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Encyonema droseraphilum sp. nov. (Bacillariophyta) and other rare diatoms from undisturbed floating-mat fens in the northern Rocky Mountains, USA

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Abstract

Relict assemblages of arctic, sub-arctic, and boreal diatoms were found intact in two undisturbed floating-mat fens at 47° north latitude and 1,830 m elevation in the Rocky Mountains of western Montana, USA. The fens support *Encyonema droseraphilum* sp. nov. and several rare northern/alpine diatom species—including eleven apparent first records for the contiguous United States—and three species of vascular plants that are imperiled in Montana. For many of the diatoms and one of the vascular plants, the fens are at the southern limit of their known distributions in North America. Twenty-seven of the 49 diatom taxa in the fens are considered at risk or declining in Germany, and similar ratings appear to be appropriate for these taxa in Montana, especially in light of global warming and human destruction of wetlands. A nearby wetland that has been disturbed by dam-building activities of beaver (*Castor canadensis*), but not by human landscape alterations, produced a diatom assemblage that contained three times more taxa than the fens but was dominated by common species, primarily *Staurosirella pinnata*. Our findings illustrate the effects of natural, intermediate disturbance on diatom species composition and underscore the importance of protecting undisturbed aquatic systems for the purpose of conserving rare species and for monitoring environmental change.

Introduction

Peatlands occur mostly in northern latitudes where cool, humid climates allow for precipitation to exceed evapotranspiration. Peatlands are best developed on low elevation, nearly level landforms having some degree of impeded drainage. The most extensive and continuous tracts of peatland are found in northern North America—notably in Canada and Alaska—and in northern Europe and Asia. Peatlands in the contiguous USA tend to be smaller and more isolated, and most are scattered among the northern tier of states and southward along major cordillera—the Appalachian and Rocky Mountains—where moderate elevation gain may compensate thermally for more southerly latitudes (Rydin & Jelgum 2006).

Peatlands are characterized by extreme environmental conditions not found in other wetland ecosystems. Cold, anaerobic, and nutrient-poor conditions limit decay of organic matter. Because the rate of organic matter accumulation exceeds the rate of decomposition, peatlands are autogenic or “self-creating” habitats. The resulting organic substrates support a number of uncommon plant communities. Due to their great masses of water-holding organic matter, peatlands are extremely stable at intermediate time scales and may persist for centuries. In the United States, the combination of habitat rarity, habitat stability, and extreme habitat conditions explain the distinctiveness of peatland vascular plant floras, as well as the high concentrations of rare species that are restricted to peatland environments (Bedford & Godwin 2003, Chadde *et al.* 1998, Rydin & Jelgum 2006). Diatom floristic studies of peatlands in the USA have typically recorded new and rare species (e.g., Reimer 1961, Stoermer 1963).

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In the Northern Rocky Mountains, peatlands are uncommon and occur mainly at lower elevations. In this region, they are represented by fens, with their water sources consisting of both groundwater and precipitation. They are even rarer southward in the Rockies, where intense solar radiation may be unfavorable for peatland plants (Larsen 1982). Intense solar radiation, summer dry periods, and steep terrain may inhibit peat development at higher elevations in the Northern Rockies (Chadde *et al.* 1998). Several plant species found in peatlands range southward along the Rocky Mountains and reach their southern limit in Montana. Twenty-one species of vascular plants from peatlands in the Northern Rockies have been designated as species of special conservation concern by the Montana Natural Heritage Program (http://mtnhp.org/), and 15 of these have been designated as sensitive species by the US Forest Service (Chadde *et al.* 1998). These species, although uncommon in the Northern Rockies, are generally secure in other parts of their ranges. All of these rare Montana peatland species are boreal or north-temperate in distribution, and disjunct or peripheral in Montana from more continuous ranges to the north (Chadde *et al.* 1998).

Floating-mat fens are a classic feature of basin or lake-fill peatlands. Roots and rhizomes of living plants and accumulated leaf litter intertwine to form a mat that develops horizontally across the water surface and floats or overlies very unstable muck below. Floating mats are ecologically stable communities because of their ability to adjust to fluctuating water levels. Floating mats have been reported to move vertically by as much as 0.75 m annually. Plant roots remain in constant contact with water and the plants avoid the inundation and drying that affect fixed or anchored mats (Chadde *et al.* 1998).

Materials and methods

Site description and sample collection

Indian Meadows Research Natural Area (IMRNA) is located on the Helena National Forest in western Montana about 90 km northwest of Helena, Montana (Fig. 1). IMRNA lies at the extreme southern end of the Canadian Rockies Ecoregion, a largely pristine, highly glaciated subregion of the Northern Rockies (USEPA 2000). IMRNA occupies a glaciated bench bordered by low hills at the head of Indian Meadows Creek, a first order tributary of the Blackfoot River. Elevations within the IMRNA range from 1692–2034 m. The area includes a diverse mix of vegetation types ranging from montane and lower subalpine conifer forests to aquatic features such as ponds, fens, and wet meadows. At the end of the Pleistocene much of the area was left covered by mixed glacial deposits. These deposits are underlain by Tertiary age rocks, which consist of volcanic tuffs near the south boundary (fen 4525) and unconsolidated sandstones and siltstones, composed of quartzites and argillites, near the north boundary (beaver pond 1241, fen 4526). Except for general atmospheric and climatic influences, the IMRNA is undisturbed by human landscape alterations. It is located at the southern limit of the Bob Marshall Wilderness Complex and part of the natural area lies within the Scapegoat Wilderness (USDA 1997).

Two floating-mat fens, one with a central pool of open water (Fig. 2), are the most distinguishing features of IMRNA. These fens support three species of vascular plants that are imperiled in Montana: *Drosera anglica* Huds. (English or great sundew), *Drosera linearis* Goldie (slenderleaf or linear-leaf sundew), and *Schoenoplectus subterminalis* (Torr.) Soják (swaying or water bulrush, fen 4525 only) (http://mtnhp.org/). The rarest of these is *Drosera linearis*: the fens at IMRNA support two of only four Montana populations of this species and the fens are at the southern limit of the species' known distribution in North America.

We collected a composite sample of surface material from near the center of each fen and from an abandoned beaver pond nearby (Fig. 1, insert). Samples from the fens were composed of material squeezed from peat, *Sphagnum*, and other vegetation, and of material in the interstitial water that surfaced in depressions created by footfalls on the floating mats. The sample from the beaver pond consisted of surface sediment, material squeezed from plants, and scrapings from rocks and logs. Samples were preserved with Lugols' iodine solution (IKI) before transporting them to the lab. Specific conductance and pH were measured in the field with a Hanna Instruments waterproof meter, model 98129, or a Horiba U-10 water quality checker.

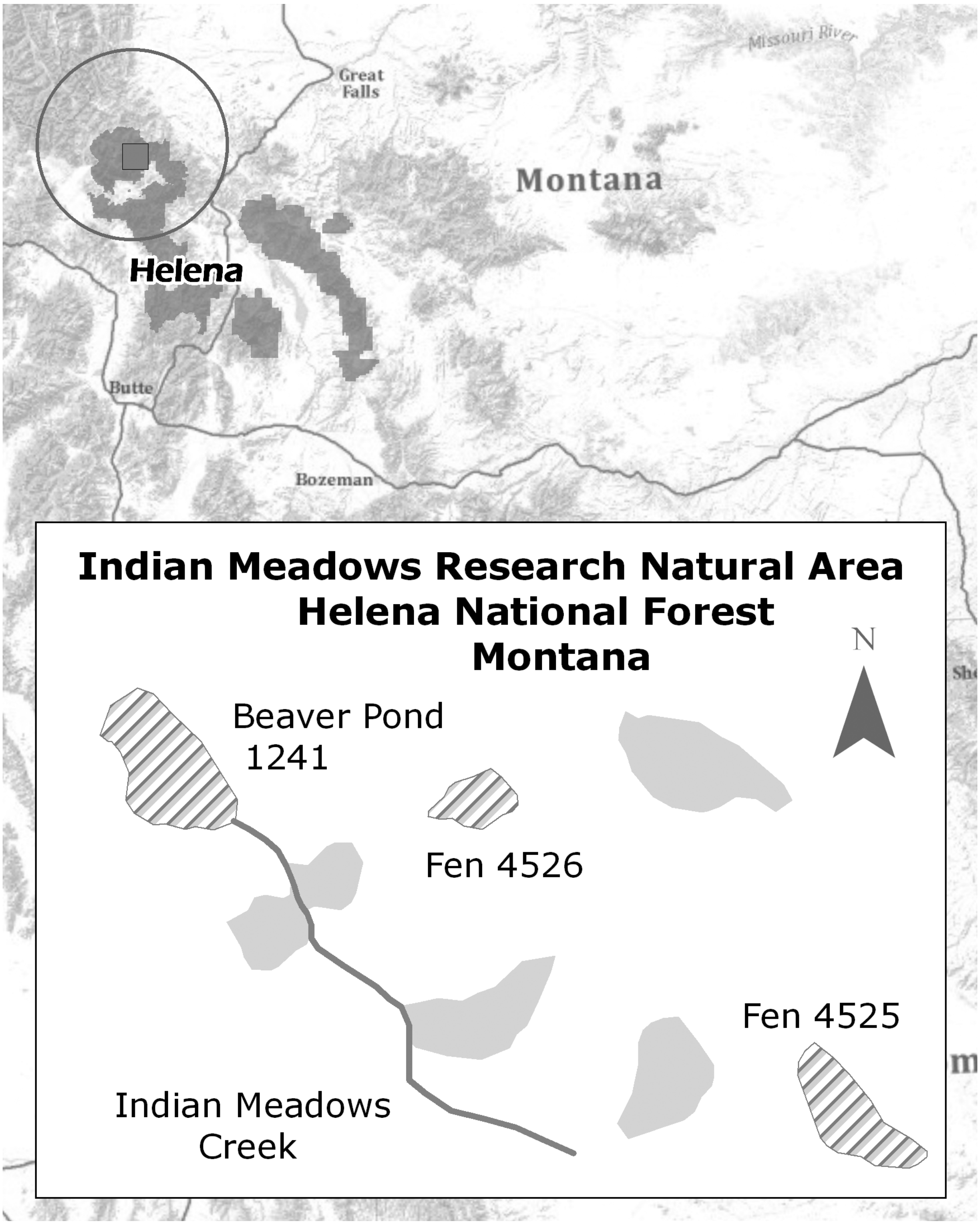


FIGURE 1: Location of Indian Meadows Research Natural Area in western Montana, USA. Inset: Site map showing relative positions of abandoned beaver pond (site 1241), floating-mat fen with central pool (site 4525), and floating-mat fen without central pool (site 4526).

Sample preparation

Samples were treated with concentrated sulfuric acid, potassium dichromate, and hydrogen peroxide to remove organic matter. After repeated dilutions of the treated material with distilled water, aliquots were dried on cover glasses and permanent mounts were prepared in Naphrax. A proportional count of 800 valves was conducted on one slide from each site at 1000X. Each slide was then scanned and additional taxa were recorded until the time required to find another taxon exceeded 10 minutes. In this way a comprehensive list of diatoms was constructed for each site. For counting, scanning, and LM photographs, we used a Leica DM LB2 research microscope with DIC optics and a Spot Insight Model 14.0 monochrome digital camera. SEM images were taken with a Hitachi S-4700 Type II cold field emission SEM at the Electron Microscopy Facility in the Division of Biological Sciences at the University of Montana. Samples were filtered, air-dried, and mounted on aluminum stubs, then sputter coated with gold and palladium using a Pelco Model 3 Sputter Coater.

Slides containing holotype specimens of the new taxon are deposited in the Montana Diatom Collection (MDC) at the University of Montana Herbarium (MONTU) in Missoula. Duplicate slides containing isotype specimens have been deposited in the MDC in Helena and in the Diatom Herbarium at the Academy of Natural Sciences of Philadelphia (ANSP).

TABLE 1: Some features of wetlands sampled for diatoms at Indian Meadows Research Natural Area, Helena National Forest, Montana, USA.

Site	Site Description	Latitude and Longitude	Plant Community Type	pH (SU)	SC (µS/cm)
1241	Abandoned beaver pond	47° 06’ 25“ N 112° 36’ 45” W	*Calamagrostis canadensis*/ *Carex utriculata*/*Salix* spp.	6.9	169
4525	Floating-mat fen with central pool	47° 06’ 01” N 112° 35’ 47” W	*Carex* spp./*Drosera* spp./ *Menyanthes trifoliata*/*Sphagnum* spp.	8.5	19
4526	Floating-mat fen without central pool	47° 06’ 19” N 112° 36’ 22” W	*Carex* spp./*Drosera* spp./ Menyanthes trifoliata	6.8	257

FIGURE 2: Floating-mat fen with central pool (site 4525). Site 4526 is similar but lacks a central pool of open water. Photo by Loren Bahls.

Results

Diatom assemblage composition

The abandoned beaver pond supported 126 diatom taxa, but over half of the valves (51%) belonged to *Staurosirella pinnata* (Ehrenberg) Williams & Round (1987: 274) (Table 2). Other taxa from the beaver pond that contributed more than 2% of the valves were all common, widespread forms: *Pseudostaurosira brevistriata* (Grunow) Williams & Round (1987: 276) (3.5%), *Staurosira venter* (Ehrenberg) Grunow (1882: 139) (3.2%), *Navicula cryptocephala* Kützing (1844: 95) (2.7%), *Achnanthidium minutissimum* (Kützing) Czarnecki (1994: 157) (2.6%), *Cocconeis placentula* Ehrenberg (1838: 194) (2.6%), *Aulacoseira italica* (Ehrenberg) Simonsen (1979: 60) (2.4%), and *Staurosira construens* var. *pumila* (Grunow) Kingston (2000: 409) (2.4%).

Contrasted to the high species richness of the beaver pond assemblage, the fens supported only 49 taxa (36 and 35 each) (Table 2). The fens also supported much more distinctive diatom assemblages composed largely of uncommon taxa. One taxon from the fens could not be identified using available floras and monographs. Ten taxa from the fens are not listed by Bahls (2009) in a checklist of diatoms from the northwestern United States and eleven are not listed by Kociolek (2005) in a checklist of diatoms from the contiguous United States (Table 2). We also show the conservation status for these fen species in Germany, where 27 of the 49 taxa are considered at risk or declining (Table 2). Below we discuss our rationale for consulting the German list as a surrogate list of imperiled diatoms for Montana.

New species description

Division **Bacillariophyta**
Class **Bacillariophyceae**
Subclass **Bacillariophycidae** D.G. Mann in Round *et al.* 1990
Order **Cymbellales** D.G. Mann in Round *et a*l. 1990
Family **Cymbellaceae** Greville 1833
Genus ***Encyonema*** Kützing 1833

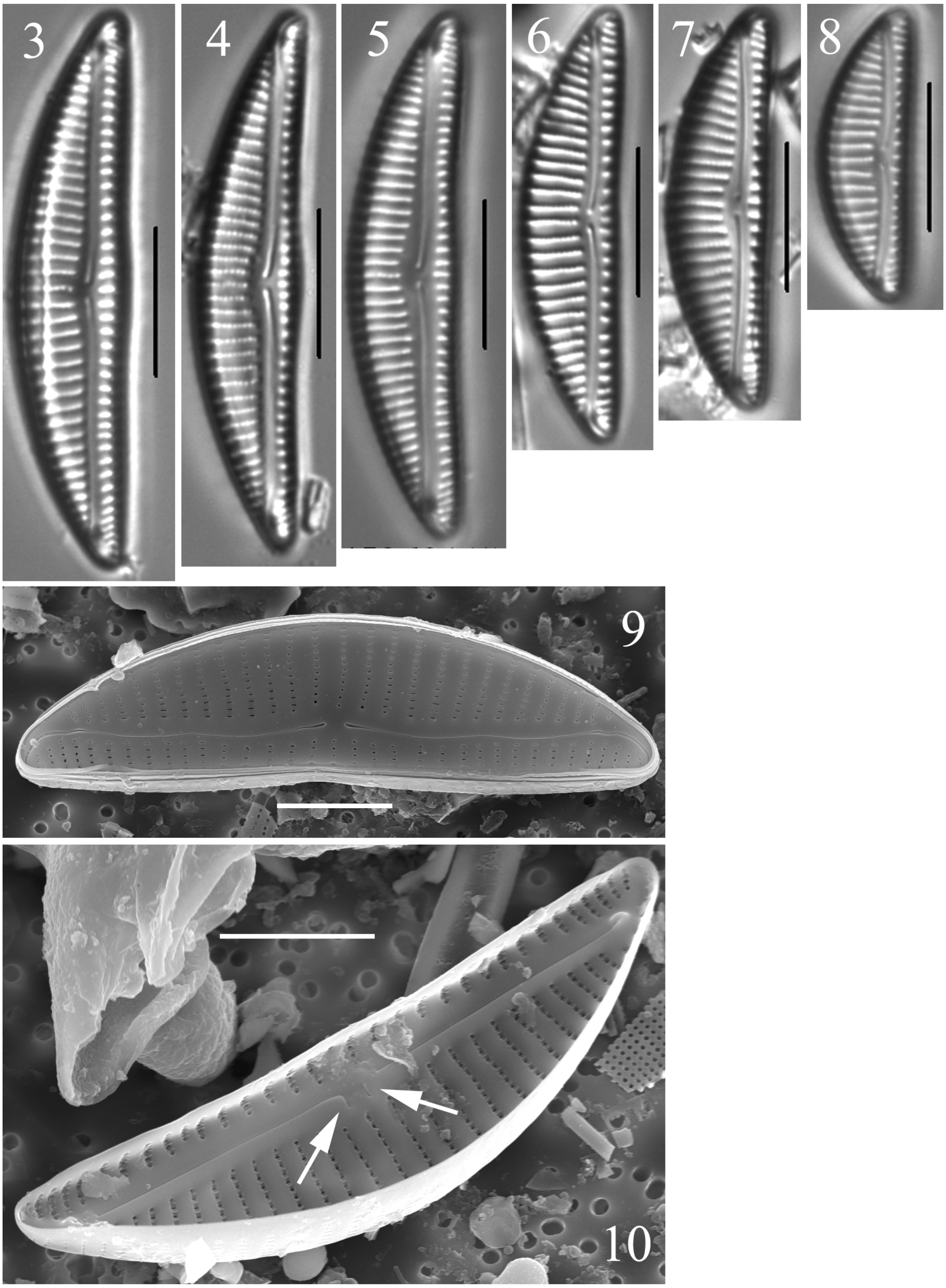
Encyonema droseraphilum Bahls, *sp. nov.* (Figs 3–10)

Valvae 20–40 µm longae, 5–9 µm latae, ratio latitudinis et longitudinis 2.8–5.0. Margo ventralis leviter tumidus in centro ad planus vel leviter concavus in speciminibus minoribus. Striae dorsalis 8–11 in 10 µm. Striae ventralis curtae, 11–13 in 10 µm, 28–32 areolae in 10 µm. Extrema proximalia fissurarum externarum rhaphis leviter expansi dorsaliter declinati, extrema terminalia versus margines ventrales declinati. Extrema proximalia fissurarum internarum rhaphis ventraliter declinati ad anguli 90º, non recurvati atque E. silesiacum var. silesiacum. Extrema terminalia fissurarum internarum rhaphis terminans in linguliformibus helictoglossis.

Valves 20–40 µm long, 5–9 µm wide. Length to breadth ratio 2.8–5.0. Ventral margin slightly tumid in center to flat or slightly concave in smaller specimens. Dorsal striae 8–11 in 10 µm. Ventral striae short, 11–13 in 10 µm. Areolae number 28–32 in 10 µm. Proximal ends of external raphe fissures are slightly inflated, deflected dorsally; distal ends are curved toward ventral margins (Fig. 9). Proximal ends of internal raphe fissures (Fig. 10, arrows) are bent dorsally at right angles, not hooked as in *E. silesiacum* (p. 184, pl. 2, fig. 7, Krammer 1997a). Distal ends of internal raphe fissures terminate in tongue-shaped helictoglossae (Fig. 10).

Type:— USA. Montana: Helena National Forest, Indian Meadows Research Natural Area, Fen 4526, 47º 06’ 19” N, 112º 36’ 22” W, collected 03 September 2009, *Sample No. 452601* collected by L. Bahls from sedge peat and interstitial water; taxon is abundant and accounts for approximately 18% of frustules in sample (Circled specimen (Fig. 4) on slide marked *MDC 452601(1)* (MONTU!) **holotype, designated here**; circled specimens on slides marked *MDC 452601(2)* (Helena!) and *GC64892* (ANSP!), **isotypes, designated here**).

Similar taxa:—This taxon is distinguished from *Encyonema silesiacum* (Bleisch in Rabenhorst) D.G. Mann (1990: 667) by its longer length-to-breadth ratio, more widely spaced dorsal striae, shorter ventral striae, and shape of the internal proximal raphe ends. Valve ends are directed ventrally, not laterally as in *E. silesiacum* var. *elegans* Krammer. This appears to be the same taxon as the *Encyonema* sp. from Kitzbühel, Schwarzsee, Österreich reported by Krammer (1997a, pl. 8, figs 6, 7).



FIGURES 3–10: *Encyonema droseraphilum sp. nov.* Figs 3–8: LM, size diminution series from the type locality. Fig. 4: Holotype specimen. Fig. 9: SEM, external valve view. Fig. 10: SEM, internal valve view. Arrows indicate dorsally bent (not curved) proximal raphe fissures. Scale bars: Figs 3–8: 10 µm; Figs 9, 10: 5 µm.

Distribution:—In North America, known only from the type locality.

Etymology:—*Drosera* refers to the genus of sundews, which are common associates of this diatom at the type locality; *philum* is from the Greek *philus*, which means "loving".

Rare taxa and new records

Here we provide morphological features, ecological information, and distribution records for selected rare taxa, including taxa recorded here for the first time from the northwestern USA and/or the contiguous USA (see Table 2).

***Encyonopsis neoamphioxys* Krammer** (1997b: p. 142, pl. 168, figs 1–7). One specimen measures 42 µm long, 5 µm wide. Striae number 13–15 in 10 µm. The type locality of this taxon is "Kitzbühel, Schwarzsee, Österreich", the same locality from which Krammer (1997a) reported our "new" *Encyonema*. *Encyonopsis neoamphioxys* has been reported by several authors from oligotrophic waters in northern/alpine regions.

***Eunotia arculus* Lange-Bertalot & Nörpel in Krammer & Lange-Bertalot** (1991: p. 213, pl. 157, figs 4–12). Valves are 18–50 µm long, 4 µm wide. Striae number 18–20 in 10 µm. Krammer & Lange-Bertalot (1991) reported *Eunotia arculus* from northern Europe in weakly acid standing waters with low conductivity. In North America, *Eunotia arculus* has been reported from lakes in northern Quebec and Labrador (Fallu *et al.* 2000).

***Gomphonema hebridense* Gregory** (1854: 607). Cleve-Euler 1955, p. 181, fig. 1274; Lange-Bertalot & Metzeltin 1996, pl. 64, figs 18–25, pl. 98, fig. 1. Valves are 21–47 µm long, 5–7 µm wide. Large specimens are tumid in the middle and tend to be cymbelloid. Striae number 15–20 in 10 µm. *Gomphonema hebridense* has been reported as a northern-alpine species from Austria, Germany, and Finland (Cleve-Euler 1955, Lange-Bertalot & Metzeltin 1996). In the USA, it has been found in low numbers in nine streams in western Montana and western Oregon (Bahls 2009), where mean pH is 6.8 and mean conductance is 247 µS/cm (Montana Diatom Database, unpublished data).

***Kobayasiella okadae* (Skvortzov) Lange-Bertalot** (1999a: 267). Nagumo & Kobayasi 1990, p. 368, figs 1–16. Synonym: *Navicula hoefleri* Cholnoky & Schinder (1953: 607). Valves are 31–37 µm long, 7–8 µm wide. Striae number 22–24 in 10 µm in the middle of the valve and 36–38 in 10 µm toward the ends. *Kobayasiella okadae* is typically found together with *K. parasubtilissima* (Kobayasi & Nagumo) Lange-Bertalot (1999a: 268) and *K. subtilissima* (Cleve) Lange-Bertalot (1999a: 268) in slightly acid waters in arctic to subarctic zones, and in temperate regions (Nagumo & Kobayasi 1990). Krammer & Lange-Bertalot (1986) report *K. okadae* (as *Navicula hoefleri*) from Scandinavia and the Alps. Lange-Bertalot & Metzeltin (1996) found *K. okadae* (reported as *Naviculadicta hoefleri*) in a Finnish lake that has low levels of conductance and inorganic nutrients and a high level of humic acid. In the United States, *K. okadae* had been reported (as *Navicula hoefleri*) only from a few oligotrophic and low conductivity lakes in New York (Camburn & Charles 2000) and Wisconsin (Diatom Paleolimnology Data Cooperative, Patrick Center, The Academy of Natural Sciences).

***Kobayasiella parasubtilissima* (Kobayasi & Nagumo) Lange-Bertalot** (1999a: 268). Kobayasi & Nagumo 1988, p. 245, figs 19–37. Synonym: *Navicula parasubtilissima* Kobayasi & Nagumo (1988: 245, 247). Valves are 31–37 µm long, 3–5 µm wide. Striae number 40–42 in 10 µm. This taxon was described from the same material from which Cleve described *Navicula* (*Kobayasiella*) *subtilissima* Cleve (1891: 37): Lake Imandra, Russian Lapland. Krammer & Lange-Bertalot (1986) report this taxon (as *Navicula subtilissima*) from high moors in the Alps and Scandinavia, usually associated with *Sphagnum* species. Fallu *et al*. (2000) reported *Navicula parasubtilissima* (from lakes in northern Québec and Labrador. In the United States, *K. parasubtilissima* has been reported (as *Navicula parasubtilissima*) from low alkalinity lakes in the Northeast

(Camburn & Charles 2000). *Kobayasiella parasubtilissima* has been reported (as *Kobayasiella subtilissima*) from 19 lakes and streams in Montana and Washington (Bahls 2009), where mean pH is 7.5 and mean conductance is 116 µS/cm (Montana Diatom Database, unpublished data).

Kobayasiella subtilissima **(Cleve) Lange-Bertalot** (1999a: 268). Kobayasi & Nagumo 1988, p. 240, figs 1–18. Synonyms: *Navicula subtilissima*, (?) *Navicula pseudobryophila* Hustedt (1942: 114). Valves are 22–24 µm long, 5 µm wide. Striae number about 36 in 10 µm. This taxon was described by Cleve from material collected in Lake Imandra, Russian Lapland, at approximately 68° north latitude. Fallu *et al.* (2000) reported *Navicula subtilissima* from lakes in northern Québec and Labrador. In the United States, *Kobayasiella subtilissima* has been reported (as *Kobayasia subtilissima*) from the Great Lakes (Stoermer *et al.* 1999). Following Krammer & Lange-Bertalot (1986), we had identified this taxon as *Navicula pseudobryophila* Hustedt (Simonsen 1987), which has the same morphological features as *Kobayasiella subtilissima*. Krammer & Lange-Bertalot (1986) report *N. pseudobryophila* from high moors in the Alps and Scandinavia, usually associated with *Sphagnum*. In the Northwest, we have six records for *Navicula pseudobryophila*, from California, Idaho, Montana, and Wyoming (Bahls 2009).

Navicula heimansioides **Lange-Bertalot** (2001: p. 87, pl. 40, figs 10–15). One valve measures 45 µm long, 6 µm wide. Striae number 14 in 10 µm at the center to 18 in 10 µm toward the ends. *Navicula heimansioides* may be distinguished from *Navicula leptostriata* Jørgensen (1948: 59) and *Navicula notha* Wallace (1960: 4) by its larger size (Lange-Bertalot 2001). *Navicula heimansioides* is widespread in electrolyte poor, circumneutral to weakly acid, oligotrophic waters. This appears to be the first published record of this taxon in the USA. In the Northwest, we have 43 records of this taxon from California, Idaho, Montana, and Oregon, where mean pH is 7.0 and mean conductance is 134 µS/cm (Montana Diatom Database, unpublished data).

Pinnularia polyonca **(Brébisson) W. Smith** (1856: 95). Krammer 2000, p. 90, pl. 95, figs 1–7. Valves are lanceolate, somewhat triundulate, widest in the middle, ends capitate and rounded. Valves measure 70–74 µm long, 9–10 µm wide. Striae consistently number 10 in 10 µm. Raphe lateral, the outer fissure weakly curved, proximal raphe ends small, bent to one side and close together. Distal raphe fissures large, ?-shaped. Axial area ¼ to ½ width of the valve, lanceolate and widening from the ends to a broad central area. This taxon is very rare; we found only two frustules—one on each of two slides. Scans of 10 additional slides that were made from sample 4526 failed to produce another frustule. In our specimens, one or two slightly longer striae occur in the central area on one side, which is a feature also shown by Siver *et al.* (2005) for specimens collected from Cape Cod (Massachusetts, USA). Krammer (1992, 2000) reports *P. polyonca* from Bavaria and as a "zonal element of the palaearctic region, rare, always isolated, [and in] waters of low electrolyte content". We have only one other record of *P. polyonca* from the Pacific Northwest (Bahls 2009) and that is from Fish Lake in Glacier National Park.

Pinnularia rhombarea **Krammer in Metzeltin & Lange-Bertalot** (1998: 185–186). Krammer 2000, p. 75, pl. 53, figs 1–10; pl. 54, figs 1–5. Valves measure 61–64 µm long, 11 µm wide. Striae number 9–10 in 10 µm. *P. rhombarea* was previously subsumed as Morphotype 3 of *P. microstauron* (Ehrenberg) Cleve (1891: 28) (Krammer 1992). Fallu *et al.* (2000) found *Pinnularia microstauron* Morphotype 3 in lakes in northern Quebec and Labrador. Krammer (2000) reports that *Pinnularia rhombarea* prefers cold, oligotrophic waters with low electrolyte content, in northern and subarctic regions. We have three other records of *P. rhombarea* from the Northwest (Bahls 2009) and all three are from lakes and fens in Glacier National Park.

Stauroneis acidoclinatopsis **Van de Vijver & Lange-Bertalot** (2004: p. 16, pl. 57, figs 1–9). Valves are 57–61 µm long, 10–12 µm wide. Striae number 24 in 10 µm (constant). Areolae number 22–24 in 10 µm. *Stauroneis acidoclinatopsis* was described from Qeqertarsuaq, West Greenland (69° N latitude), where it was found in a small shallow pool with slightly acid water (pH 6.0), low conductance (<50 µS/cm), and very low nutrient levels (Van de Vijver *et al.* 2004). Besides the fens at Indian Meadows, we have records of this species from 3 wetlands and small lakes in western Montana (Bahls 2010).

***Stauroneis heinii* Lange-Bertalot & Krammer in Lange-Bertalot & Genkal** (1999: p. 91, pl. 27, figs 1–4). Valves are elliptic lanceolate with protracted ends, 116–167 µm long, 23–30 µm wide. Striae number 15–17 in 10 µm and areolae number 16–18 in 10 µm. External proximal raphe fissures are strongly inflated and strongly curved. *Stauroneis heinii* is bipolar, having been reported from South Georgia Island (Van de Vijver *et al.* 2004) and in the Andes Mountains from Venezuela to Patagonia (Rumrich *et al.* 2000), as well as from the Canadian Arctic (Antoniades *et al.* 2008), Greenland (Van Kerckvoorde *et al.* 2000), Siberia (Lange-Bertalot & Genkal 1999), Alaska (Hein 1990), and elsewhere in western Montana, where it prefers slightly acid to circumneutral waters with low concentrations of electrolytes (Bahls 2009, 2010).

***Stauroneis indianopsis* Bahls** (2010: 85–86). Valves are linear in small specimens to linear-lanceolate in larger specimens. Apices appear pinched, very slightly protracted. Length 105–150 µm, breadth 20–25 µm. Axial area narrow, barely widening near the central area. Stauros narrow, linear or slightly expanded toward the valve margins. Raphe fissures lateral, proximal ends weakly inflated and strongly curved; terminal raphe fissures hooked. Striae radiate throughout, more so near ends, 16–17 in 10 µm. Areolae 16–18 in 10 µm. *Stauroneis indianopsis* was described elsewhere (Bahls 2010) from material collected at IMRNA. It is also known from a small lake in Missoula County, Montana, having a pH of 7.5 and conductance of 10 µS/cm (Bahls 2010).

***Stauroneis regina* Bahls** (2010: 123-124). Valves are narrowly lanceolate with rounded ends that are not or only slightly protracted. Length 142–213 µm, breadth 22–33 µm. Axial area narrow, widening slightly near the central area. Stauros narrow, rectangular, widening slightly toward the valve margins. Outer raphe fissures lateral, proximal endings inflated and curved. Terminal raphe fissures are hooked. Striae radiate throughout, 15–17 in 10 µm. Areolae 15–18 in 10 µm. *Stauroneis regina* was described elsewhere (Bahls 2010) from material collected at site 4525, IMRNA. *Stauroneis regina* is widely distributed in ponds, small lakes, and wetlands in the northern Rocky Mountains, where it prefers circumneutral waters with low concentrations of electrolytes (Bahls 2010). *Stauroneis regina* may be conspecific with *S. supergracilis* Van de Vijver & Lange-Bertalot (2004: 73).

***Stauroneis subborealis* Bahls** (2010: 151–152). Valves are linear in small specimens to lanceolate in larger specimens. Apices are protracted and broadly rounded. Length 46–142 µm, breadth 9–24 µm. Axial area narrow, widening slightly near the central area. Stauros narrow, somewhat expanded toward the valve margins. Raphe fissures lateral, proximal ends inflated and curved. Terminal raphe fissures hooked. Striae radiate throughout, 17–20 in 10 µm. Areolae 18–22 in 10 µm. *Stauroneis subborealis* was described elsewhere (Bahls 2010) from material collected at site 4526, IMRNA. *Stauroneis subborealis* has been found in a few ponds, fens, and small lakes in western Montana, where it tolerates a wide range of pH and low to moderate concentrations of electrolytes (Bahls 2010).

***Stauroneis submarginalis* Bahls** (2010: 157–158). Valves are broadly lanceolate with slightly protracted, broadly rounded apices. Length 140–186 µm, breadth 23–35 µm. A narrow line, visible in LM, runs parallel to and 2–3 µm inside the valve margins. Axial area narrow, widening slightly near the central area. Stauros narrow, rectangular, slightly expanded toward the valve margins and often containing short striae. Raphe fissures lateral, proximal ends inflated and curved (not straight). Terminal raphe fissures hooked. Striae radiate throughout, 15–17 in 10 µm. Areolae 16–20 in 10 µm. *Stauroneis submarginalis* was described elsewhere (Bahls 2010) from material collected at site 4525, IMRNA. *Stauroneis submarginalis* has also been found in several small lakes and wetlands in western Montana, northern Idaho, eastern Washington, and southern Alberta, where it prefers circumneutral waters with very low concentrations of electrolytes (Bahls 2010).

TABLE 2: Percent abundance of diatom taxa in floating-mat fens (sites 4525 and 4526) at Indian Meadows Research Natural Area, corresponding abundances in an abandoned beaver pond (site 1241), number of prior records in the Montana Diatom Database (Bahls 2009), taxa not included (FR = first report) in a checklist of U.S. diatoms (Kociolek 2005), and taxa status in the diatom Red List for Germany (Lange-Bertalot 1996): 1 = threatened by extinction; 2 = greatly at risk; 3 = at risk, imperiled; G = risk increasing; R = extremely rare; V = declining; * not at risk; ** confidently secure. A "p" for abundance indicates the taxon was observed but not counted. [1]Note: for the abandoned beaver pond (site 1241), only taxa shared with the fens are shown; see text for a list of dominant diatom taxa at this site.

Taxa	Percent Abundance			Number of Prior Records		Lange-Bertalot
	1241[1]	4525	4526	Bahls 2009	Kociolek 2005	1996
Achnanthidium deflexum (Reimer) Kingston		0.24		428		
Achnanthidium minutissimum (Kützing) Czarnecki	2.62	0.24	1.66	4570		**
Brachysira brebissonii Ross		6.16	0.12	14		*
Brachysira microcephala (Kützing) Compére	0.50	3.14		291		*
Chamaepinnularia sp. Lange-Bertalot & Krammer		0.48		5		
Encyonema droseraphilum sp. nov.			17.87	0	FR	
Encyonema neogracile Krammer	0.25	0.24	3.08	169		3
Encyonopsis neoamphioxys Krammer			p	0		2
Eolimna minima (Grunow) Lange-Bertalot	1.25		0.24	2238		**
Eunotia arculus Lange-Bertalot & Nörpel		p	3.91	0	FR	2
Eunotia flexuosa (Brebisson) Kützing	0.25	0.12		3		2
Eunotia glacialis Meister	p	0.12	5.33	18		G
Eunotia implicata Nörpel, Alles & Lange-Bertalot		p	0.24	14		G
Eunotia monodon Ehrenberg		0.36	p	26		2
Eunotia naegelii Migula	0.62	0.85	0.47	15		3
Eunotia nymanniana Grunow		1.93		1		3
Eunotia rhomboidea Hustedt		20.53	8.28	15		V
Eunotia tetraodon Ehrenberg		0.60		2		1
Frustulia crassinervia (Brébisson) Lange-Bertalot & Krammer		37.32	11.24	33		V
Frustulia saxonica Rabenhorst		0.24	0.95	7		V
Gomphonema hebridense Gregory		0.24	24.14	3	FR	V
Kobayasiella okadae (Skvortzov) Lange-Bertalot		3.38	1.07	0		1
Kobayasiella parasubtilissima (Kobayasi & Nagumo) Lange-Bertalot	p	4.11	5.68	0		V
Kobayasiella subtilissima (Cleve) Lange-Bertalot		0.24		24		2
Navicula cryptocephala Kützing	2.74		1.30	1193		**
Navicula heimansioides Lange-Bertalot	p	p		43	FR	3
Neidium iridis (Ehrenberg) Cleve		p	p	14		G
Nitzschia bryophila (Hustedt) Hustedt			0.36	152		G
Nitzschia gracilis Hantzsch	p	0.72		467		*
Nitzschia perminuta (Grunow) Peragallo	0.88	3.86	3.91	1206		*

……*continued on the next page*

TABLE 2. (Continued)

Taxa	Percent Abundance			Number of Prior Records		Lange-Bertalot
	1241[1]	4525	4526	Bahls 2009	Kociolek 2005	1996
Pinnularia divergens W. Smith		0.24		3		V
Pinnularia macilenta Ehrenberg		p		4		G
Pinnularia microstauron (Ehrenberg) Cleve		4.11	5.33	250		V
Pinnularia polyonca (Brébisson) W. Smith			p	1		R
Pinnularia rhombarea Krammer		2.54	2.96	3	FR	
Pinnularia viridis (Nitzsch) Ehrenberg	p		0.24	117		*
Pseudostaurosira brevistriata (Grunow) Williams & Round	3.50		0.71	1183		**
Sellaphora laevissima (Kützing) Mann	0.75		p	259		V
Stauroneis acidoclinatopsis Van de Vijver & Lange-Bertalot		0.12	0.12	0	FR	
Stauroneis heinii Lange-Bertalot & Krammer		0.36	p	5	FR	
Stauroneis indianopsis Bahls		p	p	0	FR	
Stauroneis regina Bahls		p		0	FR	
Stauroneis subborealis Bahls			p	0	FR	
Stauroneis submarginalis Bahls		p		0	FR	
Staurosirella leptostauron (Ehrenberg) Williams & Round			0.12	1531		**
Staurosirella pinnata (Ehrenberg) Williams & Round	51.00		0.71	1641		**
Stenopterobia curvula (W. Smith) Krammer			p	10		2
Stenopterobia delicatissima (Lewis) Van Heurck		0.24		1		3
Tabellaria flocculosa (Roth) Kützing	0.25	7.25	p	435		**
Taxa Counted	59	28	25			
Total Taxa	126	36	35			

Discussion

Global warming is shrinking the glaciers of nearby Glacier National Park (Fagre 2007), altering the hydrology of the Northern Rockies (Rood *et al.* 2005), and threatening the integrity of peatlands worldwide (Dise 2009). As a consequence, even protected fens such as those at IMRNA and the taxa they support are at risk, despite the absence of land-based threats. For unprotected peatlands and other wetlands, draining and filling for human settlement and agriculture continues to be a major threat to wetland species (Larsen 2002).

Germany and the northwestern United States have very similar diatom floras. Seventy-two percent of the diatom taxa in the Northwest are found in Germany based on a comparison of checklists for the two regions (Bahls 2009, Lange-Bertalot 1996). Both regions are within the Holarctic Kingdom of vascular plants (Takhtajan 1986), which coincides more or less with the circumboreal distribution of many diatom species in the Northern Hemisphere (e.g., see Medvedeva 2002, Metzeltin *et al.* 2009). Germany and the Northwest span similar latitudes and have similar climates, and both have mountains, coastal areas, and inland waters with very low to very high electrolyte content. For these reasons, and since there is no diatom "red list" for Montana or the United States, the German list may serve as a surrogate list of imperiled diatoms for Montana until such time as a more accurate list is prepared for this region.

"At risk" or "declining" ratings appear to be appropriate for the rare, northern, cold-loving fen diatoms at Indian Meadows and elsewhere in Montana, especially in light of global warming and continued human encroachment on wetlands. For most of these taxa, the closest records are hundreds or even thousands of kilometers removed, mainly northward. Similar and potential habitats for these taxa are rare in Montana. The two fens at IMRNA support two of only four Montana populations of the rare slenderleaf sundew (*Drosera linearis*). The other two records are from fens in the Bob Marshall Wilderness about 40 km northwest of IMRNA. The Bob Marshall fens have not been sampled for diatoms, but hold promise for supporting more rare taxa and perhaps new species.

If the new *Encyonema* sp. from IMRNA proves to be the same taxon as the one reported by Krammer (1997a) from Austria, it would be one of many diatom taxa from the European Alps to be reported in the Northern Rockies. The diatom *Distrionella incognita* (Reichardt) Williams (1990: 176-177), originally reported and known only from lakes in the foothills of the Alps, was recently found in the Northern Rockies, primarily in large fjord-like lakes at lower elevations in Glacier National Park (Morales *et al.* 2005, Bahls 2007). A recently completed survey of diatom biodiversity in Glacier National Park (unpublished) has uncovered many more northern/alpine taxa that are also found in Europe, giving floristic substance to a common nickname for Glacier National Park: America's Alps.

The new species from IMRNA and the many other rare species with widely disjunct distributions all raise a perplexing question (Williams 1994): How did they get there? There are three possible answers to this question. First, taxa that are new and unique to the fens at Indian Meadows may have evolved there from precursors that already existed in the area, for example, *Encyonema droseraphilum* from *E. silesiacum* and *Stauroneis indianopsis* from *S. heinii*. Endemism among diatoms is more common than previously thought (Mann & Droop 1996) and ancient, stable ecosystems tend to produce large percentages of endemic species. In Lake Baikal, it is estimated that endemic diatom species account for 30% (Kozhov 1963) to over 50% (Skvortzov 1937) of the diatom flora. The fens at IMRNA are not nearly as old as Lake Baikal (they began their succession at the end of the Pleistocene, about 10,000 years B.P.) but they are old enough to allow for diatom speciation, as shown by the emergence of *Stephanodiscus yellowstonensis* Theriot & Stoermer (1984: 41) from a *Stephanodiscus niagarae* Ehrenberg (1845:80) precursor over just a few thousand years in Yellowstone Lake (Theriot & Stoermer 1984, Theriot *et al.* 2006).

The second possible answer to the question of how they got there is that they have been there all along, or at least since the continental and montane glaciers began to recede. At the end of the Pleistocene it is estimated that 90% of the Northern Great Plains was under water or very wet, and areas that were not submerged supported a boreal forest vegetation interspersed with muskeg (Pielou 1991). This was before the region became drier and warm enough to support grasslands. Just west of the Great Plains, in the Northern

Rockies, recently scoured lake basins provided the physical container and a cool, wet climate provided the right conditions for the development of peatlands. At that time, habitats for boreal diatoms that require cold, oligotrophic, and circumneutral waters were much more abundant and more closely spaced than they are today. Many of the meadows or grassy "parks" at lower elevations in the Northern Rockies began as small, shallow lakes, which progressed to fens and wet meadows and finally to dry meadows. Local dispersal and interchanges of peatland diatom taxa may have occurred at first, until most of the habitats dried up and the few remaining populations became widely separated. This geographic separation of habitats and populations, along with a local progression to more dystrophic conditions, may have driven the genetic divergence and speciation noted above.

The final and least likely answer to the question of how they got there is recently, by dispersal and ecological selection. Passive, long-range dispersal of viable diatom cells between distant freshwater habitats is problematic and unproven (Harper 1999). Global history, including plate tectonics and glaciation, and the distribution histories of individual diatom taxa and groups of taxa, are sufficient to explain the current distributions of most diatoms (Kociolek & Spaulding 2000). Short-range dispersal from fen to fen, for example in the fur of amphibious animals or on the feet of shorebirds, is more likely to occur. But even this is problematic between widely separated fens.

The much larger number of diatom taxa in the abandoned beaver pond illustrates the intermediate disturbance hypothesis, which holds that biodiversity is highest when disturbance is neither too rare nor too frequent (Connell 1978, Grime 1973). For diatoms, Asai & Watanabe (2004) demonstrated that the maximum number of species occurs at intermediate levels of organic enrichment; extremely high and extremely low levels of organic pollution produce the smallest number of species. In the case of the beaver pond, the disturbance is natural, mainly flooding, which results in a shift toward more minerotrophic and limnic conditions. The IMRNA fens, on the other hand, represent undisturbed or rarely disturbed and increasingly dystrophic habitats. In peatlands of northern Minnesota, Kingston (1982) demonstrated a decrease in diatom species richness with a decrease in minerotrophy that accompanies peatland development. In another study of an adjacent lake and fen in Labrador, Kingston (1984) found that the lake diatom assemblage was composed mainly of small fragilarioid taxa, which he says are typical of post-glacial assemblages in north-temperate lakes. We found several of these same small fragilarioid taxa in the abandoned beaver pond at IMRNA. The Laborador fen, on the other hand, supported a substantially different diatom assemblage that was rich in *Eunotia* Ehrenberg (1837: 44), *Frustulia* Rabenhorst 1853: 50), and *Pinnularia* Ehrenberg (1843: 45) species, which is similar to the fen assemblages at Indian Meadows. The take home message from this is that disturbance and pollution favor common species while the absence of disturbance and pollution favors uncommon species.

In general, human activities tend to degrade water quality by increasing temperature, turbidity, sedimentation, and concentrations of inorganic salts and nutrients. Natural cold, clear and fresh oligotrophic and dystrophic waters are uncommon at temperate latitudes and are becoming more scarce with the advance of human development. Oligotrophic and dystrophic waters support unique diatom assemblages that include many new and rare species (e.g., Kulikovskiy *et al.* 2010, Lange-Bertalot & Metzeltin 1996). Most of the imperiled diatoms on the Red List for Germany are oligotraphentic and their habitats in that country and throughout much of central Europe are no longer available because of eutrophication from ubiquitous use of fertilizers (Lange-Bertalot 1996, 1999b). Undisturbed, nutrient-poor waters are therefore worth protecting, for the purpose of conserving rare species and for monitoring environmental change (Kociolek & Stoermer 2009). In the case of Indian Meadows, the United States Forest Service has designated the fens and their watershed as a Research Natural Area (RNA), making it part of a national network of RNAs that protect exemplary habitats on National Forest lands in perpetuity.

Despite their relative stability, peatlands are not immune to long-term change. At geologic time scales that allow for speciation to occur, natural wetland succession will also result in the fens' and their floras' eventual demise. As the fens progress toward wet meadows and eventually to dry meadows, more floristic changes will occur, leading ultimately to diatom assemblages composed of aerophilic taxa. This process may proceed more quickly with global warming, but with or without global warming, unless there is another glacial epoch to scour new habitats and provide a starter climate for northern diatoms, the new and rare taxa described here will become extinct or restricted to suitable surviving habitats much farther north.

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