella* species, especially in regards to the spacing of the striae. There are *Eunotia* species, for example *E. odebrechtiana* Metzeltin & Lange-Bertalot and *E. parasiolii* Metzeltin & Lange-Bertalot, with similar wide-spaced striae, but these species are easily distinguished from *A. hickeyi* based on valve morphology. *Actinella kimberlitica* is very similar in overall structure and dimensions to *E. rhomboidea* and *E. papilioforma* Furey, Lowe & Johansen. All three taxa are small, possess heteropolar valves with rounded apices, and have a slightly wider head pole. The foot pole on *A. kimberlitica* is more extended and the striae density greater than on either of the *Eunotia* species. In addition, the rimoportula on *E. papilioforma* specimens is restricted to the head pole, whereas on *A. kimberlitica* it is on the foot pole. Nevertheless, based on morphological structure, these three taxa are closely related and, as already discussed, given the heteropolar nature of the valve, *E. rhomboidea* and *E. papilioforma* may more appropriately belong in *Actinella*.

On some species of *Actinella* the base of the mantle around the apex is thickened and extended inward forming a pseudoseptum (Metzeltin & Lange-Bertalot, 1998; Kociolek *et al.*, 2001). The extent of the pseudoseptum, and on which pole it is found, varies among taxa. On most species, as is the case for *Actinella goodwinii*, the pseudoseptum is shallow and found on the foot pole. On other taxa the pseudoseptum is extensive (e.g. *A. falcifera*), or located on the head pole (e.g. *A. eunotioides* and *A. peronioides*). The presence of pseudosepta on both poles, as observed for *Actinella hickeyi*, has not been documented previously. The role of the pseudoseptum is not known, but it likely strengthens the valve and may be associated with attachment.

Based on modern analogies, the sections of the Giraffe core harbouring large concentrations of Eunotiophycidae specimens, including the heteropolar forms, likely represent relatively shallow, acidic, humic habitats (Sabbe *et al.*, 2001; Melo *et al.*, 2010; Siver & Hamilton, 2011). As a genus, *Actinella* taxa are commonly reported in highly acidic habitats with high concentrations of dissolved humic substances (Melo *et al.*, 2010), and either low (Melo *et al.*, 2010) or high (Sabbe *et al.*, 2001) dissolved salt content. In addition, morphologically similar taxa, such as *Eunotia bidentula* and *E. rhomboidea*, are consistently reported with average weighted mean pH values close to or below 5 (Camburn & Charles, 2000; Gaiser & Johansen, 2000; Siver *et al.*, 2005; Siver & Hamilton, 2011). The ecological inferences based on the eunotioid specimens are further supported by the remains of other acidophilous and acidobiontic diatoms (Siver *et al.*, 2010), as well as euglyphid rhizarians (Barber *et al.*, 2013) and scaled chrysophytes (Siver & Lott, 2012) typical of low-pH environments.

In summary, the large number of heteropolar *Actinella* taxa uncovered from the Giraffe core significantly extends the geological record of the genus, and more than doubles the number of species known from the fossil record. Most of the species have isopolar counterparts in the closely related genus *Eunotia*, implying that they are recently diverged forms. The presence of *Actinella* in the Giraffe core further demonstrates how greenhouse conditions of the middle Eocene exerted profound biogeographical reorganizations; these and other taxa with temperate to tropical

affinities are of particular utility in reconstructing the ontogeny of the Giraffe maar lake.

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