Abstract
As a contribution to our knowledge of diatom biodiversity and biogeography in the United States, high resolution light microscope images are provided for 139 diatom taxa recorded from lake, stream, spring and glacier habitats in Wrangell-St. Elias National Park, Alaska. The spring had the highest taxa richness of the four habitats that were sampled, likely owing to the relative stability of this habitat compared to the others. Most of the taxa were described from northern and alpine locations in Europe and North America and are typical of habitats in the northern Rocky Mountains, with two notable exceptions. Surirella arctica had been reported previously only from locations in the High Arctic of North America, north of 68°N latitude. Gomphonema caperatum has a disjunct distribution in montane regions of the eastern and far western contiguous United States. This may be the first record of this taxon from Alaska.

Keywords
diatoms, Alaska, diatom biodiversity, diatom biogeography, glacier diatoms

Introduction
For a land area as large as Alaska (1,717,856 km²), there are relatively few published articles on freshwater diatom taxonomy and biodiversity (Patrick and Freese 1961, Foged 1971, 1981, McLaughlin and Stone 1986, Hein 1990). All of these studies predate the general availability of scanning electron microscopy and relied on taxonomic references that today are widely considered to be incomplete and out-of-date. One recent study (Pite et al. 2009) addressed the historical morphology and abundance of two Didymosphenia species in an Alaskan Lake.
Wrangell-St. Elias National Park and Preserve (WRST) is located in the southeast corner of Alaska (Fig. 1). At 53,320 km², it is the largest national park in the United States, six times larger than Yellowstone and about the same size as the country of Croatia. It is also one of the least visited of the national parks and much of it is untracked wilderness. Elevations in the park range from sea level to 5,489 m Mt. St. Elias. The mountainous terrain and ample winter snowfall from north Pacific weather systems produce some of the largest glaciers and ice fields in the world (US National Park Service 2018).

Although diatoms have been used to assess water quality and climate change within and near WRST (Simmons 2007, Brabets et al. 2011, Griffiths 2015), these studies did not include images of voucher specimens to verify identifications. Published studies on diatom taxonomy and biodiversity in the park appear to be wanting. Here we present high-resolution LM images of 139 diatom taxa collected in early summer 2018 from a lake, a stream, a spring and a glacier in WRST. This paper is intended only as a preliminary checklist of park diatoms with images of voucher specimens (illustrated checklist). Results are discussed briefly with respect to diatom biodiversity and biogeography.

**Methods**

Samples of benthic diatoms were collected from four sites in WRST (Table 1, Fig. 1). Donoho Lake (Fig. 2) is a shallow lake surrounded by white and black spruce forest, located between the Kennicott and Root Glaciers south of Donoho Peak. Jumbo Creek is a high-gradient perennial stream that originates in the mountains east of Root Glacier and north of Kennecott Mine and Townsite. McCarthy Spring is located east of Kennicott River and serves as the water source for the town of McCarthy. Four samples were collected from Root Glacier (Figs 3, 4), one each from three open pools (moulins) on the Root Glacier Ice Field and one from melt water discharging from a smaller rock glacier on the ice field.

Substrata that were sampled at WRST collection sites were cobbles (Jumbo Creek), sediment (all sites) and peat (moulins). As there were very few diatom cells in the samples from Root Glacier pools, they were combined for the purpose of sample processing and reporting. The pools appeared to extend to the bottom of the glacier, so diatoms in the pool samples may have originated from greater depth. The Root Glacier Ice Field is up to 213 m thick at this location, which is near its confluence with the Kennicott Glacier. Collection sites on the glacier were 6 km below the massive 2,133 m Staircase Ice Fall, at the head the valley, which is the largest icefall outside the Himalayas.

Sediment samples were collected with a large-bore pipette (5 mm diameter) with a suction bulb. The pipette was rinsed with ambient water twice between collection sites. Approximately 7.5 cm³ of water and sediment was pulled from the upper 1 cm of sediment at each sample site and stored in collection bottles. At Jumbo Creek, the surface film on several cobbles was scraped into the sample bottle and some peat material was included in the moulin samples. Iodine was added to each sample within 12 hours of collection. In the laboratory, samples were treated with 30% hydrogen peroxide (H₂O₂) and heated gently for several days to remove organic matter. After
Diatoms from Wrangell-St. Elias National Park, Alaska, USA

**Table 1.** Samples collected on 29 June 2018 from WRST, Alaska. Sample numbers are for the Montana Diatom Collection and database. Slide numbers are for slides in the diatom collection at the University of Montana Herbarium, Missoula (MONTU). The numbers in the column headed “WRST” are National Park Service catalogue numbers for accession WRST-00483.

| Sample number | Site name | Latitude (°N) | Longitude (°W) | Slide number | WRST |
|---------------|-----------|---------------|----------------|--------------|------|
| 6955          | Donoho Lake | 61.5275       | -142.9580      | 50–31        | 22949|
| 6956          | Jumbo Creek | 61.5030       | -142.8972      | 50–32        | 22950|
| 6957          | McCarthy Spring | 61.4344   | -142.9278      | 50–33        | 22951|
| 6958          | Root Glacier (pools) | 61.5098 | -142.9265      | 50–34        | 22952|
| 6959          | Root Glacier (rock glacier) | 61.5122 | -142.9211      | 50–35        | 22953|

**Figure 1.** Map of Wrangell-St. Elias National Park showing approximate location of collection sites. Base map: U. S. National Park Service.

Several rinses in distilled water, cleaned diatom material was dried on cover slips and mounted permanently on glass slides using Naphrax.

One slide per sample was examined under light microscopy (LM) with differential interference contrast optics and images were captured using a Leica DM LB2 research microscope and a Spot Insight monochrome digital camera (Model 14.0). Slides examined for this study will be deposited in the University of Montana Herbarium, Missoula (MONTU) on completion of the study. Imaged diatoms were identified to the lowest practical taxonomic unit using available identification resources, mainly Patrick and...
Figures 2–4. Collection sites. 2 Donoho Lake 3 Root Glacier 4 Pool of standing water (moulin) on Root Glacier. Photos: Tara Luna.

Reimer 1966, 1975, Krammer and Lange-Bertalot 1986, 1988, 1991a, 1991b, Krammer 1997a, 1997b, 2000, 2002, 2003, Lange-Bertalot 2001, Levkov 2009, Lange-Bertalot et al. 2011 and Levkov et al. 2013, 2016. The Diatoms of North America website (INSTAAR 2018) and other sources were also consulted as needed. The INA card file at the University of California Herbarium (2018) was consulted for type localities of taxa.

Each slide was systematically scanned at 100 magnifications to locate very large taxa that might otherwise be missed while scanning at higher magnifications. After these large taxa were identified, listed and photographed, slides were examined under oil immersion at 630 and 1,000 magnifications in order to find, identify and photograph smaller taxa. A “random walk” was taken around each slide and additional taxa were listed and photographed until no additional taxa were found after 20 minutes of scanning. The number of images that were captured of each taxon is roughly proportional to the relative abundance of that taxon in a sample.
Diatoms from Wrangell-St. Elias National Park, Alaska, USA

Results

A total of 139 taxa were identified at the genus or subgenus level (Table 2, Plates 1–14). None of the species is described as new to science, but some are designated as unknowns (e.g. *Hantzschia* sp.) or as comparable to another taxon (cf.). Alternate identifications are provided for some taxa in the plate legends.

Most taxa were described from type material collected in Europe (117 taxa), mostly northern Europe (Table 2). Other type localities include North America (18 taxa) [including 2 taxa from Alaska], Africa (1), Asia (1), Japan (1), Tristan da Cunha (1) and unknown (1). The total number of taxa in each habitat ranged from 29 on Root Glacier to 61 in McCarthy Spring.

Except for McCarthy Spring, diatom cells were scarce in all of the samples, as may be expected for such austere habitats. Glacial sediment (rock flour) dominated all but the McCarthy Spring sample and often obscured specimens for photography. Capturing quality images of voucher specimens was further hindered by diatom frustules that were often broken, eroded or encrusted with lime.

Table 2. List of taxa and key to plates.

| Taxa                              | Plate | Donoho Lake | Jumbo Creek | McCarthy Spring | Root Glacier | Type Locality          |
|-----------------------------------|-------|-------------|-------------|-----------------|--------------|------------------------|
| *Achnanthidium gracillimum* (Meister) Lange-Bertalot | 4     | ×           | ×           | ×               | Japan        |                        |
| *Achnanthidium minutissimum* (Kützing) Czarnecki | 4     | ×           | ×           | ×               | Germany      |                        |
| *Amphora Ehrenberg in Kützing*     | 10    | ×           | ×           | ×               | Europe       |                        |
| *Amphora copulata* (Kützing) Schoeman & Archibald | 10    | ×           | ×           |                 | Germany      |                        |
| *Amphora inariensis* Krammer       | 10    | ×           | ×           | ×               | Finnish Lapland |                        |
| *Amphora pediculus* (Kützing) Grunow | 10    | ×           | ×           |                 | Germany      |                        |
| *Brachysira microcephala* (Grunow) Compère | 6     | ×           | ×           | ×               | Austria      |                        |
| *Caloneis alpestris* (Grunow) Cleve | 7     | ×           | ×           | ×               | Austria      |                        |
| *Caloneis falcifera* Lange-Bertalot, Genkal & Vekhov | 7     | ×           | ×           |                 | Russia       |                        |
| *Caloneis silicula* (Ehrenberg) Cleve | 7     | ×           | ×           |                 | New England, USA |                        |
| *Caloneis tenuis* (Gregory) Krammer | 7     | ×           | ×           |                 | Scotland     |                        |
| *Caloneis thermalis* (Grunow) Krammer | 7     | ×           | ×           |                 | Germany      |                        |
| *Cocconeis placenta* Ehrenberg      | 4     | ×           | ×           | ×               | Germany      |                        |
| *Cymbella alpestris* Krammer        | 9     | ×           | ×           |                 | Switzerland  |                        |
| *Cymbella cleve-eulerae* Krammer    | 9     | ×           | ×           |                 | Sweden       |                        |
| *Cymbella coleyi* Bahls             | 9     | ×           | ×           |                 | Montana, USA |                        |
| *Cymbella exsiciformis* Krammer     | 9     | ×           | ×           |                 | Germany      |                        |
| *Cymbella neovestita var. neovestita* Krammer | 9     | ×           | ×           |                 | Germany      |                        |
| *Cymbella neovestita var. islandica* Krammer | 9     | ×           | ×           |                 | Iceland      |                        |
| *Cymbopleura angustata* (W. Smith) Krammer | 9     | ×           | ×           |                 | Scotland     |                        |
| *Cymbopleura austriaca* (Grunow) Krammer | 9     | ×           | ×           |                 | Austria      |                        |
| *Cymbopleura incerta* (Grunow) Krammer | 9     | ×           | ×           |                 | Norway       |                        |
| Taxa | Plate | Donoho Lake | Jumbo Creek | McCarthy Spring | Root Glacier | Type Locality |
|------|-------|-------------|-------------|-----------------|--------------|---------------|
| Cymbopleura lapponica (Grunow) Krammer | 9 | x | x | | | Swedish Lapland |
| Cymbopleura naviculiformis (Auerswald) Krammer | 9 | x | | | | Germany |
| Cymbopleura oblongata Krammer | 9 | x | | | | Spitsbergen |
| Cymbopleura subaequalis (Grunow) Krammer | 9 | x | | | | Belgium |
| Delicata Krammer | 10 | x | | | | France |
| Delicata alpestris (Krammer) Bahls | 10 | x | | | | Austria |
| Delicata delicatula (Kützing) Krammer | 10 | x | | | | France |
| Denticula kuetzingii Grunow | 11 | x | x | | | Austria |
| Denticula tenuis Kützing | 11 | | x | | | Germany |
| Diatoma tenuis Agardh | 1 | | x | | | Scandinavia |
| Diatoma vulgaris Bory de Saint-Vincent | 1 | | x | | | France |
| Diploneis krammeri Lange-Bertalot & Reichardt | 6 | | x | | | Austria |
| Encyonema neogracile Krammer | 10 | | x | | | Finnish Lapland |
| Encyonema permisutum Krammer | 10 | | x | | | Spitsbergen |
| Encyonema silesiacum (Bleisch) Mann | 10 | | x | x | | Germany |
| Encyonopsis alpina Krammer & Lange-Bertalot | 10 | x | | | | Germany |
| Encyonopsis cesatti (Rabenhorst) Krammer | 10 | x | | | | Italy |
| Encyonopsis czarneckii Bahls | 10 | x | | | | Montana, USA |
| Encyonopsis montana Bahls | 10 | x | | | | Montana, USA |
| Encyonopsis subminuta Krammer & Reichardt | 10 | x | | | | Switzerland |
| Eucocconeis alpestris (Brun) Lange-Bertalot | 4 | x | x | | | Switzerland |
| Eucocconeis flexella (Kützing) Meister | 4 | x | x | | | Switzerland |
| Eucocconeis laevis (Østrup) Lange-Bertalot | 4 | x | x | | | Denmark |
| Eunotia arcus Ehrenberg | 4 | | x | | | Sweden |
| Eunotia valida Hustedt | 4 | | x | | | Switzerland |
| Fragilaria Lyngbye | 2 | x | x | | | Russia? |
| Fragilaria amphicephala Ehrenberg | 2 | | x | | | Oregon, USA |
| Fragilaria ripheus Ehrenberg | 2 | | x | | | Russia |
| Fragilaria tenera (W. Smith) Lange-Bertalot | 2 | | x | | | Ireland |
| Fragilaria vaucheriae (Kützing) Petersen | 2 | | x | | | Germany |
| Frustulia amosseeana Lange-Bertalot in Rumrich et al. | 2 | x | | | | Scotland |
| Gomphonema Agardh | 8 | | x | | | Germany |
| Gomphonema boeziae Lange-Bertalot & Reichardt | 8 | | x | | | Finland |
| Gomphonema capenatum Ponader & Potapova | 8 | | x | | | Virginia, USA |
| Gomphonema lateripunctatum Reichardt & Lange-Bertalot | 8 | | x | | | Germany |
| Gomphonema minuscum Krasske | 8 | | x | | | Tristan da Cunha |
| Gomphonema olivaceoides Hustedt | 8 | | x | | | Germany |
| Gomphonema pseudobohemicum Lange-Bertalot & Reichardt | 8 | | x | | | Germany |
| Gomphonema punctatum (Grunow) Reichardt & Lange-Bertalot | 8 | | x | | | Belgium |
| Gyrosigma Hassall | 6 | | x | | | Germany |
| Taxa                                                                 | Plate | Donoho Lake | Jumbo Creek | McCarthy Spring | Root Glacier | Type Locality          |
|----------------------------------------------------------------------|-------|-------------|-------------|-----------------|--------------|------------------------|
| Hannaea arcus (Ehrenberg) Patrick                                    | 2     | ×           |             |                 |              | Germany                |
| Hantzschia Grunow                                                    | 12    | ×           | ×           |                 |              | USA                    |
| Hantzschia abundans Lange-Bertalot                                  | 12    | ×           |             | ×               |              | Germany                |
| Hantzschia amphioxys (Ehrenberg) Grunow                              | 12    | ×           | ×           |                 |              | USA                    |
| Hantzschia elongata (Hantzsch) Grunow                                | 12    | ×           |             |                 |              | Germany                |
| Hantzschia hyperborea (Grunow) Lange-Bertalot                        | 12    | ×           |             |                 |              | Russia                 |
| Hygropetra balfouriiana (Grunow) Krammer                             | 7     | ×           |             |                 |              | Scotland               |
| Koeltzskrammeria acqualis (W. Smith) Bahls                           | 10    | ×           |             |                 | ×            | Scotland               |
| Lindavia antiqua (W. Smith) Nakov et al.                             | 1     | ×           |             |                 |              | Ireland                |
| Luticola mutica (Kützing) Mann                                      | 6     | ×           |             |                 |              | Germany                |
| Luticola ventricosa (Kützing) Mann                                  | 6     | ×           |             |                 |              | Germany                |
| Meridion circulare (Greville) Agardh                                 | 1     | ×           |             |                 |              | Scotland               |
| Muelleria gibbula (Cleve) Spaulding & Stoermer                       | 5     | ×           |             |                 |              | Norway                 |
| Navicula angusta Grunow                                              | 7     | ×           | ×           | ×               |              | Austria                |
| Navicula cryptocephala Kützing                                      | 7     | ×           |             |                 |              | Germany                |
| Navicula cryptotenella Lange-Bertalot                               | 7     | ×           |             |                 |              | Belgium                |
| Navicula lanceolata (Agardh) Ehrenberg                              | 7     | ×           |             | ×               |              | Germany                |
| Navicula libonensis Schoeman                                        | 7     | ×           |             |                 |              | Lesotho                |
| Navicula radiosa Kützing                                            | 7     | ×           |             |                 |              | Germany                |
| Navicula seibigiana Lange-Bertalot                                  | 7     | ×           |             |                 |              | Switzerland            |
| Navicula subconcentrica Lange-Bertalot                              | 7     | ×           | ×           |                 |              | Germany                |
| Navicula vulpina Kützing                                            | 7     | ×           | ×           | ×               |              | Germany                |
| Neidismorpha brindiformis (Krammer) Cantonati et al.                 | 5     | ×           |             |                 |              | Germany                |
| Neidium Pützer                                                      | 5     | ×           |             |                 |              | Germany                |
| Neidium bergii (Cleve–Euler) Krammer                                | 5     | ×           |             |                 |              | Scandinavia            |
| Neidium bisulcatum (Lagerstedt) Cleve                                | 5     | ×           |             |                 |              | Spitsbergen            |
| Neidium bohmmarshallensis Bahls                                     | 5     | ×           |             |                 |              | Montana, USA           |
| Neidium distinctepunctatum Hustedt                                  | 5     | ×           |             |                 |              | Austria                |
| Neidium fogedii Bahls                                               | 5     | ×           | ×           |                 |              | Alaska, USA            |
| Neidium kozlowii var. ellipticum Mereschkowsky                       | 5     | ×           | ×           |                 |              | Tibet                  |
| Nitzschia alpina Hustedt                                            | 11    | ×           |             |                 |              | Switzerland            |
| Nitzschia amphibia Grunow                                            | 11    | ×           |             |                 |              | Austria                |
| Nitzschia angustata (W. Smith) Grunow                                | 11    | ×           |             |                 |              | Sussex, UK             |
| Nitzschia dissipata (Kützing) Rabenhorst                            | 11    | ×           |             |                 |              | Germany                |
| Nitzschia dissipata var. oligotraphenta Lange-Bertalot              | 11    | ×           |             |                 |              | Austria                |
| Nitzschia exilis Sovereign                                          | 11    | ×           |             |                 |              | Oregon, USA            |
| Nitzschia fonticola (Grunow) Grunow                                  | 11    | ×           |             |                 |              | Belgium                |
| Nitzschia homburgiensis Lange-Bertalot                              | 11    | ×           |             |                 |              | Germany                |
| Nitzschia incompeca Grunow                                           | 11    | ×           |             |                 |              | Austria                |
| Nitzschia lacuum Lange-Bertalot                                     | 11    | ×           |             |                 |              | Germany                |
| Nitzschia linearii W. Smith                                         | 11    | ×           |             |                 |              | UK                     |
| Nitzschia palea (Kützing) W. Smith                                  | 11    | ×           |             |                 |              | Germany                |
| Nitzschia perminuta Grunow                                           | 11    | ×           |             |                 |              | unknown                |
| Taxa                                      | Plate | Donoho Lake | Jumbo Creek | McCarthy Spring | Root Glacier | Type Locality |
|-------------------------------------------|-------|-------------|-------------|-----------------|--------------|---------------|
| *Nitzschia pura* Hustedt                  | 11    | ×           |             | ×               |              | Germany        |
| *Nitzschia pusilla* (Kützing) Grunow      | 11    | ×           |             | ×               |              | Germany        |
| *Nitzschia sublinearis* Hustedt           | 11    | ×           | ×           | ×               |              | Austria        |
| *Odontidium hyemale* Kützing              | 1     | ×           | ×           | ×               |              | Germany        |
| *Odontidium meadow* (Ehrenberg) Kützing   | 1     | ×           |             | ×               |              | Germany        |
| *Pinnularia Ehrenberg*                    | 8     | ×           |             | ×               |              | Germany        |
| *Pinnularia kramneri* Metzeltin           | 8     | ×           |             | ×               |              | Finland        |
| *Pinnularia permicrostauron* Krammer & Metzeltin | 8 | × | | | | Finland |
| *Pinnularia sinistra* Krammer             | 8     | ×           |             | ×               |              | Germany        |
| *Pinnularia subanglica* Krammer           | 8     | ×           |             | ×               |              | Sweden         |
| *Pinnularia subcommutata* Krammer         | 8     | ×           |             | ×               |              | Belgium        |
| *Pinnularia viridis* (Nitzsch) Ehrenberg  | 8     | ×           |             | ×               |              | Germany        |
| *Placoneis abiskoensis* Hustedt           | 6     | ×           |             | ×               |              | Sweden         |
| *Planothidium lanceolatum* (Brébisson) Lange-Bertalot | 4 | × | | | | France |
| *Psammothidium helveticum* (Hustedt) Bukhtiyarova & Round | 4 | × | | | | Switzerland |
| *Pseudostaurosira robusta* (Fusey) Williams & Round | 3 | × | | | | France |
| *Rhopalodia gibba* (Ehrenberg) O. Müller  | 14    | ×           |             | ×               |              | Siberia        |
| *Sellaphora laevisima* (Kützing) Mann     | 6     | ×           |             | ×               |              | Italy          |
| *Sellaphora pupula* (Kützing) Mereschkowsky | 6 | × | | | | Germany |
| *Stauroneis amphicephala* Kützing         | 6     | ×           |             | ×               |              | Germany        |
| *Stauroneis gracilis* Ehrenberg           | 6     | ×           |             | ×               |              | French Guiana  |
| *Stauroneis reichardtii* Lange-Bertalot et al. | 6 | × | | | | Italy |
| *Stauroneis vandevijveri* Bahls           | 6     | ×           |             | ×               |              | Montana, USA   |
| *Staurosira Ehrenberg*                    | 3     | ×           |             | ×               |              | Connecticut, USA |
| *Staurosira construens* Ehrenberg        | 3     | ×           |             | ×               |              | Connecticut, USA |
| *Staurosira construens* var. venter (Ehrenberg) Hamilton | 3 | × | | | | Germany |
| *Staurosirella lapponica* (Grunow) Williams & Round | 3 | × | | | | Sweden |
| *Staurosirella leptostauron* (Ehrenberg) Williams & Round | 3 | × | | | | Germany |
| *Staurosirella pinnata* (Ehrenberg) Williams & Round | 3 | × | | | | USA |
| *Surirella arctica* (Patrick & Freese) Veselá & Potapova | 14 | × | | | | Alaska, USA |
| *Surirella minutuar* Brébisson            | 14    | ×           |             | ×               |              | France         |
| *Ulnaria ulna* (Nitzsch) Compère          | 2     | ×           |             | ×               |              | Germany        |

**Total taxa** 39 41 61 29
Plates

Plate 1. 1–4 Lindavia antiqua (6957) 5–8 Diatoma tenuis? [D. moniliformis?] (6958) 9, 10 Meridion circulare (6956) 11 Diatoma vulgaris (6955) 12–15 Odontidium mesodon (6957) 16–21 Odontidium hyemale (6957). Scale bar: 10 µm.
Plate 2. 1–10 *Fragilaria vaucheriae?* [*F. perminuta?*] (6957) 11, 12 *Fragilaria* sp. (6956) 13–18 *Fragilaria* sp. (6957) 19, 20 *Fragilaria tenera* (6956) 21 *Fragilaria sepes* (6955) 22–26 *Fragilaria amphicephala* (6957) 27 *Ulnaria ulna?* (6958) 28–31 *Hannaea arcus* (6956). Scale bar: 10 µm.
Plate 3. 1–7 *Staurosira construens* (6957) 8–10 *Staurosirella pinnata* (6957) 11–14 *Staurosira* sp. cf. *construens* var. *venter* (6957) 15 *Pseudostaurosira robusta* (6957) 16–20 *Staurosirella lapponica* (6957) 21, 22 *Staurosira* sp. (6957) 23–30 *Staurosirella leptostauron* (6957). Scale bar: 10 µm.
Plate 4. 1–4 Achnanthidium minutissimum (6955, 6956, 6957) 5 Planothidium lanceolatum (6958) 6, 7 Psammothidium helveticum (6959) 8 Eucocconeis laevis (6956) 9 Eucocconeis alpestris (6956) 10, 11 Achnanthidium gracillimum (6956) 12 Eunotia valida (6956) 13, 14 Eucocconeis flexella (6957) 15–19 Cocconeis placentula var.? (6956, 6957, 6958) 20–26 Eunotia arcus or Eunotia arcubus Nörpel-Schempp & Lange-Bertalot (6957). Scale bar: 10 µm.
Plate 5. 1–6 Muelleria gibbula (6955) 7, 8 Neidium bergii (6955) 9, 10 Neidium sp. cf. N. bisulcatum (6955) 11 Neidium sp. cf. Neidium boreale Foged (6955) 12–15 Neidium kozlowii var. ellipticum (6955) 16–18 Neidium sp. (6955, 6957) 19 Neidiopsis binodiformis (6957) 20 Neidium fogedii (6955) 21 Neidium distinctepunctatum (6955) 22–24 Neidium bobmarshallensis (6955). Scale bar: 10 µm.
Plate 6. 1 Placoneis abiskoensis Hustedt (6957) 2 Frustulia amoseana (6955) 3 Sellaphora pupula (6957) 4 Sellaphora laevissima (6957) 5 Brachyiira microcephala (6956) 6 Luticola ventricosa (6957) 7 Luticola mutica (6957) 8–10 Diploneis krammeri (6957) 11, 12 Stauroneis gracilis (6955) 13 Stauroneis amphicephala or Stauroneis ancepsfullax Bahls) (6955) 14, 15 Stauroneis vandevijveri (S. "arctic-anceps" Van de Vijver et al.) (6955) 16, 17 Stauroneis reichardtii (?) (6955) 18 Gyrosigma sp. (6955). Scale bar: 10 µm.
Plate 7. 1, 2 Navicula cryptocephala (6955) 3 Navicula seibigiana (6956) 4 Navicula cryptotenella (6955) 5, 6 Navicula angusta (6957, 6958) 7 Navicula libonensis (6955) 8 Caloneis silicula (6957) 9, 10 Caloneis falcifera (6955) 11 Caloneis tenuis (6957) 12–15 Hygropetra balfouriana (6957) 16 Navicula vulpina (6957) 17 Navicula radiosa (6957) 18 Navicula lanceolata (6958) 19–21 Navicula subconcentrica (6955, 6956) 22, 23 Caloneis thermalis (6955) 24, 25 Caloneis alpestris (6955, 6957). Scale bar: 10 µm.
Plate 8. 1 Gomphonema sp. (6957, 6959) 2 Gomphonema olivaceoides (6958) 3 Gomphonema minusculum Krasske (6958) 4 Gomphonema lateripunctatum (6956) 5 Gomphonema pumilum? (6956) 6 Gomphonema bozenae (6957) 7 Gomphonema pseudobohemicum (6958) 8–12 Gomphonema caperatum (6958) 13 Pinnularia krammeri (6955) 14 Pinnularia sinistra (6956) 15 Pinnularia subangulara (6958) 16 Pinnularia sp. (6957) 17, 18 Pinnularia subcommutata (6957) 19 Pinnularia permicrostauron (6955) 20 Pinnularia viridis (6955). Scale bar: 10 µm.
Plate 9. 1 Cymbopleura austriaca (6957) 2 Cymbopleura lapponica (6956) 3 Cymbopleura angustata (6958) 4 Cymbopleura naviculiformis (6959) 5 Cymbopleura oblongata (6956) 6 Cymbopleura incerta (6956) 7 Cymbopleura subaequalis (6958) 8, 9 Cymbella excisiformis (6958) 10, 11 Cymbella alpestris (6957) 12–15 Cymbella neocistula (6956, 6957) 16 Cymbella cosleyi (6956) 17 Cymbella cleve-eulerae (6956) 18 Cymbella neocistula var. islandica (6956). Scale bar: 10 µm.
Plate 10. 1 Encyonema neogracile (6958) 2–4 Encyonema silesiacum (6957) 5–7 Encyonema perminutum (6956) 8 Delicata delicatula (6956) 9, 10 Delicata alpestris (6956) 11 Delicata sp. (6956) 12 Encyonopsis czarneckii (6956) 13 Encyonopsis subminuta (6956) 14 Encyonopsis alpina (6956) 15, 16 Amphora sp. (6955) 17 Amphora pediculus (6957) 18 Amphora copulata (6956) 19, 20 Amphora inariensis (6957) 21–23 Encyonopsis stafsholtii (6956) 24 Encyonopsis cesatii (6957) 25 Kurtkrammeria aequalis (6958) 26, 27 Encyonopsis montana (6956). Scale bar: 10 µm.
Plate 11. 1 Nitzschia lacuum (6956) 2–7 Nitzschia fonticola (6957) 8 Nitzschia perminuta (6957) 9–11 Nitzschia alpina (6957) 12 Nitzschia inconspicua (6957) 13 Nitzschia pusilla (6956) 14 Nitzschia pura (6956) 15 Nitzschia palea (6955) 16–19 Nitzschia homburgiensis (6957) 20 Nitzschia dissipata (6957) 21 Nitzschia dissipata var. oligotraphenta (6958) 22 Nitzschia linearis (6957) 23, 24 Nitzschia sublinearis (6956, 6957) 25 Nitzschia exilis (6955) 26–28 Nitzschia amphibia (6955) 29, 30 Nitzschia angustata (6957) 31–33 Denticula kuetzingii (6955, 6957) 34, 35 Denticula tenuis (6957). Scale bar: 10 µm.
Plate 12. 1–4 Hantzschia amphioxys (6957, 6959) 5, 6 Hantzschia sp. (6957) 7, 8 Hantzschia abundans [Hantzschia amphioxys?] (6958) 9, 10 Hantzschia elongata (6955) 11–13 Hantzschia hyperborea (6955) 14 Hantzschia sp. (6955). Scale bar: 10 µm.
Plate 13. 1–3 Cymatopleura solea (6957). Scale bar: 10 μm.
Plate 14. 1–4 Rhopalodia gibba (6955) 5–9 Surirella arctica (6955) 10 Surirella minuta (6959). Scale bar: 10 µm.

Discussion

McCarthy Spring had the highest species richness of the four habitats that were sampled, likely owing to the relative stability of this habitat compared to the lake, stream and glacier habitats. That most of the type localities for these taxa are in Europe is not surprising for two reasons: 1) Most of the early work in diatom taxonomy was conducted in Europe and 2) The existence of a Holarctic or circumboreal kingdom of diatoms has been well established (Bahls 2018). Only two of the species have their type localities in Alaska: Neidium fogedii and Surirella arctica.

Most of the 139 taxa documented from WRST are typical elements of diatom associations in the Northern Rocky Mountains of Alberta, Canada and Montana, USA (Bahls, unpublished data). Two notable exceptions from the Rocky Mountain flora are Surirella arctica and Gomphonema caperatum.

Surirella arctica is a rare Arctic species that had been recorded previously only from localities in the high Arctic (Patrick and Freese 1961, Antoniades et al. 2008, Veselá and Potapova 2014, Veselá 2017). This is the first record of this species south of 68°N
latitude. Its presence in WRST at 61°N latitude is likely made possible because of the extreme Arctic-like conditions that prevail in the park.

*Gomphonema caperatum*, collected from a moulin on the Root Glacier, has a disjunct distribution in montane regions of the eastern and far western United States (Bishop 2017, Ponader et al. 2017). In the eastern U. S., it ranges from the southern Appalachians to Quebec (Ponader et al. 2017); in the West, it ranges from the Sierra Nevada Mountains in California up through the Willamette and Puget Sound basins of Oregon and Washington, respectively (Bishop 2017). Notably, it was the most common diatom on the Root Glacier and one of the few taxa from the glacier represented by more than one or two frustules, perhaps indicating a viable population in this habitat. This may be the first confirmed record of this taxon from Alaska.

The four samples reported here provide just a hint of the diatom biodiversity in this wild and immense national park. Samples from other lakes, springs, streams and glaciers and samples from other habitats (e.g. seeps and wetlands) will likely produce hundreds more taxa and provide more clues to the origins and geographic and ecological affinities of the WRST diatom flora. Elsewhere in Alaska, there are vast areas and countless diverse habitats that remain to be explored for diatoms.

**Acknowledgements**

The authors would like to thank the following WRST personnel for their assistance with this study: Peter Frank, Morgan Gantz, Caroline Ketron, Mark Miller and Desiree Ramirez.

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