



Kurtkrammeria*, a new genus of freshwater diatoms (Bacillariophyta, Cymbellaceae) separated from *Encyonopsis

Loren L. Bahls

The Montana Diatom Collection, 1032 12th Avenue, Helena, Montana 59601, USA
E-mail: eemahtuskie@gmail.com

With 116 figures and 2 tables

Abstract: The new genus *Kurtkrammeria* is erected to include 13 species assigned to *Encyonopsis* that have (1) slit-like or crescent-shaped areolae aligned lengthwise along the apical axis, (2) striae convergent at the apices, and (3) internal proximal raphe ends hooked strongly towards the dorsal side of the valve. Some species of *Kurtkrammeria* also have dorsal stigmata, apical pore fields and internal anastomosing costae at both poles, and lateral papilla-like projections from intercostae into internal areola openings. Species of *Kurtkrammeria* are reported infrequently from fossil deposits and from recent diatom assemblages. *Kurtkrammeria* is a genus of remote and undeveloped regions from the Arctic to the Tropics, in both the Old World and New World. Most species are local or regional endemics and only four species – *K. aequalis*, *K. neoamphioxys*, *K. recta*, and *K. subspicula* – appear to be widely distributed. *Kurtkrammeria* species consistently occur in oligotrophic or dystrophic waters with very low specific conductance and circumneutral pH. An extant population of the very rare *Kurtkrammeria stodderi* is described from Montana, USA. Living cells of *K. stodderi* were observed to be motile and to have plastids similar to those of *Encyonema* species. Examination under SEM reveals that *K. stodderi* also has apical pore fields at both poles.

Key words: Diatoms, *Kurtkrammeria*, *Encyonopsis stodderi*, apical pore fields, anastomosing costae, North America, Cymbellales.

Introduction

The diatom classification scheme of Round et al. (1990, p. 128) placed five genera in the family Cymbellaceae: *Placoneis* Mereschkowsky, *Cymbella* Agardh, *Brebissonia* Grunow, *Encyonema* Kützing, and *Gomphocymbella* Müller. Since then a number of new genera have been proposed for inclusion in Cymbellaceae based largely on differences in valve shape and symmetry, areolae and raphe structure, and other features observed under the scanning electron microscope (SEM). These new genera include *Afrocymbella* Krammer (2003), *Cymbellopsis* Krammer (1997a), *Cymbopleura* Krammer (2003), *Delicata* Krammer (2003), *Navicymbula* Krammer (2003), and *Oricymba* Jüttner et al. (2010). In addition, to accommodate *Encyonema*-like taxa that are symmetric or nearly symmetric with respect to the apical axis, Krammer (1997a,

p. 156) erected the genus *Encyonopsis* with *Navicula cesatii* Rabenhorst as the type species. In the ensuing Latin description, Krammer (1997a) allows for:

1. Solitary linear, lanceolate, or elliptic valves;
2. Acutely rounded or rostrate-capitate poles;
3. A moderately wide and scarcely eccentric raphe that becomes filiform near the central area and apices;
4. Proximal raphe ends inclined slightly towards the dorsal side;
5. Distal raphe fissures deflected towards the ventral side; and
6. Uniseriate striae composed of circular or elliptical areolae occluded by hymenes.

In Part 2 of his monograph, Krammer (1997b, p. 85) expands the diagnosis of *Encyonopsis* to include various forms of intermissio; areolae that are round or slit-like with their axes oriented apically or transapically; a dorsal stigma either present or absent; three distinct girdle bands; a chloroplast typical of cymbelloid genera; species that prefer oxygen-rich waters with low to moderate electrolytes; and found primarily in northern and alpine regions, but also in foothills and lowlands. For pH preferences, species span a broad range from slightly acid to alkaline.

Following this expanded diagnosis are descriptions of *Encyonopsis* species, including LM and some SEM images. From these descriptions there emerges two groups with fundamentally different valve structure:

1. Small to medium taxa in the *E. cesatii* (Rabenhorst) Krammer and *E. microcephala* (Grunow) Krammer complexes with circular or transapically elongate areolae, striae that are radiate or at most parallel at the apices, and internal proximal raphe ends confluent or weakly bent dorsally (e.g., fig. 146: 1–5, Krammer 1997b); and
2. Medium to large taxa with slit-like areolae oriented apically, striae that are convergent at the apices, and internal proximal raphe ends that are widely separated and hooked strongly to the dorsal side of the valve (e.g., *E. neoamphioxys* Krammer, fig. 168: 11–13 and *E. recta* Krammer, fig. 166: 13–15, Krammer 1997b).

A stigma is always absent in group 1 and may or may not be present in species of group 2. Species in group 1 are more numerous, more widely distributed, and have broader ecological amplitudes. Species in group 2 are far less common and are seldom reported in the literature; SEM images of both internal and external structures are scarce (e.g., *E. mantasoana* Metzeltin & Krammer in Metzeltin & Lange-Bertalot 2002, p. 24, Figs 63: 1–10; *E. stoermeri* Lange-Bertalot & Metzeltin 2009, p. 139, Figs 16: 7, 8).

Volunteer collectors recently provided the author with a large number of samples from standing waters in remote mountainous regions of western North America (Bahls 2014). Many of these samples contained populations of *Encyonopsis* species in group 2 sufficiently large enough to enable capture of SEM imagery. In this paper I provide LM and SEM imagery for two species in group 1, including the *Encyonopsis* type species (*E. cesatii*), and for seven much less common species in group 2. Three of the seven species in group 2 were described by myself (Bahls 2013) and four were described by others. All but one of the seven species in group 2 (*E. neoamphioxys*) were described

Table 1. Waters that support uncommon species of *Kurtkammeria* (species listed in Table 2) in western North America: Diatom sample locations and slide numbers in the Montana Diatom Collection (MDC), Helena, and the University of Montana Herbarium (MONTU), Missoula. Latitude and Longitude are in degrees, minutes, and seconds (DMS). AB = Alberta, BC = British Columbia, CA = California, ID = Idaho, MT = Montana, OR = Oregon, WA = Washington, WY = Wyoming.

MDC Site No.	Water Body	State/Province	Latitude N	Longitude W	MDC	MONTU
1109	Blodgett Lake	MT	461508	-1142715	P3-4-1	
1110	Kidney Lake	MT	460903	-1141702	P3-4-3	
1141	Big Creek Lake	MT	462942	-1142112	P3-4-4	
1147	Carlton Lake	MT	464101	-1141313	P3-4-10	
1154	Bramlet Lake (upper)	MT	480147	-1153313	P3-4-17	
1729	Teepee Lake	MT	480945	-1152423	P3-20-2	
1731	Pond near McDonald Mountain	MT	481045	-1153645	P3-20-4	
1741	Flower Lake	MT	482119	-1153743	P3-21-10	
1769	Meadow Lake	MT	472105	-1134544	P3-23-1	
1775	Chase Lake	ID	482732	-1164921	P3-23-20	
1792	Noseeum Lake	ID	461910	-1154608	P3-25-14	
1794	Bailey Lake	MT	460757	-1143032	P3-25-17	
1795	Gold Lake	ID	465635	-1151630	P3-25-20	
1796	Copper Lake	ID	465632	-1151559	P4-1-1	
1919	Lily Lake	ID	444953	-1143709	P4-1-4	
3815	Spring Creek	MT	481333	-1141602	114-52	30-53
4080	Johns Lake	MT	483814	-1135117	118-13	38-64
4081	Johns Fen	MT	483811	-1135122	118-14	38-65
4525	Drosera Pond	MT	470601	-1123547	123-65	36-96
4526	Drosera Fen	MT	470619	-1123622	123-66	36-97
4569	Summit Lake	AB	490028	-1140133	124-27	40-52
4909	<i>Nuphar</i> Zone, <i>Drosera</i> Pond	MT	470601	-1123547	125-70	41-7
4913	<i>Carex</i> Zone, <i>Drosera</i> Pond	MT	470601	-1123547	125-75	41-12
4947	Small Pond, Anderson Pass	WA	474151	-1231939	126-52	41-58
4948	Large Pond, Anderson Pass	WA	474149	-1231938	126-53	41-59
4957	Berkeley Park Pond	WA	465539	-1214115	126-45	41-51
4959	Dewey Lake	WA	465123	-1212853	126-47	41-53
4960	Pond above Dewey Lake	WA	465121	-1212918	126-48	41-54
4962	Clover Lake	WA	465544	-1213533	126-50	41-56
4963	Surprise Lake	WA	474008	-1210821	126-54	41-60
4993	Pond near Curly Lake	MT	453731	-1120457	126-86	41-92
4996	Pond near Schriebers Meadow	WA	484218	-1214914	126-89	41-95
4997	Nada Lake	WA	472937	-1204425	126-90	41-96
5015	Goat Rocks Pond	WA	462902	-1212922	127-8	42-14
5016	Trapper Lake	OR	423556	-1221151	127-9	42-15
5020	Saline Keys Lake	CA	371624	-1185236	127-13	42-19
5042	Boundary Trail Pond #2	WA	485908	-1195907	127-35	42-41
5043	Boundary Trail Pond #3	WA	485917	-1195746	127-36	42-42

Table 1 continued.

MDC Site No.	Water Body	State/Province	Latitude N	Longitude W	MDC	MONTU
5044	Cutthroat Lake	WA	483225	-1204043	127-37	42-43
5061	Kidder Creek tributary	CA	413033	-1230708	127-54	42-60
5064	Mount Yatza Lake	BC	522032	-1312610	127-57	42-63
5067	Lyell Point stream pool	BC	524227	-1314302	127-60	42-66
5070	Little Three Creek Lake	OR	440600	-1213820	127-63	42-69
5085	Lost Sheep Lake	MT	471608	-1134742	127-78	42-84
5092	Middle Rosary Lake	OR	433625	-1220003	127-85	42-91
5093	Jezebel Lake	OR	435043	-1215722	127-86	42-92
5105	Large Lily Pond	CA	385313	-1200700	130-2	45-8
5110	Unnamed Lake	CA	385542	-1200852	130-7	45-13
5120	Indian Henry's Pond	WA	464739	-1215019	130-17	45-23
5138	Surprise Lake	WA	474007	-1210820	130-35	45-41
5163	Crater Lake	WA	481339	-1201956	130-60	45-66
5175	Gnome Tarn	WA	472905	-1204724	130-72	45-78
5189	Shoofly Meadows #1	MT	465951	-1134341	130-89	45-95
5190	Shoofly Meadows #2	MT	465936	-1134611	130-90	45-96
5197	Pond on Windy Pass	WA	472254	-1212654	130-98	46-4
5198	Pond on Silver Peak Trail	WA	472111	-1212701	130-99	46-5
5201	Upper Big Jim Mountain Lake	WA	473945	-1204925	131-2	46-8
5206	Bigelow Tarn	WA	481249	-1202148	131-7	46-13
5207	Boiling Lake	WA	481212	-1202118	131-8	46-14
5212	Snow Lake (upper)	WA	472856	-1204522	131-15	46-21
6284	Mason Lake	WA	472530	-1213313	131-46	46-52
6287	Unnamed Pond	WA	472529	-1213203	131-49	46-55
6292	Golden Lake	WA	465258	-1215359	131-54	46-60
6302	Waterdog Lake	CA	411555	-1225833	131-64	46-70
6319	Wet Meadow	WY	425641	-1091545	131-83	46-100
6330	Azalea Lake	CA	415811	-1231759	131-94	46-89

initially without benefit of SEM images. Below I will demonstrate that group 2 species are morphologically, ecologically, and geographically distinct from species in group 1 and propose to include them in a new genus: *Kurtkammeria*.

Materials and methods

Samples were collected from small lakes (tarns), ponds, fens, and wet meadows in mountainous regions of western North America (Table 1). Most samples were collected from the North Cascade and Northern Rocky Mountains in Washington and Montana (USA), respectively, and a few from Idaho and Wyoming (USA) and from British Columbia and Alberta (Canada). Others were collected from the northern Sierra Nevada Range and Siskiyou Mountains in California (USA) and from the Cascade Range in Oregon (USA). Nearly all of the samples are from remote locations accessible

only by trail and at elevations ranging from 1000 to 3000 m a.s.l. Many of the sampled water bodies are not named on topographic maps.

At each site, diatoms were collected from all available near-shore substrata, including aquatic macrophytes, mosses, 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 (H₂SO₄), potassium dichromate (K₂Cr₂O₇) and hydrogen peroxide (H₂O₂) 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. 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 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 for this study are deposited in the Montana Diatom Collection (MDC) in Helena and the University of Montana Herbarium in Missoula (MONTU) (Table 1). The terminology of the diatom frustule follows Spaulding et al. (2010).

Results

Morphology and taxonomy of *Encyonopsis* and *Kurtkammeria*

Division: Bacillariophyta

Class: Bacillariophyceae

Order: Cymbellales D.G.Mann 1990

Family: Cymbellaceae Greville 1833

Encyonopsis Krammer sensu stricto

DESCRIPTION (Krammer 1997a, p. 156, translated from the Latin): Cells solitary, scarcely dorsiventral. Valves linear, lanceolate or elliptic; poles for the most part acutely rounded or rostrate-capitate. Raphe scarcely eccentric, moderately wide, becoming gradually filiform near the central area and apices, proximal ends inclined slightly towards the dorsal side, distal fissures deflected towards the ventral side or proceed towards the apex. Striae uniseriate, areolae round or elliptic, occluded by hymenes.

This description is still accurate for *Encyonopsis* sensu stricto. In the narrower sense, the genus *Encyonopsis* is here understood to include taxa originally assigned by Krammer (1997b) except those designated below as *Kurtkammeria* species. Features of *Encyonopsis* that are not shared by *Kurtkammeria* are:

1. Striae composed of round or transapically (not apically) elongate areolae;
2. Striae radiate or parallel (not convergent) at the apices; and
3. Internal proximal raphe ends confluent, or separate and deflected weakly (not hooked strongly) towards the dorsal margin of the valve.

As a practical matter, the second feature may be used to distinguish *Encyonopsis* species from *Kurtkammeria* species in LM. *Encyonopsis* includes all of the small- and medium-celled species in the *E. cesatii*, *E. descripta* (Hustedt) Krammer, and *E. microcephala* (Grunow) Krammer complexes (Krammer 1997b), including *E. horticola* Van de Vijver & Compère in Van de Vijver et al. (2009) and *E. neerlandica* Van de Vijver et al. (2012). It also likely includes the new small- and medium-celled *Encyonopsis* species described by Bahls (2013), but these need to be confirmed by SEM images. Here, for comparison with *Kurtkammeria*, are two examples of *Encyonopsis* from western North America – *E. cesatii* (generitype) and *E. montana* Bahls.

Encyonopsis cesatii (Rabenhorst) Krammer 1997b Figs 1–13

BAISIONYM: *Navicula cesatii* Rabenhorst 1853, Süßwasser-Diatomeen, p. 39, fig. 6: 89.

SYNONYM: *Cymbella cesatii* Grunow 1881 in A.Schmidt et al. 1874–1959, Figs 71: 48, 49.

TYPE LOCALITY: Piedmont, Italy.

LM & SEM: Striae are radiate throughout and composed of round to transapically elongate areolae. Internal proximal raphe ends are separated by the central nodule and deflected weakly towards the dorsal margin of the valve. Internally, alveoli (striae) are occluded by hymenes.

Encyonopsis montana Bahls 2013 Figs 14–26

TYPE LOCALITY: Lake McDonald, Glacier National Park, Montana, USA.

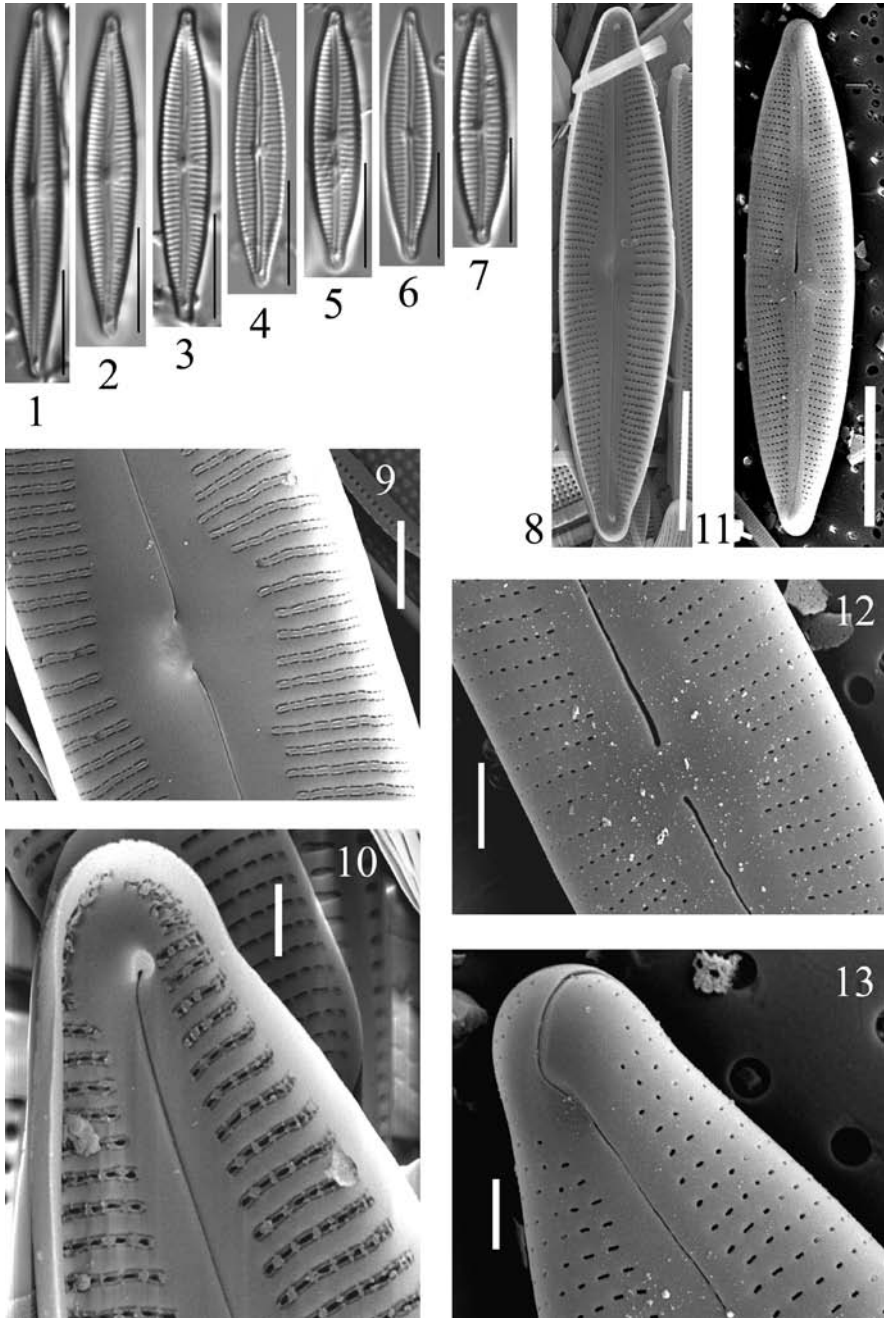
LM: See description in Bahls 2013.

SEM: Striae are radiate throughout and composed of round to transapically elongate areolae. Internally, striae are shallow alveoli occluded by hymenes (hymenes eroded in Figs 22 and 23). Internal proximal raphe ends are confluent across the central nodule, forming an intermissio. Distal raphe ends terminate in helictoglossae, which are well short of the apices and deflected towards the ventral margin of the valve.

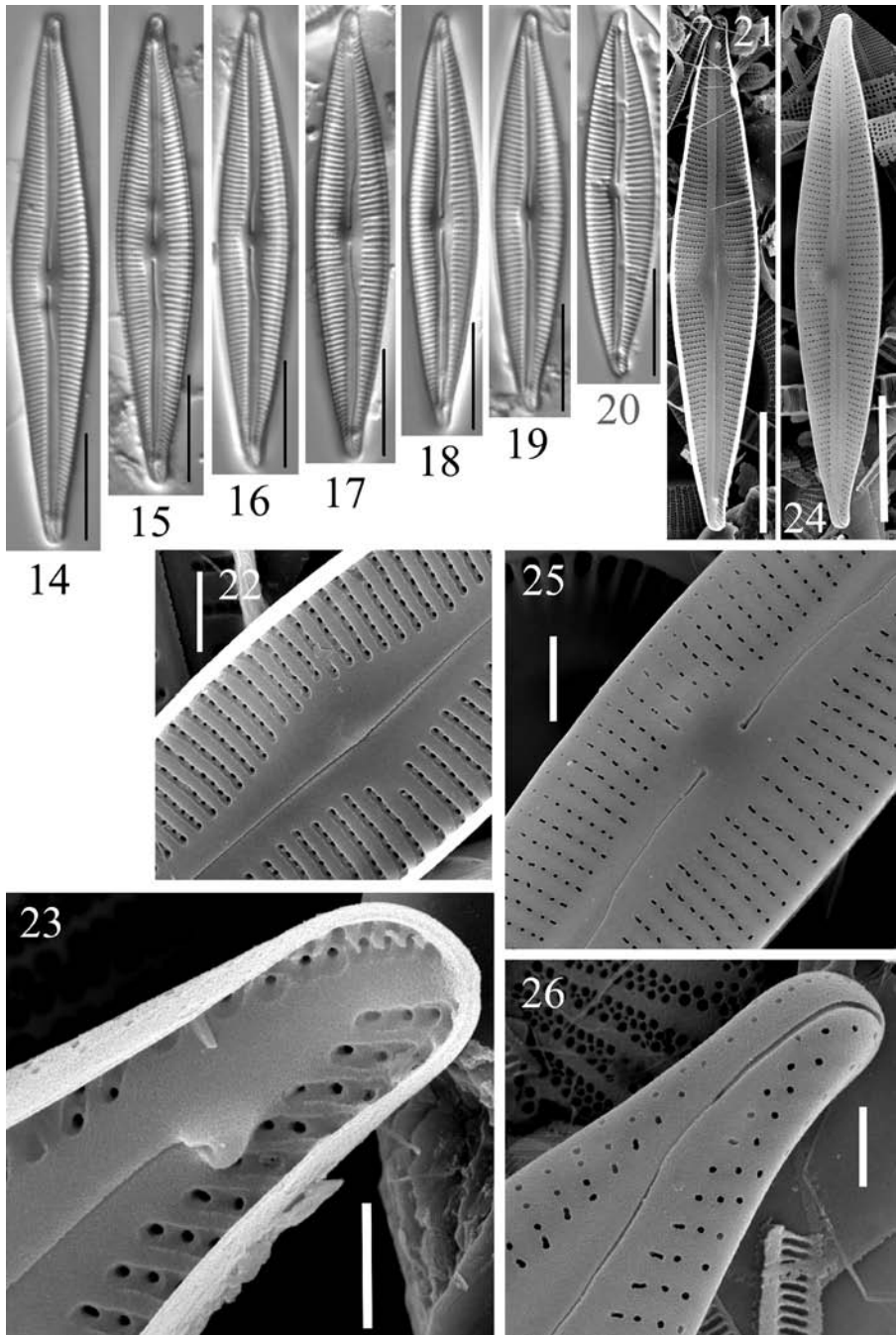
***Kurtkammeria* gen. nov.**

GENERITYPE: *Encyonopsis weilandii* Bahls 2013, Northwest Diatoms 5, p. 32, Figs 175–179.

DESCRIPTION: Cells solitary, medium to large in size. Mantles relatively deep (compared to *Encyonopsis*), cells rectangular in girdle view. Three copulae, each with a single row of poroids. Valves scarcely dorsiventral, apices sometimes slightly bent towards the ventral margin. Valves lanceolate to linear-lanceolate with rostrate, subrostrate, capitate, subcapitate or acutely to broadly rounded apices. Axial and central areas variable. Raphe lateral and somewhat sinuous, becoming filiform near the proximal and distal ends. Central pores inconspicuous and deflected slightly towards the dorsal side. Terminal fissures hooked towards the ventral margin. Transapical striae radiate near valve center, becoming parallel, then convergent near the apices. Striae continue onto the valve mantles. Middle striae more widely spaced than striae near the apices. One stigma (rarely two or three) may be present on the dorsal side of the central nodule, or stigma absent.



Figs 1–13. *Encyonopsis cesatii*. Figs 1–7: LM, Spring Creek, Montana (Site 3815). Figs 8–13: SEM, Crater Lake, Washington (Site 5163). Scale bars: Figs 1–8, 11 = 10 μ m; Figs 9, 12 = 2 μ m, Figs 10, 13 = 1 μ m.



Figs 14–26. *Encyonopsis montana*, Spring Creek, Montana (Site 3815). Figs 14–20: LM. Figs 21–26: SEM. Scale bars: Figs 14–21, 24 = 10 μm ; Figs 22, 25 = 2 μm ; Figs 23, 26 = 1 μm .

SEM: Transapical striae composed of slit-like or crescent-shaped areolae oriented with their long axes parallel to the apical axis. If present, areolae at the apices are of different shape and size. Internally, striae are represented by narrow alveoli between broad costae. Alveoli are covered by hymenes, which are usually eroded in prepared material. Where they meet the central nodule, internal proximal raphe fissures are hooked strongly to the dorsal side. Distally, raphe fissures end in helictoglossae that are deflected towards the ventral margin.

Additional features are evident under SEM on some species but not on others. These include well- to poorly-organized groups of small round areolae at both poles that resemble apical pore fields (APFs) divided by the distal raphe fissures [*K. aequalis* (W.Smith) Bahls, *K. frequentis* (Krammer) Bahls, *K. lacusglacialis* (Bahls) Bahls, *K. stodderi* (Cleve) Bahls, *K. weilandii* (Bahls) Bahls], anastomosing costae at the internal apices [*K. aequalis*, *K. frequentis*, *K. lacusglacialis*, *K. weilandii*], and lateral papilla-like structures projecting from the intercostae into the internal areolae openings [*K. aequalis*, *K. subspicula* (Krammer) Bahls, *K. weilandii*]. These features are noted below in the SEM descriptions for species. All of the following species have been described on the basis of LM observations (Krammer 1997b, Bahls 2013), so LM descriptions will not be repeated below. However, a complete description (LM and SEM) is provided for an extant population from Montana of the very rare *K. stodderi*.

***Kurtkammeria aequalis* (W.Smith) comb. nov.**

Figs 27–39

BASEONYM: *Cymbella aequalis* W.Smith in Greville 1855, Ann. Mag. Nat. Hist. 15: 255, fig. 9: 4.

SYNONYM: *Encyonopsis aequalis* (W.Smith) Krammer 1997b, p. 133, Figs 165: 1–11, 15, 16.

TYPE LOCALITY: Ben-na-Muic-Dhui, Braemar, Scotland.

SEM: Transapical striae composed of slit-like areolae oriented with their long axes parallel to the apical axis (Fig. 39). Striae radiate near valve center, becoming parallel, then convergent towards the apices (Figs 34, 37). Terminal striae composed of small round areolae at both poles (Fig. 39). Internally, there is a tendency for costae to anastomose at both poles (Fig. 36). Internal proximal raphe ends hooked strongly to the dorsal side at the central nodule (Fig. 35). Distally, raphe fissures end in helictoglossae that are deflected towards the ventral margin (Fig. 36). Internally, striae are represented by narrow alveoli between broad costae (Fig. 35). Alveoli are composed of rows of round areolae separated by broad intercostae (Fig. 35). Lateral papilla-like structures project from the intercostae into the internal areolae openings (Fig. 35). Stigma absent.

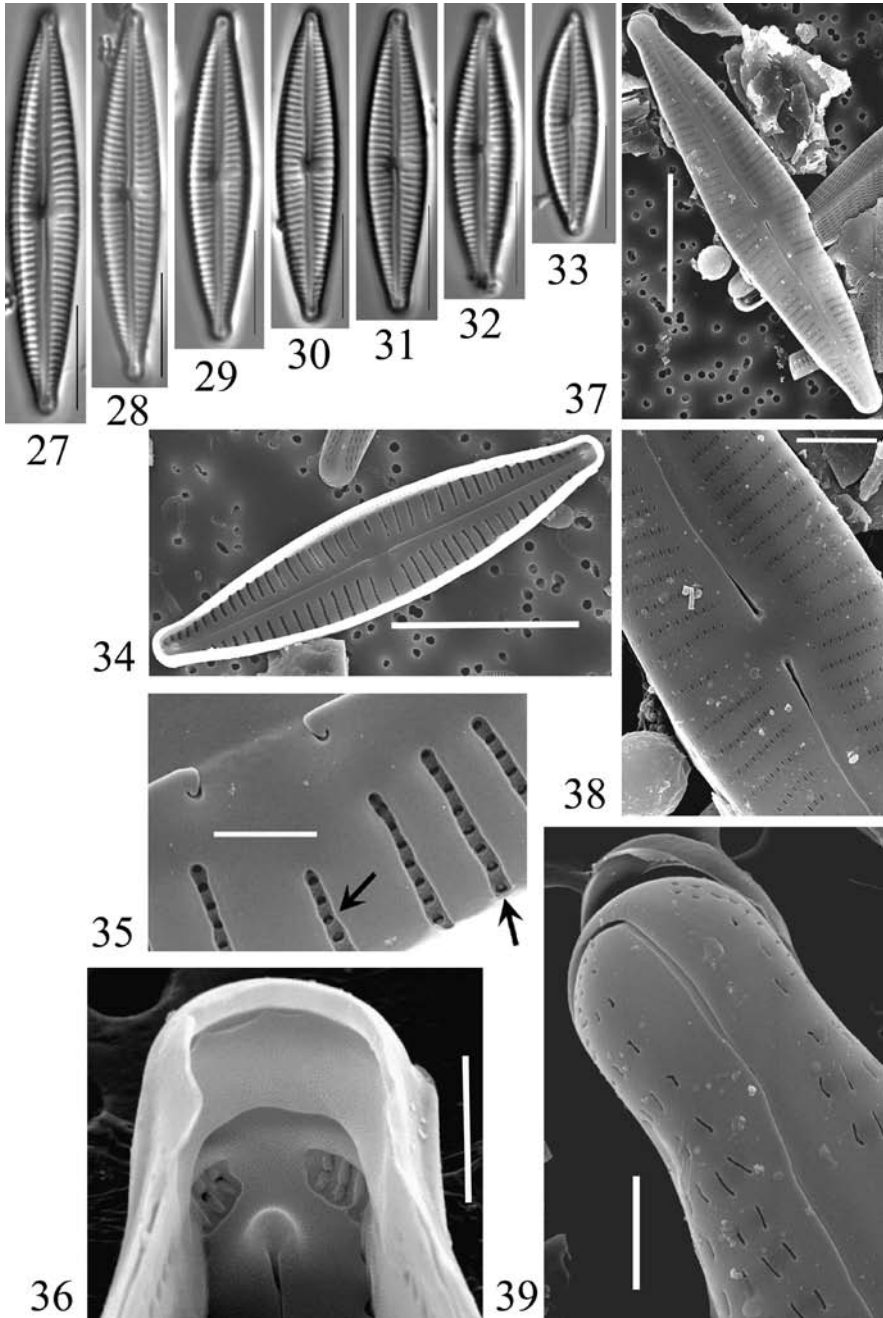
***Kurtkammeria lacusglacialis* (Bahls) comb. nov.**

Figs 40–49

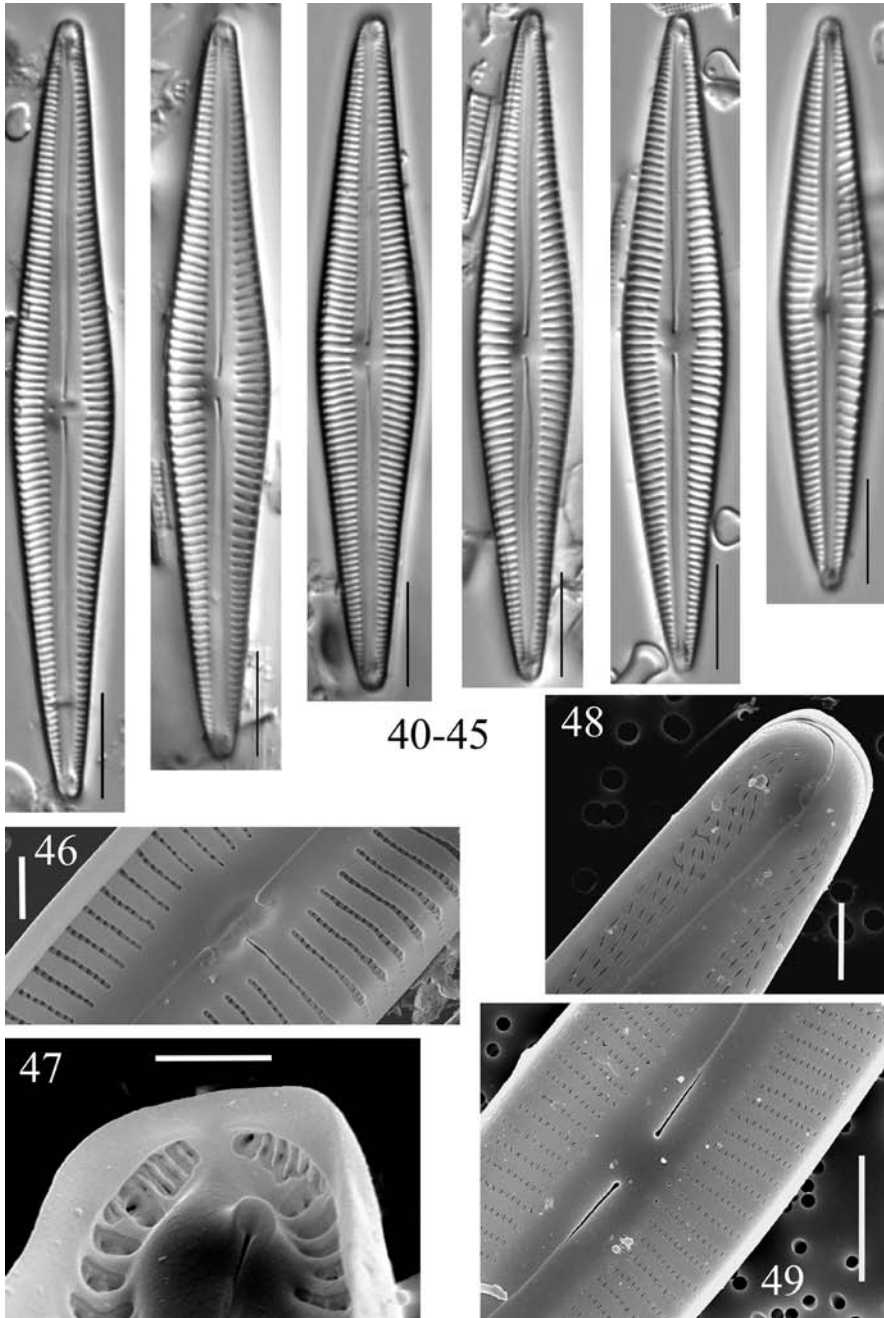
BASEONYM: *Encyonopsis lacusglacialis* Bahls 2013, Northwest Diatoms 5: 23, Figs 158–162.

TYPE LOCALITY: Summit Lake, Waterton Lakes National Park, Alberta, Canada.

SEM: Transapical striae composed of slit-like or Y-shaped areolae elongate parallel to the apical axis (Figs 48, 49). Terminal striae at both poles composed of small round pores loosely organized into simple pore fields split by the terminal raphe fissure (Fig. 48). Internally, there is a tendency for costae to anastomose at both poles (Fig. 47). Internal proximal raphe ends hooked strongly to the dorsal side (Fig. 46). Distal raphe



Figs 27–39. *Kurtkammeria aequalis*. Figs 27–33: LM, Goat Rocks Pond, Washington (Site 5015). Figs 34–39: SEM, unnamed lake, California (Site 5110). Fig. 35: Arrows point to lateral projections from intercostae into areolae. Scale bars: Figs 27–34, 37 = 10 μ m; Fig. 38 = 2 μ m; Figs 35, 36, 39 = 1 μ m.



Figs 40–49: *Kurtkrammeria lacusglacialis*. Figs 40–45: LM, various localities. Figs 46–49: SEM, unnamed lake, California (Site 5110). Scale bars: Figs 40–45 = 10 μ m; Figs 46, 48 = 2 μ m; Fig. 47 = 1 μ m; Fig. 49 = 5 μ m.

fissures end in helictoglossae that are deflected towards the ventral margin (Fig. 47). Internally, striae are represented by narrow alveoli between broad costae (Fig. 46). Internal areolae openings are round, or oblong in the apical axis, and separated by broad intercostae (Fig. 46). Stigma present; external stigma opening small and round (Fig. 49); internal stigma opening dagger-shaped (Fig. 46).

***Kurtkrammeria neoamphioxys* (Krammer) comb. nov.**

Figs 50–62

BASIONYM: *Encyonopsis neoamphioxys* Krammer 1997b, Biblioth. Diatomol. 37: 141, Figs 168: 1–7, 11–13.

SYNONYMS: *Navicula amphioxys* sensu Kützing 1844, p. 91, fig. 28: 37, *Cymbella amphioxys* (Kützing) Cleve 1894, p. 164.

TYPE LOCALITY: Kitzbühel, Schwarzsee, Austria.

SEM: Transapical striae composed of narrow crescent-shaped areolae oriented lengthwise with the apical axis and concave to the valve margins; striae continue onto valve mantle (Fig. 60). Three copulae, each with a single row of poroids (Fig. 59). External raphe fissure sinuous (Fig. 58). Central pores weakly inflated and deflected slightly towards the dorsal side (Figs 58, 60). Terminal fissures hooked towards the ventral margin (Fig. 59). Internal proximal raphe ends hooked strongly towards the dorsal margin (Fig. 61). Distally, raphe fissures terminate in helictoglossae that are deflected towards the ventral margin (Fig. 62). Internally, striae are represented by narrow alveoli between broad costae (Fig. 61). Alveoli covered with hymenes (hymenes eroded in Figs 61 and 62). Internal areolae openings are large and round and separated by narrow intercostae (Fig. 61). Stigma present; external stigma opening small and X-shaped (Fig. 60); internal stigma opening dagger-shaped (Fig. 61).

***Kurtkrammeria stodderi* (Cleve) comb. nov.**

Figs 63–75

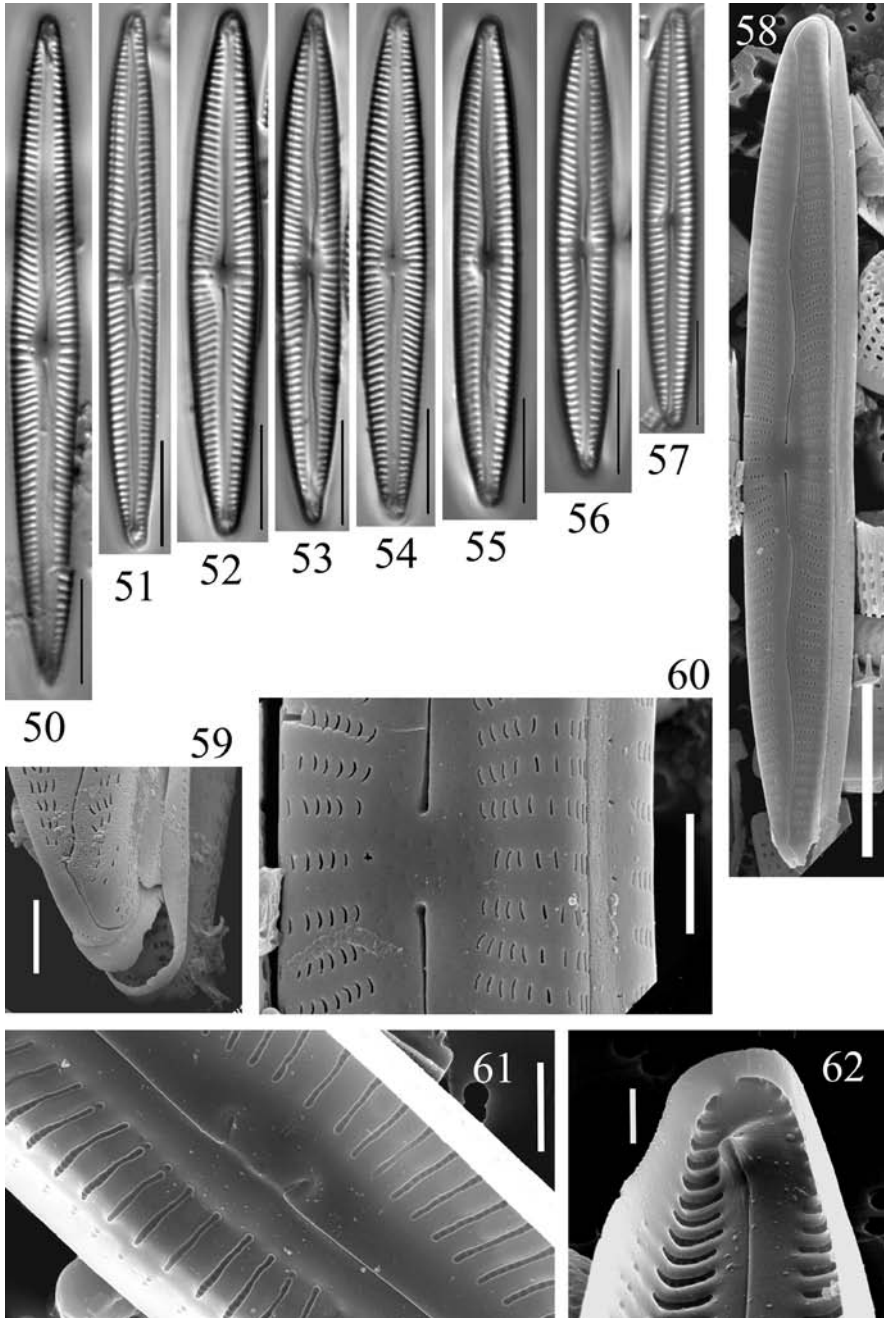
BASIONYM: *Cymbella stodderi* Cleve 1881, Kongl. Svenska Vetensk.-Akad. Handl. 18: 5, non fig. 1/5; *Cymbella stodderi* Cleve 1881 sensu Hustedt 1944 in A. Schmidt et al. 1874–1959, Atlas der Diatomaceen-Kunde, fig. 377: 1, 2.

SYNONYM: *Encyonopsis stodderi* (Cleve) Krammer 1997b, p. 162, Figs 171: 1–5; 172: 1–4.

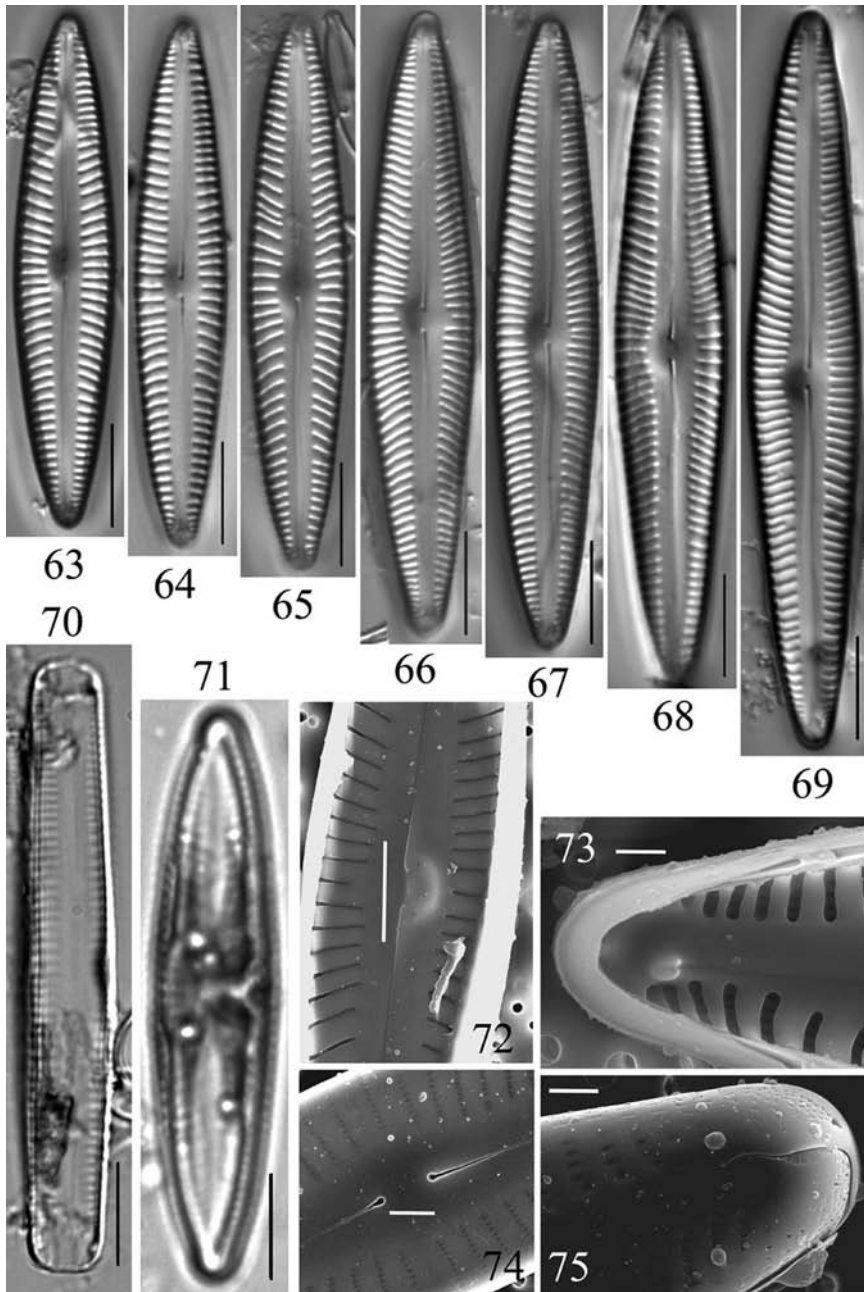
TYPE LOCALITY: Bemis Lake, White Mountains, New Hampshire, USA (fossil).

LM: Cells solitary and motile with *Encyonema*-type plastids (Fig. 71). Cells broadly rectangular in girdle view with striae extending onto deep mantles (Fig. 70). Valves broadly lanceolate with rounded, unprotracted apices (Figs 63–69). Length 50.6–72.9 μm ; width 8.9–11.8 μm . Axial area wide and confluent with a slightly wider central area. Raphe lateral, becoming filiform near the proximal and distal ends. Central pores weakly inflated and deflected slightly towards the dorsal side. Terminal fissures hooked towards the ventral margin. Striae radiate, becoming parallel and then convergent near the apices. Striae 9–10 in 10 μm at valve center, 11–13 in 10 μm near the apices. Areolae about 40 in 10 μm . Stigma absent.

SEM: Transapical striae composed of narrow slit-like areolae oriented parallel to the apical axis (Figs 74, 75). Both poles with pore fields composed of small round pores on both sides of the terminal raphe fissures (Fig. 75). Internal proximal raphe ends hooked strongly to the dorsal side at the central nodule (Fig. 72). Distal raphe fissures



Figs 50–62: *Kurtkammeria neoamphioxys*. Figs 50–57: LM, various localities. Figs 58–62: SEM, Bigelow Tarn, Washington (Site 5206). Scale bars: Figs 50–58 = 10 μ m; Figs 59–61 = 2 μ m; Fig. 62 = 1 μ m.



Figs 63–75: *Kurtkammeria stodderi*, Shoofly Meadows, Montana (Site 5190). Figs 63–71: LM. Fig. 70 is girdle view of frustule in unpreserved sample (400×). Fig. 71 is observed motile specimen with intact chloroplast in unpreserved sample (400×). Figs 72–75: SEM. Scale bars: Figs 63–71 = 10 μm; Fig. 72 = 5 μm; Figs 73, 75 = 1 μm; Fig. 74 = 2 μm.

end in helictoglossae that are deflected towards the ventral margin (Fig. 73). Internally, striae are represented by narrow alveoli between broad costae (Fig. 72). Internal areolae openings are elongate parallel to the apical axis and separated by broad intercostae (Fig. 73). Alveoli are covered by hymenes (eroded in Figs 72 and 73).

***Kurtkammeria subspicula* (Krammer) comb. nov.**

Figs 76–90

BASIONYM: *Encyonopsis subspicula* Krammer 1997b, Biblioth. Diatomol. 37: 144, Figs 168: 8, 9; 169: 1–9.

TYPE LOCALITY: Bemis Lake, White Mountains, New Hampshire, USA (fossil).

SEM: Transapical striae composed of slit-like areolae oriented with their long axes parallel to the apical axis (Figs 88, 89). Striae radiate near valve center, becoming parallel, then convergent near the apices (Figs 85, 90). Internal proximal raphe ends hooked strongly to the dorsal side at the central nodule (Fig. 86). Distal raphe fissures end in helictoglossae that are deflected towards the ventral margin (Fig. 87). Internally, striae are represented by narrow alveoli between broad costae (Figs 86, 87). Alveoli composed of rows of round areolae separated by broad intercostae (Figs 86, 87). Lateral papilla-like structures project from the intercostae into the internal areolae openings (Fig. 87). Stigma present; external stigma opening small and round (Fig. 88); internal stigma opening dagger-shaped (Fig. 86).

***Kurtkammeria treinishii* (Bahls) comb. nov.**

Figs 91–102

BASIONYM: *Encyonopsis treinishii* Bahls 2013, Northwest Diatoms 5: 31, Figs 170–174.

TYPE LOCALITY: Nada Lake, Chelan County, Washington, USA.

SEM: Transapical striae composed of slit-like or crescent-shaped areolae oriented with their long axes parallel to the apical axis or at an angle to the apical axis (Figs 101, 102). Striae radiate near valve center, becoming parallel, then convergent near the apices (Figs 101, 102). Internal proximal raphe ends hooked strongly to the dorsal side at the central nodule (Fig. 100). Distal raphe fissures end in helictoglossae that are deflected towards the ventral margin (Figs 98, 99). Internally, striae are represented by narrow alveoli between broad costae (Figs 99, 100). Alveoli are composed of rows of round areolae separated by broad intercostae (Fig. 99). Stigma present; external stigma opening small and round (Fig. 102); internal stigma opening dagger-shaped (Fig. 100).

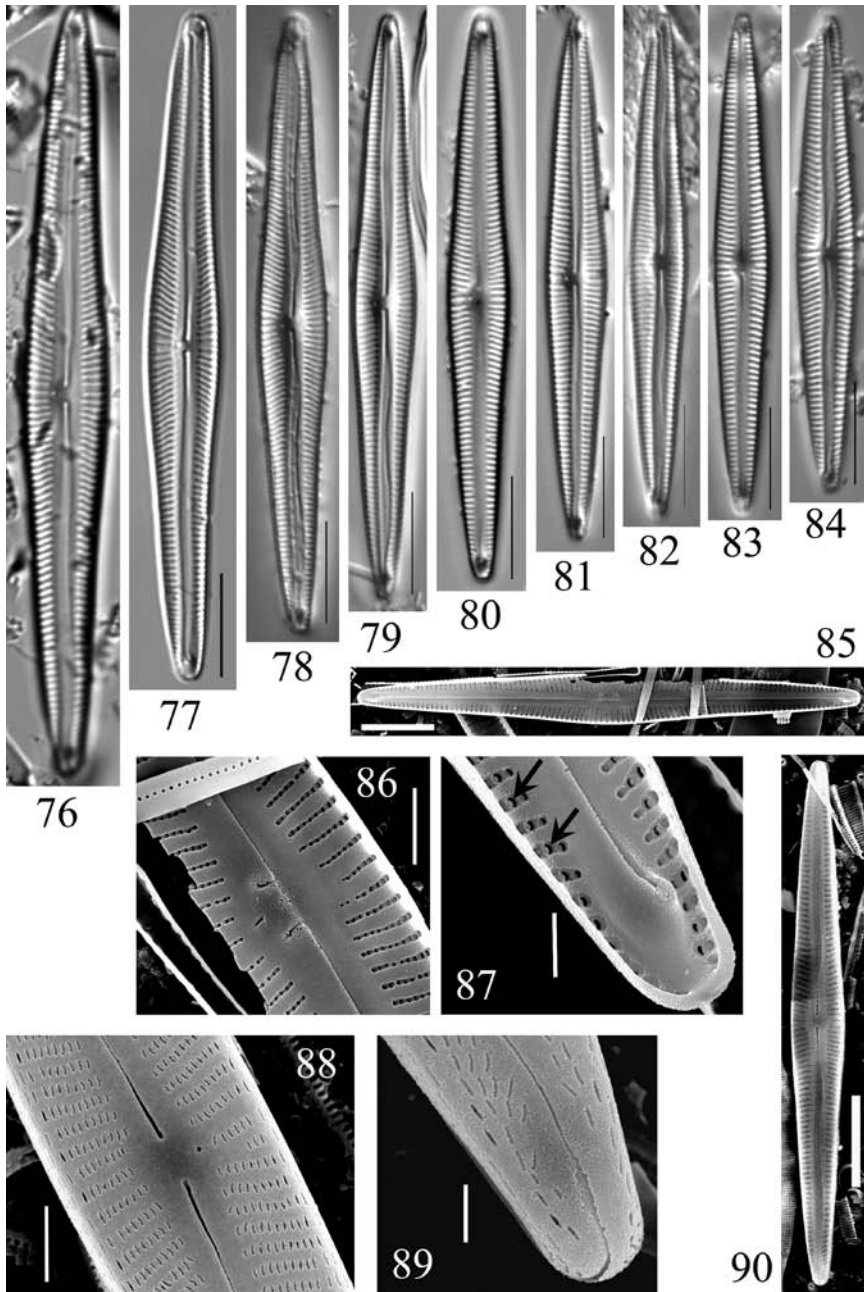
***Kurtkammeria weilandii* (Bahls) comb. nov.**

Figs 103–116

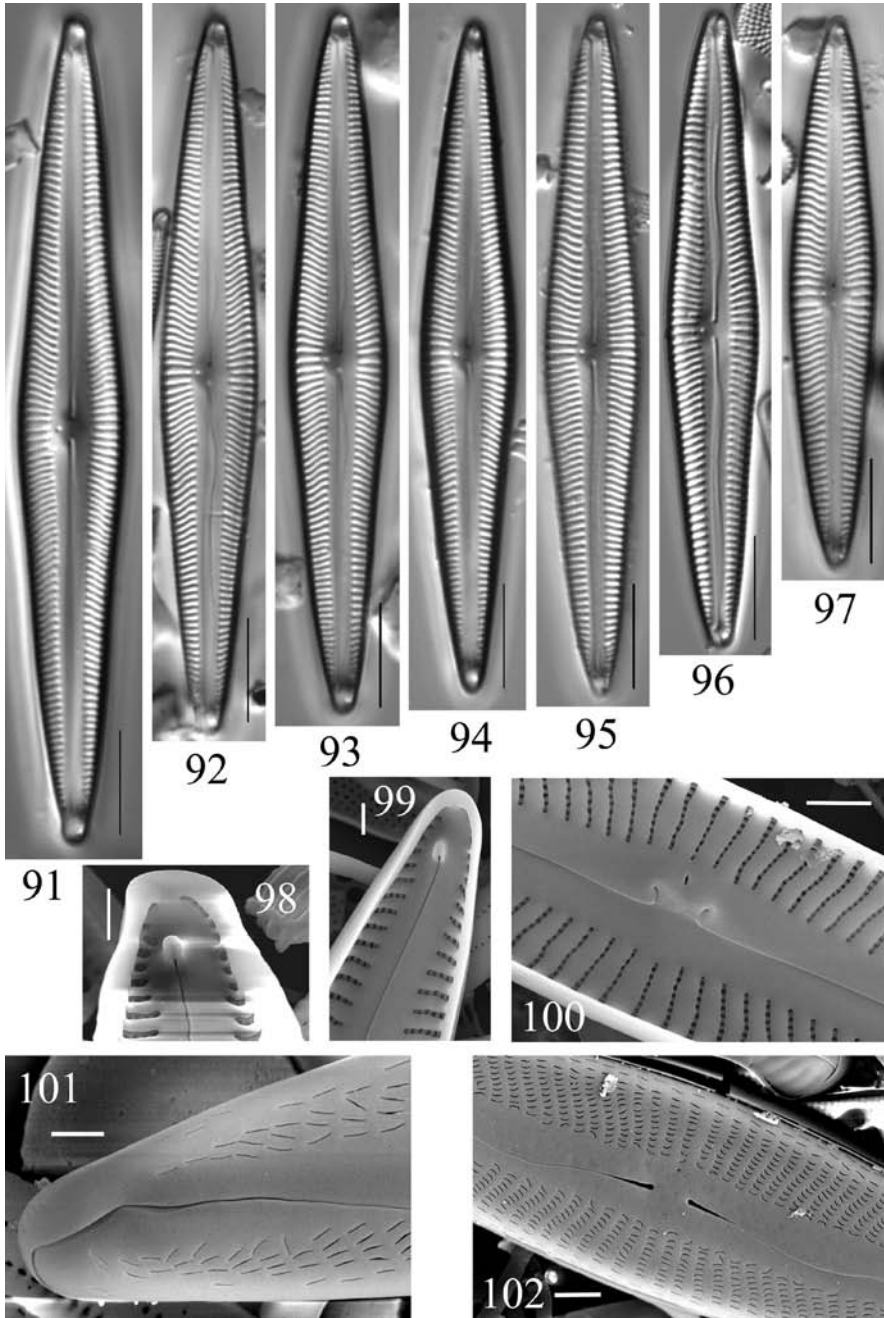
BASIONYM: *Encyonopsis weilandii* Bahls 2013, Northwest Diatoms 5: 32, Figs 175–179.

TYPE LOCALITY: Goat Rocks Pond, Lewis County, Washington, USA.

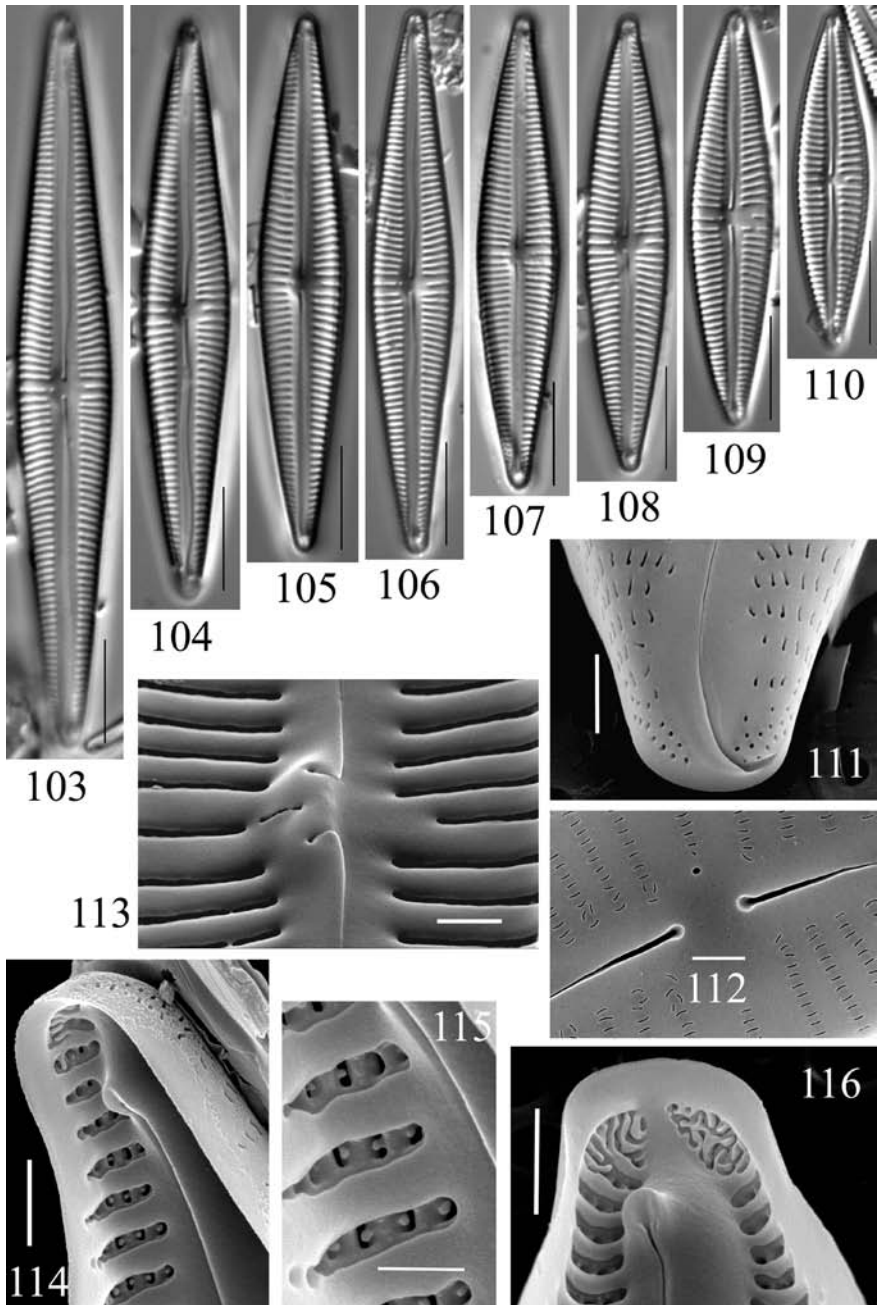
SEM: Transapical striae composed of slit-like or crescent-shaped areolae oriented with their long axes parallel to the apical axis or at an angle to the apical axis (Figs 111, 112). Striae radiate near valve center, becoming parallel, then convergent near the apices (Figs 111, 112). Terminal striae composed of small round areolae at both poles, creating simple pore fields split by the distal raphe fissure (Fig. 111). Internally, striae are represented by narrow alveoli between broad costae (Figs 114, 115). Alveoli



Figs 76–90: *Kurtkrammeria subspicula*. Figs 76–84: LM, various localities. Figs 85–90: SEM, *Nuphar* zone, *Drosera* Pond, Indian Meadows Research Natural Area, Montana (Site 4909). Fig. 87: Arrows point to lateral projections from intercostae into areolae. Scale bars: Figs 76–85, 90 = 10 μ m; Figs 86, 88 = 2 μ m; Figs 87, 89 = 1 μ m.



Figs 91–102: *Kurtkrammeria treinishii*. Figs 91–97: LM, various localities. Figs 98–102: SEM, Crater Lake, Washington (Site 5163). Scale bars: Figs 91–97 = 10 μ m; Figs 98, 99, 101 = 1 μ m; Figs 100, 102 = 2 μ m.



Figs 103–116: *Kurtkammeria weilandii*. Figs 103–110: LM, various localities. Figs 111–116: SEM, small meltwater pond, Anderson Pass, Washington. Fig. 115: Close-up view of lateral papilla-like projections from intercostae into areolae. Scale bars: Figs 103–110 = 10 μ m; Figs 111–114, 116 = 1 μ m; Fig. 115 = 500 nm.

composed of rows of round areolae separated by broad intercostae (Fig. 115). Lateral papilla-like structures project from the intercostae into the internal areolae openings (Fig. 115). At the poles, anastomosing costae and papillae create a convoluted pattern (Figs 114, 116). Internal proximal raphe ends hook strongly to the dorsal side at the central nodule (Fig. 113). Distal raphe fissures end in helictoglossae that are deflected towards the ventral margin (Fig. 116). Stigma present; external stigma opening small and round (Fig. 112); internal stigma opening dagger-shaped (Fig. 113).

The following taxa may be transferred confidently to *Kurtkammeria* based on published LM and SEM images:

***Kurtkammeria amatolensis* (Giffen) comb. nov.**

BASIONYM: *Cymbella amatolensis* Giffen 1966, Beih. Nova Hedwigia 21: 130, Figs 1: 20–23.

SYNONYM: *Encyonopsis amatolensis* (Giffen) Krammer 1997b, p. 137, Figs 183: 7–9.

TYPE LOCALITY: River in the Hog's Back Mountains, Cape Province, South Africa.

LM & SEM: Metzeltin & Lange-Bertalot 2002, Figs 61: 1–5.

***Kurtkammeria frequentis* (Krammer) comb. nov.**

BASIONYM: *Encyonopsis frequentis* Krammer 1997b, Biblioth. Diatomol. 37: 128, Figs 157: 1–11; 158: 1–3; 202: 1–6.

TYPE LOCALITY: Rio Kukenan, Venezuela.

LM & SEM: Vouilloud et al. 2010, Figs 27–33.

***Kurtkammeria kaingensis* (Vyverman) comb. nov.**

BASIONYM: *Cymbella kaingensis* Vyverman 1988, Diatom Res. 3: 259, Figs 1–6, 12–15.

SYNONYM: *Encyonopsis kaingensis* (Vyverman) Krammer 1997b, p. 139, Figs 140: 17–19.

TYPE LOCALITY: Kainga Lake (fenlands), Western Highlands, Papua New Guinea.

LM & SEM: Vyverman 1988, Figs 1–6, 12–15.

***Kurtkammeria mantasoana* (Metzeltin & Krammer) comb. nov.**

BASIONYM: *Encyonopsis mantasoana* Metzeltin & Krammer in Metzeltin & Lange-Bertalot 2002, Iconogr. Diatomol. 11: 24, Figs 63: 1–10.

TYPE LOCALITY: Lake Mantasoana, Madagascar.

LM & SEM: Metzeltin & Lange-Bertalot 2002, Figs 63: 1–10.

***Kurtkammeria recta* (Krammer) comb. nov.**

BASIONYM: *Encyonopsis recta* Krammer 1997b, Biblioth. Diatomol. 37: 132, Figs 165: 12–14; 166: 4–16.

TYPE LOCALITY: Dimade River, South Africa.

LM & SEM: Krammer 1997b, Figs 165: 12–14; 166: 4–16.

Kurtkammeria stoermeri (Lange-Bertalot & Metzeltin) comb. nov.

BASEONYM: *Encyonopsis stoermeri* Lange-Bertalot & Metzeltin 2009, Beih. Nova Hedwigia 135: 139, Figs 16: 1–8.

TYPE LOCALITY: Boquete Laguna in mountain rain forest near Bajo Mono, Panama.

LM & SEM: Lange-Bertalot & Metzeltin 2009, Figs 16: 1–8.

Distribution and ecology of *Kurtkammeria* species in western North America

Six species of *Kurtkammeria* have limited distributions in the study area (Table 2). The seventh confirmed species – *K. aequalis* – is widespread and locally abundant in lakes of the Cascade and Northern Rocky Mountains. All of the water bodies in the study area that support *Kurtkammeria* species are small standing waters at elevations exceeding 1000 m a.s.l. They are low in inorganic nutrients (dystrophic or oligotrophic) with ice-free seasons of only three or four months. Specific conductance and pH data are available for 18 of the water bodies in Table 2. Specific conductance in these 18 waters ranges from 5 to 150 μScm^{-1} with a mean value of 28 μScm^{-1} and a median value of 10 μScm^{-1} . The hydrogen ion concentration (pH) of these waters ranges from 6.00 to 7.60, with a median value of 6.50.

Most records of *Kurtkammeria* from the region consist of one to a few specimens on a strewn mount. The largest population of *Kurtkammeria* species in Table 2 was found in a small meltwater pond on Anderson Pass in Olympic National Park, Washington (Site 4947). *Kurtkammeria weilandii* was the dominant diatom species in the sample from this site. This pond is at 1361 m a.s.l. elevation, measures about 15 m in diameter, and is less than 1 m deep. The water in this pond is essentially snowmelt and rainwater.

Discussion

There is published photographic evidence that *Kurtkammeria* species occur from the Arctic to the Tropics, in both the Old World and New World, and in fossil deposits and recent diatom assemblages. Tynni (1978) reported *Cymbella amphioxys* from Lapland, and Lange-Bertalot and Metzeltin (1996) recorded this species from a Finnish lake just below the Arctic Circle. Mayama and Kobayasi (1990) reported *Cymbella amphioxys* from diatomite collected in southern Sweden. The type locality of this taxon (*Encyonopsis neoamphioxys*) is a lake in the Austrian Alps (Krammer 1997b). Scotland is the type locality of *Cymbella aequalis*, which Tynni (1978) also reported from Finland. Both species occur in western North America (Table 2). In the Sub-Antarctic region, there are unconfirmed reports of *Encyonopsis neoamphioxys* from Argentina and the South Shetland Islands, and of *E. aequalis* from Kerguelen Island (Kellogg & Kellogg 2002).

Elsewhere in the Old World, *Kurtkammeria* species have been reported from Papua New Guinea (*K. kaingensis*; Vyvermann 1988, 1991), South Africa (*K. amatolensis*, Giffen 1966, Metzeltin & Lange-Bertalot 2002; *K. recta*, Krammer 1997b), and Madagascar (*K. mantasoana*; Metzeltin & Lange-Bertalot 2002). *Kurtkammeria*

Table 2. Distribution and relative abundance of uncommon *Kurtkammeria* species in western North America. Not included is *Kurtkammeria aequalis*, which is widespread and locally abundant in lakes of the Cascade and Northern Rocky Mountains. See Table 1 for site names, locations, and slide numbers.

MDC Site No.	<i>K. lacusglacialis</i>	<i>K. neoamphioxys</i>	<i>K. stodderi</i>	<i>K. subspicula</i>	<i>K. treinishii</i>	<i>K. weilandii</i>
1109	rare					occasional
1110						occasional
1141						occasional
1147						occasional
1154	occasional					
1729				rare		
1731				rare		
1741		rare				
1769		rare			rare	
1775					rare	
1792					common	
1794	occasional				occasional	
1795	rare					
1796	occasional					
1919	occasional				occasional	rare
4080					occasional	
4081				rare		
4525				rare		
4526		occasional				
4569	occasional					occasional
4909		occasional		common		
4913		rare		rare		
4947						dominant
4948						frequent
4957			rare			
4959					rare	
4960					occasional	
4962						rare
4963					occasional	
4993		rare				
4996						frequent
4997	rare				occasional	rare
5015						occasional
5016						occasional
5020	rare				rare	
5042	common	common				rare
5043	occasional	rare				rare
5044	occasional	rare			occasional	
5061			rare			
5064						occasional

Table 2 continued.

MDC Site No.	<i>K. lacusglacialis</i>	<i>K. neoamphioxys</i>	<i>K. stodderi</i>	<i>K. subspicula</i>	<i>K. treinishii</i>	<i>K. weilandii</i>
5067						rare
5070						occasional
5085						occasional
5092					rare	
5093		rare				
5105	common					
5110	frequent					
5120						frequent
5138					occasional	
5163					common	
5175						common
5189						common
5190	rare	rare	occasional			
5197						occasional
5198						occasional
5201		rare				
5206	rare	rare				
5207					occasional	
5212	rare				occasional	occasional
6284						frequent
6287						abundant
6292						occasional
6302	rare				rare	
6319		common				
6330					frequent	
Total Re- cords	18	14	3	6	19	28

recta has also been reported from the Andes Mountains of Columbia and Venezuela (Krammer 1997b, Rumrich et al. 2000), but the other three taxa appear to be Old World endemics.

Kurtkammeria lacusglacialis, *K. treinishii*, and *K. weilandii* appear to be endemic to western North America. A fossil deposit at Bemis Lake in the White Mountains of New Hampshire (northeastern USA) serves as the type habitat for both *Encyonopsis stodderi* and *E. subspicula* (Krammer 1997b). Besides the three recent records of *E. stodderi* from western North America (Table 2), one of them confirmed as a living population, this species has also been reported from a diatomite deposit in Florida (Metzeltin & Lange-Bertalot 2007). In addition to fossil deposits at Bemis Lake and Cherryfield in northeastern USA, *E. subspicula* also occurs as a member of the recent

flora in western North America (Table 2) and, surprisingly, in the Okavango Delta of Botswana (Krammer 1997b).

Kurtkammeria frequentis is known from various black water rivers and laguna in the Amazon region of South America (Krammer 1997b, Metzeltin & Lange-Bertalot 1998, Vouilloud et al. 2010) and as a fossil in Ehrenberg material from Cayenne, Guyana, where it was reported as *Cymbella aequalis* (Reichardt 1995). *Kurtkammeria stoermeri* is known only from the type locality, a dystrophic lake in the mountain rain forest of Panama (Lange-Bertalot & Metzeltin 2009).

Encyonopsis spicula (Hustedt) Krammer, a tropical species from Sumatra (Krammer 1997b), has a dorsal stigma and the convergent terminal striae of *Kurtkammeria*, but the areolae and internal proximal raphe ends need to be examined under SEM before this species can be transferred. Other species with convergent terminal striae and thereby candidates for transfer to *Kurtkammeria* are: *Encyonopsis aequaliformis* Bahls, *E. braunii* (Hustedt) Krammer, *E. floridana* Krammer, *E. frequentiformis* Metzeltin & Krammer, *E. krasskei* Krammer, *E. kurtii* Metzeltin, *E. reichardtii* Krammer, *E. speciosa* Lange-Bertalot, Krammer & Rumrich, *E. spiculiformis* Krammer, and *E. usteri* (Krasske) Krammer.

Kurtkammeria species are reported infrequently, primarily from mountainous regions, and consistently from oligotrophic or dystrophic waters with circumneutral pH and very low dissolved solids. Vouilloud et al. (2010) report *K. frequentis* from rivers with pH values ranging from 5.1 to 6.3, conductivity of 10–16 μScm^{-1} , and low chlorophyll *a* content. These rivers are in a remote, undeveloped, and seldom visited area of the Amazon Basin. As a rule, habitats that support extant populations of *Kurtkammeria* species represent minimally-impaired reference conditions for the regions in which they occur.

Species of *Encyonopsis* are also found in similar habitats, but as a whole this genus has a much broader ecological amplitude (Krammer 1997b, Van de Vijver et al. 2009, 2012; Bahls 2013). Perhaps the most frequently reported species of *Encyonopsis* is *E. microcephala*. Although there have been problems with the identification of this species and it is often confused with similar taxa, it is generally regarded as a cosmopolitan alkaliphil that can tolerate moderate concentrations of salt (Patrick & Reimer 1975, Krammer & Lange-Bertalot 1986, Krammer 1997b). Van Dam et al. (1994) classify *E. microcephala* sensu lato as alkaliphilous and meso-eutrathentic, and report it from fresh to brackish waters.

Species of *Kurtkammeria* have a unique set of features that distinguishes the genus from *Cymbella*, *Encyonema*, *Encyonopsis*, and *Gomphonema*. The plastids, raphe system, and striae structure of *Kurtkammeria* species are most like those of *Encyonema*. But *Encyonema* species have distinct dorsiventrality and they are not known to produce apical pore fields (APFs) or stigmata (Round et al. 1990). Species of *Encyonopsis* sensu stricto have different stria and raphe structure and do not have APFs. *Cymbella* species have APFs, but they have a different raphe system and stigmata on the ventral (not dorsal) side of the central nodule (Round et al. 1990). Some species of *Kurtkammeria* with a stigma and more widely spaced central striae (e.g., *K. frequentis*, *K. weilandii*) bear a superficial resemblance to species of *Gomphonema* that have a

slightly dorsiventral aspect (e.g., *G. hebridense* Gregory, Lange-Bertalot & Metzeltin 1996, p. 246, Figs 18–25). But in *Kurtkammeria* species the raphe branches are of equal length and the valves are symmetric with respect to the transapical axis. When *Kurtkammeria* species produce APFs, they are at both poles, not just on one as in *Gomphonema*.

The nature, function, and phylogenetic significance of APFs in *Kurtkammeria* species are unknown. *Kurtkammeria frequentis* (Vouilloud et al. 2010, Figs 30, 33) and *K. stodderi* (Fig. 75) exhibit the most highly developed APFs among *Kurtkammeria* species. Since motility has been observed in cells of *K. stodderi*, these APFs apparently are not involved in producing stalks but they may function somehow in motility. Other *Kurtkammeria* species with less well developed APFs (*K. aequalis*, *K. lacusglacialis*, and *K. weilandii*) also have internal anastomosing costae at both poles (Figs 36, 47, 116). Externally and internally, these APFs are quite unlike those in *Cymbella* and *Gomphonema*. It is unclear whether they represent primitive, simple or pseudo apical pore fields. It is also unclear whether the small round terminal foramina in *Kurtkammeria* species are modified areolae, pores, poroids, or porelli.

Kurtkammeria is a compact and morphologically distinct genus that is further defined by its ecologic preferences and geographic distribution. Where they occur, species of *Kurtkammeria* may serve as indicators of minimally impaired conditions and may be used to monitor the environmental impact of human activities. There is considerable character variation within the genus, including variable development of APFs and stigmata, different levels of anastomosis of terminal internal costae, and a spectrum of internal areolar structure. Documentation of these structures may help to refine our understanding of phylogenetic relationships within the Cymbellales, a region of the diatom phylogeny that is garnering much recent attention and where several of the newly established groups that share characters with *Kurtkammeria*, such as *Encyonopsis*, are severely under-sampled (Nakov et al. 2014).

Acknowledgements

The diatom work of Kurt Krammer has informed and inspired the author for many years. This paper would not have been possible without the many samples collected by volunteers: Bill Agnew, Eric Bindseil, Beverly Boynton, Sage Clegg, Ryan Davis, Ellie Harmon, Barb Johnston, John Pierce, Leanna Taylor, Craig Weiland, Lisa White, Morris Williams, and students of Marin Academy, California. Thanks to the staff of Adventurers and Scientists for Conservation for coordinating volunteer efforts. Mark Edlund, Ingrid Jüttner, and Bart Van de Vijver provided several helpful suggestions for improving the manuscript. Jim Driver assisted with the capture of SEM images. Electron microscopy services and resources were provided by the Electron Microscopy Facility, Division of Biological Sciences, University of Montana, Missoula. The EM Facility is supported, in part, by grant #RR-16455-04 from the National Center for Research Resources (Biomedical Research Infrastructure Network program), National Institutes of Health.

References

APHA 1992: Standard Methods for the Examination of Water and Wastewater, 18th ed. – American Public Health Association, Washington, D.C.

- BAHLS, L.L. 2013: Northwest Diatoms, Volume 5. *Encyonopsis* from western North America: 31 Species from Alberta, Idaho, Montana, Oregon, South Dakota, and Washington, including 17 Species Described as New. – The Montana Diatom Collection, Helena.
- BAHLS, L.L. 2014: New diatoms from the American West – A tribute to citizen science. – Proc. Acad. Nat. Sci. Philadelphia **163**: 61–84.
- CLEVE, P.T. 1881: On some new and little known diatoms. – Kongl. Svenska Vetensk.-Akad. Handl. **18**: 1–28.
- CLEVE, P.T. 1894: Synopsis of the naviculoid diatoms. Part I. – Kongl. Svenska Vetensk.-Akad. Handl. **26**: 1–194.
- GIFFEN, M.H. 1966: Contributions to the diatom flora of South Africa. II. Diatoms from the Hog's Back region of the Amatola Mountains, Eastern Cape Province. – Beih. Nova Hedwigia **21**: 123–150.
- GREVILLE, R.K. 1833: Diatomaceae. – In: SMITH, J.E. & W.J. HOOKER (eds.): The English Flora, pp. 1824–1836, **5**: 401–415. London.
- GREVILLE, R.K. 1855: Report on a collection of diatomaceae made in the district of Braemar by Prof. Balfour and G. Lawson. – Ann. Mag. Nat. Hist. **15**: 252–261.
- JÜTTNER, I., K. KRAMMER, B. VAN DE VIJVER, A. TUJI, B. SIMKHADA, S. GURUNG, S. SHARMA et al. 2010: *Oricymba* (Cymbellales, Bacillariophyceae), a new cymbelloid genus and three new species from the Nepalese Himalaya. – Phycologia **49**: 407–423.
- KELLOGG, T.B. & D.E. KELLOGG 2002: Non-marine and Littoral Diatoms from Antarctic and Subantarctic Regions – Distribution and Updated Taxonomy. – In: WITKOWSKI, A. (ed.): Diatom Monogr., Vol. **1**, pp. 1–795. A.R.G. Gantner Verlag K.G., Vaduz.
- KRAMMER, K. 1997a: Die cymbelloiden Diatomeen: Eine Monographie der weltweit bekannten Taxa. Teil 1. Allgemeines und *Encyonema* Part. – In: LANGE-BERTALOT, H. & P. KOCIOLEK (eds.): Biblioth. Diatomol., Vol. **36**, pp. 1–382. J. Cramer, Berlin.
- KRAMMER, K. 1997b: Die cymbelloiden Diatomeen: Eine Monographie der weltweit bekannten Taxa. Teil 2. *Encyonema* part., *Encyonopsis* and *Cymbellopsis*. – In: LANGE-BERTALOT, H. & P. KOCIOLEK (eds.): Biblioth. Diatomol., Vol. **37**, pp. 1–469. J. Cramer, Berlin.
- KRAMMER, K. 2003: *Cymbopleura*, *Delicata*, *Navicymbula*, *Gomphocymbellopsis*, *Afrocymbella*. – In: LANGE-BERTALOT, H. (ed.): Diatoms of Europe, Diatoms of the European Inland Waters and Comparable Habitats, Vol. **4**, pp. 1–530. A.R.G. Gantner Verlag K.G., Ruggell.
- KRAMMER, K. & H. LANGE-BERTALOT 1986: Bacillariophyceae. 1. Teil: Naviculaceae. – In: Ettl, H., J. Gerloff, H. Heynig & D. Mollenhauer (eds.): Süßwasserflora von Mitteleuropa, pp. 1–876. Gustav Fischer Verlag, Stuttgart.
- KÜTZING, F.T. 1844: Die kieselalgen Bacillarien oder Diatomeen. – Nordhausen.
- LANGE-BERTALOT, H. & D. METZELTIN 1996: Indicators of Oligotrophy, 800 Taxa Representative of Three Ecologically Distinct Lake Types: Carbonate Buffered, Oligodystrophic, Weakly Buffered Soft Water. – In: LANGE-BERTALOT, H. (ed.): Iconogr. Diatomol., Vol. **2**, pp. 1–390. Koeltz Scientific Books, Königstein.
- LANGE-BERTALOT, H. & D. METZELTIN 2009: A dystrophic mountain lake in Panama – hot spot of new and rare Neotropical diatoms. – Beih. Nova Hedwigia **135**: 137–166.
- MAYAMA, S. & H. KOBAYASI 1990: Studies on *Eunotia* species in the classical "Degernäs materials" housed in the Swedish Museum of Natural History. – Diatom Res. **5**: 351–366.
- METZELTIN, D. & H. LANGE-BERTALOT 1998: Tropical Diatoms of South America I. – In: LANGE-BERTALOT, H. (ed.): Iconogr. Diatomol., Vol. **5**, pp. 1–695. Koeltz Scientific Books, Königstein.

- METZELTIN, D. & H. LANGE-BERTALOT 2002: Diatoms from the "Island Continent", Madagascar. – In: LANGE-BERTALOT, H. (ed.): *Iconogr. Diatomol.*, Vol. **11**, pp. 1–286. Koeltz Scientific Books, Königstein.
- METZELTIN, D. & H. LANGE-BERTALOT 2007: Tropical Diatoms of South America II. – In: LANGE-BERTALOT, H. (ed.): *Iconogr. Diatomol.*, Vol. **18**, pp. 1–877. A.R.G. Gantner Verlag K.G., Ruggell.
- NAKOV, T., E. RUCK, Y. GALACHYANTS, S. SPAULDING & E. THERIOT 2014: Molecular phylogeny of the Cymbellales (Bacillariophyceae) with a comparison of models for accommodating rate variation across sites. – *Phycologia* **53**: 359–373.
- PATRICK, R. & C.W. REIMER. 1975: The Diatoms of the United States Exclusive of Alaska and Hawaii. Volume 2, Part 1: Entomoneidaceae, Cymbellaceae, Gomphonemaceae, Epithemaceae. – *Monogr. Acad. Nat. Sci. Philadelphia* **13**: 1–213. The Academy of Natural Sciences, Philadelphia.
- RABENHORST, L. 1853: Die Süßwasser-Diatomaceen (Bacillarien) für Freunde der Mikroskopie, pp. 1–72. Leipzig.
- REICHARDT, E. 1995: Die Diatomeen (Bacillariophyceae) in Ehrenbergs Material von Cayenne, Guyana Gallica (1843). – In: LANGE-BERTALOT, H. (ed.): *Iconogr. Diatomol.*, Vol. **1**, pp. 1–99. Koeltz Scientific Books, Königstein.
- ROUND, F.E., R.M. CRAWFORD & D.G. MANN 1990: The Diatoms: Biology & Morphology of the Genera. – Cambridge University Press, Cambridge.
- RUMRICH, U., H. LANGE-BERTALOT & M. RUMRICH 2000: Diatoms of the Andes from Venezuela to Patagonia/Tierra del Fuego. – In: LANGE-BERTALOT, H. (ed.): *Iconogr. Diatomol.*, Vol. **9**, pp. 1–649. A.R.G. Gantner Verlag K.G., Ruggell.
- SCHMIDT, A. 1874–1959: Atlas der Diatomaceen-Kunde, von Adolf Schmidt, continued by Martin Schmidt, Friedrich Fricke, Heinrich Heiden, Otto Muller, Friedrich Hustedt. Reprint 1984. – Koeltz Scientific Books, Königstein.
- SPAULDING, S.A., D. LUBINSKI & M. POTAPOVA 2010: Diatoms of the United States. – University of Colorado, Boulder. Available at: <http://westerndiatoms.colorado.edu>
- TYNNI, R. 1978: Über Finnlands Rezente und Subfossile Diatomeen, X. – *Geological Survey of Finland, Bulletin* **296**, pp. 1–55, Helsinki.
- VAN DAM, H., A. MERTENS & J. SINKELDAM 1994: A coded checklist and ecological indicator values of freshwater diatoms from the Netherlands. – *Netherlands J. Aquat. Ecol.* **28**: 117–133.
- VAN DE VIJVER, B., H. LANGE-BERTALOT & P. COMPÈRE 2009: Two new freshwater diatom species (Bacillariophyceae) from a small pool in the National Botanic Garden of Belgium. – *Belg. J. Bot.* **142**: 194–203.
- VAN DE VIJVER, B., G.L. VERWEIJ, J. VAN DER WAL & A. MERTENS 2012: *Encyonopsis neerlandica*, a new freshwater diatom species (Bacillariophyta) from moorland pools in The Netherlands. – *Phytotaxa* **66**: 43–48.
- VOUILLOUD, A.A., S.E. SALA, M.N. AVELLANEDA & S.R. DUQUE 2010: Diatoms from the Colombian and Peruvian Amazon: the Genera *Encyonema*, *Encyonopsis* and *Gomphonema* (Cymbellales: Bacillariophyceae). – *Rev. Biol. Trop.* **58**: 45–62.
- VYVERMAN, W. 1988: Three new diatom taxa from the Central Highlands of Papua New Guinea. – *Diatom Res.* **3**: 259–264.
- VYVERMAN, W. 1991: Diatoms from Papua New Guinea. – In: LANGE-BERTALOT, H. (ed.): *Biblioth. Diatomol.*, Vol. **22**, pp. 1–224. J. Cramer, Berlin.