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Neidiopsis hamiltonii sp. nov., N. weilandii sp. nov., N. levanderi and N. wulffii from western North America

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Neidiopsis hamiltonii sp. nov., *N. weilandii* sp. nov., *N. levanderi* and *N. wulffii* from western North America

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Neidiopsis hamiltonii sp. nov. and *Neidiopsis weilandii* sp. nov. are described from a stream, lakes and ponds in western North America. The new species are readily distinguished from the three other published species of *Neidiopsis* by valve size, valve shape and the nature of the proximal raphe ends. In both new species, loculi along the valve margins are continuous and form hollow longitudinal canals, as in *Neidium*. Diagnostic features common to all five *Neidiopsis* species include: (1) a mix of uniseriate and biseriate striae; (2) striae arranged in two offset ranks; (3) distal raphe fissures simple (not bifurcate); (4) habitat restricted to cold oligotrophic streams, lakes and ponds with low conductivity; and (5) distribution limited to the Arctic, sub-Arctic and alpine zones of temperate regions in the northern hemisphere. Considerable variation in valve shape, including apical shape, is demonstrated in Rocky Mountain populations of *N. hamiltonii*, *N. levanderi* (Hustedt) Lange-Bertalot & Metzeltin and *N. wulffii* (Petersen) Lange-Bertalot. A comparison of morphometric data for various populations of *N. levanderi* and *N. wulffii* indicates that valves from the Rocky Mountains tend to be larger than valves from European and more northerly North American populations.

Keywords: *diatoms,* Neidiopsis*,* Neidium*, Cascade Mountains, Rocky Mountains, North America, Colorado, Montana, Washington, Canada, Bacillariophyceae, taxonomy*

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Introduction

Neidiopsis Lange-Bertalot & Metzeltin is an exclusively freshwater genus of symmetric biraphid diatoms that includes a small number of species. Distribution is restricted to the Arctic and sub-Arctic and to alpine zones of temperate regions in the northern hemisphere. Representative species are typically found in low numbers in circumneutral, oligotrophic and low-conductivity lakes and ponds (Lange-Bertalot & Genkal 1999).

Valves of *Neidiopsis* species are linear, linear–lanceolate or linear–elliptic, sometimes triundulate, with variously protracted and obtusely rounded apices. A longitudinal hyaline line runs from apex to apex along each side of the valve, interrupting the striae. Outer raphe branches are filiform. Proximal raphe ends are either straight or deflected to the same side, and they are not, or only weakly, expanded. Distal raphe fissures are simple (not bifurcate) and curved to one side. Striae are biseriate, at least in part. The girdle is composed of a few perforated bands (Lange-Bertalot & Genkal 1999, Bahls & Metzeltin 2012). *Neidium* differs from *Neidiopsis* by having marginal longitudinal canals (supposedly absent from *Neidiopsis*), bifurcate terminal raphe fissures, proximal raphe ends deflected to opposite sides and uniseriate striae (Spaulding & Edlund 2009). *Neidiomorpha* differs from *Neidiopsis* by having uniseriate striae (Cantonati et al. 2010, Spaulding 2013).

Neidiopsis currently contains three published species (CAS 2011, Silva 2013). With its distinctive triundulate valves, *Neidiopsis levanderi* (Hustedt) Lange-Bertalot & Metzeltin is perhaps the best recognized and most widely distributed of the three. It was described from material collected in Finland (Hustedt in Schmidt et al. 1874–1959) and subsequently reported from the Faeroe Islands (Hustedt 1937), the Alps (Hustedt 1961–1966), Iceland (Foged 1974), Finland (Lange-Bertalot & Metzeltin 1996) and Bear Island, Arctic Norway (Metzeltin & Witkowski 1996). Two varieties were described from Europe and have been transferred from *Navicula* to *Neidiopsis*: *N. levanderi* var. *capitata* (Krasske) Lange-Bertalot and *N. levanderi* var. *tatrensis* (Bily & Marvan) Lange-Bertalot (Krasske 1938, Bily & Marvan 1959, Lange-Bertalot in Lange-Bertalot & Genkal 1999). In North America, *N. levanderi* has been reported from Alaska (Foged 1971, 1981), Canada (Hohn & Hellerman 1963) and from the Laurentian Great Lakes (Stoermer et al. 1999). Lange-Bertalot (2001) distinguishes between two ecotypes of *N. levanderi*: a larger, more triundulate form living in oligotrophic to oligodystrophic, unbuffered waters, with low to very low mineral content

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('acidophila'), and a smaller, less triundulate form living in calcium carbonate-buffered waters, with average or higher conductivity ('calcicola').

Neidiopsis wulffii (Petersen) Lange-Bertalot in Lange-Bertalot & Genkal was described from material collected on the northeast coast of Greenland (Petersen 1924). It has since been reported from Siberia (Lange-Bertalot & Genkal 1999) and from Arctic Canada (Antoniades et al. 2008). A specimen reported as *N. wulffii* by Hohn & Hellerman (1963) from Ridley Creek, Pennsylvania is too small and finely striated to be this species and is probably new to science.

Neidiopsis vekhovii Lange-Bertalot & Genkal, the type species of the genus, was described from material collected in the Russian Arctic (Lange-Bertalot & Genkal 1999, Lange-Bertalot 2001, Lange-Bertalot et al. 2002). This species has also been reported [as *N. levanderi*] from northern Finland (Lange-Bertalot & Metzeltin 1996, Fig. 29: 3) and from Mongolia (Edlund et al. 2001a, 2001b, Metzeltin et al. 2009, Kulikovskiy et al. 2010), but it has not been reported from North America.

Here, I describe two new species of *Neidiopsis* from western North America, *Neidiopsis hamiltonii* and *N. weilandii*, based on observations under the light (LM) and scanning electron microscopes (SEM). The new species are compared with Rocky Mountain populations of *N. levanderi* and *N. wulffii*. Size diminution series are illustrated to show how these four taxa change shape during size reduction and how they may be distinguished at different sizes. Morphological features and morphometric data for Rocky Mountain populations of *N. levanderi* and *N. wulffii* are compared with original descriptions and to populations from Europe and elsewhere in North America. Finally, five unifying diagnostic features for *Neidiopsis* species are proposed.

Methods and materials

At each site, diatoms were collected from all available near-shore substrata, including aquatic macrophytes, rocks, fine sediments and woody debris, using a tablespoon or a large-bore pipette with suction bulb. Subsamples were combined in a single container and preserved with Lugol's (IKI) solution before transport to the laboratory, where they were treated with sulfuric acid (H_2SO_4), potassium dichromate ($K_2Cr_2O_7$) and hydrogen peroxide (H_2O_2) to remove organic matter (APHA et al. 1992). After several rinses in distilled water, the cleaned diatom material was mounted permanently on slides using Hyrax or Naphrax and examined under LM with differential interference contrast optics using a Leica DM LB2 research microscope and a Spot Insight Model 14.0 monochrome digital camera.

Table 1. Diatom materials examined for this study.

MDC sample no.	Accession no.	Habitat and location	Latitude N	Longitude W	pH s.u.	Conductivity $\mu S\,cm^{-1}$
497601	MONTU 41-73	Big Therriault Lake, marshy tributary, Lincoln County, MT	48.9292°	114.8789°	8.5	181
438901	MONTU 39-71	Boundary Lake, Glacier National Park, Glacier County, MT	48.9869°	114.0244°	n.d.	n.d.
408801	MONTU 38-75	Bowman Lake tributary, Glacier National Park, Flathead County, MT	48.8322°	114.1742°	n.d.	n.d.
408201	MONTU 38-66	Fish Lake, Glacier National Park, Flathead County, MT	48.6000°	113.8586°	6.7	22
124002	MDC P3-21-4	Hoskins Lake, Kootenai National Forest, Lincoln County, MT	48.8870°	115.6357°	7.6	67
408001	MONTU 38-64	Johns Lake, Glacier National Park, Flathead County, MT	48.6372°	113.8547°	7.2	30
451601	MONTU 39-84	Kootenai Lake, Glacier National Park, Glacier County, MT	48.9269°	113.9008°	8.3	112
517701	MONTU 45-80	Lake Edna, Wenatchee National Forest, Chelan County, WA	47.6570°	120.9109°	n.d.	n.d.
494501	MONTU 41-42	Mexican Cut Upper Pond No. 53, Gunnison County, CO	39.0247°	107.0675°	7.6	41
494401	MONTU 41-41	Mexican Cut Upper Pond No. 54, Gunnison County, CO	39.0250°	107.0672°	7.6	40
409505	MONTU 40-9	Parke Creek, Glacier National Park, Flathead County, MT	48.8700°	114.2642°	n.d.	n.d.
460401	MONTU 37-23	Skinner Pond No. 2, Beaverhead National Forest and County, MT	45.1722°	113.5114°	7.6	16
109801	MDC P3-3-7	Unnamed lake above Little Rock Creek Lake, Ravalli County, MT	46.0081°	114.3674°	6.4	7

Notes: CO: Colorado, MDC: Montana Diatom Collection (Helena), MONTU: University of Montana Herbarium (Missoula), MT: Montana, WA: Washington, n.d.: no data, s.u.: standard units.

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Valve measurements were made from digital images using Spot Software (version 4.5).

SEM images were captured with a Hitachi S4700 Type II cold field emission SEM. Samples were filtered, air-dried and mounted on aluminum stubs, then sputter coated with gold and palladium using a Pelco Model 3 Sputter Coater. Specific conductance and pH were measured in the field with a Hanna Instruments waterproof meter, model 98129. Slides examined in this study are deposited in the Montana Diatom Collection (MDC) in Helena and the University of Montana Herbarium in Missoula (MONTU) (Table 1). Type slides and material have been deposited at MONTU, the Academy of Natural Sciences, Philadelphia (ANSP) and the Canadian Museum of Nature (CANA). The terminology of the diatom frustule follows Spaulding et al. (2010).

Results

Neidiopsis hamiltonii *Bahls sp. nov. (Figs 1–29)*

Description

Valves are linear–lanceolate in large specimens to elliptic–lanceolate in small specimens. Valve length 19.5–43.6 μm, valve width 6.0–8.3 μm. Apices are broadly rounded, rostrate to subcapitate in the largest specimens, subrostrate and weakly protracted in small specimens. The axial area is narrow and widens gradually towards the valve center where it merges with a rhomboidal central area. The raphe is filiform with weakly expanded proximal ends. Proximal raphe ends are straight and relatively close together. Distal raphe fissures are curved toward the same side of the valve. Striae are weakly radiate at the valve center, becoming parallel toward the apices. Stria density 22–24 in 10 μm; areola density within a stria 20–26 in 10 μm. A prominent longitudinal line interrupts the striae on each side of the valve about midway between the raphe sternum and the valve margin, coming closer to the valve margin near the apices. Less prominent longitudinal lines are also evident. Plastids were not observed.

SEM morphology (external, Figs 18–23)

The valve surface curves abruptly away from the valve face (darker area in Figs 18–20) towards the deep mantle. The flat valve face extends the length of the valve and about half way toward the valve margins where it is bounded by a slight ridge that is apparent in the LM as one of the longitudinal lines. Striae are somewhat sinuous and uniseriate for most of their length, but are biseriate adjacent to the axial area near the apices. Striae surrounding the central area are uniseriate for their entire length. There is a large variation in areola size, shape and spacing. Just downslope from the valve face on the deep mantle there is a somewhat wider gap between areolae (white arrows, Figs 22, 23), creating a longitudinal hyaline line on each side of the valve. Proximal raphe ends terminate in simple pores. Distal raphe fissures are simple, not bifurcate.

SEM morphology (internal, Figs 24–29)

Valve walls are loculate, while the copulae have multiple rows of poroids (Fig. 26). Adjacent loculi along the valve margins are without intervening struts and appear to be continuous, thereby forming shallow longitudinal canals (white arrow, Fig. 26). Proximal raphe ends are simple, not deflected, and separated by a central nodule that is internally thickened as an obtuse cone (Figs 24, 27). Terminal raphe fissures end in helictoglossae (Figs 25, 26). Areolae are covered with domed hymenes (Figs 25, 26, 28). Striae are expressed internally as transversely elongate alveoli arranged in two offset longitudinal rows (Fig. 25). Two or three small, reniform foramina occur alongside each alveolus (Figs 28, 29). Foramina align in two longitudinal rows running the length of the valve (black arrows, Fig. 25). These rows appear to coincide with abrupt changes in the slope of the valve and mantle. Along the axial area are smaller alveoli, which are either biseriate near the apices (Fig. 28) or uniseriate surrounding the central area (Fig. 29).

Holotype

Slide ANSP GC 65193, acid-cleaned material GCM 5603, Academy of Natural Sciences, Philadelphia. Circled holotype specimen illustrated in Fig. 4.

Isotypes

Slide and material CANA 93594, Canadian Museum of Nature, Ottawa. Slide MONTU 41–42, University of Montana Herbarium, Missoula. Slide MDC 126-36 and material 494501, Montana Diatom Collection, Helena.

Type locality

Upper Pond No. 53, Mexican Cut Nature Preserve, Gunnison County, Colorado, USA. Collected by M. Penton, 7 July 2012.

Paratypes

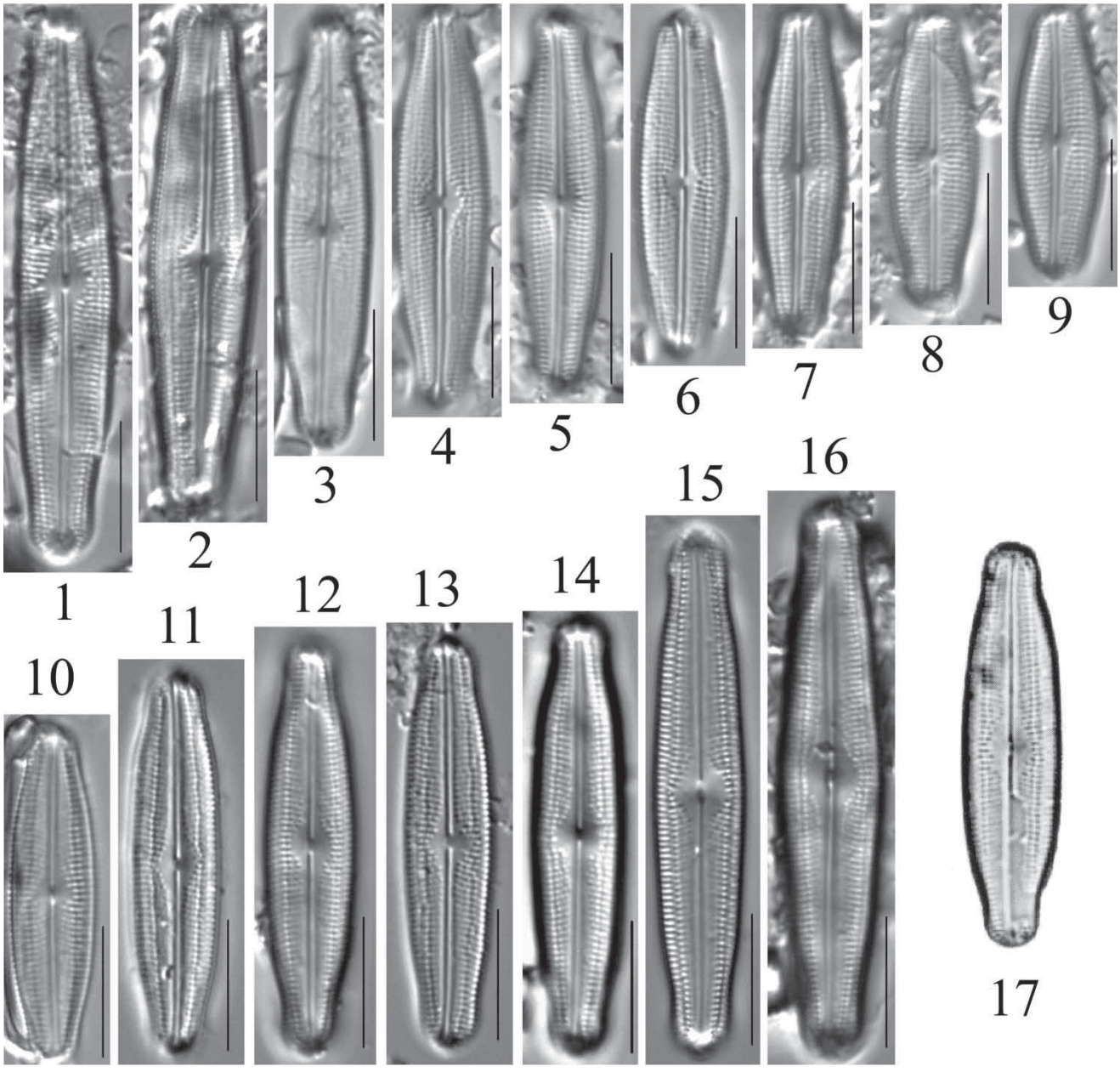
Slide MONTU 41-41, Upper Pond No. 54, Mexican Cut Nature Preserve, Gunnison County, Colorado, USA. Collected by M. Penton, 7 July 2012. Slide MDC P3-21-4, Hoskins Lake, Kootenai National Forest, Lincoln County, Montana, USA. Collected by J. Pierce, 30 August 1997.

Etymology

This species is named in honor of Paul Hamilton, Canadian Museum of Nature, in recognition of his work on North American diatoms, especially diatoms in the family Neidiaceae.

Ecology and distribution

Neidiopsis hamiltonii has been recorded from two ponds in Colorado (3450 m a.s.l.) and from Hoskins Lake in



Figs 1–17. *Neidiopsis hamiltonii* (LM). Figs 1–9. Specimens from the type locality. Fig. 4 is the circled holotype specimen. Figs 10–16. Specimens from Hoskins Lake, Kootenai National Forest, Lincoln County, Montana. Fig. 17. Specimen from 'Rocky Mountains, Canada' (Lange-Bertalot & Metzeltin 1996, Fig. 29: 6; Lange-Bertalot 2001, Fig. 101: 16). Scale bars = 10 μm.

northwest Montana (1036 m a.s.l.). The pH measured at these locations was a uniform 7.6 and specific conductance ranged from 40 to 67 $\mu S\,cm^{-1}$ (Table 1). A specimen of *N. hamiltonii* (Fig. 17) was also reported [as *N. levanderi*] from the 'Rocky Mountains, Canada' (Lange-Bertalot & Metzeltin 1996, Fig. 29: 6; Lange-Bertalot 2001, Fig. 101: 16). This specimen was collected at 'a high mountain site with oligotrophic, low conductivity water' (H. Lange-Bertalot, pers. comm.).

Remarks

Of the four other species of *Neidiopsis*, *N. hamiltonii* is most similar to *N. levanderi*. Both have straight proximal raphe ends, whereas the proximal raphe ends of *N. wulffii*, *N. vekhovii* and *N. weilandii* are distinctly bent to one side. In most cases, the smooth outline and lanceolate valves of *N. hamiltonii* easily distinguish this taxon from the linear triundulate valves of *N. levanderi*. Very small valves of *N. hamiltonii* (Fig. 9) may be distinguished from very small

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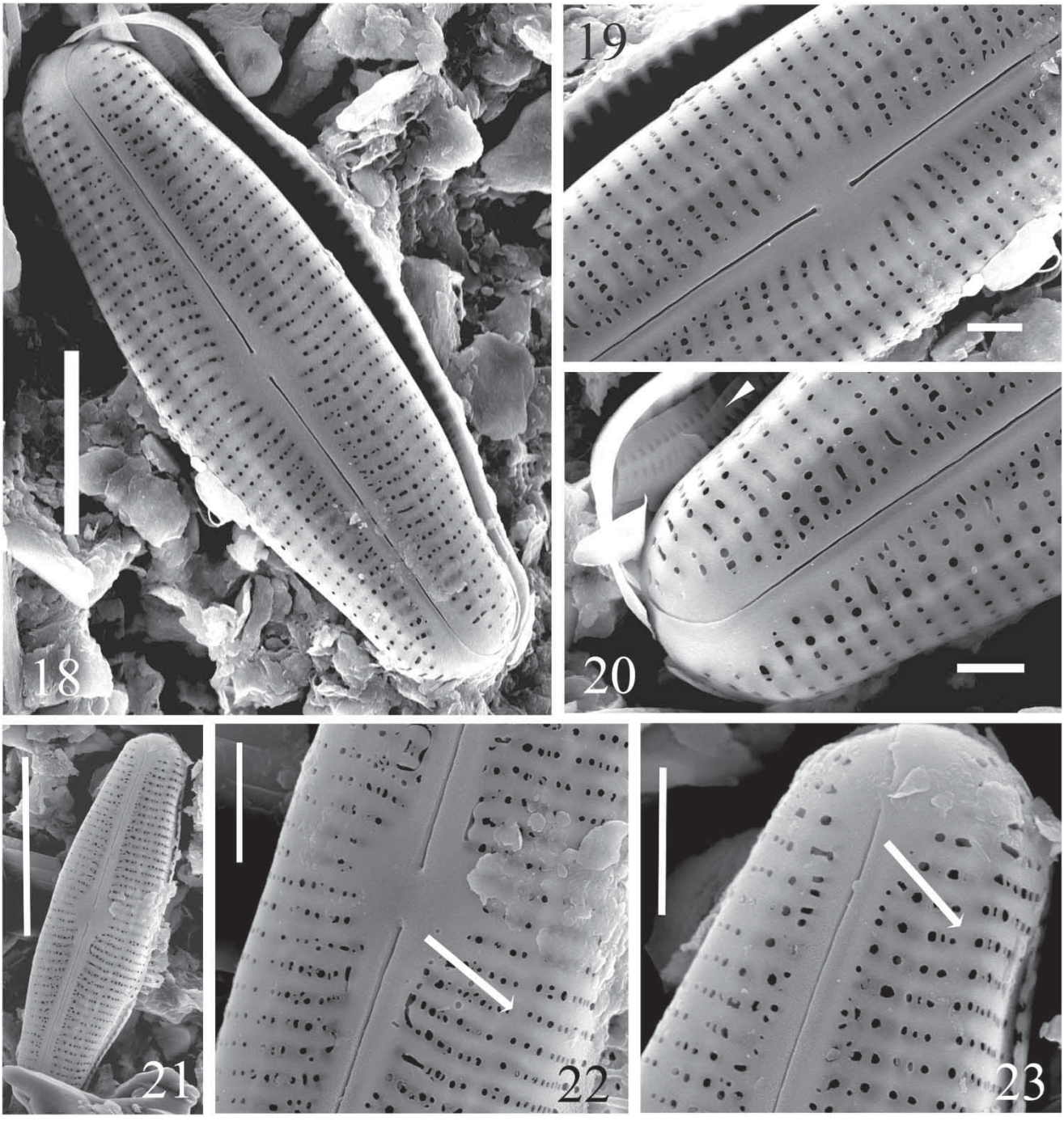
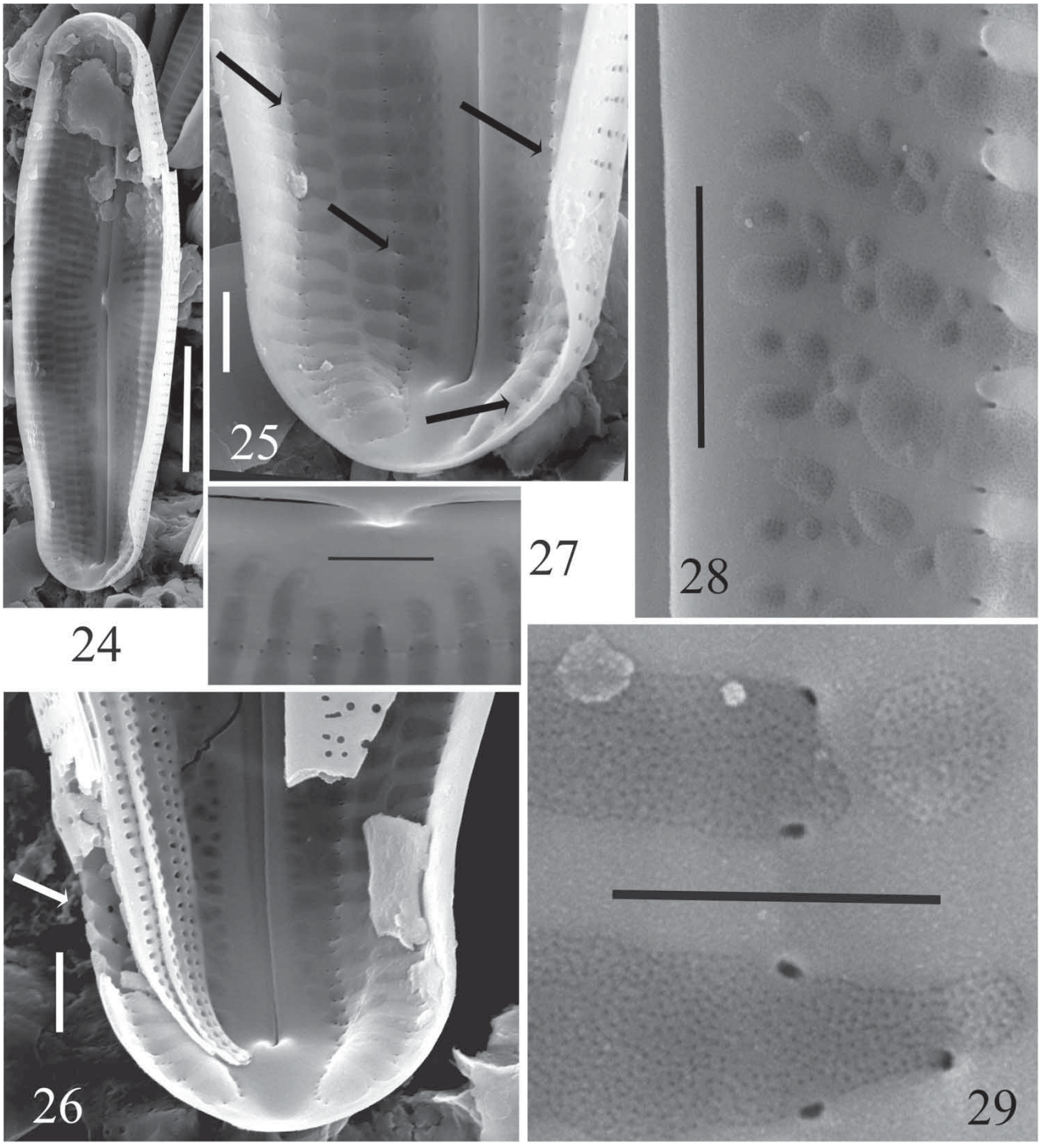


Figs 18–23. *Neidiopsis hamiltonii* (SEM, external views) from the type locality. Fig. 18. Whole valve showing central elevation of the valve face (darker region) along the apical axis and distal raphe ends curved to the same side. Fig. 19. Central region of the valve in Fig. 18 showing filiform raphe, straight proximal raphe ends, and variable spacing between areolae within striae. Fig. 20. End of the valve in Fig. 18 showing curved distal raphe fissure, areolae of various shapes and sizes, and biseriate striae along the axial area. Figs 21–23. Another specimen in oblique view showing variability in shape, size and spacing of areolae and biseriate striae along the axial area near the valve ends. A wider gap between areolae (white arrows, Figs 22–23) accounts for the distinct longitudinal lines seen in LM. Striae are uniseriate surrounding the central area. Scale bars = 10 μm (Fig. 21), 5 μm (Fig. 18), 2 μm (Figs 22–23), 1 μm (Figs 19–20).

valves of *N. levanderi* (Fig. 59) by their more elliptic shape and more closely spaced proximal raphe ends.

Under SEM, *N. hamiltonii* (Figs 18–29) shares several structural features with *N. levanderi* (Lange-Bertalot & Metzeltin 1996, Figs 29: 4, 5; Figs 30: 3–6) and *N. vekhovii* (Lange-Bertalot & Genkal 1999, Figs 41: 5–8; Figs 42: 1–4). All three species have distal raphe ends that are simple (not bifurcate) and curved to one side, and striae that



Figs 24–29. *Neidiopsis hamiltonii* (SEM, internal views) from the type locality. Fig. 24. Oblique view of the whole valve showing the inside of the mantle on the left and the outside edge of the mantle on the right. Fig. 25. Bottom end of valve in Fig. 24 showing the terminal raphe fissure ending in a helictoglossa and two offset ranks of alveoli. Inflection points where the mantle abruptly slopes away from the valve face are shown by black arrows. Fig. 26. Broken valve showing loculate wall structure, external openings of the areolae (white arrow) and the remains of two copulae. Loculi along the valve margins are without intervening struts and form shallow longitudinal canals. Alveoli with domed hymenes are evident near the valve apex. Fig. 27. Proximal raphe fissures and the central nodule of the valve in Fig. 24. Fig. 28. Close-up view of biseriate alveoli along the axial area near the valve apex. The raphe fissure is on the left and a longitudinal row of foramina is near the right edge. Fig. 29. Close-up view of simple alveoli near the central area showing porous hymenes and reniform foramina along the alveolus margins. Scale bars = 5 μm (Fig. 24), 1 μm (Figs 25–28), 0.5 μm (Fig. 29).

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are biseriate along the axial area, but uniseriate surrounding the central area. Internally, all three species have similar copulae and raphe structure, and they all have two principal rows of alveoli and smaller uniseriate or biseriate alveoli along the axial area corresponding to the single or double areolae at the proximal ends of the striae on the outside of the valve. I have been unable to find an internal SEM view of *N. wulffii* for comparison with the other species.

The abrupt change in elevation between the valve face and mantle explains why in some LM images only striae near the apical axis (Figs 11, 13), or only striae near the valve margins (Figs 10, 15), are in focus. The edge of the valve face appears to correspond to the proximal longitudinal row of foramina in the underlying alveoli (Fig. 25). The distal row of foramina appears to correspond to another abrupt change in the slope of the valve face and mantle. The offset nature of the underlying alveoli (Fig. 25) accounts for the sinuous appearance of the striae as seen externally in SEM (Fig. 18). The gap between the two underlying rows of alveoli (Fig. 25) corresponds to the overlying gap between adjacent areolae and the longitudinal hyaline lines seen in SEM (white arrows, Figs 22, 23). These features and features associated with changes in the slope of the valve face and mantle account for the prominent longitudinal lines seen in LM.

Neidiopsis weilandii *Bahls sp. nov. (Figs 30–51)*

Description

Valves are linear with weakly convex, nearly parallel margins. Valve length 39.4–65.1 μm, valve width 9.0–11.4 μm. Apices are cuneate to subrostrate and broadly rounded. The axial area is narrow and widens gradually towards the valve center where it merges with a small rhomboidal central area. The raphe is filiform with slightly expanded proximal ends that are bent toward the secondary side. Distal raphe fissures are curved toward the same side, as are the proximal raphe ends. Striae are radiate at the valve center, becoming parallel and finally convergent near the apices. Stria density 18–20 in 10 μm; areolae in the striae are very fine. A wide hyaline line runs along the valve margin from apex to apex. Plastids were not observed.

SEM morphology (external, Figs 44–47)

The flat valve face drops slightly in elevation just beside the marginal hyaline zone, where it curves abruptly to merge with the deep striated mantle (Figs 45, 46). Valve and mantle striae may be uniseriate or biseriate, or more commonly both. Striae along the axial area are always biseriate, except surrounding the central area. There is large variation in the size and shape of the areolae. At the distal edge of the mantle, each stria terminates in a long, dagger-shaped areola (Fig. 45). Distal raphe ends are simple, not bifurcate, and extend well onto the mantle (Fig. 45). Proximal raphe ends terminate in simple pores. Copulae are composed of at least two perforated bands, each with two rows of poroids, and one unperforated band.

SEM morphology (internal, Figs 48–51)

Valve walls are loculate. Adjacent loculi along the valve margins are without intervening struts, thereby forming longitudinal canals (Fig. 50). Proximal raphe ends are simple, not deflected, and separated by a central nodule that is internally thickened as an obtuse cone (Fig. 49). Terminal raphe fissures end in helictoglossae (Fig. 48). Internally, areolae are covered with porous hymenes (Figs 48, 50, 51). Striae are expressed internally as transversely elongate alveoli arranged in two offset longitudinal rows (Fig. 51). Two short linear foramina occur alongside each alveolus (Fig. 51) aligned in two longitudinal rows running the length of the valve (Fig. 48). These rows appear to coincide with changes in the slope of the valve face and mantle. A third rank of smaller, rounded alveoli occurs along the axial area (Fig. 48). These are either biseriate near the apices or uniseriate surrounding the central area.

Holotype

Slide ANSP GC 65206, acid-cleaned material GCM 5604, Academy of Natural Sciences, Philadelphia. Circled holotype specimen illustrated in Fig. 33.

Isotypes

Slide and material CANA 93608, Canadian Museum of Nature, Ottawa. Slide MONTU 45–80, University of Montana Herbarium, Missoula. Slide MDC 130-74 and material 517701, Montana Diatom Collection, Helena.

Type locality

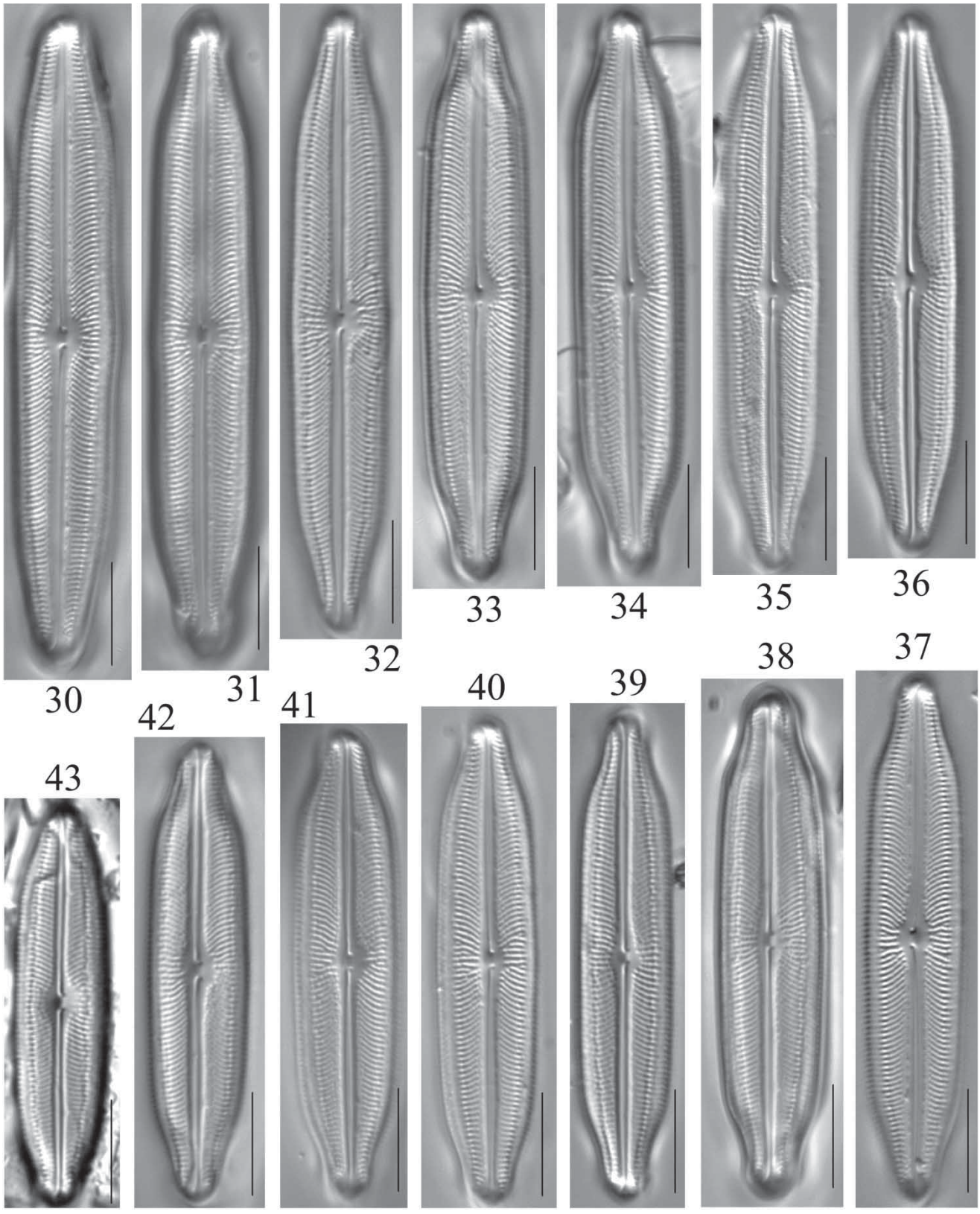
Lake Edna, Wenatchee National Forest, Alpine Lakes Wilderness, Chelan County, Washington, USA. Collected by C. Weiland, 20 September 2013.

Paratypes

Slide MONTU 39-84, Kootenai Lake, Glacier National Park, Glacier County, Montana, USA. Collected by L. Bahls, 22 July 2009. Slide MONTU 41-73, marshy tributary to Big Therriault Lake, Lincoln County, Montana, USA. Collected by L. Bahls, 18 September 2012.

Etymology

This species is named after Craig Weiland, collector of the holotype material. In 2012 and 2013, while serving as a citizen volunteer for Adventurers and Scientists for Conservation and The Montana Diatom Collection, Weiland



Figs 30–43. *Neidiopsis weilandii* (LM). Figs 30–42. Specimens from the type locality. Fig. 33 is the circled holotype specimen. Fig. 43. Specimen from Kootenai Lake, Glacier National Park, Glacier County, Montana. Scale bars = 10 μm.

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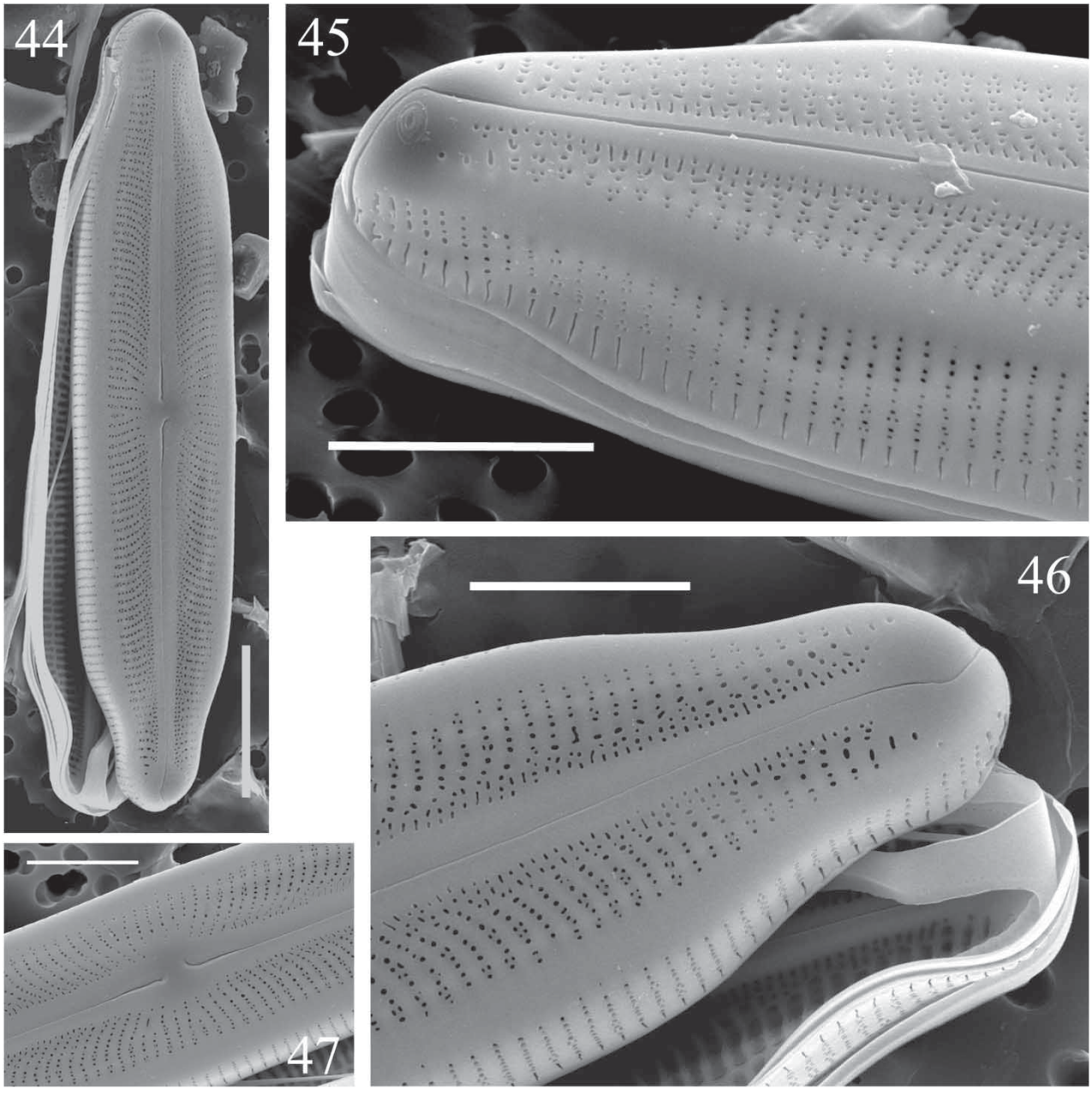

Figs 44–47. *Neidiopsis weilandii* (SEM, external views) from the type locality. Fig. 44. Whole valve partially displaced from the underlying valve. Figs 45–46. Oblique views of the valve ends showing the copulae and marginal hyaline space separating the striae on the valve face from the striae on the valve mantle. In Fig. 45 note the distal raphe fissure extending well onto valve mantle and the long dagger-shaped areolae at distal end of mantle striae. Fig. 47. Valve center. Note that striae adjacent to the central area are mostly uniseriate. Scale bars = 10 μm (Fig. 44), 5 μm (Figs 45–47).

collected diatom samples from 29 remote alpine lakes in the Cascade Mountains of Oregon, Washington, and California.

Ecology and distribution

Neidiopsis weilandii has been recorded from a small alpine lake in Washington (2060 m a.s.l.), from a small subalpine lake in Glacier National Park, Montana (1341 m a.s.l.), and from the marshy tributary of another subalpine lake in northwest Montana (1700 m a.s.l.). Water chemistry at the Washington locality is unknown but the lake probably has circumneutral pH and low concentrations of nutrients and dissolved solids. The pH at the lake in Glacier National Park was 8.3 and the specific conductance was 112 $\mu S\,cm^{-1}$ (Table 1). The marshy tributary of the subalpine lake in northwest Montana had a pH of 8.5 and a specific conductance of 181 $\mu S\,cm^{-1}$ (Table 1).

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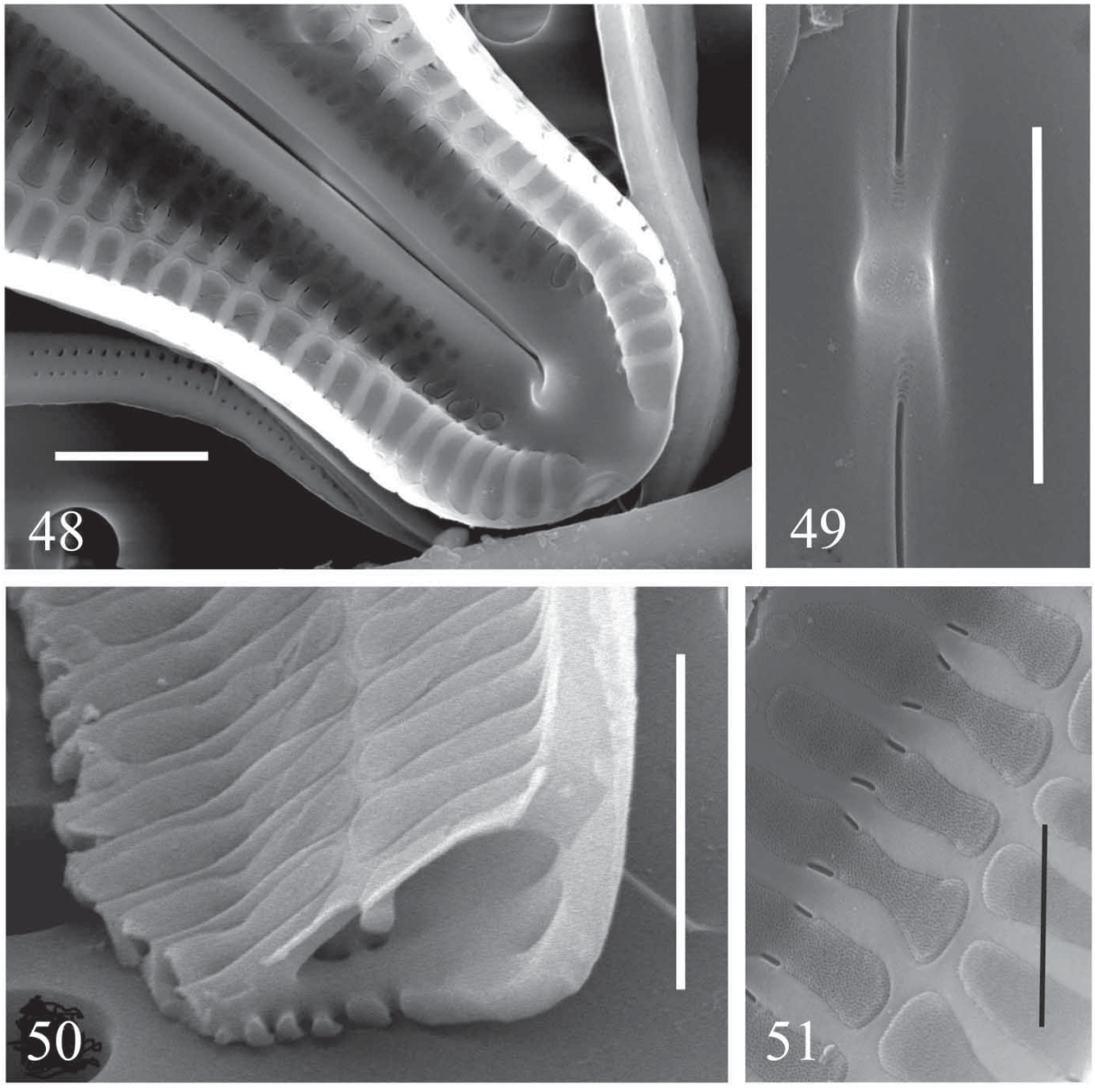

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Figs 48–51. *Neidiopsis weilandii* (SEM, internal views) from the type locality. Fig. 48. Valve end showing helictoglossa and two offset ranks of transapically elongate alveoli. Fig. 49. Central nodule. Fig. 50. Part of broken valve showing a cross-section of the longitudinal canal. At the top of the canal is a protruding piece of the valve inner wall that separates adjacent alveoli. The external openings of the areolae are evident on the bottom left. Fig. 51. Close-up view of elongate alveoli showing porous hymenes and linear foramina along the alveolus margins. Scale bars = 2 μm (Figs 48–50), 1 μm (Fig. 51).

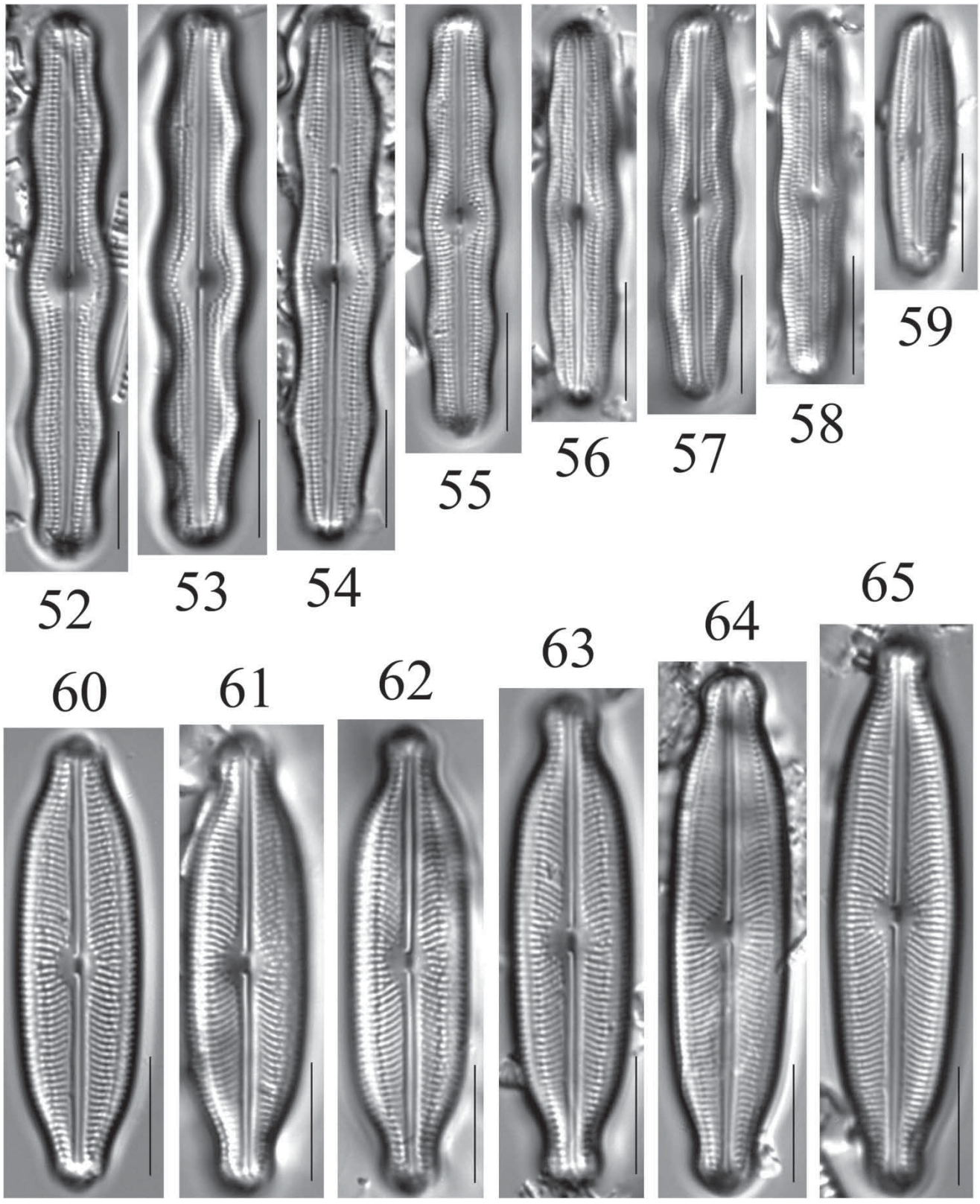
Remarks

Neidiopsis weilandii may be separated from *N. wulffii* by its larger size, more linear valves, more weakly protracted apices, more closely spaced striae and somewhat smaller central area. A specimen (Fig. 43) collected from a lake in Montana is presumably *N. weilandii*. This specimen, and a specimen collected from the marshy tributary of another Montana lake, have somewhat more closely spaced striae (20 in 10 μm) than specimens from the type locality in Washington (18–19 in 10 μm). The distinct longitudinal canal observed in this species (Fig. 50) eliminates this feature as one to distinguish *Neidium* species from species of *Neidiopsis* (Lange-Bertalot & Metzeltin in Lange-Bertalot & Genkal 1999).

Neidiopsis levanderi *(Hustedt) Lange-Bertalot & Metzeltin in Lange-Bertalot & Genkal 1999, p. 77 (Figs 52–59)*

Original description

Hustedt in Schmidt et al. 1874–1959, Figs 397: 30–32; Hustedt 1937, p. 195. Hustedt (1961–1966, p. 98, Fig. 1245)



Figs 52–65. *Neidiopsis levanderi* and *N. wulffii* (LM) from various locations in Montana. Figs 52–59. *Neidiopsis levanderi.* Fig. 52. Johns Lake, Glacier National Park, Flathead County. Figs 53–54. Fish Lake, Glacier National Park, Flathead County. Figs 55–59. Boundary Lake, Glacier National Park, Glacier County. Figs 60–65. *Neidiopsis wulffii*. Fig. 60. Skinner Pond No. 2, Beaverhead National Forest, Beaverhead County. Figs 61–63. Boundary Lake, Glacier National Park, Glacier County. Fig. 64. Bowman Lake tributary, Glacier National Park, Flathead County. Fig. 65. Unnamed lake above Little Rock Creek Lake, Bitterroot National Forest, Ravalli County. Scale bars = 10 μm.

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described *Navicula levanderi* as having 'linear valves with triundulate borders and bluntly protracted, broadly rounded, sometimes slightly capitate ends.' Valve length was given as 28–45 μm, and valve width as 6–7 μm. Stria density was 20–24 in 10 μm, striae finely punctate. Hustedt considered *Navicula levanderi* var. *tatrensis* Bily & Marvan (1959) as a synonym, and *N. levanderi* var. *capitata* Krasske (1938) as a *forma* of the nominate variety. Notably, Hustedt did not report smaller specimens that lack triundulate margins and protracted apices. He described *N. levanderi* as a 'northern-alpine, acidophilic to acidobiontic freshwater form.'

Rocky Mountain material

Rocky Mountain specimens of *N. levanderi* (Figs 52–59) range from 23 to 47 μm in length and from 6.2 to 8.9 μm in width. Most specimens are linear with triundulate margins and broadly rounded, rostrate to subcapitate apices. However, the smallest of these specimens (Fig. 59) has lanceolate valves with smooth margins and very weakly protracted apices. Stria density is 21–24 in 10 μm and areola density 20–24 in 10 μm. In the three Glacier National Park lakes where *N. levanderi* has been recorded, pH ranges from 6.7 to 7.2 and specific conductance ranges from 22 to 30 μS cm^{-1} (Table 1).

Neidiopsis wulffii *(Petersen) Lange-Bertalot in Lange-Bertalot & Genkal 1999, p. 78, Figs 42: 5, 6 (Figs 60–65).*

Original description

Petersen 1924, p. 312, Fig. 1. Petersen evidently based his description on a single valve, which was 35 μm long and 8.8 μm wide. Valve shape was 'linear–lanceolate with very slightly triundulate margins and rostrate–capitate apices.' On each side of the valve he noted 'a deep sulcus' (longitudinal line). The striae, which numbered 18 in 10 μm, were described as radiate throughout and finely punctate.

Rocky Mountain material

Rocky Mountain specimens of *N. wulffii* (Figs 60–65) are from 39 to 48 μm long and from 9.4 to 11.4 μm wide. Valves are linear–elliptic with subrostrate (Fig. 60), rostrate (Figs 61, 62) or subcapitate (Figs 63–65) apices. Valve margins are mostly convex and smooth (not perceptibly triundulate), but they are nearly flat in one specimen (Fig. 62). Stria density is 17–18 in 10 μm and areola density 20–24 in 10 μm. A distinct longitudinal line is evident near each margin. *Neidiopsis wulffii* has been recorded from five locations in the Rocky Mountains of western Montana (Table 1, Figs 60–65). Here pH ranges from 6.4 to 7.6 and specific conductance from 7 to 16 μS cm^{-1}.

Neidiopsis vekhovii *Lange-Bertalot & Genkal (1999), p. 76, Fig. 40: 10, Figs 41: 1–8, Figs 42: 1–4; Lange-Bertalot & Genkal in Lange-Bertalot (2001), p. 230, Figs 101: 22, 102: 2–8; Lange-Bertalot & Genkal in Lange-Bertalot et al. (2002)*

Neidiopsis vekhovii, the type species for the genus, is known only from Finland, the Russian Arctic and Mongolia. It has not been reported from North America. Morphological features and morphometric data for *N. vekhovii* are presented in Table 2 along with those for the four other published species of *Neidiopsis*. For *N. levanderi* and *N. wulffii*, data for Rocky Mountain populations are given separately to enable comparison with the original descriptions, with populations from Europe (Lange-Bertalot 2001) and with populations from elsewhere in North America.

Discussion

Populations of *N. levanderi* from the Rocky Mountains have somewhat wider valves than populations from Europe and elsewhere in North America (Table 2). Rocky Mountain populations also include very small specimens that lack triundulate margins. These small specimens (e.g., Fig. 59) resemble the 'calcicola' ecotype of Lange-Bertalot (2001, Figs 101: 17–21), but larger specimens in the same Rocky Mountain population (Figs 55–58) resemble Lange-Bertalot's 'acidophila' ecotype (Lange-Bertalot 2001, Figs 101: 10–15). Whether these morphological differences are a function of cell size, environmental factors or genetics remains to be resolved.

Populations of *N. wulffii* from the Rocky Mountains have larger valves than populations from Europe and more northerly sites in North America (Table 2). Smaller specimens from the Rocky Mountains (Fig. 60) may also have subrostrate apices, which have not been reported in European populations.

This study has also provided new information on stria morphology in *Neidiopsis*. *Neidiopsis wulffii* has biseriate striae throughout, except immediately adjacent to the central area, where they are uniseriate (Antoniades et al. 2008, p. 193, Fig. 120: 8). *Neidiopsis weilandii* has uniseriate and biseriate striae in roughly equal proportions, but they are always biseriate adjacent to the axial area and uniseriate surrounding the central area. The striae of the other three species are uniseriate over most of their length and biseriate only along the axial area, exclusive of the central area.

Besides being isopolar, biraphid and naviculoid diatoms with longitudinal hyaline lines and loculate valve walls, there are several distinctive features that are held in common by two or more *Neidiopsis* species, some of which may be helpful in defining the genus (Table 3). My determination of the presence or absence of these features is based on published species descriptions and SEM images (this paper, Lange-Bertalot & Metzeltin 1996, Lange-Bertalot & Genkal 1999, Lange-Bertalot 2001, Antoniades et al. 2008).

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Table 2. Morphological features and morphometric data for the five published species of *Neidiopsis*, comparing original descriptions with populations from Europe Lange-Bertalot (2001) and North America.

Species/Ref.	Valve length (μm)	Valve width (μm)	Valve shape	Valve margins	Apex shape	Proximal raphe rnds	Striae in 10 μm
N. hamiltonii	19.5–43.6	6.0–8.3	Linear–lanceolate to elliptic–lanceolate	Smooth	Subrostrate to subcapitate	Straight	22–24
N. levanderi							
Hustedt (1961–1966)	28–45	6–7	Linear	Triundulate	Bluntly protracted, broadly rounded to slightly capitate	Straight	20–24
Hohn & Hellerman (1963)	26	4.2	Linear	Triundulate	Subrostrate	Straight	20–22
Foged (1971)	23	7.5	Linear	Weakly triundulate	Rostrate	Straight	22–24
Foged (1981)	38	7	Linear	Triundulate	Rostrate	Straight	22–24
Lange-Bertalot (2001)	25–48	5.5–7.5	Linear	Triundulate	Broadly protracted and rounded	Straight	20–24
Rocky Mountains	23–47	6.2–8.9	Linear (large) to lanceolate (small)	Triundulate (large) or smooth (small)	Weakly protracted to rostrate and subcapitate	Straight	21–24
N. vekhovii							
Lange-Bertalot (2001)	30–40	5.5–6.6	Linear	Triundulate, concave	Broadly protracted and broadly rounded	Hooked to the same side	19–20
N. weilandii	39.4–65.1	9.0–11.4	Linear	Smooth	Cuneate to subrostrate	Bent to the same side	18–20
N. wulffii							
Petersen 1924	35	8.8	Linear–lanceolate	Slightly triundulate	Rostrate-capitate	Hooked to the same side	18
Lange-Bertalot (2001)	33–36	8–9	Linear–elliptic	Gently triundulate	Subcapitate	Deflected to one side	16–17
Antoniades et al. (2008)	33–39	8.5–11	Elliptic to linear–elliptic	Gently triundulate or smooth	Subrostrate to capitate	Deflected to one side	16–17
Rocky Mountains	39–48	9.4–11.4	Linear–elliptic	Smooth	Subrostrate, rostrate or subcapitate	Deflected to one side	17–18

Table 3. Shared features among species of *Neidiopsis* and whether they are consistent within (diagnostic of) the genus.

Feature	*N. hamiltonii*	*N. levanderi*	*N. vekhovii*	*N. weilandii*	*N. wulffii*	Diagnostic?
External morphology						
1. Biseriate striae	+	+	+	++	++	Yes
2. Striae in two offset ranks	+	+	+	+	+	Yes
3. Distal raphe fissures simple	+	+	+	+	+	Yes
4. Proximal raphe ends straight	+	+	−	−	−	No
5. Proximal raphe ends bent	−	−	+	+	+	No
6. Elongate distal areolae	?	?	+	++	?	?
Internal morphology						
7. Biseriate alveoli	+	+	+	+	?	?
8. Alveoli in two offset ranks	+	+	+	+	?	?
9. Alveoli with paired foramina in two rows	+	?	+	+	?	?
10. Longitudinal canal	+	?	?	++	?	?
11. Elongate alveoli with porous hymenes	+	+	+	+	?	?
12. Central nodule an obtuse cone	+	+	+	+	?	?
Plastids	?	?	?	?	?	?
Habitat	+	+	+	+	+	Yes
Distribution	+	+	+	+	+	Yes

Notes: +: feature present, ++: feature present to exaggerated degree, −: feature absent, ?: feature unknown. See Discussion for expanded explanation of features. References: this paper, Lange-Bertalot & Metzeltin (1996), Lange-Bertalot & Genkal (1999), Lange-Bertalot (2001).

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External morphological features

(1) Biseriate striae (Fig. 46). All five species of *Neidiopsis* have biseriate striae, at least in part. At a minimum, striae adjacent to the axial area are biseriate and the rest are uniseriate (Fig. 20).

(2) Striae in two offset ranks. All five species of *Neidiopsis* have two ranks of striae separated by a longitudinal hyaline line (Fig. 22). The striae in one rank are slightly offset from striae in the other rank, such that the striae may appear somewhat sinuous under SEM (Fig. 18).

(3) Distal raphe fissures simple. Distal raphe fissures of all five species are simple (not bifurcate) and bent in the same direction (Figs 20, 45). If the proximal raphe ends are also bent (*N. weilandii*, *N. wulffii*), they are bent in the same direction as the distal raphe fissures (Fig. 44).

(4) Proximal raphe ends straight (Figs 19, 22). Only two of the five species have almost straight proximal raphe ends, so this feature is not consistent across the genus.

(5) Proximal raphe ends bent (Fig. 47). Three of the five species have bent proximal raphe ends, so this feature is not diagnostic of the genus.

(6) Elongate distal areolae (Fig. 45). The ultimate distal areola in each mantle stria is long and dagger-shaped in *N. vekhovii* and *N. weilandii*. The presence of such areolae in the other three species is unknown for want of oblique valve images in SEM that include mantle striae.

Internal morphological features

(7) Biseriate alveoli. Like the external striae, the internal alveoli may be either uniseriate or biseriate. In four of the five species, alveoli adjacent to the axial area are biseriate (Fig. 28). The nature of the internal alveoli of *N. wulffii* is unknown for want of internal SEM images.

(8) Alveoli in two offset ranks (Figs 25, 48). Like the external striae, the two ranks of transapically elongate alveoli may be offset and not in line with one another. This has been demonstrated for all *Neidiopsis* species except *N. wulffii*, again for lack of internal SEM images.

(9) Alveoli with paired foramina in two rows (black arrows, Fig. 25). Each alveolus in the two ranks of transapically elongate alveoli may have an opposing pair of foramina, which are aligned in two longitudinal rows. These rows coincide with changes in the slope of the valve face and mantle. This feature has been demonstrated in *N. hamiltonii*, *N. vekhovii* and *N. weilandii*, but not in the other two species.

(10) Longitudinal canal. For *N. hamiltonii* (Fig. 26) and especially *N. weilandii* (Fig. 50), SEM views of broken valves indicate a distinct widening of the loculate walls at the junction of the valve face and mantle. These chambers are without intervening struts and therefore continuous for the length of the valve. The width and depth of these longitudinal canals appears to vary from species to species.

(11) Elongate alveoli with porous hymenes (Figs 29, 51). All four of the *Neidiopsis* species that

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have been examined internally under SEM have transapically elongate alveoli covered with porous hymenes. This feature is not unique to *Neidiopsis*. It is also present in other genera (e.g., *Biremis*, *Brachysira*, *Neidium*, *Scoliopleura*, *Scoliotropis*) (Round et al. 1990, Edlund et al. 2001a), which suggests potential relationships.

(12) Central nodule an obtuse cone (Figs 27, 49). The four species of *Neidiopsis* that have been examined internally under SEM have central nodules shaped like obtuse cones. This feature may be unique to the genus. The central nodule of *Neidium* is elongate (Round et al. 1990).

Plastids

Because of their widely scattered distribution and low abundance, the structure of plastids in living or preserved raw material has not been reported for any of the five *Neidiopsis* species.

Habitat

All five *Neidiopsis* species described to date have been reported from cold oligotrophic streams, lakes and ponds with low specific conductance, indicating a high degree of specificity in habitat preference.

Distribution

All five *Neidiopsis* species described to date have been collected from the Arctic, sub-Arctic and alpine zones of temperate regions in the northern hemisphere.

Conclusions and recommendations

In both *N. hamiltonii* and *N. weilandii*, loculi along the valve margins are continuous, without intervening struts, thereby forming hollow longitudinal canals, as in *Neidium*. The presence of this feature does not distinguish *Neidium* species from *Neidiopsis* species. Diagnostic features common to all five published species of *Neidiopsis* include: (1) striae that may be uniseriate or biseriate, or a combination of the two, but always uniseriate surrounding the central area and biseriate adjacent to the axial area; (2) striae arranged in two offset ranks separated by an intervening hyaline line; (3) distal raphe fissures that are simple (not bifurcate); (4) habitats that are restricted to cold oligotrophic lakes and ponds with low conductivity; and (5) a global distribution that is limited to the Arctic, sub-Arctic and alpine zones at temperate latitudes of the northern hemisphere. Rocky Mountain populations of *N. hamiltonii*, *N. levanderi* and *N. wulffii* display considerable variation in valve and apex shape. Montana populations of the latter two species tend to have larger valves than populations from Europe and more northerly latitudes in North America.

Living or preserved untreated specimens of *Neidiopsis* species need to be examined to determine the nature of their plastids. Internal SEM images of *N. wulffii* are needed to determine whether the internal structures of this species are consistent with those of the other four species.

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