THE *CLAYTONIA ARCTICA* COMPLEX IN ALASKA—ANALYZING A BERINGIAN TAXONOMIC PUZZLE USING TAXONOMIC CONCEPTS[1]

Stefanie M. Ickert-Bond,[2]* *David Murray,*[2] *Margaret G. Oliver,*[2,3] *Hazel K. Berrios,*[2] *and Campbell O. Webb*[2]

ABSTRACT

Trans-Beringia taxa often present complex puzzles for taxonomists, a reflection of differing traditions and opinions, taxonomic approaches, and access to material from both sides of the Bering Strait. There is wide biological variation in perceived or circumscribed taxa whose populations are widespread within the regions and yet biogeographically isolated in Asia and/or America. The *Claytonia arctica* complex is one such example; it illustrates these issues well and has been dealt with by North American and Russian botanists in decidedly different ways. We reviewed specimens and examined the various taxonomic concepts of *C. arctica* through time and source publications. The relationships (alignments) among taxonomic concepts are presented in a graphical format. We found that much of the confusion related to *C. arctica* in Beringia stems from overlooking *C. scammaniana* Hultén sensu Hultén (1939), and placing too much emphasis on the woody caudex and perennation structures, during the creation of two taxonomic concepts: *C. arctica* Adams sensu Porsild and *C. porsildii* Jurtzev sensu Yurtsev. The *C. arctica* complex (in our current sense) is an evolutionary work in progress, resulting in partially differentiated races with much overlapping variability and intergradation of characters (particularly in *C. scammaniana* according to our current sense) that have not reached the level of stability (i.e., individuals may still intergrade freely) usually associated with the concept of species in other arctic lineages.

Key words: Alignment, Beringia, *Claytonia arctica* complex, herbarium specimens, synthesis, taxonomic concepts.

It is impossible to fully understand the origin of Alaska's flora without knowing a great deal about floristic contributions from the Russian Arctic. Many plant taxa arrived in Alaska from northeastern continental Asia via the Bering Land Bridge while the Bering Strait and adjacent areas were exposed and glacier-free—the Beringian refugium—during successive intervals of continental Ice Age glaciation (Hultén, 1968; Elias et al., 1996; Ickert-Bond et al., 2009, 2013; Wen et al., 2010, 2016; Graham, 2018). During the Last Glacial Maximum (LGM) rapid climate change drove episodes of biotic expansion, interchange between Asia and America, isolation, diversification, and extinction on varying temporal and spatial scales. Boreal climates, landscapes, and vegetation changed repeatedly during the Pleistocene, affecting the movement of native taxa. These movements had large impacts on the genetic and taxonomic diversity of present-day flora and fauna (Tremblay & Schoen, 1999; Abbott et al., 2000; Hewitt, 2000; Abbott & Brochmann, 2003; Fedorov et al., 2003; Petit et al., 2003; Cook et al., 2005; Beatty & Provan, 2010), producing in Beringia and beyond a biotically distinctive region.

Differing taxonomic views on the delimitation of trans-Beringia taxa have caused taxonomic controversies due to differing traditions and opinions, taxonomic approaches, and access to material from both sides of the Bering Strait, often combined with wide biological variation in taxa whose populations are widespread within Beringia, yet biogeographically isolated in either western Beringia (Russia) or eastern Beringia (Alaska and Yukon).

Note to reader: when a taxon name is mentioned without further specification of the source that would specify the meaning (i.e., sensu) to some degree, the name is being used in our "current preferred sense." Otherwise, if the meaning being discussed is clearly not ours or we wish to distinguish it from current use, we use or reuse "sensu," "sec.," or "according to."

One important example of a Beringian taxonomic puzzle is the plant genus *Claytonia* L. (spring beauty, Montiaceae). Species in *Claytonia* sect. *Rhizomatosae*

---

[1] This research was financially supported by the National Science Foundation, Division of Biological Infrastructure, award #1759964, "ABI Innovation: Taxonomically intelligent data integration for a new Flora of Alaska." We are very grateful to Nico Franz for comprehensive review of and comments on the manuscript and to Bruce Bennett and Ian Jones for providing access to images of specimen collections from throughout the range of the *Claytonia arctica* complex.

[2] Herbarium (ALA), University of Alaska Museum of the North, University of Alaska Fairbanks, 1962 Yukon Dr., Fairbanks, Alaska 99775-6960, U.S.A.

[3] Herbarium (TENN), University of Tennessee, Temple Hall, 1818 Andy Holt Ave., Knoxville, Tennessee 37996-2800, U.S.A.

* Author for correspondence: smickertbond@alaska.edu

doi: 10.3417/2019491 ANN. MISSOURI BOT. GARD. 104: 478–494.

A. Gray ex Poellnitz (1932), with a rhizomatous habit, a stout fleshy caudex, and restricted to high northern latitudes (O'Quinn & Hufford, 2005), have been particularly misunderstood (Fig. 1): *C. arctica* Adams (1817), *C. sarmentosa* C. A. Mey. (Meyer, 1829), and *C. scammaniana* Hultén (1939) are herein referred to as the *C. arctica* complex.

Claytonia sarmentosa is morphologically distinct from *C. arctica* sensu Adams and *C. scammaniana* sensu Hultén in both above and below-ground structures. Leaves of *C. sarmentosa* are broadly spatulate and characteristically tapered at the base (Miller & Chambers, 2006). Vegetative reproduction is almost exclusively by stolons, which has been emphasized by Hultén (1939) as what distinguishes *C. sarmentosa* from *C. arctica*. We thus focus on *C. arctica* and *C. scammaniana* in most of our discussions.

There are three different traditions or approaches to delimiting the full taxonomic meaning or application of the name *Claytonia arctica*: a Russian approach championed by Volkova (1966) and Yurtsev (in Elven et al., 2011) and an American approach, based largely on the revisionary work of Miller (Miller, 2003; Miller & Chambers, 2006). Yet another view is that of the Checklist of the Panarctic Flora (PAF), which takes both approaches into account and comes to a consensus for nomenclature of arctic *Claytonia* taxa (Elven et al., 1999, 2011).

The PAF circumscribes species more broadly than done in most previous (and some current) Russian treatments but more narrowly than in some current North American treatments (Elven et al., 2011). Species rank is applied for taxa differing more or less disjunctly from their assumed relatives in several (assumed) independently inherited characters, usually also with some (assumed) reproductive barriers toward their relatives. The reproductive isolation and absence of hybridization is in most cases based on circumstantial evidence, as very little factual evidence is available for the majority of arctic plants. One important feature of the PAF is that sympatric but morphologically nonoverlapping taxa are considered species rather than subspecies (which differs from many *Flora of North America* authors). Another difference is the fact that hybridogeneous taxa are considered species in their own right, and not as hybrids, when they have an independent reproduction and sometimes also an independent range (i.e., more than a "first" hybridization event or a hybrid swarm). This is the case both with hybridization products at the same ploidy level, where some stabilization is inferred to have taken place, and with documented or assumed allopolyploids, which are rather common in the Arctic (Brochmann et al., 2004).

The difficulty of consistent identification of plants in this complex is a function of competing taxonomic theories (see above) that has resulted in many cases of renaming specimens via annotation labels. We document the frequency and nature of such switches in this paper. Alternative taxonomic perspectives on focal plant lineages can lead to the application of the same name for a different understanding of the circumscription of a taxon. These different uses are referred to as different *taxonomic concepts* (Berendsohn, 1995; Franz et al., 2008). Cases where the same valid name is applied to different circumscriptions warn us that to accurately apply a taxonomic name to a specimen we must specify the context in which the name is used, e.g., *Claytonia arctica* Adams sensu (or sec.) Porsild (1974/1975). Ideally, the presentation of a taxon in a revision, flora, or monograph should include a history of the relevant taxonomic concepts used for names and synonyms, and how they relate to each other, which was executed in exemplary fashion in Weakley's *Flora of the Southern and Mid-Atlantic States* (Weakley, 2015).

Since taxonomic circumscriptions are typically intended to delineate sets of biological traits as well as specimens or living individuals contained within a species, two such circumscribed sets can be related in five ways: identical, overlapping, not overlapping, and as a subset or superset (Franz et al., 2008). Few revisions and floras include these taxonomic concept relationships, though some good examples exist: Koperski et al. (2000), Franz and Cardona-Duque (2013), Weakley (2015), and the issue has been recognized by the biodiversity standards organization TDWG since 2005 (Taxonomic Names and Concepts Interest Group, 2006). In this review of the *Claytonia arctica* complex, we present the relationships among relevant taxonomic concepts in a graphical way. Looking forward, we anticipate that including such outlines of taxonomic concept relationships will make taxonomic summaries, such as the new Flora of Alaska (<https://floraofalaska.org>), more useful to those trying to understand taxa and aggregate specimens.

MATERIALS AND METHODS

BERINGIA

Beringia stretches from Canada's Mackenzie River to northeastern Russia's Lena River and has served as a high-latitude glacial refugium and crossroad between continents. While Sushkin (1925) recognized the importance of this unique area, the term Beringia was coined by Hultén (1937) who noted the biogeographical significance of the connection. The Beringian flora was highly diverse during the LGM, with denser, more Asian-influenced communities in the south, and sparse High Arctic communities in the north (Young, 1982). East-

Figure 1. *Claytonia scammaniana* (*J. Sias 46*, CAN-358227, seen as photograph!) showing the taxonomic complexities in the *C. arctica* complex. The specimen was first identified as *C. sarmentosa* in 1971, then as *C. arctica* sensu Porsild in 1979, and most recently as *C. scammaniana* in 1991.

west exchange has been characterized as asymmetric (Hopkins, 1979) with most taxa originating in northeastern Asia and moving to North America (Wen et al., 2010, 2016). Asymmetric dispersal was generated during glacial maxima by Beringia's western border in Siberia, which permitted Asian species to colonize the land bridge from the relatively flat and extensive plains of western Siberia.

Western Beringian topography allowed cold and glacial continental conditions to develop slightly earlier and more intensively than in the mountainous terrain of northwestern North America (Graham, 2018). The Coriolis effect also directs winds from west to east and enhanced the preferential exchange of propagules from western Beringia across the Bering Land Bridge (Gal-Chen, 1984). In contrast, eastern Beringia (Alaska and Yukon) was effectively isolated from the rest of North America by the Laurentide Ice Sheet (Pielou, 1991). Beringia is therefore key to understanding post-glacial dynamics within and among species in Alaska and the Russian Far East. Now, the flora of Beringia is on the move again, this time due to rapid anthropogenic climate change (Parmesan & Yohe, 2003; Wilmking et al., 2004; Juday et al., 2015; Phoenix & Bjerke, 2016).

THE *CLAYTONIA ARCTICA* COMPLEX

Hultén suggested that the post-glacial flora of Alaska has been associated with particular patterns of migration from Pleistocene refugia (Hultén, 1937), and in particular that *Claytonia arctica*, *C. acutifolia* Pall. ex Willd., and *C. tuberosa* Pall. ex Willd. in the sense of Hultén (1937) survived in northern Beringia coastal refugia, while *C. sarmentosa* (sensu Hultén) survived in a southern Beringian refugium. Sequence variation of the nuclear ribosomal internal transcribed spacer region (*nr*ITS) and plastid genic region *trn*K/*mat*K was extremely low within the Beringian species of sections *Claytonia* and *Rhizomatosae* (O'Quinn & Hufford, 2005), reflecting either low rates of sequence divergence within the markers used or recent divergence. Further support for a recent divergence comes from divergence time estimation based on the plastid *ycf*3-*trn*S intergenic spacer, which estimated section *Rhizomatosae* (including *C. arctica*, *C. scammaniana*, *C. sarmentosa*, and others according to Hultén, 1937) to have diverged from section *Claytonia* ca. 3.62 million years ago (Ma) (Jeffers, 2015) during the Pleistocene. A northward migration for Beringian species of section *Rhizomatosae* from low latitudes in North America was proposed by O'Quinn and Hufford (2005) based on the findings of a southern and a derived northern clade within section *Rhizomatosae*, albeit weakly supported. A more thorough analysis of sequence variation in the *C. arctica* complex is needed to address biogeographical scenarios in detail.

Claytonia is easily identified by its five showy petals, two sepalous bracts, two opposite cauline leaves, and often a basal rosette of leaves (Fig. 2). The genus is well represented in Alaska, but despite its charismatic appearance and long history of collection, there is much confusion around species delineation in the *C. arctica* complex. Porsild (1974/1975) commented on the status of *C. arctica* in North America as he understood the species in his publication *Materials for a Flora of Central Yukon Territory*. While reviewing the specimens his brother Robert had collected along the Dempster Highway in Yukon (*R. T. Porsild 477*), there was one that he determined as *C. arctica* and for which he provided a photo (Fig. 3, Appendix 1). He then cited three Alaska specimens at the Canadian Museum of Nature (CAN) from the Brooks Range that were also his *C. arctica* (*R. D. & M. Wood 341*, *L. A. Spetzman 784*, *L. A. Spetzman 1878*). His view was that *C. arctica* had been confused with *C. sarmentosa*. Next, he noted that the Seeman (1852) illustration of *C. sarmentosa* from Cape Lisburne, Alaska, was clearly not that species but *C. arctica*. Hultén (1927) provided a photo of a specimen from Kamchatka that he determined as *C. arctica*. Whereas Hultén (1968) showed *C. arctica* in the Pribilof Islands and the Aleutian Islands, it is interesting that Volkova (1966) excluded those localities from her treatment of the species for the Flora of the Russian Arctic, which includes comments on distribution in the "foreign Arctic."

TALLYING SPECIMEN DETERMINATIONS

In order to quantify the variation in names given to specimens of plants in the *Claytonia arctica* complex, we recorded all of the determinations for a representative subset of collections. Determinations included both the original label determination and all subsequent annotations (on "det. slips"). The set examined comprised 91 specimens at ALA that are currently identified as *C. arctica* and *C. scammaniana*, plus three specimens from ISC and 11 specimens from CAN including the specimens Porsild called *C. arctica* (Fig. 4, Appendix 2).

ALIGNING TAXONOMIC CONCEPT RELATIONSHIPS

While the idea of variation in the circumscription of taxa among different authors is well known to working taxonomists, the relationships among the different circumscriptions is usually only described (1) when there is a change of name, and (2) by using the general term "synonym," sometimes with the modifiers "heterotypic" or "homotypic." Taxonomic concept *mapping*, or *alignment*, aims to make the relationships among circumscriptions more explicit, using the language of mathematical set relationships (Gradstein et al., 2001; Franz et al., 2008; Franz & Peet, 2009). Generating these set relationships requires a careful

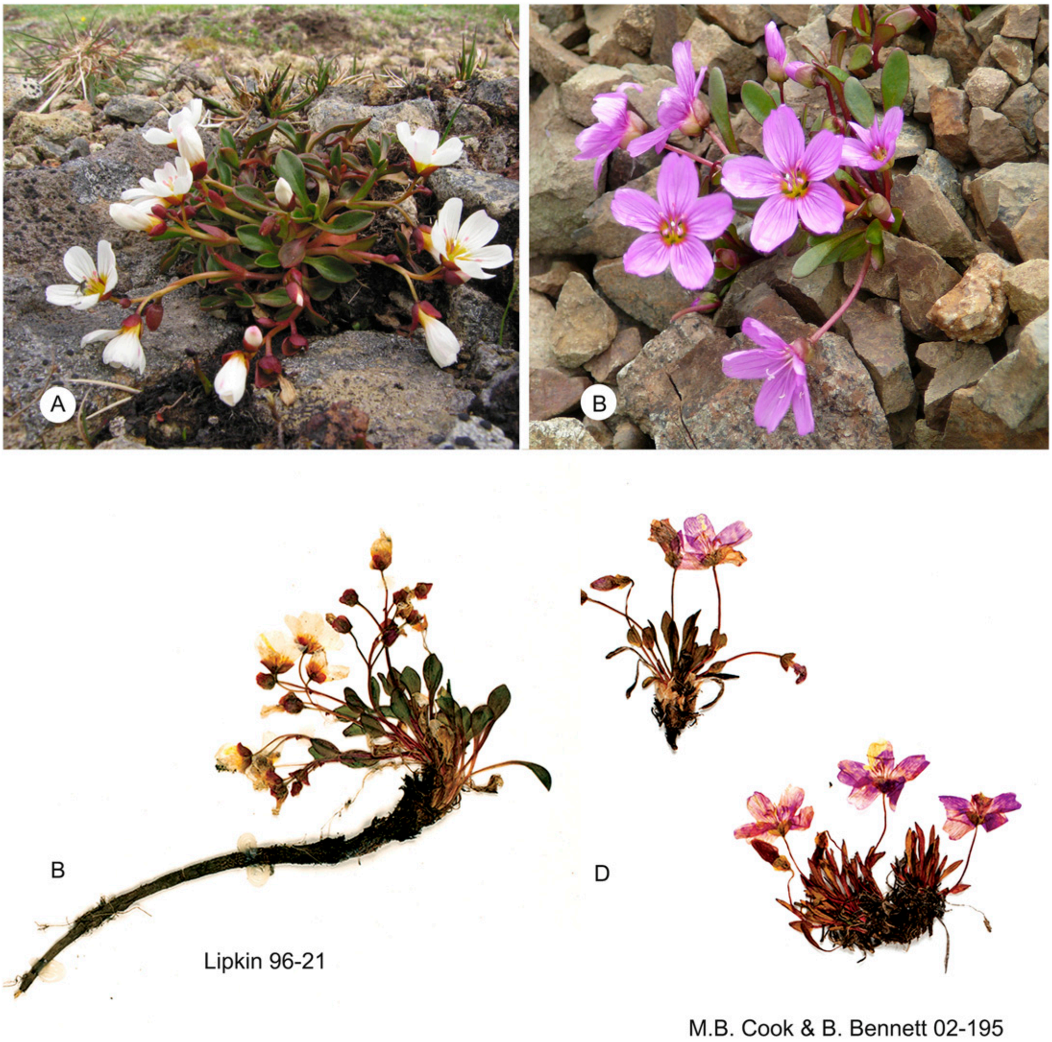
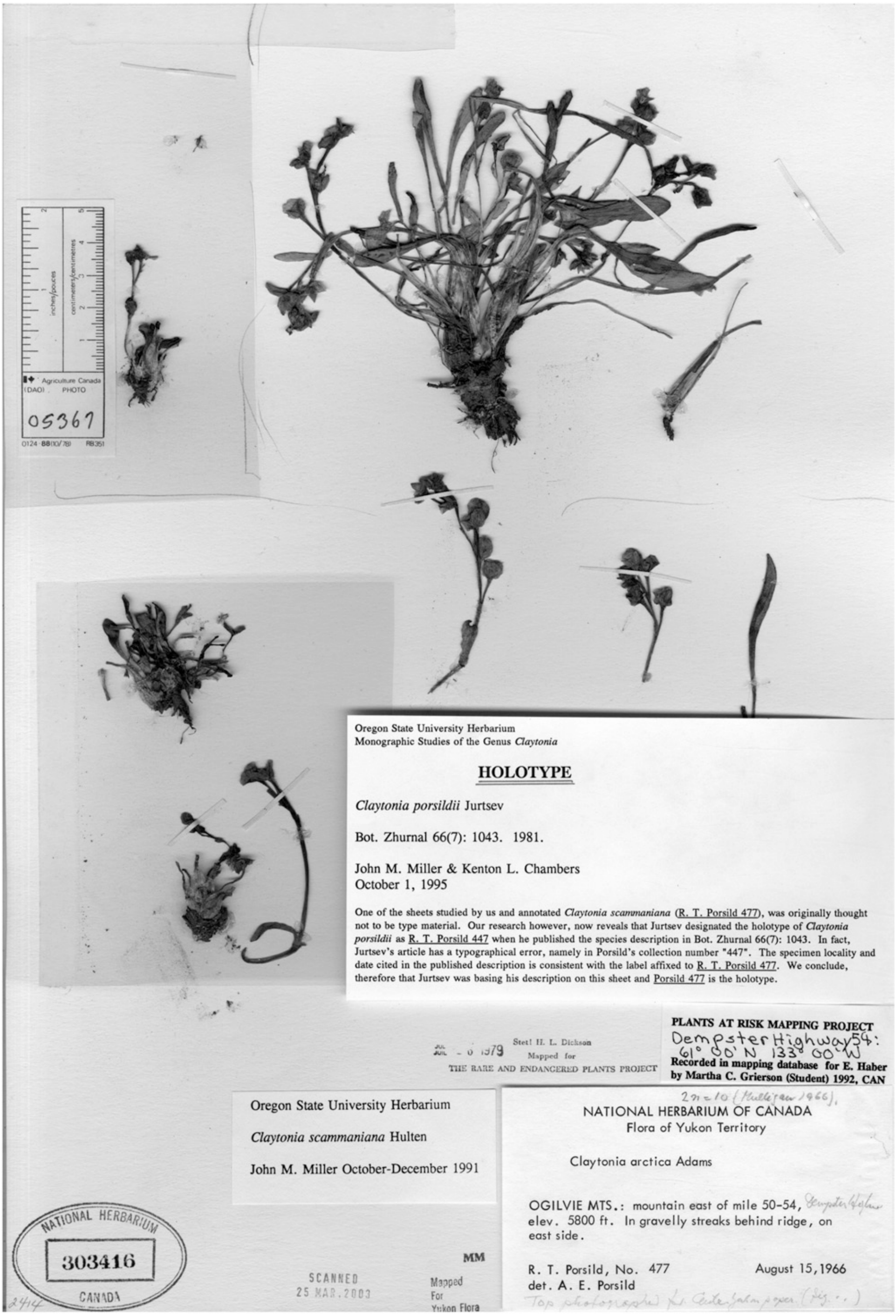


Figure 2. Overview of morphologies in the *Claytonia arctica* complex. —A. *Claytonia arctica*, photograph from Kiska Island, Alaska, by Ian L. Jones (with permission). —B. *Claytonia arctica*, plant from herbarium sheet (*Lipkin 96-21*, ALA). —C. *Claytonia scammaniana*, photograph from Denali National Park, Alaska, by Weber_sd (a Flickr user; photo licensed under Creative Commons license BY-NC-ND). —D. *Claytonia scammaniana*, plants from herbarium sheet (*M. B. Cook & B. Bennett 02-195*, ALA-V151602).

examination of the primary taxonomic literature for a taxon and a method for recording how different taxonomic concepts overlap.

Some authors have used a table-based approach to display the alignments of different taxonomic concepts (Gradstein et al., 2001; Franz et al., 2008; Weakley & Peet, 2010). Table cells are "Least Divisible Taxonomic Units" (Weakley, 2009), and rows contain the various taxonomic concepts examined in a single publication. The taxonomic concepts in other publications are placed on other rows, with corresponding taxonomic concepts aligned vertically. The set relationships between any two taxonomic concepts (*same as*, *includes*, *overlaps*, *disjunct*) can then be easily inferred, "by hand" or automatically (Webb, 2018).

While this tabular approach is a simple and elegant solution for displaying taxonomic concept relationships, we feel it is not the best method for recording the relationships while reading source publications because using a table forces the researcher to indicate set relationships for which there may be no evidence. For example, in the simple case where there has been no change in name between the original author of a taxon and a subsequent reviser it is most likely incorrect to infer and indicate an exact alignment between the original and revised circumscriptions. Usually a



Oregon State University Herbarium
Monographic Studies of the Genus *Claytonia*

HOLOTYPE

Claytonia porsildii Jurtsev

Bot. Zhurnal 66(7): 1043. 1981.

John M. Miller & Kenton L. Chambers
October 1, 1995

One of the sheets studied by us and annotated *Claytonia scammaniana* (R. T. Porsild 477), was originally thought not to be type material. Our research however, now reveals that Jurtsev designated the holotype of *Claytonia porsildii* as R. T. Porsild 447 when he published the species description in Bot. Zhurnal 66(7): 1043. In fact, Jurtsev's article has a typographical error, namely in Porsild's collection number "447". The specimen locality and date cited in the published description is consistent with the label affixed to R. T. Porsild 477. We conclude, therefore that Jurtsev was basing his description on this sheet and Porsild 477 is the holotype.

JUL - 6 1979 Stet! H. L. Dickson
Mapped for
THE RARE AND ENDANGERED PLANTS PROJECT

PLANTS AT RISK MAPPING PROJECT
Dempster Highway 54:
61° 00' N 133° 00' W
Recorded in mapping database for E. Haber
by Martha C. Grierson (Student) 1992, CAN

Oregon State University Herbarium

Claytonia scammaniana Hulten

John M. Miller October-December 1991

2n = 10 (Mulligan 1966),
NATIONAL HERBARIUM OF CANADA
Flora of Yukon Territory

Claytonia arctica Adams

OGILVIE MTS.: mountain east of mile 50-54, Dempster Highw.
elev. 5800 ft. In gravelly streaks behind ridge, on east side.

R. T. Porsild, No. 477 August 15, 1966
det. A. E. Porsild
Top photographed for Centenary paper (Fig. .)

NATIONAL HERBARIUM
303416
CANADA
2414

MM

SCANNED
25 MAR. 2003

Mapped
For
Yukon Flora

Figure 3. *Claytonia porsildii* Jurtzev (= *C. arctica* sensu Porsild) was described based on a plant illustrated in Porsild (1974/1975). B. A. Yurtsev (1981) published the name *C. porsildii* based on that photograph of *R. T. Porsild 477* (CAN-303416). Figure of the holotype of *C. porsildii* reproduced from the open-access book *The Reindeer Botanist: Alf Erling Porsild, 1901–1977* by Wendy Dathan (2012; Creative Commons license BY-NC-ND).

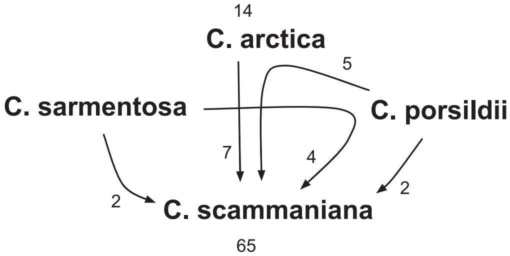


Figure 4. Diagram showing some of the changes in specimen determination (using "det. slips") for a representative set of specimens of plants in the *Claytonia arctica* complex. Numbers near *C. arctica* and *C. scammaniana* indicate the number of specimens that have been consistently identified to that name only. Numbers near an arrow indicate the number of specimens which have been re-determined as various names. Name "*C. porsildii*" includes both specimens identified as *C. arctica* sensu Porsild and *C. porsildii*. See Appendix 2 for full list of name switches and details of specimens in each class of name switch.

circumscription will be more information-rich as more variation is encountered, meaning that the most appropriate representation is that the reviser's circumscription *includes* the original taxonomic concept, but is not exactly *congruent with* it. On the other hand, a revised taxonomic concept can be more reflective of the full range of (say) phenotypic variation of a focal concept, and thus overlap with a previous one using the same taxonomic name (N. Franz, pers. comm.).

As well, there is often little or no discussion of the circumscription of taxa in non-monographic publications (e.g., floras), meaning that the only statement that can be made with confidence is that two taxonomic concepts simply *intersect* (i.e., are not disjunct). Finally, when arranging concepts in a table, implicit alignments (set relationships) must be made between concepts on different rows even when no explicit comparison of these concepts exists in the literature. While logic may support these implicit alignments (e.g., if taxonomic concept A includes B, and B includes C, then A must also include C), in other cases there the inference of transitivity for specimens assigned to multiple concepts is less precise (e.g., if A overlaps with B, and B overlaps with C, the relationship between A and C could be inclusive, overlapping, or even disjunct).

For these reasons, we used an alternative method, simply recording the taxonomic concept relationships that meet a threshold of explicitness and precision that we deem generally acceptable. The steps involved were: (1) record all relevant names, publications, and specimens in three data tables in a spreadsheet; (2) create taxonomic concepts in a fourth table, linking a name with the publication it is discussed in; (3) in a fifth table, record one of six possible set relationships among some of the pairs of taxonomic concepts (*congruent with*, *includes*, *included in*, *overlaps*, *intersects*, *disjunct*), indicating also the publication in which those relationships were discussed or from which they were inferred; and (4) in a sixth table, document the taxonomic concept applied during the identification of key specimens.

This recording process is similar to that facilitated by the software applications TaxLink (Gradstein et al., 2001) and ConceptMapper (Liu et al., 2006). Chains of relationships among taxonomic concepts can then be displayed as graphs (see Fig. 5), similar to those shown in Franz et al. (2016). These graphical chains are also an analogous representation to the taxonomic concept relationships expressed as mathematical symbols (">" includes, "<" is included in, "> <" overlaps with, "= =" is congruent with, "|" is disjunct with) in the text of Weakley's (2015) flora. The identification of specimens to particular taxonomic concepts can also be displayed in the same diagram.

RESULTS

MORPHOLOGY

Claytonia arctica in our currently used sense is a mainly northeastern Asian element with only a few populations in Alaska: Aleutian Islands, St. Lawrence Island in the Bering Sea, and on the mainland at Tin City Long Range Radar Site, Seward Peninsula (*R. Lipkin 96-21*, ALA). These plants have a particularly well-developed woody base up to a centimeter in width, from which several (seven to 10) flowering stems emerge (Fig. 2A, B), that separates it from the other two species native to Alaska (Fig. 6).

Volkova (1964) noted that as early as 1831 specimens of *Claytonia sarmentosa* from Kamchatka, the Bering Strait region, and North America, determined as *C. arctica*, can also have a distinct woody base, but neither consistently nor as well developed as in *C. arctica*. She noted that Hultén (1944) distinguished the two species on the basis of stolons at the base of *C. sarmentosa* stems and the absence of stolons in the case of *C. arctica*. Inasmuch as the stolons are brittle they are often lacking in herbarium specimens of *C. sarmentosa*. She added that *C. arctica* typically has a basal rosette of leaves, whereas *C. sarmentosa* typically does not. *Claytonia sarmentosa* in our present sense is widespread in Siberia, Alaska, the Yukon, and south to northern British Columbia. It also has been reported from the Bering Sea islands.

Claytonia scammaniana as described by Hultén (1939) is endemic to Alaska and Yukon and has long been a source of errors. It can be distinguished from *C. sarmentosa* by its narrow leaves and brownish, woody rhizome (Miller & Chambers, 2006; Fig. 2C, D). *Claytonia scammaniana* is characterized by large flowers

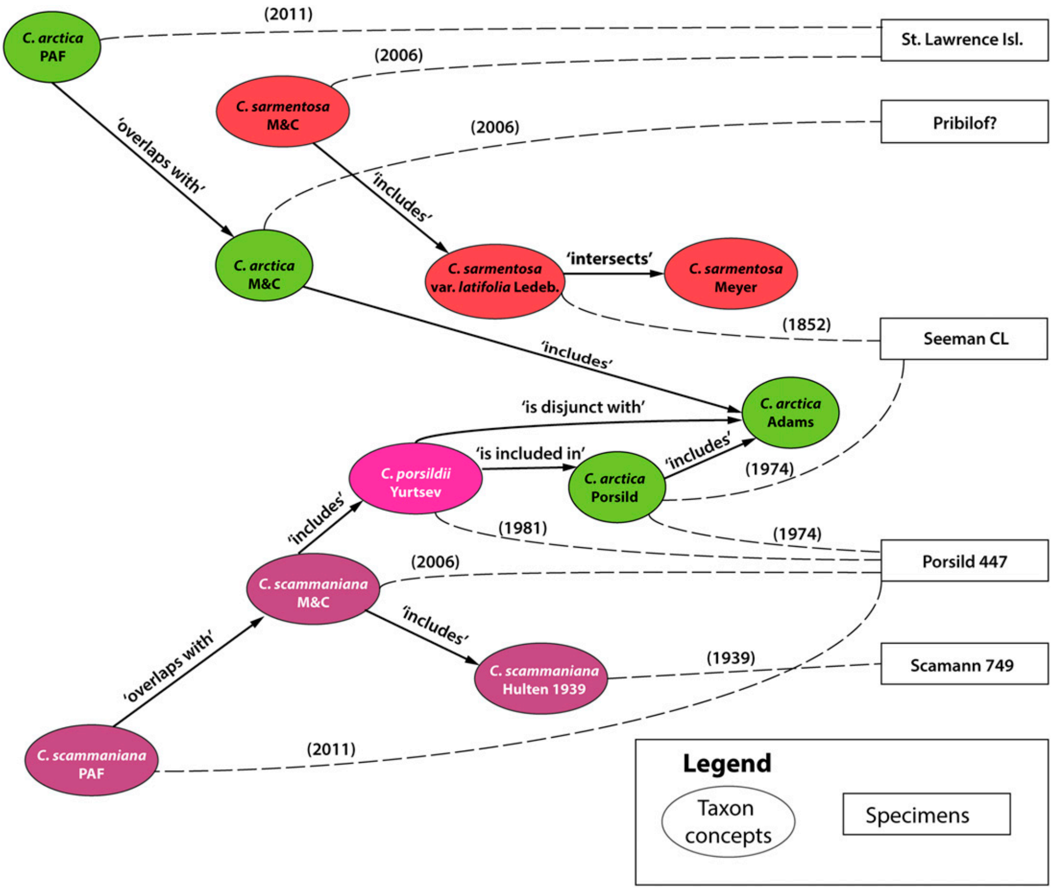


Figure 5. Diagram showing the relationships among taxonomic concepts in the *Claytonia arctica* complex, and determinations of selected key specimens. Taxonomic concepts are indicated by ovals, and the set relationships among them by the text in quotation marks above the solid line and arrow connecting them. Key specimens are indicated by rectangles on the right, and their various determinations to taxonomic concepts by dotted lines. The year in parentheses above the dotted line gives the year of the determination. Taxonomic concept labels are the species epithet (all in *Claytonia*) plus a sensu code: "PAF": Elven et al., 2011; "M&C": Miller & Chambers, 2006; "Hultén 1939": Hultén, 1939; "Yurtsev": Yurtsev, 1981; "Porsild": Porsild, 1974/1975; "Adams": Adams, 1817; "Meyer": Meyer, 1829; "Ledeb.": Ledebour, 1844. Specimen codes are: "Porsild 477": *R. T. Porsild 477* (CAN-303416); "Seemann CL": *Seemann s.n.* from Cape Lisburne; "Scamman 749": *E. Scamman 749* (GH-12291); "Pribilof?": lectotype, unknown collector and location, probably Pribilof Islands (see Miller & Chambers, 2006); "St. Lawrence Isl.": *M. L. Carlson 2012-218* (ALA-V173525). Note that this diagram does not display the complete set of alignments we recorded, and so from the point of view of logical reasoning is not self-contained.

with a pink tinge, which also sets it apart from the entirely yellow/cream flower of *C. arctica* (Fig. 2C, D). But there is much more variation than is seen in the type collection of *C. scammaniana* (Hultén, 1939).

Having reviewed *Claytonia arctica*–labeled specimens at LE in St. Petersburg, including type material, and some excellent specimens from St. Lawrence Island, it is clear that the plant illustrated in Porsild (1974/1975, fig. 3) is not *C. arctica* sensu Adams. It appeared to be an undescribed species, which is what B. A. Yurtsev concluded. He published the name *C. porsildii* Jurtzev (Yurtsev, 1981) on the basis of that photo (Fig. 3). But not having seen the specimens cited by Porsild, he had to assume that all those specimens cited in the text as examples of *C. arctica* sensu Porsild were the same. They are not (in the current prevailing view); they are *C. scammaniana*. Therefore, the basis for the name *C. porsildii* is a single specimen along the Dempster Highway in the Yukon: the holotype (Fig. 3). That is not to say there are not others like it, for we have found several at ALA (Appendix 1), but following Miller and Chambers (2006), who included material of *C. porsildii* under *C. scammaniana*, we also consider these plants *C. scammaniana*, but as edaphic extremes often associated with unstable scree slopes as found in the Talkeetna and Hayes Quadrangles in Alaska. These plants have a less-branched or unbranched rhizome, the stipules are extremely expanded, the leaves have very

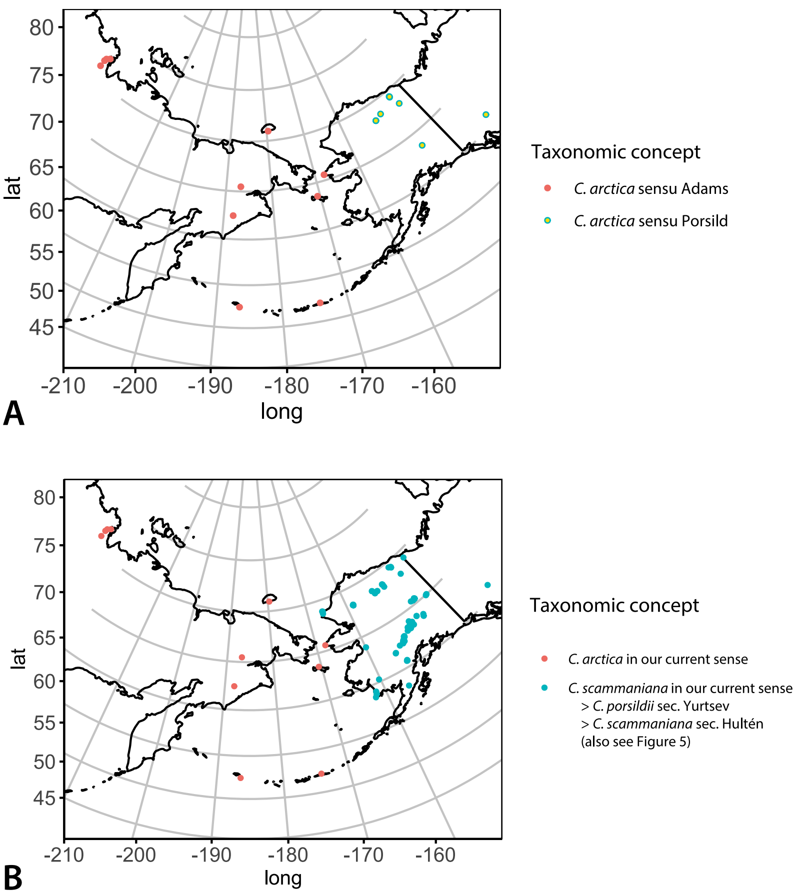


Figure 6. Distribution map of *Clayonia arctica* complex. —A. Specimens mapped of *C. arctica* Adams reviewed and those of *C. arctica* Adams sensu Porsild from collections reviewed at ALA, and selected CAN specimen. —B. All specimens in the *C. arctica* complex mapped according to our own current taxonomic concepts (see also Fig. 5 for more details). Maps were created using RgoogleMaps package in R version 3.5.1 (Loecher & Ropkins, 2015).

long petioles, and the inflorescence has more numerous flowers (Fig. 3). The plant illustrated by Seeman from Cape Lisburne, Alaska, is also *C. scammaniana*, and the plants in plate 2 of Hultén (1927) are not *C. arctica* but probably *C. sarmentosa*.

SPECIMEN DETERMINATIONS

For the 105 *Claytonia arctica* and *C. scammaniana* specimens examined, there were a total of 261 determinations. The ranges of years that different names were applied are: *C. arctica* 1903–2012; *C. arctica* sensu Porsild 1953–1980; *C. sarmentosa* 1948–1983; *C. porsildii* 1970–2003; *C. scamanniana* 1935–2006; and *Montia scamanniana* 1976 (Fig. 7). Three quarters of the specimens (79 specimens) were determined consistently (i.e., to the same taxonomic name) each time there was an annotation, while a quarter of specimens were renamed two, or even three times (Fig. 4, Appendix 2), indicating either the difficulty in identifying members of this species complex or the changes in underlying taxonomic theory about the complex.

TAXONOMIC CONCEPT MAPPING

Using the method described above, taxon names, publications, and key specimens were entered into data tables. Publications included original descriptions, revisions, and floras: Adams, 1817; Meyer, 1829; Ledebour, 1844; Seemann, 1852; Hultén, 1939, 1944; Welsh, 1968; Porsild, 1974/1975; Welsh, 1974; Yurtsev, 1981; Cody, 2000; Miller and Chambers, 2006; Elven et al., 2011 as the PAF. For each name, taxonomic concepts were isolated (i.e., name sensu taxonomic concept labels were created), and the relationships among concepts were established based on the taxonomic commentaries associated with the applications of names. The identification of key specimens to various taxonomic concepts was also recorded.

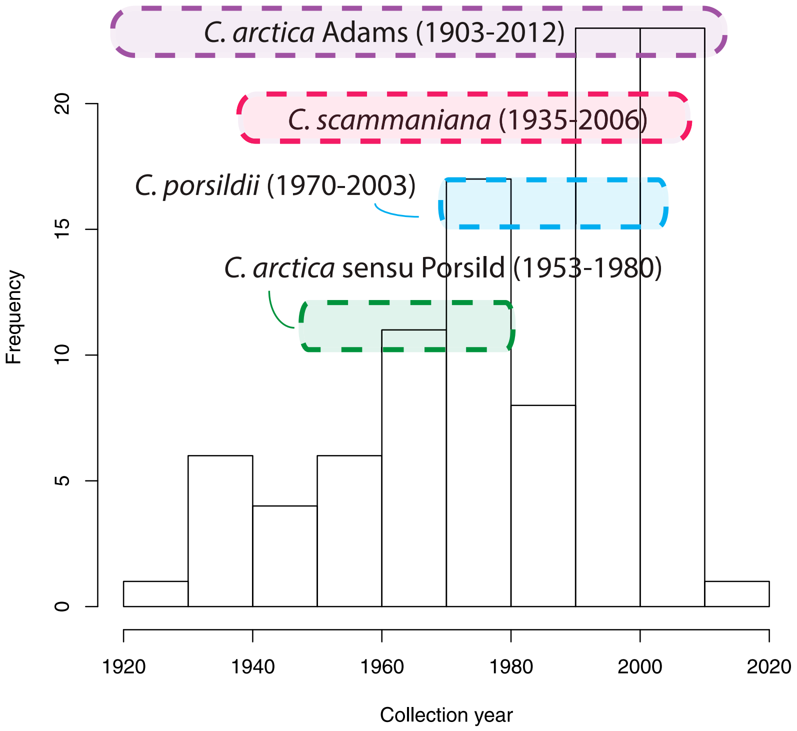


Figure 7. Histogram of year of collection for the 105 specimens of *Claytonia arctica* and *C. scammaniana* reviewed at ALA, ISC, and CAN, and selected key taxon concepts and their temporal application as inferred from annotation labels plotted.

Figure 5 shows the taxonomic concept relationships and specimen determinations for an informative subset of taxonomic concepts, displaying in a condensed fashion the following taxonomic decisions (among several others). (1) In 1974, Alf Erling Porsild extended the geographic range of *Claytonia arctica* from East Asia to include his brother's collection *R. T. Porsild 477* (Fig. 3) in the Ogilvie Mountains of Canada (and others from the Brooks Range of Alaska). (2) In 1981, Boris Yurtsev then removed the Canadian Ogilvie collection and those cited from the Brooks Range in Alaska from *C. arctica*, placing them in a new species, *C. porsildii*. The taxonomic concept *C. porsildii* sensu Yurtsev (1981) is therefore included in *C. arctica* sensu Porsild (1974/1975). (3) Both Porsild and Yurtsev failed to consider Hultén's *C. scammaniana*, but during their revision in 2006, Miller and Chambers recognized Porsild's geographically anomalous *C. arctica* specimens as *C. scammaniana*.

DISCUSSION

There are several challenges in studying high-latitude plants, such as the *Claytonia arctica* complex, resulting from frequent hybridization, reticulate evolution via genome doubling (polyploidy), inbreeding/asexuality, and the occurrence of widespread species with complex morphological variation (Brochmann et al., 2013). Both temporal and spatial biases in collecting arctic herbarium specimens are well documented (Bay et al., 2017; Väre, 2017; Huettmann & Ickert-Bond, 2018; Panchen et al., 2019). During exploration of the state of Alaska and Beringia, sampling was sparse and insufficient (Fig. 7) to evaluate accurately variation and distinguish morphological discontinuities from continuous variation. Consequently, these gaps in knowledge are likely to generate conflicting taxonomic concepts (Fig. 6). Access to Russian Far East specimens for North American researchers is particularly restricted and digitization of these specimens has lagged behind those from Alaska and Canada (but see Ivanova & Shashkov, 2017).

Specimens showing phenotypic variation and many intermediate forms did not reach the herbarium until after Porsild's *Claytonia arctica* concept (1974/1975) or Yurtsev's *C. porsildii* (1981) concept. In fact, 55 out of 105 specimens of *C. arctica* and *C. scammaniana* at ALA were collected after 1980 (Fig. 7). Not only were there few collections made prior to 1980, specimens from ALA were seldom included in revisionary work in the early 1980s. Overemphasis of perennation structures and their plasticity adds notorious complexities to the taxonomy of *Claytonia* (Volkova, 1964; O'Quinn, 2005; Miller & Chambers, 2006) and has led to confusion and misidentifications. The majority of arctic plant species reproduce both sexually and asexually (Murray, 1987; Brochmann & Steen, 1999), and arctic biomes are shaped by a diversity of life history traits reflecting perennial strategies and clonal growth, enabling plants to survive interannual climatic fluctuations (Jónsdóttir, 2011; Brochmann et al., 2013). The plasticity of underground perennation structures (such as rhizomes and stolons) enabling clonal growth in the *C. arctica* complex add further complexities to studying herbarium specimens. Botanists often fail to collect underground parts and thus structures of key taxonomic importance are often lacking or are incompletely known from a particular specimen; consequently, specimens might be misidentified.

OUR PRESENT UNDERSTANDING OF THE DISTRIBUTIONS AND MORPHOLOGIES IN THE *CLAYTONIA ARCTICA* COMPLEX

While *Claytonia arctica* occurs widespread in the Russian Far East (e.g., Taimyr, Siberia, Chukotka, Kamchatka, and Wrangel Island; Miller & Chambers, 2006; Carlson et al., 2018), in Alaska it is restricted to few populations along the Aleutian Islands (Agattu, Amchitka, Atka, and Kiska; Garroutte et al., 2018; Jones, pers. comm.), those on St. Lawrence Island (Miller & Chambers, 2006; Carlson et al., 2018), as well as a single population on the northwestern tip of the Seward Peninsula (*R. Lipkin 96-21*, Fig. 6; Nawrocki et al., 2013). Morphologically, *C. arctica* does indeed have a particularly well-developed woody base from which several flowering stems emerge, and *C. scammaniana* can also have distinct woody bases, but neither consistently nor as well developed as in *C. arctica* (Fig. 2). There is a gradual variation in this trait. Petals in *C. arctica* are all white, while becoming yellow at the base or entirely yellow/cream, never pink or pink-tinged as those of *C. scammaniana* (Fig. 2).

Claytonia scammaniana is restricted to North America, but contrary to Hultén (1939), who discussed *C. scammaniana* in his sense as "an endemic of the unglaciated central parts of Alaska," in the present sense there are several populations known from Canada (in the Kluane Range and Ogilvie, Richardson, Barn, and British Mountains of the Yukon Territory, Figs. 3, 6; Appendix 1; Cody, 2000; Yukon Conservation Data Centre, 2019). The species generally has large single flowers with a pink tinge and linear to oblong to narrowly spatulate leaves, but there is much more variation found throughout its range than is seen in the type collection of *C. scammaniana* from Porcupine Dome in Central Alaska (Hultén, 1939). The unique morphologies described under the northwestern North American *C. porsildii* (Yurtsev, 1981) have been uniformly annotated as *C. scammaniana* by Miller and are included in synonymy under *C. scammaniana* by Miller and Chambers (2006). These plants (Fig. 3) have a less-branched or unbranched rhizome, the stipules are extremely expanded, the leaves have very long petioles, and the inflorescence tends to be racemose with numerous flowers as compared to specimens from the locus classicus in Central Alaska (fig. 1 in Hultén, 1939).

We think these extreme phenotypes could represent edaphic extremes often associated with unstable scree slopes based on review of ALA specimens (Appendix 1). Parker (1989) in her review of talus and block slope assemblages in the Alaska Range listed *Claytonia scammaniana* as a member of group 2 (= block slope and talus plants) having a distinct but thin taproot and a moderately to highly branched, spreading shoot often becoming pseudo-rhizomatous. In particular, *C. scammaniana* is cited to be more commonly found in barren sites, while others in this group are found in a diversity of alpine habitats (Parker, 1989).

Microtopography and periglacial processes strongly affect distribution of snow, drainage, active soil depths, and other soil processes that can create steep gradients in ecological conditions in the Arctic (e.g., Webber, 1978; Aleksandrova, 1988; Bliss, 1997). Reduced productivity due to late snowmelt and shorter growing seasons in deep snow beds and water logging and anoxic conditions in basins with permafrost contribute to the myriad of ecological conditions in arctic environments (Jónsdóttir, 2011) that result in plasticity of trait–habitat relationships in the *Claytonia arctica* complex. Whether the extreme phenotypes seen in *C. scammaniana* are a manifestation of the habitat association with scree slopes and warrant subspecific or specific status will need a closer examination using genetic molecular tools in combination with a suitable species concept. Similarly, the profusely purple-flowering, spatulate-leaved specimens of *C. scammaniana* from serpentine barrens in the De Long Mountains, Brooks Range, in Noatak National Preserve (Appendix 1), appear morphologically distinct and warrant further phylogenetic investigation using molecular sequencing.

Claytonia sarmentosa has long been a source of problems and is morphologically distinct lacking a stout caudex and fleshy rhizomes, but possessing stolons, which *C. arctica* and *C. scammaniana* lack (see fig. 41 in Miller & Chambers, 2006; Nawrocki et al., 2013). Yet we have seen variable character expression of the aforementioned character in some *C. sarmentosa* specimens at ALA. Further genetic analysis may yet reveal that *C. sarmentosa* (strictly speaking: in our current sense) is also an element of the *C. arctica* complex.

PROMOTING TAXONOMIC CONCEPT MAPPINGS

The inclusion of taxonomic concepts and their relationships in a review or flora is helpful to anyone trying to understand the historical applications of names, for example during the compilation of specimen records for distribution mapping (Fig. 6). The taxonomic concept relationships can be presented graphically, as in Figure 5, or as symbols in text, as in Weakley (2015). Figure 5 contains these text statements:

- *Claytonia scammaniana* sec. Miller & Chambers
    - > *C. porsildii* sec. Yurtsev
    - > *C. scammaniana* sec. Hultén
- *C. porsildii* sec. Yurtsev
    - < *C. arctica* sec. Porsild
    - | *C. arctica* sec. Adams

We suggest that the graphical representation is easier to comprehend for a majority of users, especially where many concepts are involved. An additional value of presenting taxonomic concept information is that if an accepted name in a flora is associated with a complex network of preceding taxonomic concept relationships, a user should be alerted to the potential difficulty of correctly applying that name to specimens or plants in the field. Beyond its benefits to users of floras, documentation of taxonomic concept relationships permits subsequent analysis of alternative taxonomies using logical reasoning software such as Euler/X (Chen et al., 2014; Franz et al., 2016).

IMPROVING CONSERVATION OF NATURAL RESOURCES

Globally *Claytonia arctica* is considered rare (G3) and local throughout its range (21 to 100 occurrences), while the state ranking is S1S2 with typically five to 10 or fewer occurrences (NatureServe Database cited in Nawrocki et al., 2013). The scarcity of sites in North America for "true" *C. arctica* necessitates consideration by federal authorities under the United States Endangered Species Act and *C. arctica* should be considered as a candidate endangered species by both the federal government and the state of Alaska (Miller & Chambers, 2006; Nawrocki et al., 2013). While *C. scammaniana* is known from numerous localities and many individuals per population in Alaska, the species is ranked as vulnerable (N3) in Canada and (S3) in the Yukon Territory where distributions are restricted from the Kluane Range to the Tatchun Hills and Ddhaw Ghro, north to the southern and northern Richardson Mountains and the Barn, British, and Ogilvie ranges. It was first ranked in March 1989 and last reviewed in August 2015 (Yukon Conservation Data Centre, 2019). We hope that future phylogenetic work in the *C. arctica* complex will aid in evaluating the status of *C. arctica* and *C. scammaniana*, as it is clear that knowledge of phylogenetic relationships can inform conservation priorities (Faith, 1992; Pérez-Losada et al., 2009).

Literature Cited

Abbott, R. J. & C. Brochmann. 2003. History and evolution of the Arctic flora: In the footsteps of Eric Hultén. Molec. Ecol. 12: 229–313.

Abbott, R. J., L. C. Smith, R. I. Milne, R. M. M. Crawford, K. Wolff & J. Balfour. 2000. Molecular analysis of plant migration and refugia in the Arctic. Science 289: 1343–1346.

Adams, J. M. F. 1817. *Claytonia arctica* Adams. Mém. Soc. Imp. Naturalistes Moscou 5: 94–96.

Aleksandrova, V. D. 1988. Vegetation of the Soviet Polar Deserts. Cambridge University Press, Cambridge.

Bay, C., F. J. A. Daniëls & G. Halliday. 2017. The Greenland vascular plant herbarium of the University of Copenhagen. Arctic Sci. 3: 553–559.

Berendsohn, W. G. 1995. The concept of "potential taxa" in databases. Taxon 44: 207–212.

Beatty, G. E. & J. Provan. 2010. Refugial persistence and postglacial recolonization of North America by the cold-tolerant herbaceous plant *Orthilia secunda*. Molec. Ecol. 19: 5009–5021.

Bliss, L. C. 1997. Arctic ecosystems of North America. Pp. 551–683 *in* F. E. Wielgolaski (editor), Ecosystems of the World 3. Polar and Alpine Tundra. Elsevier, Amsterdam.

Brochmann, C. & S. W. Steen. 1999. Sex and genes in the flora of Svalbard – Implications for conservation biology and climate change. Pp. 33–72 *in* I. Nordal & V. Yu. Razzhivin (editors), The Species Concept in the High North–A Panarctic Flora Initiative. Skr. Norske Vidensk.-Akad. Oslo, Mat.-Naturvitensk. Kl. 38.

Brochmann, C., A. K. Brysting, I. G. Alsos, L. Borgen, H. H. Grundt, A.-C. Scheen & R. Elven. 2004. Polyploidy in arctic plants. Biol. J. Linn. Soc. 82: 521–536.

Brochmann, C., M. E. Edwards & I. G. Alsos. 2013. The dynamic past and future of arctic vascular plants: Climate change, spatial variation and genetic diversity. Pp. 133–152 *in* K. Rohde (editor), The Balance of Nature and Human Impact. Cambridge University Press, Cambridge.

Carlson, E., E. J. Trammell, T. Nawrocki & E. Noogwook. 2018. Additions to the vascular plant flora of St. Lawrence Island, Alaska: New records, rare species, and phytogeographic patterns. Rhodora 120: 1–41.

Chen, M., S. Yu, N. Franz, S. Bowers & B. Ludäscher. 2014. Euler/X: A toolkit for logic-based taxonomy integration. WFLP 2013 – 22nd International Workshop on Functional and (Constraint) Logic Programming.

Cody, W. J. 2000. Flora of the Yukon. 2nd ed. National Research Council of Canada. Monograph Publishing Program. NRC Research Press, Ottawa.

Cook, J. A., E. P. Hoberg, A. Koehler, H. Henttonen, L. Wickström, V. Haukisalmi, K. Galbreath, et al. 2005. Beringia: Intercontinental exchange and diversification of high latitude mammals and their parasites during the Pliocene and Quaternary. Mammal Study 30: S33–S44.

Dathan, W. 2012. The Reindeer Botanist: Alf Erling Porsild, 1901–1977. University of Calgary Press, Calgary.

Elias, S. A., S. K. Short, C. H. Nelson & H. H. Birks. 1996. The life and times of the Bering Land Bridge. Nature (Taipei) 382: 60–63.

Elven, R., B. Jonsell, D. F. Murray & B. A. Yurtsev. 1999. An operational species concept for the Panarctic Flora. Pp.

23–32 *in* I. Nordal & V. Yu. Razzhivin (editors), The Species Concept in the High North–A Panarctic Flora Initiative. Skr. Norske Vidensk.-Akad. Oslo, Mat.-Naturvitensk. Kl. 38.

Elven, R., D. F. Murray, V. Yu. Razzhivin & B. A. Yurtsev. 2011. Checklist of the Panarctic Flora (PAF). Natural History Museum, University of Oslo, Oslo. Previously <http://nhm2.uio.no/paf>, now <http://panarcticflora.org>, accessed 9 May 2019.

Faith, D. P. 1992. Conservation evaluation and phylogenetic diversity. Biol. Conserv. 61: 1–10.

Fedorov, V. B., A. V. Goropashnaya, M. Jaarola & J. A. Cook. 2003. Phylogeography of lemmings (*Lemmus*): No evidence for postglacial colonization of the Arctic from the Beringian refugium. Molec. Ecol. 12: 725–731.

Franz, N. & R. K. Peet. 2009. Perspectives: Toward a language for mapping relationships among taxonomic concepts. Syst. Biodivers. 7: 5–20.

Franz, N. & J. Cardona-Duque. 2013. Description of two new species and phylogenetic reassessment of *Perelleschus* O'Brien & Wibmer, 1986 (Coleoptera: Curculionidae), with a complete taxonomic concept history of *Perelleschus* sec. Franz & Cardona-Duque. Syst. Biodivers. 11: 209–236.

Franz, N., R. K. Peet & A. Weakley. 2008. On the use of taxonomic concepts in support of biodiversity research and taxonomy. Pp. 61–84 *in* Q. D. Wheeler (editor), The New Taxonomy, Vol. 76. Chapman and Hall, London.

Franz, N. M., M. Chen, P. Kianmajd, S. Yu, S. Bowers, A. S. Weakley & B. Ludäscher. 2016. Names are not good enough: Reasoning over taxonomic change in the *Andropogon* complex. Semant. Web 7: 645–667.

Gal-Chen, T. 1984. Approaches to mathematical modeling of the steppe-tundra paleoclimate. Pp. 205–218 *in* D. M. Hopkins, J. V. Matthews, Jr., C. E. Schweger & S. B. Young (editors), Paleoecology of Beringia. Academic Press, New York.

Garroutte, M., F. Huettmann, C. O. Webb & S. M. Ickert-Bond. 2018. Biogeographic and anthropogenic correlates of Aleutian plant diversity: A machine-learning approach. J. Syst. Evol. 56: 476–497.

Gradstein, S. R., M. Sauer, W. Braun, M. Koperski & G. Ludwig. 2001. TaxLink, a program for computer-assisted documentation of different circumscriptions of biological taxa. Taxon 50: 1075–1084.

Graham, A. 2018. The role of land bridges, ancient environments, and migrations in the assembly of the North American flora. J. Syst. Evol. 56: 405–429.

Hewitt, G. M. 2000. The genetic legacy of the Quaternary ice ages. Nature (Taipei) 405: 907–913.

Hopkins, D. M. 1979. Landscape and climate of Beringia during late Pleistocene and Holocene times. Pp. 15–41 *in* W. S. Laughlin & A. B. Harper (editors), The First American Origins, Affinities and Adaptations. Gustav Fischer, New York.

Huettmann, F. & S. M. Ickert-Bond. 2018. On open access, data mining and plant conservation in the Circumpolar North with an online data example of the Herbarium, University of Alaska Museum of the North. Arctic Sci. 4: 433–470.

Hultén, E. 1927. Flora of Kamchatka and the Adjacent Islands, II. Kongl. Svenska Vetensk. Handl. ser. 3, Vol. 5. Almqvist & Wiksells Boktryckeri-A.-B., Uppsala.

Hultén, E. 1937. Outline of the History of Arctic and Boreal Biota during the Quaternary Period. Lehre J Cramer, New York.

Hultén, E. 1939. Two new species from Alaska. Contribution to the flora of Alaska. Bot. Not. 1939: 826–829.

Hultén, E. 1944. Flora of Alaska and Yukon. C. W. K. Gleerup, Lund.

Hultén, E. 1968. Flora of Alaska and Neighboring Territories. Stanford University Press, Stanford.

Ickert-Bond, S. M., D. F. Murray & E. DeChaine. 2009. Contrasting patterns of plant distribution in Beringia. Proceedings of the Arctic Alaska Park Science Symposium and Beringia International Conference. Alaska Park Sci. 8: 26–32.

Ickert-Bond, S. M., F. Huettmann, I. Loera, L. Strecker, N. Sekretareva & Y. Mikhailova. 2013. New insights on Beringian plant distribution patterns. Alaska Park Sci. 12: 61–69.

Ivanova, N. V. & M. P. Shashkov. 2017. Biodiversity databases in Russia: Toward a national portal. Arctic Sci. 3: 560–576.

Jeffers, S. 2015. Spring Beauty (*Claytonia*, Montiaceae) in Beringia: New Evidence on Species Delineation from Morphometrics and Phylogenetic Analysis of Plastid and Nuclear Sequence Data. Master's Thesis, University of Alaska, Fairbanks.

Jónsdóttir, I. S. 2011. Diversity of plant histories in the Arctic. Preslia 83: 281–300.

Juday, G. P., C. Alix & T. A. Grant III. 2015. Spatial coherence and change of opposite white spruce temperature sensitivities on floodplains in Alaska confirms early-stage boreal biome shift. Forest Ecol. Managem. 350: 46–61.

Koperski, M., M. Sauer, W. Braun & S. R. Gradstein. 2000. Referenzliste der Moose Deutschlands: Dokumentation unterschiedlicher taxonomischer Auffassungen. No. 34. Schriftenreihe für Vegetationskunde. Bundesamt für Naturschutz, Bonn.

Ledebour, C. F. 1844. Flora Rossica; sive, Enumeratio plantarum in totius Imperii Rossici provinciis Europaeis, Asiaticis et Americanis hucusque observatarum. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Liu, X., R. K. Peet, N. M. Franz & L. L. Downey. 2006. ConceptMapper. Available from Science Environment for Ecological Knowledge (SEEK). <http://seek.ecoinformatics.org/>, accessed 8 July 2019.

Loecher, M. & K. Ropkins. 2015. RgoogleMaps and loa: Unleashing R Graphics Power on Map Tiles. J. Stat. Softw. 63: 1–18.

Meyer, C. A. 1829. *Claytonia sarmentosa*. Nouv. Mém. Soc. Imp. Naturalistes Moscou 1: 137.

Miller, J. M. 2003. *Claytonia*. Pp. 465–474 *in* Flora of North America Editorial Committee (editors), Flora of North America North of Mexico, Vol. 4. Oxford University Press, New York.

Miller, J. M. & K. L. Chambers. 2006. Systematics of *Claytonia* (Portulacaceae). Syst. Bot. Monogr. 78: 1–236.

Murray, D. F. 1987. Breeding systems in the vascular flora of Arctic North America. Pp. 239–262 *in* K. M. Urbanska (editor), Differentiation Patterns in Higher Plants. Academic Press, New York.

Nawrocki, T., J. R. Fulkerson & M. L. Carlson. 2013. Alaska Rare Plant Field Guide. Alaska Natural Heritage Program, University of Alaska Anchorage, Anchorage.

O'Quinn, R. L. 2005. Phylogeny, Biogeography and Evolution of Perennation Structures in Montieae (Portulaceae). Ph.D. Dissertation, Washington State University, Pullmann.

O'Quinn, R. L. & L. Hufford. 2005. Molecular systematics of Montieae (Portulacaceae): Implications for taxonomy, biogeography, and ecology. Syst. Bot. 30: 314–331.

Panchen, Z. A., J. Doubt, H. M. Kharouba & M. O. Johnston. 2019. Patterns and biases in an Arctic herbarium specimen collection: Implications for phenological research. Appl. Pl. Sci. 7(3): E01229.

Parker, C. L. 1989. A Natural History of Vascular Plant Assemblages on Block Slopes and Taluses, Alaska Range, Alaska. Master's Thesis, University of Alaska, Fairbanks.

Parmesan, C. & G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature (Taipei) 42: 37–42.

Pérez-Losada, M., G. Bond-Buckup, C. G. Jara & K. A. Crandall. 2009. Conservation assessment of southern South American freshwater ecoregions on the basis of the distribution and genetic diversity of crabs from the genus *Aegla*. Conserv. Biol. 23: 692–702.

Petit, R. J., I. Aguinagalde, J.-L. de Beaulieu, C. Bittkau, S. Brewer & R. Cheddadi. 2003. Glacial refugia: Hotspots but not melting pots of genetic diversity. Science 300: 1563–1565.

Phoenix, G. K. & J. W. Bjerke. 2016. Arctic browning: Extreme events and trends reversing arctic greening. Global Change Biol. 22: 2960–2962.

Pielou, E. C. 1991. After the Ice Age: The Return of Life to Glaciated North America. University of Chicago Press, Chicago.

Poellnitz, K. von. 1932. Claytonia sect. Rhizomatosae (A. Gray) Poelln. Repert. Spec. Nov. Regni Veg. 30: 281, 296.

Porsild, A. E. 1974/1975. Materials for a Flora of Central Yukon Territory. National Mus. Canada Publ. Bot. 4.

Roemer, J. J. & J. A. Schultes. 1819. *Claytonia joanneana*. P. 434 *in* Systema Vegetabilium, ed. 15, 5. J. G. Cottae, Stuttgart.

Seemann, B. 1852. Portulacaceae. Pp. 27–28, Plate V *in* The Botany of the Voyage of HMS Herald: Under the Command of Captain Henry Kellett, RN, CB, During the Years 1845–51. Lovell Reeve, London.

Sushkin, P. P. 1925. The wild sheep of the Old World and their distribution. J. Mammal. 6: 145–157.

Taxonomic Names and Concepts Interest Group. 2006. Taxonomic Concept Transfer Schema (TCS), version 1.01. Biodiversity Information Standards (TDWG) <http://www.tdwg.org/standards/tcs/>, accessed 9 May 2019.

Tremblay, N. O. & D. J. Schoen. 1999. Molecular phylogeography of *Dryas integrifolia*: Glacial refugia and postglacial recolonization. Molec. Ecol. 8: 1187–1198.

Väre, H. 2017. Finnish botanists and mycologists in the Arctic. Arctic Sci. 3: 525–552.

Volkova, E. V. 1964. Obzor vidov roda *Claytonia* Gronov. rasprostranennykh v S.S.S.R. Bot. Zhurn. (Moscow & Leningrad) 49: 1760–1768.

Volkova, E. V. 1966. Portulacaceae. Pp. 183–192 *in* A. I. Tolmachev (editor), Flora Arctica URSS. V. Salicaceae–Portulacaceae. Nauka Publishers, Moscow.

Weakley, A. S. 2009. Narrative for "Least Divisible Taxonomic Unit" approach to "concept mapping." Technical Report to SERNEC (SouthEast Regional Network of Expertise and Collections).

Weakley, A. S. 2015. Flora of the Southern and Mid-Atlantic States. University of North Carolina Herbarium, Chapel Hill. <http://www.herbarium.unc.edu/flora.htm>, accessed 9 May 2019.

Weakley, A. S. & R. Peet. 2010. Building a regional database of taxonomic concepts. Abstracts of the 2010 Meeting of the Botanical Society of America. <http://2010.botanyconference.org/engine/search/index.php?func=detail&aid=722>, accessed 21 August 2019.

Webb, C. O. 2018. Matrix2cleantax: Software converter from matrix representation of taxon concept alignments to CleanTax format. <https://github.com/camwebb/matrix2cleantax>, accessed 21 August 2019.

Webber, P. J. 1978. Spatial and temporal variation of the vegetation and its production, Barrow, Alaska. Pp. 37–112 *in* L. L. Tieszen (editor), Vegetation and Production Ecology of an Alaskan Arctic Tundra. Springer-Verlag, New York.

Welsh, S. L. 1968. Nomenclatural changes in the Flora of Alaska. Great Basin Nat. 28: 147–156.

Welsh, S. L. 1974. Anderson's Flora of Alaska and Adjacent Parts of Canada. Brigham Young University Press, Provo, Utah.

Wen, J., S. M. Ickert-Bond, Z.-L. Nie & R. Li. 2010. Timing and modes of evolution of eastern Asian - North American biogeographic disjunctions in seed plants. Pp. 252–269 *in* M. Long, H. Gu & Z. Zhou (editors), Darwin's Heritage Today - Proceedings of the Darwin 200 Beijing International Conference. Higher Education Press, Beijing.

Wen, J., Z.-L. Nie & S. M. Ickert-Bond. 2016. Intercontinental disjunctions between eastern Asia and western North America in vascular plants highlight the biogeographic importance of the Bering land bridge from late Cretaceous to Neogene. J. Syst. Evol. 54: 469–490.

Wilmking, M., G. P. Juday, V. A. Barber & H. S. J. Zald. 2004. Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. Global Change Biol. 10: 1724–1736.

Young, S. B. 1982. The vegetation of land-bridge Beringia. Pp. 179–191 *in* D. M. Hopkins, J. V. Matthews, Jr., C. E. Schweger & S. B. Young (editors), Paleoecology of Beringia. Academic Press, New York.

Yukon Conservation Data Centre. 2019. Rare species database. Yukon Department of Environment, Whitehorse, Yukon. <http://www.env.gov.yk.ca>, accessed 9 July 2019.

Yurtsev, B. A. 1981. Seven new taxa of flowering plants from the northeastern Asia and adjacent territories. Bot. Zhurn. (Moscow & Leningrad) 66: 1041–1046.

Appendix 1. Specimens examined.

CLAYTONIA ARCTICA ADAMS IN OUR CURRENT SENSE

RUSSIA. **Chukotka Autonomous Okrug:** Wrangel Island, heath tundra, seepage, calcareous, 70.937, –179.56, 16 Aug. 2005, *H. Solstad & R. Elven 05/0999* (ALA-V163580). **Irkutsk Oblast:** Anadyr River, upriver from Belaya, S-facing gravelly knoll, dry, 65.48, 173.21, 1 July 1995, *C. L. Parker 5794* (ALA-V121767). **Kamchatka Krai:** Koryakskoye Mtns., coarse alpine scree, 62.48, 171.86, 800 m, 16 July 1993, *C. L. Parker 4541* (ALA-V115556). **Kamchatskya Oblast:** Koryakskii natsionalnyi okrug (Koryak natl. region), Penzhinskii rayon (Penzhinskii distr.), Penzhinskii ridge, E knoll of mtn. Belaya (White), 745 m, 28 June 1975, *C. Kharkevitch & M. Gorinkov s.n.* (ALA-V110028). **Sakha Republic:** Lena River E bank, N-most ridge of Verkhoyansk Mtns., tundra meadows, luxuriant mtn. slopes, calcareous outcrops, 71.687, 127.283, 24 July 2004, *H. Solstad & R. Elven 04/0413+0724* (ALA-V154163); Lena River E bank, N-most mtn. slopes of Verkhoyansk Mtns., tundra meadows, luxuriant mtn. slopes, calcareous outcrops, 71.687, 127.283, 24 July 2004, *H. Solstad & R. Elven 04/0413+0730* (ALA-V154164); Lena River E bank, Verkhoyansk Mtns. vis-a-vis Chekurovka village, limestone slopes, seepage mire, 71.050, –127.583, ca. 300 m, 17 July 2004, *H. Solstad & R. Elven 04/0480* (ALA-V154330); Lena River E bank, Kharaulakh Mtns. 18 km S of Tit-Ary, limestone mtn. slopes, seepage mire, 71.918, –127.316, 23 July 2004, *H. Solstad & R. Elven 04/0675* (ALA-V154331); Lena River estuary, area of Lena-Nordenskiöld Research Station, NE-most Kharaulakh Mtns. & Lena River delta flat, luxuriant mtn. slopes with seepage & snowbeds, 72.185, –128.051, 28 July 2004, *H. Solstad & R. Elven 04/1002* (ALA-V154332). UNITED STATES. **Alaska:** Agattu Island, steep scree slopes, 52.472, 173.579, 137 m, 1 July 2008, *L. Kenney & R. S. A. Kaler 17* (ALA-V165606); Atka

Island, Atka village, headwaters of "Chuniisxax Cr.," fellfield area, 52.2, –174.2, 630 m, 14 Sep. 1982, *B. F. Friedman 82-67* (ALA-V81703); St. Lawrence Island, slope 30°, NE aspect, cinder cone slope, vesicular basalt rubble slope, 63.635, –170.565, 270 m, 26 July 2012, *M. L. Carlson MLC2012-218* (ALA-V173525); Seward Peninsula, Tin City, SW-facing slope, steep, unstable dry scree slope with blocky talus, sparsely vegetated, 65.57, –167.97, 250 m, 11 July 1996, *R. Lipkin 96-21* (ALA-V143814).

CLAYTONIA SCAMMANIANA HULTÉN IN OUR CURRENT SENSE

CANADA. **Yukon Territory:** Ogilvie Mtns., Dempster Highway, mtn. E of mi. 50–54, in gravelly streaks behind ridge, on E side, 61.0, –133.0, 1767.84 m, 15 Aug. 1966, *R. T. Porsild 477* (CAN-303416); Mayo distr., McArthur Mtns., growing on slate slide, 63.17, –135.92, 1829 m, *H. Bostock 163* (CAN-50920); Mayo distr., Black Ram - Hotsprings, 63.05, –135.08, *H. Bostock 206* (CAN-50919); British Mtns., alpine meadow, 69.25, –140.86, 1128.17 m, 10 July 1980, *R. Nelson et al. 43* (ALA-656). UNITED STATES. **Alaska:** Ikiakpauruk Valley, sunny, poorly drained humus, 69.5, –145.5, 762 m, 30 July 1948, *J. P. Anderson 2393* (ISC-309593); Yukon-Tanana Uplands, Mt. Prindle, ridge SW of summit, 65.461, –146.474, 1250 m, 2 July 1982, *R. Anderson 0067* (ALA-V81830); Mt. McGinnis, slope 10°, NE-facing slope, alpine habitat, growing in moist to wet mud in slide depressions, 63.5, –146.25, 1280 m, 20 July 1971, *A. R. Batten 242* (ALA-52574); approaches of Mt. McGinnis & glacier (Alaska Range), 63.5, –146.25, *J. Sias 46* (CAN 358227); Nulato Hills, N-facing slope, dark, slaty scree, growing with scattered alpine forbs, 63.88, –159.93, 800 m, 15 July 1997, *P. Caswell 96-263* (ALA-V124612); Falls Mt., Twin Lakes, NE-facing slope, loose scree, 60.63, –153.91, 903.71 m, 24 June 1995, *P. Caswell 333-95* (ALA-V120076); vic. of Galbraith Lake, well-drained W-facing slope, not too steep, mossy area, 68.467, –149.417, 975 m, 13 July 1970, *W. J. Cody 27525* (ALA-V123698); Ahklun Mtns., Limestone Ridge, mixed limestone & acidic rock scree & rocky ridge top, 59.21, –161.65, 300 m, 15 June 2004, *M. B. Cook & B. A. Bennett 02-195* (ALA-V151602); Alaska Range, W side of Easy Pass, W aspect, non-vegetated rock outcrop, talus &/or ice, with scree slope, along secondary ridgeline, 63.34, –149.78, 1469 m, 12 July 2000, *M. Duffy MD00-85* (ALA-V147723); Katmai NPP, Contact Cr., aspect 135°, slope 35°, 10% vegetation cover, talus, scattered, 58.23, –155.94, 686 m, 8 Aug. 2002, *A. Jansen, M. Carlson & I. Pearce 02-451* (ALA-V143512); Denali NPP, Mi. 62 Denali Park Rd., rock slide, 63.458, –150.233, 1122.7 m, 22 July 1959, *L. Schene 29* (ALA-8932); Cape Dyer, in a wet seepage area, 68.633, –166.2, 152 m, 20 July 1960, *L. A. Viereck & A. Bucknell 4193* (ALA-13165); Noatak Valley, Feniak Lake, serpentine barrens near NW edge of lake in dense clumps, 68.25, –158.333, 435.8 m, 10 July 1973, *S. B. Young 4611* (ALA-65825); 12 Mi. Summit, wet alpine, 65.398, –145.971, 17 July 1935, *J. P. Anderson 2393* (ISC-309593); Denali NPP, S of Divide Mtn., head of tributary stream, relatively common in moist areas of limestone gravels underlaid by abundant fines, 63.42, –149.98, 1737 m, 28 June 2001, *C. Roland 5031* (ALA-V141634); Denali NPP, Sable Pass, 63.558, –149.667, 1189 m, 2 Aug. 1954, *G. M. Frohne 54-579* (ALA-21842); Yukon-Tanana Uplands, Mt. Sorenson, aspect 360°, slope 5°, rocky alpine forb community on both sides of ridge, 65.004, –142.82, 1329 m, 29 June 2002, *M. B. Cook & B. A. Bennett 02-195* (ALA-V151602); Denali NPP, Tatina River drainage, SW aspect, in dryas-mixed ericaceous dwarf alpine scrub gravelly colluvial slopes, small opening of unstable rock & gravel, 62.4, –152.88, 955 m, 9 July 2002, *M. Duffy MD02-45* (ALA-V148793); De Long Mtns., Siniktanneyak Mtn., 5 km NW of Feniak Lake, lower SE shoulder of summit, SE-facing, gentle cobble slope with scattered seepages, patches of graminoid meadow & *Dryas* heath vegetation, serpentinized igneous bedrock, growing among cobbles & gravels in seepage areas, 68.29, –158.45, 625 m, 8 July 2001, *C. L. Parker & C. R. Meyers 10592* (ALA-V134540); Alaska Range, W end of Shellabarger Pass, aspect 206°, slope 26°, large scree slope, 62.52, –152.78, 945 m, 31 July 2001, *A. Larsen & A. Batten 01-0747* (ALA-V138801); Yukon-Tanana Uplands, SW of Mt. Sorenson, aspect 180°, slope 33°, large alpine slope composed of coarse scree slopes & rock outcrops, large areas of *Dryas*, 64.96, –143.08, 1158 m, 21 June 2002, *A. Larsen, C. Roland & A. R. Batten 02-1438a* (ALA-V146824); Cape Lisburne, N-facing slope, common in moss-rich dwarf shrub–herbaceous snowbed meadow on small ridge, 68.85, –166.1, 335 m, 1 July 1996, *R. Lipkin 96-67* (ALA-V143817); Denali NPP, Cathedral Mtn., steep alpine screes & ridge crest outcrops, 63.567, –149.6, 1120 m, 18 Aug. 1976, *D. F. Murray 6240* (ALA-V73725); Neacola Mtns., slope 20-30°, NW-facing slope, scree, sparsely vegetated moist, slumping moraine, 60.7, –153.91, 1314 m, 25 June 2001, *P. Caswell & R. Lipkin 01-120* (ALA-V136353); Cape Lisburne, occasional to common in thick moss & *Silene acaulis* polsters on moist seepy dwarf shrub herb tundra on side of rd., 68.85, –166.11, 280 m, 1 July 1996, *R. Lipkin 96-42* (ALA-V143816); Noatak Valley, Feniak Lake, outwash fan & alpine bench, serpentines, 68.25, –158.333, 670 m, 26 July 1978, *D. F. Murray 6895* (ALA-82926); De Long Mtns., Siniktanneyak Mtn., stream gully on E shoulder, serpentine barrens, 68.317, –158.333, 790 m, 9 Aug. 1977, *R. Lipkin & J. Dawe 551* (ALA-98293); Brooks Range, vic. of Anaktuvuk Pass, wet meadow drainage, 68.283, –151.417, 762 m, 10 July 1949, *L. A. Spetzman 1878* (ALA-652, CAN-211982); De Long Mtns., Siniktanneyak Mtn., N of Feniak Lake, outwash fan, very wet serpentine rubble, herb meadow, 68.317, –158.333, 530 m, 9 Aug. 1977, *R. Lipkin & J. Dawe 552* (ALA-98334); Denali NPP, top of Sable Mtn., 63.573, –149.707, 1830 m, 16 Aug. 1950, *G. Murie s.n.* (ISC-309595); Yukon-Tanana Uplands, Eagle Creek vic., E-facing slope, shrub tundra with scattered spruce, seepage, 65.45, –145.433, 792 m, 23 July 1981, *A. O. Khokhryakov, B. A. Yurtsev & A. R. Batten 6852* (ALA-V69845); Brooks Range, Mi. 257 Dalton Hwy., Atigun River valley, 68.25, –149.4, 1066.83 m, 18 July 1981, *A. P. Khokhryakov, B. A. Yurtsev & D. F. Murray 6557* (ALA-V69813); Noatak Valley, Feniak Lake, outwash fan & alpine bench, serpentines, 68.25, –158.333, 670 m, 26 July 1978, *D. F. Murray 6895* (ALA-82926); Mi. 277 Dalton Hwy., E of Galbraith Lake, W-facing slope & summit, alpine tundra, prostrate shrub-subshrub meadow & fellfield, predominantly dryas, 68.533, –149.45, 1040 m, 19 July 1977, *D. F. Murray & A. W. Johnson 6366* (ALA-79822); Alaska Range, Upper Tin Creek, NE-facing slope, loose limestone–volcanic rubble slope, 62.3833, –153.667, 1070 m, 23 June 1983, *C. L. Parker 633* (ALA-V77109); Denali NPP, Polychrome Pass, E fork Toklat River, snowbed ledge community on scree banks, low shrub, *Carex*, Gramineae, 63.558, –149.767, 1050 m, 26 June 1976, *D. Heebner s.n.* (ALA-71025); Denali NPP, vic. of Toglat River, 23 Aug. 1949, *E. L. LePage 25525* (CAN-204318, 508594); Arctic Foothills, Mi. 280 Dalton Hwy., growing along small stream in large clumps with moss in mud, moist to wet tundra on vegetated talus, 68.567, –149.5, 874.3 m, 12 July 1980, *R. Lipkin 80-87* (ALA-V75733); Denali NPP, Polychrome Pass, 63.517, –149.933, 1126 m, 24 June 1939, *A. Nelson & R. A. Nelson 3812* (ALA-658, ISC-309597); Denali NPP, McGonagall Pass, "near the top," 63.233, –150.717, 1763 m, 3 Aug. 1939, *R. Nelson, A. R. Nelson & H. Herning 43* (ALA-656); Mt. Eielson, NW slope to summit, moist tundra, fellfield knife-edge ridge, in very loose cherty, limestone talus slope, 63.417, –150.333, 1371 m, 10 July 1956, *L. A. Viereck 1190* (ALA-3504); Alaska Range, Mt. McGinnis, alpine slopes with bedrock outcrops & screes, continuous tundra mats except where active geomorphic processes & bedrock present bare mineral substrates, 63.667, –146.083, 1200 m, 9 July 1970, *D. F. Murray 3084* (ALA-V76669); Mi. 277 Dalton Hwy., W-facing slope & summit, alpine tundra, prostrate shrub-subshrub meadow & fellfield, predominantly *Dryas*, 68.533, –149.45, 1040 m, 26 July 1979, *D. F. Murray & A. W. Johnson 7007* (ALA-V77798); Denali NPP, vic. Eielson Visitors Center, steep, unstable volcanic scree, 63.433, –150.317, 1350 m, 5 Aug. 1984, *C. L. Parker 1316* (ALA-V81532); Alaska Range, Little Stony Creek, E-facing volcanic scree N of rd., 63.45, –150.28, 1200 m, 24 June 1985, *C. L. Parker 1365* (ALA-V86444); Yukon-Tanana Uplands, Mt. Sorenson, aspect 224°, slope 14°, moist spring area on S spur, 64.99, –142.93, 1584 m, 29 June 2002, *A. Larsen & D. Person 02-1627* (ALA-V146825); Togiak NWR, Cape Newenham, seepage area, 58.65, –62.08, 221.18 m, 5 July 1995, *P. Caswell 333-95* (ALA-V120076); Denali NPP, N of Ruby Peak, scattered on steep, SW-facing slope of spur ridge, 63.34, –149.91, 1127.18 m, 14 Aug. 1998, *C. Roland & M. B. Cook 3514* (ALA-V127594); Denali NPP, Upper W Fork Yentna River, steep S-facing slope, scattered in gravelly scree on steep slope with minimal plant cover, 62.52, –152.41, 442 m, 27 July 1999, *C. Roland & S. Burson 4092* (ALA-V133677); Denali NPP, W of Chedotlothna Glacier, aspect 140°, slope 226°, expansive scree slope, 62.89, –151.94, 1768 m, 20 Aug. 2001, *A. Larsen & M. Duffy 01-1175* (ALA-V138802); Endicott Mtns., NNE of Inualurak Mtn., E-facing seepage slope on blocky, carboniferous substrate, moist to wet open herbaceous vegetation, 68.23, –152.19, 1330 m, 28 July 2002, *C. L. Parker & H. Solstad 13356* (ALA-V139691); Endicott Mtns., NNE of Inualurak Mtn., moist moss depression in rocky alpine plateau, carbonate substrate, 68.23, –152.19, 1380 m, 30 July 2002, *C. L. Parker & H. Solstad 13433* (ALA-V139770); Yukon-Tanana Uplands, Eagle Summit, moist, mossy patches in *Dryas*-dwarf willow tundra near top of pass, 65.45, –145.43, 1130 m, 3 July 1997, *C. L. Parker & A. R. Batten 6963* (ALA-V122845); Nushagak–Big River Hills, Lyman Hills, alpine *Dryas*-heath slopes, growing in moist, mossy shallow depressions along ridge top, 61.9, –155.15, 650 m, 2 July 1999, *C. L. Parker & D. Blank 9001* (ALA-V128286); Endicott Mtns., S-facing moist, carbonate scree, poorly developed vegetation stripes, 68.23, –152.19, 1380 m, 30 July 2002, *C. L. Parker & H. Solstad 13434* (ALA-V139771); Arctic Foothills, Castle Mtn., alpine slopes, valleys & screes, growing in soil bank along stream, 68.56, –152.53, 885 m, 29 July 2002, *C. L. Parker et al. 12758* (ALA-V140663); Denali NPP, "area of Denali National Park," 63.73, –148.91, 524 m, Aug. 1950, *G. Murie GM-5058* (ALA-V101340); Alaska Range, N of Double Mtn., rare in loose gravel on steep, S-facing fellfield slope, 63.64, –149.51, 1158 m, 19 June 1998, *C. Roland 3040* (ALA-V127349); Alaska Range, Teklanika River canyon/Comb Peak, confined to patches in dry, loose rubble on steep, SE-facing slope, 63.97, –149.42, 886.34 m, 8 July 1998, *C. Roland 3198* (ALA-V127384); Denali NPP, W Fork Chulitna River, S slopes of canyon, scattered in scree on SW-facing slope, 63.29, –149.82, 871.18 m, 14 Aug. 1998, *C. Roland & M. B. Cook 3495* (ALA-V127583); Denali NPP, SW of Mystic Pass, aspect 136°, slope 25°, occasional in rubble & scree on SW-facing slope, 62.62, –152.59, 1067 m, 27 June 2000, *C. Roland & A. R. Batten 4303* (ALA-V141232); Denali NPP, above W fork of Chulitna River, not uncommon in scree on S-facing alpine slopes, 63.27, –149.9, 1341 m, 18 July 2000, *C. Roland & S. Carwile 4573* (ALA-V141234); Arctic Foothills, Castle Mtn., N ridge of summit area, alpine *Dryas* heath, cliffs scree & meadows along drainages, growing on steep creek bank, 68.57, –152.57, 885 m, 30 July 2002, *C. L. Parker et al. 12872* (ALA-V140944); Alaska Range, NE of Heart Mtn., steep, SE-facing slope, very loose slide rock, 62.97, –151.89, 1524 m, 10 July 1999, *C. Roland 4005* (ALA-V133676); Alaska Range, N of Heart Mtn., locally abundant on scree slope, 62.95, –152.05, 1067 m, 29 June 2000, *C. Roland 4437* (ALA-V141233); Denali NPP, Windy Cr. valley, aspect 220°, slope 27°, rare in loose rubble & patchy tundra, 63.45, –149.04, 1198 m, 9 July 1998, *C. Roland 3231-b* (ALA-V127411); Neacola Mtns., S Lower Twin Lake, scree slope, 60.63, –154.03, 771.27 m, 14 June 1996, *P. Caswell 96-263* (ALA-V124612); Alaska Range, Muldrow Glacier, ridge above glaciers, 63.3, –150.3, 1524 m, 17 July 1956, *L. A. Viereck 1367* (ALA-8265); Denali NPP, Sable Mtn., 63.575, –149.708, 1830 m, 2 Aug. 1959, *L. Schene 11* (ALA-8931); Yukon-Tanana Uplands, Eagle Creek vic., NW exposure, growing on dry, grassy knoll, 65.45, –145.433, 853 m, 6 June 1965, *J. N. Trent s.n.* (ALA-30620); Dry Creek, 50 mi. E of Healy, alpine zone consisting primarily of mats of *Dryas octopetala* on exposed sites, isolated clumps on loose talus slopes & sedge meadows in protected areas, 63.933, –147.45, 1372 m, 25 June 1962, *L. A. Viereck & K. James 5889* (ALA-82350); Yukon-Tanana Uplands, Eagle Summit, moist tundra, 65.433, –145.533, 13 July 1963, *D. Hatler dh-44* (ALA-24840); Nushagak-Big River Hills, Lyman Hills, N-facing scree, 61.93, –155.08, 755 m, 3 July 1999, *C. L. Parker et al. 9021* (ALA-V128306); Denali NPP, Polychrome Pass, in loose, sliding rock, 63.517, –149.933, 1126 m, 14 July 1939, *A. Nelson & R. A. Nelson 3812* (ALA-658, ISC-309597); Cantwell, 63.392, –148.942, 667 m, 10 July 1927, *L. J. Palmer 1914* (ALA-5545); Yukon-Tanana Uplands, Porcupine Dome, slope 19°, northern exposure, talus, alpine tundra, 65.517, –145.517, 1067 m, 26 July 1964, *L. A. Viereck 7386* (ALA-58774); Alaska Range, Tonanza River, in loose talus, 62.667, –152.5, 1142 m, 15 July 1961, *L. A. Viereck 5014* (ALA-68631); Brooks Range, Schrader Lake area, in wet moss on level ground on alluvial fan, vegetation dominated by moss & *Carex bigelowii*, 69.375, –144.967, 853 m, 28 June 1973, *A. R. Batten 242* (ALA-52574); Kilbuck-Kuskokwim Mtns., gentle slope, gravelly loam with "fair" moisture, 60.267, –160.267, 45 m, 25 May 1933, *W. B. Miller 295-c* (ALA-2879); Goodnews Bay Platinum Mine, grassy meadow above camp, grassy tundra, 58.933, –161.733, 98.933 m, 4 July 1976, *M. Williams 2601* (ALA-68920); Dry Creek, 50 mi. E of Healy, alpine zone consisting primarily of mats of *Dryas octopetala* on exposed sites, loose talus slopes & sedge meadows in protected areas, in seepage areas on exposed solifluction surfaces, 63.933, –147.45, 1524 m, 11 July 1962, *L. A. Viereck & K. Jones 5714* (ALA-82402); Kilbuck-Kuskokwim Mtns., grassy lower meadows at foot of spur of Red Mtn. (local name), but also found up to rocky ledges, 58.954, –161.742, 518.29 m, 2 July 1976, *M. Williams 3537* (ALA-68919, CAN-402161); E Fork of Kuskokwim River a.k.a. Tonzona River upper valley, loose talus slope, exposed ridge, 62.667, –152.5, 1524 m, 26 July 1961, *L. A. Viereck 5164* (ALA-68632); Alaska Range, Refuge Valley, scree slope, 63.517, –150.35, 1371 m, 17 July 1968, *S. Jones s.n.* (ALA-39518); Noatak Valley, Feniak Lake, along marshy edges of small pool near NW edge of lake, 68.25, –158.333, 435.8 m, 9 July 1973, *S. B. Young 4553* (ALA-65284); Index Mtn., 40 mi. ENE of Arctic Village, R34E, T14S, 68.25, –144.17, *L. Hettinger 209* (CAN-369669); Brooks Range, Lake Peters, abundant, "wet & mossy niggerhead tundra with *Thalictrum alpinum*," 69.33, –145, 15 July

1961, *R. D. Wood & M. Wood 341* (CAN-271431); Brooks Range, Lake Schrader, poorly drained sunny meadows on humus, 69.42, –145, 914 m, 17 July 1948, *L. A. Spetzman 784* (CAN-211981); Alaska, Brooks Range, vic. of Anaktuvuk Pass, wet meadow drainage, 68.28, –151.42, 762 m, *L. A. Spetzman 1878* (CAN-211982).

Appendix 2. Changes in determination of specimens in the *Claytonia arctica* complex.

We reviewed the changes in names given to a representative subset of specimens of the *Claytonia arctica* complex. The ALA, CAN, and ISC (on permanent loan to ALA) accession numbers for the specimens are listed below, classed by the various types of name change. These data are displayed graphically in Figure 4.

NO CHANGES (79 SPECIMENS)

C. SCAMMANIANA (65 SPECIMENS)

- *C. scammaniana* only (54): CAN-204318, CAN-508594, CAN-50919, CAN-50920, ALA-3504, ALA-V119442, ALA-V120076, ALA-V151602, ALA-24840, ALA-58774, ALA-82402, ALA-658, ALA-39518, ALA-68631, ALA-21842, ALA-30620, ALA-8265, ALA-V86444, ALA-656, ALA-V81532, ALA-V69845, ALA-71025, ALA-V73725, ALA-82350, ALA-657, ALA-V77109, ALA-V122845, ALA-V123477, ALA-V123698, ALA-V124612, ISC-309595, ISC-309593, ALA-V81768, ALA-V101340, ALA-V127349, ALA-V127411, ALA-V127583, ALA-V127594, ALA-V128286, ALA-V128306, ALA-V129313, ALA-V133676, ALA-V133677, ALA-V136353, ALA-V138801, ALA-V138802, ALA-V141232, ALA-V141233, ALA-V141234, ALA-V141634, ALA-V146825, ALA-V147723, ALA-V148793, ALA-V150049
- *Montia scammaniana* → *C. scammaniana* (3): ALA-68920, ALA-68919, CAN-402161
- *Claytonia* sp. → *C. scammaniana* (7): ALA-V134540, ALA-V139691, ALA-V139770, ALA-V139771, ALA-V140944, ALA-V143512, ALA-65284
- new species → *C. scammaniana* (1): ALA-65825

C. ARCTICA (14)

- *C. arctica* only (14): ALA-V154164, ALA-V154163, ALA-V154332, ALA-V154330, ALA-V154331, ALA-V165606, ALA-V163580, ALA-V173525, ALA-V110028, ALA-V121767, ALA-V81703, ALA-V143814, ALA-V115556, CAN-508538

ONE CHANGE (11)

C. ARCTICA → *C. SCAMMANIANA* (7)

- *C. arctica* → *C. scammaniana* (7): ALA-98334, ALA-82926, ALA-83024, ALA-98293, ALA-79822, ALA-8932, ALA-2879

C. SARMENTOSA → *C. SCAMMANIANA* (2)

- *C. sarmentosa* → *C. scammaniana* (2): ISC-309591, ALA-49595

C. PORSILDII → *C. SCAMMANIANA* (2)

- *C. PORSILDII* → *C. SCAMMANIANA* (2): ALA-V143816, ALA-V143817

TWO CHANGES (9)

C. SARMENTOSA → *C. ARCTICA SENSU PORSILD* → *C. SCAMMANIANA* (5)

- *C. sarmentosa* → *C. arctica* sensu Porsild → *C. scammaniana* (5): CAN-369669, ALA-52574, CAN-211981, CAN-211982, CAN-358227

C. PORSILDII (INCL. C. ARCTICA SENSU PORSILD) → *C. ARCTICA* → *C. SCAMMANIANA* (4)

- *C. porsildii* → *C. arctica* → *C. scammaniana* (3): ALA-V76669, ALA-V69813, ALA-V77798
- *C. arctica* sensu Porsild → *C. arctica* → *C. scammaniana* (1): ALA-V75733

OTHER DETERMINATION SWITCHES (6)

- *C. scammaniana* → *C. sarmentosa* → *C. scammaniana* (1): ALA-8931
- *Claytonia* sp. → *C. porsildii* → *C. scammaniana* (1): ALA-V140663
- *C. arctica* → *C. scammaniana* → *C. sarmentosa* → *C. scammaniana* (1): ALA-5545
- *C. arctica* sensu Porsild → *C. sarmentosa* → *C. scammaniana* (1): CAN-271431
- *C. sarmentosa* → *C. arctica* → *C. scammaniana* (1): ALA-13165
- *C. sarmentosa* → *C. arctica* sensu Porsild → *C. arctica* → *C. scammaniana* (1): ALA-652

ISSN 0026-6493 (PRINT); ISSN 2162-4372 (ONLINE)