The Canadian Field-Naturalist

Disjunctions of Needle-leaved Sedge (*Carex duriuscula*) and Thread-leaved Sedge (*Carex filifolia*) in the Husky Lakes area of Northwest Territories—first records for the Canadian true Arctic and possible Pleistocene relicts

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Catling, P.M., and B. Kostiuk. 2020. Disjunctions of Needle-leaved Sedge (*Carex duriuscula*) and Thread-leaved Sedge (*Carex filifolia*) in the Husky Lakes area of Northwest Territories—first records for the Canadian true Arctic and possible Pleistocene relicts. Canadian Field-Naturalist 134(3): 231–240. https://doi.org/10.22621/cfn.v134i3.2363

Abstract

Disjunctions are reported for Needle-leaved Sedge (*Carex duriuscula*) and Thread-leaved Sedge (*Carex filifolia*) into the Arctic region of Northwest Territories at the Husky Lakes south of Tuktoyaktuk. These are significant additions to the Canadian Arctic flora and may be part of a group of relicts of the Arctic vegetation of the Pleistocene, specifically the Tundra-steppe. The occurrence of relict vegetation east of the Mackenzie Delta is east of its frequently cited eastern limit in North America.

Key words: Cyperaceae; *Carex duriuscula*; *Carex filifolia*; phytogeography; relict; Tundra-steppe; Beringia; Northwest Territories

Introduction

The opening of the Tuk Highway (Inuvik to Tuktoyaktuk, also called the ITH), Northwest Territories (NWT) in 2018 allowed easier access to this remote region of the Canadian Arctic. Previous botanical explorations of this area were limited but included those by Mackay (1958, 1963), Cody (1965), and Corns (1974). We travelled the ITH during the summer of 2018 with the aim of improving the understanding of vascular plant diversity in the adjacent Shrub Tundra habitats. Herein we report substantial range disjunctions for two native sedges and discuss our discovery in the context of Arctic flora research. We also consider if the disjunctions are post-glacial or if they are Beringian or Pleistocene relicts.

Methods

As part of an exploration of diverse habitats, we surveyed dry slopes (P.M.C. and B.K. unpubl. data) identified with the help of aerial photography and accessed by road and foot. Our general survey protocol included walking back and forth across delineated areas of a particular vegetation type using parallel transects 2 m apart. Species were identified with the aid of Cody (1965, 2000) and Porsild and Cody (1980) and recorded. Collections were made as necessary and vouchers were deposited in the Canadian Museum of Nature and are cited below. The scientific and common names of plants are from Brouillet *et al.* (2010+). General information on plants is from the literature and relevant herbaria: University of Alaska (ALA), Bruce A. Bennett collection (BABY), Agriculture and Agri-Food Canada (DAO), and Canadian Museum of Nature (CAN). Online databases including both human observations and preserved specimens were also consulted, including GBIF (2020), ARCTOS (2020), and the Consortium of Pacific Northwest Herbaria (2020).

For the listing of Beringian taxa found in the largely unglaciated region west of the Mackenzie Delta, we accepted those: (1) Beringian species (largely confined to unglaciated northwestern North America); (2) Beringian and extending east of the Mackenzie Delta and becoming progressively more isolated eastward, in some cases extending to the region of Amundsen Gulf, but not reaching to Hudson Bay; (3) Beringian or mostly Beringian species with occurrences also in the southwestern Arctic islands; (4) Beringian species disjunct into the montane region of southwestern Alberta as well extending eastward, but not to Hudson Bay; and (5) largely Beringian and also present in the prairie region of central North America.

A contribution towards the cost of this publication has been provided by the Thomas Manning Memorial Fund of the Ottawa Field-Naturalists' Club.

The major source for distributions was Porsild and Cody (1980), but we also examined maps and distributional information for all species noted in the more recent works of Aiken *et al.* (2007), Gillespie *et al.* (2015), and Saarela *et al.* (2013, 2017, 2020). These latter works contribute to a more accurate and current representation of the distribution of vascular plants in the Arctic islands and the adjacent mainland, areas included within our definition of "Beringian taxa east of the Mackenzie delta".

Results

On the dry-tundra slopes in the Husky Lakes area (also known as Imaryuk, Inuvialuktun, and the Eskimo Lakes, ~68.8704°N, 133.5331°W) south of Tuktoyaktuk, NWT we discovered substantial range disjunctions for two native sedges: Needle-leaved Sedge (*Carex duriuscula* C.A Meyer; *Carex* sect. Divisae) and Thread-leaved Sedge (*Carex filifolia* Nuttall var. *filifolia*; *Carex* sect. *Filifoliae*). The Husky Lakes area is a series of larger lakes, lowlands, and adjacent hills extending southwest of Liverpool Bay toward Inuvik. It is a loosely defined area identified by Cody (1965, opposite p. 1) and Natural Resources Canada (2006). It is within the Reindeer Grazing Preserve studied by Cody (1965), an area of ~6 million ha for which 420 species of vascular plants were recorded and for which the actual total may be 450 including more recent collections.

The two sedges are distinctive and easily distinguished from other sedge species and each other (Figure 1). The rhizomatous *C. duriuscula* has compound spikes (3–5) forming a capitate head, and the pistillate flowers have two stigmas. The tussock-forming *C. filifolia* has long solitary spikes and the pistillate flowers have three stigmas.

Both species are characteristic and often dominant in dry prairie and are widespread in the Canadian prairie regions of southern Alberta, Manitoba, Saskatchewan, and British Columbia, as well as in unglaciated Beringia including parts of Alaska, Yukon, and NWT (Vetter 2000; Mastrogiuseppe 2002; Reznicek and Catling 2002).

Figure 1. a. Needle-leaved Sedge (*Carex duriuscula*), b. Thread-leaved Sedge (*Carex filifolia*) from the Husky Lakes area of Northwest Territories. Photos: P.M. Catling.

Discussion

Extent of disjunction

Being on the north side of the Husky Lakes, *C. duriuscula* and *C. filifolia* are north of treeline and within the Tuktoyaktuk Coastal Plain ecoregion (no. 33) of the Low Arctic Ecozone (Ecological Stratification Working Group 1996) and within, although near to the edge of, the true Arctic (CAVM Team 2003; Walker *et al.* 2005). These disjunctions (Figures 2 and 3) are therefore relevant to Canada's contribution to an understanding of circumpolar Arctic flora. Although they are the northernmost records for these species in Canada, the Holarctic *C. duriuscula* extends further north in Eurasia, reaching a northern limit on Wrangel Island (71.1948°N, 179.6549°W), off the north coast of Siberia in the Chukchi Sea (Polozova 1982). The Husky Lakes record of the exclusively North American *C. filifolia* is the northernmost in Canada and shares the title of northernmost and only Arctic occurrence in North America with two collections from coastal Alaska from slightly further north: https://www.gbif.org/occurrence/2005980149 and https://www.gbif.org/occurrence/2005980170. These specimens are not currently available for examination and are not shown on Sawtell's map (Sawtell 2012: Figure 4, p. 51). The nearest sites for both species to the disjunctions in the Husky Lakes are 350 km southwest along the "south-facing steppe bluffs" of the Porcupine River in Alaska west of the Yukon border (supported by *C. filifolia*: *D.F. Murray et al. 12107*, at 66.98°N, 142.82°W, ALA 18384; and *C. duriuscula*: *D.F. Murray et al. 12109*, at 66.98°N, 142.82°W, ALA 18386, 18391, *M.K. Reynolds s.n.* 95-586, at 66.98°N, 142.82°W, ALA

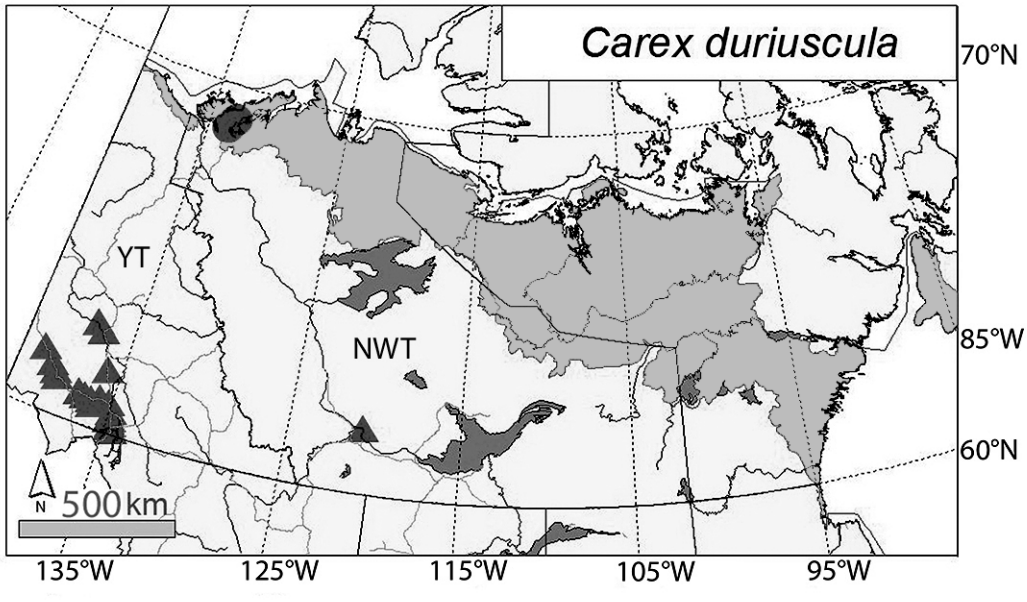

FIGURE 2. Distribution of Needle-leaved Sedge (*Carex duriuscula*) in northwestern Canada including Yukon Territory (YT) and Northwest Territories (NWT). Dots show occurrence of *C. duriuscula* in the Husky Lakes area. Triangles show occurrences elsewhere in northwestern Canada, based on Porsild and Cody (1980) and Cody (2000) and on specimens in CAN and DAO. Both types of symbols are centred on locations. The Southern Arctic Ecozone, as defined by the Ecological Stratification Working Group (1996), is shown in grey shading.

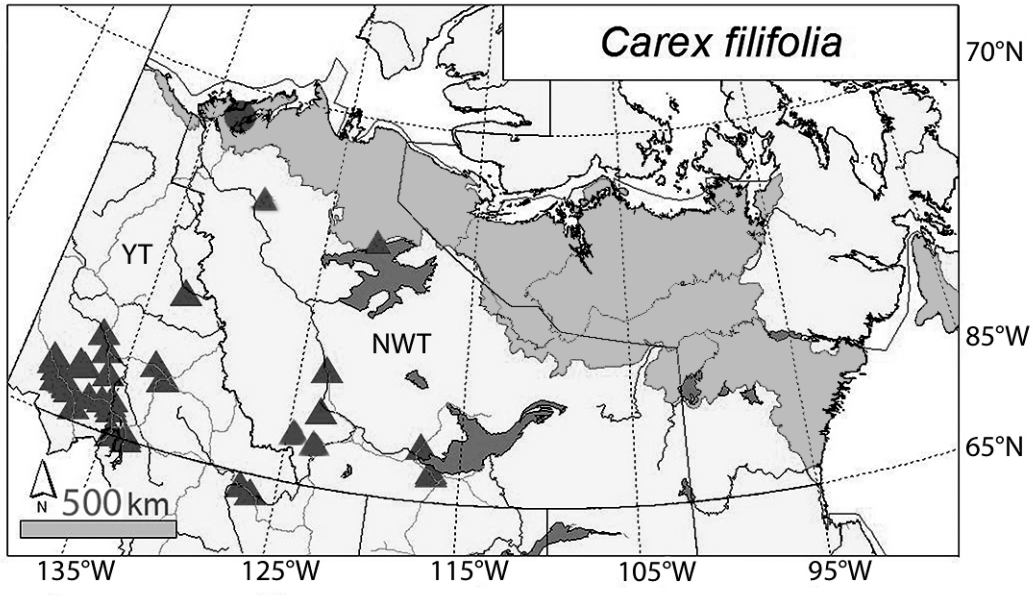

FIGURE 3. Distribution of Thread-leaved Sedge (*Carex filifolia*) in northwestern Canada including Yukon Territory (YT) and Northwest Territories (NWT). Dot shows occurrence of *C. filifolia* in the Husky Lakes area. Triangles show occurrences elsewhere in northwestern Canada, based on Porsild and Cody (1980) and Cody (2000) and on specimens in CAN and DAO. Both types of symbols are centred on locations. The Southern Arctic Ecozone, as defined by the Ecological Stratification Working Group (1996), is shown in grey shading.

13566, *R. Havenstein & J. Boron s.n.* at 66.98°N, 133.08°W, ALA 131318).

At the Husky Lakes, *C. duriuscula* is ~1000 km northwest of the only previous report in NWT near Fort Simpson (Porsild and Cody 1980 *sub Carex stenophylla* subsp. *eleocharis* (L.H. Bailey) Hultén; *W.J. Cody and K. Spicer 11450* at 61.78°N, 120.70°W, DAO, US 2456388), ~750 km north of the nearest location in Yukon on the east side of Kluane Lake (*B.A. Bennett et al. 06-0084* at 61.17°N, 138.44°W, BABY). *Carex filifolia* in the Husky Lakes is 250 km northwest of nearest locations in NWT on the east side of the Mackenzie River east of Tsiigehtchic (*DeCarlo and Kershaw s.n.* at 67.16°N, 129.97°W, CAN 10036734—a previously unpublished record) and 570 km from a site on the north arm of Great Bear Lake (Cody and Talbot 1978; Porsild and Cody 1980; whereabouts of supporting specimen[s] unclear). Other NWT sites are indicated in maps by Cody and Talbot (1978) and Sawtell (2012).

Although *C. filifolia* is shown in the Husky Lakes area by Cook and Roland (2002: 222, map 46), this *C. filifolia* map is identical to the map of *Carex eburnea* Boott (map 45) directly above it. The *C. eburnea* map (45) correctly depicts its range with the single occurrence in Yukon shown by Cody (2000: 148) and the location in the Husky Lakes shown in Porsild and Cody (1980: 178, map 231). The *C. filifolia* map (map 46) does not depict the range of *C. filifolia*, which is extensive in southwestern Yukon (Cody 2000: 149). The earlier mapping of *C. filifolia* from the Husky Lakes by Cook and Roland (2000) is thus an error based on a repeated map representing *C. eburnea*, and the report herein of *C. filifolia* from the Husky Lakes is the first.

Glacial relict or Recent (Holocene)

Habitats of *C. duriuscula* and *C. filifolia* in the Husky Lakes are small 200–5000 m^2 southwest (SW)-facing slopes of 30–45° dominated by a rich herb and graminoid cover (Figure 4). They are anomalies in a landscape strongly dominated by Shrub Tundra, wetlands, and lakes. During the period of climate changes between 4500 and 9500 years ago (Ritchie 1977, 1984), the extensive dry ground herb and graminoid cover is believed to have shrunk to these very small and widely scattered remnants. Shrub Tundra became predominant on higher ground as climate stabilized. The sloping habitats, due to their angle and SW orientation, receive more direct sunlight than the surrounding landscapes and are thus warmer and able to retain

Figure 4. A habitat of Needle-leaved Sedge (*Carex duriuscula*) in the Husky Lakes area of Northwest Territories (lower right), 27 June 2018. The sedge and associated plants are the same species that dominate the more extensive remnants of Tundra-steppe in Russia. The flora suggests a more eastern historical presence of this habitat in Canada than previously thought. The surrounding Shrub Tundra dominated the landscape after 4500 years ago. The slope is warmer and drier than the surrounding landscapes and was thus able to retain a rich relict flora associated with the previously drier climate. Photo: P.M. Catling.

a rich flora, once more extensive, that is associated with a previously drier climate.

Although we prefer a relict hypothesis to explain the occurrence of the two sedges and many other Beringian plants in the Husky Lakes region, there are other explanations. One of these is postglacial migration. However, this would not explain the restricted area occupied by the plants because the moist postglacial environment would have been unsuitable for plants of dry situations and it requires long-distance dispersal to small, isolated areas of occurrence. If the relictual populations are considered equivalent to islands, the small size of the island targets and the increasing distance to western or southern sources suggests that postglacial dispersal is unlikely according to the fundamentals of island biogeography where dispersal is negatively influenced by island size and distance (MacArthur and Wilson 1967).

Long distance dispersal has recently been suggested to be common in Arctic plants and possibly even relatively frequent (Alsos *et al.* 2015). However, there is a distinct eastern and western flora in the Canadian Arctic. Isolated disjunctions from the west to the east (and *vice versa*) are unusual. Major disjunctions from the south to the north are also unusual. However, there may have been extensive late glacial or postglacial dispersal over long distances within some major phytogeographic regions as suggested by Shönswetter *et al*. (2008). Although some Beringian species may have colonized areas west of the Mackenzie Delta from the west and/or south in postglacial times, it becomes difficult to explain why so many species of varying ecology and provenance have approximately the same eastern limit west of the Mackenzie Delta (see below) unless there was a landscape boundary, such as continental ice, that existed until a period of rapid climate change.

Another possible explanation is very recent introduction, which could explain why previous botanical surveys in the very extensive area east of the Mackenzie Delta (Mackay 1958, 1963; Cody 1965; Corns 1974), and plant collections made in the area as part of grazing studies by G. Scotter in 1965 and 1966 (CWS-Edmonton, DAO) and J. Lambert in 1968 and 1969 (CCO, DAO) noted by Porsild and Cody (1980) did not record these plants. The area was a wilderness with only a winter road connecting Inuvik and Tuktoyaktuk until the Tuk Highway opened in 2018. Consequently, there was insufficient human traffic to explain the disjunctions as recent dispersal by humans. The very large size of the area, isolated and rare occurrence of disjuncts, and the short duration and incomplete coverage of previous botanical surveys can readily explain how these disjunct species were overlooked.

There is also a possibility of introduction with Reindeer (*Rangifer tarandus*). The Husky Lakes are part of the Reindeer Grazing Preserve, so *C. duriuscula* may have been introduced with the Reindeer. The Reindeer originated in Kotzbue Sound, Alaska, but before that they had been imported from Siberia between 1891 and 1902 (Scotter 1972; Treude 1975). The herd of 3400 animals was driven along the coast starting in 1929, arriving on the east bank of the Mackenzie in 1935. *Carex duriuscula* has not been found along this west and north coast of Alaska or north coast of Yukon (Hultén 1968; Cody 2000; Arctos 2020; GBIF 2020). It seems unlikely that its seeds would be carried along the coast to NWT during this five year journey of a continuously moving herd in which only 10% of the original animals survived (Treude 1975).

Relicts of a past vegetation

Because Canada was covered by the Laurentide and Cordilleran Ice sheets until ~12 000 years ago, it was only the unglaciated landscape of the northwest, i.e., eastern Beringia, where the Pleistocene megafauna, including herbivores such as Eastern Moose (*Alces alces* L. subsp. *americana*), Alaskan Moose (*Alces alces* L. subsp. *gigas*), Steppe Bison (*Bison priscus* Bojanus), Helmeted Muskox (*Bootherium bombifrons* Harlan), Giant Moose (*Cervalces latifrons* Johnson), Cabilline Horse (*Equus* sp. 1), Hermione Horse (*Equus* sp. 2), Woolly Mammoth (*Mammuthus primagenius* (Blumenbach)), Muskox (*Ovibos moschatus* Zimmermann), Dall Sheep (*Ovis dalli* Nelson), Caribou (*Rangifer tarandus* L.), and Saiga Antelope (*Saiga tatarica* L.), roamed the somewhat controversial Tundra-steppe (Matthews 1979; Cwynar and Ritchie 1980; Blinnikov *et al.* 2011; Stuart 2015). The Arctic Steppe Biome, also known as the Mammoth-steppe and the largest biome that ever existed on earth, may have extended east to the Mackenzie Delta (Matthews 1979; Guthrie 1990; Elias *et al.* 2000).

Within NWT the unglaciated landscape also included a downward extension into the Mackenzie Mountains. An area of Pleistocene Tundra-steppe may have existed east from the Mackenzie Delta, the frequently-cited eastern boundary, to the Caribou Hills, the Husky Lakes, the Tuktoyaktuk Peninsula, the Anderson River, and north to Banks and Victoria Islands, based on mapping of unglaciated landscapes (Dyke *et al.* 2002, 2003; Dyke 2004). This is further supported by Pleistocene faunal remains, including horses (*Equus* spp.), Steppe Bison, Woolly Mammoths, and Saiga Antelope, most mapped and discussed by Harrington (2007) and Zazula *et al.* (2009). Saiga Antelope are valuable paleoenvironmental indicators of dry, steppe-like, grasslands (Harrington and Cinq-Mars 1995; Harrington 1998).

They occurred on the Baillie Islands, which are 270 km northeast of the Husky Lakes disjuncts, 15 000 years ago (Harrington and Cinq-Mars 1995) and prior to vegetation change in the region, which began 9500 years ago. At this time the dominant regional vegetation apparently changed from graminoid and herb-dominated Tundra-steppe to spruce forest or parkland and this was replaced by Dwarf Shrub Tundra after 4500 years ago, this persisting to the present (Ritchie 1977, 1984).

The two disjunct sedges are of particular interest as possible indicators of the Pleistocene Tundra-steppe east of the Mackenzie Delta for three reasons:

(1) As plants of dry ground capable of existing as dominants, adapted to grazing pressure and preferred food of some surviving large mammalian grazers (e.g., Hoefs 1979; Vetter 2000; Bazha *et al.* 2009; Reinecke *et al.* 2017; Chitry *et al.* 2019), the two sedges have characteristics that are expected in plant species associated with Pleistocene megafauna. Herbs may have played a more important role in megafaunal diet and the Tundra-steppe may have been a patchwork of dry, mesic, and wet habitats including extensive dry grasslands (Willerslev *et al.* 2014). However, there can be little doubt that the megafauna was adapted to the dry grasslands based on tooth structure (e.g., Guthrie 1990) and other anatomy, and it may have been adapted particularly to these two sedges.

(2) The two species draw attention to the existing phytogeographic evidence for a relict flora based on restricted distributions. The continental portion of the eastern extension of unglaciated landscape described above is treated as Phytogeographical Province 3 by Porsild and Cody (1980: 1–3) partly on the basis of "a few Amphi-Beringian species". In fact, there are more than a few restricted Beringian species that may be regarded as potential Pleistocene relicts in this area. We estimate 80 Beringian species (depending on how strictly they are defined) based on the maps in Porsild and Cody (1980). These represent 17.7% of the local flora of ~450 species (Cody 1965, P.M.C. and B.K. pers. obs.). They include plants of (1) wetlands such as Spruce Muskeg Sedge (*Carex bigelowii* Torrey ex Schweinitz subsp. *lugens* (T. Holm) T.V. Egorova) and Arctic-flower (*Wilhelmsia physodes* (Fischer *ex* Seringe) McNeill); (2) moist saline shores such as Marsh Felwort (*Lomatogonium rotatum* (L.) Fries var. *rotatum*) and Northern Primrose (*Primula borealis* Duby); (3) Shrub Tundra such as Narrow-leaved Sawwort (*Saussurea angustifolia* (L.) de Candolle) and Steven's Meadowsweet (*Spiraea stevenii* (C.K. Schneider) Rydberg), and (4) species of dry ground. It is the last group that has often been emphasized in discussion of the Arctic-steppe biome relicts because of the presumed dry conditions leading to a previously more widespread plant community of drier ground dominated by herbs and grasses. There are 45 restricted Beringian species of drier ground mapped for this area by Porsild and Cody (1980; Tables 1, 2 and 3). This is an impressive list of potential relicts. The two disjunctions are not only additions increasing the list to 47 species but are particularly good examples of potential relicts. This group is an important reminder of the value of local floristic information as one of many local proxies that need to be used to elucidate the character of the Pleistocene Arctic (Blinnikov *et al.* 2011).

(3) *Carex duriuscula* is a valuable species upon which to build the concept of existing relict Tundra-steppe in NWT because it expands the context of the idea to include some of the better-known examples. In his extensive discussion of the relict steppe vegetation in Asian (western) Beringia, Yurtsev (1982: 162, 163, 168, 169, 171) also mentions dominant species and he alludes to *C. duriuscula* more than to any other. He illustrated a steppe dominated by *C. duriuscula* in the Indigirka River valley (Yurtsev 1982: Fig. 3, 152). He considered "the vegetation of Wrangel Island to be the closest living analog to the sort of vegetation that clothed northern Beringia during Pleistocene time" (Yurtsev 1982: 157). An extensive area dominated by *C. duriuscula* is described as an indicator and dominant of rich steppe habitats, with 50–60 associated species on Wrangel Island. *Carex duriuscula* and Prairie Sagebrush (*Artemisia frigida* Willdenow) were considered as "true steppe plants" by Yurtsev (1982: 174). The Siberian examples of putative Tundra-steppe relicts are extensive and they include all slope aspects of the landscape. The Indigirka Steppe is 30 km long and up to 4 km wide and Wrangel Island, with an area of 7511 km^2, off the north coast of Siberia, was the last stand of the Mammoth, in this case the unusually small Wrangel Island Dwarf Mammoth (*Mammuthus primigenius* subsp. *wrangeliensis* Garutt, Averianov & Vartanyan), which died out only 4000 years ago (Vartanyan *et al.* 1995).

Carex filifolia has been discussed by Vetter (2000) as part of relict grasslands in southwestern Yukon. In this area it is a co-dominant species with *A. frigida*.

Among the close associates of *C. duriuscula* and *C. filifolia* in the Husky Lakes are Prairie Sagebrush, Purple Reedgrass (*Calamagrostis purpurascens* R. Brown), Blunt Sedge (*Carex obtusata* Liljeblad), Weak Arctic Sedge (*Carex supina* Willdenow *ex* Wahlenberg var. *spaniocarpa* (Steudel) Hultén), and Prairie Pasqueflower (*Pulsatilla nuttalliana* (de Candolle) Berchtold *ex* J. Presl (*P. multifida*)). Yurtsev (1982) mentions these as dominant species in the Russian Tundra-steppe. These are more than just rare potential relicts scattered over the land-

TABLE 1. Dry land species largely restricted in Canada to Beringia and its eastern limit (Phytogeographical Province 3) as mapped by Porsild and Cody (1980) and other sources (see Methods). Many of these also occur eastward to Amundsen Gulf and the southwestern Arctic Islands. Scientific names are in alphabetical order by genus and species.

Scientific name	Common name
Androsace chamaejasme Wulfén ex Host subsp. *lehmanniana* (Sprengel) Hultén (*A. chamaejasme* var. *arctica*)	Lehmann's Fairy-candelabra
Arnica griscomii Fernald subsp. *frigida* (C.A. Meyer ex Iljin) S.J. Wolf (*Arnica louisiana* subsp. *frigida*)	Griscom's Arnica
Artemisia borealis Pallas subsp. *richardsoniana* (Besser) Korobkov (*Artemisia richardsoniana*)	Richardson's Wormwood
Artemisia tilesii Ledebour	Tilesius Wormwood
Astragalus australis var. *glabriusculus* (Hooker) Isely (*Astragalus richardsonii*)	Aboriginal Milk-vetch
Astragalus bodinii E. Sheldon	Bodin's Milk-Vetch
Bupleurum americanum J.M. Coulter & Rose	American Thoroughwax
Carex petricosa Dewey var. *petricosa*	Rock-dwelling Sedge
Cnidium cnidiifolium (Turczaninow) Schischkin	Jakutsk Snow Parsely
Dryas punctata Juzepczuk	Sticky Mountain Avens
Elymus macrourus (Turczaninow) Tzvelev (*Agropyron sericeum*)	Silky Wildrye
Eremogone capillaris (Poiret) Fenzl var. *capillaris* (*Arenaria capillaris* var. *nardifolia*)	Thread-leaved Sandwort
Erigeron porsildii G.L. Nesom & D.F. Murray	Porsild's Fleabane
Erigeron yukonensis Rydberg	Yukon Fleabane
Eurybia sibirica (Linnaeus) G.L. Nesom (*Aster sibiricus*)	Siberian Aster
Gentianopsis detonsa (Rottbøll) Ma subsp. *detonsa* (*Gentianopsis richardsonii*)	Sheared Gentian
Koenigia alaskana (Small) T.M. Schuster & Reveal var. *glabrescens* (Hultén) T.M. Schuster & Reveal (*Polygonum alaskanum*)	Alaska Wild Rhubarb
Lupinus arcticus S. Watson	Arctic Lupine
Micranthes reflexa (Hooker) Small (*Saxifraga reflexa*)	Yukon Saxifrage
Oxytropis borealis var. *viscida* (Nuttall) S.L. Welsh (*Oxytropis glutinosa*)	Sticky Locoweed
Oxytropis campestris var. *varians* (Rydberg) Barneby (*Oxytropis hyperborea*)	Variable Locoweed
Packera hyperborealis (Greenman) Á. Löve & D. Löve (*Senecio hyperborealis*)	Boreal Groundsel
Phlox richardsonii Hooker (group)	Richardson's Phlox
Poa ammophila A.E. Porsild	Sand Bluegrass
Polemonium acutiflorum Willdenow ex Roemer & Schultes	Tall Jacob's-ladder
Polemonium boreale Adams	Northern Jacob's-ladder
Polemonium pulcherrimum Hooker	Showy Jacob's-ladder
Potentilla hookeriana Lehmann (*Potentilla nivea* var. *hookeriana*)	Hooker's Cinquefoil
Salix phlebophylla Andersson	Skeleton-leaved Willow
Silene involucrata subsp. *tenella* (Tolmachew) Bocquet (*Melandrium taimyrense*)	Taylor's Arctic Catchfly
Silene repens Patrin (*S. repens* ssp. *purpurata*)	Pink Catchfly
Symphyotrichum pygmaeum (Lindley) Brouillet & S. Selliah (*Aster pygmaeus*)	Pygmy Aster
Taraxacum alaskanum Rydberg	Alaska Dandelion
Tephroseris frigida (Richardson) Holub (*Senecio atropurpureus*)	Purple-haired Groundsel

scape of Phytogeographical Province 3 east of the delta. Coherent isolated communities exist that are in many ways similar to those in Russia identified by a Russian authority.

Although Yurtsev's work is a favourite and classical reference for relict Tundra-steppe, there have been more recent studies that have also indicated *C. duriuscula* as a dominant species of such relicts (Schweger 1997; Reinecke *et al.* 2017; Chitry *et al.* 2019). Other recent work has suggested that only partial analogues will be found because Tundra-steppe was likely a herbivore-driven biome (Zimov *et al.* 1995), and most of the keystone herbivores are now extinct. Regardless of how complete our concept of Tundra-steppe vegetation is, the disjunct sedges may be an informative part of it.

Voucher specimens

Carex duriuscula C.A. Meyer, Needle-leaved Sedge —CANADA, NORTHWEST TERRITORIES: Husky Lakes:

Table 2. Beringian and prairie species of dry ground in Phytogeographical Province 3. Some populations that occurred south of the continental ice sheet during the glacial period may have simply moved north into the present prairie region. The restricted Beringian populations may have persisted from the Pleistocene. Based on mapping by Porsild and Cody (1980) and other sources (see Methods). Scientific names are in alphabetical order by genus and species.

Scientific name	Common name
Agoseris glauca (Pursh) Rafinesque var. *dasycephala* (Torrey & A. Gray) Jepson (*Agoseris glauca scorzoneraefolia*)	Alpine Agoseris
Anticlea elegans (Pursh) *Rydberg* (*Zigadenus elegans*)	Mountain Death Camas
Artemisia frigida Willdenow	Prairie Sagebrush
Bromus pumpellianus Scribner	Pumpelly's Brome
Carex obtusata Liljeblad	Blunt Sedge
Festuca altaica Trinius	Northern Rough Fescue
Pulsatilla nuttalliana (de Candolle) Berchtold ex J. Presl (*Pulsatilla ludoviciana*, *Anemone patens*)	Prairie Pasqueflower

Table 3. Beringian and montane (mostly southwestern Alberta) species of dry ground in Phytogeographical Province 3. Those populations that occurred south of the cordilleran ice sheet may have moved into the mountains and foothills afterward. Those in Beringia may represent long time persistence in this region. Based on mapping by Porsild and Cody (1980) and other sources (see Methods). Scientific names are in alphabetical order by genus and species.

Scientific name	Common name
Plantago canescens Adams	Hairy Plantain
Salix barrattiana Hooker	Barratt's Willow
Salix farriae C.R. Ball	Farr's Willow
Senecio lugens Richardson	Small Black-tip Ragwort

southwest-facing steep (45°) slope, 68.8704°N, 133.5331°W, 28 June 2018, *P.M. Catling & B. Kostiuk 2018338* (DAO); southwest-facing 40° slope, 69.1010°N, 133.0868°W, 11 July 2019, *P.M. Catling & B. Kostiuk 2019400* (CAN 10102106).

Carex filifolia Nuttall var. *filifolia*, Thread-leaved Sedge—Canada, Northwest Territories: Husky Lakes: southwest-facing hilltop, 69.1833°N, 133.0158°W, *P.M. Catling & B. Kostiuk 2019410* (CAN 10102107, DAO).

Author Contributions

Both authors contributed to all parts of the study.

Acknowledgements

Jeff Saarela and Bruce Bennett kindly provided many helpful comments. Jennifer Doubt assisted with the examination of specimens at The Canadian Museum of Nature and the preparation of vouchers.

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Received 19 September 2019
Accepted 21 August 2020
Associate Editor: J.M. Saarela