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REVISION OF THE STELLARIA CALYCANTHA (CARYOPHYLLACEAE)
COMPLEX AND TAXONOMIC NOTES ON THE GENUS

By

Richard K. Rabeler

A DISSERTATION

VOLUME I

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Botany and Plant Pathology

1986

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ABSTRACT

REVISION OF THE STELLARIA CALYCANTHA (CARYOPHYLLACEAE) COMPLEX AND TAXONOMIC NOTES ON THE GENUS

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The extensive morphological variation exhibited in Stellaria calycantha (Ledeb.) Bong. and two related species (S. crispa Cham. & Schldl. and S. obtusa Engelm.) in North America has resulted in these taxa being interpreted in many different ways. There is little consensus among modern floristic works as to the number of species and varieties that should be recognized in this complex.

Numerical methods emphasizing multivariate approaches for analyzing morphological variation, studies of plants in culture, and field observations were employed in an attempt to circumscribe the taxa in the complex as they occur in North America. Stellaria obtusa is easily segregated from the other species. Several characteristics, including sepal venation and seed morphology, indicate a close relationship between S. crispa and S. calycantha. The classification of S. calycantha is realigned, with the number of often-cited taxa reduced from eight to three; three varieties based mainly on inflorescence characteristics are synonymized. Two species (S. calycantha and S. borealis Bigelow) and one subspecies (S. borealis subsp. sitchana (Steudel) Piper) are recognized on the basis of morphological features;

segregation of S. calycantha and S. borealis is independently supported by cytological information. The hybrid formula S. borealis × S. longifolia is proposed, providing the first recognition in American literature of the hybrid formed between S. borealis and S. longifolia Muhlenb. ex Willd.

Evidence is presented for a North American origin of the complex with subsequent dispersal to both Europe and the Far East. Plant protection efforts are reviewed in light of the proposed taxonomy, an analysis of post-1960 collections of the taxa, and field studies.

A description of the genus Stellaria and its nomenclatural synonymy are provided along with a list of taxa thought to be currently accepted and chromosome numbers that have been reported for these taxa.

To
Martin and Ruth Rabeler
and
Karen Elizabeth Studer

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ACKNOWLEDGMENTS

Before proceeding with the entire list of people who have been of assistance during this work, I should like to make special mention of several individuals who have made significant contributions either to the project itself or to my psychological well-being in the last several years.

I thank Dr. John H. Beaman for encouragement and guidance on this project.

Dr. Thomas Duncan must be mentioned prominently in appreciation of all that he did to facilitate my visit to Berkeley. His provision of housing, access to the UC herbarium computer system, assistance in preparing the data set, getting it to run, and discussing what the voluminous output meant was invaluable. His additional help in running further analyses after my return to East Lansing is greatly appreciated.

Special thanks also to Dr. John K. Morton for sharing his thoughts on the Stellaria calycantha complex and allowing me to inspect his collections, both living and preserved, including 58 chromosome vouchers.

Drs. Jay R. Harman, John K. Morton, Donald O. Straney, and Ralph E. Taggart participated on my guidance committee and provided critical remarks on the text. Dr. Robert K. Jansen assisted me through discussions on approaching the project and selecting numerical techniques to be utilized. Dr. Robert R. Smith, my undergraduate adviser, peaked my early interests in systematic botany and offered

encouragement during my annual visits.

Dr. Edward G. Voss gave considerable assistance in interpreting several sections of the International Code as they applied to several odd nomenclatural situations in Stellaria.

My parents, Martin and Ruth Rabeler, and my fiancée, Karen E. Studer, have provided invaluable encouragement on many occasions.

Dr. Ove Almborn helped in determining the first publication of Stellaria alpestris. Dr. Lincoln Constance reviewed my ideas on typification of Stellaria obtusa. Consultants from the Computer Laboratory User Information Center, Michigan State University, provided assistance in designing the discriminant analysis. Dr. Cheryl A. Crowder scanned the C. F. Baker works in the RSA library, and attempted to locate Stellaria borealis specimens at BM and K. Darwin Dale prepared seed photographs (Figure 40). Dr. Barbara Ertter assisted in developing an autonym list, provided information on the itinerary of C. A. Purpus, and helped me access the correspondence of T. S. Brandegee. George F. Estabrook gave some helpful hints on deciphering the results of the NT-SYS analyses. Dr. John J. Furlow provided a copy of the NT-SYS manual. Roy E. Gereau supplied a copy of a letter from T. S. Brandegee to G. Engelmann which proved to be the answer to the discrepancy between specimen labels and the description of S. obtusa. Angus Gunn provided comments on the label of the Boott collection of Arenaria alpestre in LIV. Dr. Ronald L. Hartman provided recent collections of S. calycantha and S. borealis from Wyoming and information on S. americana. Dr. Larry Heckard provided desk space in the Jepson Herbarium.

Dr. Eugene E. Hutton supplied a collection of Stellaria borealis from West Virginia. Dr. David M. Johnson and Nancy Murray gave several hints on preparing plant descriptions and text formatting. Dr. Askeell Löve provided an important clue in locating the description of S. calycantha subsp. pilosella. Gary Martin provided information on his similar study of the Arenaria lanuginosa complex. Dr. Chris Meacham assisted me via several discussions of numerical taxonomy theory. Dr. Larry E. Morse supplied Stellaria records from the database on rare plant status maintained by The Nature Conservancy. Karen E. Studer assisted in plotting several NT-SYS analyses and making seed/capsule counts. Mary S. Taylor supplied information on C. F. Baker types. Mary M. Walker provided biographical information on Jacob Bigelow and suggested that a Boott collection could be at LIV. Curt M. Whitcomb translated Zhukova's remarks on diploid S. calycantha in Siberia. Dr. Steven J. Wolf provided information on G. Engelmann useful in the typification of S. obtusa. Dr. Richard Zander provided comments on the Bigelow collection from BUF.

Several individuals deserve mention for contributing information that enhanced my field efforts: Robin Day (New Brunswick), Don Henson (Manistique, Michigan), Dr. Paul Monson (northeastern Minnesota), Drs. Dale H. Vitt and Diana Horton (Alberta and British Columbia), and the Superintendents of Crater Lake, Glacier, Lassen Volcanic, Mt. Rainier, and Olympic National Parks for permission to collect specimens in their areas.

Roy E. Gereau, Brian T. Hazlett, Dr. Brent D. Mishler, Nancy Murray, Jacinto Regalado, and Dr. Anton A. Reznicek deserve mention for their roles in helping me procure the literature that was required to

complete the taxonomic portion of this study.

Curators of the following herbaria provided loans of specimens of Stellaria calycantha and related species treated in this work: A, ALA, ALTA, BH, BUF, CAN, CAS, CM, COLO, CORD, CS, CU, DAO, DS, DUL, DWC, F, GH, ISC, JEPS, LE, LKHD, LIV, MICH, MIN, MO, MT, MTMG, ND, NDG, NEBC, NFLD, NY, NYS, ORE, OSC, PAC, PENN, PH, RM, S, TRH, UBC, UC, UPS, US, UTC, VT, WIS, WS, WTU, WVA.

I appreciate the hospitality of the curators of A, ALTA, BH, CM, CRATER LAKE, CU, DUL, F, GFND, GH, JEPS, JKM, MARY, MCTF, MICH, MO, MT RANIER, NA, ND, NDG, NY, PAC, PENN, PH, RSA, UBC, UC, UMBS, US, WAT, and WTU during my visits there.

In addition, the efforts of personnel at several institutions should be noted for looking for specimens that could have been, but were not, in their respective collections: N. Hallé (P), I.C. Hedge (E), G.M. Keleher (WIN), G. Ll. Lucas (K), Linda Rader (WVA), Marian F. Rodman (MASS), Lisa A. Standley (WELC), and Roy Vickery (BM).

The assistance provided by library personnel at the Library of Congress, National Agricultural Library, GH-A, NY, and PH was also most appreciated during the visits I made to their facilities. The Interlibrary Loan Office at Michigan State University deserves mention for some of the minor miracles they "performed" in getting obscure items I requested.

The administration of Lyman Briggs College (now Lyman Briggs School) contributed a great deal through both salaries to me as a graduate assistant, and later, as an instructor and through travel money for several herbarium visits. Field work in 1980 was in part financed via a scholarship received from the Graduate School and money from the

University of British Columbia in payment of some of the expenses incurred in presenting a laboratory demonstration during the Botany '80 meetings.

INTRODUCTION

Members of the Stellaria calycantha (Ledeb.) Bong. complex have been described and treated in many different ways during the 194 years since Michaux made the first collection of S. calycantha. Most attention has focused on the subdivision of S. calycantha into subspecies, varieties, and even forms; over 70 names exist for plants now referred to S. calycantha.

The situation is particularly noticeable in North America where most of the morphological variation is found. Differences in recent North American treatments emphasize this point. Fernald (1940) considered S. calycantha to include seven varieties. Hultén (1968) accepted five of Fernald's varieties, moving two of them to S. sitchana Steudel and adding a subspecies. Hitchcock (in Hitchcock & Cronquist, 1964) modified Fernald's position still further by elevating S. calycantha var. simcoei (Howell) Fern. to S. simcoei (Howell) C. Hitchc.

On the other hand, several workers have suggested that some of the variation, particularly that described among populations in eastern North America, may not deserve taxonomic recognition. Wiegand and Eames (1926) indicated that the differences in inflorescence presentation among plants found near Ithaca, New York, might be environmentally induced, hardly justifying Fernald's (1914) separation of three varieties. Schlising and Iltis (1962) expressed similar reservations about variation in Wisconsin plants, noting that the varietal assignment

of a young specimen could not be satisfactorily determined. Voss (1985) echoed similar feelings noting "these varieties ... are not always well marked."

Both Hultén (1968) and Hitchcock (in Hitchcock & Cronquist, 1964) noted uncertainty about the boundaries of certain taxa, a situation that would be resolved through a monographic study of the group. The widely differing views on the taxonomic circumscription of S. calycantha suggested the need for a serious investigation. It is the intent of this study to circumscribe the members of the S. calycantha complex on the basis of as much evidence as possible. Questions addressed include: How much of the expressed variation deserves taxonomic recognition? Have more (or fewer) taxa been described than are needed to account for variation in the S. calycantha complex?

Problems of taxonomic circumscription in Stellaria are not restricted to the species level. The most recent treatment of Stellaria approaching worldwide coverage was published in 1934 (Pax & Hoffmann, 1934), including an infrageneric classification little modified from that presented by Fenzl (in Endlicher, 1836-1840) and a list of species only partially assigned to that classification scheme. Although a complete treatment of the genus is beyond the scope of this work, it is appropriate to consider the impact of floristic and taxonomic research since 1934 and how it has contributed to our knowledge of the genus Stellaria.

HISTORICAL ACCOUNT

AN OVERVIEW OF STELLARIA

Since the nomenclatural trail followed in various treatments of S. calycantha has lead into several genera besides Stellaria, a brief inspection of the history surrounding the application of the name Stellaria is appropriate. The discussion is organized into sections as follows: a) original description and concept of Stellaria, b) Alsine - is it correct for Stellaria?, and c) early genera that are now considered to be in Stellaria.

Original description and concept of Stellaria

Prior to 1753, the several species of Stellaria known at that time were included in Alsine, a genus established by Tournefort and subsequently adopted by Linnaeus and described in his Genera Plantarum ed. 1. (1737).

The name Stellaria first appeared when Linnaeus (1753) listed eight species in Species Plantarum ed. 1 and subsequently described the genus under Decandria Trigynia in his Genera Plantarum ed. 5 (1754). The generic description by Linnaeus (Figure 1) gives a good characterization of the typical Stellaria flower and includes the feature most often used in segregating Stellaria from Arenaria, namely the presence of bifid petals. It is clear from his inclusion of "Alsine Tournef. 126" (a reference to plate 126 in Tournefort's Institutiones Rei Herbariae of

1700 fide Stearn, 1960) following "504. Stellaria" and the very similar text found in both his 1737 description of Alsine and this description of Stellaria that Linnaeus intended to replace both Tournefort's Alsine and his earlier Alsine with Stellaria. Green (in Hitchcock & Green, 1929) selected S. holostea L., a species included by Linnaeus (1753) in his original treatment, as the type of Stellaria.

Alsine - is it correct for Stellaria?

The only generic name which some have suggested should replace Stellaria is Alsine. Linnaeus (1753, 1754) described Alsine in a similar manner to Stellaria. The description (Figure 2) was based on two species, Alsine media L., now Stellaria media (L.) Villars, and A. segetalis L., now Spergularia segetalis (L.) G. Don.

A careful inspection of Linnaeus' (1754) text illustrates that Alsine in Genera Plantarum is clearly different from Tournefort's Alsine. Linnaeus' placement of Alsine in his Pentandria Trigynia emphasized the five-merous androecium he described for A. media, a character that is very common in S. media, but is rather atypical in the other species of Stellaria and not mentioned in his earlier Alsine description (Linnaeus, 1737). The description of Alsine is less specific than that of Stellaria, and in at least one instance, not entirely accurate. As Sprague (1920) noted, "the description of the petals as longer than the sepals fits neither [A. media nor A. segetalis]." Sprague (1920) and McNeill (1962) both concurred with Britton's (in Britton & Brown, 1913) selection of A. media as the type of Alsine.

A major study presenting the Stellaria vs. Alsine argument and all

of the other uses (and misuses) of Alsine was published by T. A. Sprague (1920). From the title, "Stellaria or Alsine", I suspect the intent of his work was to dispel the notion that Alsine should replace Stellaria. After being abandoned in the early 1800's, Sprague noted that the reappearance of the idea could be traced to a proposal by Britton (1893) which reads as follows:

"Alsine, L. Sp. Pl. 272 (1753). I note that this generic name must, on the recognition of priority of place, and the beginning of nomenclature in 1753, clearly displace Stellaria, L. Sp. Pl. 421 (1753)."

The phrase "priority of place" refers to the rule in the Rochester Code (1892) that priority is to be interpreted to apply to both date of publication and the place where the name appears in the publication (Lawrence, 1951). In other words, Alsine was to replace Stellaria since Alsine appeared on an earlier page than did Stellaria.

The action of Britton (1893) was in direct conflict with the International Code in effect both then (the Paris Code fide Lawrence, 1951) and now, where the name chosen by the first author to combine two names published in the same year (i.e. of equal priority) is accepted (Voss et al., 1983; Art. 57.2).

Determination of the first author to select Stellaria over Alsine is not a simple matter. McNeill (1962) listed the first author as Scopoli (1772), but as Sprague (1920) correctly pointed out, Scopoli maintained the genus Alsine for S. media (under Pentandra Trigynia), the other two species which Linnaeus placed in Alsine (A. segetalis and A. mucronata L.) not occurring in the range of Scopoli's work. Scopoli

(1772) thought that the "Alsines genus naturale" included the Linnaean genera Sagina, Alsine, Moehringia, Stellaria, Arenaria, and Spergula but, that in following the "methodi sexualis", Sagina, Alsine, and Moehringia must be separated from the others which he grouped in Stellaria.

Sprague (1920) credited Cirillo (spelling fide Stafleu & Cowan, 1976) with uniting the genera under Stellaria, transferring A. media to S. media (L.) Cirillo in 1784. Although Cirillo (1784) mentioned Alsine media within his treatment of Stellaria, he did not make the transfer; the combination S. media (L.) Cirillo does not exist! The combination of Alsine into Stellaria should be attributed to Villars (1789), who made the combination when he transferred A. media to S. media and specifically included both five- and ten-stamened plants. Alsine is retained in Stellaria since Villars' transfer preceded Gaertner's revival of Alsine in reference to Minuartia in 1791 (Sprague, 1920).

Sprague (1920) and Lawrence (1951) both mention a primary reason for the dichotomy between the use of Alsine or Stellaria for names in the S. calycantha complex. The acceptance of the American Code by N. L. Britton (and others at the New York Botanical Garden) and the objections raised by Asa Gray at Harvard gave early 20th Century American botanists a "choice"; follow Britton and accept Alsine or Gray and use Stellaria. From the literature that I have seen, it appears that the Britton school had more influence on the writers of that day.

Sprague (1920) noted the disposition of Alsine was "a distinct advantage, as it has been applied to three different genera [Stellaria, Spergularia, and Minuartia via a third species added by Linnaeus in 1762] and is now quite ambiguous." McNeill (1962) summarized his

opinion on the status of Alsine as "the name falls into disuse (so long as Stellaria media is regarded as congeneric with S. holostea)."

Nevertheless, Alsine appeared in 1974 in still another form. Löve and Löve (1974) thought that S. media "undoubtedly is misplaced in the genus Stellaria, morphologically, and especially cytologically" and, in noting McNeill's position on Alsine, revived it in a strict sense to include only S. media and close relatives. To my knowledge, this usage has not gained wide acceptance.

Early genera that are now considered to be in Stellaria

Eight generic names have been published that are now accepted as synonyms of Stellaria. These will be discussed in chronological order of publication: Stellularia (1748, 1773), Spergulastrum (1803), Micropetalon (1805), Larbrea (1816), Bigelowia (1817), Adenonema (1835), Schizotechium (1841), and Hylebia (1868).

a. Stellularia

Stellularia has appeared on various occasions, but always applied in the same sense. Linnaeus used Stellularia in place of Alsine in his Systema Naturae (1748). Hill (1751) also used Stellularia in the same fashion in A General Natural History, considering that Stellularia "comprehends the Alsine of Tournefort." Given the appearance of Stellularia on the same page (p. 436) of the second edition of this work (fide Farr et al., 1979) published in 1773 (fide Stafleu & Cowan, 1979; note their statement about the two editions being nearly identical), Stellularia of Hill is an illegitimate name since it was used as a

substitute for Stellaria L.

The most recent appearance of Stellularia was in Kuntze's Revisio Generum Plantarum (1891) in which he argued that Stellaria L. (1753) should be considered a synonym of Stellularia L. (1748); he made Stellularia combinations for all the species of Stellaria of which he was aware. He rejected his own argument when he placed both genera in synonymy of Alsine L., consistent with his acceptance of 1737 as the starting point for priority (see his Codex in Post & Kuntze, 1903).

b. Spergulastrum or Micropetalon

The genus name Spergulastrum was published by Michaux in 1803. The reason behind the rejection of Spergulastrum in favor of Micropetalon is difficult to decipher since I can get no clear statement from any source as to why Spergulastrum is, as Rafinesque (1818) called it, "the bad name Spergulastrum Michaux."

Michaux (1803) described Spergulastrum, noting that it had the habit and the calyx of Stellaria and the following characteristics:

"COR. petala aut nulla aut calyce conspicue minora, integra. STAM. 10. PIST. stigmata 4, sessilia, ligulato-setacea. CAPS. ovata, calyce longior, 4-valvis, &c."

or (my translation)

petals none or entire, conspicuously shorter than the calyx; stamens 10; stigmas 4, sessile, ligulate-setaceous; capsule ovate, longer than the calyx, 4-valved.

Three species were included in Spergulastrum: S. lanuginosum Michaux (now Arenaria lanuginosa (Michaux) Rohrb.), S. gramineum Michaux (now

Stellaria longifolia Muhlenb. ex Willd.), and S. lanceolatum Michaux which refers to Stellaria borealis Bigelow. He went on to note that the number of stigmas and "rariore petalorum defectu" (petals rarely wanting) set Spergulastrum apart from Spergula, probably one of the only times that Spergula and members of Stellaria and Arenaria were placed that close in a classification.

Persoon (1805) defined Micropetalon on a very similar set of characters, namely a 5-parted calyx; petals being minute, entire, or none; capsule ovate, longer than the calyx, 4-valved. He then cited "(Habitaee Stellariae. Spergulastrum. Mich.)" and listed the same three species that Michaux included. He concluded his treatment with the following statement: "Hae plantae genus naturale cum Stellariis efficere videntur." [these plants seem to form a natural genus with Stellaria]. This statement is intriguing since it indicates he did not feel the separation between Micropetalon and Stellaria was very great.

Pursh (1814) followed Persoon (1805), although he created an orthographic variant by citing the genus as Micropetalum. Nuttall (1818) followed Persoon in accepting Micropetalon, but noted it to be "a trifling genus which ought to be united with Stellaria." He removed M. lanuginosum (Michx.) Pers. for having a 6-toothed capsule, placing it in Stellaria as S. elongata Nutt., a transfer which he felt rendered "that genus [Micropetalon] unnatural."

In addition to noting Spergulastrum as a "bad name," Rafinesque (1818) also thought that Micropetalon lanuginosum should be removed. He noted that since it was apetalous, M. lanuginosum more properly belonged either in Bigelowia or Ballarion. Torrey (1824) united Micropetalon with Stellaria, stating that "I entirely agree with Mr. Nuttall that the

genus MICROPETALUM is founded on too trifling characters to be separated from STELLARIA to which I have accordingly united it." On the other hand, Amos Eaton continued the separation of these genera, inadvertently adding combinations for S. longifolia under Micropetalum (in Eaton, 1829) and Micropetalon (in Eaton, 1833).

Torrey (1824) noted Michaux's Spergulastrum combinations in synonymy, but offered no hints as to his opinion of the problems with that name. Fernald (1914) noted Persoon's transfer of Spergulastrum lanceolatum to Micropetalon, but gave no further details. McNeill (1962) listed Spergulastrum as a synonym (in part) of Arenaria subg. Leiosperma McNeill, but did not mention Micropetalon. Farr et al. (1979) listed Micropetalum and Micropetalon as synonyms of Spergulastrum. I surmise that one possibility for Persoon's action and Rafinesque's comment is one of semantics. Michaux mentioned that his plants had the habit and calyx of Stellaria, but gave them a name reminiscent of Spergula from the styler condition that was important in the Linnean sexual system that Michaux followed.

The only combinations that had ever been made in Spergulastrum were the three of Michaux until 1981 when Weber (in Weber et al., 1981) made the combination Spergulastrum lanuginosum Michx. subsp. saxosum (A. Gray) W. A. Weber. Weber did not discuss the reason for his action. I consider this move to be an unnecessary resurrection of a genus in which Michaux included unrelated taxa and which is separated from Stellaria on characteristics which, as will be shown later, can vary on the same Stellaria borealis plant.

c. Larbrea

Larbrea was published by St. Hilaire (1816) to accomodate the perigynous (rather than hypogynous) stamen insertion that he noted in Stellaria aquatica Pollich (= S. alsine Grimm). Godron (1842) emended the genus, picking up on the character which he noted was first reported by St. Hilaire. He added three more species to Larbrea, and added a series of floral characters to maintain Larbrea as distinct from his emended concept of Stellaria (S. holostea, S. nemorum L., and S. pentagyna Gaudin [= Myosoton aquaticum (L.) Moench]). A more appropriate level for Larbrea was afforded the name by Fenzl (in Endlicher, 1836-1840 [Stellaria, p. 969, published in 1840 fide Stafleu & Cowan, 1976]), who placed Larbrea in synonymy with one of his "sections" of Stellaria.

d. Bigelowia

Bigelowia was published by Rafinesque (1817) to accomodate a plant reported by Bigelow (1816) as Arenaria seu Stellaria. The only character separating Bigelowia from either Stellaria or Arenaria is petal condition, Rafinesque believing that an apetalous plant could not belong to either genus. Bigelowia was not adopted by other North American botanists, and in an action taken "on the definite understanding that all well-known generic homonyms should, as far as possible, be conserved" (Green in Rehder et al., 1935), became a nomen rejicienda against the more widely used Bigelowia A. DC.

e. Adenonema

Adenonema was described by Bunge (1835) for a Russian species which he felt was distinctive in its perigynous stamen structure and five-valved capsule bearing a single seed. Fenzl (in Endlicher, 1840; in Ledebour, 1841-1843 [Stellaria, p. 375-395, published in 1842 fide Stafleu & Cowan, 1979]) included Adenonema as a subgenus of Stellaria, a position which has received little if any argument.

f. Schizotechium

Reichenbach apparently is the only author who elevated subg. Schizotechium Fenzl to the generic level, a move made without explanation in his Herbarienbuch (1841). Fenzl (in Endlicher, 1840) separated subgenus Schizotechium from all other groups in Stellaria on the basis of the few (2-3) ovules and seeds (1, rarely 2) found in Stellaria crispata Wallich, the only species Fenzl cited in subgenus Schizotechium.

g. Hylebia

The final genus in this category is Hylebia, published by and used solely by Fourreau (1868). This is a simple elevation of Koch's (1837) Stellaria sect. Hylebia, created to segregate S. nemorum from all other species of Stellaria on the basis of an elongated columella.

TAXONOMIC HISTORY OF STELLARIA CALYCANTHA

The description and naming of the variation present in the various members of the Stellaria calycantha complex has been a subject of interest to both European and American botanists. The purpose of this section is to trace the development of the current nomenclature, summarizing the various treatments which have been proposed since Michaux published the first name applicable to the complex in 1803.

This account has been divided into two sections; major European treatments and treatments based on North American material.

Major European treatments

Background information on the major treatments of European members of the S. calycantha complex which influenced nomenclatural concepts used for North American material is presented here. Consideration of European taxonomic activity in the Stellaria calycantha complex is divided into several sections to correspond with the appearance of the major revisionary works of Fenzl (in Ledebour, 1841-1843), Fries (1842-1845), and Regel (1862).

Nomenclature prior to 1842

Ledebour (1815) first used the epithet calycantha when he published the description of Arenaria calycantha Ledeb. based on a Tilesius collection from "Sibiria orientali," probably made in 1804 or 1805 (fide Hultén, 1927). The polynomial diagnosis that he provided before the

longer description is as follows: "A. foliis oblongis acutis sessilibus basi ciliatis, pedunculis axillaribus unifloris diphyllis." [leaves oblong, acute, sessile with a ciliate base, peduncles axillary with one flower and two bracts]. He also noted that this species had a calyx of five oblong, acute, membranous-margined sepals and stamens shorter than the calyx. The absence of petals evidently puzzled Ledebour since he wondered whether the plant was always apetalous or if the petals fell early.

Arenaria calycantha is often listed as being published in 1812. This date probably was gleaned from the title page of Mémoires de L'Académie Impériale des Sciences de St. Pétersbourg Volume 5, which also includes the text "Avec L'Histoire de L'Académie pour L'Année 1812", with the date 1815 appearing at the bottom of the page. An inspection of the volume reveals that "L'Histoire is just that; a 30 page article at the beginning of the volume. The text "Conventuel exhibuit die 19 Januarii 1814" on the title page (p. 514) of Ledebour's article indicates the paper was read in 1814, placing publication no earlier than late 1814 in any case.

The initial Scandinavian treatment of Stellaria calycantha can be traced to C. J. Hartman (1818) and his recognition of S. uliginosa Murray β alpestris Hartman. He separated β alpestris from S. uliginosa on the basis of linear-lanceolate (vs. oblong) leaves and solitary one-flowered peduncles (vs. subaggregated, often branched peduncles). The combination Stellaria alpestris Hartman first appears in the second edition of his Handbok i Skandinaviens Flora (Hartman, 1832), with the 1818 combination noted in synonymy.

E. M. Fries, another key player in the early taxonomy of Stellaria

in Scandinavia, also enters the scene in 1832 by describing Stellaria alpestris Fries and two polynomial "varieties" in his Novitiarum Florae Suecicae Mantissa Prima (1832). Although these probably can be considered varieties, there is no direct mention of a rank for taxa preceded by a Greek letter in his work. The only names stated as varieties in direct reference to these combinations appear on the labels of specimens which Fries distributed as part of his Herbarium Normale exsiccatae. His "varieties" are as follows: "α. foliis omnibus conformibus" and "β. foliis ad axillas caulis in bracteis suppressis, unde caulis apice paniculatus.", a major distinction being leaves of uniform size in α vs. smaller ones ("bracteis suppressis") in β. Fries noted his "variety" α (at least in part represented by the 1837 distribution of S. alpestris var. aliflora Fries) was based on Hartman's S. uliginosa β alpestris, while his "variety" β (distributed in 1842 as S. alpestris var. paniculata Fries) was based on "Stell. uliginosa alpina" of Laestadius. An inspection of Laestadius (1822) reveals the proper combination is S. graminea L. β alpina Laest. within which he had included S. uliginosa sensu Wahlenb. and comments on Hartman's S. uliginosa β alpestris.

The presence of two 1832 publications which include different descriptions of S. alpestris suggests that the priority should be investigated. Neither Krok (1925) nor Stafleu and Cowan (1976, 1979) give information besides "1832" for the publication date of the works. The reference to "Hartm. Scand. ed. 2. p. 123" in Fries (1832) indicates that Fries' work, the first 16 pages [Stellaria alpestris is on pages 10 and 11] published as a dissertation defended on 9 May 1832 (O. Almborn, pers. comm.), appeared after Hartman's volume. Thus, Stellaria

alpestris Fries must be treated as a later homonym of S. alpestris Hartman.

Fenzl and the first varieties of S. borealis

Fenzl's treatment of the Alsineae in Ledebour's Flora Rossica is of critical importance to the taxonomy of Stellaria calycantha. Fenzl (in Ledebour, 1841-1843 [Stellaria, p. 375-395, published in 1842, fide Stafleu & Cowan (1979)]) accepted S. borealis (as shown in Figures 3 and 4) and segregated the taxon into two varieties based primarily on petal absence (α [var.] apetala) or presence (β [var.] corollina). Both varieties were subdivided again into unnamed *lusus* entities to deal with leaf shape and margin variation (in α) and calyx length (in β). Fenzl's α and β designations can be accepted as varieties since he does mention several times in his Stellaria text "var. α , var. β ," etc., allowing a rank to be associated with his names.

Fenzl's usage of the names Arenaria calycantha and Stellaria calycantha deserve some comment. As I will note later, one of the major arguments that occurred in dealing with the American nomenclature of S. calycantha revolved around whether Arenaria calycantha and Stellaria calycantha were really conspecific. Fenzl apparently thought that they belonged together in α apetala, but did make an interesting, if partial, separation in his *lusi*. This suggests that he found some variation in material he associated with S. calycantha that was absent in A. calycantha, but not enough to clearly segregate them even at the *lusus* level!

The entries for S. alpestris Fries in Figures 3 and 4 are confusing. The only Fries work quoted in the text is his "Novit. Fl.

suec. mant. I," the 1832 publication. Based on inspecting Fries (1845) and his redefinition of S. alpestris, I feel it best to assume that S. alpestris α (1832) is included in Fenzl's var. apetala while Fries' α and β both can be considered elements in Fenzl's var. corollina.

Another observation that can be drawn from Fenzl's (in Ledebour, 1842) assignments is that he included diverse elements in his S. borealis var. corollina. Fries (1845) later segregated S. alpestris var. paniculata as his emended S. alpestris, a name which applies to S. borealis $\times$ S. longifolia hybrids. Fenzl specifically referred S. brachypetala Bong., treated here as S. borealis subsp. sitchana (Steudel) Piper, to "Lus. 2", but made no similar assignment for S. alpestris or S. mollis Wirzen 1839 (non Schldl. 1816.), the latter a plant described from Finland that seems misplaced since Wirzen (1839) stated that the inflorescence is ebracteate.

Fries and the emendation of Stellaria alpestris

As shown by label text (Herb. Normale VII no. 34, MO, S, UPS), Fries was aware of the different interpretations of S. alpestris when he distributed S. alpestris var. paniculata in 1842. He discussed the various ways in which S. alpestris had been treated, including the major differences between his 1832 treatment with both varieties and Hartman's restriction of it to apply to only var. aliflora. Fries concluded by noting that his 1832 definition of S. alpestris was correct, proven in his mind since he felt var. paniculata to be more typical of S. alpestris.

It is evident from an inspection of Novitiarum Florae Suecicae Mantissa Tertia that Fries (1842-1845 [S. alpestris and S. borealis, (p.

194-197) published 1845 fide Stafleu & Cowan (1976), not 1842 as often reported] further modified his ideas on the relationship of Stellaria alpestris, S. borealis, and S. calycantha. First, he retained S. alpestris but in a restricted sense from his 1832 concept to include only his strictly scarious-bracted S. alpestris var. paniculata, just as he suggested on the label in 1842. He recognized S. borealis as including two varieties, Fenzl's var. corollina (cited by Fries as a variety and defined in a similar manner) and var. calycantha Fries. Under var. corollina, he cited "St. alpestris a. Fr. Nov. Mant. II". It is most likely a reference to S. alpestris α as defined in his Mantissa Prima (Fries, 1832) since there is no mention of S. alpestris in his Mantissa Altera (Fries, 1839). His S. borealis var. calycantha, based on Bongard's S. calycantha, included S. alpestris Hartman and S. alpestris var. aliflora Fries, a name that Fries associated (and published as "var. aliflora" (Fries, 1837)) with an apetalous plant that he distributed in 1837. From the context of Fries (1845) treatment, Fernald's (1914) statement on the non-equality of S. alpestris α of Fries (1832) and var. aliflora Fries (1837) appears correct, contradicting Fries earlier intention of equating the two collections of S. alpestris that he distributed in his Herbarium Normale with the polynomial "varieties" in his 1832 text. The similarity of his description of var. calycantha and assignment of synonyms to that of Fenzl's var. apetala suggests that var. calycantha could be dismissed as a superfluous name for S. borealis var. apetala.

The work of Eduard Regel

Regel's (1862) treatment of S. borealis in his report on the plants from several expeditions to Russia and Russian North America seems at first glance to resemble Fenzl's work, but there are some intriguing differences. An outline of his classification is presented in Figures 5 and 6.

First, infraspecific names preceded by a Greek letter suggest he was using the same concepts as Fenzl, but Regel repeatedly used the German word "Formen" when referring to them. Hultén (1928, 1937a) cited Regel's names in synonymy, but did not associate any rank with them. Since Regel specified "Formen" and used two infraspecific levels, Article 35.3 of the International Code [where a single infraspecific level is used in a pre-1890 publication, names can be assumed to represent varieties (Voss et al., 1983)] is inoperative, leaving little choice but to consider them as forms. Secondly, he used Fenzl's α apetala and β corollina in very different ways, including the redefinition and naming of included *lusus* entities, along with splitting Stellaria crista Cham. & Schldl. and sensu Fenzl into fractions that he added to his forms of S. borealis (more on this matter later).

Regel's separation of S. calycantha and S. borealis into different forms (calycantha to α apetala, borealis to β corollina) is unfortunate but understandable given Bigelow's (1824) description of S. borealis. Within the description, Bigelow (1824) stated that S. borealis possessed petals about equal to the sepals, but in the very next paragraph noted that most plants that he had seen were apetalous.

There is no mention of the taxa that Fenzl included in his S.

borealis var. corollina. Regel (1862) commented on this when he made the following statement: "Die St. borealis corollina Fenzl halten wir fur eine eigne, durch die zu rispenformigen Trugdolden vereinigten Blumen, gut unterschiedene Art." (We consider St. borealis corollina Fenzl to be a very distinct species, the flowers gathered into panicle-forming cymes.). Regel (1862) instead described Stellaria fenzlii Regel, noting S. borealis β corollina Fenzl and S. borealis β Hook. in the synonymy. True S. fenzlii, found only in northeastern Asia, has broad leaves, reminiscent of some specimens of S. calycantha but clearly much larger in both length and width, all bracts of reduced size and bearing scarious margins, and short hairs at each node (see Schischkin in Komarov & Shishkin, 1936; Ohwi, 1965).

1863 - present

There are very few contributions from the European arena after the appearance of Regel's work in 1862. Modern treatments (e.g. Chater & Heywood in Tutin et al., 1964; Jalas & Suominen, 1983) have accepted S. calycantha without infraspecific taxa.

Behm (1887) described S. laxa Behm from Scandinavia, an entity that Murbeck (1899) referred to S. calycantha (his S. alpestris) while Gürke in Richter (1899) placed it in his "Species dubiae et non satis notae." Murbeck (1899) retained S. alpestris Hartman for S. calycantha, but noted that the often apetalous plants he considered as S. alpestris forma calycantha (Ledeb.) Murbeck were the predominant form seen in northern Europe.

Several of the "combinations" noted since 1863 deal with recognition of the hybrid that can form between S. borealis and S.

longifolia. Norman (1893) described S. borealis × S. friesiana (S. friesiana Ser. in DC. is now considered to be a synonym of S. longifolia), making him one of the first to suggest hybrid parentage for these plants. Murbeck (1899) described S. alpestris × longifolia, and through his synonymy it was possible to deduce the proper placement of S. alpestris sensu Fries as referring to hybrid material. Hultén (1928) listed S. calycantha × S. longifolia for plants he discovered in the Kamchatka region.

Stellaria yesoalpina Nakai, a Japanese member of the Stellaria calycantha complex, was described in 1929. I have not seen material of this plant, but Ohwi (1965) considered it a synonym of S. calycantha.

The only taxon described in the S. calycantha complex since 1940 outside North America is S. calycantha subspecies pilosella Kozhevnikov (1974) published the description of this taxon in a footnote of a table in an article on the flora of the Telekaj Gorge in Chukotka (Eastern Siberia), noting the plant to be very pubescent. From an inspection of an isotype of S. calycantha subsp. pilosella (Kozhevnikov s.n., LE), it is not necessary to consider this entity further since it does not resemble any North American material. The plant more closely resembles a pubescent form of S. longifolia, and I see no reason for maintaining it in the S. calycantha complex.

Nomenclature applied to North American material

This discussion is divided into sections corresponding to a) the two major schools of thought prior to 1914 (establishment and usage of Stellaria borealis for all variation vs. usage of S. borealis and additional taxa), b) the major change that Fernald's work brought in 1914, and c) subsequent developments.

Application of Names Prior to 1914

a. Eastern Plants - Establishment of Stellaria borealis

Andre Michaux (1803) published the first name applied to Stellaria calycantha in North America, describing Spergulastrum lanceolatum Michaux based on a collection from northeastern Québec that he probably made in August of 1792 (Michaux's Journal in Sargent, 1889). He described the species as follows:

"S. glabrum : foliis utrinque angustato-lanceolatis : floribus petaliferis.", adding an "OBS. Interdum stigmata 3. Petala brevissima, ovalia."

or glabrous: leaves from both sides narrowly lanceolate : flowers with petals. Styles occasionally 3. Petals very short, oval.

An inspection of a photograph of the type (Michaux s.n., IDC microfiche 6211; 62: 18, MICH) revealed that the plant he collected would be considered in many treatments as S. calycantha, treated here as S. borealis.

Persoon (1805) transferred Spergulastrum lanceolatum to the genus Micropetalon, forming the combination Micropetalon lanceolatum (Michaux) Pers. The reasons for this transfer are obscure; see "Early genera that

are now in Stellaria" for discussion. Pursh (1814) followed Persoon, but created an orthographic variant when he cited the species as Micropetalum lanceolatum in his Flora Americae Septentrionalis. Torrey's (1824) transfer of Spergulastrum lanceolatum to Stellaria as Stellaria lanceolata (Michaux) Torrey is invalid because of the existence of the earlier S. lanceolata Poiret, a species described from the Straits of Magellan (Poiret in Lamarck, 1806). Even if Volponi's (1983) suggestion that the type of S. lanceolata Poiret may not even be a member of the Caryophyllaceae is confirmed, the name would remain to block the transfer. Stellaria lanceolata does not appear in the literature after Torrey and Gray (1838-1840) listed it in synonymy under S. borealis.

Another set of names was generated from the collections that Bigelow described in his 1816 article on the White Mountains of New Hampshire. Bigelow (1816) was uncertain of the generic assignment for the plant, citing it as "Arenaria seu Stellaria" and describing it as follows:

"caule anguloso; foliis oblongis, acutis, enervibus; pedunculis solitariis elongatis, floribus apetalis."

or stem angular; leaves oblong, acute, without nerves; peduncles solitary, elongate, flowers apetalous.

Rafinesque (1817) decided that, since the apetalous condition seen in this plant precluded its inclusion in either entire-petalled Arenaria or bifid-petalled Stellaria, Bigelow's plant rightfully "constituted a peculiar genus" which he named Bigelowia. He named the plant Bigelowia montana Raf. and included Bigelow's Latin description of Arenaria seu Stellaria and his own translation of that text. There is no indication

that Rafinesque actually examined specimens of B. montana, the combination probably being one of his bibliographic combinations as described in Merrill (1949). In what appears to be a normal occurrence in the writings of Rafinesque, a typographical error resulted in a reference to Bigelowia in a later publication (Rafinesque, 1819) appearing as Bigelonia. Jackson (1893-1895; 1: 302 published in 1893 fide Stafleu & Cowan, 1979) actually made the combination Bigelonia montana Raf. ex B. D. Jackson. The same brief reference (Rafinesque, 1819) contains another little-known binomial for Bigelow's plant, namely Arenaria montana Raf. Although Rafinesque (1819) listed "Big.M.", his reference for Bigelow's 1816 work, after the combination, it must be of his own construction since he is the only one to apply the epithet montana to Bigelow's plant.

Bigelowia montana is the first binomial to be applied to Bigelow's plant. It appears that no other authors used either this or the other combinations which Rafinesque published - not even Bigelow mentioned it in the description of Stellaria borealis (Bigelow, 1824). Rafinesque's name was not transferred to Stellaria and would not displace Bigelow's more familiar name if S. borealis is treated as a species (as proposed here) since making a transfer at this time would result in the creation of a later homonym of Stellaria montana Pierrat, published in 1880 for a European plant (Greuter et al., 1984).

Stellaria borealis Bigelow first appears in Bigelow's Florula Bostonensis (1824) based on collections, both his own and those of others, from the White Mountains. His Latin description is as follows:

"S. foliis ovali-lanceolatis; pedunculis axillaribus, elongatis, unifloris; petalis calyci subaequalibus."

or [Bigelow's translation] "Leaves oval lanceolate, peduncles axillary, elongated, one-flowered; petals about equal to the calyx."

Between this description and the other characteristics that he mentioned in his 1824 treatment, it is obvious that the 1816 and 1824 phrases refer to the same plant in all facets except petal condition. The reason for the abrupt change in this aspect is unknown, but from the text following his 1824 description one suspects that he felt that plants without petals may be incomplete:

"This plant generally occurs without petals, in which state I discovered it on the White mountains in July, 1816. I have since received it several times from the same place but always in the apetalous state, until last year, when Messrs. Greene and Little found it there in August with complete flowers."

This name was used by most authors to refer to S. calycantha plants from eastern North America until Fernald (1940) accepted the arguments of Hultén (1928, 1937a) in considering S. calycantha as including S. borealis.

Two exceptions to the above statement exist. The various editions of Eaton's Manual of Botany for North America represent the only sources I have seen in which Micropetalon lanceolatum is recognized after the binomial S. borealis was published. Micropetalum lanceolatum was first treated in the 3rd edition (Eaton, 1822), with S. borealis joining it in the 5th edition (Eaton, 1829). Eaton (1833) corrected Micropetalum to Micropetalon in his 6th edition, but retained both species in their respective genera in both the 7th (Eaton, 1836) and the final (eighth) edition of his work (Eaton & Wright, 1840).

The other exception to usage of S. borealis for plants from eastern North America is the "interlude" of consideration of Stellaria as a synonym of Alsine (see An Overview of Stellaria) when Britton (in Britton et al., 1894) treated S. borealis as Alsine borealis (Bigelow) Britton.

b. Western Plants

The situation in western North America is more complex, a situation in line with the greater variation exhibited there. Attempts of botanists to describe this variation involved one of two strategies, either the description of infraspecific taxa within S. borealis or the adoption of S. borealis and other names at the species level.

i. Adding varieties to Stellaria borealis

Hooker (1829-1834) listed three varieties (α , β , and γ nana, varietal status confirmed by his use of "var. α " references in text) under S. borealis [p. 94-95 published in 1830, fide Stafleu & Cowan (1979)] based on his inspection of collections from the northern areas of the continent. Variety α , as he noted, matched specimens of S. borealis of Bigelow that he received from Dr. Francis Boott. His β was described as "panicula minus foliosa, rarius bracteata", a plant with an expanded panicle and small bracts replacing the leaves among the flowers of α . Stellaria borealis γ nana was a dwarf form from the Rocky Mountains which later authors (e.g., Macoun, 1883) have referred to S. umbellata Turcz. ex Karelín. & Kir.

The synonymy surrounding var. β is of interest in illustrating some of the complex name shuffling which has taken place in the S. calycantha

complex. Fenzl (in Ledebour, 1842) listed var. α under his S. borealis var. apetala lusus 1, but placed var. β under S. crassifolia Ehrh. var. linearis Fenzl. Regel (1862) followed Fenzl in listing var. β with S. crassifolia, but also included both Hooker's var. β and the very similar var. β of Torrey and Gray (1838-1840, p. 185 published in 1838) in the synonymy of his S. borealis segregate S. fenzlii Regel without citation of any North American collections. In volume 1 of the Synoptical Flora of North America, Robinson (1897) considered S. fenzlii Regel as a synonym of S. borealis var. corollina Fenzl but also included var. β of Hooker under S. crassifolia, continuing the dual placement of Regel (1862). An inspection of specimens of Hooker's var. β (NY, PH) indicates that it clearly should be placed in S. borealis as treated here. Robinson's (1897) treatment "brought back" var. β into S. borealis, but as will be discussed later, the nomenclature he used was inappropriate.

Torrey and Gray (1838) included two unnamed varieties (α and β , varietal status conferred by a reference to "Vars. α & β " under Stellaria longipes Goldie on the same page as the beginning of their treatment of S. borealis.), β applied to plants with "upper leaves reduced to bracts (not scarious); cyme spreading." These varieties are not named and should not be confused with the S. borealis var. β crispa Fenzl ex Torrey & A. Gray which appears in the Supplement to Volume 1 (Torrey & Gray [1838-1840], p. 675, published in 1840). Comparing the descriptions of these "varieties β " makes it clear that Torrey and Gray did not consider them to be equivalent.

Gray (1867) described S. borealis var. alpestris A. Gray, based on a collection from the south shore of Lake Superior (Robbins 62a, GH).

His intent was to segregate plants with "later flowers more cymose, and their bracts small and partly scarious, also the seeds obscurely reticulated or roughish," the condition that Fernald (1914) would later name as his S. borealis var. floribunda Fern., here included in S. borealis subsp. borealis.

Although Gray (1867) cited the authority for the epithet as "S. alpestris Fries, S. fenzlii Regel," I feel it appropriate to follow Brewer & Watson (1876), Howell (1881 [1883 fide Stafleu & Cowan (1979), but see Howell, 1887; Lange, 1953], and Farwell (1918) in citing it as a combination formed by Gray. Since Robbins 62a is not equal to the European material included in S. alpestris Fries (Fries' applied S. alpestris to plants which are examples of the S. borealis × S. longifolia hybrid), I think that Fernald (1914) was correct in relegating Gray's combination to synonymy. Although Farwell (1918) argued that Gray's reference to S. alpestris Fries "is merly [sic] a case of misidentification and cannot invalidate Gray's varietal name," the confusion surrounding the various definitions makes alpestris an ambiguous name, which as emended by Fries (1845) is most applicable not to S. borealis but to the hybrid S. borealis × S. longifolia.

Gray (1873) brought another European name into American literature when he used S. borealis var. corollina Fenzl for an Oregon collection (Hall 55, F[4], GH[2], MO, NY[2], UC, US[2]) which is treated here as S. borealis subsp. sitchana. Fernald (1914) rejected the use of this combination for American material. He noted that use of this name solely for plants with a paniculate inflorescence was incorrect since Fenzl (in Ledebour, 1842) made no such statement in his description. After noting the various elements present in S. borealis var. corollina

(see section entitled "Major European treatments" for an elucidation of them), Fernald (1914) pointed out that "subsequent European authors have interpreted [S. borealis] var. corollina merely as the form of S. borealis with petals and there is no clear reason why we should do otherwise." I agree with Fernald's logic for two reasons. First, the idea of defining varieties on the presence or absence of petals, a character state that is quite variable (as I will show, even on the same plant) is not an appropriate concept in the S. calycantha complex. The mixed nature of Fenzl's var. corollina and Regel's rather different interpretation represent usage of an ambiguous taxon. Cooley (1892) used S. borealis var. corollina in the same sense as Gray, in this case for an Alaskan collection.

Gray (1873) suggested that his earlier S. borealis var. alpestris and var. corollina should be combined, including "S. alpestris Fries. The same collected at Lake Superior by Dr. Robbins" in his later entry for var. corollina. Stellaria borealis var. alpestris was maintained for the Robbins collection in the next (6th) edition of Gray's Manual of Botany (Watson & Coulter, 1890). Robinson (1894, 1897) was the first to include var. alpestris A. Gray in synonymy of Gray's concept of S. borealis var. corollina, citing collections by Robbins (Lake Superior) and Howell (Oregon). This treatment was unfortunate since dissimilar elements were united under the same misapplied name; the Robbins collection represents S. borealis subsp. borealis while the Howell collection which Robinson would most likely have seen (Howell 388, GH) represents S. borealis subsp. sitchana. The use in Robinson (1897) appears to be the last such application of S. borealis var. corollina to North American plants.

The inclusion of S. fenzlii in synonymy by Gray (1867) and Robinson (1894, 1897) under S. borealis vars. alpestris or corollina respectively requires some additional comment. This most likely comes from Regel's (1862) assignment of Fenzl's S. borealis var. corollina to his S. fenzlii. Hultén (1928) noted that S. fenzlii was distinct from S. calycantha in most cases, but did describe S. calycantha × fenzlii. His later treatment of this hybrid as S. sitchana (Hultén, 1937a) reinforces the distinctness of western material (such as the Hall collection) from S. fenzlii. "True" S. fenzlii is restricted to northeastern Asia (see Hultén, 1928; Schischkin in Komarov & Shishkin, 1936; Ohwi, 1965) and has not been reported from North America (Hultén, 1968; Rice et al., 1982; Scoggan, 1978).

Britton (in Britton et al., 1894) also placed the Robbins and Hall collections within a single taxon, but in this case used the alpestris concept of Gray (1873) within Alsine, forming A. borealis var. alpestris (Fenzl) Britton or, corrected to reflect Gray's description of var. alpestris, var. alpestris (A. Gray) Britton. Piper (1906) followed Britton's usage of Alsine but since Piper followed the Philadelphia Code in recognizing the subspecies as the only infraspecific level (Cronquist, 1955), the combination A. borealis subsp. alpestris (A. Gray) Piper was formed.

Kurtz' (1894) study of plants collected on the 1882 Krause expedition to southeastern Alaska added three names at the form level. These have very brief descriptions: S. borealis f. apetala (leaf margin ciliate), f. subcorollina (very ciliate), and f. corollina (large). Two other names are listed, f. "macrantha" and f. "glauescens" but are without published descriptions, making them nomina nuda. In spite of

the existence of Regel's (1862) S. borealis f. apetala and f. corollina, I feel that these combinations should be attributed to Kurtz. The type of Stellaria borealis forma apetala Kurtz (Krause & Krause 336, CORD) is a specimen of S. borealis subsp. borealis; all of the collections that I have seen which bear Regel's combination are either S. crispa, S. calycantha, or S. borealis subsp. sitchana. An inspection of the type of S. borealis forma corollina Kurtz (Krause & Krause 280, CORD) shows it is referable to S. borealis subsp. sitchana, while Regel's S. borealis f. corollina also included material (lusus csachalinensis) now referred by Schischkin (in Komarov & Shishkin, 1936) to S. fenzlii.

Under his treatment of S. sitchana var. bongardiana (Fern.) Hultén, Hultén (1944) noted that "It seems probable that REGEL'S report of S. borealis f. macrantha and borealis f. corollina major from Chilcat R. and Portage Bay in Pl. Radd. loc. cit. are referable to this species." I consider this to be incorrect for three reasons. First, the names and locations are cited exactly as in Kurtz (1894). Second, there is no trace of these names in the Pl. Radd. reference that Hultén refers to here - Regel (1862). Third, the collections of Drs. Krause were made in 1882, 20 years after the appearance of Regel (1862).

ii. Adoption of Stellaria calycantha and other names

For the beginning of the use of Stellaria calycantha we must turn to Russia and the early expeditions that visited the coast of Alaska. The 1826 publication of Chamisso and Schlechtendal contains descriptions of plants from collections made at Unalaschka by Chamisso in 1817. Chamisso and Schlechtendal (1826) mentioned two taxa of interest here. Stellaria aquatica Cham. & Schldl. (non Pollich) is referable to S.

calycantha, their collections clearly not equal to S. alsine Grimm, the correct placement for the plants Pollich (1776) described. Hultén (1937a) thought that S. graminea (non L.) as used by Chamisso and Schlechtendal possibly was referable to his S. sitchana var. bongardiana, an opinion that I can neither substantiate nor reject since I did not see any Chamisso collection of S. graminea.

Bongard (1833) made the combination Stellaria calycantha (Ledeb.) Bong. after inspecting material that Mertens had collected from Sitka, Alaska. He considered Arenaria calycantha Ledeb. to be conspecific with his material, basing his decision at least in part on the opinion of Meyer who had seen the type of A. calycantha ("fide amiciss. D. Meyer, qui specimina originalia vidit"). Bongard also thought it more properly treated as a Stellaria, making the statement "Habitus jam indicat, Stellariae potius speciem, quam Arenariae esse," [habit now indicates this species is a Stellaria rather than Arenaria].

The date of publication of Bongard's work is not 1832 as Fernald (1914) and Hitchcock (in Hitchcock and Cronquist, 1964) have cited. Although the title page of Ledebour's article indicates "Lu le 4 Mai 1831," the title page of Mémoires de L'Academie Imperiale des Sciences de St. Pétersbourg, Sixieme Série Volume 2 bears the date 1833, with the reverse of this page bearing the text "publie par ordre de l'Academie en Novembre 1833." Hultén consistently cited the publication as 1833 in his various works (1928, 1937a, 1944) as did Schischkin (in Komarov and Shishkin, 1936) as well as Pole on the label of a specimen of S. calycantha distributed by LE (Herb. Flor. URSS 3113, leg. R. Pole in 1917, MICH), suggesting that both Hultén and Russian sources thought that 1833 is indeed the correct date.

The first names given to plants referable here to S. borealis subsp. sitchana also appear in 1833. Bongard (1833) described a plant with simple erect stems, linear-lanceolate leaves, and petals and capsules shorter than one-half the length of the sepals as Stellaria brachipetala Bong. while considering a similar plant with flaccid or ascending stems, linear or linear-lanceolate leaves, petals longer than one-half the length of the sepals, and capsules scarcely longer than the calyx to be Stellaria longifolia. It appears that he was unaware that Bunge (in Ledebour, 1830) had already described Stellaria brachypetala Bunge, making S. brachipetala a later homonym. Steudel (1840-1841, [Stellaria, p. 635-637, published in 1841 fide Stafleu & Cowan (1985)]) corrected the situation by publishing S. sitchana Steudel to replace Bongard's S. brachipetala.

It appears that Fernald (1914) was one of the first botanists to note the nonequivalence of S. longifolia sensu Bongard and S. longifolia Muhlenb. ex Willd, correctly considering it within S. borealis. Fernald (1914) chose the name S. borealis var. bongardiana Fern., basing his decision on both Bongard's (1833) description and "a sheet of the Mertens collection [of S. longifolia] in the Gray Herbarium." He considered Bongard's (1833) inclusion of "Cyma dichotoma" in the description of S. brachipetala and the absence of a similar phrase in Bongard's description of S. longifolia to mean that S. brachipetala had a dichotomous cyme while S. longifolia of Bongard did not. The GH specimen (Mertens s.n., without date, GH) is a mixed collection of two young stems of S. borealis subsp. sitchana with an unexpanded cyme (the mature flowers appearing to be axillary), one sterile stem referable to the same taxon, and one stem of S. calycantha. This sheet bears little

resemblance to a Mertens collection at LE (Mertens 18, without date, LE), labeled S. longifolia Muhl. in the hand of Bongard (checked against samples of his labels in Lipschitz & Vassilczenko, 1968) and bearing the number (18) found in Bongard (1833). This specimen matches the protologue of Bongard's (1833) S. longifolia, includes one stem with a dichotomous cyme (contrary to Fernald's assumption), is annotated in an unknown hand as S. brachypetala, and is referable to S. borealis subsp. sitchana as treated here. This suggests that Fernald's S. borealis var. bongardiana is based on a misidentification by Bongard and an unwarranted assumption by Fernald.

The first American work to include Bongard's names is Torrey and Gray (1838). As noted before, they also defined varieties within S. borealis. In addition, they list S. calycantha and S. brachypetala (their spelling probably a typographical error), citing "Sitcha, Bongard" as the locality and source of the citation.

Most American works subsequent to Torrey and Gray and prior to 1897 do not segregate S. calycantha and S. brachipetala, following one of the aforementioned varietal schemes in recognizing many-flowered plants. Macoun's (1883) reference to collections from Macleod's Lake, British Columbia "which completely accord with the description of this species [S. calycantha] and are altogether unlike any form of S. borealis we possess" marked its initial appearance in Canadian literature and the beginning of the revival of its use in American literature. Most Macoun specimens of S. calycantha subsp. calycantha are labeled S. borealis. This reflects his subsequent adoption of S. borealis, apparently in reaction to correspondence he received from S. Watson and N. L. Britton (transcribed on Macoun, Herb. Geol. Surv. Canada 4772, CAN acc. no.

51545), indicating their acceptance of S. borealis.

The year 1897 proved quite eventful in nomenclatural developments in our story. Robinson (1897) accepted S. calycantha for the western plants with ovate leaves, agreeing with Macoun in noting S. calycantha as being "a species referred by Fenzl, l.c. 382, and by various American writers to S. borealis, but, as it seems, rightly restored to specific rank by Prof. Macoun." Rydberg (1897) transferred S. calycantha to Alsine as A. calycantha (Ledeb.) Rydb. in a brief report on rare Montana plants.

Howell (1897) made two contributions in his Flora of Northwest America. First he proposed Alsine simcoeii Howell for the pubescent plants that he first collected in 1880 in the Simcoe Mountains of southern Washington. An 1880 collection of these plants (Howell s.n., US) with a label originally in his hand but rewritten by John Donnell Smith suggests Sereno Watson had proposed, but apparently never published, the name Stellaria crispa "var. pubescens" for these plants. Instead of accepting Gray's var. corollina concept for the larger western plants, Howell chose Alsine brachypetala (Bong.) Howell, following Bongard (1833) who described Stellaria brachipetala Bong. from Merten's collections from Sitka, Alaska. Howell followed Bongard's example one step further in that his Alsine brachypetala is also a later homonym! In this case, the earlier combination was formed by Opiz (1826) for a Czechoslovakian collection now more appropriately referred to Stellaria media (e.g. Graebner, 1916-1917).

From my investigation, P. A. Rydberg holds the distinction of being the only American botanist to recognize any entity in the Stellaria calycantha complex bearing the epithet alpestris at the species level.

He created Alsine alpestris (Fries) Rydb., citing S. alpestris Fries of 1832 as the basionym (Rydberg, 1912), and subsequently maintained it along side both A. borealis and A. calycantha in the later Flora of the Rocky Mountains and Adjacent Plains (Rydberg, 1917) as in Figure 8. From the description in Rydberg (1917), I assume that he was using it in a similar sense to Gray for many-flowered plants with scarious-margined upper inflorescence bracts, but I cannot confirm this since I have not seen any specimens bearing his annotations using this combination.

The disposition of Alsine viridula Piper (1913) and St. John's (in St. John & Warren, 1925) subsequent transfer of A. viridula to Stellaria is of interest to this discussion in part because of previous misinterpretations. Piper cited Leiberg 1396 at US as the type and noted Piper 2328 as a paratype. Both Piper and St. John maintained Alsine (and Stellaria) viridula separately from both S. borealis and S. obtusa Engelm. (St. John even in the most recent edition [1963] of his Flora of Southeastern Washington), in spite of the actual relationships with both taxa. All but two of the specimens of Leiberg 1396 inspected in this study are plants of S. calycantha. The US specimen of A. viridula is a large plant of S. obtusa as are one isotype (NY) and the cited paratype, probably providing the reason for the description being very close in many respects to S. obtusa.

American Nomenclature since 1914

Fernald's revision of S. borealis was published in 1914. His study was the first to seriously survey the species throughout North America and to carefully incorporate most of the significant contributions of the Russian and European botanists via their studies of plants from the

vicinity of Sitka, Alaska.

Fernald considered S. borealis to include six elements as shown in Figure 7, naming five varieties: vars. bongardiana Fern., floribunda Fern., isophylla Fern., simcoei (Howell) Fern., and sitchana (Steudel) Fern. On a grossly simplified level, vars. floribunda and isophylla represented the small-fruited, narrow-leaved plants primarily found in eastern North America, vars. sitchana and bongardiana the larger-fruited plants of the West, and vars. borealis and simcoei the primarily western plants with small fruits, broader leaves and, in the latter case, pubescent stems. A similar division stressing the presence of a well-developed inflorescence with reduced scarious bracts vs. plants with mostly axillary flowers was applied in both the small- and large-fruited, narrow-leaved plants; vars. floribunda and sitchana included plants with large cymes, while vars. isophylla and bongardiana applied to plants with axillary flowers.

Fernald (1914) retained S. borealis as the lead species for his treatment rather than S. calycantha because of his skepticism over the equivalence of S. calycantha of Bongard and A. calycantha of Ledebour. He was most troubled by Ledebour's description of the peduncle of A. calycantha as possessing two ovate bracts, suggesting to himself that the taxon was a true Arenaria rather than a Stellaria. He was convinced that Bongard had a specimen of the plant that had been traditionally identified as S. calycantha, but was convinced that it was not Arenaria calycantha.

Many, but not all, post-1914 treatments of S. borealis have followed Fernald's (1914) alignment. The comparison between Piper and Beattie (1915) and Rydberg (1917) shown in Figure 8 illustrates just how

different American treatments of these species had become, with Rydberg's work being among the last to favor the multiple species approach. Piper and Beattie (1915) were among the first to adopt Fernald's concepts of vars. sitchana and bongardiana in their Flora of The Northwest Coast, Piper following the American Code and creating combinations at the subspecies level for these taxa. Davidson and Moxley (1923) treated Californian material in a slightly different fashion, forming in the process the combination Alsine bongardiana (Fern.) Davidson & Moxley.

The first challenge to Fernald's taxonomy came in 1928 when Hultén questioned the separation of S. calycantha and S. borealis. He noted Fernald's contention that S. borealis was identical with S. calycantha of Bongard, but not A. calycantha of Ledebour. Hultén (1928) stated his position succinctly by stating "the type-specimen in Hb. Hort. Petrop. of Arenaria calycantha LEDEB. which I have seen is identical with our plant, and it must therefore bear the name Stellaria calycantha."

Another major difference between the treatments of Hultén and Fernald appeared when Hultén recognized Stellaria sitchana Steudel and made the combination S. sitchana var. bongardiana (Fern.) Hultén in 1937. Hultén (1937a) felt that "they [S. calycantha vars. bongardiana and sitchana] differ so widely from typical S. calycantha that they must be regarded as a separate species to which I give the name S. sitchana Steud." He restated the characters that Fernald used to separate these taxa from his other varieties and discussed four additional characteristics which he felt distinguished these taxa from S. calycantha. Hultén noted S. sitchana had "styles about twice as long," a quadrangular scabrous stem, and in many cases, flowers bearing short

petals, while S. calycantha had "a smooth, not quadrangular stem and no petals." He also felt that "Fernald's varieties have a geographical area of their own," another property that he thought supported his argument. In correcting his earlier (Hultén, 1928) incorrect treatment of S. sitchana as S. calycantha × S. fenzlii, he noted that "in characteristics it is fairly intermediate between those two species."

Fernald reacted to Hultén's position with a paper in 1940 in which he addressed both issues that were raised by Hultén. He reluctantly accepted Hultén's idea on the conspecific nature of S. calycantha and S. borealis. As Fernald (1940) stated, "There is, consequently, no course, assuming that the plant Hultén examined was the actual type and that he correctly understood the characters of S. borealis, but to take up the very imperfectly described S. calycantha." He added that he did this "with the reservation that a good photograph of the type, when it can be secured, may change the interpretation."

Fernald (1940) made the appropriate combinations for all of the varieties he described in 1914 and added another element to the puzzle by publishing S. calycantha var. laurentiana Fern. for material from the Gaspé Peninsula and Anticosti Island which he felt bore strong resemblances to S. calycantha var. bongardiana (Fern.) Fern. of the West except for the absence of reflexed fruiting peduncles. Indeed, some authors (e.g. Scoggan, 1978) have merged S. calycantha var. laurentiana with S. calycantha var. bongardiana, giving rise to reports of S. calycantha var. bongardiana from Québec (e.g. Bouchard et al., 1983).

Fernald (1940) also firmly restated his reasons for not segregating S. calycantha vars. bongardiana and sitchana as a segregate species. Fernald's (1940) approach consisted in part of text and plates

illustrating his difficulty in noting how, as Hultén (1937a) stated, "in general appearance [*S. sitchana* vars. *sitchana* and *bongardiana*] differ considerably from typical *S. calycantha*." He countered Hultén's additional morphological character of petals vs. none by quoting passages from descriptions by Michaux, Bigelow, Hooker, and Torrey and Gray, noting the presence of petals in North American *S. calycantha*. He illustrated the scabrous stem of a collection of *S. calycantha* var. *isophylla* to counter the difference of a scabrous vs. smooth stem. Fernald's (1940) concluding sentence summarized his position: "Until some stable character besides the tardy reflexing of the peduncles is demonstrated for the western *Stellaria sitchana* I must continue to retain it within the plastic and wide-ranging *S. calycantha*."

After inspecting material from interior Alaska and adjacent portions of the Yukon, Hultén (1944) described *S. calycantha* subsp. *interior* Hultén. He noted these plants resembled *S. calycantha* var. *floribunda* (Fern.) Fern., but differed in "its small leaves, small flowers and scabrous stem." Hultén (1944) felt it to be a distinct entity, although he admitted that some overlap with typical *S. calycantha* was occasionally noted.

Most recent authors (e.g. Hitchcock & Cronquist, 1964; Scoggan, 1978) have followed either Fernald (1940), Hultén (1937a, 1944), or some combination thereof when treating *S. calycantha*, there being but a few additional changes since the appearance of the works of Fernald and Hultén. Boivin (1951) described a series of collections from Alberta and British Columbia as *S. calycantha* var. *latifolia* J. Boivin, a glabrous plant with very broad leaves, a very reduced inflorescence, and few flowers with short sepals. Apparently Boivin himself dismissed the

importance of this combination since he included it only in synonymy under S. calycantha in his treatment of Stellaria in his Flora of the Prairie Provinces (1968-1969). This name is referred to S. borealis subsp. borealis here.

Hitchcock (in Hitchcock & Cronquist, 1964) made the most recent nomenclatural change when he raised S. calycantha var. simcoei to the species level, Stellaria simcoei (Howell) C. Hitchc., noting the pubescent stem as a distinctive characteristic. G. N. Jones thought likewise some years earlier, the combination "Stellaria simcoei (Howell) G. N. Jones" appearing on one of his collections (G. N. Jones 9647, WS) made in 1936, but it was apparently never published (A. Jones, pers. comm.). The appearance of A. simcoei Howell in synonymy under S. calycantha in his treatment of the flora of Mt. Rainier (Jones, 1938) suggests that it may have been a brief thought.

NUMERICAL TAXONOMIC STUDIES

One conclusion that can be drawn from the preceding overview of taxonomic treatments of the Stellaria calycantha complex is that there are differences of opinion on what taxa are to be recognized. Some of these differences, e.g. the Hultén - Fernald debate over the recognition of S. sitchana, reflect different interpretations of the character variation present in the S. calycantha complex. Numerical phenetics provides an objective means for analysis of character variation patterns without either 1) making a statement about their evolutionary history or 2) a priori weighting any of the characters before observing their behavior in the analysis (Duncan & Baum, 1981). Various phenetic methods have been successfully employed in deciphering variation patterns in species complexes (e.g. Whitehead & Sinha, 1967; Barber, 1980; Duncan, 1980); for a more general index to botanical studies using these techniques, see Baum et al., [1985]). Duncan and Baum (1981) reviewed the uses and misuses of numerical phenetics, noting the usefulness of such techniques in the recognition of patterns of similarity.

The approach taken in this section is twofold. First, a series of cluster and factor analyses are presented, the results illustrating the multivariate distribution of characters and the resulting clustering of populations into groups which represent probable taxa in the S. calycantha complex. After the groups have been established, discriminant analysis, a technique requiring a priori group assignment

(Sneath & Sokal, 1973), will be employed to test the groups and the appropriateness of the taxonomy suggested by them.

Methods: sample selection - criteria and comments

The sample chosen as the data set for the numerical analyses is based on the assumption that an Operational Taxonomic Unit (or OTU, Sneath & Sokal, 1973) is equal to one herbarium sheet chosen to represent a population in which there is variation. Sneath and Sokal (1973) recommended the use of individuals as OTUs in studies where either the establishment of species or infraspecific variation was being studied; both topics are of interest here.

Over 5,000 herbarium specimens of the various taxa of the Stellaria calycantha complex were examined in the process of selecting the OTUs for this study. A sample size of 150 was suggested by G. Martin and T. Duncan (pers. comm.) as being appropriate to illustrate the inherent variation in the complex; Martin has employed a similar sample size in his work on the Arenaria lanuginosa complex. The 165 (163 in final analyses) specimens selected for analysis were chosen following three criteria: 1) representation of the geographic range of the members of the complex, 2) representation of the morphological variation present in the included taxa, and 3) use of complete specimens that would add as much information as possible on that population to the data set.

Only collections gathered directly from wild populations were measured. One chromosome voucher (Hedberg 3092b, DAO), although an interesting specimen, was excluded from the sample since it had been grown in Sweden (see Hedberg, 1967) rather than the place of seed collection (Schefferville, Québec).

Thirty-four characters, listed in Tables 1 and 2, were selected and measured. The characters selected for this study included those traditionally used to segregate variation in the complex (see Fernald, 1940; Hitchcock in Hitchcock & Cronquist, 1964; Hultén, 1968) and several others noted during the course of specimen analysis. Binary and qualitative multistate characters were scored following multiple observations of the character on the herbarium sheet. In the few cases where more than one character state was observed in a population, the population was scored for the "majority state" for that character. Five measurements of each quantitative character were taken from each herbarium sheet wherever possible, a lesser number substituted where five replicates were not present. Measurements of large features (e.g. stem length) were made with a millimeter ruler, while an ocular micrometer calibrated in millimeters at 10X was employed for small features (e.g. seed length). Qualitative characters were evaluated at 10X whenever necessary (e.g. papillose condition of stems, etc.), and often at 30X when the state was unclear at 10X. All averages calculated from the multiple measurements were rounded to two decimal places. Since the measurements include either one or two decimals, carrying averages to any additional digits would overrepresent the accuracy of the measurements.

Separate codes were assigned to distinguish between two different "No Data" situations. A value of zero was assigned where the character did not exist in the OTU being measured. One example involves character states designed to measure cymose inflorescence characters in OTUs with axillary inflorescences. In cases where data were missing for a character that should be present (e.g. open capsule length on an OTU

with immature capsules), a value of 99 was assigned.

The OTU-character matrix was prepared in part on a Zenith Z-100 computer and completed using a Freedom 200 VDT connected to a Gifford Systems 8/16 computer at the University of California - Berkeley Herbarium. The data matrix is available from the author.

OTUs were labeled to include both taxonomy and geography, in part to be able to track OTUs fitting the traditional views of Fernald. The first two letters represent possible taxon identity as follows: CR - S. crispera, EB - eastern S. calycantha var. bongardiana (Fernald's S. calycantha var. laurentiana), EC - eastern S. calycantha var. calycantha, EF - eastern S. calycantha var. floribunda, EI - eastern S. calycantha var. isophylla, OB - S. obtusa, SB - S. calycantha vars. sitchana and bongardiana (and S. calycantha subsp. interior Hultén), SI - S. calycantha var. simcoeii, and WC - western S. calycantha var. calycantha. The remaining letter(s) represent abbreviations for states and provinces, the number added to distinguish different OTUs from the same state. Complete label data and determinations are given in Appendix B for each OTU.

Commentary on the methodology

The quality of herbarium specimens placed limitations on the number of specimens available for the final set. Many of the older collections are rather poor, often lacking the basal portion of the stem. They were often collected early in the season so the full expansion of the inflorescence cannot be noted. Several specimens included in the final set were not complete, but were used as the best available material illustrating the morphological diversity in several geographic regions.

Basing this study on a selected fraction of the available material could suggest that the data set is not as representative of random variation as possible. Although the choice and number of characters are often carefully discussed in introductory text and articles, recommendations concerning the number of OTUs that should be included in a study are often missing from these treatments (e.g. Doyle, 1986; Dunn & Everitt, 1982; Sneath & Sokal, 1973). Hu et al. (1985) noted that the classification produced from the exemplar method (or the use of individual specimens to represent variation within a taxon [described in Sneath & Sokal, 1973]) using a small sample size may be less representative than one based on a larger sample. Crovello (1968) noted that adding OTUs to a study changed the results slightly. Such changes did not occur on a random basis, but only involved relationships among OTUs most similar to those being added; new groups were not defined, but existing ones became more dense.

A larger sample may be more desirable because there is less influence from individual variation due to environmental and developmental plasticity (Hu et al., 1985), but as they note, the use of a larger data set may not be an ideal solution. One approach to simplifying the OTU-character matrix when many OTUs (e.g. over 500) are sampled involves summarizing character information for each taxon in the study. Barber (1980) followed this approach in calculating grand means of the averages of individual taxa as did Hu et al. (1985) in determining character mean vectors for each taxon studied. One of the distinct disadvantages of this approach is that the OTUs must be sorted into taxa before the analysis. Since one of the powerful aspects of a phenetic analysis is to produce clusters, selecting the taxa ahead of

time seems to add a great degree of subjectivity.

Selecting only a limited number of measurements per plant can also affect the results. The occurrence of a rare character state may be missed if it is only seen after the requisite number of measurements on that sample has been completed. In spite of the desirability of measuring a consistent number of replicates of a character per population, the use of a herbarium specimen to represent a population is itself a limiting factor. Often there are only a few examples of a structure present on a collection. The presence of wrinkled leaves, hidden flowers, empty capsules, etc. adds to the problem of getting a large sample of some characters in some populations. In the cases where it was not possible to make five measurements, the importance of many measurements became evident as the influence of a single "odd" value was more easily seen when the averages were calculated.

Comments on character analysis

The following information is presented to explain the reasoning that I used in determining the states and/or measurements of characters that often have been interpreted in various ways.

A. Stem length and the number of flowers per stem

Measurements for both stem length and number of flowers per stem were taken from main stems, not just axillary branches. Stem length was measured from either the lowermost evident stem segment (top-clipped material was avoided if at all possible) or the uppermost root. All flowers present on both main and any axillary branches arising from those stems were counted.

Measurement of stem length was often difficult since members of the S. calycantha complex often are tufted perennials which can send out long axillary shoots. The practice of some collectors of grabbing a stem makes stem length determination from a herbarium sheet difficult since the stem on the sheet may have been an axillary sprig from a much larger plant, giving subsequent taxonomists a distorted view of the size and habit of the plant.

B. Inflorescence characters

i. Herbaceous vs. scarious margin of the upper inflorescence bracts

Fernald (1940) used the presence of a wide scarious margin on the uppermost inflorescence bracts as a diagnostic character of S. calycantha var. floribunda, the alternative being bracts that are entirely herbaceous. A number of specimens do have mostly-scarious uppermost bracts. Unfortunately, the character is not as clearcut as Fernald suggested, necessitating the addition of an intermediate character state. On several specimens, a narrow white margin was present on the uppermost bracts (e.g. Garton 1878, DAO), margins that closely resemble those of the middle bracts of some plants that eventually produced tiny mostly-scarious bracts subtending the uppermost flowers (e.g. Cochrane & Cochrane 9795, MSC).

ii. Measurement of leaves/bracts above the basal flower

Various features of the inflorescence have been used by past workers in segregating Stellaria calycantha into infraspecific taxa. Most of the interest has focussed on the size of the uppermost bracts in

relation to those subtending the basal flowers, the relative number of flowers, and the presence/absence of a wide scarious margin on the uppermost bracts. In an attempt to quantify these features, the following inflorescence characteristics were measured: number of flowers/stem; number of nodes bearing flowers; and the length and width of leaves subtending the lowermost flower, the flowers two nodes above the basal flower, and the uppermost flowers.

The objective in including these characters was two fold. First, a clear differentiation between plants with axillary flowers and those with cymose inflorescences could be established; plants with strictly axillary inflorescences would lack the branching pattern and bract modification (if any) associated with cyme formation. Second, the tendency to have all similar-sized bracts vs. a reduction to tiny upper bracts could be measured.

The measurements of uppermost inflorescence bracts were taken from bracts subtending open flowers. Inflorescence bract characters were measured from bracts of the terminal inflorescence. A number of plants also bore axillary inflorescences of similar shape but smaller size (e.g., Rabaler 473, MSC). Inclusion of data from axillary inflorescences was deemed inappropriate since the bracts of these inflorescences often differed dramatically in size from bracts occupying the same position in the terminal inflorescence. In some cases, the uppermost flowers of an OTU were at the second node above the basal flower. Where this occurred, the data for the uppermost and second node above the base were duplicated.

iii. Measurement of the pedicel

Pedicel length was measured from the junction of pedicel and stem to the base of the expanded receptacle for pedicels bearing mature capsules.

C. Floral characters

i. Measurements of the calyx

The length of the calyx, both at anthesis and in fruit, has been a central feature in most of the previous treatments of this complex. One of the first problems I encountered in measuring Stellaria specimens was determining the juncture of the calyx and the receptacle. Melchior (1964) noted that members of the subfamily Alsinoideae have free or basally connate sepals. In the case of Stellaria calycantha and relatives, the calyx is briefly connate basally, in most cases obscuring the exact boundary between the calyx and receptacle. This boundary is marked with a color difference just below the juncture of adjacent sepals in many S. calycantha flowers; the sepals are brighter green than the slightly brownish receptacular area (e.g. Garton 1878, DAO). Since this difference was much less obvious in many collections (totally obscured in both S. obtusa and S. crispa and many S. calycantha flowers bearing capsules), it was of limited use.

A second clue to this boundary was in the veins leading into the sepals, these often being elevated into noticeable ridges near the juncture. Although it would have been more convenient to measure only the free portion of the calyx, use of the venation pattern and other features noted above should provide more reliable data. In all cases

where the other characters were not particularly evident, I always included a small portion of the sepal below this juncture, reflecting the continuation of the sepals beyond the sinus.

ii. Petals:

Two simple presence-absence characters were chosen here. Stellaria crispera and S. obtusa flowers are nearly always apetalous, while S. calycantha and S. borealis flowers often are either petalous or apetalous. When petals are present, most are considerably shorter than the sepals, but occasional flowers were found where the petals were approximately the same length as the sepals. As noted in the text on Floral Morphology, individual S. borealis plants can exhibit both apetalous flowers and others containing a variable number of small petals, forcing the occasional use of "majority-coding" for this character.

iii. Styles:

Hultén (1937a) noted that the length of the style branches was useful in segregating S. sitchana from his concept of S. calycantha, but parenthetically noted that often these were broken on herbarium material. I measured styles that, from all appearances, were intact. As it turned out, many of these measurements were taken from styles still attached to developing capsules. This should not be detrimental to the analysis since the styles attained maximum length during their period of receptivity and do not appear to shrink noticeably after pollination has taken place and fruit development has been initiated. The styles of Stellaria are either curled or relatively straight;

measurements used here were taken from uncurled styles in an attempt to represent their maximum length.

iv. Capsules:

Capsule measurements were taken from the apex of the capsule to the base as estimated from receptacular shape; individual capsules were not dissected from flowers on each collection. From those "free" capsules that were examined (e.g., J. F. Collins et al. in 1900, GH), it was evident that the capsules did extend below the sinuses of the free portions of the sepals and that a measurement near the receptacle-sepal line discussed above was appropriate.

Measurements of both unopened and opened mature capsules were noted. Since the act of pressing was found to "open" some immature capsules prematurely (e.g. Rabaler 484, MSC), I tried to restrict the measurement of open capsules to those containing mature seed which would have been ready for dispersal.

v. Seeds

The terms "length & width" are applied to this material following Berggren (1981) as shown in Figure 42.

Rejected characters

One of the most commonly used diagnostic characters for S. crispa (e.g. Hitchcock in Hitchcock & Cronquist, 1964) is the presence of a hyaline, crisped leaf margin. An inspection of the material at hand revealed that many of the populations of all taxa investigated exhibited a variable amount of this character, negating its diagnostic value.

Another character that has been suggested as useful in distinguishing S. calycantha is the presence of darkly colored capsules. A discussion of the variation in this character is appropriate. First, it is best to consider this a developmental feature that appears gradually over time in populations showing darkened capsules. Second, the darkening that has been noted appears to be caused by two different sources. Some capsules actually become darkly pigmented with age, changing from their initial green to a finely mottled dark red color (e.g. Rabeler 551, MSC) or even black (Shacklette 7443, MICH). In other plants, (e.g. Piper 4412, US) the "dark color" is not the result of pigmentation but rather is provided by the maturing seeds within nearly transparent capsules. For these reasons, the use of a simple character referring to darkened capsules is not appropriate.

FACTOR AND CLUSTER ANALYSES

The Numerical Taxonomy System of Multivariate Statistical Programs (NT-SYS) of Rohlf et al. (1979), Version 4 Level 3 installed on the IBM 3081 mainframe at the University of California-Berkeley, was used to generate the various cluster and factor analyses.

Outline of analyses performed

The following programs were employed in producing each NT-SYS analysis that will be discussed. Program names are taken from Rohlf et al. (1979). Parenthetical abbreviations appearing below will be used in subsequent text to refer to the appropriate techniques.

STAND: Standardization, or more appropriately in this case, scaling of the data. Gower's scaling formula is employed with each character ranged so that the maximum value of the character is set at 1, the minimum set at 0 according to the following formula: $X_i - X_{\min} / X_{\max} - X_{\min}$, where X_i is a character value, $X_{\min}$ and $X_{\max}$ being the minimum and maximum values for that character in the data set (Sneath & Sokal, 1972). This procedure allows the mixing of measurements taken in different units (e.g. number of styles, seed length) with discrete character data (e.g. leaf pubescence) since the process ranges the data over a common unitless scale. Sneath and Sokal (1972) recommended Gower's scaling procedure for studies in which a mixture of binary and multistate characters is used (as in the present case).

SIMINT: Two matrices are formed using this procedure. First, average distance (Euclidean distance divided by the number of characters [Sneath & Sokal, 1973]) coefficients are calculated and placed in a matrix using the DISTANCE option. A character correlation matrix is formed using the CORRELATION option (Rohlf et al., 1979).

TAXON: An Unweighted Pair-Group Method with Arithmetic Averages (UPGMA) analysis of the average distance matrix is performed. This algorithm clusters OTUs on the basis of calculating the average dissimilarity between an OTU and an existing cluster (Sneath & Sokal, 1973).

MXCOMP: A cophenetic correlation coefficient is derived from the comparison of the average distance matrix with a cophenetic matrix produced in the previous step. This coefficient provides a measure of how effective the UPGMA phenogram summarizes the information in the distance matrix (Jackson & Crovello, 1971).

MST: The calculation of a single-linkage cluster from the average distance matrix. A minimum spanning tree (MST), listing OTUs and the distances separating them, and a single-linkage (SL) cluster matrix are produced.

PHEN: Produces a phenogram from the single-linkage cluster matrix formed by MST.

COPH: Calculates a cophenetic matrix from the MST single-linkage cluster matrix.

SUBSETS: A routine used to find the most distinctive clusters. The "Low" option was chosen, matching the clusters on common low values. Identified subsets will have members which exhibit less dissimilarity with each other than any one member exhibits with an OTU outside of the

subset (Rohlf et al., 1979).

GOWER: A procedure used to transform the average distance matrix into a matrix from which plots can be made of OTUs onto eigenvectors in a linear vector space (Rohlf et al., 1979).

FACTOR: Two factor analyses were performed. First, a principal coordinates analysis (PCO) was performed on the transformed average distance matrix. Sneath and Sokal (1973) noted that this technique allows the derivation of principal components (and therefore a spatial projection of the OTUs) directly from a Euclidean distance matrix. The principal components analysis (PCA) is normally computed from a matrix of product moment correlation coefficients (Sneath & Sokal, 1983). Three unweighted factors were derived from each analysis.

Second, a principal components analysis (PCA) was performed on the correlation matrix of characters in order to determine both character correlation with the components and relative character loadings. Three unweighted factors were derived from each analysis.

MXPLOT: This routine was used to plot the results of the factor analyses of distance matrices, each plot illustrating OTUs vs. two of the three factors derived in the analysis.

Methods used in presentation of results

Results will be presented from four sources: minimum spanning trees (MST), UPGMA phenograms, principal coordinate scatter diagrams (PCO), and principal component analyses (PCA) of character correlation matrices.

The first step in the analysis of the output from each NT-SYS run was the derivation of the MST. The MST is constructed to produce the

shortest overall path among all OTUs without forming any loops. OTU-OTU relations are based on the average distance matrix, each segment of length proportional to the dissimilarity between OTUs (Abbott et al., 1985). The result is a graphic representation which can be used to illustrate OTU relationships as they exist in multidimensional space (Abbott et al., 1985; C. Meacham, pers. comm.).

The relationship between OTUs and distance makes the MST useful in the analysis of principal coordinate projections to determine the degree of local distortion of such relations as portrayed in PCO scatter diagrams. The use of PCO instead of PCA allows this matching since, as noted above, PCO can operate directly on a distance matrix (Sneath & Sokal, 1973). Since the PCO projection is summarizing a portion of the variation over the entire data set in producing a two dimensional scatter diagram, local distortions are possible which can place OTUs which are not nearest neighbors in multidimensional space adjacent to one another in the reduced dimensions of a PCO scatter diagram (Sneath & Sokal, 1973). Linking points on a scatter diagram with the corresponding segments from a MST overcomes this difficulty (Abbott et al, 1985).

A reason for using MST's instead of UPGMA or SL phenograms is found in the reliance on cluster formation in phenograms, an activity which, as shown below, may obscure actual OTU relationships.

The SL clustering algorithm begins with joining the same two OTUs that are linked first on an MST, the closest two OTUs in multidimensional space (Abbott et al., 1985). Clusters are then added in order of greatest similarity, being joined to preceding clusters at the level where the first link is made between OTUs in both clusters

(Abbott et al., 1985). Another way to interpret the SL algorithm is to note that an OTU is added to a cluster based on the degree of similarity which it exhibits to its nearest neighbor within the cluster (Sneath & Sokal, 1973).

UPGMA is an average clustering method, computing the average similarity of an OTU to an existing cluster (Sneath & Sokal, 1973). Crovello (1968) noted that the most accurate portion of a UPGMA phenogram is near the tips since the OTUs which are initially clustered exhibit the greatest similarity to each other. The calculation of average similarity between this cluster and all other OTUs acts to increase the distortion of OTU-OTU relationships.

Although phenograms display clusters of OTUs, a comparison of the MST (Figure 19), the SL phenogram (Figure 10), and the UPGMA phenogram (Figure 11) for the S. crista cluster illustrates three reasons not to rely solely on phenograms. The OTU CRAU1 is linked to six other OTUs on the MST shown in Figure 13. These links are obscured in the cluster-addition algorithms used to generate the phenograms in Figures 10 and 11. Since one of the criteria in a phenetic investigation is to elucidate overall similarity, it seems logical to expect that several very similar OTUs could all show a close allegiance to a single OTU.

Second, the placement of distant OTUs was distorted by both of the phenogram algorithms. While the relations between close OTUs are often closely approximated in a phenogram, distant relationships are often distorted. As an example, the MST link between OTUs OBOR2 and OBWA2 is not included in either phenogram since there is no mechanism by which a distant OTU (e.g. OBWA2) can be placed with its nearest neighbor (OBOR2) if that neighbor is on an inner branch of a cluster (e.g. OBOR2 in both

phenograms). Again, the MST seemed a better representation of overall similarity in that a distant OTU could be added to the OTU judged to be its nearest neighbor, the desired result in a study of phenetic similarity. Such "outliers" either accumulated at the base of a phenogram or were placed at the base of clusters in positions that, upon inspection of specimens, seemed inappropriate.

A comparison of the MST and the two phenograms illustrates the danger in relying on a single method for making conclusions about the membership of a cluster. In the case of the cluster suggested for S. obtusa, the MST (Figure 12) includes only the 17 OB OTUs, separating these OTUs from all other OTUs by a link considerably longer than any OTU-OTU segments within the cluster. The treatment in the SL phenogram (Figure 10) is similar, although the linkage of this cluster to the remaining OTUs is made through a different OTU pair (OBWA2 - WCUT1) than in the MST. The cluster including all of the S. obtusa OTUs suggested in the UPGMA phenogram (Figure 11) also includes the OTUs WCUT1 and WCNV1. A relationship of these OTUs to the S. obtusa OTUs is suggested by the SL Phenogram via their placement at the base of Figure 10, but not in the MST (segments linking these OTUs are included in the PCO scatter diagram in Figure 9).

A similar case can be made using the different projections of the S. crispa OTUs. Both of these situations reinforce the observation that no single two-dimensional representation of the OTUs can contain all of the information on the distribution and relationships of these OTUs as they occur in multidimensional space (Ingrouille, 1986).

The PCA analyses of character correlation matrices are useful in presenting an approximation of the contributions that character variance

is making to the factors displayed in the PCO scatter diagrams. An inspection of the character loadings in Table 3 reveals both an absence of loadings with an absolute value of greater than 0.5 and small differences separating the contributions of many of the variables. These situations are present in all but one of the PCA analyses and may influence the significance that can be attached to the PCA analyses. Since each factor is "constructed" from a combination of many characters, each making a small contribution, the total variance in these characters is more likely to be spread among the entire set of axes; in this case 33 axes (1 per character) are required to precisely locate the OTUs in space (Doyle, 1986). Since this does reduce the effectiveness of the PCA in reducing the dimensionality needed to summarize the character variation, the PCA data presented here may be of limited utility.

Initial NT-SYS runs were made using the entire data set of 165 OTUs (complete data on these specimens provided in Appendix C) and 34 characters (listed in Tables 7 and 8). Subsequent runs were made employing various subsets of OTUs and characters (as described below) to both measure the contribution of quantitative and qualitative characters to the resulting clusters and to inspect OTU distributions when well-defined clusters are removed.

Character 6, sepal margin width, was removed after initial runs since, although useful in *S. obtusa*, there were too many cases where OTUs representing small plants of *S. calycantha* exhibited a mixture of states.

Data reported are taken from runs subsequent to the removal of OTUs EFNY1, a specimen which was later determined to be *S. borealis* × *S.*

longifolia, and SBUT3, an isotype of S. palmeri (Rydb.) Tidestrom, which although labeled as S. borealis, turned out to be S. longipes.

Results

The results of the NT-SYS analyses will be presented in the following order.

1. Analysis of entire data set, all characters.
2. Contributions of qualitative and quantitative characters in cluster formation.
3. The clusters representing S. crisper and S. obtusa.
4. Resolution of S. calycantha and S. borealis relationships.

1. Analysis of entire data set, all characters

The first analyses were calculated from a matrix including the entire set of 163 OTUs and 33 characters. The cophenetic correlation coefficient of the UPGMA phenogram for this matrix is 0.79. Three factors were calculated from the distance matrix, summarizing 31.66, 15.72, and 10.82% of the trace variance respectively. The PCO diagram giving both the best OTU separation and the least apparent distortion from the MST was that of factor 1 vs. factor 2 illustrated in Figure 9 and marked with evident clusters.

PCA of the correlation matrix of characters produced eight components with eigenvalues greater than 1.0, indicating that the characters are not highly correlated. The first three components each had eigenvalues of 3.5 or greater, accounting for 59.31% of the trace variance; the character loadings of these components are given in Table 3. The first component includes contributions from many quantitative

characters, with leaf, style, and open capsule lengths making the greatest contributions. Sepal characteristics, inflorescence type, and seed width contribute to the second component, while leaf width measurements make the largest contributions to the third component.

The PCO scatter diagram shown in Figure 9 illustrates that two small clusters and one larger one have been formed, with most of the points below a diagonal placed from the upper left corner to the lower right corner of Figure 9 more loosely dispersed. Identification of the OTUs and superposition of the MST on the PCO reveals that all 17 of the S. obtusa OTUs were placed in the cluster in the lower right quadrant near the Factor 2 axis. A single link from OTU OBMT1 to WCOR1 connects the cluster to the other OTUs on the PCO scatter diagram. The 21 S. crispata OTUs likewise are clustered together, forming an elongate group in the upper right quadrant near the Factor 1 axis. A single link from OTU CRBC2 to EION2 connects to cluster to the remaining OTUs.

The larger cluster in the upper left quadrant contains OTUs representing various taxa within Fernald's S. calycantha. Many of these OTUs are from populations in eastern and northern North America while the majority of the OTUs below the diagonal represent western populations; overlap in both groups precludes interpretation of the split as entirely representative of a geographic division in the variation patterns. Two MST links between this cluster and the OTUs below the diagonal (segments between OTUs EFQU1 and EFWV1, WCUT1 and WCNV1) illustrate that OTUs that represent the same taxon have been segregated by long distances in this projection. A similar situation occurs between two OTUs representing S. calycantha var. simcoei; OTU SIWA3, located just above the diagonal in the lower right quadrant, is

linked by the MST to SIOR1 in the lower left quadrant.

The presence of these long segments between similar OTUs suggests that the projection in Figure 9, while clearly portraying the S. obtusa and S. crispa clusters, may not be clearly illustrating the relationships among the remaining S. calycantha OTUs. After inspecting a PCO scatter diagram of an early run of the 165 x 33 matrix similar to Figure 9, G. Estabrook noted (pers. comm.) that an improved ordination of the relationships among the OTUs thought to represent S. calycantha could be obtained if clearly segregated clusters were removed. PCO ordinations illustrate the most different pairs or clusters of OTUs most clearly, with such distances contributing to both axis formation and relative position of the OTUs being projected (G. Estabrook, pers. comm.). Doyle's (1986) comments on PCA analysis advise a similar course of action; if evident clusters appear in the results, separate analyses of the clusters should be performed to "help clarify the relationships within each group." This rationale is also used by Johns and Estabrook (in press fide Estabrook and Duncan) in their study of wild and cultivated Solanum.

Since the clusters containing S. crispa and S. obtusa OTUs were both near the edge of the PCO scatter diagram and the axes, the presence of these clusters was both contributing to the axes being projected and distorting the presentation of the other clusters. Removal of the S. obtusa and S. crispa clusters allows a closer inspection of the relationships among the S. calycantha OTUs; this ordination would not be influenced by the large distances between S. calycantha and the other taxa (especially S. obtusa).

Analyses in which the S. obtusa and S. crispa OTUs have been

deleted will be presented in Part 4 of this discussion.

2. Contributions of qualitative and quantitative characters in cluster formation

The S. calycantha complex has traditionally been described with a combination of qualitative and quantitative differences. After viewing the results from the entire data set (see Figure 9 and Table 3), I was curious to investigate the individual effect of qualitative and quantitative data on the clustering exhibited in the patterns produced by the analysis of the entire data set. Could clusters be recognized on the basis of using only one of the two types of characters? Analyses were made using all OTUs with discrete qualitative characters (163 x 13 matrix) and continuous quantitative data (163 x 20 matrix). Results are presented as character loadings from PCA of the characters (Tables 4 and 5), simplified MSTs (Figures 14 and 16), and the PCO scatter diagram from the 163 x 20 (Figure 15).

A. Qualitative characters - 163 x 13 matrix

The significant contribution that is made by the qualitative characters is illustrated in the clusters and trends present in a simplified version of the MST (Figure 14). The cophenetic correlation coefficient for the UPGMA phenogram is 0.866, higher than the 0.790 recorded from the analysis of all OTUs for all characters, indicating that the UPGMA phenogram more accurately summarizes the information in the distance matrix in this analysis (Jackson & Crovello, 1971). A PCO scatter diagram of factor 1 vs. factor 2 formed a pattern similar to that in figure 16, with CR and OB clusters at the same positions. Three factors were calculated from the distance matrix, summarizing 33.38,

19.17, and 13.05% of the trace variance respectively.

PCA of the correlation matrix of characters produced five components with eigenvalues greater than 1.0, indicating that the characters are not highly correlated. The first three components each had eigenvalues of 1.6 or greater, accounting for 63.59% of the trace variance, the character loadings of these components given in Table 4.

The first component includes contributions from sepal shape and nerving, inflorescence type, seed surface and capsule shape, characters that would be used to easily identify S. obtusa and, to a somewhat lesser degree, S. crispa. Petal characteristics, capsule shape, and leaf midrib pubescence contribute to the second component, while leaf pubescence, sepal nerve length, and petal characteristics are favored slightly in the third component. The presence of petal characteristics in both the second and third components indicates a significant contribution by these features, a situation which should be noted in subsequent analyses.

The clusters illustrated in Figure 14 are either groups of OTUs separated from one another by zero-length segments or, as in the case of those designated by asterisks, clusters of OTUs representing the same taxon. Several of the often-recognized taxonomic entities are evident in Figure 14. Stellaria obtusa OTUs cluster tightly and sit apart from all other taxa, the WCUT1 - OBMT2 segment being the longest (0.481) on the tree. The eastern OTUs sort into several clusters, somewhat but not exactly along the lines of Fernald's taxonomy of S. borealis. The diverse position of the four EC OTUs suggests a potential problem in recognizing Fernald's S. calycantha var. calycantha as a separate taxon in eastern North America. The close association of the two EB OTUs with

EI and EC OTUs illustrates similarities in OTUs which would have been judged by Fernald to represent different varieties; Fernald's S. calycantha var. laurentiana is difficult to segregate from his vars. calycantha and isophylla on qualitative features. The segregation of EF OTUs into three groups is based on two factors, as shown in Figure 14. One split of these OTUs is based solely on presence (4 EF OTUs) vs. absence (9 EF OTUs) of petals, a character that is variable in S. calycantha and S. borealis, especially in eastern populations. Maintaining such a separation would be reminiscent of recognizing Fenzl's segregation of apetalous (S. borealis var. apetala) and petalled (S. borealis var. corollina) plants. Three of the apetalous EF OTUs have a papillose stem, placing them on the the line leading to OTUs approaching Hultén's S. calycantha subsp. interior.

Stellaria crispera OTUs exhibit unity on all qualitative character states, forming a tight zero-length segment network, connected to other OTUs via OTU EBQ1, one of the two OTUs representing Fernald's S. calycantha var. laurentiana. Many of the SB OTUs segregate into two clusters, the separation reflecting the fact that these OTUs probably represent different taxa. The 14 SB OTUs in the lower right of Figure 14 represent what Fernald called S. calycantha (or S. borealis) vars. bongardiana and sitchana. On the other hand, the nine SB OTUs connected via intermediates to the EF clusters are smaller northern plants exemplifying Hultén's S. calycantha subsp. interior. SI OTUs, representing S. calycantha var. simcoeii are found in two groups, also reflecting the petal presence/absence situation noted among the EF OTUs. Most SI OTUs are segregated from most WC OTUs, a situation reflecting the difference in pubescence characters between S. calycantha vars.

calycantha and simcoei.

B. Quantitative characters - 163 x 20 matrix

The data set consisting solely of quantitative characters produced a far different result, as illustrated by the PCO scatter diagram in Figure 15 and the simplified MST shown in Figure 16. The cophenetic correlation coefficient is 0.78, lower than that of the entire data set (0.79) or the qualitatives alone (0.866). This indicates that a UPGMA phenogram derived from this analysis would give a less accurate summary of the distance matrix than one summarizing the matrix from the qualitative characters alone, but one of similar accuracy to a UPGMA phenogram summarizing the entire data set. Three factors were calculated from the distance matrix, summarizing 47.63, 12.87, and 9.90% of the trace variance respectively. The PCO scatter diagram of factors 1 vs. 2 is illustrated in Figure 15.

PCA of the correlation matrix of characters produced four components with eigenvalues greater than 1.0, indicating, not surprisingly, that the quantitative characters exhibit a greater degree of correlation. The first three components each had eigenvalues of 2.1 or greater, accounting for 70.36% of the trace variance, the character loadings of these components given in Table 5.

The first component includes eigenvalues greater than for 14 of the 20 characters, indicating that many of the characters are each making similar contributions to an ordination of the OTUs; the five with the largest eigenvalues being leaf, stem, and pedicel lengths. Sepal length, seed width, and upper leaf width contribute to the second component, while the third component is composed of a mixture of

characters including the number of flowers and nodes with flowers, the width of lower leaves, and length of styles.

Since none of the OTUs share identical measurements, there are no zero-length segments on this MST, obscuring most of the clusters shown in Figure 14. This situation contributes to the lack of evident clusters in the PCO scatter diagram for this analysis (Figure 15). The most evident clusters on the MST include the CR and OB OTUs, in part due to the combination of characters favoring these groups noted in the third component of the PCA character analysis. The connection of OB OTUs to the S. calycantha complex occurs via OBWY1 - SIC01, with the inflorescence (represented via upper leaf measurements of zero in OTUs with axillary inflorescences [all OB and CR OTUs]) and slightly larger dimensions (especially style length) as evident differences between the two OTUs. The CR OTUs attach via the CRQC1 - WCYU1 segment, with differences reflected in upper leaf measurements (zero in CRQC1) and the shorter pedicels, shorter styles, and longer sepals of CRQC1.

Tracing the size of plants through both the CR and OB clusters revealed an interesting pattern: a small OTU participates in a linkage to a diminutive S. calycantha OTU with OTUs becoming increasingly larger away from that linkage. Given the emphasis on size characteristics in the quantitative characters (see Tables 1 and 5), such a result is not surprising. More importantly, it reflects the often-seen confusion between S. obtusa, S. crispa, and small plants of S. calycantha; misdetermined specimens of any of these three taxa are likely to be specimens of one of the other listed species. Without such diagnostic qualitative features as seed surface texture, sepal shape, and leaf pubescence, the segregation of small plants of these species becomes

much more difficult. Although there often is little difficulty in distinguishing S. crista and S. obtusa from S. calycantha, the line between S. crista and S. calycantha is less clear, a situation that will be discussed later.

The only grouping among the remaining OTUs that approaches a cluster including OTUs often joined in a traditional taxonomy is the branch including 20 of the WC (S. calycantha var. calycantha) and SI (S. calycantha var. simcoeii) OTUs, an intermixing possible in the absence of pubescence characters. These plants are grouped together by shorter styles and mostly ovate leaves, features that are important in segregating these OTUs.

The remainder of the S. calycantha complex is best described by trends rather than distinct clusters that could be used for taxonomic interpretation of the group. The trends illustrated in Figure 16 and described below are based on an inspection of character values of OTUs and observing changes that occur along MST segments joining the indicated OTUs.

In addition to the general trend of enlargement beginning at OTU SIC01, the tree illustrates several developmental courses that could have been followed in the production of larger plants, most of these to be treated here as S. borealis. Most of the OTUs beyond SBYU2 in Figure 16 have longer leaves, the segments of the MST leading to OTUs with the common linear-lanceolate or oblong leaf shape of the larger plants. Three major lines of differential development can be seen along the MST segments linked to OTU EION1. First, increasing the number of flowers in conjunction with a slight narrowing of the leaves leads to OTUs resembling large specimens of Fernald's S. calycantha var. floribunda.

OTUs toward and beyond SBWY1 have longer leaves, sepals, and capsules than OTU EION1. These OTUs include five EI OTUs and, on a separate branch, most of the OTUs which would be identified as Fernald's S. calycantha var. sitchana. Finally, plants sometimes identified as S. calycantha vars. isophylla and bongardiana are found in the lower left corner of Figure 16, characterized by larger upper leaves of the inflorescence than would be found in OTU EION1.

In summary, not only do these groups contain OTUs representing different taxa, but an inspection of the entire MST for this analysis would reveal little if any semblance of geographical unity that should be apparent in any clusters that are to be used in defining variation within a wide ranging species.

Summary

A comparison of the results of the two analyses presented above illustrates that, in spite of the very different patterns produced for the majority of the S. calycantha complex, a cluster of all S. obtusa and all S. crispa OTUs is defined in both analyses. Although linkage of the S. obtusa cluster to the remainder of the MST is accomplished via different S. obtusa OTUs in each analysis, in each case it involves an OTU representing a small, ovate-leaved specimen of S. calycantha; the placement of S. obtusa is similar in each analysis.

The situation involving S. crispa OTUs is similar in that all OTUs representing that taxon are clustered together in analyses using all characters and both analyses based on partial character sets. In this case, the link between S. crispa and the remaining OTUs does not involve OTUs representing the same taxon. In two analyses, the link is made via

eastern OTUs that will be treated as S. borealis (EION2 - entire character set; EBQA1 - qualitatives only), while an OTU representing a small western plant of S. calycantha (WCWY1) is involved in the link with S. crispa in the quantitatives - only analysis.

In analyses using only a portion of the data, it has been shown that qualitative data will produce both a MST and a PCO scatter diagram more closely resembling those produced from the entire data set. Meyer (1980) reached the same conclusion in her investigation of Pisum sativum. Why should this occur? The use of an unweighted algorithm gives equal consideration to each character, but scaling the data to produce the average distance matrix actually adds a weighting factor in favor of characters with either few states or a very narrow range of variation. The most dramatic example occurs in the case of binary characters - scaling a 0,1 character places a 0 and 1 in the data set. This tendency can be offset by converting quantitative characters into qualitative multistate characters, as seen in Duncan (1980). This approach was not used because I did not want to bias the results by subdividing the quantitative data, and thus segregating character variation divisions a priori. I thought it more important to investigate what the overall variation illustrated.

3. The clusters representing S. crispa and S. obtusa

The phenetic distinctiveness of both Stellaria crispa and S. obtusa from other members of the S. calycantha complex is suggested by the results of most of the analyses thus far discussed. Each cluster will be described below, the MSTs shown in Figures 12 and 13 derived from the 163 OTUs x 33 characters analysis summarized in Figure 9 and Table 3.

A. Stellaria obtusa

The MST illustrating the S. obtusa cluster is provided in Figure 12. The 17 S. obtusa OTUs are linked by distances of less than 0.097, relatively short distances when compared to many of the distances encountered among S. borealis OTUs in Figures 21 and 22. A segment of length 0.333 connects S. obtusa through OBMT1 to WCOR1, the S. calycantha OTU smallest in overall stature included in the analysis. Changes in inflorescence type, sepal apex shape, petal presence, and seed surface texture occur on this OBMT1 - WCOR1 segment, with quantitative characters of these OTUs being comparable. WCOR1 was originally identified as S. obtusa, a situation commonly encountered among specimens of very tiny S. calycantha plants from the Cascades.

OBWA2 deserves special mention since it represents an isotype of S. washingtoniana Robinson (Allen 157, MSC). Although not usually associated with S. obtusa in modern synonymy (e.g. Hitchcock in Hitchcock & Cronquist, 1964), it clearly clusters with the S. obtusa OTUs in the PCO scatter diagram (Figure 9), the MST (Figure 12), and the UPGMA phenogram (Figure 11); only in the SL phenogram (Figure 10) is OBWA2 noted as being distant from the other S. obtusa OTUs. It is set off from OBOR2 by a greater distance than any other S. obtusa OTU pair, in part due to the pubescent stem of OBWA2, a unique occurrence in the cluster, and its slightly larger lower leaves and longer pedicels.

The MST can be used as a basis for phytogeographic conclusions. In the case of S. obtusa, the cluster outlines a species found in the mountains of western North America, from California and Colorado in the south to southern British Columbia and Alberta in the north. OBUT2 is

distinctive in being connected to four OTUs, illustrating morphological similarity to several OTUs from other portions of the range of the species.

B. Stellaria crispa

The MST for the S. crispa cluster is shown in Figure 13. Twenty of the 21 OTUs are linked by distances less than 0.087; CROR2 is joined to CRWA4 by a segment of length 0.169. A segment of length 0.248 joining CRBC2 to OTU EION2, connects Stellaria crispa to the other OTUs in the analysis. Qualitative differences in leaf margin pubescence, inflorescence type, extent of sepal nerves becoming evident in fruit, and seed surface texture occur along this segment. Significant quantitative differences appear since CRBC2 has, as do most S. crispa OTUs, shorter leaves, pedicels, and styles, but longer sepals than EION2.

The position of OTU CRAU1 in the cluster (Figure 13) is interesting. It is connected to six other OTUs from widely separated areas. This OTU occupies similar positions in analyses in which only qualitative or quantitative data were used; it is placed on a zero-length branch in the MST of the qualitative analysis (Figure 14) and connected to five CR OTUs in the quantitative analysis (Figure 16). CRAU1 was collected in the Aleutian Islands near the northwestern extreme of the range. The morphological similarity to southern populations could serve as evidence of the post-Pleistocene migration from southern areas noted in the discussion of phytogeography of S. crispa (see Phytogeography text).

In contrast to S. obtusa, it is much more difficult to explain the

relation of S. crispa to the S. calycantha complex via the CRBC2 - EION2 segment on either morphological or phytogeographic grounds. The vastly different appearances of EION2 and CRBC2 are readily apparent, EION2 an erect plant with a distinct inflorescence, CRBC2 a very small trailing plant with few axillary flowers. Since none of the characters are weighted, the MST algorithm is looking for measures of overall similarity. Although separated by a long distance (only seven branches of the tree are longer), EION2 was judged to be most similar to the S. crispa cluster. Similar character states in EION2 and CRBC2 include all qualitative characters except the four noted above, stem length, style number, open and closed capsule length, and seed width. Stellaria crispa is a western species, which while usually very distinctive, is more likely to be confused with and related to some of the small western S. calycantha plants. OTU EION2 is similar to other eastern OTUs, but has a papillate stem, a characteristic more common in plants found in northwestern Canada.

The attachment of the S. crispa cluster to SIWA1 via CROR2 at the 0.2555 level in the SL phenogram (Figure 10) may have more phytogeographic significance than the CRBC2 - EION2 link described above. A comparison of these OTUs reveals several similarities, the most evident being their common possession of few flowers, an absence of petals (odd among SI OTUs), and short styles. The placement of the cluster near SBCA3 is significant since SBCA3 is a large plant that resembles (and usually clusters with [e.g. Figures 19 and 23]) plants of the taxon here treated as S. borealis subsp. sitchana in stature and inflorescence, but certainly S. crispa in leaf shape.

Taxonomy

The combination of distant connections to the remaining OTUs in the S. calycantha complex which are based on changes in several characters and short segments connecting members within the clusters suggests that separation of S. crispa and S. obtusa from the remaining OTUs is warranted. The clear separations maintained in most projections using the entire suite of characters and those where only qualitative or quantitative characters were employed suggests that recognition of these taxa at the species level is warranted.

The connection of the S. obtusa cluster at the very base of both the SL phenogram (Figure 10) and the UPGMA phenogram (Figure 11) illustrates that S. obtusa OTUs are distinct from all other OTUs, suggesting that S. obtusa could be distantly related to the S. calycantha complex. The distinctness of the S. obtusa cluster is confirmed by the results of the analysis of the 163 x 33 matrix using the SUBSETS program. Of the 55 subsets recognized by the program, six involve OB OTUs. While five of the 14 subsets with the smallest diameters involve pairs of OB OTUs, I think it far more significant that subset 33 includes all 17 OB OTUs. This subset has the most members (17) and is defined with a smaller diameter (0.158), or maximum distance (dissimilarity) between OTUs within the cluster, than six other subsets. Subset 33 also has the largest minimum gap (0.333), or minimum distance (dissimilarity) between an OTU inside the cluster and an OTU outside of the cluster, of any of the subsets; the score of 0.333 is equal to the length of the WCOR1 - OBMT1 segment from the MST. This last feature is important since by the definition of the algorithm (Rohlf et al., 1979), subset 33 is the most

distinct cluster, considered by the program to be well separated from all other OTUs.

The fact that S. *crispa* was not clustered with the small western OTUs of S. *calycantha* except in the SL phenogram (Figure 10) with which it has sometimes been confused is a result that was not expected.

4. Resolution of S. *calycantha* and S. *borealis* relationships

A. Analyses using all characters

Analyses of a 125 OTU (21 S. *crispa* and 17 S. *obtusa* OTUs excluded) 125 x 33 character matrix were calculated to examine the relationships within the S. *calycantha* OTUs in accord with the arguments presented at the end of the text for Part 1. The cophenetic correlation coefficient of the UPGMA phenogram for this matrix is 0.733, indicating the phenogram is a less accurate summary of the distance matrix, possibly a reflection of the effect of removing the OB and CR clusters. The PCO scatter diagram giving the best separation and least distortion from the MST was that of factor 1 vs. factor 2 illustrated in Figure 17 and marked with suggested clusters. Three factors were calculated from the distance matrix, summarizing 24.24, 20.14, and 12.33% of the trace variance respectively.

PCA of the correlation matrix of characters produced eight components with eigenvalues greater than 1.0, indicating, as in the 163 x 33 matrix, that the characters are not highly correlated. The first three components each had eigenvalues of 2.6 or greater, accounting for 52.27% of the trace variance, the character loadings of these components given in Table 6. The first component includes many quantitative characters, with leaf, stem, sepal, and closed capsule lengths making

the largest contributions. Leaf width and margin characteristics contribute to the second component, while petal and sepal features contribute to the third component.

The PCO scatter diagram (Figure 17) illustrates that greater separation among the remaining OTUs was obtained after removing S. obtusa and S. crispa OTUs, with the formation of what appear to be three nicely separated clusters. A closer inspection of both the trends in the MST and the OTUs themselves suggests that the present results are indeed close to a final clustering, but require additional refinement before being accepted as indicative of the taxonomy of the group.

The large cluster at the bottom of the PCO includes most of the elongate-leaved plants primarily found in eastern and northern North America, a rather tight group with the exception of several distant OTUs (e.g. SBMC2). The most evident group of OTUs within that cluster is the 9 EF OTUs representing S. borealis var. floribunda at the lower left of the cluster, their smaller upper leaves helping to segregate them from other eastern OTUs.

Most of the OTUs in the upper left quadrant of the PCO scatter diagram (Figure 17) form a cluster representing the small ovate-leaved, short-styled western plants usually classified as S. calycantha vars. calycantha and simcoei. All but one of the OTUs with eigenvalues greater than 0.107 along the factor 1 axis in the upper right quadrant of Figure 17 are all large western plants often identified as either S. calycantha var. sitchana or var. bongardiana.

One problem in accepting this scatter diagram as the basis for the taxonomy is evident from the above description of the clusters; the OTUs between the two upper clusters are not accounted for. These OTUs

represent a diverse assortment of specimens primarily from western localities with characteristics setting them in many ways between the eastern material in the lower cluster and the sitchana-bongardiana cluster.

After the MST for this analysis was superimposed on Figure 17, several interesting situations in the portion of the tree shown in Figure 18 became apparent. If one follows the branch from WCAK2 through WCWY1, all of the taxa bear WC or SI OTU abbreviations, while most others on both sides of WCAK2 do not. All but one of the OTUs in the upper right quadrant of Figure 17 are connected via OTU SBCA6 to OTU EIMA1, an adjacent OTU to WCAK2. Furthermore, four of the EF OTUs are placed in the upper left quadrant of Figure 17. Placing the EFQU1 - EFWV1 MST segment on the PCO scatter diagram indicates that the locations of these two OTUs are clearly distorted on the PCO; compare the EFQU1 - EFWV1 segment to the EIWI2 - EFQU1 segment depicted in Figure 17; these are similar length MST segments in Figure 18. Why should this occur?

The answer was surprisingly simple, and showed the power of binary characters in forming the pattern of the MST. An inspection of OTUs reveals that the EFQU1 - EFWV1 segment is a major division of the MST. Not only are there quantitative differences between these populations, but EFWV1 has petals! All OTUs below EFWV1 in Figure 18 have petals, while all of the taxa on the EFQU1 side of that segment (i.e. at the top of Figure 18 and in the lower cluster of Figure 17) lack petals. Petal condition was added as two binary characters, one presence-absence and a second for relative length. As noted in the section on floral biology, apetalous flowers are more common on eastern plants than ones with one

or more petals. The situation is reversed in western North America; 9 of 14 SI OTUs, all SB OTUs (sensu S. calycantha var. sitchana), and all WC OTUs on this MST have petals.

The character loadings in Table 6 affirm the large contribution of petal characters to the PCO. Not only do they contribute the majority of their effect to component 3, but also the loading scores for these characters exceed all others among the first three components.

When the PCO scatter diagram is examined with the "petals - no petals" situation in mind, it becomes evident that these characters have produced a major dichotomy. Except for the 4 SI OTUs near the horizontal axis, the axis is also a dividing line between petals (above) and no petals (below). The 4 EF OTUs just above the axis are most closely related to the EF OTUs in the lower quadrant, much of the distance being distortion from these characters. Similar distortion is also present in the presentation of the 4 apetalous S. calycantha var. simcoeii OTUs near the axis, their nearest neighbors being petal-bearing SIOR1 among the SI OTUs in the upper portion of the quadrant.

B. The 125 x 31 matrix - the effect of removing petal characters

Analyses were run using a 125 x 31 matrix after the removal of petal characters. The cophenetic correlation coefficient for the UPGMA phenogram for this matrix is 0.735, very close to the 0.733 of the 33 character matrix. The PCO scatter diagram giving the best separation and least distortion from the MST was that of factor 1 vs. factor 2 illustrated in Figure 19 and marked with evident clusters. Three factors were calculated from the distance matrix, summarizing 29.12, 16.43, and 13.48% of the trace variance respectively.

PCA of the correlation matrix of characters produced eight components with eigenvalues greater than 1.0, indicating that the characters are not highly correlated. The first three components each had eigenvalues of 1.9 or greater, accounting for 53.14% of the trace variance.

Since the loadings of the first two components in this analysis are virtually identical in size and rank to those of the 125 x 33 matrix, the only loadings of significance here are those of the third component (Table 7). Removal of the two petal characters changed the nature of the third component significantly, increasing the number of characters with eigenvalues greater than 1 from five to nine. The five largest values now belong to characters representing sepal nerve length, leaf midrib and stem pubescence, and seed dimensions.

The MST will be presented in segments as the major taxa are discussed. The following plan will be followed in describing each cluster:

1. Presentation and description of the MST.
2. Comparison of the MST to the PCO and discussion of distortion.
3. Taxonomy of the cluster.

i. Stellaria calycantha

Most of the OTUs in the lower left quadrant of Figure 19 are members of this cluster, encompassing the delicate plants found at high altitudes in the western areas of the continent.

The MST for this cluster is presented in Figure 20, including the attachment through ECGR1 to the remaining OTUs. This tree is characterized by only one tight cluster (around SIID2, in part due to

the stem and leaf midrib pubescence of these OTUs) and by many taxa attached rather distantly to each other. The WCWY1 - WCAK2 - WCAU1 - ECGR1 segment is clearly a transition area between the clusters, being characterized by the character changes including those illustrated in Table 8. OTUs WCAU1 and WCAK2 are somewhat intermediate in having longer leaves, but share the shorter styles and sepals of WCWY1 as well as the tendency to produce a more globose capsule which becomes more fully expressed in OTUs beyond WCWY1.

The WCCA2 - SIWY1 segment is the juncture between glabrous plants (WCCA1) and very pubescent plants (SIWY1) which were identified as S. calycantha var. simcoei. Since the distant WC OTUs beyond SIOR2 are also glabrous, the placement of pubescent SI OTUs between two groups of glabrous plants suggests that pubescence features are less important than recent treatments of these taxa would indicate.

Comparison of the MST and PCO scatter diagram for this cluster reveals an intermixing of the WC and SI OTUs, a situation that should occur if pubescence features are not emphasized. Superposition of the MST on the PCO scatter diagram reveals that, except for OTU SBAB2, all OTUs in the cluster are related through a single connection with OTUs outside of the cluster. This suggests a significant difference between the clusters, one that I have chosen to recognize at the species level. Stellaria calycantha is retained for OTUs within the cluster while S. borealis is "resurrected" for the plants with longer styles and generally more elongate leaves.

Although they can be separated by the characters listed in Table 8, it is interesting to note the nearest neighbors to the S. calycantha OTUs are several OTUs from the New England states, the other area where

Fernald (1940) thought S. calycantha var. calycantha was found.

Taxonomy: Although showing as separated from WC members on the MST, the taxonomic recognition of S. calycantha var. simcoei (the SI OTUs) borders on the subjective. Characters including overall leaf shape, capsule length and shape, and the short styles are shared by WC and SI OTUs. The criteria that most easily segregate SI and WC OTUs are all pubescence features (leaf margin, leaf midrib, and stem), illustrating the segregating power of binary characters.

Based on previous experience with the variability of pubescence features in the Caryophyllaceae (see Rabeler, 1985) and variability exhibited in S. calycantha (e.g. the mixing of pubescent leaves and lower leaf midribs [as in S. calycantha var. simcoei] and a glabrous stem [as in S. calycantha var. calycantha] in OTU SIWAl), I cannot support taxonomic recognition of the pubescent plants, even as a variety within S. calycantha.

ii. Stellaria borealis

This large cluster includes all of the OTUs on the PCO in Figure 19 not included in the Stellaria calycantha cluster. S. borealis OTUs generally have elongate leaves, ovoid capsules, and styles over 1.0 mm long. The MST for the S. borealis cluster is presented in Figures 21 and 22. Several clusters appear in this portion of the MST, so the decision to recognize only two taxa must be explained. A brief description of the MST follows.

Three groups of OTUs are evident from left to right across the MST illustrated in Figure 21. The line from ECGR1 to EION2 includes eastern OTUs with non-reflexed peduncles, most of which have been placed in S.

calycantha (or S. borealis) var. isophylla in recognition of their few flowers and large upper leaves. The two EC OTUs have leaves which approach an ovate shape present in S. calycantha; their placement along the line leading to that cluster is appropriate. Ten EF and 1 SB OTU form a cluster based on the upper leaves becoming mostly scarious in these OTUs in conjunction with a more prominent floral display and an increase in leaf length. The remaining line of OTUs leading from SBAU1 includes 20 OTUs. This group is separated from other clusters on this end of the MST by the presence of reflexed peduncles, longer leaves, and slightly longer capsules.

Two main lines are evident in the MST in Figure 22. The 24 OTUs on the left side of Figure 22 have papillate stems and leaf margins. They often have shorter and more oblong leaves and somewhat smaller flowers than OTUs in Figure 21. Many of these populations, originally assigned to SB OTUs in this analysis, could be placed into Hultén's S. calycantha subsp. interior. The other group of OTUs leads from SBYU1 toward OTUs representing Fernald's S. calycantha (or S. borealis) var. sitchana (OTU SBQC1 beginning that group) consisting of papillate-stemmed plants which have slightly larger flowers and larger upper leaves than the "interior" group. A discussion of OTUs treated here as S. borealis subsp. sitchana will be deferred until later in this discussion since those OTUs are to be recognized as a distinct cluster.

There is a bias in the MST which occurs at the juncture between Figures 21 and 22. The segment joining OTUs SBQA6 and SBYU1 represents the dividing line between OTUs with glabrous or pubescent stems (Figure 21) and those with distinctly papillate stems (Figure 22). I consider this to be a less severe situation than that of the petal bias since the

distribution of the papillate stem condition is more consistent, being found in most of the OTUs from the northern areas of Canada and in many of the OTUs in the Rocky Mountains. Folding Figure 22 under Figure 21, and thus placing the smaller papillate plants closer to the EI and EF OTUs on the left side of Figure 21 and the larger papillate plants closer to the group of EI and SB OTUs on the right side of Figure 22 reduces the effect of stem pubescence; this reduces the distance between papillate and the non-papillate plants with which they cluster in Figure 19. Since the MST is generated by the program as a list of segments but with no clue on their spatial orientation, the possibility of such a folding cannot be completely discounted.

The PCO scatter diagram (Figure 19) shows this cluster as a reasonably compact group with the rather obvious exception of the distant OTUs near the upper edge of the scatter diagram. These are OTUs with both a large number of flowers and a wide scarious leaf margin, matching S. calycantha (or S. borealis) var. floribunda of Fernald. The influence of those characters on the PCO factors accounts for the distorted (when compared to the MST) placement of the EF OTUs on the PCO scatter diagram. Other trends which are operating to spread the OTUs in Figure 19 include general increases in stem, leaf, sepal, and style length along the X axis.

Taxonomy: Although subclusters in this cluster appear to indicate that segregation of at least two taxa is prudent, knowledge of an important feature of the plants suggests that recognition of all but one of these clusters is of little value. Evidence presented by Wiegand and Eames (1926) and Schlising and Iltis (1962) and personal experience noted in the text on Floral Morphology suggests that recognition of S.

calycantha (or S. borealis) var. floribunda, primarily differing from other OTUs in inflorescence structure (number of flowers and bract size and texture), is not meaningful and may be dependent at least in part on habitat conditions.

It is somewhat tempting to segregate the smaller papillate-stemmed OTUs often identified as S. calycantha subsp. interior. All of the plants have papillose stems and leaf margins, similar to those found in both S. borealis subsp. sitchana and S. longifolia. This is a feature only weakly exhibited (if at all) in other S. calycantha and S. borealis plants. Inspection of OTUs of the "interior" group suggests a tendency toward shorter and slightly wider leaves and the production of flowers with smaller dimensions in these plants. Most collections of S. borealis from an area extending from central Alaska and northwestern Canada, southward only in the Rockies as well as a small number of collections in eastern Canada (near Hudson Bay in Ontario eastward into Québec) could be identified as S. calycantha subsp. interior. Superposition of the MST on the PCO scatter diagram revealed, however, that these OTUs did not form a distinct cluster. Rather, the OTUs disperse among other S. borealis OTUs when stem pubescence is not emphasized.

An inspection of the MST and PCO scatter diagram of this cluster reveals two other interesting items about Fernald's classification. The four OTUs which I thought might represent S. calycantha var. calycantha as he recognized it in the East did not segregate clearly from other eastern material in either the MST or the PCO scatter diagram. Fernald's S. calycantha var. laurentiana disappears easily, EBQU1 (holotype of S. calycantha var. laurentiana) and EBQA1 (paratype) being

only a few OTUs removed from EINH2, the type specimen of Fernald's S. calycantha var. isophylla, in the MST. These OTUs did not cluster either distantly from other eastern OTUs or close to each other, giving no basis for taxonomic recognition.

Three OTUs should be removed from the S. borealis subsp. borealis cluster since, although acting in the analyses as perfectly "normal" large plants with a prominent inflorescence, they represent S. borealis × S. longifolia hybrids. SBAK2, SBC01, and SBWA2 each have sharply smaller, mostly scarious leaves at the first node above the basal flower, a S. longifolia characteristic which is usually expressed in the hybrids.

iii. Stellaria borealis subsp. sitchana

This cluster occupies over one-half of the lower right quadrant of Figure 19 and represents large papillate plants common to wet areas along the Pacific Coast which were recognized by Fernald as S. calycantha (or S. borealis) vars. sitchana and bongardiana.

The MST for most S. borealis subsp. sitchana OTUs is shown in Figure 22, the segment between OTUs SBWY1 and SBQC1 marking the division between S. borealis subspp. borealis and sitchana. All OTUs beyond SBWY1 have distinctly longer sepals and capsules, features which in combination with the sharply reflexed pedicels and papillose stems distinguish the OTUs of the subspecies. Most plant dimensions increase in size as one progresses from SBQC1 toward either SBAK3 or SBSD1.

The cluster in the lower right quadrant of Figure 19 emphasizes both the distance between some of the larger OTUs and the sometimes close resemblance between large western OTUs that approach S. borealis

subsp. sitchana in a number of features. The representation of the closest S. borealis subsp. sitchana OTUs in both Figures 19 and 22 is good. Distortion in Figure 19 increases the length of the SBWY1 - SBQC1 segment, making the connection to the remaining S. borealis subsp. borealis OTUs more distinct than it often appears in nature.

All but one of the OTUs inside the boundaries of the cluster are connected to SBQC1 on the MST. The unconnected OTU is SBCA3, a specimen from a California population which is referable to S. borealis subsp. sitchana in spite of its glabrous stem and rather ovate upper leaves.

Two OTUs not included in the S. borealis subsp. sitchana cluster should be included on the basis of inspection of the specimens these OTUs represent. SBOR1 resembles other specimens of S. borealis subsp. sitchana except for the possession of smaller sepals and narrower upper inflorescence bracts than most other plants. SBAU1 closely resembles most S. borealis subsp. sitchana specimens except for the lack of sharply ridged sepals, a characteristic which may not be as constant as these data suggest.

Taxonomy: After slight modification, this cluster becomes a unified entity for the large western plants primarily found along the Pacific coast and to some degree in the northern Rocky Mountains of the United States.

A study of the MST and the PCO scatter diagram shows that the retention of S. borealis vars. sitchana and bongardiana within S. borealis as maintained by Fernald (1914) is appropriate. These results illustrate that although OTUs often identified as these varieties do form a cluster, the cluster is by no means as distinct as those formed by S. crispa and S. obtusa.

On the other hand, there is little evidence for segregating S. borealis vars. sitchana and bongardiana from one another. OTUs SBCA1 and SBCA2 are both from the same collection (Tracy 795, UC), done intentionally to see if a few-flowered and a many-flowered plant would cluster very differently. Although the distance between them is distorted in Figure 22, they are both related to SBCA5 on the MST and, as will be seen in Figure 23, the UPGMA algorithm links these OTUs to each other - as they should be! Stellaria borealis var. bongardiana is not recognized in this treatment.

C. Removal of Stellaria calycantha - a 93 x 31 matrix

The Stellaria borealis cluster delimited in the previous analysis was analyzed in the absence of S. calycantha OTUs. The cophenetic correlation coefficient for the UPGMA phenogram of this matrix is 0.733, very close to the 0.735 obtained in the 125 x 31 matrix.

Removal of the S. calycantha OTUs resulted in lengthened MST distances, some OTU rearrangements on the MST and spreading of the OTUs on the PCO scatter diagram, but did not result in substantial changes to the OTU clusters described from the MST in Figures 21 and 22.

The UPGMA phenogram from this analysis gives the best picture of possible groups within S. borealis, each marked on Figure 23. OTUs in groups 1 and 2 have few flowers and large upper inflorescence bracts, with reflexed pedicels and slightly larger capsules separating group 1. These OTUs would fall into Fernald's S. borealis var. isophylla. Group 3 OTUs share herbaceous upper inflorescence bract margins with groups 1 and 2, being separated from those groups by papillose stems and leaf margins and the smaller size of the upper inflorescence bracts in these

plants. Nearly all group 3 OTUs would be considered as members of Hultén's (1944) S. calycantha subsp. interior. OTUs in groups 4 and 5 all have small, mostly scarious upper inflorescence bracts and most have numerous flowers. Most OTUs in group 4 are eastern plants which would key to S. borealis var. floribunda in Fernald (1914), while those in group 5 are larger western OTUs which would key to S. borealis var. floribunda, S. calycantha subsp. interior, or S. borealis var. sitchana (SBOR1). All OTUs in group 6 have the longer, narrower leaves and larger floral dimensions associated with S. borealis subsp. sitchana. All unlabeled OTUs are connected remotely to other OTUs on the MST, their appearance at the base of the phenogram not necessarily illustrating any relationship.

In simple terms, groups 1 through 5 reflect the sorting of OTUs on a combination of stem pubescence, number of flowers, and upper inflorescence bract margin texture. There appears to be little justification for recognizing any of these groups if they are not all consistently treated.

On the other hand, group 6 appears to stand alone from the other groups. The branch point of SBMT1 (the OTU closest to the group 6 cluster) is next to that of EINY1 (the OTU "leading" to groups 1 - 5), suggesting a dichotomy between groups 1 - 5 and 6 that deserves recognition. Therefore, groups 1 - 5 are being recognized as S. borealis subsp. borealis and group 6 as S. borealis subsp. sitchana.

Suggested Classification

The following classification of the Stellaria calycantha complex is suggested from the results of the factor and cluster analyses.

Stellaria obtusa

Stellaria crispa

Stellaria calycantha

Stellaria borealis subsp. borealis

Stellaria borealis subsp. sitchana

DISCRIMINANT ANALYSIS

Discriminant analysis is useful in assessing the separation between pre-defined groups. Each OTU is assigned to a group before a discriminant analysis is performed, a major difference between this technique and cluster analysis. Each discriminant function represents a linear combination of variables which specifies an axis that maximizes the spatial separation between the centroids of groups as they appear in multidimensional space (Abbott et al., 1985). The algorithm used to calculate a discriminant function analyzes a function of the "maximal variance between groups relative to the pooled variance within groups" (Sneath & Sokal, 1972).

After the axes are determined, the scores of individual OTUs can be calculated and plotted. In this classification phase, a set of equations is calculated for each OTU, one equation for each group in the analysis. Each equation is formed by multiplying a linear discriminant (or classification) coefficient and a data value, repeating the process for each variable, summing these products, and adding them to a constant. The resulting set of classification scores, one for each group, is used to assign OTUs; an OTU is placed in the group represented by the highest score from the equations for that OTU. A priori group assignments for OTUs are compared to those predicted on the basis of the classification equations, providing a measure of the predictive ability of the equations.

Suggested group assignments are provided for OTUs that, according to the algorithm, have less than a 50% chance of belonging to the group to which they have been assigned (Klecka in Nie et al., 1975).

It is unfortunate that OTUs with missing data are not analyzable with discriminant analysis because some of the most distinctive plants of a group may be missing one or more features. This limitation makes it impossible to create a group for the S. borealis × longifolia hybrids unless all fruit variables are excluded from the analysis. For this reason, the three hybrids have been excluded from the discriminant analysis data set.

The Direct method was chosen for the discriminant algorithm. All variables enter into the analysis at the outset with the resulting discriminant functions created from the entire set of variables rather than, in the case of stepwise procedures, from a subset of variables (Klecka in Nie et al., 1975).

OTUs with missing values for variables which enter the discriminant analysis have been included in the classification phase; the group mean is substituted for the missing data value (Klecka in Nie et al., 1975). Since all variation in the data set is not necessarily represented in the subset of "complete-data" OTUs, group definitions may be narrower than if all OTUs were considered. This is apparent when analyses where OTUs with missing values are excluded from classification are compared to analyses where all OTUs are classified; a decline in the percentage of "grouped cases correctly classified" is both expected and observed. Noting how additional OTUs are placed into the groups that have been defined in an analysis provides a clue on the amount of variation in a taxon that is represented in the OTUs used in defining the groups. How

likely (or not) are correct group assignments going to be made?

Analyses were performed using the DISCRIMINANT program of SPSS-6000 Version 9.0 (Northwestern University conversion of SPSS) on a Cyber 750 at Michigan State University. The taxonomic - geographic OTU identification code described earlier is also used here.

The initial OTU group assignments reflect the results obtained from NT-SYS minimum spanning trees (Figures 12 - 14, 16, 18, 20 - 22) and the UPGMA phenogram shown in Figure 23. OTU groups representing the division of Stellaria calycantha into vars. calycantha and simcoei and the recognition of Stellaria calycantha subsp. interior are initially recognized to allow further consideration of the merits of recognizing these taxa.

Group assignment codes and the number of OTUs initially assigned to each group are as follows:

1 - <u>S. obtusa</u>	- 17 OTUs
2 - <u>S. crispa</u>	- 21 OTUs
3 - <u>S. calycantha</u> var. <u>calycantha</u>	- 18 OTUs
4 - <u>S. calycantha</u> var. <u>simcoei</u>	- 14 OTUs
5 - <u>S. borealis</u> subsp. <u>sitchana</u>	- 17 OTUs
6 - <u>S. borealis</u> subsp. <u>borealis</u>	- 49 OTUs
7 - <u>S. calycantha</u> subsp. <u>interior</u> Hultén	- 24 OTUs

Results

The results are presented as a series of analyses conducted on both the complete data set and various subsets. The following questions were posed:

1. Are the initial group concepts supportable or are some of these groups separable only by a complex combination of characters?
2. What characters are useful in discriminating between the groups? How do they vary between the groups under consideration?

3. Are the groups suggested by the clustering algorithm also portrayed, or is there a different result?

1. Analysis of all OTUs, all characters

As a starting point, the discrimination among the 160 OTUs was investigated, the resulting groups representing 81 of the 160 OTUs that had complete data. Thirty-two of the 33 variables entered the analysis (LEAFMID [lower leaf surface midrib pubescence] is constant within each group and was not used), with six discriminant functions, accounting for 90.98, 5.49, 1.88, 0.97, 0.53, and 0.15% of the variation respectively, used in plotting and classification. Results of this analysis are summarized in Table 9, a scatterplot shown in Figure 24.

Just as in the clustering analysis of the 163 x 33 matrix, S. obtusa (group 1) and S. crispa (group 2) are the most clearly separated groups in the scatterplot (Figure 24), both from themselves and from all other groups. From the list of discriminant coefficients in Table 9, formation of the S. obtusa and S. crispa clusters is favored since all of the OTUs representing these taxa lack petals and cymose inflorescences. The latter characteristic is noted not only in the character INFLTYP, but also in the listed leaf characters (e.g. LF2ALN and LF2AWD) for which all OTUs except S. obtusa and S. crispa have non-zero values.

The remaining five groups are not distinctly separated in this analysis. Most Stellaria calycantha var. calycantha (group 3) and S. calycantha var. simcoei (group 4) OTUs are found near their respective group centroids (1 OTU of each group is a prominent exception). A similar situation exists for S. borealis subsp. borealis (group 6) and

S. calycantha subsp. interior (group 7). The occurrence of several OTUs of S. borealis subsp. sitchana (group 5) plotted among group 6 and 7 OTUs indicates that the OTUs being added during the classification phase differ in some respects from those contributing to the group statistics and that a relationship of these OTUs with those in groups 6 and 7 is suggested. Stellaria borealis subsp. sitchana is segregated on a number of size criteria, and is closest to groups 7 and 4 on the basis of pubescence characters.

The results of the classification phase emphasized the distinctness of the S. obtusa and S. crispa clusters. All S. obtusa OTUs and S. crispa OTUs were correctly assigned, while all misassignments were confined to the S. borealis and S. calycantha groups. This suggests that exclusion of these clusters may produce a different result that would favor separation among the S. borealis and S. calycantha clusters.

2. Analysis of all OTUs, 31 characters

I thought it appropriate to increase the number of OTUs contributing to the group statistics to determine the effect such an action might have on group definition and subsequent assignment of OTUs. One variable*, CAPOPLN (the length of an open capsule), was deleted. This variable was the only missing value in 15 OTUs, was not among the 10 variables making the largest contributions to the first discriminant function, and did not have a discrimination coefficient greater than

*[The variable for lower leaf surface midrib pubescence was also deleted, but this action had no effect here since it was constant for each group and therefore not included in the initial analysis].

|0.63| in any of the six functions calculated in the first analysis.

These factors suggested that the effect of deletion of CAPOPLN would not outweigh the benefits of adding OTUs to the analysis.

The discrimination among the 160 OTUs on the basis of 31 characters was investigated, the resulting groups representing 96 of the 160 OTUs that had complete data. Six discriminant functions, accounting for 84.40, 9.57, 3.65, 1.31, 0.79, and 0.28% of the variation respectively, were used in plotting and classification. Results of this analysis are summarized in Table 10, a scatterplot shown in Figure 25.

As in the initial analysis, S. obtusa (group 1) and S. crispa (group 2) are the most clearly separated, both from themselves and from all other groups. The relative contributions of the variables to each of the discriminant functions are similar (compare Tables 9 and 10), the most evident changes being the sharply lower contributions by four variables representing petal characteristics (PETALS and PETLNTH) and leaf measurements two nodes above the basal flower (LF2ALN and LF2AWD). The discriminant coefficients of these variables are more consistent with those of the other variables in this analysis. The majority of the characters still deal with inflorescence features, emphasizing the differences between groups 1 - 2 and the S. borealis and S. calycantha clusters.

An inspection of the scatterplot in Figure 25 illustrates that removal of the two characters did not change the basic pattern of the scatterplot. Stellaria obtusa and S. crispa OTUs remained distinctly separated from all other groups (one group 3 OTU excepted). A slightly greater separation between the centroids of groups 3, 4, 6, and 7 is evident as well as the proximal placement of the centroids of groups 3

and 4 (S. calycantha vars. calycantha and simcoei) and those of groups 6 and 7 (S. borealis subsp. borealis and S. calycantha subsp. interior). The placement of group 5 (Stellaria borealis subsp. sitchana) is very similar to that in the first analysis although the number of OTUs plotted near the group centroid is greater here.

The small increases in the percentages of correct assignments suggest that the larger sample contributing to the group statistics produced groups which included more of the variation present in the OTUs in the data set. This is reflected both as an increase in the percentage of correctly assigned OTUs and, in the case of OTUs pre-assigned to groups 3, 4, and 5, as a decrease in the number of groups into which the program placed these OTUs. This latter point is best exemplified among OTUs identified as S. borealis subsp. sitchana (group 5). In the first analysis (Table 9), the eight misassigned OTUs were distributed among groups 3 (one OTU), 4 (two OTUs), 6 (three OTUs), and 7 (two OTUs). In this analysis, one of the eight OTUs is placed in group 5, while the remaining seven now are assigned to group 6.

3. Analysis of Stellaria calycantha and S. borealis OTUs, all characters

As suggested from the analyses presented above, S. obtusa and S. crispa have been clearly separated both from each other and from the remaining groups, while resolution within the groups traditionally treated as S. calycantha is incomplete. Excluding OB and CR OTUs from subsequent runs would focus group discrimination on the central S. calycantha complex.

The discrimination among 122 OTUs (17 S. obtusa and 21 S. crispa OTUs excluded from the original set of 160 OTUs) on the basis of 31

characters was investigated. The resulting groups represented 59 of the 122 OTUs that had complete data, the lower fraction of contributing OTUs reflecting the greater percentage of S. calycantha and S. borealis OTUs with data missing for at least one variable. Thirty-two of the 33 variables entered the analysis (LEAFMID [lower leaf surface midrib pubescence] was constant within each group and was not used), with four discriminant functions, accounting for 58.00, 29.62, 10.25, and 2.15% of the variation respectively, used in plotting and classification. Results of this analysis are summarized in Table 11, a scatterplot shown in Figure 26.

The statistics in Table 11 illustrate that groups defined within S. calycantha are somewhat more difficult to segregate when outlying groups are removed from the analysis. The percentage of variance represented by the first discriminant function is much smaller than in the analyses including S. crispa and S. obtusa. The contributions of the variables in this case are similar to those in Table 9, with a very strong emphasis on petal and inflorescence features; PETALS and PETLNTH make a greater contribution here, especially to the second discriminant function.

The separation among the five groups suggested in Figure 25 becomes somewhat more distinct in this analysis (see Figure 26). Groups 3 (S. calycantha var. calycantha) and 4 (S. calycantha var. simcoei) are close to each other, but separated from the three other clusters. Centroids of groups 6 and 7 (S. borealis subsp. borealis and S. calycantha subsp. interior) are also plotted close to each other. The clearest separation among the five groups involves group 5 (S. borealis subsp. sitchana), a situation that in part may be caused by the much larger

stature of most S. borealis subsp. sitchana OTUs. It should also be noted that most group 5 OTUs are widely dispersed from the centroid for group 5, suggesting that OTUs contributing to group statistics may not be very representative of the other OTUs that have been assigned to S. borealis subsp. sitchana.

A comparison of Tables 9 and 11 illustrates the percentages of correct assignments of S. borealis and S. calycantha OTUs in the classification phase to be very similar; the elimination of S. crispa and S. obtusa OTUs had little effect on the accuracy of group assignment. Misassignments of group 3 and 4 OTUs into groups 5 - 7 were limited to two of 32 OTUs. All but two of the misassignments involving S. borealis OTUs were made to other S. borealis taxa.

These observations suggest a major dichotomy in the S. calycantha complex between groups 3 and 4 (S. calycantha varieties) vs. the group set 5 - 7 (S. borealis subspecies), one that must be considered in further analyses of the complex.

4. Stellaria calycantha and S. borealis, adding OTUs to the analysis

OTU assignment results in Tables 9 and 11 illustrate the difficulty in forming group statistics from a small number of OTUs and then trying to fit other OTUs into these groups. Increasing the number of OTUs contributing to the group statistics by selectively removing characters as in Part 2 above would increase the information content of the analysis phase. It is likely that the additional variation included in the group definitions will permit higher correct assignment percentages in one or more of the S. calycantha and S. borealis groups.

Seven characters were selected for removal. LEAFMID, lower leaf

surface midrib pubescence, was eliminated since it was a constant character in each group (see section 5. A. for additional comments). The dimensions of leaves two nodes below the basal flower (LFBLN and LFBWD) were often missing since the lower leaves of S. calycantha and S. borealis plants often shrivel and sometimes fall from the plant during late summer; 15 OTUs lacked only these data. Fernald (1914) carefully noted that capsule measurements were made from mature, but unopened capsules. I measured both closed and open capsules, noting that, as one might expect, the opened ones were slightly longer. I also noted that open capsules were absent from a number of collections, especially S. borealis subsp. sitchana OTUs. Deletion of CAPOPLN, the length of the open capsule, adds an additional six OTUs to the sample. Although the number of styles (STYNO) varies in nearly every OTU, the variable is not a major contributing variable in the four discriminant functions in Table 11.

The last two characters to be removed, PETALS and PETLNTH, bear special mention. At the outset of the study, I thought that the inclusion of petal presence and length of petals would be useful information. After discovering the contribution these characters made in segregating taxa in the cluster analyses and in the discriminant analyses of S. calycantha OTUs presented above, I think it best to discard these characters. While indeed most of the OTUs in groups 3, 4, and 5 do have petals, and most in 6 and 7 do not, the OTUs in these groups with the "unusual" condition were very distinctly, albeit unnaturally, segregated in the cluster analyses. The observed variation in petal number among flowers of a cultured plant of S. borealis subsp. borealis (see Floral Morphology text) suggests that group segregation

based on petal characters may be of little utility.

The discrimination of S. calycantha and S. borealis on the basis of 26 characters was investigated. The resulting groups are based on 84 of the 122 OTUs; an increase of 25 OTUs. Four discriminant functions, accounting for 61.34, 22.89, 12.19, and 3.58% of the variation respectively, used in plotting and classification. Results of this analysis are summarized in Table 12, a scatterplot shown in Figure 27.

A comparison of the results in Tables 11 and 12 reveals several interesting items. The percentage of variance accounted for by the first discriminant function increased while the canonical correlation of that function decreased in Table 12, indicating slightly more variation was accounted for by a discriminant function which was slightly less correlated with the dummy variables defining group memberships (Klecka in Nie et al., 1975). Discriminant coefficient values are far different in magnitude (only one value exceeding |1.0| in Table 12), illustrating both the removal of the "strong" petal characters and by the addition of OTUs which make the groups less distinctive from one another.

The scatterplot of this analysis (Figure 27) illustrates that the basic arrangement of the groups is the same as that portrayed in Figure 26. The separation between S. calycantha (groups 3 and 4) and S. borealis subsp. borealis and S. calycantha subsp. interior (groups 6 and 7) is more clearly shown. OTUs in group 5 (S. borealis subsp. sitchana) are plotted much closer to the group centroid than in Figure 26, while the distances between the centroid of group 5 to those of groups 6 and 7 decrease, more suggestive of the relationship of these taxa being proposed than the distances shown in Figure 26.

The overall percentage of correct OTU assignments increases

significantly, the largest individual increases occurring in S. calycantha var. calycantha (72.2% to 100%) and S. borealis subsp. sitchana (52.9% to 88.2%). The only group in which the assignment percentage declined was S. calycantha var. simcoei (group 4) where one OTU assignment was changed from var. simcoei to var. calycantha. The separation between S. calycantha (groups 3 and 4) and S. borealis (groups 5 - 7) is also shown in the classification results, with all but one of the 12 misassigned OTUs placed into a group representing the same species as their pre-assigned group.

5. Should all five Stellaria calycantha and S. borealis groups be taxonomically recognized?

One point that has been emphasized in each of the analyses is the similarity of S. calycantha vars. calycantha and simcoei (group pair 3 - 4) and of S. borealis subsp. borealis and S. calycantha subsp. interior (group pair 6 - 7). Each group has been recognized as a distinct entity within the S. calycantha complex by one or more workers. Evidence from the cluster analysis suggested that continued recognition of each group may not be justified (see Figure 19). The scatterplot in Figure 27 indicates a similar possibility given the close proximity of the centroids of groups 3 and 4 and those of groups 6 and 7 within their respective point clouds. Testing these groups via discriminant analyses seems an appropriate measure. If treated separately, what characters make significant contributions to the discriminant functions?

Analyses will be presented for each case using the same suite of 26 variables as described in section 4.

A. Stellaria calycantha vars. calycantha and simcoei

As noted elsewhere, members of groups 3 and 4 are usually segregated into either different varieties of S. calycantha, or different species (e.g. Hitchcock in Hitchcock & Cronquist, 1964), based on the pilose stem of S. calycantha var. simcoei vs. the glabrous stem of S. calycantha var. calycantha.

The discrimination of S. calycantha vars. calycantha and simcoei was investigated with two analyses, the groups in both representing 20 of the 32 OTUs assigned to these taxa at the outset of the study. Eighteen of the 26 variables in the set used in Part 4 entered the first analysis (eight variables failed the tolerance test, a test used to eliminate variables that are constant within a group and variables that, if used, would contribute to large rounding errors in the calculation of discriminant coefficients [Klecka in Nie et al., 1975]).

Eighteen of the same 26 variables entered the second analysis, but the sets of 18 are not identical. One variable, STEMPUB (stem pubescence), was intentionally deleted for the second analysis to investigate the discriminant result in the absence of stem pubescence. SEPFRLN (length of sepals in fruit), deleted during the first analysis since it failed the tolerance test, was included in the second analysis. One discriminant function was calculated for each analysis and used in plotting and classification. Results of these analyses are summarized in Table 13, the histograms shown in Figures 28 and 29.

One interesting condition (and limitation) of the discriminant algorithm will be discussed before the results in Table 13 are described; the exclusion of variables which are constant either

throughout the data set or within a group. While the former case was expected, the latter situation has a significant bearing on this analysis. In this case, two variables were excluded for being constant throughout the data: PEDRFLX (reflexing of the pedicel) and SEEDSUR (seed surface). Stellaria calycantha var. simcoei (group 4) OTUs are the only OTUs in the data set where the midrib of the lower leaf surface is pubescent. Although it would seem that this character would be useful in delimiting group 4 OTUs, the program excluded LEAFMID from the analysis. A similar situation involving stem pubescence was narrowly avoided since OTU SIWAl has a glabrous stem, preventing a uniform character state in group 4.

The information in Table 13 suggests that S. calycantha vars. calycantha and simcoei could be separated on characters other than the pilose vs. glabrous stem condition, although the separation is less distinct and OTU assignment is less accurate. Two variables make large contributions to the discriminant functions in both analyses, namely LFBLN (length of leaves subtending the basal flower) and PEDLN (pedicel length). Other variables with large discriminant function coefficients in one of the analyses often have much smaller coefficients in the other analysis (e.g. compare coefficients of INFLTYP and SEPAPEX).

The assignment of OTUs was not perfect in either analysis, with the removal of stem pubescence changing the predicted group assignments for six OTUs. Four additional S. calycantha var. simcoei OTUs are placed among S. calycantha var. calycantha OTUs. The predicted group assignments change for two S. calycantha var. calycantha OTUs, but are not reflected in the classification summary of the second analysis because they are offsetting changes; OTU WCNV1, misassigned in the first

analysis, joins group 3 in the second analysis while OTU WCCA4 is transferred to group 4 in the second analysis.

It is evident from the decrease in the percentage of correct S. calycantha var. simcoei OTU assignments in the second analysis that the separation obtained in the absence of STEMPUB forms two groups which would not be representative of the present varieties. This makes recognition of the separation a choice between using a combination of characters which would not include the most noticeable difference between different plants representing S. calycantha or using the current system based on pubescence differences. In light of the variability of pubescence in S. calycantha (e.g. OTU SIWA1 with leaf pubescence as other OTUs of S. calycantha var. simcoei but with a glabrous stem), keeping groups 3 and 4 separate would produce a classification that would be of little utility.

B. Relationships within S. borealis - groups 5, 6, and 7

Before group 6 - 7 relationships are examined, an analysis of groups 5 - 7 is necessary. Stellaria borealis subsp. sitchana (group 5) OTUs were set apart from remaining S. borealis OTUs in the UPGMA phenogram (see Figure 23 and have been likewise segregated in each of the discriminant analyses. Will a similar pattern hold when the groups are isolated from groups 1 - 4?

The discrimination of S. borealis OTUs on the basis of the 90 OTUs originally assigned to groups 5 - 7 was investigated with the groups formed on the basis of 64 of the 90 OTUs having complete data. Twenty-five of the 26 variables from the set described in Part 4 entered the analysis (CAPSHAP [capsule shape] was constant in each group), with two

discriminant functions, representing 73.24 and 26.76% of the variation respectively, used in plotting and classification. Results of this analysis are summarized in Table 14, a scatterplot shown in Figure 30.

As illustrated in Figure 30, a larger separation exists between S. borealis subsp. sitchana OTUs (group 5) on one hand and those of S. borealis subsp. borealis and S. calycantha subsp. interior (groups 6 and 7 respectively) on the other. Most of the variables making the largest contributions to the first discriminant function emphasize the larger size of some characters of S. borealis subsp. sitchana plants; NERVLNTH (sepal nerve length), NODEFLW (nodes bearing flowers), LFBLN (leaf length at basal flower), and SEPFRNLN (length of sepals in fruit). STEMPUB (stem pubescence), LEAFTIP (uppermost leaf margin), and SEPANLN (length of sepals at anthesis) make the largest contributions to the second discriminant function which separates S. borealis subsp. borealis from S. calycantha subsp. interior.

C. Stellaria borealis subsp. borealis vs. S. calycantha subsp. interior

As the OTUs for this study were measured, it became apparent that plants in the northern portion of the range might represent a distinct entity within the complex. Many of these plants could be distinguished from the lanceolate-leaved plants of the East by their papillate stems, somewhat smaller flowers, and smaller leaves. Hultén (1944) felt these comprised a distinct race within the complex, describing them as S. calycantha subsp. interior. Given their overall similarity to the plants of the East and the close relations seen in both the cluster and discriminant analyses, I was curious to see what a discriminant analysis on group 6 and 7 OTUs alone would illustrate.

The discrimination of S. borealis subsp. borealis and S. calycantha subsp. interior was investigated, the groups based on 53 of the 73 OTUs originally assigned to these taxa. Twenty-four of the 26 variables in the set described in Part 4 entered the analysis (INFLTYP [inflorescence type] and CAPSHAP [capsule shape] were constant in each group), with one discriminant function derived and used in plotting and classification. Results of this analysis are summarized in Table 15; a histogram is shown in Figure 31.

Of the four variables with coefficients exceeding $|0.75|$ for the discriminant function, STEMPUB [stem pubescence] makes the largest contribution. The variables representing leaf (inflorescence bract) dimensions two nodes above the basal flower (LF2ALN and LF2AWD) both have relatively high coefficients. Although these leaves are often smaller in plants of S. calycantha subsp. interior, S. borealis subsp. borealis OTUs exhibit either larger leaves (Fernald's S. calycantha var. isophylla) or leaves of a very similar size (Fernald's S. calycantha var. floribunda) to those found in S. calycantha subsp. interior. The importance of LEAFTIP [uppermost leaf margins] reflects the presence of wide scarious upper leaf margins in OTUs resembling Fernald's S. calycantha var. floribunda (here included in group 6); these rarely occur in S. calycantha subsp. interior OTUs.

The contribution of LEAFPUB (leaf pubescence) represents a similar pattern to that of stem pubescence. Most of the plants with papillose stems (all S. calycantha subsp. interior OTUs, a few S. borealis subsp. borealis OTUs) bear leaves with prominent marginal papillae and few if any short cilia.

Several of the other variables represent size differences,

suggesting that the smaller features of many of these plants may be distinctive; a closer view reveals this may be a difficult position to support. Stellaria calycantha subsp. interior plants sometimes have fewer flowers than those of S. borealis subsp. borealis, but variance in this feature can also be attributed to differences in plant maturity, making reliance on such differences discomfoting. Differences in LFBLN and LFBWD (the dimensions of length of leaves subtending the basal flower) are evident between S. calycantha subsp. interior OTUs and most of the longer-leaved OTUs which Fernald would recognize as S. calycantha var. isophylla, but not between some S. calycantha subsp. interior OTUs and those OTUs which resemble S. calycantha var. floribunda.

One interesting result of the classification phase involves the placement of the large papillate-stemmed OTU SBMT1. This OTU was assigned to group 6 since clustering results and the large size of many features of the plant indicated it would not be part of the S. calycantha subsp. interior group. One of the three group 6 OTUs to be placed into group 7 was SBMT1, indicative of the discriminating power of stem pubescence.

In summary, S. borealis subsp. borealis and S. calycantha subsp. interior are most simply separated by stem and leaf pubescence, followed by tendencies in OTUs of the latter taxon toward somewhat smaller flowers. Although one may develop a certain gestalt feeling toward S. calycantha subsp. interior OTUs, this feeling may in part be influenced by the smaller overall aspect of the plant produced in the open, unshaded areas where these plants occur. The differences between S. calycantha subsp. interior and S. borealis subsp. borealis suggest that S. calycantha subsp. interior plants more likely represent small members

of a continuum within S. borealis subsp. borealis.

D. Could Stellaria borealis subsp. borealis be split in eastern North America?

Before concluding this examination of different arrangements within the S. calycantha complex, one further possibility can be considered. Fernald (1914) used differences in bract size, bract texture, and number of flowers to recognize S. borealis vars. isophylla and floribunda; OTUs often identified as these varieties are both included in group 6. Examination of the PCO plot shown in Figure 19 and the UPGMA phenogram in Figure 23 suggests a distinction between the EF OTUs and all other eastern OTUs. Various authors (Wiegand & Eames, 1926; Schlising & Iltis, 1962; Voss, 1985) have suggested problems in recognizing these varieties.

The discrimination of S. borealis vars. isophylla and floribunda was investigated, the groups formed on the basis of 26 of the 32 OTUs in the data set from eastern North America that represent these taxa. All of these OTUs were originally assigned to S. borealis subsp. borealis, with OTU group assignments here changed to indicate their identity as either S. borealis var. floribunda (group 5) or S. borealis var. isophylla (group 6). Twenty-one of the 26 variables used in Part 4 entered the analysis. Five variables failed the tolerance test: four (INFLTYP [inflorescence type], SEPAPEX [sepal apex shape], CAPSHAP [capsule shape], SEEDSUR [seed surface]) are constant among all OTUs in the analysis; the fifth variable NERVLNTH [sepal nerve length] is nearly constant among the OTUs. One discriminant function was used in plotting and classification. Results of this analysis are summarized in Table 16, a histogram illustrated in Figure 32.

In addition to the 32 OTUs noted above, the two OTUs representing Fernald's S. calycantha var. laurentiana and the four OTUs that represent plants which could fit Fernald's (1940) concept of eastern S. calycantha var. calycantha were included as unclassified OTUs, allowing the program to place them into one of the two groups. Twenty-three OTUs representing material assignable to S. calycantha subsp. interior were included to note their classification assignments when S. borealis vars. floribunda and isophylla are recognized.

In spite of 100% correct assignment of all grouped OTUs, the high discriminant coefficients, and the separation shown on the histogram in Figure 32, the closeness of S. borealis vars. isophylla and floribunda appears when the variables making large contributions to the discrimination equation are inspected.

Of the six characters with discriminant coefficients exceeding |3.9| in Table 16, five are directly related to the inflorescence; LEAFTIP (upper leaf margin texture [herbaceous vs. narrow or wide scarious]), FLWSTEM (number of flowers per stem), NODEFLW (number of nodes bearing flowers), and LFTPLN - LFTPWD (dimensions of the uppermost leaves [inflorescence bracts]). Given both the real and potential variability in the form and extent of the inflorescence (see also comments under Floral Morphology) and the problems inherent in classifying young material correctly, I see little reason for splitting the eastern OTUs.

Placement of the ungrouped OTUs that had been included in this analysis indicated that all but one of these 29 OTUs could be placed into S. borealis var. isophylla as described in this analysis. Both of the S. calycantha var. laurentiana (EB) OTUs and the four "eastern

calycantha" (EC) OTUs were placed near the S. borealis var. isophylla OTUs. Placement of the S. calycantha subsp. interior OTUs produced a 1 to 22 split between assignments to S. borealis vars. floribunda and isophylla respectively, many of these OTUs placed farther from the S. borealis var. floribunda OTUs than the majority of S. borealis var. isophylla OTUs. This appears to be a contradiction since the smaller upper leaves and usually numerous flowers of S. calycantha subsp. interior give them a superficial resemblance to the S. borealis var. floribunda OTUs. An inspection of the data set and the discrimination coefficients reveals the influence of the strong contribution made by the margin of the uppermost leaves. While the majority of S. calycantha subsp. interior OTUs have a prominent inflorescence, all but four had herbaceous upper leaf margins, increasing the chance of assignment near the var. isophylla OTUs. One of those having scarious uppermost leaves (WCYU3) was placed in the S. borealis var. floribunda cluster.

6. The case for three groups within Fernald's Stellaria calycantha

As a result of the above analyses on close group pairs, it was evident that the recognition of three groups within S. calycantha and S. borealis was more logical than the previous five-group concept. Group assignments of the 122 OTUs originally assigned to groups 3 - 7 were changed to the following (1, 2 previously assigned to S. obtusa and S. crispa OTUs respectively):

- 3 - S. calycantha - S. calycantha vars. calycantha and simcoei
- 4 - S. borealis subsp. sitchana
- 5 - S. borealis subsp. borealis - all eastern OTUs and S. calycantha subsp. interior

The discrimination of the three S. borealis and S. calycantha groups described above was investigated, the groups based on 84 of these 122 OTUs and the set of 26 characters described in Part 4. Two discriminant functions, accounting for 73.89 and 26.11% of the variation respectively, were used for plotting and classification. Results of this analysis are summarized in Table 17; a scatterplot of the 122 OTUs is shown in Figure 33.

A comparison of Tables 12 and 17 illustrates the differences between five-group (Table 12) and three-group (Table 17) classifications. The first discriminant function in the three-group analysis (Table 17) accounts for 12.5% more variance than that of the five-group analysis (Table 12), with a very similar canonical correlation (0.9579 vs. 0.9593 respectively). LF2ALN (leaf length two nodes above the basal flower) and STYLN (style length) make the greatest contributions to the first function in both analyses, while LFBLN (leaf length at the basal flower) has the largest coefficient in function 2 in both analyses.

The assignment of OTUs to their respective groups produced a higher percentage of correct placements (95.90% in Table 17 vs. 90.16% in Table 12), primarily the result of merging groups 3 - 4 and 6 - 7 and thus eliminating nine misassignments. The five OTUs which were misassigned in this analysis were treated in the same manner in the five-group analysis.

Three of the four characters with the largest discriminant coefficients for function 1 in Table 17 illustrate a simple correlation in S. calycantha and S. borealis. Interpreting the positive and negative signs as longer (+) or smaller (-), the variables suggest that

style length and the length of the leaf subtending the basal flower both increase in length while the width of that same leaf decreases. Most S. calycantha OTUs have short styles and short, wide leaves. Many S. borealis subsp. borealis OTUs have both longer styles and longer, proportionately narrower leaves. The trend continues into S. borealis subsp. sitchana, where the longest styles were seen in conjunction with leaves which most closely approached a linear-lanceolate condition.

The similarity in the first two discriminant functions, the scatterplots (Figures 27 and 33), and the classification percentages could be interpreted as favoring the five-group approach. The advantage of the three-group concept becomes clear when the previous analyses of close group pairs 3 - 4 and 6 - 7 are inspected. In both of these cases, separations of OTUs are made on the basis of combinations of characters. These characters include qualitative features that can vary widely in the groups being segregated (e.g. pubescence in S. calycantha vars. calycantha and simcoeii) and quantitative characters I think are more indicative of a continuum (e.g. sepal length in S. borealis subsp. borealis vs. S. calycantha subsp. interior) rather than a clear dividing line between groups.

7. Addition of Stellaria crispa and S. obtusa - all OTUs, 31 characters

With the above classification of S. calycantha and S. borealis OTUs in mind, it is also appropriate to inspect the modified groups when S. obtusa and S. crispa are included in the analysis.

The discrimination of the five groups as defined in Part 6 was investigated, the groups including 96 of the 160 OTUs using the 31 characters described in Part 2. Four discriminant functions, accounting

for 85.78, 9.33, 3.58, and 1.31% of the variation respectively, were used in plotting and classification. Results of this analysis are summarized in Table 18; a scatterplot is shown in Figure 34.

The effect that group reduction had on discrimination and classification of the complex is very small, as seen by comparing the data in Table 18 with those in Table 10. The first discriminant function in the three group analysis accounts for an additional 1.3% of the variance and maintains the high correlation to the data. The variables with canonical coefficients exceeding $|1.0|$ are the same in Functions 1 - 4 in Table 10 and those in Table 18. The overall percentage of correct OTU assignments increases from 86.87 to 91.88%, a change entirely due to merging former groups 3 - 4 and 6 - 7.

The scatterplot for this analysis (Figure 34) is very similar to that produced from the seven-group analysis (Figure 25). The separation of S. obtusa and S. crispa (groups 1 and 2 respectively) from S. calycantha and S. borealis (groups 3, 4, and 5) is maintained, appearing more significant than distances between groups 3 through 5. This picture is in good agreement with the results of the cluster analysis (see Figures 9 and 19).

Although not clearly shown by the position of group centroids in the scatterplot (Figure 34), the distance between groups 4 and 5 is slightly shorter than that between 3 and 5, weakly supporting the treatment of 3 and 4 - 5 as species (S. calycantha and S. borealis respectively) and 5 as a subspecies (S. borealis subsp. sitchana) of 4. The most obvious "glitch" on the scatterplot is the group 3 OTU near group 2 points. WCNV1 is a young plant resembling S. calycantha in most respects except its possession of an axillary inflorescence.

8. A speculative view - What if the inflorescence is ignored?

Although not considered in recent taxonomic treatments, S. *crispa* was occasionally treated in the older literature as a variety of S. *borealis* (see description of S. *crispa*). After specimens of both S. *crispa* and S. *calycantha* which had been misidentified were inspected, it was evident that the inflorescence is a convenient character for segregating the two taxa in many situations. I thought it would be interesting to conduct a discriminant analysis in which inflorescence characteristics are ignored. Is the significant separation between S. *obtusa*, S. *crispa*, and the S. *calycantha* - S. *borealis* clusters maintained? If not, what rearrangements are evident? What effect does this have on classification of the OTUs?

The discrimination of the S. *calycantha* complex in the absence of inflorescence features was investigated, the resulting groups including 100 of the 160 OTUs in the data set. Twenty-four variables entered the analysis; the following variables were deleted from the list of 31 variables used in the previous analysis: LEAFTIP (uppermost leaf margin), INFLTYP (inflorescence type), NODEFLW (number of nodes of flowers), and all measurements of leaves above the basal flower (LF2ALN, LFTPLN, LF2AWD, LFTPWD). Four discriminant functions, accounting for 59.44, 21.94, 13.54, and 5.07% of the variation respectively, were used in plotting and classification. Results of this analysis is summarized in Table 19; a scatterplot is shown in Figure 35.

The data from this analysis contribute several important concepts to the classification of the S. *calycantha* complex, seen most clearly when Tables 18 and 19 and Figures 34 and 35 are compared. The first

discriminant function in Table 19 accounts for 26.3% less of the total variance, although the canonical correlation is only 0.0126 lower. A comparison of the lists of discriminant function coefficients in Tables 18 and 19 reveals that, in the absence of inflorescence characteristics, greater importance is assumed by seed surface morphology, sepal characters, and style length; key characters useful in identifying these taxa.

The scatterplot in Figure 35 shows the most significant results. First, the distance between S. *crispa* and S. *calycantha* is significantly reduced from that in Figure 34. Because the distance between the S. *obtusa* cluster and all other groups was maintained, S. *crispa* may be more closely related to S. *calycantha* than suggested by previous analyses. Indeed, as will be illustrated later, several of the character states found in S. *crispa* resemble those found in either S. *calycantha* or S. *borealis* subsp. *sitchana*.

Classification results were surprising - the overall percentage of correct assignments increased by 2.49% when the inflorescence characters were eliminated. Since the assignment of both S. *obtusa* and S. *crispa* OTUs was 100% correct regardless of the inflorescence characters, the increase in correct assignments occurs in the S. *calycantha* and S. *borealis* groups. OTUs now correctly assigned include one S. *calycantha* OTUs, one S. *borealis* subsp. *sitchana* OTU, and two S. *borealis* subsp. *borealis* OTUs.

What effect should these results have on the taxonomy of the complex? If one were to adopt a taxonomic stance akin to that of the Mediterranean school, as described by Bolos and Vigo (1974) and extended by Greuter et al. (1984), S. *calycantha* could be considered an aggregate

species with S. crispa a member of that aggregate. Stellaria crispa would be thought of as distinct from S. calycantha, but by differences not considered sufficient to warrant recognition of the taxa as separate species. In light of the presence of the inflorescence as an easily seen character and the habitat differences between S. crispa and S. calycantha that are not reflected in the data set, I am not in favor of uniting S. crispa and S. calycantha into a single taxon. From experience in Petrorhagia (Rabeler, 1985), I find that the aggregate species concept does not always describe either the morphology or biology of the plants as well as one might wish. In the present case, the trailing habit of S. crispa is a significant feature maintained in culture and, combined with the axillary flowers and sepal and seed characteristics, allows ready recognition of the plants, with only a rare individual causing one to pause before assigning it to S. crispa.

SUGGESTED CLASSIFICATION

The classification of the Stellaria calycantha complex suggested from the factor and cluster analyses is supported by the results of the discriminant analyses. The proposed treatment, illustrated in Figure 44, will be the source of names in subsequent text.

CHROMOSOME NUMBERS

Chromosome counts have been recorded for 50 species of Stellaria (see Appendix D for a listing), or about 25% of the 203 species that are listed in Appendix D. Pogan et al. (1981) summarized Stellaria as including a "series of cytotypes with the basic numbers of 10, 11, 12, 13 and 14." Before reporting $x = 15$ for the first time, Morton (1984a) noted that while " $x = 10, 11, 12$, and 13 have been reported for the genus, ... almost all of the native North American species that have been examined have a base number of 13."

All known chromosome counts for taxa in the Stellaria calycantha complex are presented in Tables 20 and 21, the majority being unpublished counts provided through the courtesy of Dr. John K. Morton. Nearly all cytological work has been performed on North American material, there being but two counts from Europe and one from the Soviet Union. A base number of $x = 13$ can be assumed for the complex, nearly all counts being some multiple of 13.

I have examined voucher specimens for all counts based on North American material listed in Tables 20 and 21 (except for Löve & Löve S3424 from Manitoba which could not be located [not in COLO or MT as indicated in Löve & Löve, 1982] and Chinnappa CC200 and CC1436, these reports discovered too recently to allow an inspection of the vouchers), allowing correct identification and placement within the taxonomy derived from the numerical analyses.

Stellaria obtusa

The six counts for S. obtusa listed in Table 20 suggest that many populations of this species are tetraploids or of higher ploidy levels. At least one population from Alberta, near the northern edge of the species' range, is diploid. Inspection of the vouchers for Morton's counts did not reveal any noticeable morphological differences which could be used to segregate the plants with different ploidy levels from one another.

J. K. Morton (pers. comm.) suggested that all of the numbers thus far reported could be explained through a complicated series of crossing events, requiring the formation of a triploid hybrid ($2x [26] \times 4x [52] = 3x [39]$), the formation of an amphidiploid from the triploid to form a hexaploid ($6x = 78$), and a subsequent backcross of a hexaploid and a tetraploid plant ($6x[78] \times 4x [52] = 5x [65]$). This would require outcrossing and most likely subsequent radiation of the species in the various forms to the present range. Additional counts over the range of S. obtusa are required for confirmation or rejection of this hypothesis.

Stellaria crispa

All counts except one indicate that this species is diploid. The voucher for the $2n = 52$ count reported by Chinnappa (1985) has not been seen; the possibility that it was misidentified cannot be eliminated at this time.

Stellaria calycantha

The seven counts assignable to S. calycantha show this taxon to be diploid. The commonality of the diploid number in S. calycantha and S. crispa is interesting in light of the close positions these taxa assume in the discriminant analysis when the inflorescence characters were eliminated, reflecting possible ancestral ties.

Merging Stellaria simcoei into S. calycantha, rather than with S. calycantha subsp. interior as Hultén (1958) and Hitchcock (in Hitchcock & Cronquist, 1964) suggested, is supported by cytological evidence. Two of the five North American counts representing S. calycantha, Hartman 2926 (RM) and Morton & Venn NA7341 (JKM), were made from plants that would be identified as with Stellaria simcoei if one chose to recognize that taxon.

Stellaria borealis subsp. borealis

This subspecies is tetraploid, all but three counts being either $n = 26$ or $2n = 52$.

The counts listed in Table 21 reveal two important points about the taxonomy and distribution of the subspecies. First, S. borealis is more widely distributed than diploid S. calycantha, being found throughout the North American range of the species. This result would be expected if, as often suggested (Lewis, 1967), polyploidy confers some adaptive ecological advantages. The scant information from European populations indicates that plants in Scandinavia are tetraploids.

Secondly, all populations from eastern North America that have been counted are tetraploid. The presence of tetraploid material from the summit of Mt. Washington, New Hampshire (Löve & Löve 7562, COLO; Morton

s.n., JKM) confirms the placement of these plants with other eastern material rather than with western S. calycantha var. calycantha as suggested by Fernald (1940).

Stellaria borealis subsp. sitchana

All counts of this taxon are tetraploid, confirming the alignment of S. borealis subsp. sitchana with S. borealis suggested by the numerical analyses.

Stellaria borealis × S. longifolia

Each of Morton's counts for this material shows $2n = 39$. The plants are apparently sterile triploids resulting from crosses between diploid S. longifolia and tetraploid S. borealis.

In concluding this section, I think it appropriate to comment on the taxonomy of Stellaria calycantha in light of the cytological evidence presented above.

First, I believe that recognition of diploid and tetraploid populations of plants commonly referred to S. calycantha as separate species (S. calycantha and S. borealis respectively) is warranted. Ecologically, S. calycantha plants are found at high elevations in the south part of the range; they are not often collected from sites where S. borealis has been reported. In areas of co-occurrence (e.g. Jasper National Park, Alberta), collections that I have examined are clearly either S. borealis or S. calycantha; no specimens exhibiting an intermediate morphology suggesting a hybrid derivation have been seen. Cytological evidence suggests that S. calycantha and S. borealis are not

exchanging genes through hybrid formation, the only $2n = 39$ counts being those of S. borealis × S. longifolia hybrids. The statement that genes are never exchanged between S. calycantha and S. borealis might be inappropriate, but from available evidence it appears that they are behaving as independent entities.

Second, I think that evidence from the numerical analyses suggests that the variation recognized within S. borealis should be given a status below that of species. It is clear from trying to segregate S. borealis subspp. borealis and sitchana that genetic interchange is taking place. While most S. borealis subsp. sitchana plants are readily identified, the boundary with subsp. borealis becomes indistinct along the contact zone between the taxa in the Rocky Mountains and in coastal Alaska. Additional discussion of the difficulties encountered in segregating specimens of these taxa is presented in the descriptions of the taxa within the Taxonomic Treatment.

HYBRIDIZATION

The impact of hybridization in the Stellaria calycantha complex is unknown. The only clear examples of hybridization in nature involve crosses between S. borealis and S. longifolia. Several potential hybrids involving taxa within the complex are suggested from morphological features exhibited on several specimens and will be briefly mentioned.

Stellaria borealis × S. longifolia

Norman (1893) was the first to propose hybrid status for these plants, describing them as S. borealis × S. friesiana. He presented a detailed comparison of the characteristics of the hybrids with those of the parental species; a translated summary appears in Figure 36. He noted that the anthers often did not dehisce, remaining unchanged after anthesis, and that pollen was either sparse and imperfectly developed or absent. Norman (1893) reported that while capsules were rarely formed, mature seed was not known. He indicated that the hybrids were found throughout continental arctic Norway.

As Norman's description suggests, these plants resemble a mixing of leaf and stem characteristics of S. borealis with inflorescence and floral features of S. longifolia. The inflorescence is often axillary, a condition common in S. longifolia but rare in S. borealis. J. K. Morton (pers. comm.) has suggested that the hybrids account for most of the anomalies he saw in collections thought to be S. borealis. All

putative hybrid specimens that I have seen were sterile, with little evidence of even the formation of an aborted capsule. Characteristics of the hybrid are maintained in material transplanted to a greenhouse (J.K. Morton, pers. comm.).

J. K. Morton (pers. comm.) suggested that hybrid plants may arise spontaneously, possibly the result of a chance cross-pollination event where the two species coexist. He has seen the hybrid appear in pots containing seeds from vouchered collections of S. borealis and S. longifolia. The plants are vigorous perennials in cultivation just as they appear to be in wild situations where they grow (Morton's observations).

J. K. Morton (pers. comm.) thought that one variable contributing to the morphology of the hybrid may be which species serves as the female parent. Much of the morphological variation among hybrid plants occurs in leaf width and petal length, with some plants more closely resembling S. longifolia (narrower leaves, larger petals) or S. borealis (wider leaves, shorter petals). Studies have not been attempted to establish the validity of this suggestion.

The details related above are similar to those reported by Chinnappa (1985) from his study of the hybrid between tetraploid S. longipes and diploid S. longifolia. He discovered that artificial crosses of these taxa often produced seed that, when germinated, formed vigorous plants showing a combination of characters intermediate between those of the parent plants.

Specimens suggesting hybrids

Stellaria obtusa and S. crispa

From the limited studies of cultured plants, I noted that these species can take on a very similar aspect in cultivation, S. obtusa plants gaining longer internodes and a more viny appearance. Careful inspection of the plants revealed that most other morphological differences between the two species could still be used to clearly assign them to their "proper" species. If a fertile hybrid did form, I would expect the seed to reflect a combination of the very different morphologies of the parental species, just as is seen in Petrorhagia nanteuillii (Rabeler, 1985).

A collection from the Olympic Peninsula, Washington (Jones 8463, WS, WTU) most closely approaches a combination of morphological features that may be present in a hybrid between S. obtusa and S. crispa. In this case, the plants most closely resemble S. crispa, but the leaves bear a few basal cilia similar to those of S. obtusa. A few flowers are present, each having sepals that are acute and ribbed as in S. crispa. The absence of fruit suggests that, if indeed this is a hybrid population, the cross may be sterile. Plants of both species normally bear mature fruit many weeks before the 6 September collection date.

Stellaria obtusa and S. calycantha

A collection from western Montana (Thomas 11244, DS) resembles S. obtusa (annotated as S. obtusa by W. A. Weber in 1982), but several characteristics suggest features normally associated with S. calycantha. The leaves have the shape and short petiole normally found in S. obtusa,

but the thinner and more translucent character of those of S.
calycantha. The sepals are 2 - 3 mm long, acute, and have a wide
scarious margin, while the styles are about 0.75 mm long, which are
features of S. calycantha. Immature capsules were present, suggesting
that the plants were fertile.

PHYTOGEOGRAPHY

The Caryophyllaceae are thought to have arisen in Laurasia (Raven & Axelrod, 1974) about midway through the Tertiary. The oldest pollen remains clearly assignable to the Caryophyllaceae are Oligocene in age (38 to 27 my BP fide Raven & Axelrod, 1974), while the oldest macrofossils are among Pliocene (10 to 2.5 my BP) deposits (Muller, 1970). If Chandler's (1964) assignment of the pollen of Hantsia to the Caryophyllaceae is accepted, the origin would be moved back slightly to the Late Eocene, most of her records being from the Bartonian Age. It seems probable that derivation of the species complexes within the Caryophyllaceae took place in areas comprising modern-day Europe, Asia, and North America.

The map shown in Figure 37, modified from Hultén (1958) and Jalas & Suominen, 1983), illustrates the world range of the Stellaria calycantha complex. If the current ranges of each of the five taxa in the complex were plotted on Figure 37, a pattern of one widespread taxon and four of more limited ranges would appear. The tetraploid S. borealis subsp. borealis (see map in Figure 53) is found throughout the range shown in Figure 37, although it is very rare west of the Rocky Mountains in the United States. The remaining four taxa are not known from eastern North America. Two of these taxa, S. crista (map in Figure 48) and S. borealis subsp. sitchana (map in Figure 55) are common in coastal areas from the Aleutian Islands to California. Stellaria calycantha (map in

Figure 51) inhabits coastal Alaska and higher sites in both the Coast Ranges and the Rocky Mountains. The last taxon, Stellaria obtusa (map in Figure 46), occurs in the Rockies and Coast Ranges but not in Alaska.

A North American origin of the complex is most consistent with the biogeographical events of the past, the location of the diploid S. calycantha, and the fact that virtually all of the differentiation within the complex occurs in the North America taxa. Subsequent limited migrations of S. borealis eastward into Scandinavia and westward into eastern Asia would be required to complete the presently-known distribution of the complex.

One complication that clouds such a discussion is the paucity of reports of Caryophyllaceae in the fossil record in North America. Caryophyllaceae pollen is not often reported in North American palynological studies, being a minor component in the few studies in which I found it mentioned (Spear & Miller, 1976; Heusser, 1978; Watts, 1979). In part this situation reflects the large pollen loads produced by trees vs. the smaller amounts from insect-pollinated herbs; trees often dominate the pollen representation in a core. A similar situation exists with respect to macrofossils, with only a few reports of seed remains having been made (Birks, 1976; Miller & Thompson, 1979; N.G. Miller, pers. comm.). The only factors that I could foresee complicating the preservation and/or identification of other plant parts involves the small size and their sometimes delicate nature. The following discussion is therefore both speculative and tentative.

Pre-Pleistocene Distribution

The presence in Alaska of Stellaria crispa, S. calycantha, and both subspecies of S. borealis recognized in this treatment suggests that the complex could have arisen there, near what Hultén (1937b) would consider the evolutionary center for many northern species, with subsequent dispersal to sites to the east and south. Chinnappa (1985) made a similar suggestion concerning the origin of the Stellaria longipes complex because of the occurrence of all morphotypes and cytotypes of S. longipes in "the north western region of North America."

Hultén (1958) proposed that the present arctic-alpine flora was probably widespread during the relatively mild climate of the Tertiary. If the current distribution of the species is any indication of the range of these taxa prior to the Pleistocene ice advances, it could follow that Stellaria borealis was widely distributed across North America. The extent of the range and the members of the complex actually in existence during the Tertiary is unknown.

The origin of tetraploid Stellaria borealis is a difficult question to answer in a simple manner. We cannot look among past representatives of the taxa since fossil remains are unknown. The degree of morphological similarity between some populations of present day diploid S. calycantha and tetraploid S. borealis subsp. borealis is high, suggesting that an autopolyploid situation may be involved. Mulligan and Porsild (1969) observed that differences between a diploid and its autotetraploid derivative would be mostly quantitative; several of the differences between S. calycantha and S. borealis are quantitative. Mitotic figures of both diploid S. calycantha and

tetraploid Stellaria borealis chromosomes (in Zhukova, 1980) do not reveal any evident differences that would immediately suggest a hybrid origin.

One question often asked in studies involving polyploids is their age. Stebbins (1984) noted that they may range from being very old to very recent in origin, but cautioned on the difficulty in establishing such ages. The cytological and morphological similarity between the tetraploid plants found in Europe and those found in eastern North America could suggest an early derivation of the tetraploid. The most likely time for a North American - European migration would be during the late Tertiary prior to the complete opening of the North Atlantic, when plant migrations could still occur freely (Raven & Axelrod, 1974).

On the other hand, some northern diploid Stellaria calycantha and tetraploid S. borealis plants exhibit a great deal of morphological similarity, evidence that might suggest a more recent origin of the tetraploids from the diploids somewhere in the Northwest. In either case, eastward dispersal of the tetraploids would bring the plants to eastern North America, where dispersal, most likely by chance if a recent origin is accepted, to Europe would have occurred. Knaben (1985) proposed a similar scheme of Alaskan derivation and eastward dispersal for Papaver lapponicum.

The Pleistocene Epoch - where did the Stellaria calycantha complex hide?

Questions regarding where species occupying northern environments were found during the Pleistocene glaciations continue to attract considerable attention. Morphological trends evident in present-day members of the Stellaria calycantha complex suggest that refugia in

unglaciated Alaska and areas south of the ice in both eastern and western North America may have included some elements of the complex as summarized in Figure 38. Gradual dispersal from these areas could have produced the present-day distributions.

a. A Southeastern refuge

Since nearly all of the eastern North American populations of Stellaria borealis occur in areas that were covered with ice during at least one Pleistocene ice advance (see Figure 38), the progenitors of many of these plants most likely were displaced southward.

The map of full-glacial vegetation at 18,000 years BP presented by Delcourt and Delcourt (1979) suggests areas from present day West Virginia southward through Tennessee, a region covered at that time by jack pine-spruce-fir or cool temperate mixed forests potentially similar to forests where Stellaria borealis is currently found, may have served as a refuge. Another possible area would be the lower Mississippi embayment, in light of the spruce-larch assemblage that Delcourt and Delcourt (1979) show for that region.

Since a few populations at the far northern extent of the range of Stellaria borealis subsp. borealis are found in treeless tundra, the possibility of survival closer to the ice mass should be considered. On the basis of pollen data, Watts (1979) suggested tundra, dominated by grasses and ericaceous shrubs similar to that now found in northern Québec, was present in southeastern Pennsylvania during the glacial maximum. A similar condition may have existed elsewhere near the edge of the ice mass; Watts (1983) reported a similar tundra association existed in southern Minnesota.

The occurrence of Stellaria borealis in northeastern West Virginia has been interpreted by Hutton (1962) as indicating an area where the species could have survived during the Pleistocene. Hutton's interpretation could be correct if S. borealis was found among the species of the grass-herb tundra described above since, as Watts (1979) noted, the area would have been covered by tundra vegetation, a spruce-fir forest not appearing there until approximately 12,000 years BP.

Plant migrations following the most recent Wisconsin glacial maximum in eastern North America are thought to have started about 14,000 years BP, probably coinciding with an increase in average annual temperature which Watts (1979) thought allowed northern forest species such as spruce to move north to the ice boundary. Watts' (1979) report of a small amount of Caryophyllaceae pollen in sediments deposited about 13,000 years BP at a glaciated site (Tannersville, PA) suggests that early migrations could have included some northern Caryophyllaceae species such as Stellaria borealis.

Before completing discussion of the eastern region, a few comments will be made concerning the large Stellaria borealis plants found in some areas around the Gulf of St. Lawrence. Fernald (1925) identified these plants as S. borealis var. sitchana (changing this to S. calycantha var. laurentiana in 1940), noting this taxon as one of over 500 species of boreal and western plants with disjunct distributions in the Gulf of St. Lawrence which he thought indicated the likelihood that these plants survived the Pleistocene in situ on unglaciated highlands (or nunataks).

Recent reviews of the subject (Drury, 1966; Morriset, 1971) suggested there are far fewer endemic or disjunct plants in the Gulf of

St. Lawrence region, noting those still recognized as such are limited to calcicolous habitats where, as Morriset (1971) suggested, they may have been relegated by the readvancing forest. Morriset (1971) cited evidence for at least some glaciation in most areas of the Gulf of St. Lawrence, stating that the few areas which may have been exposed were not extensive enough to have housed all of the rich flora of the region, the flora instead migrating to some coastal refugia.

Since these plants are best interpreted as large forms of S. borealis subsp. borealis, I think it is much more likely that they represent populations which are growing in optimal habitats rather than remnants of a distinctive relict population.

b. Western refuges

1. The southern Rocky Mountains

Weber (1965) accepted Hultén's (1958) thoughts on the broad extent of the circumpolar flora, suggesting that much of the present-day high elevation flora was present in the southern Rockies (south of the central Wyoming deserts) prior to the Pleistocene. The species assemblage reflected a series of invasions from the north, bringing a number of species with Asian or Alaskan affinities to the area which most likely occupied a larger area of the western states than their present ranges would suggest. Since this area escaped continental glaciation, it would seem likely that the current flora could represent both a portion of the pre-Pleistocene distributions and a source area for northward expansion after the retreat of the glaciers.

The presence of additional active mountain glaciers in the western states during the Pleistocene probably caused displacement of high

elevation species to lower elevations. Baker (1983) noted that tundra was probably found at middle and upper altitudes along the Rockies from Montana to New Mexico, with the tree-line at least 500 m below present-day elevations.

The most likely candidate for placement in a western refuge within the Rockies is Stellaria obtusa. The current distribution as scattered populations in mountainous areas (see Figure 46) suggests that the species has not dispersed widely from areas it could have inhabited, supporting Baker's (1983) conclusion that post-glacial elevational migrations are more likely than latitudinal floristic migrations in that region.

A similar case can be made for many populations of Stellaria calycantha. The availability of habitat for these high-elevation plants in the western states argues for an earlier dispersal of S. calycantha to the region followed by an assumption of the present range after the Pleistocene.

2. The Pacific Northwest

Heusser (1965) noted that palynological evidence suggested the presence of lush forest growth similar to the present-day forests in lowlands near and south of the Olympic Peninsula. Ice-free areas of the Olympic Peninsula might have taken an appearance similar to that of modern hemlock-spruce forests of coastal Alaska, suggesting this would be an ideal place for some populations of Stellaria crispa and S. borealis subsp. sitchana during glacial times.

The cooling period following the Hypsithermal temperature maximum (10,000 - 7,000 years BP in Washington vide Baker, 1983) may have had a

significant effect on the present distribution of the above species.

Baker (1983) noted that the cooling allowed species common to the Pacific Coast forests to move inland, "reaching northern Idaho in the last few thousand years." A similar migration by populations of chiefly coastal S. crispa and S. borealis subsp. sitchana would be an attractive explanation of their current ranges.

3. California and the southern Coast Range Mountains

Current ranges of the taxa within the Stellaria calycantha complex suggest that some populations of each taxon could have been found in California, although I have no information to suggest they were found in areas significantly beyond their presently known ranges.

4. An Alaskan refuge

The presence of a plant refuge in unglaciated central Alaska is suggested from palynological evidence, but, as noted by Heusser (1965, 1983), its existence prior to Wisconsin glaciation is not firmly established. Ager (1983) noted that such a refugium would have been tundra covered with herbs and a few woody plants; the idea of it serving as a major forest refugium cannot be supported by current evidence. Besides this area, there is some evidence that small refugia may have existed along the Alaska-British Columbia coast, providing local populations for dispersal onto the barren areas after the last ice retreat (Heusser, 1965).

As indicated above in the discussion of pre-Pleistocene distribution, the present-day occurrence of all but one of the taxa within the complex in Alaska makes the concept of an Alaskan refugium an

inviting one. The close alliance of Stellaria crispa populations in Alaska with those to the south as suggested in the minimum spanning tree derived in the cluster analysis could be interpreted in a number of ways: strictly northward radiation from southern refugia, southward radiation from an Alaskan refugium, or some combination of both. As Stebbins (1984) noted, there is no "one way" directionality in these past migrations which would prohibit a multi-directional reinvasion of glaciated areas.

If the current distributions of S. crispa and S. borealis subsp. sitchana are indicative of their pre-Pleistocene ranges, survival in Alaska would be doubtful because of the glaciation of coastal Alaska from the expansion of ice fields in the Alaska and Aleutian Ranges (Hamilton & Thorson, 1983). Evidence of extensive glaciation in the Aleutian Islands presented by Heusser (1978, 1983) would make their survival there also doubtful.

One group of plants which supports dispersal from, if not also a refugium in, Alaska is the tetraploid Stellaria borealis subsp. borealis plants with papillose stems and small flowers which Hultén (1944) described as S. calycantha subsp. interior. These plants are common in Alaska, including interior areas near the postulated refugium, and similar habitats eastward into the Northwest Territories, but do not often occur south of British Columbia. If they survived the Pleistocene in a southern refuge, there should be more plants with similar characters among the populations now extant in southern areas. Dispersal of these plants to the east and subsequent mixing among the eastern plants with larger flowers has led to both the current trend of "papillate plants in the north" among eastern plants and the very slight

differences which now separate them from other S. borealis subsp. borealis plants in the Northwest. Les (1986) suggested a similar reinvasion of the Northwest Territories by Ceratophyllum demersum, in part based on fossil evidence which suggested reinvasion had occurred faster than what would be expected if all populations were derived from refugia far to the south.

Merging of eastern and western populations of Stellaria borealis

Péwé's (1983) projections of glacial boundaries as they might have looked during the most recent glacial maximum (from 22,000 to 15,000 years BP) and after a period of retreat (10,000 years BP) are illustrated in Figure 38. The Cordilleran (western) and Laurentide (eastern) Ice Sheets, which had converged at the glacial maximum, retreated at different rates, creating an ice-free corridor through central Canada between the retreating glaciers (Heusser, 1983). Les (1986) thought that this corridor represented a meeting point for Ceratophyllum demersum populations migrating from eastern and western refugia.

A similar situation may have taken place in Stellaria borealis subsp. borealis. A westward dispersal of propagules from glabrous-stemmed populations (the common condition in plants from eastern North America), combined with an eastward dispersal of papillose-stemmed populations (the common character in western populations) could explain the occurrence of both glabrous-stemmed and papillose-stemmed plants in Saskatchewan and Manitoba.

A look at the Asian distribution

If the Stellaria calycantha complex did originate in North America, the only portion of the current distribution of the complex which has not been discussed is that in far eastern Asia. Based on the locations of these populations, two possible dispersal routes might have been employed; the first across the Bering Strait to Chukotka (the portion of Siberia directly opposite the Seward Peninsula of Alaska), the second from the Aleutian Islands leading to the Kamtchatka Peninsula via the Commander Islands.

The presence of a few populations of Stellaria calycantha in Chukotka suggests that at least one migration event across the Bering Strait occurred, possibly via the Bering Land Bridge sometime between the late Pliocene and middle Pleistocene (Yurtsev, 1972). Although the results of several studies (listed in Yurtsev, 1972) have suggested that the dominant trend of plant and animal migration was from Asia to America, there are a number of North American species with ranges which just barely get into northeastern Asia (Yurtsev, 1972). I would consider Stellaria calycantha a good candidate to add to this list.

The presence of both Stellaria calycantha and, according to Hultén (1937a), S. borealis subsp. sitchana on the Kamchatka Peninsula combined with their presence in the Aleutians makes the route between them suggested by Yurtsev (1972) tempting. Although this route was apparently available well into the Pleistocene, I would suggest that dispersal to Kamtchatka may have taken place before the Pleistocene.

In 1928, Hultén described Stellaria calycantha × fenzlii from Kamchatka, from collections which he later regarded as S. sitchana.

Although I have not been able to examine any of the collections he cited, a photograph appearing in Hultén (1928) suggests that some interaction with Stellaria fenzlii has indeed taken place; the illustrated plants have inflorescence characters resembling S. fenzlii. The Asian populations probably were dispersed subsequently southward via a number of islands to reach northern Japan.

Before leaving the subject of Asian distribution, mention should be made of one species present in the Aleutians which apparently did not reach Asia. Although now found on the outermost of the Aleutian Islands, Stellaria crispa is only known from North America. One might speculate that an expansion into the Aleutians did not occur until late in Pleistocene time after opening of the Bering Sea. The presence of Caryophyllaceae pollen (less than 2% of the sample) in sediments of 4000, 6000, and 10,000 years BP on Adak Island of the Middle Aleutians suggests that reinvasion could have taken place soon after deglaciation and the formation of a sedge-Salix-Empetrum community (Heusser, 1978).

FLORAL MORPHOLOGY

Inflorescence

Two inflorescence types are found in taxa of the Stellaria calycantha complex. The only taxa that consistently have strictly axillary inflorescences are S. obtusa and S. crispa; they are rarely found in S. calycantha or S. borealis plants.

Stellaria borealis vars. bongardiana and isophylla are often described as having axillary flowers, but a close inspection of most specimens of S. calycantha and S. borealis reveals a cymose inflorescence. As noted in the case of the cyme from cultured S. borealis subsp. borealis plant 21-1 depicted in Figure 39, the cymes can be incomplete (missing flowers or bracts at nodes), or disguised by larger leaf-like bracts, but the basic cymose branching form and order of flower opening (numbers in Figure 39) remain unmistakable.

Two other situations can occur which camouflage the basic cyme. In some cases (e.g. Piper 4412, US; and R. T. Ogilvie s.n., UBC), an inflorescence forms and flowers appear at most but not all lower nodes of the inflorescence. In this case, the stem tips, instead of ending in flowers, resume normal leaf production thus simulating the form expected in an axillary inflorescence.

In addition to the terminal inflorescence, an axillary flower or small inflorescence can be present below the terminal inflorescence (e.g. Rabaler 479, MSC; Shacklette 7433, MICH). Even in these cases,

the terminal inflorescence is evident, and certainly an interpretation of these plants as having primarily axillary flowers or inflorescence is tenuous at best.

Variation in inflorescence bracts

Stellaria borealis vars. sitchana and bongardiana are often segregated from each other by differences in inflorescence features: the presence of many flowers subtended by reduced bracts in S. borealis var. sitchana vs. few flowers in axillary groupings with bracts of size similar to the leaves in S. borealis var. bongardiana. Hitchcock (in Hitchcock & Cronquist, 1964) noted that the two varieties intergrade imperceptibly. In specimens that have been identified as these taxa by various workers (including Fernald), the differences appear more temporal and developmental than variation which could reliably segregate taxa. Many of the few-flowered specimens were collected early in the season (as evidenced by both the collection date and the absence of fruit), or represent populations growing in shaded areas.

As noted earlier, Fernald (1914) used the presence of a wide scarious margin on the reduced uppermost inflorescence bracts as a diagnostic character of S. borealis var. floribunda. According to his description, S. borealis var. isophylla plants should have bracts that are entirely herbaceous. Unfortunately, this feature is not as clearcut as Fernald suggested. On several specimens, a narrow white margin was present on the uppermost bracts, one that resembles those of the middle bracts of some plants that eventually produced the tiny mostly-scarious bracts. One collection (Voss 14715, LKHD) exhibited another combination of characters; two plants bearing bracts with entirely herbaceous

margins and one plant which had bracts with the narrow white margins.

Table 22 provides a comparison of the inflorescences of Rabeller 649 (MSC) collected in Ontario, with inflorescences produced in culture at East Lansing, Michigan on plant 21-1 grown from seed from this plant. These data indicate that, at least for one population, plants that normally bear a small number of flowers among leafy bracts have the potential to produce plants with larger many-flowered, small-bracted inflorescences. Besides producing more flowers on most stems, the change in bracts from leaf-like to scarious illustrates plasticity in a character which has been used in previous treatments to segregate varieties.

Flower size vs. inflorescence position

Flower size is not constant within the inflorescence, a trend of size reduction being most clearly seen in plants with a large inflorescence. For example, the lowermost flower is the first to appear in a cyme. It is often borne on the longest petiole, with the petioles subtending upper flowers becoming gradually shorter toward the top of the inflorescence. Thieret 7639 (F) illustrates the diminution very clearly, with flowers and capsules at the apex of the inflorescence considerably smaller than basal ones.

Flowers

The presence of small, inconspicuous flowers unites the taxa in the Stellaria calycantha complex. Data (see Table 23) gathered from the cultured Ontario plants of S. borealis subsp. borealis indicate that the number of floral parts present is variable among different flowers of an

individual plant. Most flowers are pentamerous except in S. obtusa where many flowers are tetramerous.

Calyx

The sepals are very briefly basally fused, with free portions being lanceolate or less frequently ovate-elliptic. The apex is normally acute, less commonly obtuse. A scarious, often whitish margin is present in all taxa in the complex, varying from a very narrow (less than 0.1 mm) obscure band in some specimens of S. obtusa and S. calycantha to a wider band in S. crispa and S. borealis subsp. borealis. Reports of white flowers in predominantly apetalous S. crispa are probably based on the petal-like appearance which the wide scarious margin often produces. Three sepal veins become raised as nerves in most taxa, becoming easily seen either at the base near the fusion point of adjacent sepals or prominent, especially in fruit, over the entire length of the sepal. Sepal length does increase during the maturation of the capsule in all taxa.

Corolla

Petals, when present, are thin, white, deeply bifid to the base with each segment linear-lanceolate to occasionally elliptic in shape, without a claw, and with a blunt or rounded apex. The only petals exceeding the length of the calyx were found in cultured material, with herbarium and field collections bearing petals from at most equal to less than one-fourth the length of the calyx. Petal number is variable (see Table 23), with all combinations between 0 and 5 (including fractions) possible. The corolla is persistent after anthesis, with

petals visible in flowers bearing mature capsules.

Androecium

Two whorls of stamens are present, the outer opposite the sepals, the inner opposite the petals. Stamen number equals either twice the number of sepals or fewer if abortion occurs. Nectaries are present at the base of the outer stamens. Most stamen abortion occurs among inner stamens; Warming (1921) noted that 1 - 3 stamens were often aborted. Stamens are bent outward or are erect in an open flower, and are normally shorter than the sepals. Unless the plant has been attacked by anther smut, Ustilago violacea (see text below), the anthers often become detached from the filaments after anthesis. Anther color is variable in live material, with yellow, pink, and red often reported; dried anthers are tan in color. The pollen grains are white and spherical, those for Stellaria borealis noted by Nilsson & Praglowski (1963) as being 30 - 40 μ in diameter with fewer than 15 pores.

Styles

The number of styles is variable; most often 3 - 5 are present. Style length is less variable than number, most styles being either short and curved outward or longer and initially erect, spreading outward at maturity. Styles are papillate from base to apex.

Fruit

The fruit is a dehiscent, globose to ovoid capsule up to two times the length of the calyx. The number of capsule valves is usually recorded as equalling twice the number of styles, with most capsules

composed of six valves. Many cases where two styles were attached to the same capsule segment were seen, suggesting that the relationship between style number and capsule segment number is not absolute. The capsule is initially green, later becoming either translucent, light tan, or commonly dark red or black. Kaden and Kirpicznikov (1965) define this fruit type as a "*Cerastiocarpium trimerum disjunctive dorsicidum*".

Seed

Seeds of species of the *Stellaria calycantha* complex are elliptic to obovate with the hilum prominent or more often within a shallow or pronounced marginal notch. Surfaces are either smooth, indistinctly roughened, rugulose, or reticulate-furrowed, with base colors being either slightly lustrous red-brown or brown, or a dull gray-black (terminology adapted from Berggren, 1981).

Effects of anther smut, *Ustilago violacea*

Smut fungi, which produce a violet-colored spore mass within the enlarged anthers of a flower, are known to attack many members of the Caryophyllaceae as shown by lists compiled by Zundel (1953) and Lindeberg (1959). *Ustilago violacea* (Pers.) Roussel [or, if the apparent biological difference between those infecting species of Caryophyllaceae subfamily Alsinoideae and those on species of subfamily Silenoideae is recognized, var. *stellariae* (Sowerby) Savile] has been reported from Europe on 10 species of *Stellaria*, including *S. borealis*, *S. longifolia*, and *S. borealis* × *S. longifolia*.

Several collections of *S. borealis* subsp. *borealis* included both

smut-infected and smut-free plants, illustrating the effects of anther smut on normal growth. While the leaves of some infected plants are slightly smaller, the most evident differences are found in the flowers. The flowers are often slightly smaller than those of uninfected plants, a condition also reported in smut-infected Dianthus (Spencer & White, 1951). The anthers are often nearly twice the size of uninfected anthers, dark red in color, and persistent even in the oldest flowers on the plant. Spores are often found on other flower parts, giving the flowers a reddish cast visible on recently collected herbarium specimens. While not totally suppressed as in Dianthus (Spencer & White, 1951), gynoecial development is interrupted. The styles are often shorter than those present in non-infected plants and all infected plants examined were devoid of capsules.

SEED MORPHOLOGY

Seed morphology is a particularly useful character in delimiting taxa in the Caryophyllaceae. Morton (1972) illustrated differences in seed size and surface features useful in distinguishing Stellaria media and S. pallida (Dumort.) Piré. Crow (1979) found seed morphology a key feature in determining species relationships in Sagina. Wofford (1981) surveyed the seed morphology of 13 species of Arenaria in the southeastern United States and was able to distinguish all but two pairs of closely related species on seed testa characters.

I became aware of the diagnostic power of seed morphology during my study of Petrorhagia (Rabeler, 1985). For example, seed testa patterns illustrated the intermediate position of Petrorhagia nanteuillii (Burnat) P. Ball & Heyw., a tetraploid species presumably derived from an "old" cross between P. prolifera (L.) P. Ball & Heyw. and P. velutina (Guss.) P. Ball & Heyw.; the seed had the reticulate pattern and shape of P. prolifera while exhibiting a papillate nature similar to seeds of P. velutina.

A seed from each of the taxa recognized in this treatment of the Stellaria calycantha complex is illustrated in Figure 40. Three basic variations in testa morphology were noted, as shown in the key in Figure 41.

Figure 40 illustrates that the seeds of S. obtusa (Figure 40a) are very different from other members of the complex. These seeds are

transversely elliptic, being wider than tall while most seeds of other taxa are elliptic along an axis parallel to (or through) the hilum. The hilar area often protrudes instead of being recessed in a marginal notch. Epidermal cells have angled rather than sinuate margins, adjoining margins forming small furrows between the mostly flat cells. Very little variation was noted in different samples of S. obtusa seeds.

A comparison of S. obtusa seeds with those from the 14 species of Stellaria illustrated in Berggren (1981) show S. obtusa seeds to be very different from other species of Stellaria in regard to basic shape, protruding hilum, and relatively flat epidermal cells. Such differences reinforce the separation between S. obtusa and the other members of the S. calycantha complex but also could suggest that the relationship between S. obtusa and other members of the genus may be less certain than other morphological characteristics indicate.

Before the remaining members of the complex are discussed, Wyatt's (1984) study of seed variation in Arenaria uniflora (Walter) Muhlenb. will be considered. As he noted, many studies illustrating seed surfaces focus on the "typical" distinctive pattern which is then used to clearly delimit taxa. After noting significant variation in the seed testa, he suggested that "a cautious approach does seem warranted" when using seed surface features to segregate taxa.

Wyatt's suggestion should be kept in mind when interpreting seed data from the Stellaria calycantha complex. Although the seeds illustrated in Figure 40 are "typical" of those found most commonly in S. crispa and S. calycantha, some variation (see below) is present which prevents clear taxon segregation on seed testa characters.

The only previous photographs and detailed description of S.

calycantha seeds appear in Berggren (1981). Since her work is based on Scandinavian material, her description pertains to S. borealis subsp. borealis. Berggren (1981) noted a great deal of similarity between S. borealis and S. longifolia, seeds of both being henna brown in color with a smooth or "very finely dimpled or rugulose" surface where the central portion of the epidermal cells is raised slightly to form the wrinkled appearance. Most seeds of S. borealis subsp. borealis (Figure 40b) fit this description, being essentially smooth or with a very indistinctly roughened surface as viewed at 30X.

Seeds from S. calycantha (Figure 40d) are very similar to those of S. borealis subsp. borealis (Figure 40b), the illustrations here emphasizing a difference in surface roughness and epidermal cell separation which is often indistinct. These taxa cannot be differentiated on the basis of seed testa features.

The seeds of S. borealis subsp. sitchana (Figure 40e) are usually clearly roughened. These seeds often have a deeper marginal notch and are slightly taller and narrower than those of the other taxa in the complex. Epidermal cells appear to be randomly arranged except along the margin where a clear pattern of concentric rows becomes apparent. Stellaria crispa seeds (Figure 40c) are very similar, the epidermal cells being slightly lower and seed dimensions more closely approaching those of S. calycantha.

The proposed taxonomy of the complex is partially reflected in seed testa patterns. Stellaria obtusa is set off from the remaining taxa, a separation which will be seen in the numerical analyses; the seed serves as a clear marker of this species in cases where other vegetative aspects have led to a mistaken identification as S. crispa. Stellaria

crispa seeds are usually more rugulose than those of S. calycantha, but overall similarity reflects the close relationship illustrated when inflorescence characteristics are ignored. The presence of a smooth surface in S. calycantha, S. borealis, and S. longifolia suggests a close relationship between the two species, a notion supported by the existence of hybrid individuals of S. borealis × S. longifolia as noted in Europe (Norman, 1893), Asia (Hultén, 1928), and most recently in North America by Morton (1984b).

Seed testa morphology is not in accord with the classification proposed here in the case of two taxa. The rugulose seeds of both S. borealis subsp. sitchana and S. crispa suggest a close heritage. This is reflected in the discriminant analyses most clearly when inflorescence characters are eliminated, where characters such as sepal nerve length are then selected as discriminating characters.

Typical seed morphology favors Hultén's (1937a) recognition of S. sitchana as a species distinct from S. borealis subsp. borealis. Most collections determined as S. borealis subsp. sitchana have strongly wrinkled seeds, but occasional specimens (e.g. Christ 11190, NY) have seeds that have a much smoother surface similar to that of many populations of S. borealis subsp. borealis.

The reverse situation also occurs among some populations assignable to S. borealis subsp. borealis, indicating that the separation between S. borealis subsp. borealis and sitchana is not complete. Several populations from northwestern Canada and the western United States resemble other populations of S. borealis subsp. borealis except for distinctly rugulose seeds very similar to those of S. borealis subsp. sitchana.

POLLINATION BIOLOGY

Pax and Hoffmann (1934) defined a general form of floral presentation for members of the Alsinoideae (including Stellaria) in the following manner. The flowers are often small, with white petals and are usually open wide. Floral odor and nectar may or may not be present. The flowers would be accessible to both long- and short-tongued insects, with bees and flies being the most common visitors. Reduction trends evident in some genera lead to apetalous flowers, selfing, and cleistogamy.

Knuth (1908) presented information on the pollination biology of 14 species of Stellaria. Most species had either protandrous or homogamous flowers, and were described as being self-pollinated during late anthesis "as a last resource" (Knuth, 1908). Mention of smaller female flowers distributed gynodioeciously (or less often monodioeciously) was included for 10 species, suggesting it may be a common occurrence among members of the genus.

Among Knuth's accounts are two of particular interest. First, he included information on S. friesiana var. alpestris which, by my interpretation, would refer to the hybrid S. borealis × S. longifolia. Lindman noted that plants in Norway were either protogynous and became homogamous through long-persisting stigmas or were protandrous. In both cases, contact of the anthers and stigmas in late anthesis resulted in "automatic self-pollination" (Knuth, 1908).

Secondly, Knuth (1908) summarized the findings of Lindman and Warming (discussed below under Warming, 1921) from study of Stellaria borealis in Norway and Greenland. Lindman reported that the plants at Dovrefjeld (Norway) had homogamous flowers which could be self-pollinated when "anthers of the longer stamens come into contact with the stigmas" late in anthesis (Knuth, 1908).

Warming's (1921) review of the floral biology of Arctic species of the Caryophyllaceae included comments on S. borealis specimens from Greenland, Norway, and Russia. Most flowers were apetalous, homogamous, and self-pollinated via "long styles which curve backwards and are thrust among the stamens" (Warming, 1921).

Warming (1921) reported gynodioecy in S. borealis specimens from northwestern Russia, consisting of female flowers with smaller petals (if present), partially (or mostly) abortive stamens and stigmatic papillae which might be slightly larger than in hermaphroditic flowers. Although noting that gynodioecism was found in several arctic species, he suggested that, in light of the reduced number of pollinators in arctic areas, production of female flowers was a disadvantage, possibly a reflection of poor plant health. I could not confirm the occurrence of gynodioecism in North American populations.

One of the purposes for culturing populations of taxa of the Stellaria calycantha complex was to gather information on floral biology. Only four of the nine taxa of Stellaria cultured flowered: S. media, S. alsine, S. obtusa, and four populations of S. borealis subsp. borealis. Stellaria graminea, S. longifolia, S. calycantha, and S. crispa did not flower and only a single flower was produced by one plant of S. borealis subsp. sitchana. Since they were all grown in similar

conditions (see Appendix C) and two of the species that did not flower (*S. graminea* and *S. longifolia*) grow in the East Lansing area, bringing *Stellaria* into flower in culture was more difficult than expected. Given this situation, the information I can present is necessarily limited.

The general pollination strategy which I propose for *Stellaria borealis* subsp. *borealis* and *S. obtusa* involves presentation of open flowers with small but potentially attractive (if petals are present) displays. Self pollination can take place if no insects visit the flowers. A similar process probably occurs in both *S. calycantha* and *S. crispa*, but experimental confirmation is lacking. The primarily apetalous flowers in the latter taxon may indicate a greater reliance on self-pollination, although the slightly more prominent scarious sepal margin may play a small role as a pollinator attractant.

I could not determine if any relationship exists between flowers that bear petals and success in cross pollination of *S. borealis* subsp. *borealis*, although it seems logical that flowers with petals would be more attractive to potential pollinators. Martin (1979) thought that petalled plants that he studied in northern Michigan were attracting insects. Small drops of nectar were noted in both petalous and apetalous flowers of cultured plants from Ontario, suggesting that some reward is present for the occasional insect visitor. Stamens appeared before the styles had completely elongated, suggesting that at least some flowers could be protandrous.

The presence of small white cocoons attached to the summit of capsules on plants from Manitoulin Island, Ontario (Morton NA9308 [JKM]), the Gaspé Peninsula, Québec (Morton NA4059 [JKM]; Rabeler 637 MSC),

Waldo Co., Maine (C. H. Knowlton s.n. in 1940 [NEBC]), and Rutland Co., Vermont (W. W. Eggleston s.n. in 1893 [CU, F, MICH, MIN, NY]) offer evidence of insect visitation to S. borealis subsp. borealis, most likely a microlepidopteran (J. K. Morton, pers. comm.) in this case.

Floral Duration

Stellaria borealis subsp. borealis

I was able to follow the daily progression of flowering on two cultured plants of S. borealis subsp. borealis from Ontario from 18 April to 5 June (25 - 29 May excepted) 1984. Each inflorescence that appeared was sketched in order to determine both the order of flowering and to identify individual flowers for determining the number of floral parts and time of opening and closing. An example of the inflorescence diagram is shown in Figure 39, with duration of flowering summarized in Table 24.

The data on floral duration in Table 24 support the concept of the basic pollination process proposed above. Most of the flowers remained open for one to four days with no diurnal opening and closing cycle as seen in some Caryophyllaceae (e.g. Dianthus armeria L., Petrorhagia prolifera, where one flower per inflorescence opens in the morning and closes in the evening - personal observations). This situation is reminiscent of that described by Philipp (1975) for S. longipes where flowers remained open for 4 - 12 days. As noted by Knuth (1908), styles and stamens are not proximal in the early open flower, but stamens and styles did establish contact near the end of the flowering period.

A trend toward an increase in the number of flowers open in a given

inflorescence as the day length increased was observed, until the number of flowers decreased with the completion of flowering; a condition expected of the determinate cyme.

The longer mean duration for stem 1 of plant 21-1 may have been environmentally induced, with a combination of both increasing day length and increased daytime temperature resulting in later flowers being open a shorter time. All but three of the 24 flowers opening between 18 April and 18 May were open at least four days, while only two of the 12 flowers (for which complete data are available) opening after that date were open longer than three days. Since none of the other shoots began flowering before 15 May at the earliest, the "longer duration flowers" did not appear in these data.

The results in Table 24 must be interpreted with caution because flowering took place at a time when most plants in a native setting would not be in flower. Given the normal mid-late summer flowering of these plants in Ontario, the flowering of S. borealis subsp. borealis in May and June in East Lansing, Michigan, shows that these plants are day neutral; day length would be decreasing from the maximum at the summer solstice (22 June).

One factor which might be a more likely measure is total heat accumulation, which would be increasing in mid-late summer as the combination of continental warming and continued long exposures of solar radiation on the atmosphere brings warmer temperatures to more northerly areas of the continent (Daubenmire, 1974; J. R. Harman, pers. comm.). MacDonald et al. (1984) reported that temperature had a greater influence on growth of Stellaria longipes than photoperiod. In their studies, S. longipes plants required a minimum of three long, warm days

before stem elongation was initiated, while a minimum of "50 days of winter cold" appeared to be necessary for a plant to flower. The "off-season" flowering observed in cultured S. borealis subsp. borealis and S. obtusa suggests these plants may behave in a similar manner.

Stellaria obtusa

One of the Stellaria obtusa plants flowered briefly in March of 1985, indicating that this species is also day neutral. The absence of both petals and significant scarious sepal margins makes the flower very inconspicuous against the green stems. Data on the duration of each of the 12 flowers are not available.

Evidence for self-pollination

Stellaria borealis subsp. borealis

Confirmation of self-pollination comes both from Martin's (1979) study of wild material and my observations of cultivated plants.

Martin (1979) tested both insect and self-pollination strategies by emasculating some flowers (forcing cross pollination) and sealing another set of flowers in plastic bags (forcing self-pollination). Normal capsules and seeds were produced by both groups of flowers.

After noting the high number of capsules being formed from flowers on the cultured Ontario plants, I suspected self-pollination was being carried out. The plants were grown in a room where very few flying insects were seen (methods given in Appendix C). Neither the occasional housefly nor the varying concentrations of adult thrips were ever seen visiting an open flower. Crawling mites were noted, but given their size and habits, the chances of them effecting a pollination are very

remote.

Selfing was confirmed by enclosing a portion of the inflorescence of stem 1, plant 21-2 in plastic. Flowers which were still in bud at the time of bagging opened normally and produced seed which both looked normal and could be germinated.

Stellaria obtusa

The 12 flowers on plant 23 were produced while the entire plant was enclosed in plastic. Since there were no insects inside the bag, self pollination must have occurred, producing seed which both looked normal and could be germinated. This indicated that self pollination was successful in a species with significantly shorter styles than those found in S. borealis subsp. borealis.

Seed production

To get an indication of the number of ovules produced and seeds formed in a capsule, individual closed capsules were collected from cultured plants. Each capsule was dissected in a petri dish with all seeds and fragments attached to cellophane tape to simplify counting the immature and mature seeds contained in a capsule. These data, summarized in Table 25, are limited to those taxa where flowering material was available.

Inspection of the capsules revealed that seeds were of two distinct sizes. Seeds near the summit of the capsule were similar in size, color, and surface features to mature seeds of the species (see Figure 40). The remaining seeds were light brown in color, much smaller (approximately 0.3 x 0.3 mm), and mostly near the base of the capsule,

suggesting that maturation of seeds proceeds basipetally.

If all of the seeds counted in a capsule matured, between 20 and 35 seeds could be expected in the average S. borealis capsule, 20 - 25 in S. obtusa. The data also reveal that in most cases there is more variation in the proportion of immature/mature seeds in a capsule than in the total number of seeds. This situation reflects the presence of flowers of different ages, an expected occurrence in plants producing multiple flowers in inflorescences where not all flowers are open simultaneously. Given that the greatest observed ratio between mature seeds and total seeds in a capsule was 52% (from S. obtusa count of 12/23), these data also suggest that actual seed production is significantly lower than the potential numbers noted above. Inspection of other specimens confirmed this observation, with only a few capsules (these mostly the larger capsules of S. borealis subsp. sitchana) containing even 20 seeds.

Two factors may explain the reduced seed production. First, given the numerous variables involved in pollination and subsequent fertilization, I assume that the chances of every egg being fertilized are rather slim. Second, the physical size of the capsule may be a limiting factor, the total number of mature seeds in some way limited by the space available in the capsule. This is apparent in S. obtusa where the capsule walls are thinner and are often seen to be distorted by the expanding seeds. The combination in many specimens of S. borealis subsp. sitchana of a longer capsule and seeds that appear to be slightly narrower and longer (see Figure 40e) may illustrate one process which could increase the number of seeds, especially in light of the larger number of mature seeds seen in the capsules on these plants.

DISPERSAL

Literature on dispersal of Stellaria is limited, most references focusing on the ubiquitous Stellaria media. Since some of the dispersal modes known for S. media may apply to members of the S. calycantha complex, a brief summary of these methods seems appropriate.

Anemochory, or wind dispersal, is important in S. media. The ripe, often erect, capsules separate into six segments allowing wind movement to knock seeds out of the capsules (Sobey, 1981). In commenting on how S. media could have gotten to Surtsey Island (Iceland), Berg (1983) downplayed this method, noting that S. media did not have any specialized dispersal mechanisms and was for all practical purposes "a short-distance dispersal plant in the extreme."

Berg (1983) instead suggested that endozoochory, in the Surtsey case most likely via birds, may be a regular dispersal mechanism in S. media. Sobey (1981) listed four grazing animals and four birds in which fecal samples had included viable S. media seeds. McRill (1974) found evidence that earthworms had ingested and subsequently excreted S. media seeds, suggesting that earthworm casts may be an important site for seedling establishment at short distances from the parent plant.

Ridley (1930) reported several other methods for dispersal of S. media including harvesting by ants and dispersal by adhesion (via mud) to boots and animal feet. Stellaria media has also been reported as a contaminant in commercial seed mixtures (Ridley, 1930). Ridley (1930)

also reported that Borza and Bujoreau were able to germinate S. media seeds after they had been submerged in water from the Black Sea for 90 days (Ridley, 1930).

Seed Dispersal in the Stellaria calycantha complex

I concur with Martin (1979) that dispersal via wind is at best a short-range phenomenon for most populations of Stellaria borealis. It may be a possibility for plants growing in open, exposed areas (such as roadsides in extreme northwestern Canada), but certainly not for populations of S. calycantha or S. borealis growing in shaded, swampy areas where there is very little wind or for S. crispa plants growing prostrate on the forest floor. The downward pointing capsules found in many S. borealis subsp. sitchana plants would not favor wind dispersal.

Endozoochory could be a possibility, but likely of less importance than in S. media, since none of the taxa in the S. calycantha complex are plants of fields and pastures where either birds or most grazing animals are likely to ingest the seeds. Martin (1979) suggested that an animal eating S. borealis would eat both seeds and capsules; he noted many empty capsules on the plants he studied in northern Michigan. I have not seen evidence of mass grazing on S. calycantha or S. borealis plants.

Reindeer may play a small role in dispersal of S. borealis. Ridley (1930) noted that Ekstam and Hart found that reindeer exhibit a preference for S. longifolia, suggesting this as contributing to dispersal of the species. Heinitz listed S. alpestris among species which have been found in fecal samples (Ridley, 1930). Given that Heinitz' work took place in Scandinavia and the application by some of

the name S. alpestris to S. borealis, I suspect that he may have been referring to S. borealis. This idea could apply in North America since caribou do occur in some areas where S. borealis is found (compare maps of Alaska in Palmer [1922] and Palmer [1926] with Figures 13 and 53). I hasten to add that a more likely candidate for such dispersal is S. longipes. This species is more likely to be found in tundra situations than is either S. borealis or S. calycantha and is cited in several studies of reindeer and caribou nutrition (e.g. Thing, 1980) as a forage species.

The contribution that ants and earthworms might make is unknown, but S. crispa capsules might make a tempting target for ant harvesting since they often lie on or near the forest floor.

Dispersal by adhesion may be an important dispersal mechanism, especially via mud adhering to animals frequenting wet areas. Wind dispersal might account for a few instances, but as noted above, some taxa appear to be poorly suited for taking advantage of that system. Once a seed capsule is ripe, seeds can always be dropped near the parent plant, promoting survival of the extant colony, but not dispersing the colony. Since many S. calycantha and S. borealis populations are found in wet areas, seeds lodged in mud subsequently attached to an animal could be transported over long distances and, if deposited at a favorable site, start a new population. J. K. Morton (pers. comm.) has suggested adhesion on the feet of birds as a likely means for species to reach islands.

The occurrence of the majority of populations of the taxa in the S. calycantha complex in habitats near, and sometimes in, water courses suggested to Martin (1979) an obvious route of dispersal - streams and

rivers. One prerequisite in such a scheme would be the ability of Stellaria propagules to float for at least short distances.

Van der Pijl (1982) noted that most floating seeds are in some way unwettable, floating with the assistance of the surface tension of the water; breaking surface tension often causes seeds to sink. Factors such as chemical consistency of the seed testa, presence of bristles, or pits which could trap air help some seeds float.

A discussion of such a possibility with Dr. J. K. Morton led to a simple experiment patterned after one he performed with seeds from the flora of Manitoulin Island. Four seeds of eight taxa of Stellaria were placed in bottles of water obtained from a local pond; each bottle was agitated twice daily to periodically disturb the surface tension that often caused the seeds to cluster together at (or near) the surface. The results, summarized in Table 26, indicate that all but one of the taxa did float for varying lengths of time, all seeds eventually sinking.

The results indicate that the length of time that a Stellaria seed can float is not simply determined by seed size. While the largest seeds in the group (S. graminea) did sink first, the next two sets of seeds to sink were those of S. media (large seeds) and S. alsine (smallest seeds of the eight taxa).

Seed surface pattern may have an effect on seed flotation. Hauptli et al. (1978) and Clark and Jernstedt (1978) noted that tuberculate seeds and nutlets float longer than relatively smooth seeds since air could be trapped among the tubercles. Hauptli et al. (1978) found that species of Limnathes occurring in wet areas indeed had tuberculate nutlets while those of drier areas had smooth nutlets. Wyatt (1984)

found the reverse situation in Arenaria uniflora, where rough seeds were found among populations from the driest sites.

In the present experiment, seeds with the smoothest surfaces (S. borealis, S. calycantha, and S. longifolia) had the largest average values for seed flotation, followed closely by S. obtusa with reticulate - furrowed, but not strongly tuberculate, seeds. The three species which sank first each have seeds with prominent surface projections, suggesting that at least among the species of Stellaria tested, a tuberculate seed surface is not an advantage in prolonging flotation.

The comparison of seed surface roughness to species habitat preference does not produce a clear correlation. Of the four species with the roughest seeds, two are weedy and can frequent relatively dry sites (S. media and S. graminea), one is found in moist, shaded areas (S. crispa), and one in wet sites (S. alsine). The species with smooth seeds (S. borealis, S. calycantha, and S. longifolia) are most prevalent in moist or wet situations.

Van der Pijl (1982) noted that floating seeds should sink if surface tension is broken, a situation I did not find entirely applicable to Stellaria seeds. Unless a seed sank, seeds often clustered together at the surface or floated just under the surface of the water. Continued flotation after repeated agitation suggests that dispersal of most taxa via water would not be restricted to very quiet pools, but could occur in small streams.

Although the length of time shown may be exaggerated over that occurring in a natural environment, the fact remains that floating propagules could be a viable dispersal route for these plants. The germination potential of the seeds tested is not known, but given my

experience with germinating similar seeds in petri plates, I suspect that such dispersal would not adversely affect most seeds.

Vegetative Propagation

Since all taxa in the Stellaria calycantha complex are perennials, the total reliance on production of an overwintering propagule, which is a necessity for an annual species, is absent; energy channeled to flower and seed production can be channeled to vegetative propagation.

Warming (1921) reported the formation of "pale, very slender subterranean runners - shoots bearing 'scale leaves' in S. borealis, placing the species along with six other species of Stellaria in what he called "The Cerastium arvense type" of vegetative propagation. He considered these stems arising from basal nodes to be true subterranean structures rather than ones that accidentally became buried by debris.

Plants arising from such runners were observed in some of the cultured plants of S. borealis subsp. borealis, but not in either S. crispa or S. obtusa. These were seen most clearly as small plants that arose during the first year of growth some distance from the single plant originally inserted in a pot. Damage to the main portion of the plant (cutting after severe insect injury) stimulated growth of these smaller plants, suggesting activity similar to axillary buds when a terminal apex is damaged.

Ankei (1982) conducted a study of the reproductive biology of seven species of Stellaria in Japan. He noted that one method of dispersal, formation of creeping stems, was rare in S. media and S. neglecta, but common in the others tested. These stems rooted at the nodes (except, as he noted, during the flowering period) and subsequently became

separate plants (ramets).

The formation of creeping stems in taxa of the Stellaria calycantha complex was easily demonstrated in culture. Creeping stems formed at the bases of many plants. In one case, such a stem of a plant of S. borealis subsp. borealis became several decimeters in length. Most of these stems remained above the soil, curving upward if an obstruction to horizontal travel was encountered; only rarely did they point downward into the soil. Nodal roots formed on erect and creeping stems of plants of each taxon subjected to very humid conditions. Placing cuttings in water produced similar root production from stem nodes.

Nodal rooting from above-ground stems was occasionally noted on specimens of S. crispa and S. obtusa collected late in the growing season. Plants of these taxa often have flowers at lower nodes (formed early in the season) of stems which continue to elongate during the remainder of the season. This suggests a strategy of producing seeds near the present plant and then sending stems outward. The increased axillary stem growth exhibited by plants possessing nodal roots would support a strategy of active vegetative propagation.

TAXONOMIC TREATMENT

SPECIMENS EXAMINED

Many of the data for this study were gathered from over 5000 herbarium specimens representing North American collections from the following 63 herbaria [all symbols for herbaria cited follow Holmgren et al. (1981) with the exception of JKM (personal herbarium of Dr. John K. Morton) and the two national park collections listed]: A, ALA, ALTA, BH, BUF, CAN, CAS, CM, COLO, CORD, CRATER LAKE, CS, CU, DAO, DS, DUL, DWC, F, GFND, GH, ISC, JEPS, JKM, LE, LKHD, LIV, MARY, MCTF, MICH, MIN, MO, MSC, MT, MTMG, MT RAINIER, NA, ND, NDG, NEBC, NFLD, NY, NYS, ORE, OSC, PAC, PENN, PH, RM, S, TRH, UBC, UC, UMBS, UPS, US, UTC, VT, WILLU, WIS, WS, WTU, WUD, WVA. A subset was selected from these collections for use in numerical analyses; see Appendix B for a list of specimens used for that study. Measurements cited are based primarily on the specimens used in the numerical study; a millimeter rule and an ocular micrometer calibrated in millimeters at 10X magnification were used. Field observation and collection of Stellaria were concentrated in western North America (1980) and in eastern North America (1981). Ninety-eight voucher specimens documenting this work are deposited at MSC.

Abbreviations for authors are taken from Meikle (1980), periodicals from Botanico-Periodico-Huntianum (Lawrence et al., 1968), and major works from Stafleu and Cowan (1976, 1979, 1981, 1983, 1985) where possible, with additional abbreviations from Tutin et al. (1976, 1980).

Conventions used in Specimen Citations

The following abbreviations appear within specimen citations. The use of periods conforms with rules in the CBE Style Manual, 4th edition (CBE Style Manual Committee, 1978). Capitalization of abbreviations reflects usage in the specimen citations.

Bor.	- Borough	Mtn	- Mountain
ca	- circa	Mtns	- Mountains
CG	- Campground	Nat.	- National
Co.	- County	Prov.	- Provincial
Dist.	- District	RS	- Ranger Station
Exped.	- Expedition	Rd.	- Road
Fl.	- Flora	Sta.	- Station
ft	- foot	St.	- Street
HQ	- Headquarters	St. Park	- State Park
hwy	- highway	T#R#S#	- Township, Range, Section (Public Land Survey)
jct.	- junction	Terr.	- Territory, Territories
km	- kilometer	Twp	- Township
m	- meter	vic.	- vicinity
mi	- mile		
Mt	- Mount		

Locality information in the specimen citations has been paraphrased, with latitude and longitude information provided by the collector given where state/provincial subdivisions are not known. Variations in label text of duplicates specimens of the same collection and information added to clarify localities are placed in brackets.

The initials of the collectors (where known) appear in citations of unnumbered collections.

The number of duplicates of collections awaiting distribution from MSC is indicated by a number following the herbarium abbreviation.

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1754. pro parte. Alsine L. emend. A. Löve & D. Löve, Preslia 46: 128. 1974. Lectotype: A. media L. (fide: Britton in Britton & A. Brown, Ill. Fl. N. U.S. ed. 2. 2: 41. 1913. & Sprague, Bull. Misc. Inform. 1920: 316. 1920.).

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Pursh, Fl. Amer. Sept. 1: 319. 1814. orth. var. Micropetalum
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Type: not designated.

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St. Hil. emend. Godron, Observ. Alsin. 17. 1842. Type: L. aquatica
(Pollich) A. St. Hil., non C. aquaticum L.

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sect. Alsinae et Stellariae verae.

Leucostemma Benth. in Wallich, Cat. n. 642. 1828, nomen.; Benth. ex
Don, Gen. Hist. 1: 449. 1831. Type: not designated.

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non Alsinella Moench, Methodus 222. 1794.

non Alsinella Sw., Summa Veg. Scand. 17. 1814.

non Alsinella Gray, Nat. Arr. Brit. Pl. 2: 655. 1821.

non Alsinella Hornem. Nomencl. Fl. Danic. 33. 1827.

Adenonema Bunge., Mém. Acad. Imp. Sci. St.-Petersbourg Divers Savans.

2: 548. 1835. & Verz. Altai Pfl. 36. 1836. Type: A. petraeum Bunge.

Schizotechium (Fenzl) Reichb., Deut. Bot. Herb.-Buch. 205. 1841. Type:

Stellaria crispata Wallich ex Don.

Stellaria L. emend Godron, Observ. Alsin. 20. 1842, excl. S.

pentagyna Gaudin. Type: not designated.

Hylebia (Koch) Fourr., Ann. Soc. Linn. Lyon. ser. 2. 16: 347. 1868.

Type: H. nemorum (L.) Fourr.

Alsine subg. Stellaria (L.) E. H. Krause in Sturm, Deutschl. Fl. ed.

2. 5: 51. 1901.

Tytthostemma Nevski, Trudy Bot. Inst. Akad. Nauk SSSR, Ser. 1, Fl.

Sist. Vyss. Rast. 4: 305. 1937. Type: T. alsinoides (Boiss. & Buhse) Nevski.

Mesostemma Vved., Bot. Mater. Gerb. Bot. Inst. Uzbekistansk. Fil.

Akad. Nauk SSSR. 3: 4. 1941. Type: M. karatavica (Schischkin)

Vved., non S. kotschyana Fenzl (Rechinger, 1981).

Generic names excluded from Stellaria

Alsinella Sw., Summa Veg. Scand. 17. 1814.

Stated in Jackson (1893-1895) and Rechinger (1979) as Stellaria

p.p. Swartz (1814) indicated Alsinella as equal to "Alsine Wahl.

Fl. Lapp.;" Alsinella thus was published as a replacement genus.

All species are now referred to Arenaria sensu lato.

Ballarion Raf., Amer. Monthly Mag. & Crit. Rev. 1: 442. 1817. nomen;

Amer. Monthly Mag. & Crit. Rev. 2: 266. 1818. Type: Spergulastrum

lanuginosum Michaux. Rather than being referred to Stellaria (Jackson, 1893-1895; Merrill, 1949), Ballarion belongs in synonymy under Arenaria subg. Leiosperma.

Dichodon (Bartling ex. Reichb.) Reichb., Nom. 205. 1841. Type: D. dubium (Bast.) Ikonn. Provencheria J. Boivin, Naturaliste Canad. 93: 644. 1966. nomen superfl. Type: P. cerastoides (L.) J. Boivin.

Myosoton Moench, Methodus 225. 1794. Myosanthus Desv., J. Bot. Agric. 3: 227. 1816. Malachia Fries, Fl. Hall. 77. 1818. Larbrea Ser. in DC., Prodr. 1: 395. 1824, non Larbrea A. St. Hil. (1816), non Larbraea A. St. Hil. ex Dumort. (1827), non Larbrea A. St. Hil. emend. Godron (1842). Malachium Fries ex Reichb., Fl. Germ. Excurs. 795. 1832. orth. var. Malacion St. Lager, Ann. Soc. Bot. Lyon 8: 183. 1881. orth. var. Type: M. aquaticum (L.) Moench - from Cerastium aquaticum L. Stellaria L. emend. Godron, Observ. Alsin. 20. 1842. pro parte. Stellaria pentagyna Gaudin.

Pseudostellaria Pax in Engl. & Prantl, Nat. Pflanzenfam. ed. 2. 16c: 318. 1934. Krascheninikovia Turcz. ex Besser, Flora 17: 1, Beibl. 9. 1834. nomen. orth. var. Krascheninnikowia Turcz., Bull. Soc. Imp. Naturalistes Moscou 11: 89. 1838. nomen. Krascheninikovia Turcz. ex Fenzl in Endl., Gen. Pl. 968. 1840. orth. var.; corrected, Art. 73. (Schaeftlein, 1957). Krascheninnikowia Turcz., Bull. Soc. Imp. Naturalistes Moscou 15: 609. 1842; Fenzl in Ledeb. Fl. Ross. 1: 373. 1842. Krascheninikowia Turcz. ex Fenzl in Endl., Gen. Pl. Suppl. 4(3): 56. 1850. orth. var. Krascheninikowia Turcz. ex Fenzl emend. Maxim., Prim. Fl. Amur. 57. 1859. orth. var. Krascheninnikowia Turcz. ex Fenzl emend. Korsh., Izv. Imp. Acad. Nauk, ser. 5, 9: 38. 1898. Alsine sect. Krascheninikovia? (Turcz.)

Kuntze in T. Post & Kuntze, Lex. Gen. Phan. 20. 1903.

Krascheninnikowa Turcz. ex T. Post & Kuntze, Lex. Gen. Phan. 310.

1903. orth. var. Type: P. rupestris (Turcz.) Pax, fide: Mizushima,
Bull. Bot. Surv. India 7: 66. 1965.

non Krascheninnikovia Gueldenst., Novi Comment. Acad. Sci. Imp.
Petrop. 16: 551. 1772.

non Krascheninikova Cothen., Disp. Veg. Meth. 5. 1790. orth. var.

non Kranikofa Raf., Princ. Fond. Somiol. 30. 1814., nomen., orth.
var.

non Kraschennikofia Raf., Princ. Fond. Somiol. 30. 1814., nomen.,
orth. var.

non Krascheninikofia Raf., Fl. Tellur. 1: 86. 1837 ("1836").,
nomen., orth. var.

non Kranikovia Raf., Fl. Tellur. 1: 86. 1837 ("1836")., nomen.,
orth. var.

non Kraschenikofia Raf., Fl. Tellur. 1: 92. 1837 ("1836").,
nomen., orth. var.

non Krasnikovia Raf., Fl. Tellur. 1: 92. 1837 ("1836"). orth.
var.

non Kraschnikovia Turcz. ex Ledeb., Fl. Ross. 3: 402. 1849.

non Krascheninnikowa Gueldenst. ex T. Post & Kuntze, Lex. Gen.
Phan. 310. 1903. orth. var.

non Krascheninnikowa Ledeb. ex T. Post & Kuntze, Lex. Gen. Phan.
310. 1903. orth. var.

Low annual or perennial herbs, rarely xerophytic. Stems erect or
trailing, internodes angled or not, glabrous, pilose, or scabrous.

Leaves simple, opposite, blades ovate, elliptic, cordate, lance-linear, or linear; blades usually glabrous, very rarely with sharp points, ventral midrib rarely pilose; margin glabrous to ciliate or papillate; sessile, bases often clasping or abutting the stem, forming a short sheath, or truncate, cordate, to attenuate with a distinct $\pm$ winged petiole; exstipulate. Flowers on slender pedicels, either solitary and axillary or in bracteate, often lax, terminal or axillary cymes; bracts either resembling lower leaves in size and texture or much smaller in size and mostly scarious. Flowers perfect, subhypogynous or perigynous, 5(4)-merous; sepals 5(4), free or briefly basally connate, often glabrous, margin often scarious; petals 5 (or fewer), white, deeply 2-cleft, without claw, often longer than sepals, sometimes wanting; stamens 10(8) in two whorls or fewer (to 1 - 3); ovary superior, unilocular, styles 3, seldom 2 or 4 - 5(6, rarely 7), free; ovules many, seldom reduced to 2 - 6; Capsule ovoid or oblong to globose, longer than or equalling the calyx, opening by 6, seldom 4 or 8 - 10(12, rarely 14?) valves. Seeds (1)-few to many, brown or red-brown (rarely gray-black), globose to elliptic in outline, surface papillate or rugulose, less commonly smooth, (0.5)0.6 - 1.6 mm long x 0.5 - 2.7 mm wide (Berggren, 1981). Pollen spheroidal, polyantoporate, 30 - 40(60) μ in diameter, pores often 10 - 15(20) (Nilsson & Praglowski, 1963), surface verrucate to spinulose (Candau, 1978). X = 10-13, 15, most species X = 13.

Type: Stellaria holostea L., fide Green (in Hitchcock & Green, Nom. Prop. Brit. Bot. 155. 1929.).

After describing the subfamilies Alsinoideae and Silenoideae, Cullen (in Heywood, 1978) summarized a major problem in the

Caryophyllaceae with the following statement: "both of these subfamilies are well distinguished and easily recognized, though the recognition of genera within them is taxonomically difficult and controversial." A close inspection of the nomenclature surrounding Stellaria reveals it to be no exception to Cullen's comment. Myosoton Moench, Dichodon (Bartling in Reichb.) Reichb., and Pseudostellaria Pax have sometimes been associated with (or included in) Stellaria since they include plants that in some way resemble Stellaria, but current evidence suggests they should be recognized as separate entities. On the other hand, Tytthostemma Nevski and Mesostemma Vved. (including Leucostemma Benth. ex Don), although typically treated as small sections seemingly peripheral in Stellaria, are not considered to "have a better home." I will treat names in these two categories separately.

Genera excluded from Stellaria

1. Myosoton

Myosoton was published by Moench (1794) based on Cerastium aquaticum L. This plant has been difficult to place since the ovate-lanceolate leaves and bifid petals resemble S. nemorum (Bentham, 1862) or a large S. media while the presence of 5 styles (like Cerastium, but alternate rather than opposite the sepals), and an ovate capsule with 5 bifid valves (unlike Cerastium, approaching Stellaria) combine to make it a recognizable entity (Rabeler et al., in press). Since that time, Myosoton has been retained as a distinct genus (Myosoton, Myosanthus Desv., Larbrea Ser. ex DC. (non A. St. Hil.), Malachium Fries ex Reichb.) or sometimes placed within Stellaria. Pax (1889) was the last

to include Myosoton in Stellaria on the basis of capsule shape, treating it as subg. Myosoton Pax, using the presence of 5 styles to separate subg. Myosoton from the remaining species of Stellaria. The combination of morphological features noted above and a base chromosome number of $x = 14$ ($2n = 28$, all counts except one [$n = 10$; Moore, 1973]; Goldblatt, 1985; Moore, 1977) not found in Cerastium and reported only once in Stellaria ($n = 14$ in S. vestita; Goldblatt, 1981) argue for continued separation.

ii. Dichodon

Dichodon (Bartling ex Reichb.) Reichb. is a generic name still used occasionally for nine species (*fide* Ikonnikov, 1973 & 1976) which are also intermediate between Cerastium and Stellaria, in that they resemble Cerastium plants in habit (Mertens & Koch, 1831), but possess 3 (rarely to 5) styles and a 6- (rarely to 10) toothed capsule (Ikonnikov, 1976), the teeth being flat rather than revolute (Jalas et al., in Tutin et al., 1964).

Dichodon was first recognized as an unranked portion of Stellaria by Mertens and Koch (1831) and later noted as a Stellaria sect. Dichodon (Bartling ex. Reichb.) Koch, being defined by Koch (1837) as having a capsule dehiscing by apical teeth and an elongated column, uniting these plants with Stellaria on the common number of styles. Fenzl (in Endlicher, 1840) transferred Dichodon to Cerastium, starting the current trend of recognizing these plants as species of Dichodon (or the superfluous Provencheria J. Boivin [1966]) or Cerastium, Dichodon being treated as Cerastium subg. Dichodon (Bartling ex Reichb.) Fenzl or Cerastium sect. Dichodon (Bartling ex Reichb.) Boiss. Chromosome

information supports both separation from Stellaria and recognition at some level in or near Cerastium. Löve and Löve (1975) list $x = 19$ as the base number for Dichodon (all counts they list from three species are $2n = 38$), a number foreign to Stellaria, but more consistent with Cerastium, in which several species have been reported as $2n = 36$ (Goldblatt, 1985). The report of Shildneck and Jones (1986) of $n = 18$ for Cerastium dubium (Bast.) Guépin (= D. dubium (Bast.) Ikonn.) suggests that inclusion of Dichodon within Cerastium may be appropriate.

iii. Pseudostellaria

Pseudostellaria Pax was first described as a genus, later combined with Stellaria, and now is accepted by most at the generic level. The first name given these plants, Krascheninnikowia Turcz. ex Fenzl (name appearing in 1834 [Besser, 1834], description in 1840 [Fenzl in Endlicher, 1840], orthographic correction by Schaeftlein [1957]) is a later homonym of Krascheninnikovia Gueldenst., a genus in the Chenopodiaceae described in 1772 (Farr et al., 1979). The usage of the later homonym continued for nearly 100 years until Pax (in Pax & Hoffmann, 1934) published Pseudostellaria, allowing the production of several more orthographic variants to add to the collection already formed (six from the pen of Rafinesque alone in his works on correction of spelling!) from Gueldenstaedt's earlier name. Schaeftlein (1957) noted that Russian botanists proposed conservation of Krascheninnikowia against Pseudostellaria at the 1954 Paris Congress, a proposal that was rejected.

Pseudostellaria as originally described (Fenzl in Endlicher, 1840) contained one Russian species which resembled S. nemorum, but had

emarginate (resembling Arenaria rather than Stellaria) petals, and roots bearing small globose tubers, the latter character mentioned outside of the formal description. Maximowicz (1859) emended Krascheninnikowia, noting that the two species that he had examined had dimorphic flowers; large male flowers near the apex of the plant and small bisexual flowers near the base; neither of Fenzl's characters appeared in his description. Bentham (1862) thought that basing a genus on dimorphic flowers, while the first report he was aware of in the Caryophyllaceae, was unwise since that characteristic "has been ascertained to exist in so many different Polypetalous orders, and to be so frequently not even of specific value." Instead, he treated it as a section of Stellaria. Regel (1862) accepted Krascheninnikowia in its original sense for K. rupestris, but thought Maximowicz' K. sylvatica was better treated as a Stellaria, forming subg. Pawlowskya Regel defined on the basis of dimorphic flowers. Pax (1889) was uncertain what fate Krascheninnikowia should have, treating it just after Stellaria, but not integrating it into the Stellaria treatment.

Recent work has indicated that Pseudostellaria can be defined by a combination of characters (including those given above) as a genus distinct from both Stellaria and Arenaria, with spinule- or glochid-tipped seed tubercles being a useful and unique character (Mizushima, 1965c). In addition, several Stellaria species, mostly from subsect. Insignes (Fenzl) Pax & K. Hoffm., have been found to belong to Pseudostellaria, including one of the common western "Stellaris", P. jamesiana (Torrey) W. A. Weber & R. L. Hartman (Weber & Hartman, 1979).

Generic names synonymous with Stellaria

Tyttthostemma and Mesostemma (including Leucostemma) include xerophytic species growing in eastern and central Asia which have traditionally been associated with Stellaria, but have recently been split away by some workers of the region.

The monotypic genus Tyttthostemma Nevski includes S. alsinoides Boiss. & Buhse, a plant placed in Stellaria sect. Pseudalsine by Boissier (1867). Nevski (1937) defined Tyttthostemma and segregated it from Leucostemma Benth. (now placed in either Stellaria or Mesostemma [see below]) by having 4 perigynous (rather than hypogynous) stamens, a six- (rather than many-) ovuled ovary, and briefly bifid petals.

Vvedensky (in Botschantzev & Vvedensky, 1941) included two pentamerous species of Stellaria which have two styles and four-valved capsules in the genus Mesostemma. He segregated Mesostemma from Leucostemma Benth. ex Don by the presence of two styles and from Tyttthostemma by a pentamerous calyx and corolla. His distinction from Leucostemma is incorrect on two accounts. First, Don (1831) clearly indicated "styles 2" in the description of Leucostemma. The second point is more obscure since it involves an inaccuracy in the original description. In his commentary on the Caryophyllaceae, Bentham (1862) noted that Leucostemma was "a genus I originally proposed for two Himalayan species with tetramerous flowers." Don (1831) is the first work to include a description of Leucostemma based on "Benth. mss. in Lin. soc. Herb." but stated "Calyx 5-leaved. Petals 5", certainly not the intent of Bentham from his later comments! Fenzl (in Endlicher, 1840) treated Leucostemma as Bentham intended, citing a later source

(plate 21 in Royle's Illustrations of the Botany of the Himalayan Mountains, published in 1834 fide Stafleu & Cowan, 1983) from which he apparently got his information.

Ikonnikov (1976) expanded Mesostemma, incorporating Stellaria sect. Leucostemma as a section. This meant that the genus, united on possession of two styles and four-valved capsules, now had one pentamerous section (Vvedensky's original two species) and one tetramerous section (species from Leucostemma).

Apparently in ignorance of Ikonnikov's work, Rechinger (1981) "updated" the description of Mesostemma. Several aspects of his treatment complicate the use of Mesostemma. First, he indicated the type of the genus as being different from the one listed as "Typus generis" by Vvedensky (in Botschantzev & Vvedensky, 1941), a violation of the International Code (see Voss et al., 1983; Guide for the determination of types, T.1). He listed Leucostemma in synonymy, but his description does not allow for any tetramerous species! The primary distinctions between Mesostemma and Stellaria emphasize the xerophytic habit, two styles, four-valved capsule bearing one (or few) ovules that result in one (or a few) seeds.

Kozhevnikov (1983) discussed the various treatments of these plants in his review of Stellaria in Central Asia. He preferred to keep Mesostemma, Leucostemma, and Tytthostemma within Stellaria, downplaying the merosity differences in noting that the relationship between Leucostemma and sect. Adenonema (Bunge) Turcz. may be closer than otherwise reported. In describing two new species with two styles and four-valved capsules, he noted a clear affinity to S. arenaria Maxim., a five-merous species with three styles, suggesting that one of these

species, S. maximowiczii Kozhevnik., may be a link between sects.

Leucostemma and Adenonema.

While it might be convenient to sweep all of the bistylous members out of Stellaria, it cannot be done with the above-mentioned genera as presently defined. The most recent definition of Mesostemma does not account for some of the variation that should be included if one is to believe the cited synonymy; Kozhevnikov's (1983) ideas suggest that Ikonnikov's (1976) concept of Mesostemma may be faulty. Since these genera are being defined on some of the same characters that are shown to vary within Stellaria (e.g. hypogynous vs. perigynous stamen insertion) and sometimes within the same species (4 vs. 5-merous condition in S. obtusa and S. calycantha), I think that it is most appropriate to retain them in Stellaria until better evidence for segregation is provided.

Stellaria: distribution, size, and infrageneric treatment

Stellaria is often described as a genus whose members are primarily found in cooler areas of northern and southern temperate areas with some species at higher elevations of the tropics (Baker & Burger, 1983). Several of the species, most notably Stellaria media (L.) Villars, are cosmopolitan weeds. Some species are known from arctic and alpine areas, e.g. S. decumbens Edgew. found at elevations over 6100 m in the Himalayas (Polunin & Stainton, 1984). A few central Asian species have adopted a xerophytic habit; see Ikonnikov (1976) and Kozhevnikov (1983) for reviews of these species.

Most sources cite Stellaria as including about 100 species (Kozhevnikov, 1983), with estimates ranging from 75 (Marie-Victorin,

1964) to 120 (Willis, 1973). I think all of these sources underestimate the number of species of Stellaria. After compiling a list of Stellaria species from an exhaustive search of many floras and recent treatments of the genus and attempting to eliminate synonyms and the ever-present differences between treatments, I still can account for 202 names (and one species said to be undescribed in southern Australia [Cunningham et al. 1981]). A list of species names of Stellaria is presented in Appendix D along with the primary sources consulted.

Several factors may be contributing to this increased size estimate. Older estimates would not account for species that have been described recently. I am aware of 14 new species described since 1971 (all but three from Asia; two additional Asian taxa were recently raised to the species level). Differences in how several species complexes within Stellaria (e.g. S. media, S. longipes) should be treated adds (or subtracts) several names to the list in Appendix D, depending on how much of the variation is recognized at the species level. The inclusion of the genera Mesostemma and Tytthostemma adds 10 species but all have been described previously in Stellaria.

A related area in which there is a great deal of confusion involves the infrageneric treatment of Stellaria. Although a complete review of the problem is not appropriate for presentation here, a few comments about the state of such a classification do seem timely.

The most recent treatment of Stellaria which could be considered worldwide in scope is that of Pax and Hoffmann (1934), in which they present a scheme based on the work of Fenzl (in Endlicher, 1836-1840) augmented by sections described by Bentham (1862) and Boissier (1867). Several attempts have been made to refine this scheme, but most of the

proposed changes cannot be accepted because of nomenclatural problems. Schischkin (in Komarov & Shishkin, 1936) and Popov (1957) both presented more detailed schemes involving species in the U.S.S.R., but most of their series names are invalid since they are accompanied by Russian (rather than Latin) descriptions. Ke's (1985) treatment of 44 species of Stellaria in China is also accompanied by infrageneric taxa. But, as in the Russian works, nomenclatural problems seem to be the rule rather than the exception; sect. "apetalum" lacks a designated type, two of Schischkin's invalid series names are used, and several series names, which, from the numbering of the series, should be present, are not mentioned in the text. Mizushima (in Hara, 1966) and Morton (1984a) both cite problems in placing species within the extant sectional classification, suggesting the need for a complete assessment of the characters being used to define the various groups.

Recent work in Stellaria

Recent investigations involving species of Stellaria have focused on floristics and studies aimed at assessing relations within species complexes.

Floristic work has been concentrated in central Asia where workers including Ikonnikov (1976), Kozhevnikov (1983), and Rechinger (1981, 1985) have described new species and subspecies as additional material has become available. Ke's (1985) recent work on Stellaria of China, although including a faulty sectional treatment, gives us a look at how Chinese taxonomists have been dealing with Stellaria. Recent works by Moore (1983), Pedersen (1983), and Volponi (1983) have added to our knowledge of Stellaria in southern South America.

Breeding, cytological, electrophoretic, and numeric studies have been employed in recent efforts to resolve the taxonomy of four species complexes within Stellaria. The Stellaria media complex has received most of the attention, in part due to the cosmopolitan distribution and often weedy habit of S. media sensu stricto. The only published studies I am aware of that discuss the use of electrophoresis (Verkleij et al., 1980), flavonoids (Scholte, 1978), and numerical taxonomy (Whitehead & Sinha, 1967) on species of Stellaria involve members of the S. media complex. Gadella and Kliphuis have studied the cytology of the S. graminea L. complex as it occurs in the Netherlands, a paper by Gadella (1977) summarizing many of their findings. Chinnappa and Morton have investigated the S. longipes complex from a biosystematic standpoint, concentrating on phenotypic plasticity, crossing experiments, and cytological investigations. Their work is contained in several papers, but especially Chinnappa and Morton (1984). Dr. Chinnappa has expanded these investigations of S. longipes, recent studies including an investigation of the influence of temperature and photoperiod on stem elongation (MacDonald et al., 1984), interspecific hybridization (Chinnappa, 1985), and electrophoresis of seed proteins (Gifford & Chinnappa, 1986).

The Stellaria calycantha complex is the fourth species group. Dr. J. K. Morton has been interested in this complex for a number of years (pers. comm.), concentrating his efforts, as in the S. longipes complex, on cytological aspects of the species. Except for an abstract (Morton, 1984b), his results are still unpublished, with chromosome information appearing in this treatment graciously provided by Dr. Morton.

KEY TO SPECIES OF THE STELLARIA CALYCANTHA COMPLEX .
INCLUDING OTHER SPECIES FREQUENTLY CONFUSED WITH THEM

- 1 Leaves broadly ovate, ovate, triangular ovate, or elliptic, margins various, but not papillate; petals shorter than sepals or absent
- 2 Flowers axillary and solitary, mostly apetalous
 - 3 Sepals obtuse, nerves obscure; capsules globose; seeds grayish black, finely reticulate-furrowed S. obtusa
 - 3 Sepals acute, prominently nerved; capsules ovoid; seeds brown, rugulose S. crispa
- 2 Flowers borne in a distinct cyme (herbaceous bracts may disguise it), or flowers rarely few and seemingly axillary; flowers with or without petals
 - 4 Flowers subtended by tiny scarious bracts
 - 5 Flowers borne in an umbel-like terminal cyme S. umbellata
 - 5 Cyme axillary, not umbel-like S. alsine
 - 4 Flowers subtended by herbaceous bracts
 - 6 Stems glandular-pubescent; capsules included within the calyx S. littoralis
 - 6 Stems glabrous or pilose, pubescence not glandular; capsules normally extending beyond calyx
 - 7 Seeds tuberculate, mostly over 0.9 mm long; stems pubescent in lines, lower leaves mostly petiolate S. media

- 7 Seeds smooth or with some rounded tubercles, mostly under
0.9 mm long; capsule walls darkened; stem pubescence (if
present) not in lines, lower leaves rarely petiolate

..... S. calycantha

- 1 Leaves oblong, lanceolate, lance-linear, or linear, margins various

- 8 Petals longer than the sepals, occasionally just barely so

- 9 Bracts subtending nearly all flowers small, scarious (at most
with a green midrib).

- 10 Plants often shining and glaucous; leaves mostly stiff and
erect, keeled below

..... S. longipes

- 10 Plants not shining; leaves not stiff or keeled

- 11 Cymes mostly axillary; leaves linear to lance-linear; leaf
margins very finely papillate roughened (use at least 15x
lens), not basally ciliate; seeds smooth or minutely
roughened

- 12 Leaves linear; all flowers subtended by scarious
bracts; petals longer than sepals

..... S. longifolia

- 12 Leaves linear to lance-linear, basal flower (and
occasionally others) subtended by herbaceous bracts;
petals shorter than to longer than the sepals; capsules
rarely formed

..... S. borealis

× S. longifolia

- 11 Cymes terminal; leaves lanceolate to narrowly elliptic; leaf
margins not roughened, sometimes ciliate at base; seeds
distinctly wrinkled.

..... S. graminea

- 9 Bracts subtending the flowers herbaceous (uppermost bracts sometimes scarious) and/or flowers solitary.
- 13 Plants mostly glabrous, often shining and glaucous; leaves acute, mostly stiff and erect, keeled below
- S. longipes
- 13 Plants glabrous but not shining; leaves acute to more often obtuse, not stiffened or keeled
- S. crassifolia
- 8 Petals shorter than or at most equal to the sepals, or absent
- 14 All flowers subtended by tiny scarious bracts; leaf margins smooth
- 15 Flowers borne in an umbel-like terminal cyme
- S. umbellata
- 15 Cyme axillary, not umbel-like
- S. alsine
- 14 Bracts subtending the flowers herbaceous (uppermost bracts sometimes scarious) and/or flowers solitary; leaf margins often ciliate or papillate
- 16 Cymes terminal; leaves above the basal flower gradually reduced in size; scarious bracts (if present) only among uppermost flowers
- S. borealis
- 16 Cymes axillary; leaves above the basal flower sharply reduced in size; most upper flowers subtended by small scarious bracts; capsules rarely formed
- S. borealis
- × S. longifolia

KEY TO TAXA OF THE STELLARIA CALYCANTHA COMPLEX.

- 1 Sepals obtuse, nerves obscure (center nerve sometimes evident near base); capsule globose, walls not darkened; seeds grayish black, finely reticulate-furrowed; flowers strictly axillary

..... 1. S. obtusa

- 1 Sepals acute, very rarely obtuse, nerves evident; capsule globose or ovoid, translucent or darkened; seeds brown, smooth to distinctly rugulose; flowers axillary, or more commonly in terminal cymes

- 2 Flowers axillary (terminal branching may rarely simulate a cyme), often borne near the base of trailing stems; sepal nerves becoming evident ridges extending to the herbaceous apex; plant glabrous; leaves ovate or elliptic; styles 3, very rarely 4; seeds rugulose, especially along edges

..... 2. S. crispa

- 2 Flowers borne in a distinct cyme (herbaceous bracts may disguise it), or rarely few and seemingly axillary; sepal nerves evident in lower half of sepals, less often extending to the herbaceous apex; plant glabrous or more often with leaf margins pubescent and/or papillate and stems glabrous or papillate; leaves ovate or more often lanceolate to lance-linear; styles often 4 - 5; seeds often appearing smooth or indistinctly roughened, less frequently tuberculate

- 3 Cymes terminal, very rarely axillary; leaves above the basal flower gradually reduced in size; scarious bracts (if present) only among uppermost flowers; petals, if present, shorter than or at most equal to the sepals; leaves ovate to lance-linear

- 4 Leaves ovate, ovate-lanceolate, to elliptic, mostly 2.5 cm or less long; styles 0.4 - 0.9(1.2) mm, mostly curved; sepals at

anthesis mostly shorter than 2.5 mm; capsule globose to globose-ovoid; stems glabrous or pubescent above, never papillate

..... 3. S. calycantha

- 4 Leaves mostly lanceolate to lance-linear or oblong, occasionally ovate-lanceolate, to 6 cm long; styles usually 0.9 - 2 mm long, erect, later spreading; sepals at anthesis to 4 mm long; capsule ovoid; stems glabrous or papillate above, rarely pubescent

..... 4. S. borealis

- 5 Fruiting pedicels usually erect, sometimes arching, seldom reflexed; upper stems glabrous or less frequently papillate; sepals at anthesis to 3 mm long, in fruit rarely longer than 3.3 mm long, less than one-half the length of mature capsule; nerves usually evident in lower half of sepals; closed capsule rarely longer than 4.5 cm, open capsule rarely longer than 5.1 cm (then stems only rarely papillate); seeds smooth or indistinctly rugulose

..... 4a. S. borealis subsp. borealis

- 5 Fruiting pedicels sharply reflexed, sometimes arching, rarely erect; stems papillate, rarely glabrous; sepals at anthesis longer than 2.8 mm long, in fruit rarely shorter than 3.1 mm long, mostly longer than one-half the length of mature capsule; nerves usually evident nearly to tip of sepals; closed capsule rarely shorter than 3.7 cm, open capsule normally longer than 5.1 cm; seeds usually rugulose

..... 4b. S. borealis subsp. sitchana

3 Cymes axillary; bracts above the basal flower sharply smaller, scarious; petals shorter than to longer than the sepals; leaves linear to lance-linear; capsules rarely formed

..... 5. S. borealis ×

S. longifolia

COMPARISON OF PROPOSED TAXONOMY TO RECENT TREATMENTS

The treatments of Stellaria calycantha appearing in recent floristic manuals are often based in part on one of two classification schemes; that of Fernald (1940) or the treatment used by Hitchcock (in Hitchcock & Cronquist, 1964) supplemented by Scoggan (1978). The taxonomy proposed here is compared to these systems in Figures 43 and 44.

The recognition of both S. calycantha and S. borealis revives a concept most recently used in North America by Rydberg (1917). Such a separation reflects the biological differences between these taxa presented earlier that have been obscured by almost all keys and treatments of the complex since Fernald's (1914) revision of S. borealis.

Fernald (1940) recognized seven varieties of Stellaria calycantha. As shown in Figure 43, several of the varieties which he recognized are placed in synonymy within either S. borealis or S. calycantha in the present classification. Fernald's (1940) concept of S. calycantha var. calycantha included western plants accepted here as S. calycantha and eastern plants that have the floral, capsule, and cytological characters associated with S. calycantha subsp. borealis as described in the preceding key. Stellaria calycantha var. simcoei represents a pubescent

form of S. calycantha; the variability of pubescence in S. calycantha noted in this study (see text on the Discriminant Analysis of this species) and in other members of the Caryophyllaceae (see Rabeler, 1985) suggests that varietal recognition is inappropriate. Phenotypic variation in inflorescence development makes the distinction between Fernald's S. calycantha vars. isophylla and floribunda and vars. sitchana and bongardiana indistinct in many cases, while growth on a favorable substrate explains the larger nature of plants which Fernald (1940) would place in S. calycantha var. laurentiana.

The classification presented by Hitchcock (in Hitchcock & Cronquist, 1964) diverges more from the proposed treatment than does Fernald (1940) and is less desirable for a number of reasons. Scoggan's (1978) inclusion of S. calycantha var. latifolia within his S. calycantha var. calycantha is incorrect. Although the ovate leaves of S. calycantha var. latifolia suggest those of S. calycantha, all other characteristics place it in S. borealis subsp. borealis; see Figure 19 for placement of OTU SBAB3, an isotype of S. calycantha var. latifolia. Although the recognition of S. calycantha vars. bongardiana and sitchana by Hitchcock (in Hitchcock & Cronquist, 1964) and Scoggan (1978) in part parallels the inflorescence conditions as described by Fernald (1940), their inclusion of S. calycantha vars. floribunda, isophylla, and laurentiana in S. calycantha var. bongardiana is incorrect. This alignment places three taxa referable to S. borealis subsp. borealis into a taxon referable to the larger western S. borealis subsp. sitchana. Their placement of S. calycantha var. floribunda (reduced scarious bracts) within S. calycantha var. bongardiana, a taxon they described as having herbaceous bracts which are only slightly reduced,

is particularly inappropriate!

Hitchcock's definition and synonymy of Stellaria simcoe forms an unnatural taxon for small, pubescent plants. As shown in the numerical analyses, recognition of Stellaria simcoe is not acceptable since the segregation of this taxon from S. calycantha is based entirely on pubescence features. While plants which Hultén (1944) would have included in his S. calycantha subsp. interior can sometimes have small ovate leaves, the presence of a papillate stem, longer styles, ovoid capsule, and a tetraploid chromosome complement emphasize the non-equivalence of Hultén's S. calycantha subsp. interior and S. calycantha as treated here. Stellaria washingtoniana is S. obtusa with a pilose stem; seed characteristics confirm such an alignment.

•

1. Stellaria obtusa Engelm., Bot. Gaz. (Crawfordsville) 7: 5. 1882.

Alsine obtusa (Engelm.) Rose, Contr. U.S. Natl. Herb. 3: 569. 1896.

TYPE: USA. COLORADO. Gunnison Co.: Anthracite Creek, 1881,

T. S. Brandeggee s.n. (neotype, here designated, UC!; isoneotypes, GH!, NY!).

Stellaria washingtoniana Robinson, Bot. Gaz. (Crawfordsville) 25:

166, pl. 13, fig 4. 1898. Alsine washingtoniana (Robinson) A. A.

Heller, Cat. N. Amer. Pl. ed. 2. 4. 1900. TYPE: USA.

WASHINGTON. Pierce Co.: Alder woods, upper valley of the

Nesqually, 18 June 1895, Q. D. Allen 157 (holotype, GH!;

isotypes, CAN!, CS!, DS!, F [1!+Photo!], GH!, MIN!, MO!, MSC!,

NY!, RM!, UC[2!], US[2!], VT!, WS!).

Alsine viridula Piper, Contr. U.S. Natl. Herb. 16: 207. 1913. pro

parte excl. isotypes examined except NY. Stellaria viridula

(Piper) H. St. John, Prelim. List Pl. Kaniksu Natl. Forest 1: 6.

1925. pro parte. TYPE: USA. IDAHO. Kootenai Co.: Springy

places in cañ[ny]ons, ridges south from Wiessner's Peak, 1700 m,

28 July 1895, J. B. Leiberg 1396 (holotype, US!; isotypes, DS!,

F!, GH!, MO!, NY!, ORE!, RM!, UC!). PARATYPE: USA. WASHINGTON.

Walla Walla Co.: Along streams [GH] (rivulets[WS]) in woods, Blue

Mtns, 17 July 1896, C. V. Piper 2328 (GH!, WS!).

Perennial herbs, often matted. Stems trailing, rarely erect,
(2.4)3 - 23(28) cm long, often branched; nodes sometimes bearing roots;
internodes glabrous, or rarely pilose, sometimes ridged. Leaves simple,
opposite, blades ovate, orbicular, or elliptic, (1.6)2 - 12(18) mm long,
(0.7)0.9 - 7(9) mm wide, apex acute, base truncate to attenuate, margin

smooth, with long cilia from base to halfway to apex or glabrous, occasionally undulate; leaves sessile or often with a petiole to 2(3) mm. Flowers axillary, one per node, (1)2 - 9(16) per stem. Flowers perfect, sepals 5 (often 4), ovate, basally connate, (1.2)1.7 - 2.5(2.7) mm long at anthesis, (1.7)1.9 - 3(3.5) mm long in fruit, nerves obscure, center nerve sometimes evident near base, apex obtuse or very rarely slightly acute, margin scarious, rarely exceeding 0.1 mm width; petals 0; stamens 10(8) or fewer; styles 3(4), white, usually curved, (0.2)0.3 - 0.5(0.6) mm long, stigmatic along entire length. Capsules globose to globose-ovoid, walls membranous, tan or translucent, (2)2.3 - 3.3(3.8) mm long unopened, 2.4 - 3.5(4) mm long opened, valves 6, pedicels (3)3.5 - 12(17) mm long, not reflexed, glabrous. Seeds reddish brown (immature) to grayish black (mature), transversely elliptic, 0.5 - 0.7 mm long, 0.5 - 0.75 mm wide, finely reticulate-furrowed, raised tubercles absent. $2n = 26, 52, 65$ (Morton, unpub.); ca 78 (Hartman, 1971). Figures 40a and 45.

DISTRIBUTION: The species is found at widely scattered sites in the mountains of western North America, from central British Columbia and Alberta southward in both the Coast Ranges to California and the Rockies to Colorado. Stellaria obtusa occurs at elevations from 730 to 3350 meters, except in the Olympic Peninsula where riverside populations occur below 300 meters. Plants with pubescent stems previously identified as Stellaria washingtoniana were restricted to the Olympic Peninsula and Mt. Rainier. Reports of S. obtusa occurring in southern Alaska (Hitchcock in Hitchcock & Cronquist, 1964; Boivin, 1966; Straley et al., 1985) could not be substantiated; Alaskan specimens at DAO annotated as S. obtusa by Boivin proved to be S. crispa. Straley et al.

(1985) reported S. obtusa from Lillooet and Mount Robson Provincial Park, British Columbia; these reports could not be confirmed. Figure 46.

ECOLOGY: Stellaria obtusa is often found as matted plants along streams, either in mossy bank vegetation under Salix and/or Alnus or on sand/gravel bars, and in damp shaded woodlands and meadows. All collections from forested lands have been made in coniferous woods (pine, spruce, fir, cedar, etc.) except in Utah and Colorado where the species occurs in aspen and aspen-fir forests. Some collections have been made from more exposed sites such as talus slopes and cliffs, indicating that S. obtusa is at least somewhat tolerant of dry soils.

Flowering is noted from late May through mid September, with fruit present on most of the earliest collections. Three collections of W. N. Suksdorf bearing mature fruit and collection dates between 31 March and 23 May (Suksdorf, Riverbank, Bingen, s.n. 31 Mar 1900 [WS]; Garden [from river bank], Bingen, s.n. 23 May 1900 [WS]; Garden, Bingen, s.n. 27 Apr 1907 [WS]) were excluded from consideration since they may be from cultivated plants. Suksdorf lived in Bingen, Washington (Weber, 1944), a town along the Columbia River, elevation about 30 meters. The absence of other collections of S. obtusa from any other sites below 300 meters suggests that Suksdorf may have transplanted some plants from an unspecified riverbank to his garden, making collections from these plants.

PROTECTION STATUS: At the present time S. obtusa is listed as rare only in two Canadian provinces (see Table 27) near the northern limit of its range. Although listed as a "Special Species" in Colorado in Kartesz & Kartesz (1977), it does not appear in a listing prepared from the database maintained by The Nature Conservancy (1986) of species

considered to be rare in at least one state. The absence of an entry for Stellaria obtusa in a recent flora of the Gunnison Basin, Colorado (Barrell, 1969) should not be interpreted as extirpation from the region where the type of S. obtusa was collected, but more likely the absence of collections from the Gunnison area at the herbaria (COCO, COLO, CS) that Barrell (1969) consulted. No specimens of S. obtusa from the Gunnison Basin were included in loans received from COLO and CS, while a 1961 collection (Iltis & Iltis 18886, WIS) from the Crested Butte area confirms it is still present in the Gunnison Basin.

Collections made after 1960 shown in Figure 46 illustrate that S. obtusa has been collected recently in most portions of the range. Two or more post-1960 collections were examined in this study from each state or province except Washington.

COMMON NAMES: The common names applied to S. obtusa are listed in Table 28. The reference to the obtuse, or blunt, sepals is appropriate, as is the use of "Rocky Mountain" since many of the populations are indeed found at sites in the Rockies. The last two names in the list were used for S. washingtoniana, considered here as a synonym of S. obtusa.

REPRESENTATIVE SPECIMENS: CANADA. ALBERTA. Improvement Dist. 6: Bank of Carbondale Creek, S of Blairmore, 23 Jul 1949, Budd 1632 (CAN, DAO [photo of CAN]). Waterton Lakes Nat. Park: Along trail to Bertha Lake, 4200 ft, 13 Sep 1925, Malte & Watson 2627 (CAN, COLO, DAO [photo of UAC], MIN, RM, UC, WTU); parking lot at last shelter, Twin Lakes Trail, 6300 ft, 15 Aug 1969, Kuijt & Blais 2949 (ALTA, CAN); Little Row Lake, 2 Jul 1971, J. K. Morton s.n. (JKM); foot of avalanche slide,

Cameron Lake, 2 Jul 1971, Morton NA4694 (JKM); path to Bertha Lake, 3 Jul 1971, Morton NA4723 (JKM).

BRITISH COLUMBIA. Cariboo Dist.: Edge of Summit Creek, 7.5 mi N of Barkerville on road to Bowron Lake, 3900 ft, 9 Aug 1953, Calder, Savile, & Ferguson 14925 (DAO). Kootenay Dist.: On sand and gravel bar in Sand Creek, 3.5 mi NNE of Galloway, 3400 ft, 29 May 1958, Taylor & Ferguson 922 (DAO). Similkameen Dist.: Cliffs and talus slopes, 40 mi W of Trail, 10 mi N of WA boundary, 5000 ft, 3 Aug 1964, Scoggan 16087 (CAN). Yale Dist.: Lake House, Skagit River, 12 Jul 1905, Macoun, Herb. Geol. Surv. Canada 79601 (CAN [mixed with S. crispa], NY).

USA. CALIFORNIA. Alpine Co.: Gabbot Meadows, Stanislaus Nat. Forest, 1970 m, 19 Jun - 19 Jul 1913, Eggleston 9507 (US). Butte Co.: On gravel bars by Butte Creek, Jonesville, 1500 m, 18 Jul 1931, Copeland, UC Herbarium 636 (CAS, CU, DS, F, GH, MICH, MIN, MO, ORE, RM, UC, UTC, WIS, WTU). Glenn Co.: Plaskett Meadows, 6000 ft, 4 Aug 1943, Howell 19011 (CAS, DS, F, GH, NY). Humboldt Co.: Lower end of Brett Hole, Trinity Summit, 5200 ft, 23 Jul 1935, Tracy 14161 (UC). Modoc Co.: Parker Creek Canyon, 5600 ft, 14 Jul 1932, Payne 682 (CAS). Nevada Co.: W side of Donner Pass, near Norden, ca 7000 ft, 14 Jul 1943, Howell 18297 (CAS). Placer Co.: Near Yuba River below Cisco, 5500 ft, 25 Jul 1919, Heller 13298 (CAS, CU, DS, F, GH, MO, NY, PH, US, WIS). Plumas Co.: Stream bank, Drakesbad, 5500-6000 ft, 21 Jul 1960, Howell 35798 (CAS, OSC). Siskiyou Co.: Finley's Upper Camp, head of N Fork of Salmon River, 18 Aug 1928, Kildale 6467 (DS). Tehama Co.: Brokeoff Mtn trail, ca 7500 ft, 19 Aug 1960, Howell 36116 (CAS). Tuolumne Co.: Beehive, N of Hetch Hetchy, Yosemite Nat. Park, 6550 ft, 22 Jul 1938, Mason 11960 (UC).

COLORADO. Gunnison Co.: Ruby, 9500 ft, 7 Aug 1901, Baker 706 (GH, MO, NDG, NY, US); slopes and streams, path from Redwell Basin to Peeler Basin, 4 - 5.5 mi WNW of Crested Butte, 10000 - 11000 ft, 18 Aug 1961, Iltis & Iltis 18886 (WIS). Routt Co.: Beaver dam outlet along trail between Slavonia & Mica Creek, 30 mi NE Steamboat Springs, Routt Nat. Forest, 29 Jul 1951, Weber 7088 (CAS, COLO, CS, DAO, MIN, RM, WS, WTU).

IDAHO. Adams Co.: Shore of Black Lake, Weiser [Payette] Nat. Forest, 8 Aug 1937, Christ 8641 (NY, UC). Bannock Co.: Topons Creek, Cache [Caribou] Nat. Forest, 7500 ft, 6 Aug 1929, Wright KEW-193 (RM). Bear Lake Co.: Limestone ridge N of Bloomington Peak, 13 mi W of Bloomington, 10 Jul 1949, Christ & Christ 18810 (NY). Blaine Co.: Banks of Wood River, at base of Galena Grade, 14 mi N of Ketchum, 25 Jul 1946, Christ 15819 (NY). Boise Co.: Summit of Boise-Lowman Hwy, 6800 ft, 16 Jul 1944, Hitchcock & Muhlick 9973 (BH, CAN, CAS, DS, NY, RM, UC, US, UTC, WS, WTU); along two-track E of ID 21, 21 mi SW of Lowman, Boise Nat. Forest, T7N R7E S20 NW 1/4, 6100 ft, 12 Aug 1980, Rabaler 534 (MSC + 1). Bonner Co.: Roadside, Priest River Expt. Forest, 10 Aug 1943, Daubenmire 43106 (WS, WTU). Boundary Co.: On trail of E slope of Continental Mtn, 25 mi W of Porthill, 7 Jul 1946, Christ & Smith 15277 (NY). Caribou Co.: Log in grassy meadow, Gravel Creek CG, Grays Range, 22 mi NNE of Soda Springs, T6S R43 S2, 6700 ft, 19 Jul 1971, Holmgren & Marttala 5518 (DAO, DS, UTC, WTU). Franklin Co.: Headwaters of Logan River, Franklin Basin, 2 mi N of UT state line, 8000 ft, 15 Jul 1958, Anderson 1348 (NY, UC, WTU). Idaho Co.: damp slopes, Josephine Lake, 7600 ft, 15 Jul 1969, Munz & Davidson 18228 (DAO, OSC). Kootenai Co.: Springy places in cañ[ny]ons, ridges S from Wiessner's Peak, 1700 m, 28 Jul 1895, Leiberg 1396 (NY, US only). Shoshone Co.: Sandy ground,

Little North Fork Clearwater River, Clearwater Camp, T43N R5E S17, 4 Aug 1941, Wilson 461 (UC, WS). Teton Co.: By creek in foothills, Bates, 13 Jul 1934, Christ 5345 (NY). Valley Co.: Near Big Creek [Summit], 13 mi E of Cascade, 25 Jun 1934, Jones 5009 (GH, US).

MONTANA. Flathead Co.: 30 m NE of Johns Lake, 0.3 mi S of Glacier Hwy 1, near NE end of Lake McDonald, Glacier Nat. Park, 4360 ft, 15 Aug 1980, Rabaler 546 (MSC). Gallatin Co.: Bridger Mtns, 7000 ft, 14 Jun 1897, Rydberg & Bessey 4014 (F, GH, NDG, NY[2], RM, US). Glacier Co.: Gravel overflow channel E of Wilbur Creek, 100 m S of bridge of trail to Swift Current Pass, due W of Swift Current Campground, Glacier Nat. Park, 4900 ft, 16 Aug 1980, Rabaler 552 (MSC). Granite Co.: drying hillside near Daly Creek on Skalkaho Rd., 7000 ft, 9 Aug 1933, Hitchcock 2064 (CAS). Lewis and Clark Co.: E slope of China Wall near N end, Sun River Primitive Area, Lewis and Clark Nat. Forest, 27 Jul 1948, Hitchcock 18942 (WTU). Meagher Co.: Wet meadowland along Checkerboard Creek, NE of base of Castle Mtns, 8 Jul 1945, Hitchcock & Muhlick 12134 (NY[2], WS, WTU). Mineral Co.: Headwater of Deer Creek, 0.6 mi SW of Deek Peak, 8 mi SW of Alberton, Lolo Nat. Forest, T13N R24W S1 SW 1/4, 5400 ft, 3 Sep 1971, Stickney 2438 (RM). Park Co.: Cooke City, without date, J. K. Morton s.n. (JKM).

OREGON. Grant Co.: Indian Springs, Blue Mtns, Malheur Nat. Forest, 5 Aug 1946, Maguire & Holmgren 26892 (NY, UC, UTC). Hood River Co.: White River, road to Mt Hood, 19 Jul 1926, Abrams 11427 (DS, NDG). Klamath Co.: W bank of Munson Creek, 25 m NE of Stop 2 on Godfrey Glen Nature Trail, 1.8 mi NE of Mazama, Crater Lake Nat. Park, 6000 ft, 5 Aug 1980, Rabaler 496 (MSC). Umatilla Co.: Boggy meadow near Langdon Lake, 14 Jul 1944, Peck 22296 (CAS, UC, WILLU). Union Co.: Gravel bar, West

Eagle Creek Meadow, T5S R43E S31, ca 5500 ft, 18 Jul 1964, Mason 6979 (ORE). Wallowa Co.: Moist woods, Lostine River Rd., near the Pole Bridge, T2S R43E S16, 4100 ft, 28 Jun 1969, Mason 8199 (ORE); creek along logging road off Sheep Creek, 15 mi SE of Joseph, ca 5600 ft, 18 Jul 1971, Mason 8900 (JKM, ORE, WS). Wasco Co.: Near Eight Mile Creek, Mount Hood Nat. Forest, 3830 ft, 21 Jul 1933, Jones 4095 (CAS, WTU[2]).

UTAH. Cache Co.: Margin of Tony Grove Lake, Bear River Range, 8000 ft, 4 Aug 1938, Maguire & Snell 16042 (CAN, CU, RM, US, UTC[2], WTU [not ex J. W. Thompson 22116]). Salt Lake Co.: Alta, Wasatch Mtns, 10000 ft, 29 Jul 1879, Jones 1096 (DS, RM[2]); in Populus-Abies forest, N-facing slope near rd. leading to Salamander Lake, Lambs Canyon, E of Salt Lake City, T1S R3E S28 SWNW, 8100 ft, 21 Jul 1974, Arnow 4139 (NY). Sanpete Co.: Pleasant Creek, above Manti-LaSal Nat. Forest boundary, 7700 ft, 23 Jul 1976, Lewis 4354 (UTC). Utah Co.: Mt Timpanogos, Wasatch Mtns, 25 Jul 1930, Garrett 5587 (F).

WASHINGTON. Clallum Co.: Sol Duc Hot Springs, Aug 1931, Jones 3694 (WTU). Columbia Co.: By streams in moist ravines, Blue Mtns, 11 June 1897, Horner B95 (GH). Grays Harbor Co.: gravel bar of Quinault River, 10 mi above Lake Quinault, 30 Jun 1933, Jones 3958 (WTU[2]). Jefferson Co.: Hoh River, 9 Sep 1935, Jones 8422 (WTU). Mason Co.: Damp woods, Lake Cushman, Aug 1895, Piper 2238 (GH). Pend Oreille Co.: in Picea-Abies/Pachistima climax, few mi E of N Baldy, 25 Jul 1957, Daubenmire 5774 (WS). Pierce Co.: Upper valley of the Nesqually [Mt Rainier], 18 June 1895, Allen 157 (CAN, CS, DS, F[1+Photo], GH[2], MIN, MO, MSC, NY, RM, UC[2], US[2], VT, WS). Skamannia Co.: Barley Meadow, South Prairie, 31 Aug 1893, W. N. Suksdorf s.n. (WS). Walla Walla Co.: Along streams [GH] (rivulets [WS]) in woods, Blue Mtns, 17 July 1896, Piper 2328 (GH,

WS). Whatcom Co.: Thick mats on gravel along Slate Creek Barron, Mt Baker Nat. Forest, 23 Jun 1939, Muenschner 10046 (CU, DS, GH, UC, US, WS, WTU).

WYOMING. Carbon Co.: Along stream, Rambler, ca. 16 mi W of Encampment, Medicine Bow Nat. Forest, 9400 ft, 9 Jul 1969, Hartman 2914 (RM). Lincoln Co.: Mtns near Cottonwood Lake, E of Smoot, 7700 ft, 28 Jul 1923, Payson & Armstrong 3619 (CU, GH, ISC, MO, MSC, PH, RM). Teton Co.: West De Lacy Creek, Yellowstone Nat. Park, 4 Aug 1899, Nelson & Nelson 6298 (CM, CU, GH, MIN, MO, NDG, NY, RM[2], US).

NOMENCLATURAL HISTORY: Engelmann (1882) described S. obtusa from material collected in western Colorado by T. S. Brandegees in 1881, noting that it was "closely allied to S. crispa of the northwest but readily distinguishable." Rose (1896) transferred S. obtusa to Alsine (Alsine obtusa (Engelm.) Rose), making a combination of relatively brief usage.

Robinson (1898) described Stellaria washingtoniana Robinson from material collected on Mt. Rainier by O. D. Allen in 1895 (Allen 157 (CAN, CS, DS, F[1 + photo], GH[2], MIN, MO, MSC, NY, RM, UC[2], US[2], VT, WS). He noted the affinities of S. washingtoniana were "obviously with S. obtusa Engelm., S. crispa Cham. & Schlecht., and S. calycantha Bong." This species was segregated from S. obtusa on the basis of having a pubescent stem, thin leaves that may be puberulent and ciliate near the base, and a pubescent calyx; he noted S. obtusa as "essentially glabrous [sic], and has thicker obtuser apparently glaucescent leaves and sepals."

I found that collections previously identified as S. washingtoniana resembled S. obtusa except for possessing a pubescent stem, indicating a

relationship with S. obtusa rather than with S. simcoeii as Hitchcock (in Hitchcock & Cronquist, 1964) suggested. After over 330 specimens of S. obtusa were examined, it appeared that the stem pubescence found on Allen 157 represents an uncommon local variation. Material similar to Allen 157 was limited to four collections from the Olympic Peninsula. Although these plants may represent a little-known taxon, the close morphological resemblance of these plants to S. obtusa except on pubescence suggests that taxonomic recognition is not warranted.

As noted before, a portion of S. viridula (Piper) St. John, published as Alsine viridula by Piper (1913) on the basis of Leiberg 1396 (DS, F, GH, MO, NY, ORE, RM, UC, US) is referable to S. obtusa. Piper's description reads like one for S. obtusa in many ways and the holotype (US!), one isotype (NY!), and the cited paratype (Piper 2328, GH, WS) are specimens of S. obtusa.

TYPIFICATION: In the protologue, Engelmann (1882) stated the location as "Western Colorado on the tributaries of Gunnison River, alt. 9,000 to 10,000 feet, in damp grounds, T. S. Brandegee." Since the types for species that Engelmann described are for the most part at MO (Stafleu & Cowan, 1976), it was interesting to note that no specimens bearing this locality description were received from MO nor did Dr. Steven J. Wolf locate any Brandegee collection of S. obtusa made early enough to be considered as type material during his study of Engelmann type material at MO. Dr. Wolf (pers. comm.) noted that there is almost always a specimen bearing the exact text used in Engelmann's descriptions.

The source of Engelmann's phrasing was located in a letter which Brandegee sent to Engelmann on 13 November 1881, from "Coal Ck. Canon,

Colorado", received by Engelmann on 21 November. The following text explains Brandegees' thoughts on S. obtusa:

"I enclose a plant which I think has not yet been sent East by me - Perhaps it is an apetalous Arenaria, it is common covering the damp ground in some places for quite an area - alt. 8000 to 10,000"

and indicates that Brandegees sent Engelmann a specimen collected in 1881. A note on the letter indicates that Engelmann answered Brandegees' letter the same day. Unfortunately, Engelmann's response is not among the T. S. Brandegees correspondence housed at UC and GH.

Three replicates of a T. S. Brandegees collection made in 1881 and labelled in Brandegees' hand (fide labels illustrated in Ewan, 1942) were located (GH, NY, UC), the label reading as follows.

"Stellaria obtusa Eng. n. sp.
Bot. Gazette. VII. I.
Anthracite Ck, Colorado
Coll. T. S. B. 1881."

The inclusion of the citation for the description indicates that Brandegees prepared the labels either after the publication appeared or after Engelmann had provided the information to him. Although the label information does not resemble that found in the Engelmann description, several pieces of evidence suggest that these specimens are from the original gathering by Brandegees.

The salutation of the letter is of interest for two reasons.

"Yours truly,
T.S. Brandegees
Irwin
D.S.P. and P.R.R. Colorado"

Ewan (1942) noted that Brandegees was supervising a surveying crew that was planning the location of a railway from Gunnison northwestward through the valley of Ohio Creek in 1881, confirmed by the salutation. Irwin, Colorado is about three miles north of the source of Ohio Creek

and near the start of both Anthracite Creek and Coal Creek, all three creeks being tributaries of the Gunnison River. An inspection of the other Colorado collection localities listed by Ewan (1942) reveals Brandegee's 1881 trip was his only one in this area, all other sites being south and/or southeast of the Gunnison area.

In the absence of a specimen from Engelmann's collection, it is appropriate to designate a neotype for S. obtusa. I have selected the Brandegee collection from UC (Figure 45) as the neotype (filed at UC as a holotype), the remaining specimens (GH, NY) serving as isoneotypes. Although it is quite probable that these collections would have been made at the same time as the specimen which Brandegee sent to Engelmann, none of them can be designated as lectotype since there is no evidence that Engelmann would have actually studied these collections when he described S. obtusa (see Voss et al., 1983; Guide for the Determination of Types, T.4.[a]). Brandegee's personal herbarium was deposited at UC; this specimen bears the stamp "Brandegee Herbarium". The inscription "part of type" in an unknown hand appears just above Brandegee's label, suggesting that another botanist also felt that it was part of the gathering that Brandegee sent to Engelmann.

2. Stellaria crispa Cham & Schldl., Linnaea 1: 51. 1826.

Stellaria borealis (Ledeb.) Bong. var. crispa (Cham & Schldl.) Fenzl
ex Torrey & A. Gray, Fl. N. Amer. 1: 675. 1840. Stellularia
crispa (Cham & Schldl.) Kuntze, Rev. Gen. 1: 55. 1891. Alsine
crispa (Cham & Schldl.) Holzinger, Contr. U.S. Natl. Herb. 3:
216. 1895. TYPE: USA. ALASKA. Aleutian Islands: Semina 12,
Unalaschka 17 [date?; 1817 from type description], L. A. von
Chamisso s.n. (lectotype, here designated, LE!, ex herb
Chamisso).

Stellaria borealis (Ledeb.) Bong. forma α apetala (Fenzl) Regel lusus
c. crispa Regel, Bull. Soc. Imp. Naturalistes Moscou 35: 277.
1862. pro parte. ORIGINAL MATERIAL: USA. ALASKA. Aleutian
Islands: Unalaschka, without date, J. F. G. Eschscholtz s.n.
(LE!)

Perennial herbs, sometimes matted. Stems trailing, sometimes
initially erect or supported by other plants, 5.5 - 38.7(60.5) cm long,
often branched; roots occasionally formed at nodes; internodes glabrous,
often ridged. Leaves simple, opposite, blades ovate or elliptic,
(1.1)1.5 - 18(34) mm long, (0.6)1.5 - 11(18) mm wide, apex acute or
acuminate, base truncate, cordate, or attenuate, entirely glabrous,
margin smooth, scarcely hyaline, often undulate; leaves sessile or often
with a petiole to 2(3) mm. Flowers axillary, one per node, more
frequent below, 1 - 14(25) per stem. Flowers perfect, sepals 5(rarely
4), basally connate, lanceolate, 1.8 - 3.6(4.2) mm long at anthesis,
(2)2.5 - 4.1(4.8) mm long in fruit, nerves 3, becoming evident ridges
extending to apex, glabrous, apex acute to acuminate, margin scarious,

exceeding 0.1 mm width; petals 0(rarely 1 - 5), white, deeply 2-cleft, less than 1/2 X the sepals; stamens 10(8) or fewer; styles (1 - seen once, 2)3(rarely 4), white, usually curved, 0.5 - 0.9(1.2) mm long, stigmatic along entire length. Capsules ovoid, walls membranous, translucent, 2.8 - 5(6) mm long unopened, (2.9)3.6 - 5.1(6) mm long opened, valves 6, pedicels (1.2)3 - 16(33) mm long, seldom reflexed, glabrous. Seeds reddish brown (immature) to brown (mature), elliptic to circular-elliptic, 0.6 - 1.0 mm long, 0.5 - 0.9 mm wide, rugose, especially along edges. $N = 13$ (Taylor & Mulligan, 1968), $2n = 26$ (Morton, unpub.), 52 (Chinnappa, 1985). Figures 40c and 47.

DISTRIBUTION: Stellaria crispa is found from the Aleutians Islands eastward along coastal Alaska and southward along the North American coast into northern California, with the range extending inland to include southern British Columbia, Alberta, Idaho, and Montana. Collections have been made at elevations from sea level to 2290 meters, with the majority from coastal and valley sites below 900 meters.

Stellaria crispa has been listed as occurring in montane areas at elevations to nearly 3350 meters in California (Munz & Keck, 1959; Weeden, 1981), with Munz and Keck (1959) and Munz (1974) noting the range extends further southward to include the San Bernardino and San Jacinto Mountains near Los Angeles. All material labeled as Stellaria crispa collected above 2200 meters as well as collections from southern California were found to be specimens of Stellaria calycantha. Other published references to Stellaria crispa which are based on misidentified specimens of S. calycantha include Gillett et al. (1961; Lassen Volcanic National Park, Gillett 999, CAS, MSC, and UC), Heckard and Hickman (1985; Snow Mountain, Colusa Co., Heckard with Hickman 5277,

JEPS) and Twisselmann (1967; Kern Co., Twisselmann 6465 and 7758, both at CAS). The description accompanying Ferlatte's (1974) report of S. *crispa* from the Trinity Alps suggests that his material is probably S. *calycantha* (voucher [Ferlatte 1058, HSC] not seen).

Stellaria *crispa* has also been reported from Nevada and Wyoming, although no specimens of S. *crispa* from these states were examined. The reference to S. *crispa* in Esmeralda Co., Nevada in Lloyd and Mitchell (1973) is based on Duran 3312 (UC), also a collection of S. *calycantha*. Material seen from Yellowstone National Park and Sheridan Co., Wyoming, which was labeled as S. *crispa* is S. *calycantha*, negating the record for Wyoming in Dorn (1977). Shaw's (1976) report of S. *crispa* from Teton Co., Wyoming could not be confirmed.

ECOLOGY: Stellaria *crispa* is often found growing over and among other low herbaceous plants under Alnus and Salix along streams, in moist woods and forest openings, in roadside ditches, and on beaches in the forest/beach ecotone. Many collections are of plants growing among mats of moss in spruce-fir, hemlock-cedar, redwood, and maple-Douglas Fir forests. Munz and Keck (1959) noted S. *crispa* as being found in three communities in California; Northern Coastal Scrub, Redwood Forests, and Mixed Evergreens.

Flowering is noted from late March through late August, with mature fruit present in southern areas by mid-April. The earliest flowering dates reported are from coastal sites, with many collections (except those from the Aleutian Islands) made after late June bearing only mature fruit.

PROTECTION STATUS: Although a listing for S. *crispa* appears in several publications (see Table 29), it appears that no state or

provincial agency currently recognizes S. crispa as a rare plant. As noted in Table 29, the listing for the Yukon Territory (Douglas et al., 1981) is based on a misidentified collection of S. borealis subsp. borealis (Anderson 9323, CAN). Stellaria crispa is noted as rare in Alberta in two publications, but not in the list prepared by Argus and White (1978) outlining the rare plants of Alberta.

Many collections have been made since 1960 (see Figure 48), reinforcing the notion that the species does not appear to require monitoring in most portions of its range.

COMMON NAMES: The common names which have been applied to Stellaria crispa are listed in Table 30. Most names either commemorate one of the botanists who first described it (A. Chamisso) or make reference to the usually undulate ("crisped") leaf margin of these plants. As noted above, that feature is certainly noticeable in S. crispa, but similar leaf crisping is seen in S. obtusa and S. calycantha.

REPRESENTATIVE SPECIMENS: CANADA. ALBERTA. Improvement Dist. 6: Between N Kootenay Mtn and Lynx Creek camp, Carbondale River region, 5000 ft, 16 Jul 1971, Packer & Silberhorn 1971-147 (ALTA, CAN). Waterton Lakes Nat. Park: Path to Bertha Lake from Waterton, 3 Jul 1971, Morton NA4725 (JKM).

BRITISH COLUMBIA. Cariboo Dist.: Hungary Creek ca. 15 mi ESE of Purden Lake, 2500 ft, 2 Aug 1974, V. J. Krajina, J. Polar, & C. Parsons s.n. (UBC). Cassiar Dist.: Sandy creek bank, Haines Rd. Mile 45, 250 m, 17 Jul 1956, Taylor, Szczawinski, & Bell 1536 (GH, UBC). Coast Range 2 Dist.: Spider Island, mossy slopes along beach, 10 Jul 1939, McT. Cowan 11668 (CAN [2]). Coast Range 3 Dist.: Hanging in streamers over stump,

Neekis River, Don Peninsula, 2 Aug 1939, McCabe 7395 (UC). Coast Range
 5 Dist.: Slope of Hudson Bay Mtn above Sylvan Mine, 9 mi W of Smithers,
 13 Jul 1954, Calder, Savile, & Ferguson 12935 (DAO, GH). Kamloops
 Dist.: Tranquille Range, Kamloops, 3900 ft, 28 Jul 1937, Soper 40-370
 (DAO). Kootenay Dist.: Columbia Gorge, Revelstoke, 1600 ft, 2 Jul 1905,
Shaw 845 (CM, COLO, GH, MIN, NY, PENN, PH, US). New Westminster Dist.:
 Spanish Banks, Vancouver, 28 May 1944, Eastham 11390 (ALTA, DAO, UBC,
 UC, WIS); University Endowment Lands, Marine Drive, Vancouver, 16 Jul
 1980, Morton & Venn NA13485 (JKM); 0.1 mi E of jct. of Dewdney Trunk Rd.
 - 288th St., E of Haney, 17 Jul 1980, Rabeller 426 (MSC + 4). Osoyoos
 Dist.: Beaver lake near Winfield, 4400 ft, 26 Jul 1952, V. J. Krajina
s.n. (UBC). Peace River Dist.: By river, W of Solitude Mtn, on hwy from
 Dawson Creek to Pine Pass, 2400 ft, 13 Jul 1960, Calder & Kukkonen 26878
 (DAO, GH, NY, OSC). Queen Charlotte Dist.: Graham Island, logged over
 areas back from beach, W outskirts of Queen Charlotte City, 26 May 1957,
Calder, Savile, & Taylor 20908 (DAO, DS, NY, OSC, WS, WTU); Moresby
 Island, roadside bank, Moresby Logging Camp, Cumshewa Inlet, 28 May
 1957, Calder, Savile, & Taylor 20957 (COLO, DAO); Graham Island, gravel
 of roadside ditch, 2.5 mi SE of Prot Clements, 3 Jun 1964, Calder,
Taylor, & Sherk 34600 (DAO); Graham Island, mossy flats, N end of Dawson
 Inlet, 15-16 Jun 1964, Calder, Taylor, & Sherk 35128 (DAO); Moresby
 Island, summit on road between Gillatt Arm of Cumshewa & Peel Inlet, 19
 Jun 1964, Calder & Taylor 35211 (DAO). Similkameen Dist.: Bear Creek,
 Penticton, S of main road to Keremeos, 20 Aug 1937, M. Stoner s.n. (UBC).
 Vancouver Island - Barclay Dist.: Trail from Bamfield to Bachena Bay, 11
 Jun 1961, Calder & MacKay 30301 (DAO, WS). Vancouver Island - Clayoquot
 Dist.: About 4 mi N of NE end of Kennedy Lake on Tofino - Alberni Road,

14 May 1961, Calder & MacKay 29089 (DAO, DS, UBC, UC). Vancouver Island - Renfrew Dist.: Forest edge, Jun - Jul 1901, Rosendahl & Brand 41 (CAN, COLO, DS, GH, MIN, MO, MSC, NY, PH, RM, UC[2], US). Vancouver Island - Rupert Dist.: log line of sandy beach, SW of Orchard Point, Brooks Peninsula, 0-30 ft, 16 Aug 1975, Pinder-Moss 1278 (DAO, UBC). Yale Dist.: Roadside bank, 12 mi W of RS on Hope - Princeton Hwy, Manning Prov. Park, 16 Jul 1953, Calder & Savile 10604 (DAO).

USA. ALASKA. Alaska Peninsula: NW section of Chowlet Island, steep beach slope, Sutwik Island Quad., 56°02'N 156°42'W, 5 m, 13 Jul 1977, Hatch 181 (ALA, UBC). Chugach Nat. Forest: Evans Island, Port San Juan, 3 Aug 1948, Eyerdam 5980 (CAN, MO, MT). Glacier Bay Nat. Monument: Station 20, Glacier Bay, 18 or 21 Jul 1929, Cooper & Andrews 263 (F, ISC, MIN). Haines Bor.: Pyramid Harbor, 1883, T. Meehan s.n. (PH). Juneau Bor.: Shaded cliff, Funter Bay, 0 ft, 7 Jun 1915, Walker & Walker, RM Herbarium 696 (CM, DS, GH, MO, NY, RM, UC, WS); wet woods, Juneau, 1 Jun 1940, Anderson 6239 (ALA[2], CAN, DAO, GH, PH, RM, S, WTU). Kenai Peninsula Bor.: Wet bank, Hope, 6 Jun 1941, Anderson 6616 (ISC, PH, RM, WTU). Ketchikan Gateway Bor.: Shady bog, Wrangell, 15 May 1915, Walker & Walker, RM Herbarium 642 (CM, DS, F, GH, MO, NY, RM, UC, WS). Kodiak Island Bor.: Kodiak Island, roadside, 4 mi N of village through pine wood to Mill Bay, 1 Jul 1936, Hutchinson 181 (MO); in valley near stream and lagoon, Olga Bay, 15 Jun 1938, Looff & Looff 285 (BH, DAO, GH, MO, ND, NY, OSC). Matanuska-Susitna Bor.: Alaska Range Dist., E shore of Kroto Lake, 1.5 mi E of the road from Peters Creek to Petersburg, ca 20 mi NW of Talkeetna, T27N R8W, 1122 ft, 3 Jul 1980, Siplivinsky 193 (COLO). Sitka Bor.: E coast of Baranof Island, forest/beach ecotone, S side of Cascade Bay at base of large slide area,

Tongass Nat. Forest, T56S R67E S9, 10 ft, 18 Jun 1980, Muller 3569 (ALA, WTU). Yakutat Quad.: Slopes of mesa, Tanis Mesa Camp, 2 mi S of Tanis Lake, 59°15'N 138°30'W, 21 Jun 1967, Argus & Chunys 6282 (CAN).

ALASKA. Aleutian Islands: Akutan Island, Akutan, Aug 1935, J. Rudd s.n. (WTU). Atka Island, 11 Jul 1932, Eyerdam 1293 (CAN, CAS, DS, NY, US). Attu Island, high beach, W side of Chichagof Harbor, 8 Jul 1945, Hardy 168 (ALA, CAS, CU, MIN, MO, PH, S, UC, WTU); Attu Island, near creek, Attu Village site, Chic[h]agof Harbor, 12 Jul 1945, Van Schaack 598 (GH, MICH, US). Bogoslof Island, Umnak Quad., 53°56'N 168°02'W, 20 Jul 1980, Friedman 80-148 (ALA). Carlisle Island, 15 Jul 1932, Hultén 6599 (S). Shemya Island [in Semichi Islands], 1944, K. K. Bohnsack s.n. (MICH). Unalaska Island, Unalaska, 20 Jul 1938, Anderson 4118 (ISC, UC).

CALIFORNIA. Amador Co.: Panther Creek, 4800 ft, 13 Jun 1895, Hansen 1102 (DS, F, MIN, MO, NY, US). Calaveras Co.: Bear Valley, 29 May 1898, A. Eastwood s.n. (F, UC). Glenn Co.: Canyon of Snow Basin Creek, 12 Aug 1943, Howell 19289 (CAS, DS, F, GH). Humboldt Co.: Near mouth of Raccoon Creek, 15 Jul 1950, Tracy 19042 (CM, UC, VT, WTU). Marin Co.: Near Olema, Aug 1898, Davy 4343 (UC). Mendocino Co.: Pine barrens ca 3 mi SE of Fort Bragg, 200 - 300 ft, 26 Jun 1955, Thomas & Thomas 670 (DS). Nevada Co.: Rainbow Tavern, Donner region, ca 6000 ft, Jul 1936, H. M. Pollard s.n. (CAS). Plumas Co.: Lassen Peak, Jul 1896, Bruce 850 (MO). Shasta Co.: Goose Valley, 29 Jun - 11 Jul 1912, Eastwood 877 (CAS). Siskiyou Co.: Mud Creek Canyon, 6500 ft, 22 Aug 1940, Cooke 15461 (BH, COLO, NDG, NY).

IDAHO. Benewah Co.: Alder Creek, 19 Jun 1927, Jones 719 (WS). Boise Co.: Summit of Boise-Lowman Hwy, ca 6300 ft, 16 Jul 1944,

Hitchcock & Muhlick 9982 (CAS, NY, UC, WS, WTU). Bonner Co.: Kalispell Creek, 5 Aug 1934, Christ 6068 (NY, US). Boundary Co.: Smith Creek, 10 mi due W of Port Hill, 4600 ft, 13 Jul 1936, Rossbach & Rossbach 252 (DS, RM, WTU). Cassia Co.: Creek edge, Howell's Canyon, T13S R24E, 7500 ft, 18 Jul 1940, Davis 2793 (MO, UC). Clearwater Co.: Moist mountainside, 4 mi SE of Cedars RS, on road to Osier Ridge, 29 Jul 1947, Christ 17096 (NY). Idaho Co.: Disturbed area along S side of FS 373, opp. Wagon Mtn Trail, 1.15 mi E of US 12, Lolo Pass Info. Center, Clearwater Nat. Forest, T38N R15E S15 NE1/4, 5250 ft, 12 Aug 1980, Rabaler 541 (MSC + 1). Kootenai Co.: Moist [Wet] places [or Low grounds], Jul 1892, Sandberg 1081 (DS, ISC, MIN, MO, NYS, PH,). Latah Co.: Valley of Pine Creek, 29 Jun 1892, Sandberg, MacDougal, & Heller 527 (CAS, CS, DS, F, GH, MO, NY, US); along stream, N side of Cedar Peak, 2 Jul 1936, Dillon & Dillon 754 (CM, UC, WS, WTU). Lemhi Co.: Near S side of Salmon River, 12 mi W of Salmon, 12 Jul 1945, Christ & Ward 14685 (NY). Madison Co.: Pinus contorta / Vaccinium globulare area, Targhee Nat. Forest, T4N R42E S14 NW 1/4, 7000 ft, 25 Jun 1979, Dieffenbach, Glennon, Holte, Mel, Pearson, & Vieth, s.n. (RM). Nez Perce Co.: Lake Waha, 2000 - 3500 ft, 25 Jun 1916, Heller & Heller 3307 (CU, DAO, MIN, MO, NY, UC, US). Owyhee Co.: Springy slope, 3 mi S of Silver City, 10 Jul 1944, Christ 14318 (NY). Shoshone Co.: Freezeout Springs, Coeur d'Alene Nat. Forest, T54N R1E S14, 3 Jul 1980, S. N. Stephenson s.n. (MSC).

MONTANA. Flathead Co.: Ole Creek, Glacier Nat. Park, 30 Jun 1934, Maguire, Maguire, & Maguire 15470 (CU, GH, RM, UC). Gallatin Co.: Upper Bracket Creek, 8 Aug 1899, J. W. Blankinship s.n. (NY). Glacier Co.: Thickets, Midvale, 29 Jul 1903, Umbach 582 (COLO, F, GH, MIN, MSC, NY,

RM, US, WIS). Lake Co.: Skidoo Creek about 5 mi up road from Hwy 35, 4000 ft, 13 Jul 1966, Woodland 600 (DS). Ravalli Co.: Mossy seeps, Bass Creek Trail, Bitterroot Mtns, 4800 ft, 28 Jun 1977, Lackschewitz 7347 (COLO, NY).

OREGON. Benton Co.: Mary's Peak, Corvallis, 800 ft, 17 Jun 1916, Gilbert 143 (OSC, US). Clackamas Co.: Lake Oswego, 6 May 1928, Thompson 4140 (DS, MO, US). Clatsop Co.: Jct. of Saddle Mtn Rd. and Hwy 2 [26] 10 mi SE of Seaside Junction, T5N R9W S24 N 1/2, 30 May 1962, Steward & Steward 7091 (DAO, DS, GH, ISC, NY, OSC, UBC). Columbia Co.: Near Clatskanie, 15 May 1927, Thompson 2420 (DS, MO, PH). Curry Co.: Moist woods, Port Orford, 27 Jun 1919, Peck 8573 (GH, WILLU). Deschutes Co.: Bank near Sisters RS, 27 Jun 1919, Ferris & Duthie 579 (DS). Douglas Co.: Beaver-dam lake just W of Limpy Rock, N of North Umpqua River, upstream from Steamboat RS, Umpqua Nat. Forest, T26S R2E S7, 3500 ft, 19 Jun 1976, Chambers 4221 (ORE, OSC). Hood River Co.: Pool along N side of road to Hood River Meadows CG, 0.25 mi E of jct. with road to Hood River Meadows Ski Lodge, at Bennett Pass, Mt Hood Nat. Forest, T3S R9E S11 SW1/4, ca 4600 ft, 3 Aug 1980, Rabaler 485 (MSC + 1). Jackson Co.: Beaver Creek, Siskiyou Mtns, T2W R40S S7, 2600 ft, 16 Aug 1949, Whittaker 345 (WS). Josephine Co.: Near Grayback Creek, 10 m S of FS 3941 (Grayback Rd.), 1.6 mi E of OR 46 (14.4 mi E of Cave Junction), Siskiyou Nat. Forest, T39S R6W S29 SW1/4, 6 Aug 1980, Rabaler 499 (MSC + 2). Lane Co.: Mouth of Cummins Creek, 14 Apr 1934, Eastwood & Howell 1496 (CAS, UC, WS); shaded hillside, Clover Ridge, T17S R11W S5, 900 ft, 16 Jun 1938, Detling 2966 (ORE). Lincoln Co.: Waldport, 25 Jul 1924, Peck 13486 (PH, WILLU). Marion Co.: Shady damp woods, Silver Creek, Jun 1871, Hall 54 (CAS, F[2], GH, MO[2], NY[3], US). Multnomah Co.: Among

rocks in Oneonta Creek, Oneonta Gorge within 150 m of Columbia Scenic Drive, Mt Hood Nat. Forest, T1N R6E S9 N1/2, 3 Aug 1980, Rabeler 483 (MSC + 1). Polk Co.: Falls City, 7 May 1921, Nelson 3581 (NYS, PH). Tillamook Co.: Along shore at Wheeler, 14 May 1939, Muenschner & Muenschner 15298 (CU). Union Co.: Vernal pool bed, 4 mi NW of Starkey HQ, Starkey Forest & Range Expt. Sta., T3S R34E S32, 24 Jul 1975, Naas & Naas 3118 (RM). Wallowa Co.: Downey's Gulch, 2300 ft, 16 Jun 1897, Sheldon 8321 (F, GH, MO, NY, RM, US). Wasco Co.: Banks of White River, 8 Sep 1898, Langille 66 (US). Washington Co.: Forest Grove, 3 Jun 1893, F. E. Lloyd s.n. (NY[3]); Scroggins Creek, 26 May 1928, Thompson 4309a (DS, MO, PH, US).

WASHINGTON. Chelan Co.: Nadal Lake by trail to Snow Lakes, Wenatchee Mtns, 4500 ft, 11 Aug 1952, Thompson 17155 (NY). Clallum Co.: Cleared land, Port Crescent, 9 Jul 1904, Lawrence 252 (UC, WS, WTU). Columbia Co.: Creek bottom, Wolf Fork of Touchet River, 30 May 1925, St. John, Davison, & Scheibe 7009 (DS, UC, WS). Grays Harbor Co.: near [4 mi N of] New London, 10 Jun 1897, Lamb 1171 (DS[2], F, MO, ND, NY, PH). Island Co.: Whidbey Island, Goose Rock, Deception Pass Park, 8 Jun 1936, Smith 881 (WS, WTU). Jefferson Co.: Near O'Neil Creek Shelter, 1200 ft, 1 Jul 1938, Rossbach & Rossbach 484 (CAS, DS, WTU). King Co.: Moist woods, University of Washington campus, 15 May 1929, Benson 1387 (DS, MO, WTU); Seattle, 1 Aug 1933, W. J. Eyerdam s.n. (MO). Kitsop Co.: Shady bank, Illelee Park, N of Bremerton, 22 Jul 1945, Schallert 19409 (MSC). Klickitat Co.: Near shaded springs, Bingen Mtn, 25 Jun 1906, Suksdorf 5668 (WS, WTU). Lewis Co.: E of hwy ditch, ca 0.1 mi S of Nisqually River, Mt Rainier Nat. Park, 4000 ft, 1 Aug 1980, Rabeler 477 (MSC + 1). Mason Co.: Maple woods at edge of Scott's Prairie, near

Shelton, 11 May 1935, Jones 6520 (WTU). Okanogon Co.: Summit of Muckamuck Lookout, 6300 ft, 26 Jun 1931, Thompson 6986 (DS, GH, MO, PH, UC, WTU). Pacific Co.: Nahcotta, 10 Jun 1952, T. Kincaid s.n. (CAS). Pend Oreille Co.: Seepage area, edge of clearcut, Coyote Creek, T37N R44E S30, 5200 ft, 10 Jul 1969, Layser 964 (WS). Pierce Co.: Upper valley of the Nesqually [Mt Rainier], 12 Jun 1895, Allen 156 (CAN, CS, DS, F[2], GH[2], MIN, MO, MSC, NY, RM, UC, US, VT, WS); N of Tahoma Creek, S of Indian Henry's Camp trail, Mt Rainier Nat. Park, 3120 ft, 31 Jul 1980, Rabaler 471 (MSC + 1). San Juan Co.: San Juan Island, Friday Harbor, 25 Jun - 1 Aug 1917, Zeller & Zeller 877 (CAS, CM, GH, MIN, NY). Skamannia Co.: Shady wet places [Butterfly Lake fide W. Weber annotation, WTU], 10 Jul 1891, Suksdorf 1863 (F, GH, ISC, MIN, MO, MSC, NY, UC, US, WS, WTU). Snohomish Co.: Open bogs at Big Four Inn, 1900 ft, 15 Jun 1940, Thompson 14673 (COLO, GH, MO, US, WS, WTU). Spokane Co.: Latah Creek, 28 Jul 1916, Suksdorf 8964 (WS). Thurston Co.: Saint Martin's College campus, Olympia, 3 May 1974, C. Abair s.n. (MIN). Wahkiakum Co.: Altoona, 20 Jul 1909, W. N. Suksdorf s.n. (WS). Walla Walla Co.: Blue Mtns, 17 Jul 1896, C. V. Piper s.n. (WS). Whatcom Co.: Fountain Lake, 8 Jun 1929, Muenschner & Muenschner 5399 (BH, CU).

NOMENCLATURAL HISTORY: Chamisso & Schlechtendal (1826) described S. crispa from specimens that Chamisso collected at Unalaska in 1817. Except for a time during the mid-1800's when some authors thought that S. crispa Cham. & Schldl. was better treated as a variety or form of S. borealis and the later usage of Alsine to replace Stellaria (Alsine crispa (Cham. & Schldl.) Holzinger, published in 1895), there has been little dispute over the name for this plant.

Fenzl was apparently the first to consider S. crispa as a variety

of S. borealis. In the Supplement to their Flora of North America, Torrey and Gray (1838-1840, pp. 674-675 published in 1840) noted that Fenzl made the combination S. borealis β crispa Fenzl in his important monograph on the Alsineae, a portion of which they noted "is already published (in Annal. Wiener. Museum.).". Unfortunately, it appears that the work was never published. McNeill (1962) noted Fenzl's contributions were limited to his 1833 dissertation on phytogeography and his treatments in Endlicher's Genera Plantarum (1840) and Ledebour's Flora Rossica (1842). Reichardt (1880) listed three articles by Fenzl that appeared in the Annalen des Wiener Museums, one describing Acanthophyllum and two containing his monograph of the Molluginaceae. Given this situation, Torrey and Gray's usage becomes the first for the combination. The authorship should be S. borealis var. β crispa (Cham. & Schldl.) Fenzl ex Torrey & A. Gray, reflecting Torrey and Gray's publication of Fenzl's combination. Fenzl made no mention of S. borealis β crispa in his treatment of S. crispa in Ledebour (1842), a rather curious situation in light of both Torrey and Gray's reference to Fenzl's work and Fenzl's references to Torrey and Gray in various places in the Flora Rossica treatment.

The equivalence of β to variety is based on several pieces of evidence. As noted elsewhere, Fenzl refers to "var. α & β " in several places in his Stellaria treatment in Ledebour (1842), suggesting strong evidence of his belief in their equivalence. Torrey and Gray (1838) also use Greek letters to signify varieties including a reference to "Vars. α & β " under Stellaria longipes on the same page as the beginning of their treatment of S. borealis. Following Article 35 of the International Code (Voss et al., 1983) is difficult here since we would

would be trying to determine the meaning of Fenzl's ranks as used in a publication that apparently does not exist. Rothrock (1868) is the first to use "var. crispa" in text, most likely following Torrey and Gray's (1840) position rather than making a new combination as the synonymy that Hultén (1944) lists under S. crispa suggests. Torrey (1874) treated S. crispa as a variety of S. borealis based on discovering plants he and Asa Gray considered intermediates, but did not give an authorship to the combination - strange, considering the usage of Fenzl's combination in Torrey and Gray (1840). Turner (1886) is the most recent work I have seen that followed Torrey's concept of S. crispa.

As mentioned above, Fenzl later (in Ledebour, 1842) accepted S. crispa. A comparison of Fenzl's description with that of Chamisso and Schlechtendal (1826) suggests that Fenzl expanded his concept of S. crispa. For example, Fenzl (in Ledebour, 1842) described the leaves as "ovatis ellipticis sive lanceolatis acutis v. acuminatis" [ovate elliptic or lanceolate, acute or acuminate], while Chamisso and Schlechtendal (1826) noted the leaves as "brevissime petiolata, ovata, acuminata" [briefly petiolate, ovate, acuminate]. Fenzl (in Ledebour, 1842) added two unnamed lusi based on pedicels 1 - 1 1/2 times longer than the calyx vs. pedicels being 2 - 5 times longer than the calyx, a distinction unique to his taxonomy.

It is evident that Fenzl (in Ledebour, 1842) considered S. borealis and S. crispa related, but separate species from a statement he placed after his S. crispa treatment: "A praecedente vix specie bene distincta, facile tamen distinguenda" or, From the preceding species [S. borealis was treated immediately before S. crispa] scarcely distinct, however

easily distinguished.

Regel (1862) expressed a desire to consider S. *crispa* as an entity within S. *borealis*. For reasons summarized earlier, Regel's names should be considered to be published at the level of form. In addition, he was unsatisfied with Fenzl's treatment of S. *crispa*, especially his inclusion of "narrow-leaved petal-bearing" plants. Regel (1862) split S. *crispa* sensu Fenzl into two portions as outlined in Figure 49.

Regel's contention of non-equivalence of S. *crispa* sensu Fenzl on the basis of admission of narrow leaves may be valid, but not on the issue of the presence of petals. Chamisso and Schlechtendal (1826) noted that S. *crispa* had petals that were "minima, calycem dimidium aequantia minorave, usque ad basin bifida, plura saepies abortiunt" [petals minimal, less than one-half the length of the calyx, bifid through to the base, more often abortive]. Fenzl (in Ledebour, 1842) followed this concept very closely in stating "petalis 3-5 calyce subdimidio brevioribus: laciniis angustissimis v. nullis" [petals 3-5, shorter than 1/2 the length of the calyx: divisions very narrow or absent]. There is nothing in Fenzl's description equivalent to Regel's definition of petal length in his S. *borealis* β *corollina* lusum a. *crispa*. An inspection of collections from LE bearing Regel's names reveals that Regel's β *corollina* a. *crispa* is not S. *crispa* at all. Hultén (1944) is correct in placing a Peters collection bearing that name under his S. *sitchana* var. *bongardiana*.

A. A. Lindsey reinterpreted Robinson's (1898) suggestion of affinities between S. *washingtoniana* and S. *crispa* when he formed the combination S. *crispa* "var. *washingtoniana* (Robinson)" on the label of a collection from Mt. Rainier (A. A. Lindsey s.n. in 1935 [CU]). I can

find no evidence that this combination was ever published; if it had been, the combination would become a synonym under S. calycantha since the specimen is a collection of pubescent-stemmed S. calycantha.

TYPIFICATION: A lectotype can be designated for S. crispa. Specimens from Chamisso's voyage to Alaska are found in 15 herbaria (Lanjouw & Stafleu, 1954), with the first set and Chamisso's original herbarium at LE (Stafleu & Cowan, 1976). Information received from LE indicated that the type of S. crispa was "unavailable" (loan invoice), although one collection that most likely was used by Chamisso and Schlechtendahl in their description (1826) was included in the loan received.

The label of the specimen selected as the lectotype (Figure 47) reads as follows:

crispa
Stellaria undulata
Semina 12
Unalaschka 17
Hb. Chamiss.

Interpreting the "17" as 1817 would make this one of the specimens which Chamisso collected on the voyage of the Rurik. "Semina 12" is probably a reference to the number of seeds, "12 sperma" included in the text (Chamisso & Schlechtendal, 1826) following the description. The label is in Chamisso's hand (fide comparison to Burdet, 1974) and is from Chamisso's herbarium, making it the best candidate for material which was actually used in writing the description. The crossed-out epithet "undulata" suggests that Chamisso and Schlechtendal may have intended to give this plant a different name.

3. Stellaria calycantha (Ledeb.) Bong., Mém. Acad. Imp. Sci. St.-

Pétersbourg, Sér. 6, Sci. Math. 2: 127. 1833.

Arenaria calycantha Ledeb., Mém. Acad. Imp. Sci. St. Pétersbourg

Hist. Acad. 5: 534. 1815. Stellaria borealis Bigelow forma α

apetala (Fenzl) Regel lusus a. ciliata Regel, Bull. Soc. Imp.

Naturalistes Moscou 35: 277. 1862. pro parte. Alsine calycantha

(Ledeb.) Rydb., Bull. Torrey Bot. Club 24: 244. 1897. TYPE:

USSR. In Sibiria orientali, without date (1804-1805 fide Hultén,

1927), Tilesius s.n. (holotype, LE, negatives provided!; photo -

MSC!, JKM!).

Alsine simcoeii Howell, Fl. N.W. Amer. 1: 83. 1897. Stellaria

borealis Bigelow var. simcoeii (Howell) Fern., Rhodora 16: 150.

1914. Stellaria calycantha (Ledeb.) Bong. var. simcoeii (Howell)

Fern., Rhodora 42: 255. 1940. Stellaria simcoeii (Howell) C.

Hitchc., Univ. Wash. Publ. Bot. 17(2): 310. 1964. TYPE: USA.

WASHINGTON. Klickitat Co.: In wet places top of Simcoe Mtns, Jul

1880, T. Howell s.n. (lectotype, here designated, ORE!(Acc. #

04593); isoelectotypes, GH!, ORE(2!), WS!).

Perennial herbs, sometimes matted at high elevations. Stems erect, rarely trailing, (2.5)4.5 - 25(35.5) cm long; internodes glabrous or pilose, occasionally ridged. Leaves simple, opposite, blades ovate, elliptic, or occasionally oblong, (2.6)5 - 24(40) mm long, (1.1)2.4 - 9.5(19) mm wide, apex acute, base rounded or attenuate, glabrous or with dorsal midrib pilose, margin smooth, glabrous, or with long cilia from base to halfway to apex, occasionally sparsely ciliate to the leaf tip, occasionally undulate; leaves sessile or rarely with a very short

petiole. Inflorescence a lax terminal cyme, rarely axillary with one terminal flower, flowers 1 - 11(29) per stem; bracts resembling leaves, (1.2, 2.3)2.8 - 14(19) mm long, 0.6 - 6(9) mm wide, margin herbaceous, or rarely with a narrow scarious margin, glabrous or ciliate as in leaves. Flowers perfect, sepals 5 or 4, ovate, basally connate, (1.3)1.4 - 2.5(3) mm long at anthesis, (1.6)1.7 - 2.8(3.6) mm long in fruit, nerves either obscure, raised in lower half of sepals, or rarely extending to the tip, apex acute, rarely obtuse, margin scarious, occasionally exceeding 0.1 mm width; petals 0 - 5, white, deeply 2-cleft, to $1/2$ X the sepals; stamens 10(8) or fewer; styles (2)3 - 5(6, 7 - seen once), yellowish or white, usually curved, (0.4)0.5 - 0.9(1.2) mm long, stigmatic along entire length. Capsules globose to globose-ovoid, walls membranous, usually dark brown or black at maturity, (2.0)2.3 - 4(4.4) mm long unopened, 2.7 - 4.5(5) mm long opened, valves 6, 8, or 10(12?), pedicels (3.5)6 - 23(49) mm long, erect, not reflexed, glabrous. Seeds reddish brown (immature) to brown (mature), 0.5 - 0.8(0.9) mm long, 0.4 - 0.7(0.8) mm wide, smooth or with small rounded tubercles. $N = 13$ (Taylor & Mulligan, 1968; Kruckeberg, unpublished); $2n = 26$ (Hartman, 1971; Morton, unpublished data). Figures 40d and 50.

Stellaria crispa and Stellaria calycantha have often been confused, especially at high elevation sites where S. calycantha becomes a small, glabrous, few-flowered plant which may assume a matted appearance reminiscent of S. crispa. The formation of a terminal cyme is the normal condition in S. calycantha, while all flowers of S. crispa are axillary, a condition only rarely obscured by irregular branching in some S. crispa collections. These plants normally have weakly-ribbed calyces, one or more short petals, four or more styles, globose-ovoid

capsules often much exceeding the calyx, and seeds which are smooth or just barely roughened; characters either rare or unknown in S. *crispa*. In areas where both species are found, there is little evidence of hybridization, most collections being easily recognized as either S. *crispa* or S. *calycantha*; the generally earlier flowering of S. *crispa* no doubt reduces hybridization possibilities.

Populations of S. *calycantha* from Alaska differ slightly from most of those found in the southern end of the range. While "southern" plants often are either entirely glabrous or have pubescent leaves and stems, Alaskan collections often have cilia along the leaf margins and glabrous stems. The northern populations often have more elongate leaves, closely approaching a shape common in S. *borealis*. The longest sepals present in S. *calycantha* plants are found in specimens from Alaska.

DISTRIBUTION: Stellaria *calycantha* is found in the mountains of western North America. Collections have been made from the Pribilof and Aleutian Islands of Alaska, the south central Alaska, and southward along the Coast Ranges to southern California and the Rocky Mountains to New Mexico. Most plants were collected at elevations between 1220 and 3720 meters. Stellaria *calycantha* reaches lower coastal sites only in southern Alaska and northwestern British Columbia. Figure 51.

Hitchcock's (in Hitchcock & Cronquist, 1964) doubt about the existence of S. *calycantha* subsp. *calycantha* in the Pacific Northwest may have in part lead to Layser's (1971) reporting what he thought to be the first occurrence of the taxon in Washington. The cited collection (Layser 310, NY, WS), however, is S. *borealis* subsp. *sitchana*.

I have seen only one report of S. *calycantha* being considered as an

introduced plant. Calder, Taylor, and Ferguson suggested that their 1954 collection of S. calycantha at the Mt. Thornhill lookout near Terrace, BC was "Introduced?" (Calder, Taylor, & Ferguson 14875 [DAO]).

ECOLOGY: This species is often found growing in mats of moss in and along cold streams, often found under Salix or Alnus or in coniferous forests. Some collections are from damp meadows, tundra, and talus slopes, indicating that S. calycantha also inhabits sunny, exposed areas.

Flowering occurs from late June through September, with a collection from coastal Alaska with a few flowers and fruit present in early June. Collections from some high altitude populations in California and Nevada indicate that flowering may begin even later, with no fruit formed as of 10 - 11 August.

PROTECTION STATUS: Reports that now would be referred to S. calycantha as treated here are listed in Table 31. Plant conservation efforts have recognized S. calycantha and S. simcoei as separate taxa, with more emphasis placed on locating and monitoring S. simcoei. This position is exemplified by comparing the Idaho data on the two names from the database of The Nature Conservancy (1986). Stellaria calycantha is listed as a species known from a large number of locations (or individuals), but of some concern in Idaho, while their record for S. simcoei indicates it is known from a far smaller number of localities/populations in Idaho.

Monitoring of S. calycantha is appropriate given the fragility of the habitat in which these plants grow and the small numbers of plants in some populations. These plants occupy areas which, at least at the present moment, are either not threatened by imminent development or are

already afforded some protection through the National Park Service. After I gained a field knowledge of habitat preferences of these plants, populations could be located easily.

COMMON NAMES: The common names which have been applied to taxa treated here within S. calycantha are listed in Table 32. The previous recognition of pilose plants as a separate species (S. simcoei) has attracted several common names for these plants. After eliminating the names that also apply to S. borealis subsp. borealis (see Table 34), those including "Simcoe Mountain" as referring specifically to the pilose plants, very few names remain. Weeden's (1981) use of "interior" for California plants arose no doubt from Munz and Keck's (1959) use of S. calycantha subsp. interior for California plants referred here to S. calycantha. Northwestern Stitchwort, the name chosen by Kartesz and Kartesz (1977) for S. simcoei, seems the best choice for the species since most of these plants are indeed found in the Pacific Northwest.

REPRESENTATIVE SPECIMENS: CANADA. ALBERTA. Banff Nat. Park: Wet meadow by lake, Sunshine Ski Lodge, Fatigue Pass, 7 Aug 1945, Porsild & Breitung 13925 (CAN). Improvement Dist. 6: Along streamlet, Carbondale River, Crowsnest area, 5000 ft, 17 Jul 1961, R. T. Ogilvie s.n. (DAO [photo of UAC], UBC). Waterton Lakes Nat. Park: Twin Lakes Trail, 5900 ft, 29 Jul 1969, Blais & Nagy 2309 (ALTA, CAN).

BRITISH COLUMBIA. Cariboo Dist.: McLeod's Lake, 24 Jul 1875, Macoun, Herb. Geol. Surv. Canada 3 (GH). Cassiar Dist.: gorge between Landslide and Forget-Me-Not Ridges, S face of Ghost Mtn, Gladys Lake area, 57°35'N 128°47'W, 5000 ft, 14 Jul 1975, J. Pojar s.n. (UBC); Mile 46, Haines Road, 200 m, 15 Jul 1956, Taylor, Szczawinski, & Bell 1405 (GH, UBC). Coast Range 4 Dist.: NE slope of Hierochloë Peak, Ilgachuz

Mtns, 52°45'N 125°15W, 6300-6500 ft, 15-25 Aug 1972, Taylor, Beil, Marchant, & Oliver 5709 (DAO, UBC). Kootenay Dist.: Asulkan Valley, near 51°30'N, 5000 ft, 17 Aug 1904, Petersen 509 (CM, GH, MO, NY, PENN, PH, US). Lillooet Dist.: below Mt Matier, 14.5 mi E of Mount Curry village, 5800-6000 ft, 7 Aug 1974, Pinder-Moss & Schofield 922 (DAO, UBC). New Westminster Dist.: Glacial moraines, Sphinx Glacier foreland, Garibaldi Park, 5000 ft, 26 Jul 1965, B. Fraser s.n. (UBC). Peace River Dist.: Outlet, E end of Fern Lake, 4500 ft, 5 Aug 1977, Argus & Haber 10630 (CAN, COLO). Queen Charlotte Dist.: Moresby Island, mtn at W end of Mosquito Lake, Cumsheewa Inlet, 2600 ft, 24 Aug 1957, Calder & Taylor 23740 (DAO); Moresby Island, talus slopes above Lake Takakia, 10 mi S of Moresby Logging Camp, 1900-2400 ft, 25-30 Jul 1964, Calder & Taylor 36357 (DAO).

NORTHWEST TERRITORIES. MACKENZIE DIST.: Terminal moraine, near Flat River, Mackenzie Mtns, 62°02'N, 128°10'W, 5500 ft, 8 Aug 1967, Spicer 1694 (DAO).

YUKON TERRITORY. Streamlet, Mile 100, Haines Highway, ca 4000 ft, 14 Aug 1967, Schofield & Crum 8293 (CAN, UBC).

USA. ALASKA. Alaska Peninsula: cracks in sea cliff, NW section of Chowiet Island, 56°02'N 156°42'W, 30 m, 13 Jul 1977, Hatch 185 (ALA, DAO, UBC). Brooks Range area: Mountains, NW of Walker Lake, upper Kopuk River, 16 Aug 1950, Jordal 3991 (BH, MICH). Chugach Nat. Forest: Port San Juan, Evans Island, 15 Jul 1948, Eyerdam 5886 (CAN, MO). Glacier Bay Nat. Monument: shore of Muir Inlet, 29 Jun 1967, Argus & Chunys 6402 (CAN, GH, RM). Kenai Peninsula: Trail Creek, Seward, 570 ft, 26 Jun 1980, Helmstetter 80-101 (ALA). Ketchikan Gateway Bor.: Disappearing Lake, near Chickamin Glacier, 21 mi NW of Hyder, 17 Jul 1941, McCabe

8998 (NY, UC, UTC, WTU[2]). Matanuska-Susitna Bor.: Peters Hills Mtns, 26 mi NW of Talkeetna, T29N R8W, 3000-3300 ft, 20 Jul 1980, Siplivinsky 811 (COLO).

ALASKA. Aleutian Islands: Amchitka Island. Pond 32, SW of NW end of Charlie Runway, 28 Jun 1962, Reich & McCann 439 (ALA, CAN, F, ISC, WVA); bare rock in the tundra, near Infantry Road and Cyril Cove, 11 Aug 1966, Shacklette 7443 (MICH, S). Unalaska Island. Sea-beach at Dutch Harbor, 3 Jul 1899, Jepson 104 (UC). Pribilof Islands: Tolstoi, St. Paul Island, 12 Jul 1923, E. C. Johnston s.n. (GH, MT).

CALIFORNIA. Colusa Co.: Cirque between E and W Peaks of Snow Mtn, ca 10 mi W of Stonyford, ca 6700 ft, 1 Jul 1980, Heckard with Hickman 5277 (JEPS). Fresno Co.: Huntington Lake, 20 Jul 1943, H. M. Pollard s.n. (CAS); Bubbs Creek Canyon, in vic. of Vidette Meadows, 9500-10000 ft, 21 Jul 1948, Howell 24815 (CAS). Inyo Co.: Cirque at head of Lone Pine Canyon, E of Mt Muir, vic. of Mt Whitney, 12200 ft, 20 Aug 1937, Sharsmith 3314 (CAN, DS, GH, UC). Mono Co.: below Spuller Lake, Lake Valley, Harvey Monroe Hall Natural Area, E base of White Mtn, 8 Sep 1940, Clausen 1824 (CAS, DS[2], UC). San Bernardino Co.: High Creek, San Bernardino Mtns, 23 Aug 1923, Peirson 4158 (JEPS). Shasta Co.: Wet meadow above Paradise Meadow, NE of Lassen Peak, Lassen Volcanic Nat. Park, 8200 ft, 8 Aug 1957, Gillett 999 (CAS, MSC, UC). Siskiyou Co.: Sunny gravelly edge of streamlet, Jaynes Canyon, Siskiyou Mtns, T47N R10W S12, 6400 ft, 26 Jul 1935, Wheeler 3697 (GH, MO, NY, US). Tehama Co.: Along cold spring drainage into ditch, W side of CA 89, S of Sulphur Works Entrance, Lassen Volcanic Nat. Park, 6550 ft, 10 Aug 1980, Rabeler 518 (MSC + 1). Tuolumne Co.: NW plateau of Mt Dana, 11150 ft, 18 Sep 1936, Sharsmith 2333 (DS, GH, UC).



COLORADO. Arapaho Co.: Mountain torrent, at foot of Berthoud Pass, US 40, Winter Park side, 7 Jul 1974, Morton & Venn NA7341 (JKM). Clear Creek Co.: Between Mt Bancroft and James Peak, Loch Lomond, 11140 ft, 8 Aug 1972, Weber, Koponen, & Nelson 14523 (BH, CAN, COLO, CS, UTC). Larimer Co.: Headwaters of Beaver Creek, 50 mi W of Fort Collins, 9500-10000 ft, 19-20 Jul 1898, C. S. Crandall s.n. (MSC); seepage slope, 2 mi from Estes Park entrance, Rocky Mountain Nat. Park, 7 Jul 1974, Morton & Venn NA7325 (JKM). Pitkin Co.: Above hwy betwn Lincoln Gulch and Lost Man Camp, Roaring Fork River, 9500 ft, 9-13 Jul 1963, Weber 12085 (COLO).

IDAHO. Boise Co.: Stream edge above Bull Trout Lake, 35 mi W of Stanley, 6900 ft, 3 Aug 1941, Cronquist 3607 (MO, UTC). Elmore Co.: Near Big Roaring River Lake, 20 mi N of Pine, 8000 ft, 25 Aug 1947, Meyer & Meyer 2345 (F, MO, NY, UC). Kootenai Co.: Packsaddle Peak, 6 Aug 1892, Sandberg, MacDougal & Heller 865 (CAS, GH, NY, US); springy places in Cañ[ny]ons, ridges S from Wiessner's Peak, 1700 m, 28 Jul 1895, Leiburg 1396 (DS, F, GH, MO, ORE, RM, UC; excl. NY, US). Valley Co.: West End Creek, tributary to Sugar Creek, Stibnite area, T18N R9E S2 NE1/4, 6500 ft, 11 Jul 1980, Grimes & Packard 1792 (NY).

MONTANA. Beaverhead Co.: Blair Lake, T15S R1E S2 NW 1/4, 8130 ft, 25 Jul 1979, Lowry 2630b (MO). Cascade-Judith Basin Cos.: Long Baldy, Little Belt Mtns, 7000-8000 ft, 19 Aug 1896, Flodman 431 (GH, MIN, MO, US). Glacier Co.: W bank of Lunch Creek, 0.75 mi E of Logan Pass Summit, Glacier Nat. Park, 6400 ft, 15 Aug 1980, Rabeler 549 (MSC). Madison Co.: Spanish Basin, Madison Range, 6000 ft, 18 Jul 1896, Flodman 430 (MIN, MO, NDG, NY[2], US).

NEVADA. Elko Co.: Upper basin meadow, Hayes Creek, Independence Mtns, 11 Aug 1943, Maguire & Holmgren 22452 (GH, NY, UC, UTC).

Esmeralda Co.: Chiatovitch Creek, White Mtns, 10300 ft, 16 Jul 1931, Duran 3122 (UC). White Pine Co.: Lehman Creek Basin, Wheeler Peak, Snake Range, 8200 ft, 2 Aug 1941, Maguire 21067 (DAO, DS, GH, NY, UC, UTC[2], WS, WTU).

NEW MEXICO. Colfax Co.: On jeep trail roadcut, 1 mi S of Clear Creek Camp, Philmont Scout Ranch, Cimmaron, 10200 ft, 27 Jul 1968, Hartman 2496 (RM). Santa Fe Co.: Stream in aspen woods, road to Santa Fe Basin, ca 10000 ft, 26 Jun 1974, Morton & Venn NA7099 (JKM).

OREGON. Deschutes Co.: W end of Paulina Lake, 2100 m, 29 Jul 1894, Leiberg 581 (DS[3], F, GH, MO, NY, ORE, RM, US); Park Meadow, E fork of Park Creek, Three Sisters Wilderness, W of Bend, 6150 ft, 14 Aug 1953, Ireland 3274 (ORE); S bank of Paulina Creek, E of top of Paulina Creek Falls, 6300 ft, 4 Aug 1980, Rabaler 490 (MSC + 1). Harney Co.: Steens Mtn region, 17 mi E and 9.75 mi due S of Frenchglen, T33S R33E S12, 8000 ft, 18 Aug 1954, Hansen 988 (OSC, WS, WTU). Hood River Co.: Pool along N side of road to Hood River Meadows CG, 0.25 mi E of jct. with road to Hood River Meadows Ski Lodge, at Bennett Pass, Mt Hood Nat. Forest, T3S R9E S11 SW1/4, 6 Aug 1980, Rabaler 486 (MSC + 1). Klamath Co.: Along banks of tributary of Munson Creek, near Castle Crest Wildflower Garden, Crater Lake Nat. Park, 6475 ft, 5 Aug 1980, Rabaler 494 (MSC + 2). Linn Co.: Spring W of Carpenter Mtn lookout, H. J. Andrews Expt. Area, T15S R6E S7, 5000 ft, 25 Jul 1968, Franklin 775 (RM). Wallowa Co.: Wet bank, Ice Lake, Wallowa Mtns, 14 Jul 1934, Peck 18525 (WILLU).

UTAH. Duchesne Co.: N shore of Third Chain Lake, Krebs Basin, SE slope of Mt Emmons, 11000 ft, 21 Jul 1933, Hermann 5174 (MO). Juab Co.:

Head of Tom Canyon, above Stewart's Cabin, Deep Creek Range, 9000 ft, 5 Aug 1944, Holmgren, Skanchy, & Walker 3606 (GH, NY, US, WS, WTU[2]).

Summit Co.: In dense mats, streamside in deep ravine, Henrys Forks Basin, Uinta Mtns, 10900 ft, 12 Aug 1936, Maguire, Hobson, & Maguire 14591 (CAN, UTC, WTU).

WASHINGTON. Chelan Co.: Stevens Pass, Cascade Mtns, 4000 ft, 26 Jul 1934, Jones 5700 (GH). Klickitat Co.: Wet places, top of Simcoe Mtns, Jul 1880, T. Howell s.n. (GH, ORE[3], WS). Okanogan Co.: 16 mi up Boulder Creek Road, T37N R23E S32-33, 1 Jul 1958, Hitchcock & Muhlick 21641 (DS, NY, RM, WS). Pend Oreille Co.: Near Bunchgrass Meadow, T37N R44E S25 NE1/4, ca 5000 ft, 5 Aug 1967, Layser 263 (NY). Pierce Co.: Paradise River, Mt Rainier, 25 Aug 1895, Allen 159 & 159a (CAN, CS, DS, F, GH [2 + 1 159a only], MIN, MO, MSC, NY, RM, UC, VT, WS). Skamannia Co.: wet shady places [Butterfly Lake fide W. Weber annotation, WS, WTU], 10 Jul 1891, Suksdorf 2194 (F, GH(2), MIN, MO, MSC, MT, NY, UC, US, WS, WTU). Whatcom Co.: Below glaciers on Heliotrope Ridge, Mt Baker, 7500 ft, 11 Aug 1934, Thompson 11247 (US, WTU); mtn rivulet, Chain Lakes, Mt Baker Nat. Forest, 20 Aug 1939, Muenschner 10571 (COLO, CU, DS, F, GH, NY, PH, UC, US, WS, WTU); open alpine slopes, Coleman Glacier, Mt Baker, 6 Aug 1963, Kruckeberg 5690 (WTU). Yakima Co.: Mt Adams, 15 Aug 1882, T. J. Howell s.n. (CM, F, MICH, MIN[2], MO, NY[4], ORE[2], OSC, PH, US); along streams, Mt Paddo [Adams], 6-7000 ft, 17 Sep 1894, Suksdorf 2302 (F, GH[2], ISC, MIN, MO, NDG, NY[3], ORE, UC[2], US, WS, WTU); streambanks, Mt Paddo [Adams], 6-7000 ft, 17 Sep 1894, Suksdorf 2303 (F, GH[2], ISC, MIN, MO, NDG, NY[2], NYS, US, WS).

WYOMING. Albany Co.: 1/2 way up W side of Snowy Range Pass [WY 230], Medicine Bow Mtns, 5 Jul 1974, Morton & Venn NA7286 (JKM). Carbon

Co.: Ferris Mtns, 25 Jul 1898, Nelson 4973a (RM); Big Creek Park, 10 mi W of Hwy 230, Medicine Bow Nat. Forest, 8500 ft, 9 Jul 1969, Hartman 2911 (RM). Fremont Co.: 1 mi W of Fiddler Lake, W of Lander, Shoshone Nat. Forest, 9800 ft, 5 Aug 1969, Hartman 2926 (RM). Teton Co.: East De Lacy's Creek, Yellowstone Nat. Park, 7500 ft, 10 Aug 1897, Rydberg & Bessey 4013 (CAN, F, GH, NDG, NY).

TYPIFICATION: The oldest name for these plants is Arenaria calycantha Ledeb., published in 1815. The label of the type specimen (Tilesius s.n., LE, photo at JKM!, MSC!), shown in Figure 50, is in the hand of Ledebour (checked against samples of his handwriting in Burdet [1979] and labels in Lipschitz & Vassilczenko [1968]). The specimen can be clearly identified as Stellaria calycantha, confirming Hultén's (1928) statement about the conspecificity of A. calycantha and S. calycantha (Ledeb.) Bong.

Although a definitive statement about the ploidy level of the type collection cannot be made, there is a distinct possibility that it is a diploid plant. The plant came from eastern Siberia, the only area outside of western North America where a diploid chromosome count of S. calycantha has been recorded (Zhukova, 1980). Oblong leaves are more typical of tetraploid plants, but are occasionally seen in short-styled material in southwestern Alaska. Capsule shape is not entirely conclusive since one capsule is subglobose, while the other is ovoid. Ledebour (1815) did not describe the styles and unfortunately they are not visible in the photographs.

It might be argued that Chamisso and Schlechtendahl's (1826) assignment of a plant resembling S. calycantha to S. aquatica Poll., a

combination published in 1776 (Pollich, 1776) should be considered. Their usage is clearly a misidentification, S. aquatica Poll. being a synonym of S. alsine Grimm (= S. uliginosa Murray), a plant with small axillary, scarious-bracted cymes.

Excluding the misidentification by Chamisso, the first name applied to American material with characteristics matching those of S. calycantha is Stellaria calycantha (Ledeb.) Bong. Bongard (1833) based his combination on collections of Dr. Mertens made at Sitka, noting that he thought it to be conspecific with Ledebour's earlier A. calycantha. An inspection of Mertens collections (GH, LE) indicates that the plants he had are clearly S. calycantha as recognized here; delicate plants with small leaves, short curved styles, and small subglobose capsules.

An inspection of the specimens received from LE revealed a curious situation which I feel deserves some attention. A problem arises from the notation of "(p.p)" on the label of a Mertens collection in Bongard's hand (comparison via sample in Lipschitz & Vassilczenko, 1968) bearing both the name and number (No. 19) used in Bongard's (1833) description of S. calycantha. There is a second sheet at LE with the same label data, but bearing material of S. crispa. Could Ledebour's description of S. calycantha be based on a mixed collection? Evidence that I have assembled suggests not.

First, Bongard (1833) recognized S. crispa, noting it as "20." in his list, citing that he had nothing to add to Chamisso's description. Second, the description of S. calycantha includes several descriptors which apply nicely to the first sheet (i.e. S. calycantha), but not to the second sheet (i.e. S. crispa). The stem length of "5 - 7 pollices" (pollex = approximately 1 inch, per Stearn, 1966) fits the S. calycantha

plants, but is clearly exceeded by one of the stems on the second sheet. The description of the leaf margin as "pilis albis margine lanuginosa-ciliata" applies to S. calycantha, but not to S. crispa. The simple statement "Cyma dichotoma" also indicates that he had a specimen of S. calycantha, the material on the second sheet with strictly axillary flowers not at all suggesting a cyme.

A statement made by Fernald (1914) lends further credence to the argument. In commenting on the correctness of applying Bongard's S. calycantha to the small northwestern plants, Fernald (1914) noted "Bongard's own species, ... as shown by a cotype [= isotype, fide Lawrence, 1951] in the Gray Herbarium labeled by Bongard himself as well as by his description, ..." The specimen that Fernald refers to (K. H. Mertens s.n., GH) is labeled S. calycantha in Bongard's hand (checked against Lipschitz & Vassilczenko, 1968) and matches the plants on the first of the "19(p.p)" sheets at LE. Further searching at GH revealed a collection of S. crispa (K. H. Mertens s.n., GH) bearing the same label inscription and handwriting, adding to the argument that Bongard indeed did consider these plants to represent different species.

Torrey and Gray (1838) introduced the name to American literature, translating Bongard's description for their text. Macoun (1883), Piper (1906), and Rydberg (1917) segregated S. calycantha from S. borealis on about the same set of characters as those used in this treatment.

4. Stellaria borealis Bigelow, Fl. Boston. ed. 2. 182. 1824.

Perennial herbs. Stems erect, sometimes reclining or matted, (3)9 - 72(110) cm long; upper internodes glabrous or less frequently papillate, often ridged. Leaves simple, opposite, blades oblong to lance-linear, rarely ovate or linear, (5)7.5 - 54(87) mm long, (0.9)1.8 - 9(22) mm wide, apex acute, base truncate, rounded, or rarely attenuate, glabrous, margin sparsely ciliate to the tip, with or without intermixed papillae, or papillate with minute basal cilia, rarely glabrous; leaves sessile or rarely with a petiole to 3 (rarely to 5) mm. Inflorescence a lax terminal (very rarely axillary) cyme, rarely axillary with one terminal flower, flowers (1)5 - 43(280) per stem; bracts resembling leaves or uppermost reduced and mostly scarious, 1 - 45(58) mm long, (0.3)0.6 - 9(11) mm wide, margin herbaceous, or with a wide scarious margin, pubescence as in leaves. Flowers perfect, sepals 5, seldom 4, basally connate, ovate to lanceolate, (1)1.3 - 3.7(4.1) mm long at anthesis, (1.6)1.9 - 4.2(4.7) mm long in fruit, nerves becoming evident ridges in lower half of the sepals, or less frequently extending to the tip, apex acute, very rarely obtuse, margin scarious, exceeding 0.1 mm width, margins occasionally ciliate; petals 0 - 5, if present, white, deeply 2-cleft, less than 1/2 X (rarely equal to) the sepals; stamens 10(8) or fewer; styles (2)3 - 4(6), white, erect and later spreading, (0.6)0.9 - 1.8(2.0) mm long, stigmatic along entire length. Capsules ovoid, wall membranous, translucent or darkened, (2.1)2.9 - 7 mm long unopened, (2.7)3.6 - 7 mm long opened, valves 6 - 10(12), pedicels (3)6 - 33(65) mm long, erect, arching, or sometimes reflexed, glabrous. Seeds reddish brown (immature) to brown (mature), (0.6)0.7 - 0.9(1.0) mm long, 0.5 - 0.7(0.9) mm wide, surface appearing only

indistinctly roughened, or occasionally tuberculate. $N = 26$ (Morton, unpublished); $2n = 48$ (Knaben, 1968); 52 (Löve & Löve, 1966; Hedberg, 1967; Hartman, 1971; Löve & Löve, 1982; Chinnappa, 1985; Morton, unpublished).

4a. Stellaria borealis Bigelow subsp. borealis

Stellularia borealis (Bigelow) Kuntze, Rev. Gen. 1: 55. 1891.

Alsine borealis (Bigelow) Britton, Mem. Torrey Bot. Club 5: 149.

1894. TYPE: USA. NEW HAMPSHIRE. Coos Co.: White Mtns. alp.

The origl. station [of Bigel. - NY only], without date, E.

Tuckerman s.n. (neotype, here designated, DWC!; isoneotype, NY!).

Spergulastrum lanceolatum Michaux, Fl. Bor.-Amer. 1: 275. 1803.

Micropetalon lanceolatum (Michaux) Pers., Syn. Pl. 1: 509. 1805.

Micropetalum lanceolatum (Michaux) Pursh, Fl. Amer. Sept. 1: 320.

1814, orth. var. Stellaria lanceolata (Michaux) Torrey, Fl. N.

Mid. U.S. 453. 1824, non Poiret (1806). Stellaria borealis

Bigelow var. floribunda Fern., Rhodora 16: 151. 1914. pro parte.

Stellaria calycantha (Ledeb.) Bong. var. floribunda (Fern.)

Fern., Rhodora 42: 255. 1940. pro parte. TYPE: CANADA. QUÉBEC:

Riv. Sagney, Qus Mistasinus, in borealibus Americae

septentrionalis, without date [Aug 1792 fide Michaux in Sargent

(1889)], A. Michaux s.n. (lectotype, here designated, P, IDC

microfiche 6211, card 62, specimen 18 [MICH!]).

Bigelowia montana Raf., Amer. Monthly Mag. & Crit. Rev. 1: 442. 1817.

Arenaria montana (Raf.) Raf., J. Phys. Chim. Hist. Nat. Arts. 89:

259. 1819. Bigelonía montana Raf. ex B.D. Jackson, Index Kew. 1: 302.

1893, nom. sphalm. Original material: USA. NEW HAMPSHIRE.

Coos Co.: summit of Mt Washington, J. Boott, Aug 1816. not seen.

Stellaria uliginosa Murray β alpestris Hartman, Kongl. Vetensk. Acad.

Handl. (ser. 3, vol. 6). 1818: 145. 1818. Stellaria alpestris

Hartman, Handb. Skand. Fl. ed. 2. 123. 1832, non Fries (1832,

emend. 1845). Original material: SWEDEN. Jamtland, at the foot

of Mt. Areskutan, 1813, L. L. Laestadius s.n. (UPS!).

Stellaria borealis α Hook., Fl. Bor.-Amer. 1: 94. 1830. Original

material: CANADA. Fort Norman, J. Richardson. not seen.

Stellaria borealis β Hook., Fl. Bor.-Amer. 1: 95. 1830. Original

material: CANADA. Franklin's Journey, without date (1821?), J.

Richardson s.n. (NY! - ex Torrey).

Stellaria alpestris Fries, Novit. Fl. Suec. Mant. I. 10. 1832, excl.

β . Stellaria alpestris var. aliflora Fries, Cat. Herb. Norm. III,

no. 31. 1837. Stellaria borealis Bigelow var. calycantha

(Ledeb.) Fries, Novit. Fl. Suec. Mant. III. 196. 1845.

?Stellaria alpestris forma calycantha Murb., Bot. Not. 1899: 213.

1899. Original material: SWEDEN. Herjedal, bor. occid.

Funnesberget, Aug, without year, K. F. Thedenius, Fries Herb.

Normale Fasc. III, No. 31 (MO!, SI, UPS!).

Stellaria borealis Bigelow var. α apetala Fenzl in Ledeb., Fl. Ross.

1: 382. 1842. Original material not seen.

Stellaria borealis Bigelow var. β corollina Fenzl in Ledeb., Fl.

Ross. 1: 382. 1842. Original material not seen.

Stellaria borealis Bigelow var. alpestris A. Gray, Manual. ed. 5. 93.

1867, non Fries (1832, emend. 1845). Stellaria borealis Bigelow

var. corollina Robinson, Proc. Am. Acad. 29: 286. 1894, non Fenzl

(1842), pro parte. Alsine borealis Bigelow var. alpestris

Britton, Mem. Torrey Bot. Club 5: 149. 1894. Alsine borealis
 Bigelow var. alpestris Britton & A. Brown, Ill. Fl. N. U.S. 2:
 24. 1897, pro parte. Stellaria borealis Bigelow var. floribunda
 Fern., Rhodora 16: 151. 1914, pro parte. Stellaria calycantha
 (Ledeb.) Bong. var. floribunda (Fern.) Fern., Rhodora 42: 255.
 1940, pro parte. TYPE: USA. MICHIGAN. Keweenaw Co.: Head of
 Portage Lake, Lake Superior, 1863, J. W. Robbins 62a (lectotype,
 here designated, GH!).

Stellaria borealis Bigelow forma apetala Kurtz, Bot. Jahrb. Syst. 19:
 366. 1894. TYPE: USA. ALASKA: Gebiet des Lynn-Canals: schattige
 ufer des Takhn, 20 Jul 1882, A. & A. Krause 336 (Holotype, B
 [destroyed?]; isotype, CORD!).

Stellaria borealis Bigelow var. isophylla Fern., Rhodora 16: 150.
 1914. Stellaria calycantha (Ledeb.) Bong. var. isophylla (Fern.)
 Fern., Rhodora 42: 255. 1940. Stellaria calycantha (Ledeb.)
 Bong. var. isolepis Welsh, Anderson's Fl. Alaska. 96. 1974, orth.
var. TYPE: USA. NEW HAMPSHIRE. Cheshire Co.: Gap Mtn, Troy, 13
 Jun 1898, E. L. Rand & B. L. Robinson 459 (holotype, GH!;
 isotype, NEBC!).

Stellaria calycantha (Ledeb.) Bong. var. laurentiana Fern., Rhodora
 42: 255, pl. 602, fig 1, 4. 1940. TYPE: CANADA. QUÉBEC. Gaspé-
 Ouest Co.: Calcareous sea-cliffs and rock slides by the Gulf of
 St. Lawrence, Christie, 25 Jul 1922, M. L. Fernald & A. S. Pease,
 Fl. Quebec 25058 (holotype, GH!; isotypes, CAN!, MT!, [NY!]).

Stellaria calycantha (Ledeb.) Bong. subsp. interior Hultén, Acta
 Univ. Lund. n.s. 40(1): 648. 1944. TYPE: CANADA. YUKON
 TERRITORY. Bonanza Creek, Dawson, 12 Jun 1914, A. Eastwood 196

(holotype, S!; isotypes, CAN!, CAS[2!], GH!, UC!, US!).

Stellaria calycantha (Ledeb.) Bong. var. latifolia J. Boivin, Canad.

Field-Naturalist 65: 7. 1951. TYPE: CANADA. ALBERTA.

Strathcona Co.: Spruce woods, 1/8 mi N [or few rods S, just S] of Davis Lake, 5 mi SE of Fort Saskatchewan, 24 Jul 1945, G. H.

Turner 4590 (holotype, DAO!; isotypes, ALTA!, UBC!).

Perennial herbs. Stems erect, sometimes matted (3)9 - 40(59) cm long; upper internodes glabrous or less frequently papillate, very rarely pubescent, often ridged. Leaves simple, opposite, blades oblong to lanceolate, rarely ovate, (5)7 - 36(68) mm long, (0.9)1.8 - 7.5(16) mm wide, apex acute, base truncate, rounded, or rarely attenuate, glabrous, margin sparsely ciliate to the tip, with or without intermixed papillae, or papillate with tiny basal cilia, rarely glabrous; leaves sessile or rarely with a petiole to 3(very rarely 5) mm. Inflorescence a lax terminal (very rarely axillary) cyme, rarely axillary with one terminal flower, flowers (1)5 - 44(123) per stem; bracts resembling leaves or uppermost reduced and primarily scarious, 0.9 - 20(30) mm long, (0.3)0.6 - 5.5(7.5) mm wide, margin herbaceous, or with a wide scarious margin, pubescence as in leaves. Flowers perfect, sepals 5, seldom 4, basally connate, ovate or sometimes lanceolate (1)1.3 - 3.0(3.5) mm long at anthesis, (1.6)1.9 - 3.3(4.7) mm long in fruit, nerves becoming evident ridges in lower half of the sepals, rarely beyond, apex acute, very rarely obtuse, margin scarious, exceeding 0.1 mm width, margin occasionally ciliate; petals 0(- 5), if present, white, deeply 2-cleft, less than 1/2 X the sepals (very rarely equalling the sepals); stamens 10(8) or fewer; styles (2)3 - 4(6), white, erect and later spreading, (0.6)0.9 - 1.6(1.9) mm long, stigmatic along entire

length. Capsules ovoid, walls membranous, translucent or darkened, (2.1)2.9 - 4.5(5.2) mm long unopened, (2.7)3.6 - 5.1(6) mm long opened, valves 6 - 10(12), pedicels (3)6 - 33(42) mm long, erect, sometimes arching, seldom reflexed, glabrous. Seeds reddish brown (immature) to brown (mature), (0.6)0.7 - 0.9(1.0) mm long, 0.5 - 0.7(0.9) mm wide, surface appearing only indistinctly roughened, or occasionally tuberculate. $N = 26$ (Morton, unpublished); $2n = 48$ (Knaben, 1968); 52 (Löve & Löve, 1966; Hedberg, 1967; Hartman, 1971; Löve & Löve, 1982; Chinnappa, 1985; Morton, unpublished). Figures 40b and 52.

Plants of Stellaria borealis subsp. borealis collected after mid-July which bear flowers but no fruit should be inspected carefully since they may represent S. borealis $\times$ S. longifolia plants (see description of that taxon). If enlarged reddish anthers are present, the specimen may be a S. borealis subsp. borealis plant infected with anther smut (Ustilago violacea); a characterization of infected plants is given in the discussion on Floral Morphology.

DISTRIBUTION: Stellaria borealis subsp. borealis is the most widely distributed taxon within the S. calycantha complex. Plants are found from Alaska across northern Canada into Québec, Labrador, and Greenland southward in the East to a single population in northern West Virginia and many sites around Lake Superior and in the West as widely scattered populations in the Rocky Mountains as far south as Utah. Although most populations of S. borealis along the Pacific Coast between British Columbia and California represent S. borealis subsp. sitchana, a few collections of S. borealis subsp. borealis have been made in California, Oregon, Washington, and British Columbia. Bosseaux (1965)

reported Stellaria borealis in his floristic study of St. Pierre and Miquelon; this report could not be confirmed. Stellaria borealis subsp. borealis has been collected at elevations from sea level to 1917 meters in eastern North America and sea level to 3500 meters in western North America. Western populations are known from elevations over 1015 meters except in northwestern Canada and Alaska. Figure 53.

Two reports of Stellaria borealis subsp. borealis outside of the range shown in Figure 53 have been noted, one of which can be discounted. Fernald (1950) listed S. calycantha var. floribunda as present in Arizona. The GH specimen of Palmer 55 bears Fernald annotations as S. borealis (and later S. calycantha) var. floribunda. The collection locality is listed as "Beaver City" on that sheet, the title of the printed label is "Southern Utah, Northern Arizona, &c."; Palmer collected it at Beaver City, Utah (fide McVaugh, 1956). Neither Stellaria calycantha or S. borealis is not known from Arizona (Lehr, 1978).

Stellaria calycantha is reported from Becker Co., Minnesota in the Atlas of the Flora of the Great Plains (Great Plains Flora Association, 1976) and in Larson (1986). G. E. Larson (pers. comm.) stated the specimen supporting this record might be at NDA; this report could not be confirmed.

The only reports of Stellaria borealis being considered as an introduced plant are referable to S. borealis subsp. borealis. Polunin (1940) thought a collection that he made near an old house at Burwell, Labrador, represented material which was "just possibly introduced. Ownbey and Ownbey gave no reason, but included the phrase "Probably introduced" on the label of their 1948 collection of S. borealis from

Susie Island, Minnesota (Ownbey & Ownbey 1037; MIN, NY, UC, WS). C. E. Garton noted that S. borealis was expanding onto recently constructed road shoulders west of Thunder Bay in 1981, describing one collection as "clearly adventive after [sic] road construction" (Garton 20172; CAN, LKHD, MICH).

The summary of the collections of Stellaria borealis subsp. borealis plants infected with anther smut, Ustilago violacea, in Table 35 indicates that the occurrence of this fungus on Stellaria borealis is, as McCain and Hennen (1986) suggest could be the case for many pathogenic fungi, more common and widespread than any previous information would suggest. All of the records of U. violacea on Stellaria listed by Zundel (1953) are from Europe except for a report on S. borealis from Greenland. The only North American records of U. violacea on Stellaria which Savile (1953, 1957) had seen were a collection of S. calycantha from Kenai Peninsula, Alaska, and an occurrence on S. longipes at Yellowknife, Northwest Territories. As noted in Table 35, smut-infected plants of S. borealis subsp. borealis examined were collected from nine Canadian provinces and two states, the earliest collection made in northern Manitoba in 1854 (McTavish s.n. [CAN]).

ECOLOGY: Stellaria borealis subsp. borealis has been collected in a wide variety of habitats. Many collections are from populations in spruce - fir sphagnum bogs, cedar swamps, stream banks, willow and alder thickets, and wet deciduous or coniferous forest openings. Limestone cliffs and river gravel support many populations in eastern Canada, some being the source of the large plants which Fernald (1940) described as S. calycantha var. laurentiana. Stellaria borealis also inhabits

roadside ditches and damp tundra in northern areas of Canada.

Flowering has been reported as early as 8 May in New York, with most collections from late May (early June in the West) through early September bearing flowers. The first killing frost of the growing season may signal the end of flowering; a few flowering collections have been made as late as 9 October. Fruit is present in southern areas by early June (mid-July in the Northwest).

PROTECTION STATUS: Reports that are attributable to S. borealis subsp. borealis are shown in Table 33. The Manitoba record in Kartesz and Kartesz (1977) is suspect on the basis of the absence of the taxon from the provincial listing (White & Johnson, 1980) and the range data provided in this study. As noted in the numerical analyses, plants from Québec referred to either S. calycantha vars. sitchana or laurentiana are luxuriant specimens of S. borealis subsp. borealis which, although appearing large in many features, do not merit separate taxonomic recognition. Bouchard et al. (1985) listed S. calycantha var. sitchana among their compilation of 408 rare plants found in Québec, but did not include it in their list of 85 plants which they suggest as "priority cases for future research and preservation."

After eliminating these records, the remaining reports of rarity are from the southeastern portion of the range of S. borealis subsp. borealis, where the taxon is known from only a few sites. From my experience in trying to locate populations of S. borealis in the eastern United States, I would hasten to add a note of support to these listings; the only locality in this region where it appears to be common is the summit of Mt. Washington, New Hampshire. In spite of the large number of older collections from the Middle Atlantic and New England

states, only a very few collections made since 1960 (see Figure 53) were encountered in this study. No recently collected specimens were seen from Connecticut, Rhode Island, or New Jersey, although Snyder and Vivian (1981) reported it as extant in two counties in New Jersey in 1980. This rarity is largely attributable to habitat loss from development as the population of this region has increased over the last century.

Although not recognized yet through any formal listings, a similar situation may be developing in the Great Lakes region, as the accompanying map (Figure 53) illustrates. Collections made since 1960 are from the northern portions of each state while early collections show that the range of S. borealis subsp. borealis extended further southward. As I discovered through growing the various taxa, S. borealis subsp. borealis would grow under culture in East Lansing, nearly 200 miles south of the nearest post-1960 collection. The very limited tolerance to drought expressed by these plants suggests that destruction of cold bogs in southern areas to be a primary factor in reducing its frequency.

In answering a question about the whereabouts of Lake Harriet, G. B. Ownbey (pers. comm.) suggested habitat destruction associated with the expansion of Minneapolis as a key factor in eliminating southern populations of northern plants (e.g. S. borealis) from the bogs that formerly were found near the Twin Cities. If similar development activity occurs in northern sections of the Great Lakes States, S. borealis in that region may also be threatened.

COMMON NAMES: The common names which have been applied to S. borealis var. borealis are listed in Table 34. Most recent authors

appear to agree on the use of "Northern" as part of the name, the second word being of their preference for Chickweed, Starwort, or Stitchwort.

REPRESENTATIVE SPECIMENS: CANADA. ALBERTA. Banff Nat. Park: Boggy ground, foot of Squaw Mtn near Banff, 4500 ft, 22 Jul 1899, McCalla 2407 (ALTA, CU, NY, US, WTU). Improvement Dist. 14: Beside trail between Red Rock Lake and Wildhay River, [Willmore] Wilderness Park, ca 4600 [ft], 24 Jul 1965, Packer 3378 (ALTA, DAO). Improvement Dist. 18: S shore of Cold Lake, E side of French Bay, on AB - SK boundary, 15 Jul 1968, Dumais & Anderson 3376 (ALTA, JKM); S of Primrose Lake, 17 Jul 1968, Dumais & Anderson 3469 (ALTA, JKM). Improvement Dist. 22: 17 mi S of Keg River, 26 Jul 1958, Boivin & Perron 12717 (DAO, GH, MT, NY). Jasper Nat. Park: In woodland, Miette Hot Springs, 27 Jun 1971, Morton NA4609 (JKM). Kananaskis Country: Dry watercourse in woods, Livingstone Falls campsite on Coldwell [Coleman?] - Kananaskis Rd, 30 Jun 1971, Morton NA4648 (JKM). Strathcona Co.: Spruce woods, few rods S of Davis' Lake, 5 mi SE of Fort Saskatchewan, 24 Jul 1945, Turner 4590 (ALTA, DAO, UBC). Waterton Lakes Nat. Park: Cameron Lake, 5500 ft, 5 Aug 1969, Nagy 2688 (CAN). Wood Buffalo Nat. Park: Edge of woods, Ft. Fitzgerald, 30 Jun 1950, Cody & Loan 4110 (ALTA, CU, DAO, LKHD, MT, PAC).

BRITISH COLUMBIA. Cassiar Dist.: On river gravel, 2nd crossing of Bell Irving River, 99.5 mi N of Stewart, Cassiar Hwy, 1 Aug 1980, Morton & Venn NA13674 (JKM); gravelly roadside, ca 3 mi S of Alaska Hwy on Cassiar Hwy, 3 Aug 1980, Morton & Venn NA13684 (JKM); stream gravel, 15 km N of Stikine River crossing, Cassiar Hwy, 3 Aug 1980, Morton & Venn NA13690 (JKM). Coast Range 5 Dist.: Spruce/Fir forest, road to Babine Lake, ca 10 mi E of Smithers, 2700 ft, 8 Jul 1974, V. J. Krajina & J.

Pojar s.n. (UBC). Kamloops Dist.: Alpine slopes of Chipuin Mt, Marble Mtns [NE of Lillooet], 6000 ft, 21 Jul 1938, Thompson & Thompson 605 (CAN, GH, ISC, WTU). Kootenay Dist.: Asulkan Valley, [near] Glacier, 4100-6000 ft, 19 Jul 1906, Brown 621 (GH, MO, NY, PH, US). Peace River Dist.: Stream bank thickets, vic. of Sikanni River, approx. 57°14'N 122°43'W, 26 Jun 1943, Raup & Correll 10281 (A, CAN, MICH, MIN, MSC, RM, UBC, US, WS); roadside, Alaska Highway, 30 mi E of Summit Pass, 27 Aug 1943, Raup & Correll 11562 (A, CAN, S); gravel pit, N of Muncho Lake, Mile 472, Alaska Hwy, 28 Jul 1968, Morton NA2000 (JKM); roadside, S of Summit Lake, Km 626, Alaska Hwy, 20 Aug 1980, Morton & Venn NA14137 (JKM). Similkameen Dist.: On river gravel above Base Camp, Cathedral Provincial Park, SW of Penticton, 21 Jul 1980, Morton & Venn NA13519 (JKM). Yale Dist.: Old rock slide, E side of Lightning Lake, 4000 ft, 13 Jul 1960, Beamish & Vrugtman 60748 (LKHD, UBC).

MANITOBA. Churchill area: Fort Churchill, 27 Jul 1948, Gillett 2258 (DAO, ISC, MO, MT, RM, US, WIS); W bank of Townsite Slough, Churchill, 23 Jul 1954, Beckett M-28-6 (MIN). Lynn Lake area: Roadside in sandy clay, 1 Oct 1957, Krivda L.L. 39 (DS, NY). Nejanilini Lake area: Stunted forest, Duck Lake (SE arm of Nejanilini Lake), 59°22'N 97°46'W, 11 Aug 1950, Scoggan & Baldwin 8300 (CAN, GH, MIN, MT). Nueltin Lake area: Below falls of Thlewiaza River out of Nahili Lake, 59°43'N 100°08'W, 23 Jul 1961, Baldwin 2271 (CAN, GH, MICH, MT, WS). Riding Mtn Nat. Park: Stream gravel, Hwy 10, 3 km S of N gate, 50°49.7'N 100°04'W, 9 Jul 1979, Cody 24376 (DAO).

NEW BRUNSWICK. Charlotte Co.: In shingle at top of beach, S shore of White Head Island, Grand Manan, 5 Aug 1927, Weatherby & Weatherby 5751 (CAN, GH, US). Kent Co.: Cedar bog, 3.1 mi E along main park rd.,

0.4 mi S along Olivier Rd, Kouchibouguac Nat. Park, 5 Jul 1978, Munro 1960 (DAO[2], MT, NYS). Madawaska Co.: Banks of the Grand River, about 1 mi E of Flemming, 4 Jul 1927, Malte & Watson 244 (CAN).

Northumberland Co.: Stream edge, Mt Carleton, 5 Aug 1960, Smith & Clattenburg 20083 (DAO). St. John Co.: Gravel of spring, Big Salmon, River Bridge, 13 Jul 1962, Smith, Roland, Erskine 20858 (DAO, MTMG).

NEWFOUNDLAND. Bonavista North Dist.: Birch forest, E of Northwest Brook, about 3 mi upstream, Bay d' Espoir, 800 ft, 14 Jul 1961, Damman 1005 (MT). Carbonear Dist.: Grassy slopes, SE section of Baccalieu Island, 16 Jul 1960, Rouleau 5650 (NFLD). Grand Falls Dist.: N bank of Exploits River, below the falls, Grand Falls, 6 Jul 1911, Fernald & Wiegand, Fl. Newfoundland 5388 (CU, GH, PH). Green Bay Dist.: Shore of Dildo Run, New World Island, Notre Dame Bay, 18 Jul 1911, Fernald & Wiegand, Fl. Newfoundland 5389 (CAN, CU, DS, GH, PH). Humber Dist.: Slaty bank, near Curling, Humber Arm, Bay of Islands, 31 Aug 1929, Fernald & Long, Fl. of W Newfoundland 1679 (GH, PH); dry limestone ridges, E of the Darmston Quarry, Corner Brook, 5 Jul 1948, Rouleau 95 (CAN, DAO, MT, NFLD, NY, US). St. Barbe Dist.: Site of microwave tower, summit of Portland Head, 50°08'N 57°38'W, 560 ft, 2 Jul 1974, Hay & Bouchard 75-123 (CAN, MT); gravelly shore, NF 430, ca 7 km N of Bellburns, 22 Aug 1978, Morton & Venn NA12408 (JKM); in moss at base of limestone shelf, E side of NF 430, 2 km S of road to Bartlett's Harbor, 28 Jul 1981, Rabaler 618 (MSC + 1). St. Georges-Port Au Port Dist.: Border of brook, Green Gardens, Cape St. George, 20 Jul 1922, Mackenzie & Griscom 11055 (GH[2]). White Bay Dist.: Dripping limestone ledges, Cook Point, Pistolet Bay, 13 Aug 1925, Fernald, Gilbert & Hotchkiss, Fl. NW Newfoundland 28184 (CU, GH, ISC, PH); springy swale, Anse aux

Sauvages, 11 Aug 1925, Fernald, Wiegand, & Long, Fl. NW Newfoundland 28195 (CU, GH, PH).

NEWFOUNDLAND/LABRADOR. Belle Isle Straits area: Sand-bank bordering beach, Forteau, 14 Aug 1925, Long, Fl. Labrador 28125 (CU, GH, PH). Cartwright area: Cartwright, 21-22 Jul 1928, M. Q. Malte s.n. (CAN, GH). Churchill Falls area: Spray zone, Churchill Falls, 29 Jul 1972, Olsen 508 (NFLD[2]); Churchill Falls, 16 Aug 1972, H. C. Duthie s.n. (JKM). Goose Bay area: Roadsides, near the mouth of Otter Creek, 20 Jul 1969, Rouleau 11221 (MT, NFLD); stream banks, Goose Bay, 26 Jun 1950, Gillett & Findlay 5121 (DAO, GH, MIN, MT, NY, RM, UBC, US). Labrador City area: Smoky Mtn, near Labrador City, 12 Jul 1967, Hustich 360 (CAN). Nain area: At head of N side of Lake Tasisuak, Fraser Canyon, ca 100 km inland from Nain, 0 ft, 11 Aug 1973, Shepherd & Matthews 112 (CAN, NFLD).

NORTHWEST TERRITORIES. KEEWATIN DIST.: Spruce muskeg, NW extremity of Nueltin Lake, mouth of Windy River, 6 Aug 1947, Harper 2388 (CAN, MICH, MIN, PH). Hudson Bay Islands: Bill of Portland Island, Manitounuk Islands, 16 Aug 1935, Doult 2680 (CM, F). James Bay Islands: North Twin Island, 53°18'N 80°00'W, 23 Jul 1973, T. H. Manning s.n. (CAN).

NORTHWEST TERRITORIES. MACKENZIE DIST. Arctic Red River area: Roadside in taiga area, Dempster Hwy, 32 km W of Arctic Red River, 11 Aug 1980, Morton & Venn NA13866 (JKM). Fort Providence area: Roadside, Mackenzie River - Yellowknife Hwy Mile 68.2 N, 12 Jul 1961, Thieret & Reich 7639 (DAO, F, US). Fort Simpson area: Cleared ground around Community Centre, Fort Simpson, 12 Jul 1955, Cody & Matte 8758 (DAO, DS, GH, MIN, NY). Fort Smith area: Roadside, Seven Mile Lake, 27 mi W of Fort Smith, 60°02'N 112°38'W, 22 Jul 1950, Cody & Loan 4650 (DAO); bank

of Little Buffalo River, 32 mi W of Fort Smith, 60°02'N 112°48'W, 25 Jul 1950, Cody 4730 (DAO, F). Great Bear Lake area: Beach, Sawmill Bay, NE tip of Leith Peninsula, 6 Jul 1948, Shacklette 2858 (MICH). Hay River area: Along road, E to ford over Kakisa River, Enterprise - Mackenzie River Hwy, 1 Jul 1959, Thieret & Reich 4905 (A, CAN, DAO, F, NY, US). Inuvik area: Lakeshore, peat bog, area of Mackenzie Delta, 67°58'N 133°41'W, 23 Jul 1966, Owen-Larsen 247 (UBC). Keele River area: 2 mi below Canadian Wildlife Services Camp, 64°12'N 127°25'W, 1400 ft, 28 Jun 1971, Cody & Scotter 19274 (CAN). Norman Wells area: By Bosworth Creek, Norman Wells, 20 Jul 1953, Cody & Gutteridge 7399 (CAS, DAO, F, GH, MIN, MO, UBC, US). Yellowknife area: Roadside ditch, near Giant Mine, 62°27'N 114°22'W, 30 Jun 1949, Cody & McCause 2335 (DAO, PENN, US); roadside ditches, Yellowknife, 17 Jul 1949, Cody & McCause 2677 (BH, CM, DAO, DUL, MICH, UBC, UC).

NOVA SCOTIA. Colchester Co.: Woods along North River, Lower Five Islands, 29 Jun 1960, Smith, Clattenburg, Quinten, & Chase 19614 (DAO). Inverness Co.: Cliff, Cheticamp River, 4 mi E of LeBlanc Brook, 10 Jul 1953, Smith, Schofield, Taylor, Webster, & Slipp 7798 (DAO, MT). Yarmouth Co.: Spring-rill in barrens, Tusket, 15 Jul 1920, Long & Linder, GH Exped. Nova Scotia 21201 (CAN, GH, PH).

ONTARIO. Algoma Dist.: On tussocks in boggy ditch, Hwy 17 at entrance to Lake Superior Prov. Park, 4 mi S of Michipicoten River, T30 R22, 6 Jul 1971, Garton 14313 (CAN, ISC, LKHD, MCTF, MICH). Cochrane Dist.: Opening in black spruce, Hudson Bay lowlands, S of Ogoki along Ogoki River, 51°38'N 85°57'W, 9 Aug 1956, Baldwin, Porsild et al. 6760 (CAN, LKHD). Kenora Dist.: Depression between river terrace, junction of the Fawn and Poplar Rivers, 26-28 Jul 1952, Moir 944 (CAN, MIN).

Manitoulin Dist.: Woodland edge, road to Mississagi Lighthouse from Meldrum Bay, Dawson Twp, Manitoulin Island, 17 Jul 1976, Morton & Venn NA9308 (JKM); by seasonal stream in cedar forest, bay at Indian Reserve, Cockburn Island, 3 Aug 1983, Morton & Venn NA15126 (JKM). Nipissing Dist.: Cache Lake, Algonquin Park, 5 Jul 1900, Macoun, Herb. Geol. Surv. Canada 23524 (MO, NY, US); 23534 (CAS, CAN). Ottawa-Carleton Co.: Wet pasture, Munster, Goulbourn Twp, 19 Jun 1947, Dore 47-171 (DAO, MO). Thunder Bay Dist.: Cedar bog, N side of Little Pigeon Bay, Crooks Twp, Lake Superior, 17 Jul 1952, Garton 1878 (DAO, LKHD, MT, MIN, UBC); gravelly shore, N shore of Paradise Island, 20 mi SE of Nipigon, 5 Aug 1956, Garton 2965 (DAO, DUL, LKHD, MIN); woodland, Leadman Islands group (State Islands), off Terrace Bay, 16 Jun 1971, Morton NA4536 (JKM); road shoulder, Sagnagons Lake access Rd. at White Pine Reserve, 48°23N 90°43W, 6 Jul 1981, Garton 20254 (CAN, LKHD, MICH, UBC).

PRINCE EDWARD ISLAND. Kings Co.: Brook in woods, Harmony, 7 Jul 1914, Fernald & St. John, Fl. Prince Edward Island 11054 (CAN, CU, GH, PH). Prince Co.: Brackish marsh, Green's Shore, Summerside, 12 Jul 1912, Fernald & St. John, Fl. Prince Edward Island 7452 (CAN, CAS, GH, MT, [NY], PH, US). Queens Co.: Woods near railway station, Wood Island, 29 Jul 1914, Fernald & St. John, Fl. Prince Edward Island 11055 (CAN, GH, MT, NY, US, WS).

QUÉBEC. Abitibi Co.: Spirit Lake (Abitibi), 9 Jul 1918, Marie-Victorin 8483 (GH, MT, US). Argenteuil Co.: Bois très humide dans les sphaignes, St-Adolphe [-d'Howard], 5 Jul 1947, Rolland-Germain 6212 (MT, NY, UC, WIS); 6213 (CAS, CM, CU, DAO, DS, F, GH, MIN, MT, NY, RM, WS, WVA). Baie James Terr.: Bas de la falaise d'argile, Rupert House, 51°30'N, 11 Jul 1945, Dutilly & Lepage 14134 (CAN, GH); sous les Salix

en haut du rivage, Vieux-Comptoir, 52°37'N 78°42'W, 31 Jul 1954, Lepage 32098 (DAO, MT). Chicoutimi Co.: Fossé - Bord de la nouvelle route, Rivière Ste-Marguerite, Canton Labrosse, ca 48°24'N 70°07'W, 17 Aug 1964, Coyouette [sic, Cayouette?] & Brisson 64797 (DAO). Duplessis Co.: Sables decapes, chemin de fer mi 146, Jiggs, Petit lac Manicouagan, 23 Jul 1962, M. Maldagne & G. Lemieux s.n. (DAO). Gaspé-Est Co.: High sea cliffs of Forillon Peninsula, Cap Rosiers, 24 Jul 1975, Churchill 7572464 (MARY, MICH). Gaspé-Ouest Co.: Calcareous sea-cliffs and rock-slides, by the Gulf of St. Lawrence, Christie, 25 Jul 1922, Fernald & Pease, Fl. Quebec 25058 (CAN, GH, MT, [NY]); crumbling cliffs, NE end of St. Anne des Monts, 13 Aug 1970, Morton NA4073 (JKM); fire road near summit, St. Pierre des Monts, 13 Aug 1970, Morton NA4091 (JKM); around lake below summit, Mt Jacque Cartier, 14 Aug 1970, Morton NA4109 (JKM); roadside ditch, S side of QU 132, 1.1 km W of Rivière Ste. Marthe, 10 Aug 1981, Rabaler 637 (MSC + 2). Gatineau Co.: Meach Lake, 17 Jul 1923, Malte 432/23 (CAN, MICH, MSC). Magdalen Islands: Ile du Havre-aux-Maisons, 16 Aug 1919, Marie-Victorin & Rolland-Germain 9894 (GH, ISC, MT[2], UC, WS). Matane Co.: Sur le platin di schiste au sommet, Mont Blanc, 1075 m, 5 Aug 1938, Boivin 450 (CAN, CAS, CU, DAO, F, ISC, MICH, MO, MT, PH, RM, UC, WIS, WS); gravel of forest road up Mt Logan from St. Octave de l'Avenir, 12 Aug 1970, Morton NA4020 (JKM); upper slopes of Mt Logan, 12 Aug 1970, Morton NA4059 (JKM). Megantic Co.: Runnel by power line track, slopes of Silver Mtn, Black Lake, Thetford Mines area, 9 Jun 1976, Morton & Venn NA8906 (JKM). Nouveau-Québec: Willow swamp, 3 mi W of camp, Fort Chimo area, 58°07'N 68°23'W, 23 Aug 1945, Calder 2729 (DAO, MO, MT, US); along small stream at camp, Fort Chimo area, 58°07'N 68°23'W, 5 Aug 1948, Calder 2380 (DAO, MT); Knob Lake, 2 mi E of

Schefferville, 9 Aug 1959, Hedberg 3092b (DAO, [UPS]); Lac Payne, 59°17'N 73°25'W, 16 Aug 1965, Legault 8168 (CAN, DAO, MT, MTMG, UBC, VT). Rimouski Co.: On serpentine ledges, S side of Ha Ha Bay, Bic, 9 Jul 1969, Morton NA2934 (JKM); on crumbling shale scree by sea and coastal rock crevices, between St. Fabien-sur-Mer & Cap a la Carre, 9 Aug 1970, Morton NA3926 (JKM); rocks around coast, Bic Island, 10 Aug 1970, Morton NA3966 (JKM). Rivière-du-Loup Co.: Shore of Presque Isle, Cacouna, 23 Jul 1880, G. G. Pringle s.n. (VT[2]). Saguenay Co.: Forestville, 31 Jul 1963, Cinq-Mars, Rousseau, & Bonneau 63-834 (DAO, GH, MT[2], MTMG, UBC, UC). Saguenay Co. - Mingan area: Grassy shore, Point au Maurier, Charnay, 16 Jul 1915, St. John, Herb. Geol. Surv. Canada 90434 (CAN, GH). Saguenay Co. - Anticosti Island: Prairie naturelle, Rivière Ferree, 15 Aug 1926, Marie-Victorin & Rolland-Germain 25621 (CAN, GH, MT[2], PH); anfractuosité de rocher, Tête a la Vache: 2 mi E of Rivière Galiote, 18 Jul 1942, Rousseau 52368 (CAN, CAS, CU, F, ISC, MICH, MO, MT[2 + photocopy], NY, UC, US, WIS, WS). Temiscouata Co.: Lac St-Hubert, Jul 1913, [Marie-] Victorin 163 [163n on NY] (GH, MT, MTMG, NY, NYS, US[3], WTU).

SASKATCHEWAN. Beauval area: E shore of Little Amyot Lake, 12 mi NW of Beauval, Hwy 155 mile 70, 55°11'N 107°50'W, T71N R13W, 19 Jul 1970, Harms 16950 (DAO). Hasbala Lake area: Muskeg, edge of small lake, 3 1/2 mi W of Hasbala Lake, 59°55'N 102°05'W, 13 Jul 1963, Argus 219-63 (CAN, COLO, GH, RM). Melfort area: Edge of a field, 6 mi S of (DAO, CAN only) Crooked River, 8 Jul 1940, Breitung 621 (ALTA, CAN, DAO, NY, VT); 1 mi N, 5 mi W of Wallwort, 14 Jul 1940, Breitung 652 (ALTA, CAN, DAO). Prince Albert Nat. Park: Lakeshore, Hanging Heart Lake, Waskesiu, 53°59'N 108°11'W, 19 Jul 1966, Baldwin & MacPherson 10497 (CAN, LKHD,

MICH, MO, MTMG).

YUKON TERRITORY. Dawson area: Independence Creek, 1 Aug 1902, Macoun, Herb. Geol. Surv. Canada 58410 (CAN, NY); Bonanza Creek, Dawson, 12 Jun 1914, Eastwood 196 (CAN, CAS[2], GH, S, UC, US); lush area about cabin, near 31 Mile cabin on 60 Mile Road, 64°15'N 140°18'W, 14 Aug 1949, Calder & Billard 4494 (DAO, MT, S); steep gravelly mud slide, Klondike Hwy, 4 mi S of Dempster Hwy jct., 6 Aug 1980, Morton & Venn NA13721 (JKM); roadside gravel bank, Bonanza Creek, Dawson, 7 Aug 1980, Morton & Venn NA13737 (JKM). Dempster Highway: dry earth bank, N side of Mile 22, 16 Jun 1969, Packer 1969-229 (ALTA); ca 25 mi N of Dawson, 3 Aug 1968, Morton NA2170bis (JKM); roadside, North Fork Pass, Km 77, 8 Aug 1980, Morton & Venn NA13762 (JKM); roadside, bridge below Tombstone campsite, Km 70, 16 Aug 1980, Morton & Venn NA14040 (JKM). Faro area: Wet gravel and clay bank, road to Cyprus Anvil lead-zinc mine from Faro, off Campbell Hwy, 17 Aug 1980, Morton & Venn NA14050 (JKM). Koidern area: Alaska Hwy at White River, 21 Jul 1944, Anderson 9323 (CAN, ISC); roadside, Alaska Hwy, near Koidern, 31 Jul 1968, Morton NA2072 (JKM). Mayo area: Hight Gulch, tributary to Minto Creek, 63°45'N 136°10'W, 4000 ft, 15 Jul 1967, Porsild 831 (CAN, MSC[p.p]; not COLO). South Canol Road: Bog hummocks, Upper Ross River valley, Canol Road Mile 95, 3600 ft, 11 Jul 1944, Porsild & Breitung 10366 (CAN, GH); roadside gravel, Km 112 and 148, 18 Aug 1980, Morton & Venn NA14087 (JKM); gravel bank, Km 94, Quiet Lake, 18 Aug 1980, Morton & Venn NA14089 (JKM). Watson Lake area: Roadside clearing, Campbell Hwy, 33 mi N of Watson Lake, 21 Aug 1970, Harms 17183 (CAN, DAO, GH, RM).

DENMARK. GREENLAND. Godthaab, 64°11'N, 19 Aug 1936, J. Lagerkranz s.n. (RM). Skjoldungen Dist.: Eqalungmiut (Dronning Maries Dal),

63°28'N 41°55'W, 13 Aug 1970, Astrup & Kliim-Nielsen, G.B.U. 864 (MO, MTMG, NY). Tunugdliarfik: Majut, 61°04'N 45°35'W, 150 m, 29 Aug 1962, Hansen, Hansen, & Petersen 2171 (DAO).

USA. ALASKA. Arctic National Wildlife Range: Sadlerochit Spring, 69°40'N 144°24'W, 300 m, 8 Aug 1978, Murray 6923b (ALA). Chicken area: Franklin, Forty Mile District, 12 Jul 1941, Anderson & Gasser 7194 (ALA, CAN, ISC, UTC); gravelly roadside, Logging Cabin Creek, Taylor Hwy, S of Chicken, 2 Aug 1968, Morton NA2116 (JKM). Fairbanks North Star Bor.: Miller House, on Steese Highway, 115 mi N of Fairbanks, 2100 ft, 2-26 Jul 1937, Scamman 750a (GH); gravel bar, Fossil Creek, White Mtns, 21 Jul 1953, Gjaerevoll 685 (CAN, S[2], [TRH]); Fairbanks, 15 Jul 1961, E. Hultén s.n. (A, S, US). Gakona area: Steppe bluff, Gakona, ca 2 km E of Gakona Junction, 62°18'N 145°20'W, 9 Jul 1981, Khokhryakov, Yurtsev, & Murray 6228 (ALA). Juneau Bor.: Terminal moraine, Taku Inlet, 11 Jun 1915, Walker & Walker, RM Herbarium 702 (DS, GH, MO, NY, RM). Kenai Bor.: Roadside, vic. of Eagle River, Anchorage, 2 Aug 1947, Dutilly, LePage, & O'Neill 21844 (CAN, DAO). Kodiak Island Bor.: Sturgeon River, 19 Jul 1899, Coville & Kearney 2237 (F, US). McGrath area: Sphagnum bogs, Kuskokwim River drainage basin, 62°57'N 155°36'W, 21 Aug 1949, Drury 3117 (ALA, GH). Nome area: Nome, 26 Jun 1938, Anderson 3641 (GH, ISC, S). Tok area: Talus slope, 35 mi SW of Tok, Milepost 91, Slana-Tok Hwy, 8 Jul 1968, Welsh & Moore 8052 (ALA, ISC, NFLD).

CALIFORNIA. Tulare Co.: Moist places, n. Middle Tule River, 7000-8000 ft, Apr - Sep 1897 [May fide B. Ertter], Purpus 5131 (GH, MO, UC, US).

COLORADO. Arapaho Co.: Mountain torrent, foot of Berthoud Pass, US 40, Winter Park side, 7 Jul 1974, Morton & Venn NA7340 (JKM). Clear

Creek Co.: Near rivulet in forest, Idaho Springs, 11 Aug 1942, Degener & Peiler 16883 (NY, RM). Jefferson Co.: Cub Creek Picnic Ground, Arapahoe Nat. Forest, T6S R71W S31, 8400 ft, 11 Jul 1981, Colson, Wittmann, & Wittmann 1821 (CM). Pitkin Co.: Valley of Roaring Fork River, between Aspen and Lost Man CG, 8000-10200 ft, 9-13 Jul 1963, Weber 12079 (DAO).

CONNECTICUT. Litchfield Co.: North Canaan, 24 Jun 1909, Blewitt 645 (NEBC). Middlesex Co.: Bottom of trap talus, Pistopang Mtn, Durham, 9 Sep 1918, Weatherby 3377 (NEBC). New Haven Co.: Brook in woods, Waterbury, 17 Jun 1910, Blewitt 660 (NEBC). Windham Co.: Spring-fed rivulet, Thompson, 28 Jun 1920, Weatherby 4687 (GH, NEBC, US).

IDAHO. Custer Co.: Rocks near brook, Bear Creek below Parker Mtn, 6500 ft, 18 Jul 1916, Macbride & Payson 3337 (CM, DS, GH, MO, NY, RM, US).

MAINE. Aroostook Co.: Mossy woods, Fort Fairfield, 6 Jul 1893, Fernald, Maine Flora 17 (CAN, F, GH[2], MIN[2], MO, MSC[2], NEBC, NY, UC, US); recent clearing, valley of Limestone River, Limestone, 22 Jun 1898, Fernald 2277 (NEBC); springy woods in disintegrated volcanic rock, Haystack Mountain, 10 Jul 1902, E. F. Williams, J. F. Collins, & M. L. Fernald s.n. (GH, MT, NEBC). Lincoln Co.: White Island, off Boothbay, 5 Jul 1903, J. R. Churchill s.n. (MO, NEBC). Oxford Co.: Wet ledges and rocky slopes of Twin Peaks, Bowmantown, 24 Jul 1975, Campbell, Eastman, & Richards 3287 (NEBC). Penobscot Co.: Swamps, Orono, 4 Jul 1890, M. L. Fernald s.n. (F, GH, NEBC); wet muddy bank, Lower Penobscot Valley, Veazie, 15 Sep 1897, M. L. Fernald s.n. (NEBC).

MASSACHUSETTS. Franklin Co.: In water, S end of Pocuntuck, Deerfield, 20 May 1964, R. G. Poland s.n. (MO). Hampden Co.: Roadside rill, Mt Shatterack, Montgomery, 15 Jul 1930, Seymour 782 (DAO, MO, VT,

WIS). Middlesex Co.: Wet sphagnous meadow, R. F. Root's swamp, Concord, 11 Jun 1921, R. J. Eaton s.n. (NEBC).

MICHIGAN. Alcona Co.: Lake shore, Harrisville, 12 Jun 1888, W. J. Beal s.n. (BH, MSC). Alger Co.: Margin of woods, Grand Marais, 25 Aug 1916, Dodge 556 (NY). Alpena Co.: Bottom of Dehring [Limestone] Sink #3, [7 mi N of Lachine], T32N R6E S16 NW 1/4, 12 Jun 1980, Gereau 454 (MSC + 6). Charlevoix Co.: Trail in moist woods, French Bay, SW side of Beaver Island, 26 Jun 1958, Voss 6936 (MICH). Cheboygan Co.: Creek bank, Fontinalis run, N shore of Burt Lake, 26 Jul 1927, Ehlers 3535 (DS, MICH, UMBS, WIS). Crawford Co.: Grayling, Jul 1922, C. V. Piper s.n. (GH, US). Delta Co.: SW shore of Bear Lake, 0.5 mi S of FR2436, T43N R18W S36 SW1/4, 24 Jun 1980, Rabeler 364 (MSC + 1). Emmet Co.: N shore of Waugoshance Point, 21 Jul 1979, Martin 94 (MICH, UMBS). Gogebic Co.: Woods between Johnston Springs and Moss Lake, Sylvania Recreation Area, 19 Jul 1968, Voss 12722 (MICH). Houghton Co.: pond margin, Jacobsville Quarry, 15 Jul 1950, Richards 3611 (MICH, PAC). Keweenaw Co.: Woods near Lake Superior shore, Calumet Water Works, 24 Jul 1936, Hermann 8272 (MO, NY, US); boreal forest, Passage Island, Isle Royale Nat. Park, 9 Aug 1975, Voss 14715 (LKHD, MICH). Luce Co.: sandy ditch, E Lake Manistique, 28 Jul 1936, Hermann 8301 (MICH, MIN, NA, NY, PH). Mackinac Co.: forest depression, NE side of Round Island, 16 Jul 1980, Voss 15334 (LKHD, MICH). Montmorency Co.: E. O. Avery's woods, Hilliman, 8 Jul 1898, C. F. Wheeler s.n. (MSC). Roscommon Co.: Cedar swamp, 6 mi S of Dept. of Conservation Training School, Higgins Lake, 10 Jun 1951, Rogers 7415 (WUD). Sanilac Co.: Tamarack swamp near Palms, 6 Sep 1917, Dodge 388 (MICH, NY).

MINNESOTA. Cook Co.: S side of NE promontory of Susie Island,

Susie Islands near Grand Portage, 13 Aug 1948, Ownbey & Ownbey 1037 (MIN, NY, UC, WS). Hennepin Co.: Meadow, Lake Harriet, May 1890, G. B. Aiton s.n. (MIN). Itasca Co.: 3 mi S of Swan Lake, 13 Jun 1947, Moore & Huff 19558 (MIN). Lake Co.: Wet rocks, Two Harbors, 8 Jul 1891, Sandberg 446 (CU, MIN, US). St. Louis Co.: Armstrong Lake, near Ely, 15 Jul 1946, Jones 18191 (MIN[2], MO, MT); spruce forest N of Wahlston on Hwy 35 [MN 135], 14 Jul 1954, Lakela 17882 (DAO, DUL, LKHD, MIN, PENN).

MONTANA. Flathead Co.: W bank of Avalanche Creek, 10 m NW of Avalanche Lake, 2.2 mi SW of Hwy 1, Glacier Nat. Park, 3930 ft, 15 Aug 1980, Rabeler 547 (MSC + 3). Glacier Co.: Slough borders, Midvale, 29 Jul 1903, Umbach 584 (F, MSC, NY, RM, US, WIS); N bank of Two Medicine Creek, 1.2 mi W of Two Medicine Entrance Station, Glacier Nat. Park, 4880 ft, 16 Aug 1980, Rabeler 551 (MSC + 3). Madison Co.: Limekiln Cañon, Bozeman area, 6000 ft, 16 Jun [MO & MTMG only] and 8 Sep 1905, Blankinship 89 (CAN, F, MO, MTMG, PH, US).

NEVADA. Elko Co.: Lamoille Canyon, S of Scout Camp, 3 Sep 1941, Holmgren 1978 (GH, NY).

NEW HAMPSHIRE. Cheshire Co.: Open woods, Gap Mtn, Troy, 13 Jun 1898, Rand & Robinson 459 (GH, NEBC). Coos Co.: Tuckerman's Ravine, Mt Washington, 30 Jul 1890, J. R. Churchill s.n. (MO); on damp schistose gravel, summit of Mt Washington, 1930 m+, 10 Sep 1931, Fernald, Pl. Gray. Exsiccatae 548 (BH, CAN, CAS, COLO, CU, DAO, DS, F, GH, ISC, MICH, MIN[2], MO, MSC, MT, [NA], NEBC, NY, NYS, PAC, PENN, PH, RM, UC, WIS, WS, WTU, WVU); E facing cliff, Huntington's Ravine, 5000 ft, 27 Jul 1958, Löve & Löve 7562 (COLO); rock crevices at base of WMTW-TV antenna, E exposure, S of Mt Washington summit, White Mtn Nat. Forest, 6250 ft, 13 Aug 1981, Rabeler 642 (MSC + 4). Hillsboro Co.: Woods, Bassett Mtn,

New Ipswich, 6 Jun 1896, M. L. Fernald s.n. (MIN, NEBC). Rockingham Co.: Swampy edge, South Hampton, 15 Jul 1967, Hodgdon & Holland 15850 (NEBC).

NEW JERSEY. Sussex Co.: on the Kittatinny Mtns, near Walpack Centre, 17 Jun 1882, H. H. Rusby & N. L. Britton s.n. (PH); wooded swamps, High Point, 12 Sep 1909, Mackenzie 4406 (NY[2]).

NEW YORK. Albany Co.: Marsh near New Salem, 6 Jun 1931, House 18249 (CU, NYS). Allegany Co.: Rushford, 31 May 1907, M. S. Baxter s.n. (BH). Cayuga Co.: Swamp S of Lake Como, Summer Hill Twp, 1306 ft, 13 Jul 1947, Clausen, Flora of New York 7094 (NYS). Chemung Co.: Woods, NE corner of Van Etten, 3 Jun 1915, MacDaniels & Eames, Flora of New York 4018 (CM, CU, GH). Chenango Co.: Lake MacDonough, MacDonough, 10 Aug 1929, House 16880 (NYS). Cortland Co.: SE of Virgil, Town of Lapeer, about 2000 ft, 23 Jun 1940, Palatier, Cohn, & Carr, Flora of New York 20161 (CU). Delaware Co.: Stamford, 2300 ft, 3 - 10 Jul 1909, Taylor 624 (NY). Essex Co.: Wet woods near Minerva, 30 Jun 1927, House 14545 (MT, NYS); Rivulet, edge of road, N of Underwood, W of Euba Mills, ca 1350 ft, 10 Jul 1962, Smith & Miller 33653 (NYS). Franklin Co.: Pickerel Pond, near Stony Creek Mtn, 29 Jun 1899, W. W. Rowlee, K. M. Wiegand, & G. T. Hastings s.n. (CU, PAC). Hamilton Co.: Near Long Lake, 3 Jul 1924, House 10208 (NYS). Herkimer Co.: border land, Lake Warren, 4 Jun 1903, Haberer 2376 (GH). Lewis Co.: Cold brook, E of Parkers (Montague), 1900 ft, 13 Jun 1927, Hotchkiss 2309 (NYS). Madison Co.: Swamp S of Fenner, 29 Jun 1930, House 17651 (GH, NYS). Oneida Co.: Swamps N of New London, 14 Jun 1925, House 10889 (NYS). Oswego Co.: Jackson Hill, Volney, 27 Jun 1895, W. W. Rowlee & K. M. Wiegand s.n. (CU). Otsego Co.: Summit Lake marsh, Springfield, 8 Jun 1930, House

17385 (NYS). St. Lawrence Co.: cold swamps, Canton, 30 May 1914, Phelps 426 (CAN, CU, GH, NY, US). Sullivan Co.: Roadside bank, along Neversink River below Claryville, 25 Jun 1934, Jones, Phillips, & Stebbins 10 (GH, NYS). Tompkins Co.: Springs in hills SE of Brookton, 24 Jul 1918, Wiegand & Eames, Flora of New York 9871 (CU, GH, MICH, MO). Ulster Co.: Roadside in Rondout Valley, 1/2 mi E of Peekamoose Lodge, Town of Denning, 1465 ft, 28 Jul 1956, Wilkins 9067 (PH). Washington Co.: marsh along Lake George, Pilot Knob, 1 Aug 1942, House 28859 (CU, NY, NYS, PENN). Wayne Co.: Arbor-vitae swamp, E of Clyde, 23 Jun 1917, Wiegand, Flora of New York 8069 (CU, GH).

OREGON. Baker Co.: Rock Creek, 6 mi W of Haines, 10 Aug 1915, Peck 7028 (WILLU).

PENNSYLVANIA. Bedford Co.: meadow, 1 1/2 mi NNW [of] Pavia, 1540 ft, 5 Jul 1939, Berkheimer 1068 (PENN, PH). Blair Co.: Pool along secondary channel of Loup Run, 2.8 mi NW of Tipton, 1440 ft, 26 May 1982, Kunsman 4233 (PAC). Cambria Co.: Sphagnum bog, 3 mi N of Ebensburg, 5 Jun 1942, Wood 2048 (PENN). Centre Co.: Wet place along Wallace Run, 4 mi N of Unionville, 2 Jun 1941, Wahl 986 (CU, GH, ISC, MO, PAC, PENN, UC, WS). Elk Co.: Field, 2 mi N of Weedville, 17 Jun 1940, Wahl 699 (CU, GH, ISC, PAC, PENN, WS; not UC). Erie Co.: South Junction Paradise (PENN), Park (CM), 8 Jul 1879, G. Guttenburg s.n. (CM, PENN). Jefferson Co.: Ravine along McKee Run, 1.5 mi ENE of Desire, 24 Jun 1947, Wahl 2853 (GH, ISC, PAC, UC, WS). Lackawanna Co.: Wooded swamp along US 6, 0.75 mi WSW of Clark Summit, 6 Aug 1946, Glowneke 8328 (PENN). Lycoming Co.: Woods, 3 mi N by E of Salladasburg, 30 Jun 1959, Wahl 19176 (PAC, PENN). McKean Co.: Mt Jewett, 14-18 Sep 1922, Q. E. Jennings s.n. (CM). Monroe Co.: Ledge, 3 mi N of Tobyhanna Mills, 4 Jul

1893, Taylor s.n. (PH). Northampton Co.: streamlet, Bangor, 11 May
 1909, B. Long s.n. (GH). Pike Co.: South Stirling, 11 Jun 1906, B. Long
s.n. (PENN). Sullivan Co.: Shady Nook, Lopez to Bella Sylva, 9 Aug
 1908, Stone 10073 (PENN). Tioga Co.: Grand Canyon, Harrison Park, 10 mi
 SW of Wellsboro, 24 Jun 1939, O. E. Jennings s.n. (CM). Warren Co.:
 Sulphur swamps near Pine Valley, 11 Jun 1927, J. Bright s.n. (CM[2],
 PENN, WVA). Wayne Co.: Upper Woods Pond, 2 mi NNE of Cold Spring, 26
 Jun 1954, Wahl 14326 (PENN).

RHODE ISLAND. Providence Co.: Woonsocket, without date, E. Flint
s.n. (GH).

UTAH. Beaver Co.: Beaver City, 1877, Palmer 55 (CAN, GH, MO[2],
 NY[2], US). Summit Co.: Fish Lake, 9000 ft, 3 Aug 1894, Jones 5730 (F,
 MO, MSC, NY, RM[2], UC).

VERMONT. Caledonia Co.: Rill along Route 302, Groton, 19 Jul 1950,
Seymour 18845 (NEBC). Essex Co.: Clearing, Miles Pond, Concord, 4 Jul
 1963, Seymour 21338 (MO). Lamoille Co.: Mt Mansfield, 5 Jul 1897,
Greenman 2403 (GH). Orleans Co.: Swamp, Willoughby, 15 Jul 1898, G. C.
Kennedy s.n. (NEBC). Windham Co.: By a spring, Jamaica, 24 Jun 1964,
Seymour 21601 (MO, NEBC).

WASHINGTON. Whatcom Co.: Spring along Slate Creek, W of Harts
 Pass, 29 Jul 1940, Ownbey & Meyer 2326 (CAS, CU, DS, GH, ISC, MIN, MO,
 NY, OSC, PAC, UC, WIS, WS).

WEST VIRGINIA. Tucker Co.: Cold pool at base of cranberry bog,
 Dolly Sods, 4000 ft, 24 Aug 1984, E. E. Hutton Jr. s.n. (MSC + 3).

WISCONSIN. Ashland Co.: Jumble of rock and driftwood over
 claybank, near boat dock, S end of Devils Island, T53N R3W S15 NW1/4, 30
 Jul 1980, Cochrane & Cochrane 9197 (MSC). Bayfield Co.: Near Herbster,

5 Jul 1897, Cheney 6795 (WIS). Douglas Co.: Cedar swamp, jct Hwy P and Brule River, ca 1 mi N of Solon Springs, T45N R11W S8, 11 Jul 1969, Koch 5800 (LKHD, WIS). Florence Co.: Mossy sedgy seepage in Thuja woods, N-facing slope at S end of Pickerel Lake, T40N R17E S7, 30 Jun 1964, Iltis & Turner 22059 (UC, WIS). Forest Co.: Boggy woods, N side of Hwy 52, 0.7 mi E of jct with Hwy W, T34N R14 S11 SE 1/4, 8 Aug 1971, Nee 4468 (WIS). Marathon Co.: Woods, Mosinee Hill, Wausau, 21 May 1932, Fassett, Drescher, & Sicker 14061 (GH, MT, WIS). Oneida Co.: Valley of Wisconsin River near Rhinelander, 17 Jul 1893, Cheney 1770 (WIS). Vilas Co.: Old beaver dam, Siphon Creek, T42N R8E S13, 14 Jun 1961, Schlising & Schlising 1950 (UC, WIS).

WYOMING. Albany Co.: Near stream, Snowy Range near Snowy Range Lodge, 8900 ft, 18 Jun 1969, Hartman 2862 (RM); willow swamp at ski area, E slope of Medicine Bow Mtns, 6 Jul 1974, Morton & Venn NA7306 (JKM). Lincoln Co.: Stream bank, Hills E of Afton, 7500 ft, 27 Jun 1923, Payson & Armstrong 3294 (CU, GH, ISC, MO, MSC, PH, RM). Teton Co.: Little Firestone River, 21 Jul 1919, J. Bright s.n. (CM, MSC).

TYPIFICATION: One problem encountered in this study was locating any specimens that represented type material for Stellaria borealis. Many topotypes exist, the most widely distributed being a collection Fernald made in 1930 (Plantae Exsiccatae Grayanae 548) and subsequently sent to 100 (and possibly as many as 125) herbaria (Howard in Walker et al. 1986); 29 specimens of Fernald's collection were examined in this study. Neither in his review of the American variation in Stellaria borealis (Fernald, 1914) nor in his extensive arguments on whether S. borealis should be included in S. calycantha (Fernald, 1940) is any mention made of type material of S. borealis. Pease (1964) did not list

any Bigelow collection of S. borealis; his listings were based on inspection of specimens at GH, NEBC, UNA, and earlier records compiled at NY, US, and the South Natick Historical, Natural History, and Library Society (now at GH fide specimen of Robbins 62a, GH). I could not find any Bigelow material in either the general collection or type folders at GH.

Only a single specimen bearing a label in the hand of Bigelow (verified in comparison with sample in Burdet, 1979) was located among the requested loans. The locality is given as "Mt. Washington, N.H." but no date is given. Dr. Richard Zander noted on the loan invoice from BUF that it "was probably obtained in the 1860's by G. Clinton [the period when Clinton was building his herbarium (Gray, 1886)], and is probably a topotype." I concur with his reasoning since the name that Bigelow wrote on the label, Stellaria borealis, was not used by him in his initial description of the plant (Bigelow, 1816) where he noted it as Arenaria seu Stellaria. Pease (1964) listed Bigelow as collecting in Coos County, NH in 1841, this report based on "a single sheet of Cassiope" that Pease found and reported in an earlier work (Pease, 1917). The use of Stellaria borealis on the label without any indication of its significance as a new species suggests it may be from this trip.

Another point should be noted that complicates the picture. Bigelow (1816) mentioned that his catalogue included the plants that he found at the summit in July, with others listed as a result of the "botanical zeal" of Mr. F. Boott who made a second trip with his brother to the summit in August. In his 1816 work, Bigelow lists "August 25" opposite the entry for Arenaria seu Stellaria, giving the reader the

impression that he was basing this entry solely on a Boott collection. Rafinesque (1817) repeated Bigelow's text in his description of Bigelowia montana, making an August, 1816 Francis Boott collection the type of B. montana.

Two Francis Boott collections were located, one from US, the other from LIV. The first is labeled "S. borealis? Boston, N.A. F. Boott. 1816." Unfortunately, this specimen is a mixed collection of Cerastium fontanum and Moehringia lateriflora. The name would have been added later since Bigelow did not publish Stellaria borealis until 1824.

The specimen obtained from LIV is clearly the same plant that Bigelow described. It is from the "White Mountains N. America", identified as "Arenaria alpestre Species Nova" but without date. Given the ambivalence of Bigelow in his first mention of Stellaria borealis as Arenaria seu Stellaria, this specimen may indeed represent one of the Boott collections in question. Based on details in his obituary (Gray, 1864), any North American collections would have been made prior to his departure for England in 1820; clearly prior to the publication of S. borealis in 1824 (but see Pursh, 1917: p. 170, footnote 2 for reference to a possible later trip). I found no mention of Arenaria alpestre in any literature; this may have been a name that Boott intended to publish. The lack of any reference to it in either of Bigelow's subsequent Florulas (1824, 1840) suggests that Bigelow was unaware of Boott's name. Furthermore, there is no conclusive evidence that it was collected at the summit of Mt. Washington since the July 1816 expedition in which Bigelow and Boott participated did climb other peaks in the White Mountains (Bigelow, 1816; Gray, 1864), and Graustein (1964) described Boott's 1817 trip as a "collecting trip in the mountains."

Even if a Boott collection could be located, it would not serve as a type for Stellaria borealis unless chosen via neotypification.

Bigelow (1824) included the following text after the description of

Stellaria borealis:

"This plant generally occurs without petals, in which state I discovered it on the White mountains in July, 1816. I have since received it several times from the same place but always in the apetalous state, until last year, when Messrs. Greene and Little found it there in August [of last year] with complete flowers."

The absence of any mention of either Boott or his 1816 collection is curious since Bigelow had earlier (1816) attributed the discovery of S. borealis (then Bigelow's Arenaria seu Stellaria) to Boott rather than to himself.

The collections that Bigelow (1824) mentioned would have been used by Bigelow in preparing his description of Stellaria borealis; they would be syntypes. Pease (1917) restated the above citation from Bigelow (1824) and followed it with a very discouraging sentence: "Who these intermediate collectors of the apetalous plant were we cannot tell." He suggested that John Locke and George Emerson could have gathered the plants, but no specimens bearing their names were seen. No collection of Benjamin Greene or Henry Little was received in the loans from herbaria where their material is deposited fide Index Herbariorum, part II [Greene at BSN, now GH (Lanjouw & Stafleu, 1957); Little at PH (his herbarium was presented to PH in 1829 per Graustein, 1964) and GH or NY? (Chaudhri et al., 1972)].

The list in Pease (1964) entitled "Type Localities in Coos County" includes the location of several type specimens, but is not of direct value since Pease (1964) included "only names still valid." One listed taxon, Prenanthes trifoliata (Cass.) Fern. var. nana (Bigelow) Fern., is

based on a collection from the White Mountains made in August by "Mr. Little". Since Bigelow published this species (as Prenanthes alba var. nana) in 1824 and Little only made a single trip to the White Mountains prior to 1824 (Pease, 1964), Little's collection of P. alba var. nana was most likely made at the same time as the Little collection of Stellaria borealis which Bigelow (1824) refers to in his description. Since Pease (1964) did not cite the location of Little's Prenanthes collection and Milstead (1964) did not see it while preparing his revision of Prenanthes, this clue is of little value.

Given the above situation, I see little choice but to designate a neotype. An undated collection of Tuckerman (Tuckerman s.n. (DWC, NY) made as early as 1837 (fide Pease, 1964) has been selected. The phrasing on the label "The origl. station [of Bigel. - NY only]" indicates that he was familiar with the location from which Bigelow made his first collections. Tuckerman segregated this as "form alpina" (a name which he apparently never published) to distinguish it from plants he collected from lower elevations, a specimen of which is also present on the DWC sheet. This is indicative of Tuckerman's knowledge of the plant which Bigelow described.

- 4b. Stellaria borealis Bigelow subsp. sitchana (Steudel) Piper in Piper & Beattie, Fl. N.W. Coast 147. 1915.

Stellaria brachipetala Bong., Mém. Acad. Imp. Sci. St.-Petersbourg, Sér. 6, Sci. Math. 2: 126. 1833, non Bunge (1830), nec Jessen (1879). Stellaria brachypetala Bong., in Torrey & A. Gray, Fl. N. Amer. 1: 186. 1838, nom. sphalm. Stellaria sitchana Steudel, Nomencl. Bot. ed. 2. 2: 637. 1841. Alsine brachypetala (Bong.) Howell, Fl. N. W. Amer. 82. 1897, non Opiz (1826). Stellaria borealis Bigelow var. sitchana (Steudel) Fern., Rhodora 16: 151. 1914. Stellaria calycantha (Ledeb.) Bong. var. sitchana (Steudel) Fern., Rhodora 42: 255. 1940. TYPE: USA. ALASKA. Sitka, without date, [1827 fide Hultén, 1940], K. H. Mertens s.n. (lectotype, here designated, LE!).

Stellaria borealis Bigelow forma α apetala (Fenzl) Regel lusus a. ciliata Regel, Bull. Soc. Imp. Naturalistes Moscou 35: 277. 1862. pro parte. Original material: USA. ALASKA. Aleutian Islands: Unalashka, without date [1827 fide Hultén, 1940], K. H. Mertens s.n. (LE!).

Stellaria borealis Bigelow forma β corollina (Fenzl) Regel lusus a. crispa Regel, Bull. Soc. Imp. Naturalistes Moscou 35: 278. 1862. Original material: USA. ALASKA. In insula Sitka, without date [1827 fide Hultén, 1940], K. H. Mertens s.n. (GH!, LE[2!]); Sitka, without date, Bongard s.n. (LE!).

Stellaria borealis Bigelow forma corollina (Fenzl) Kurtz, Bot. Jahrb. Syst. 19: 366. 1894. TYPE: USA. ALASKA. Gebiet des Lynn-Canals: Portage Bay, feuchte Stellen am Meeresufer, 16 Jul 1882, A. & A. Krause 336 (holotype, B [destroyed?]; isotype, CORD!).

Stellaria borealis Bigelow forma subcorollina Kurtz, Bot. Jahrb.

Syst. 19: 366. 1894. TYPE: USA. ALASKA. Gebiet des Lynn-Canals, 26 Jun 1882, A. & A. Krause 324a (holotype, B [destroyed?]; isotype, CORD!).

Stellaria borealis Bigelow var. bongardiana Fern., Rhodora 16: 151.

1914. Stellaria borealis Bigelow subsp. bongardiana (Fern.)

Piper & Beattie, Fl. N.W. Coast 147. 1915. Alsine bongardiana (Fern.) Davidson & Moxley, Fl. South. Calif. 133. 1923.

Stellaria sitchana Steudel var. bongardiana (Fern.) Hulten, Fl.

Aleut. Isl. 164. 1937. Stellaria calycantha (Ledeb.) Bong. var. bongardiana (Fern.) Fern., Rhodora 42: 255. 1940. Original material: USA. ALASKA. Sitka, without date [1827 fide Hulten, 1940], K. H. Mertens s.n. (GH!); not Mertens 18 (LE!).

Stellaria calycantha × fenzlii in Hultén, Kongl. Svenska

Vetenskapakad. Handl. ser. 3. 5(2): 64. 1928. fide Hultén, Fl.

Aleut. Isl. 178. 1937. Original material: USSR. Kamtchatka. not seen.

Perennial herbs. Stems erect or sometimes reclining, (14)17 - 72(110) cm long; upper internodes papillate or rarely glabrous, usually ridged. Leaves simple, opposite, blades oblong to lance-linear, rarely ovate, (5)17 - 54(87) mm long, (1.3)2.5 - 9(22) mm wide, apex acute, base truncate or rounded, rarely attenuate, glabrous, margin papillate with minute cilia near the leaf base or rarely glabrous; leaves sessile or very rarely with a short petiole. Inflorescence a lax terminal cyme, rarely axillary with one terminal flower, flowers (2-10)17 - 41(280) per stem bracts resembling leaves, (1.6)3.6 - 45(58) mm long, (0.5)0.9 - 9(11) mm wide, margin herbaceous, or rarely with a wide scarious margin,

papillate (or rarely glabrous) as in leaves. Flowers perfect, sepals 5, basally connate, ovate to lanceolate, (2.4)2.8 - 3.7(4.1) mm long at anthesis, 3.1 - 4.2(4.5) mm long in fruit, nerves becoming evident ridges extending to the tip, rarely only in lower half of the sepals, apex acute, margin scarious, exceeding 0.1 mm width, margin occasionally ciliate; petals 5 or fewer, white, deeply 2-cleft, most 1/2 X the sepals, occasionally as long as the sepals; stamens 10 or fewer; styles (2)3 - 4(5), white, erect and later spreading, (1)1.2 - 1.8(2.0) mm long, stigmatic along entire length. Capsules ovoid, wall membranous, translucent or darkened, (3.1)3.6 - 6.5(7) mm long unopened, (4.6)5.1 - 7 mm long opened, valves 6 - 8(10), pedicels (12)16 - 30(65) mm long, sharply reflexed, or rarely arching, glabrous. Seeds reddish brown (immature) to brown (mature), (0.7)0.8 - 1.0 mm long, (0.5)0.6 - 0.8 mm wide, surface tuberculate or occasionally appearing only indistinctly roughened. N = 26 (Morton, unpublished); 2n = 52 (Chinnappa, 1985; Morton, unpublished). Figures 10e and 54.

I cannot agree with Hultén (1937a, 1944) in his segregation of S. calycantha vars. sitchana and bongardiana into a separate species (S. sitchana vars. sitchana and bongardiana). Although S. borealis subsp. sitchana plants often look very distinctive and are easily separated from S. borealis subsp. borealis, the distinction between the two subspecies becomes very slight when considering specimens from the Rocky Mountains and some areas in Alaska. Both varieties in these areas have papillate stems and leaves, with ciliate leaves restricted to S. borealis subsp. borealis. While sepal nerving is usually a useful feature, some specimens of S. borealis subsp. sitchana exhibit very

weak, short nerves suggesting S. borealis subsp. borealis. Flowers on large plants of S. borealis subsp. borealis and small plants of S. borealis subsp. sitchana (often those collected above 1065 meters elevation) may have very similar calyx and capsule measurements, complicating the segregation of these varieties.

The relative lengths of the calyx and capsule offer one clue to variety assignment in such cases. Stellaria borealis subsp. sitchana plants have long, often lanceolate sepals which usually enclose one-half or more of the mature capsule. The calyx of S. borealis subsp. borealis is often very short in relation to the capsule, the often ovate sepals rarely covering the lower half of the capsule. Capsules of S. borealis subsp. sitchana are less likely to become darkly pigmented, but this latter feature is not consistently expressed in either variety.

Specimens of Stellaria borealis subsp. sitchana collected at sites above 1000 meters in central and southern California often exhibit a strong resemblance to S. crispa. These plants can be segregated from S. crispa by the presence of an inflorescence, flowers containing petals, and papillate stems and leaves; characters only rarely seen (not at all in the case of the latter two characters) in S. crispa.

Plants of Stellaria borealis subsp. sitchana collected after mid-July which bear flowers but no fruit should be inspected carefully since they may represent S. borealis × S. longifolia plants (see description of that taxon). If enlarged reddish anthers are present, the specimen may be a S. borealis subsp. sitchana plant infected with anther smut (Ustilago violacea); a characterization of infected plants is given in the discussion of Floral Morphology.

DISTRIBUTION: Stellaria borealis subsp. sitchana is found along

the Pacific Coast from the end of the Aleutian Islands southeastward to central California, with a number of populations in the Rocky Mountains of Idaho and Montana. While most populations have been gathered from coastal locations, S. borealis subsp. sitchana has been collected at elevations to 1500 meters, with one site at 1830 meters in Idaho and ones at 2257 and 2745 meters in south central California. Figure 55.

Eight smut-infected collections of S. borealis subsp. sitchana were seen, five of these being collections made since 1967. The occurrence of U. violacea specimens of S. borealis subsp. sitchana from northern Washington (Rabaler 467 [MSC + 3] and 470 [MSC]) may represent the first collection of Ustilago on Stellaria in the Pacific Northwest; Shaw (1973) listed U. violacea as occurring in the Pacific Northwest, but not on Stellaria.

ECOLOGY: S. borealis subsp. sitchana is commonly found in wet roadside ditches, marshes, and thickets along river and creek banks in coastal Pseudotsuga and Thuja-Tsuga forests. Rubus, Salix, and Alnus species are common associates. Stellaria borealis subsp. sitchana plants scramble over, and in some cases are supported by, foliage of adjacent herbs. Plants of S. crispa grow in similar habitats and are often found nearby.

Flowering is reported from mid-May through early September, with an occasional flower seen on specimens collected in late April and even early November. Mature fruit is present in southern areas by early June.

PROTECTION STATUS: No reports referable to S. borealis subsp. sitchana have been seen.

COMMON NAMES: The common names applied to Stellaria borealis subsp.

sitchana are listed in Table 36. The only unique name is Sitka Starwort, Northern Starwort being used in a number of the references below to refer to both S. borealis subsp. borealis and sitchana.

REPRESENTATIVE SPECIMENS: CANADA. BRITISH COLUMBIA. Cassiar Dist.: N of Dragon Lake on Terrace-Watson Lake Road, 55°N 128°W, 500-1000 ft, 1 Jul 1973, Beamish, Pojar, & Wade 730054 (DAO, UBC); river gravel, tributary of main river, Cassiar Hwy, 78 km N of Hwy 16, 1 Aug 1980, Morton & Venn NA13665 (JKM); in wet gravel by road and river, Stewart Hwy, W side of pass, 1 Aug 1980, Morton & Venn NA13669 (JKM). Coast Range 5 Dist.: Bog between Hwy 16 and C.N.R. tracks, N of Smithers, just S of Kathryn Lake, 1600 ft, 19 Jul 1974, V. J. Krajina, J. Pojar, & C. Parsons s.n. (UBC). Kootenay Dist.: Road shoulders and ditches, New Denver-Kaslo road, few mi E and W of Whitewater Creek, Slocan, 3500 ft, 15 Jul 1975, Beamish, Luitjens, Carey, & Campbell 750279 (DAO, UBC). New Westminster Dist.: Wet roadside, Garibaldi, Vancouver, 6 Sep 1969, Morton NA3335 (JKM); 0.1 mi E of jct. of Dewdney Trunk Rd. - 288th St., E of Haney, 17 Jul 1980, Rabaler 425 (MSC + 4); roadside ditch, W end of Spanish Banks, Vancouver, 23 Jul 1980, Morton & Venn NA13536 (JKM). Queen Charlotte Dist.: Moresby Island, logged-over woods at margin of village, Alliford Bay, 27 Jun 1957, Calder, Savile, & Taylor 21857 (DAO, MO, UC). Vancouver Island - Alberni Dist.: Thickets, bottom land, Prairie Farms Alberni, 10 Jul 1917, W. R. Carter s.n. (GH). Vancouver Island - Cameron Dist.: Opening in forest by East Cameron River at bridge on Port Alberni Road, 25 Aug 1975, Morton NA8368 (JKM). Vancouver Island - Cowichan Lake Dist.: Ditch along forestry road, about halfway up Mt. Masachie, Lake Cowichan, 26 Jul 1980, Morton & Venn NA13576 (JKM). Vancouver Island - Renfrew Dist.: Tall weeds, sandy

soil, Jun-Jul 1901, Rosendahl & Brand 53 (CAN, COLO, DS, GH, MIN, MO, MSC, NY, RM, UC[2], US). Vancouver Island - Rupert Dist.: Upper end of Claud Elliot Lake, Tsitika River watershed, 1000 ft, Jul 1973, Roemer 156 (UBC). Yale Dist.: Gravel bar, Boy's Town, Hope-Princeton Hwy, 2300 ft, 11 Jul 1960, Beamish & Vrugtman 60643 (DAO, LKHD, UBC).

USA. ALASKA. Alaska Peninsula: small stream, SW section of Chowiet Island, 56°02'N 156°42'W, 2 m, 19 Jul 1977, Hatch 232 (ALA). Chugach Nat. Forest: Copper River, Delta, near USFS Tiedeman Slough Cabin, 60°25'N 145°28'W, 9 Jul 1977, Batten & Bente 77-278 (ALA). Juneau Bor.: Wet meadow, Eagle River, near Juneau, 28 Jun 1940, Anderson 6238 (ALA[2], CAN, DAO, GH[2], PH, RM[2], UTC, VT). Ketchikan Gateway Bor.: Clearings, Wrangell, 19 Jun 1915, Walker & Walker, RM Herbarium 731 (CM, DS, F, GH, MO, NY, RM, WS). Kodiak Island Bor.: gravel above beach, near Cannery Station, Olga Bay, 22 Jun 1939, Looff & Looff 728 (BH, DAO, GH, MO, NY[3], UBC); among tall grasses, Port Vita (CAS, 1 DS spec) Raspberry Island, 15 Jul 1939, Eyerdam 3130 (CAN, CAS, COLO, DS[2], GH, ISC, UC[2], WS). Middleton Island: Roadsides, near airstrip and base, 59°25'N 146°20'W, 2 Aug 1956, Thomas 6278 (CAN, DS, UC, US, WTU). Sitka Bor.: Sitka, 6-9 Sep 1904, Piper 4412 (MO, US); tundra back of and NE of Sitka, 18 July 1929, Heller 14968 (PH, UC, UTC, WTU).

ALASKA. Aleutian Islands: Adak Island, Hillside behind enlisted Navy personnel barracks, ca. 30 m, 14 Jul 1974, Hein 170 (ISC). Amchitka Island, Roadside marshes N of Fox Runway, 14 Jul 1962, Reich & McCann 564 (ALA, CAN, F). Attu Island, vic. of naval base, Massacre Bay, SE part of island, 26 Aug 1949, Miller 1293 (CAN, MICH, US). Unimak Island, False Pass, Jul 1936, Jones 8811 (811 on 1 ORE spec) (CAS, ISC, ORE[2], OSC, UC).

CALIFORNIA. Humboldt Co.: Moist places, Eureka, 0 to 200 ft, 22 May 1900, Tracy 795 (DS, GH, RM, UC, US); meadow at Box Camp, Trinity Summit, 4800 ft, 24 Aug 1947, Tracy 17904 (DAO, UC, UTC, WS, WTU). Kern Co.: Shirley Meadows, Greenhorn Range, 5 Aug 1957, Twisselmann 4134 (CAS). Marin Co.: Point Reyes, Jul 1903, Elmer 4552 (CAS, DS, MIN, MO, NY, UC, US). Mariposa Co.: Bridal Veil Meadows, Yosemite Nat. Park, 4000 ft, 13 Jul 1911, Hall 9105 (UC); Wawona: 4000 ft, 20 Jun 1924, Howell 428 (CAS). Mendocino Co.: Noyo, 1866, Bolander 4718 (CU, F, GH, MO, NY, UC, US). Sonoma Co.: N half of Lower Pitkin Marsh, 9 Jun 1951, Rubtzoff 153 (DS).

IDAHO. Adams Co.: W Branch of Goose Creek, S side of ID 55, 4.1 mi E of US 95 - ID 55 jct., New Meadows, Payette Nat. Forest, T19N R2E S27, 13 Aug 1980, Rabaler 539 (MSC + 3). Boise Co.: W bank of Beaver Creek, 0.5 mi N of Beaver Creek Camp, 14.7 mi SW of Lowman on ID 21, Boise Nat. Forest, T7N R7E S3 NE1/4, 12 Aug 1980, Rabaler 535 (MSC + 3). Bonner Co.: Overflow meadows at mouth of Pack River on Lake Pend Oreille, 16 Jun 1940, Christ 11190 (NY, WS). Idaho Co.: banks of Sheep Creek, 3 mi from the Snake River in Snake River Canyon, 11 May 1939, Meyer 1607 (GH, MO, US, WS[2]). Latah Co.: Moist places near Julietta, 8 Jun 1892, Sandberg, MacDougal, & Heller 349 (CAS, CS, DS[2], F, GH, MO, NY, US). Nez Perce Co.: Forests, 3500 ft, 29 Jul 1896, Heller & Heller 3476 (CU, DAO, DS, MIN, MO, MSC, NDG, NY [2, 1 ex BKL], PH, UC, US).

MONTANA. Glacier Co.: Overflow stream bed E of Wilbur Creek, 100 m S of trail to Swift Current Pass, due W of Swiftcurrent CG, Glacier Nat. Park, 4900 ft, 16 Aug 1980, Rabaler 553 (MSC + 1). Missoula Co.: Rattlesnake Creek, 5 mi [N] out of Missoula, 17 Jul 1921, Kirkwood 1100 (CAS, DS[2], F, GH, ISC, MO, NY, ORE, PH, UC). Ravalli Co.: Hamilton,

4000 ft, 16 Jun 1906, Blankinship 89a (DS, RM, UC).

OREGON. Benton Co.: Frazier Creek, W of Canterbury Circle, NE of Corvallis, T11S R5W S24, 67.5 m, 15 Jun 1980, Halse 2238 (DAO, NY, OSC, UTC). Clackamas Co.: Summit of meadow, Mt Hood, 21 Jul 1965, Faegri F167 (OSC). Clatsop Co.: Bank of Necanicum River, S side US 26 at Saddle Mtn State Park Road, 2 Aug 1980, Rabaler 479 (MSC + 2). Columbia Co.: Beaver Creek Falls, 10 Jul 1922, Abrams 8833 (DS, MO, RM, WILLU). Curry Co.: Port Orford, 27 Jun 1919, Peck 8570 (BH, GH, MO, NY). Harney Co.: Upper Emmigrant Creek, 4 Aug 1912, Peck 1780 (WILLU). Jackson Co.: Sykes Creek Crossing, near Wimer, 18 Jun 1892, Hammond 39 (MO, NY[2], RM, US). Josephine Co.: stream near Rd. 3941, 14.2 mi E of Cave Junction, Siskiyou Nat. Forest, 2160 ft, 22 Jun 1973, Denton 2518 (NY, WTU). Lane Co.: Water Board Park, off US 126, 25 mi E of Eugene, 19 Jul 1975, Mason 10219 (ORE). Marion Co.: Thickets, Valley of the Willamette, Salem, 1871, Hall 55 (F[4], GH[2], MO, NY[2], UC, US[2]). Multnomah Co.: Willamette Heights, Portland, 7 Jul 1902, Sheldon S.10830 (DS, F, GH, MIN, NY). Wallowa Co.: Horse Creek Cañon, 1750 ft, 25 May 1897, Sheldon 8164 (MO, NY).

SOUTH DAKOTA. Lawrence Co.: Along creek, near Deadwood, 28 Jun 1929, Palmer 37610 (GH).

WASHINGTON. Clallum Co.: Seepage along trail, Boulder Creek CG, 8.5 mo SW of Elwha RS, Olympic Nat. Park, 2061 ft, 28 Jul 1980, Rabaler 455 (MSC + 3). Grays Harbor Co.: Hoquiam, 6 Jun 1897, Lamb 1159 (F, MIN, MO, NY, PH); back of Quinault, 25 Jun 1902, Conard 157 (GH, MIN, NY, PENN, PH, US, WS). Island Co.: Whidby Island, Jun 1898, N. L. Gardner s.n. (UC). Kitsap Co.: Orchard Point, Jul 1895, Piper 2313 (GH[2], NY, US, WS, WTU). Klickitat Co.: Springs in woods, 15 May Jun

1895, Suksdorf 730 (or s.n.) (CAN, DS, F[2], MO, NY[2], US, WS).

Okanogan Co.: Nason Creek, 650 m, 30 Jul 1893, Sandberg & Leiber 605 (CAN, CAS, GH, NY, ORE, UC, US, WS). Pend Oreille Co.: E side of Pend Oreille, S of Ione, ca 2200 ft, 4 Jun 1967, Layser 310 (NY, WS). Pierce Co.: Upper valley of the Nesqually [Mt Rainier], 27 May 1895, Allen 155 (CAN, CS, DS, F[2], GH, MIN, MO, MSC, NY, RM, UC, US, VT, WS); W shore of Fish Creek, 3.6 mi N of main park road (E of Nisqually Station), Mt. Rainier Nat. Park, 2950 ft, 31 Jul 1980, Rabeler 473 (MSC + 4).

Snohomish Co.: Trail edge near boardwalk, Ice Caves Trail, N of Stillaguamish River bridge, S of Fed. Hwy 7, 15 mi E of Monte Cristo RS, Verlot, T30N R10E S33 NE1/4, 30 Jul 1980, Rabeler 466 (MSC + 2).

Thurston Co.: Along fence rows, head of Elds Inlet (Mud Bay), 5 mi W of Olympia, 11 Jun 1940, Meyer 1779 (CU, DAO, GH, ISC, MO, NY, RM, UC, US, WS). Whatcom Co.: Shore of Baker Lake, 26 Jun 1933, Muenschner & Muenschner 5820 (CU, UC).

The combination Stellaria borealis subsp. sitchana is attributed to Piper for several reasons. In his 1906 Flora of Washington, Piper stated that his nomenclature followed the Philadelphia Code. One provision of that Code involved the designation of the subspecies as the only infraspecific level, varieties relegated to horticultural usage (Cronquist, 1955). In both Piper (1906) and Piper and Beattie (1915) any new trinomial combination that Piper designated is noted as a "subsp. nov."

Unfortunately, Piper followed the lead of other proponents of the American Code in his failure to designate new combinations for infraspecific names originally published as varieties (Cronquist, 1955).

In the treatment of S. borealis in Piper and Beattie (1915), the trinomials S. borealis sitchana Fernald and S. borealis bongardiana Fernald are listed. It is clear that Piper intended these to be subspecies from the text following the names in which he stated "While the lowland subspecies S. borealis bongardiana ..." The authorship is listed as Piper rather than Piper and Beattie since all new combinations that are designated in Piper and Beattie (1915) carry Piper's name, not Piper and Beattie; see p. 397 of Piper and Beattie (1915) for a summary of new combinations in that work.

TYPIFICATION: Fernald (1914) was the first to propose S. borealis var. sitchana, later (Fernald, 1940) making the combination under S. calycantha. Neither he nor Hultén (1937) in the latter's treatment of the taxon as S. sitchana designated a type for this name. This can be readily corrected using an original Mertens collection from LE.

A Mertens collection (K. H. Mertens s.n., without date, LE) is chosen as the lectotype for S. borealis subsp. sitchana. It bears the name proposed by Bongard (S. brachipetala Bongard) in Bongard's hand (checked against samples of his labels in Lipschitz & Vassilczenko, 1968), but unfortunately lacks the number (17) appearing in Bongard (1833). The specimen matches the protologue closely (except capsules absent) and, except for the lack of an evident sharply reflexed pedicel, is clearly representative of the taxon as currently recognized.

5. Stellaria borealis Bigelow × S. longifolia Muhlenb. ex. Willd.

Stellaria alpestris β Fries, Novit. Fl. Suec. Mant. I. 10. 1832.

Stellaria alpestris Fries var. paniculata Fries, Cat. Herb.

Normale VII, no. 34. 1841 (1842). Stellaria alpestris Fries,

Novit. Fl. Suec. Mant. III. 194. 1845. sp. emend., non Hartman

(1832). Stellaria friesiana Ser. in DC. * alpestris (Fries)

Hartman, Handb. Skand. Fl. ed. 7. 131. 1858. Stellaria borealis

× S. friesiana in J. Norman, Fl. Arct. Norv. Sp. 19. 1893.

Stellaria alpestris × longifolia in Murb., Bot. Not. 1899: 214.

1899. Original material: SWEDEN. Lappon. Torn. Karesuando, July

[year ?], L. L. Laestadius, Fries Herbarium Normale Fasc. VII,

No. 34 (UPS!, original set; MO!, S!).

?Stellaria graminea L. β alpina Laest., Kongl. Vetensk. Acad. Handl.

(ser. 3, vol. 10) 1822: 335. 1822. TYPE: Lappland, 1821, L. L.

Laestadius (S?). not seen.

Stellaria hybrida Doerfler, Herb. Norm. no. 5240. 1911, non Rouy &

Fouc. (1896), nec Bég. (1910). TYPE: Lappland. In pratis ad

Alamuonie prope "Muonia" (Lat. bor. 68), July 1905, Montell,

Herb. Norm. 5240 (BM - fide J. K. Morton).

Stellaria calycantha × longifolia in Hultén, Kongl. Svenska

Vetenskapakad. Handl. ser. 3. 5(2): 65. 1928. Original material:

USSR. Kamtchatka. not seen.

Perennial herbs. Stems erect or sometimes reclining, (22)30 - 55 cm long; upper internodes papillate or glabrous, often ridged. Leaves simple, opposite, blades lance-linear to linear, 15 - 35 mm long, (0.5)1 - 4(6) mm wide, apex acute, base truncate or rounded, glabrous, margin

papillate with or without minute cilia near the leaf base, rarely ciliate to the tip; leaves sessile or rarely with a very short petiole. Inflorescence a diffuse axillary (rarely terminal) cyme, flowers (6)15 - 20(25) per stem; bracts subtending lowermost flower usually resembling leaves, others sharply smaller and mostly scarious, 1.5 - 4.2 mm long, 0.4 - 1.3 mm wide, margin wide and scarious, papillate (or rarely glabrous) as leaves. Flowers perfect, sepals 5, basally connate, (1.6)2 - 3(3.9) mm long at anthesis, ovate to lanceolate, nerves becoming evident ridges in lower half of the sepals, or nerves extending to the tip, apex acute, margin scarious, exceeding 0.1 mm width; petals often 5, white, deeply 2-cleft, from 1/2 to 1 1/2 X the length of the sepals; stamens 10(8) or fewer; styles (2)3(4), white, erect and later spreading, 1.1 - 1.7(2.2) mm long, stigmatic along entire length. Pedicels 16 - 40 mm long, erect, glabrous. Capsules reported as rarely formed (Norman, 1893), not seen in North American material; seeds not known. $2n = 39$ (Morton, unpublished). Figure 56.

The combination of lanceolate to lance-linear leaves, flowers subtended by one or more herbaceous bracts below and tiny scarious bracts above, flowers with petals usually equal to or longer than the sepals, and the absence of capsules would be indicative of S. borealis × S. longifolia plants. Since most plants of S. borealis have both flowers and fruits by midsummer, a plant with these characteristics without fruit would most likely be either a hybrid plant or one infected with anther smut, Ustilago violacea; the spore mass formed in the enlarged, reddened anthers would be diagnostic of the latter plants.

DISTRIBUTION: Very few collections of S. borealis × S. longifolia

have been made (Figure 57), several of these being mixed gatherings of hybrid plants and one of the putative parents. It is reasonable to expect the occurrence as occasional plants where ranges of the two species overlap. Comparison of Hultén's (1968) map of the range of Stellaria longifolia with those for S. borealis (Figures 53 and 55) indicates that the species overlap throughout most of the range of S. borealis except in the Aleutian Islands, western Alaska, northern Mackenzie District and Yukon Territory, California, and most of Northeastern Québec/Labrador. Although very little elevation data was available from collections examined, a similar elevation range to that of S. borealis is suggested, with collections known from the low elevations (Mississagi Island in the Great Lakes) to at least 2440 meters.

Flowering was noted from early June through early August.

ECOLOGY: Specimens of S. borealis × S. longifolia occur along creek edges, in swampy woodlands, and on damp slopes.

PROTECTION STATUS: None

COMMON NAMES: No common names are known.

SPECIMENS EXAMINED: CANADA. ALBERTA. Kananaskis Country: Livingstone Camp, Coleman [from site of NA4648?]; grown from seed in greenhouse at Waterloo, collected 25 Mar 1976; without date, J. K. Morton s.n. (JKM).

ONTARIO. Algoma Dist.: Swampy woodland, Mississagi Island (North Channel), 6 Jun 1977, Morton & Venn NA10410 (JKM); 7 Aug 1977, Morton & Venn NA10726 (JKM).

YUKON TERRITORY. On gravel, Start of Dempster Hwy, ca 25 mi from Dawson City, 3 Aug 1968, Morton NA2170 (JKM).

USA. ALASKA. Matanuska Bor.: Matanuska, 10 Jul 1931, J. P.

Anderson s.n. (ISC).

COLORADO. Clear Creek Co.: Along shaded Little Bear Creek, Idaho Springs, 13 Aug 1942, Degener & Peiler 16815 (F, MO, NY, RM). Larimer Co.: Seepage slope in woodland, ca 2 mi from Estes Park entrance, Rocky Mountain Nat. Park, 7 Jul 1974, Morton & Venn NA7326 (JKM).

CONNECTICUT. New Haven Co.: Small stream in woods, Southbury, 13 Jul 1917, Harger 7009 (NEBC, UC).

NEW YORK. Oneida Co.: Shady flats of a stream around sand bog, Deerfield, 10 Jun 1901, Haberer 2264 (GH).

WASHINGTON. Skamania Co.: Little White Salmon River below Berry Creek, 26 Jun 1895, Suksdorf 2438 (WS).

WYOMING. Albany Co.: Willow swamp, E side at ski area, Medicine Bow Mtns, near Laramie, 6 Jul 1974, Morton & Venn NA7309 (JKM).

The hybrid formula proposed for this plant takes into account the morphological and chromosomal evidence which indicates that only tetraploid S. borealis plants are involved in the hybrid combination. A name for this taxon is not proposed since I think that, as is stated in Recommendation H.10B of the International Code (Voss et al., 1983), the hybrid formula conveys more information about the parentage of the hybrid than would naming the nothotaxon. In addition, the widely scattered, apparently infrequent occurrence of these plants (Figure 57) and their apparent sterility suggests that these plants result from a chance fertilization event which is not self-replicating except possibly via local vegetative propagation; these conditions would also suggest a hybrid formula is more appropriate than a binomial name (S. J. Wolf, pers. comm.).

Prior to recognition of these plants as hybrids, they were often referred to Stellaria alpestris. After Fries emended his concept of Stellaria alpestris in 1845, little is seen of the name. Although I earlier thought the name was to be associated with S. longifolia, it appears that the emended S. alpestris is associated with S. borealis × S. longifolia. Murbeck's (1899) treatment of Stellaria in northern Europe is very useful in understanding the various definitions of Stellaria alpestris. He used S. alpestris Hartman as including S. borealis, S. calycantha (defined as a form of S. alpestris), but excluded S. alpestris β of Fries. He cited Fries Herbarium Normale f. III no. 31 as an exsiccatae of this taxon; Fries' distribution of S. alpestris var. aliflora does indeed represent S. calycantha. Murbeck's S. alpestris thus is equal to S. calycantha.

The next taxon that Murbeck (1899) listed was S. alpestris × longifolia under which he listed the following synonymy: S. graminea L. β alpina Laest., S. alpestris β Fries, both listed by Fries (1845) in his synonymy of S. alpestris. Murbeck also listed S. friesiana Ser. β [* in original publication of Hartman (1858)] alpestris (Fries) Hartman, and S. borealis × friesiana Norman. These names apply to the plants in question since S. friesiana is a synonym of S. longifolia Muhlenb. ex Willd. Murbeck (1899) cited Fries Herbarium Normale f. VII no. 34 as an exsiccatae, material that matches one of the possible forms that S. borealis × longifolia plants can take. Gürke (in Richter, 1899) independently came to a similar conclusion concerning the status of S. alpestris Fries in citing it in synonymy under S. borealis × friesiana. Gürke did not cite an author after S. borealis × friesiana, a curious situation in light of his attributing other combinations to Norman

(1893) including S. friesiana × graminea.

In spite of past usage, S. alpestris cannot be used for the hybrid plants. As noted before, both Fries and Hartman described S. alpestris in 1832 in slightly different manners, Fries (1832) including both S. borealis and material assignable to the hybrid S. borealis × S. longifolia. The first usage of the name by Hartman (1832) in 1832 makes Fries' 1845 definition of S. alpestris a later homonym.

UNCERTAIN TAXA

1. Stellaria graminea L. sensu Cham. & Schldl., Linnaea 1: 49. 1826, non
L. Original material from Unalaschka. not seen.

Hultén (1937a) preceded this taxon with a question mark in his synonymy under S. sitchana var. bongardiana. I cannot support or refute Hultén's position since no Chamisso collections of S. graminea were seen.

2. Stellaria borealis Bigelow forma apetala (Fenzl) Regel lusus a.
glabra Regel, Bull. Soc. Imp. Naturalistes Moscou 35: 277. 1862.

Regel (1862) listed two collections from Alaska ["Sitka (Lutke). Unalaschka (Eschscholtz)."] and included a portion of both Stellaria borealis sensu Torrey and Gray (1838) and Stellaria crispa sensu Fenzl (in Ledebour, 1842) in synonymy. I have not seen any material bearing this name.

3. Stellaria borealis Bigelow forma β corollina (Fenzl) Regel lusus b.
dahurica Regel, Bull. Soc. Imp. Naturalistes Moscou 35: 278. 1862.

Regel (1862) described this lusus on the basis of a Sensinoff collection from Dahuria (southeastern Siberia per Stearn, 1966). I have not seen any material.

4. Stellaria borealis Bigelow forma β corollina (Fenzl) Regel lusus csachalinensis Regel, Index. Sem. Hort. Petrop. 1863: 33. 1863.

Schischkin (in Komarov & Shishkin (1936) listed this form in synonymy with Stellaria fenzlii Regel. No material has been examined.

5. Stellaria borealis Bigelow var. γ nana Hooker, Fl. Bor.-Amer. 1: 95. 1830. Original material: CANADA. Rocky Mountains, T. Drummond. not seen.

Macoun (1883) listed this variety in synonymy with Stellaria umbellata Turcz. Robinson (1894, 1897) placed "S. borealis, var. Hook." in synonymy with S. umbellata, although he did not specify whether it was var. γ nana. No material labeled S. borealis var. nana was received in loans for this study.

6. Stellaria mollis Wirzen, Geogr. Pl. Prov. Casan. 43. 1839, non Willd. ex. Schldl (1816), non Fischer ex DC (1823), nec Klotzsch (1862). Original material from Finland, not seen.

Fenzl (in Ledebour, 1842) included S. mollis Wirzen in synonymy under S. borealis var. corollina. I cannot confirm his action.

7. Stellaria laxa Behm, Bot. Not. 1887: 181. 1887, nec Merr. (1905), nec Muschler (1911). Original material from Jamtland, Sweden, not seen.

Murbeck (1899) included S. laxa Behm in synonymy under S. calycantha (his S. alpestris). Gürke (in Richter, 1899) considered S. laxa as a "Species dubiae et non satis notae." I cannot comment on these treatments since I have not seen any specimens of S. laxa.

8. Alsine alpestris (Fries) Rydb., Bull. Torrey Bot. Club. 39: 315.
1912.

Rydberg (1912) cited Stellaria alpestris Fries of 1832 as the basionym. Although I suspect Rydberg used this combination much as Gray did with his S. borealis var. alpestris, I cannot confirm this thought since I have not seen any Rydberg collections bearing this name.

9. Stellaria yesoalpina Nakai, Bot. Mag. (Tokyo) 43: 450. 1929. TYPE:

JAPAN. Yeso: in humidis frigidis secus torrentis montis

Daisetsusan prov. Ishikari, T. Nakai (TI).

Both Mizushima (1965b) and Ohwi (1965) place S. yesoalpina in synonymy with S. calycantha. I have not seen any material of this taxon.

REJECTED TAXA

1. Alsine palmeri Rydb., Bull. Torrey Bot. Club 39: 315. 1912.

Stellaria palmeri (Rydb.) Tidestrom, in Tidestrom & Kittell, Fl. Arizona & New Mexico 92. 1941. TYPE: USA. UTAH. Iron Co.: Bear Valley, 1877, E. Palmer 54 (holotype, NY [ex Columbia]; isotypes, GH!, MO!, NY!)

A species of Stellaria that has often been overlooked is Stellaria palmeri Tidestrom. Rydberg (1912) described it as Alsine palmeri based on E. Palmer 54 collected in 1877, with Tidestrom (in Tidestrom & Kittell, 1941) transferring it to Stellaria. Rydberg (1912) noted that the type was originally determined as "Stellaria borealis by Dr. Watson but is evidently not closely related to it", and suggested it may be closer to Stellaria edwardsii. Welsh (1982) considered it as a synonym of Stellaria obtusa. An inspection of three undesigned isotypes of Palmer 54 (GH, MO, NY [not the ex Columbia College specimen that Rydberg (1912) refers to) revealed that Rydberg's observation was correct. The presence of petals about equal to or slightly surpassing the sepals and a wrinkled, but not reticulate seed places it outside of either S. calycantha, S. borealis, or S. obtusa. Instead, it is a small specimen of S. longipes.

The collection locality for Palmer 54 has also been misinterpreted. Rydberg (1912) cited it as "Beaver Valley" while Welsh (1982) cited it as "Beaver Co., Beaver Valley." In his biography of Edward Palmer,

McVaugh (1956) made a good case for interpreting "Beaver" as an error, the actual locality being Bear Valley in northeastern Iron County, an area where Palmer is known to have collected before moving north to Beaver later in July of 1877. Only one of the three sheets of Palmer 54 that I have seen includes any locality information besides the label heading "Southern Utah, Northern Arizona, etc."; the GH specimen is from Bear Valley. This situation may have been aggravated by the fact that Palmer 55 is from Beaver City, Utah and is mounted on the same sheet (a practice also followed on the MO and NY specimens). I suspect "Bear" and Beaver" could have been thought to be the same at the time the collections were prepared at GH.

2. Alsine polygonoides Rydb., Fl. Colorado 128. 1906, non Prantl (1884).

nomen nudum. Original material: USA. COLORADO. Mineral Co.: Near Pagosa Peak, 12000 ft, Aug 1899, C. F. Baker 307 (MO, NDG, RSA).

Harrington (1964) incorrectly placed Alsine polygonoides in synonymy with Stellaria obtusa. Weber's (1961) inclusion of the name in synonymy with Stellaria irrigua Bunge is correct.

Weber annotated the NDG collection of Baker 307 with the Rydberg (1906) reference as the publication of A. polygonoides, although no description or reference to one is provided there by Rydberg. M. S. Taylor (pers. comm.), currently compiling a list of types based on C. F. Baker collections, has been unable to locate a published description of A. polygonoides.

3. Stellaria borealis Bigelow forma glaucescens Kurtz, Bot. Jahrb. Syst. 19: 366. 1894. nomen nudum. Original material: USA. ALASKA. Gebiet des Lynn-Canals: Portage Bay, 6 Aug 1882, A. & A. Krause 408 (holotype, B [destroyed?]; isotype, CORD!).

Kurtz (1894) did not provide a description for this name.

4. Stellaria borealis Bigelow forma macrantha Kurtz, Bot. Jahrb. Syst. 19: 366. 1894, nomen nudum. Original material: USA. ALASKA. Gebiet des Lynn-Canals: [Meer?] Strandwiesen an der Mündung des Tschutkat [Chilcatflusses in pub.], 21 Jul 1882, A. & A. Krause 324 (B [destroyed?], CORD).

Hultén (1944) thought S. borealis forma "macrantha" was referable to S. sitchana var. bongardiana. Besides being a nomen nudum, Krause & Krause 324 (CORD) is a specimen of S. humifusa Rottb.

5. Stellaria calycantha (Ledeb.) Bong. subsp. pilosella Kozhevnik., Bot. Zurn. (Moscow & Leningrad) 59: 513. 1974. TYPE: USSR. Central Chukotka, in systemate fl. Czantalveergyn, ad ostiam fl. Telekaj sinistram, in luco relicto gramineto Chosenia arbutifoliae [from description, label of collection is written in Cyrillic], 9 Jul 1972, Yu I. Kozhevnikov s.n. (holotype, LE?; isotype, LE!).

As noted earlier, inspection of the isotype suggested this is a pubescent form of S. longifolia, not S. calycantha or S. borealis.

6. Stellaria oxyphylla Robinson, Bot. Gaz. (Crawfordsville) 25: 165, pl. 13, fig 5. 1898. Alsine oxyphylla (Robinson) A. A. Heller, Cat. N. Amer. Pl. ed. 2. 4. 1900. TYPE: USA. IDAHO. Kootenai Co.: St. Joseph River, Wies[s]ner's Peak, Alt. 1800 ft, 8 Jul 1892, J. H. Sandberg, D. T. MacDougal, & A. A. Heller 608 (holotype, US!; isotypes, GH!, NY!, PH!).

Inspection of type material reveals this species should be placed in synonymy with Pseudostellaria jamesiana (Torrey) W. A. Weber & R. L. Hartman.

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REVISION OF THE STELLARIA CALYCANTHA (CARYOPHYLLACEAE)
COMPLEX AND TAXONOMIC NOTES ON THE GENUS

By

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A DISSERTATION

VOLUME II

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Botany and Plant Pathology

1986

APPENDICES

APPENDIX A

TABLES AND FIGURES

504. STELLARIA * *Alfina Tournef.* 126.

CAL. *Perianthium* pentaphyllum: *foliis* ovato-lanceolatis, concavis, acutis, patentibus, persistentibus.
 COR. *Petala* quinque bipartita, plana, oblonga, marcescentia.
 STAM. *Filamenta* decem, filiformia, corolla breviora: *alterna* breviora. *Anthera* subrotunda.
 PIST. *Germen* subrotundum. *Styli* tres, capillares, patentes. *Stigmata* obtusa.
 PER. *Capsula* ovata, tecta, unilocularis, sexvalvis.
 SEM. plurima, subrotunda compressa.

or (my translation)

CALYX. Perianth 5-leaved: leaves ovate-lanceolate, concave, acute, spreading, persistent.

COROLLA. Petals 5, bifid, flat, oblong, persistent.

STAMENS. Filaments 10, filiform, shorter than the corolla: Alternates shorter. Anthers subrotund.

PISTIL. Ovules subrotund. Styles 3, capillary, spreading. Stigmas obtuse.

FRUIT. Capsule ovate, hidden, unilocular, 6-valved.

SEED. many, subrotund, compressed.

Figure 1. Description of Stellaria from Linnaeus (1754).

342. ALSINE.

CAL. *Perianthium* pentaphyllum: Foliolis concavis, oblongis, acuminatis.

COR. *Petala* quinque, æqualia, calyce longiora.

STAM. *Filamenta* quinque, capillaria. *Antheræ* subrotundæ.

PIST. *Germen* subovatum. *Styli* tres, filiformes. *Stigmata* obtusa.

PER. *Capsula* ovata, unilocularis, tecta.

SEM. plurima, subrotunda.

or (my translation)

CALYX. Perianth 5-leaved: leaves concave, oblong, acuminate.

COROLLA. Petals 5, uniform, longer than the calyx.

STAMENS. Filaments 5, capillary. Anthers subrotund.

PISTIL. Ovules subovate. Styles 3, filiform. Stigmas obtuse.

FRUIT. Capsule ovate, unilocular, hidden.

SEED. many, subrotund.

Figure 2. Description of Alsine from Linnaeus (1754).

Figure 3. Classification of Stellaria borealis α apetala presented by Fenzl (in Ledebour, 1842). Personal translation of Fenzl's Latin text follows in parentheses.

Stellaria borealis Bigelow α apetala:

"floribus omnibus v. plurimis apetalis, paucioribus 2-3 petalis, plerumque 4gynis, seminibus laevissimis."

(flowers all or many apetalous, a few with 2-3 petals, the majority 4-gynous, seeds very smooth.)

Lusus 1. "Folia majora plerumque ovata basi subciliata v. glaberrima patentia obsolete reticulato-venosa margine haud crispata."

(Most larger leaves ovate, base subciliate or clearly glabrous, margin barely reticulately-veined, not at all crisped.)

Lusus 2. "Folia plurima oblonga v. elliptico-oblonga plerumque distincta ciliata erecta manifeste reticulato-venulosa margine saepe subundulata."

(Most leaves oblong or elliptic-oblong, mostly distinctly ciliate, erect, margin clearly reticulately-veined, often subundulate.)

Lusus 3. "Folia plurima productius ovato-lanceolata v. lanceolata plerumque distincte ciliata demum flaccide reflexa manifeste reticulato-venulosa margine rarius subundulata."

(Most leaves longer, ovate-lanceolate or lanceolate, mostly distinctly ciliate, eventually flaccid, reflexed, clearly reticulate-veined, margin rarely subundulate.)

S. borealis α Hooker (Lus. 1)

S. alpestris Fries (in part to var. β examined)

Arenaria calycantha Ledeb. (Lus. 2)

Stellaria calycantha (Ledeb.) Bong. (Lus. 1 et 2)

Spergulastrum lanceolatum Michaux

Stellaria borealis Bigelow β corollina:

"floribus omnibus 5petalis v. paucissimis 3petalis, plurimis
3gynis, seminibus dorso obsoletissime rugulosis, foliis
lanceolatis rarius ovato- v. oblongo-lanceolatis."

(flowers all 5 petaled or very few 3 petaled, many 3-gynous, seeds
 obsoletely rugulose on the back, leaves lanceolate rarely ovate-
 or oblong-lanceolate.)

Lusus 1. "Calyces 1 - 1 1/2 lin. longi. Caules plerumque abbreviati
debiles.

(Calyx 1 - 1 1/2 lines long, stems mostly short, weak.)

Lusus 2. "Calyces plerumque 2 lin. longi. Caules saepe erecti
longifolii elongati."

(Calyx 2 lines long, stems often erect and elongate.)

S. alpestris Fries "l.c. !"

S. brachypetala Bongard (Lus. 2)

S. mollis Wirzen

Figure 4. Classification of Stellaria borealis β corollina presented by Fenzl (in Ledebour, 1842). Personal translation of Fenzl's Latin text appears in parentheses.

Stellaria borealis Bigelow

α apetala Fenzl.: "petalis nullis v. minimis."

(petals none or minimal.)

Lusus a. ciliata: "foliis lanceolatis v. elliptico-lanceolatis, basi v. circum ciliolatis. - Folia plana v. rarius margine crispula."

(leaves lanceolate or elliptic lanceolate, basally or entire margin ciliate. Leaves flat or margin rarely crisped.)

A. calycantha Bong. [sic]

S. calycantha Torr. & Gray

Lusus b. glabra: "foliis lanceolatis v. anguste lanceolatis, glabris. - Folia margine saepe crispa."

(leaves lanceolate or narrowly lanceolate, glabrous. Leaf margin often crisped.)

S. borealis sensu Torrey & A. Gray ex parte.

S. crispa sensu Fenzl ex parte.

Lusus c. crispa: "foliis ovato-lanceolatis, glabris, margine saepe crispis."

(leaves ovate-lanceolate, glabrous, margin often crisped.)

S. crispa Cham. & Schldl.; Fenzl in Ledeb.

ex parte.

Figure 5. The classification of Stellaria borealis α apetala of Regel (1862). Personal translation of Regel's Latin text follows in parentheses.

Stellaria borealis Bigelow

β corollina: "petalis calycem dimidium aequantibus v.
superantibus."

(petals equal or longer than one-half of the calyx)

S. borealis Bigelow, S. borealis α Hook.,

S. crispa sensu Fenzl ex parte.

Lusus a. crispa: "foliis anguste lanceolatis, margine glabris
crispis."

(leaves narrowly lanceolate, margin glabrous,
crisped.)

Lusus b. dahurica: "foliis oblongo-lanceolatis, planis, tenuibus,
glabris."

(leaves oblong-lanceolate, flat, thin,
glabrous.)

Figure 6. Classification of Stellaria borealis β corollina of Regel (1862). Personal translation of Regel's Latin text follows in parentheses.

Figure 7. Key from Fernald (1914) outlining his Stellaria borealis classification.

Figure 8. A comparison of two circa 1915 treatments for Stellaria borealis and related species in the western United States.

Mature calyx 2-3.5 (rarely 4) mm. long: mature but unopened capsule 3-5 (rarely 5.5) mm. long.

Leaves ovate, ovate-lanceolate or elliptic-lanceolate, the primary ones 0.7-2.5 cm. long.

Branches glabrous or essentially so1. S. borealis.

Branches densely pilose2. var. Simcoei.

Leaves lanceolate to lance-linear, the primary ones 2.5-5.5 cm. long.

Upper leaves long and but slightly reduced, herbaceous throughout;
flowers few, axillary and terminal3. var. isophylla.

Upper leaves much reduced to short scarious-margined bracts:

flowers numerous in terminal cymes4. var. floribunda.

Mature calyx 4-5.5 mm. long: mature capsule 5-8 mm long: leaves

lanceolate to lance-linear, the primary 2.5-8 cm. long.

Upper leaves long and but slightly reduced, herbaceous throughout:

flowers few, axillary and terminal5. var. Bongardiana.

Upper leaves much reduced to short scarious-margined bracts: flowers
numerous in terminal cymes6. var. sitchana.

Figure 7

I. Piper and Beattie (1915)
Flora of the Northwest Coast

Stellaria borealis

S. borealis subsp. bongardiana

S. borealis subsp. sitchana

S. crispa

S. washingtoniana

II. Rydberg (1917)
Flora of the Rocky Mountains
and Adjacent Plains

Alsine borealis

A. calycantha

A. alpestris

A. brachypetala

A. crispa

A. obtusa

A. washingtoniana

Figure 8

Table 1. Qualitative characters and recognized character states chosen for Stellaria calycantha analyses.

- 1 Uppermost leaves/bracts:
 - 0 - herbaceous
 - 1 - with narrow scarious margin
 - 2 - with wide scarious margin
- 2 Leaf margin:
 - 0 - glabrous/cilia rare
 - 1 - long cilia at base
 - 2 - basal cilia tiny, margin papillate
 - 3 - sparsely ciliate to tip
 - 4 - papillate & sparsely ciliate to tip
- 3 Leaf midrib: 0 - glabrous 1 - pubescent
- 4 Inflorescence:
 - 0 - strictly axillary
 - 1 - axillary with a single terminal flower
 - 2 - axillary with a minimal inflorescence
 - 3 - in lax terminal cyme
- 5 Fruiting pedicel: 0 - reflexed 1 - not reflexed
- 6 Sepal margin:

0 - herbaceous	2 - wide scarious (over .1mm)
1 - narrow scarious ($\leq .1\text{mm}$)	
- 7 Sepal apex: 0 - acute 1 - obtuse
- 8 Nerves of sepals in fruit:

0 - not raised as ridges	1 - nerves become evident ridges
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- 9 Length of sepal nerve ridges:

0 - NA	2 - beyond 1/2 to entire herbaceous part of sepals
1 - lower 1/2 of sepals	
- 10 Petals: 0 - present 1 - absent
- 11 Petals present:

0 - NA	2 - equal to sepals
1 - shorter than sepals	3 - longer than sepals
- 12 Stem pubescence on upper nodes:

0 - glabrous	1 - pubescent	2 - papillose
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- 13 Capsule shape: 0 - ovoid 1 - globose-ovoid
- 14 Seed surface texture:

0 - smooth	3 - finely reticulate
1 - indistinctly roughened	4 - wrinkled
2 - lightly rugose-warty	

Table 2. Quantitative characters chosen for Stellaria calycantha analyses.

- 15 Number of flowers per stem
- 16 Number of nodes above basal flower bearing flowers
- 17 Length of flowering stem - (cm)
- 18 Length of leaves two nodes below basal flower - (mm)
- 19 Length of leaves subtending basal flower - (mm)
- 20 Length of leaves two nodes above basal flower - (mm)
- 21 Length of leaves subtending uppermost flower - (mm)
- 22 Width of leaves two nodes below basal flower - (mm)
- 23 Width of leaves subtending basal flower - (mm)
- 24 Width of leaves two nodes above basal flower - (mm)
- 25 Width of leaves subtending uppermost flower - (mm)
- 26 Length of fruiting pedicel - (mm)
- 27 Length of sepals at anthesis - (mm)
- 28 Length of sepals in fruit - (mm)
- 29 Number of styles
- 30 Length of styles - (mm)
- 31 Length of mature unopened capsule - (mm)
- 32 Length of mature open capsule - (mm)
- 33 Seed width - (mm)
- 34 Seed length - (mm)

Figure 9. PCO scatter diagram of factor 1 vs. factor 2, 163 OTUs x 33 characters, illustrating Stellaria obtusa and S. crista clusters, and one cluster among the S. calycantha OTUs. Segments connecting OTUs are taken from the MST for this analysis. * - one OTU, 2 - two OTUs at that location.

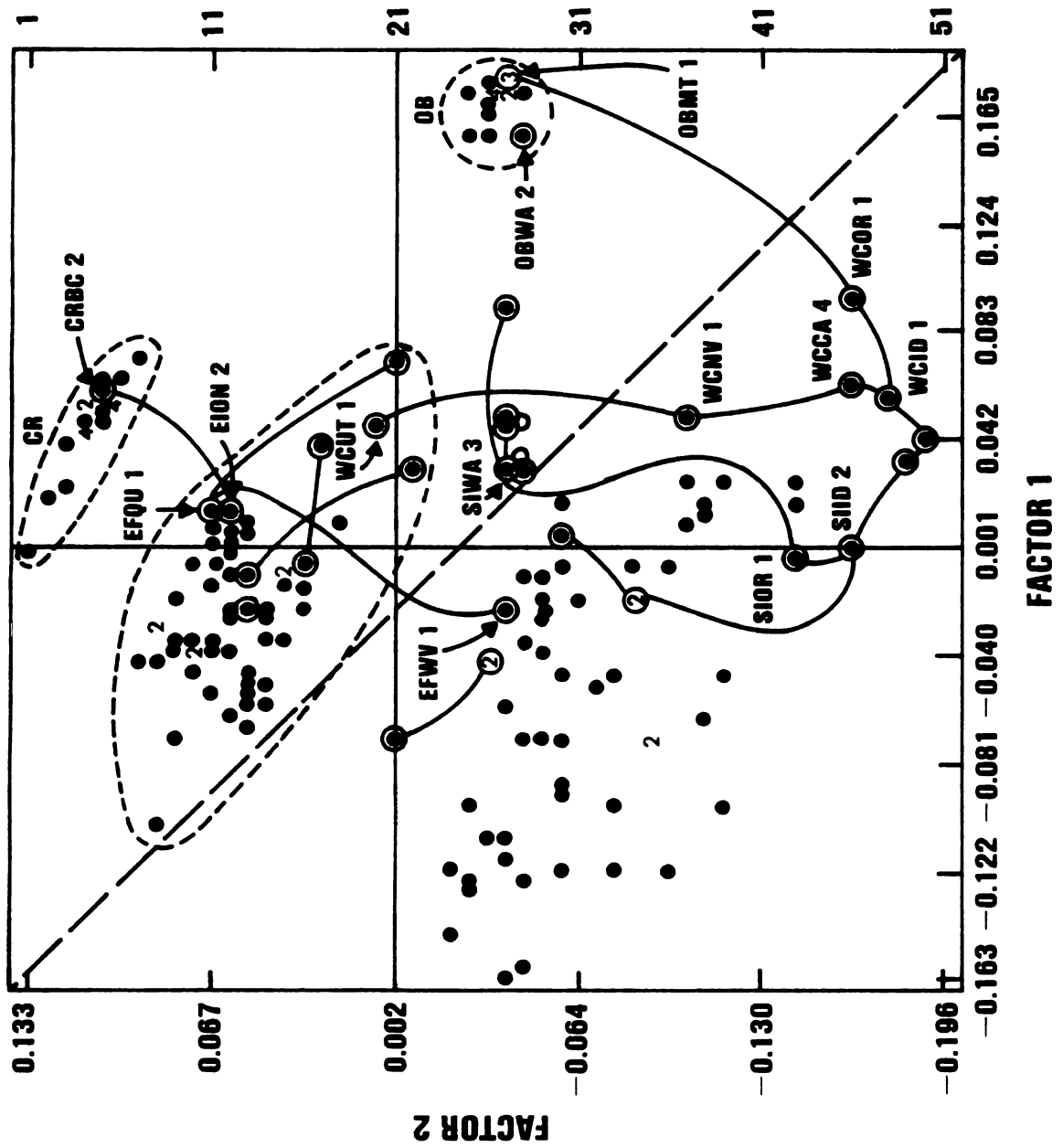


Figure 9

Table 3. Character loadings for three components of PCA analysis of 163 OTUs x 33 characters.

Character	Component 1	Component 2	Component 3
Margin of uppermost leaves	.024	-.087	.351
Leaf pubescence	.124	-.247	.195
Lower leaf midrib pubescence	-.033	-.171	-.094
Inflorescence type	.187	-.306	.130
Pedicle reflexing	-.165	-.057	-.063
Sepal apex shape	-.205	.005	-.159
Sepal nerve presence	.188	.054	.255
Sepal nerve length	.137	.248	.161
Petal presence/absence	-.103	.158	.061
Petal length	.105	-.132	-.033
Stem pubescence	.118	-.089	.082
Capsule shape	-.186	-.147	-.233
Seed surface	-.153	.245	-.144
Number of flowers per stem	.131	-.027	.146
Number of nodes of flowers	.217	-.154	.137
Stem length	.213	.155	-.060
Leaf length,			
two nodes below base flower	.256	.004	-.063
Leaf length, at basal flower	.245	.023	-.158
Leaf length,			
two nodes above base flower	.235	-.111	-.191
Leaf length, at uppermost flower	.207	-.114	-.258
Leaf width,			
two nodes below base flower	.165	.068	-.267
Leaf width, at basal flower	.130	.082	-.345
Leaf width,			
two nodes above basal flower	.199	-.194	-.220
Leaf width, at uppermost flower	.156	-.193	-.276
Pedicle length	.224	-.093	-.122
Length of sepals at anthesis	.129	.290	-.115
Length of sepals "in fruit"	.137	.342	-.111
Style number	.044	-.230	-.019
Style length	.233	-.023	.183
Length of closed capsule	.213	.223	.066
Length of open capsule	.230	.121	.137
Seed width	.061	.307	-.043
Seed length	.213	.162	.127

Figure 10. Sections of SL phenogram, 163 OTUs x 33 characters, illustrating Stellaria obtusa and S. crispa clusters. Level = similarity value of an OTU.

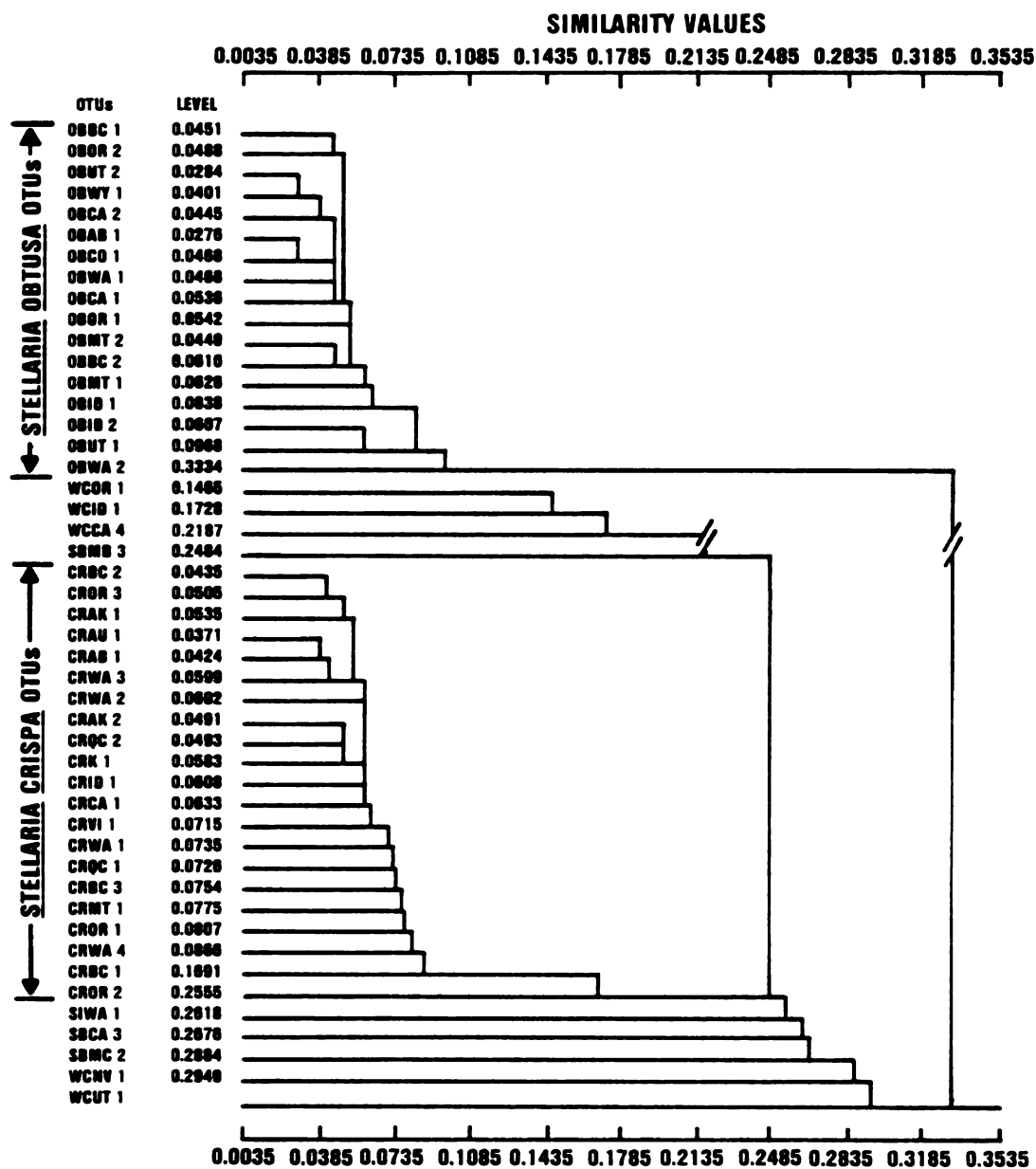


Figure 10

Figure 11. Sections of UPGMA phenogram, 163 OTUs x 33 characters, illustrating Stellaria obtusa and S. crispa clusters. Level = similarity value of an OTU.

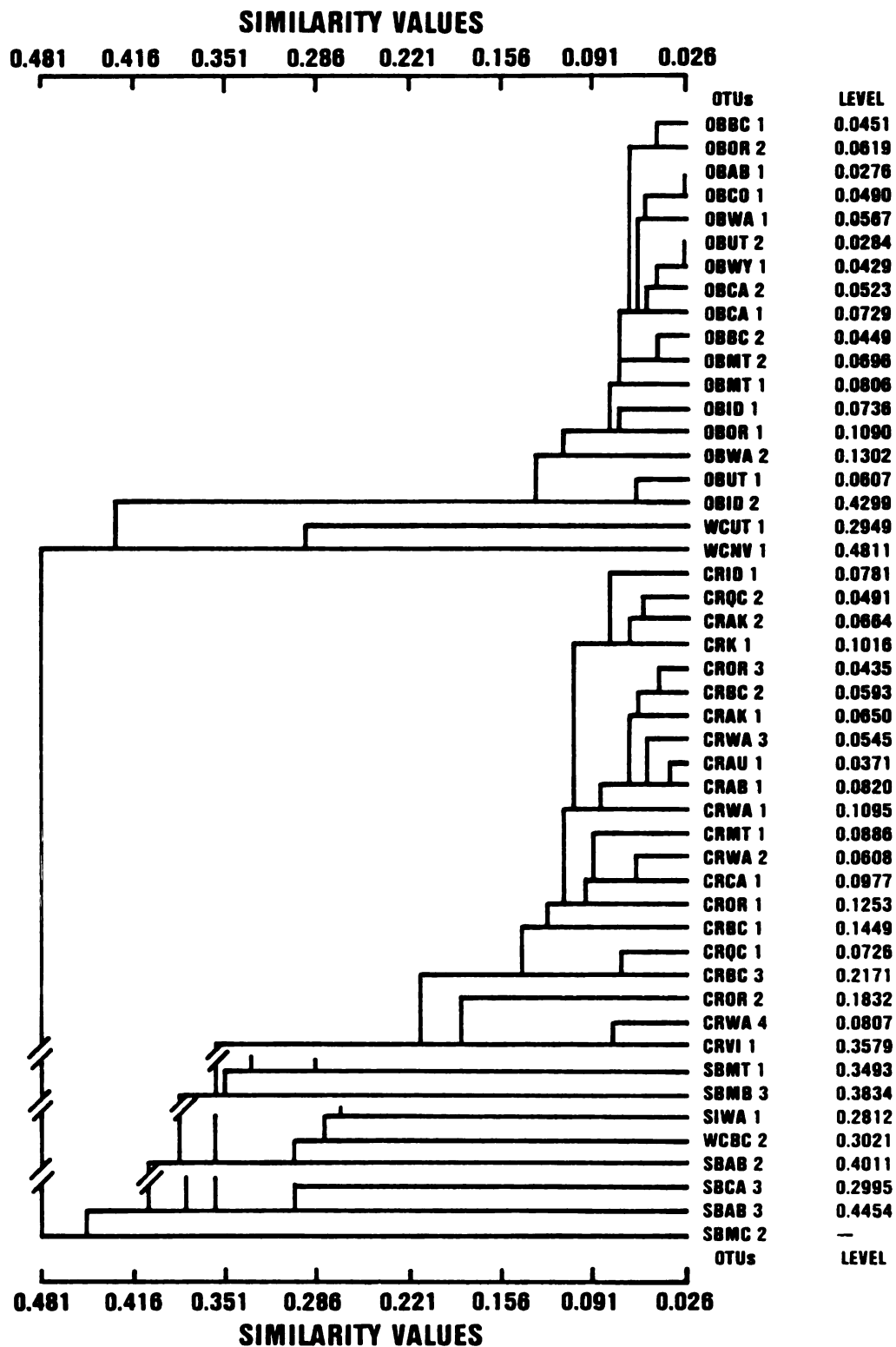


Figure 11

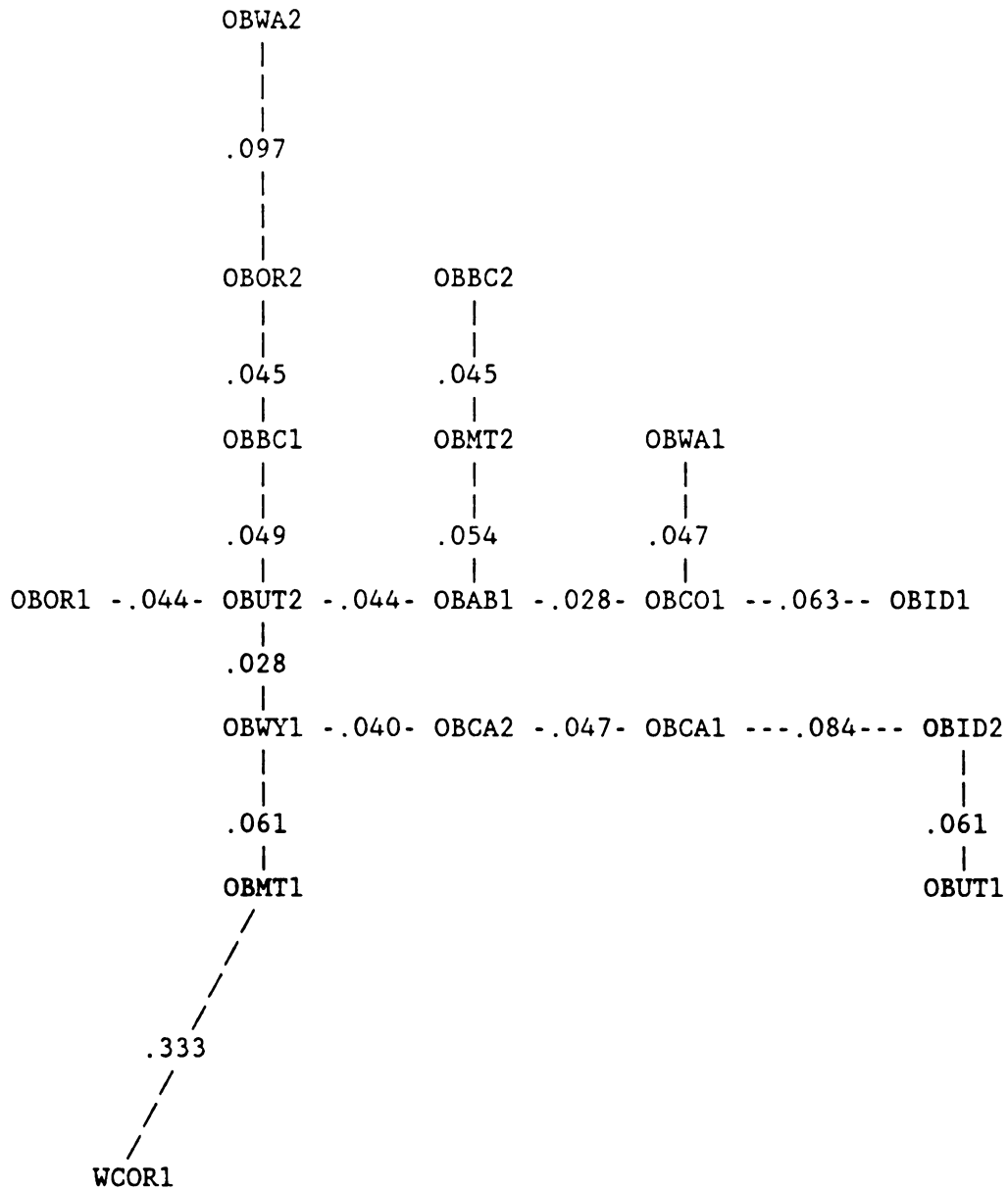


Figure 12. MST of Stellaria obtusa cluster, 163 x 33 matrix.

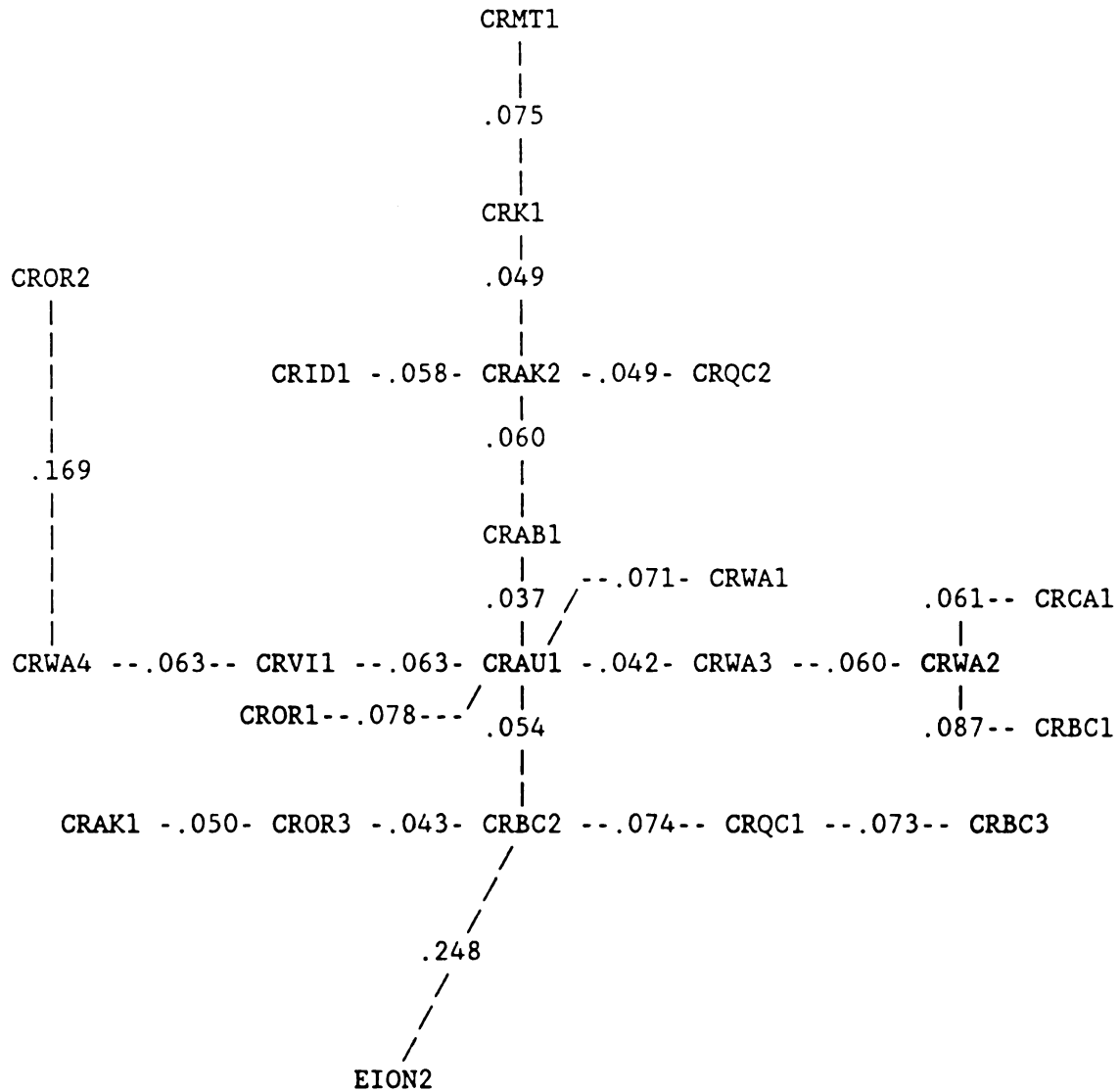


Figure 13. MST of Stellaria crisper cluster, 163 x 33 matrix.

Table 4. Character loadings for three components based on PCA analysis of 163 OTUs x 13 characters.

Table 5. Character loadings for three components based on PCA analysis of 163 OTUs x 20 characters.

Table 4

Character	Component 1	Component 2	Component 3
Margin of uppermost leaves	.143	-.006	.355
Leaf pubescence	.259	-.104	.491
Lower leaf midrib pubescence	.021	-.348	.038
Inflorescence type	.373	-.228	.269
Pedicel reflexing	-.207	-.128	.147
Sepal apex shape	-.394	-.118	.070
Sepal nerve presence	.382	.262	-.055
Sepal nerve length	.245	.334	-.407
Petal presence/absence	-.212	.472	.370
Petal length	.216	-.447	-.396
Stem pubescence	.222	-.090	-.052
Capsule shape	-.309	-.402	.054
Seed surface	-.364	.116	-.254

Table 5

Character	Component 1	Component 2	Component 3
Number of flowers per stem	.144	-.033	.428
Number of nodes of flowers	.223	-.163	.398
Stem length	.261	-.155	.087
Leaf length, two nodes below base flower	.300	-.027	.096
Leaf length, at basal flower	.302	-.042	-.031
Leaf length, two nodes above base flower	.282	-.216	-.026
Leaf length, at uppermost flower	.253	-.223	-.206
Leaf width, two nodes below base flower	.217	-.010	-.325
Leaf width, at basal flower	.192	-.032	-.400
Leaf width, two nodes above basal flower	.236	-.319	-.099
Leaf width, at uppermost flower	.192	-.314	-.269
Pedicel length	.257	-.123	-.004
Length of sepals at anthesis	.169	.350	-.192
Length of sepals "in fruit"	.184	.397	-.166
Style number	.039	.296	.057
Style length	.232	.026	.307
Length of closed capsule	.245	.283	.126
Length of open capsule	.249	.171	.199
Seed width	.090	.339	-.170
Seed length	.218	.200	.062

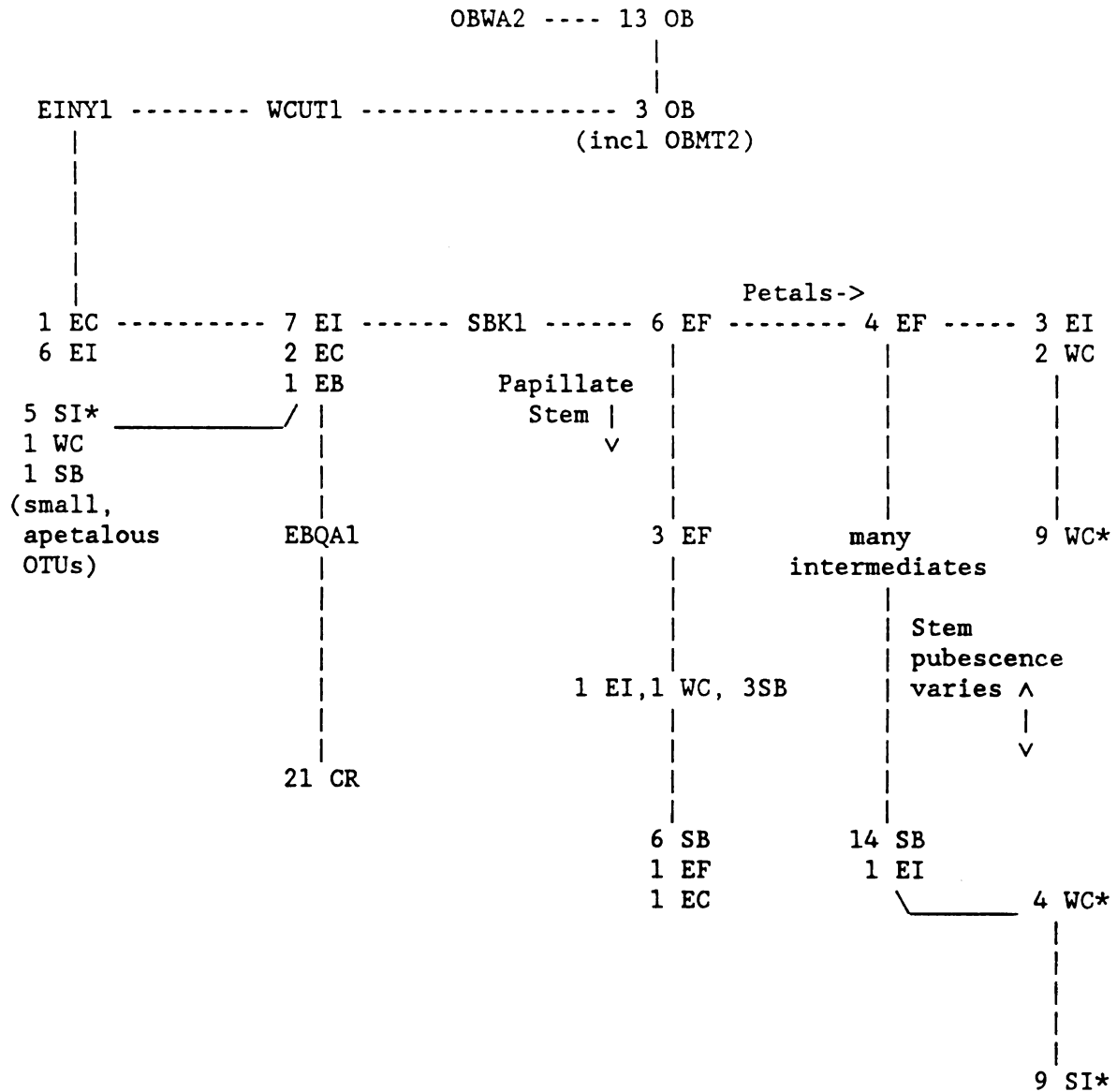


Figure 14. Simplified MST of 163 x 13 matrix, illustrating major clusters of OTUs. * = cluster not composed of zero-length segments.

Figure 15. PCO scatter diagram of factor 1 vs. factor 2, 163 OTUs x 20 quantitative characters. * = one OTU, 2 = two OTUs at that location.

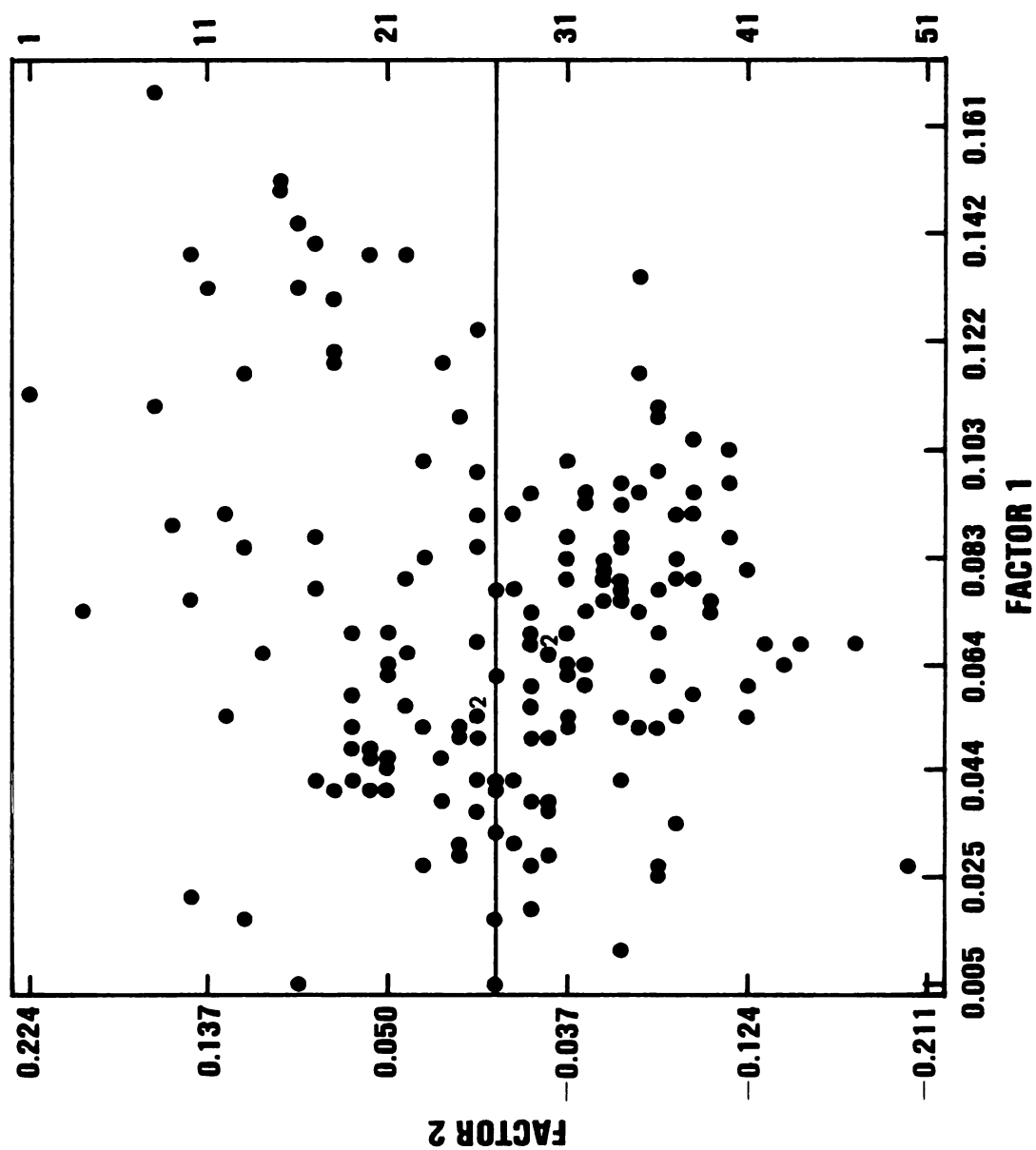


Figure 15

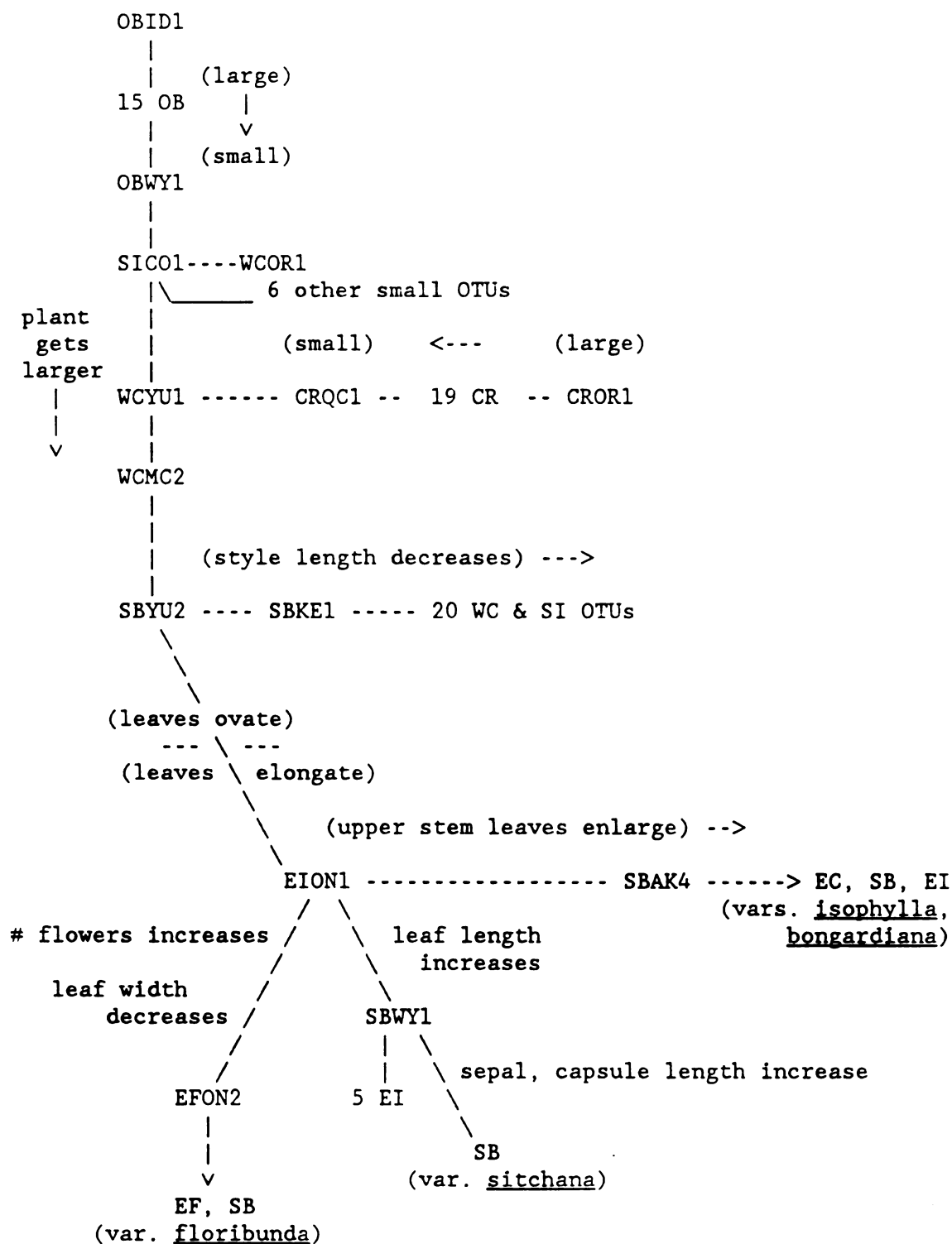


Figure 16. Simplified MST of 163 x 20 matrix.

Figure 17. PCO diagram of factor 1 vs. factor 2, 125 Stellaria calycantha and S. borealis OTUs x 33 characters. Segments connecting OTUs are taken from MST for this analysis.
* - one OTU, 2 - two OTUs at that location.

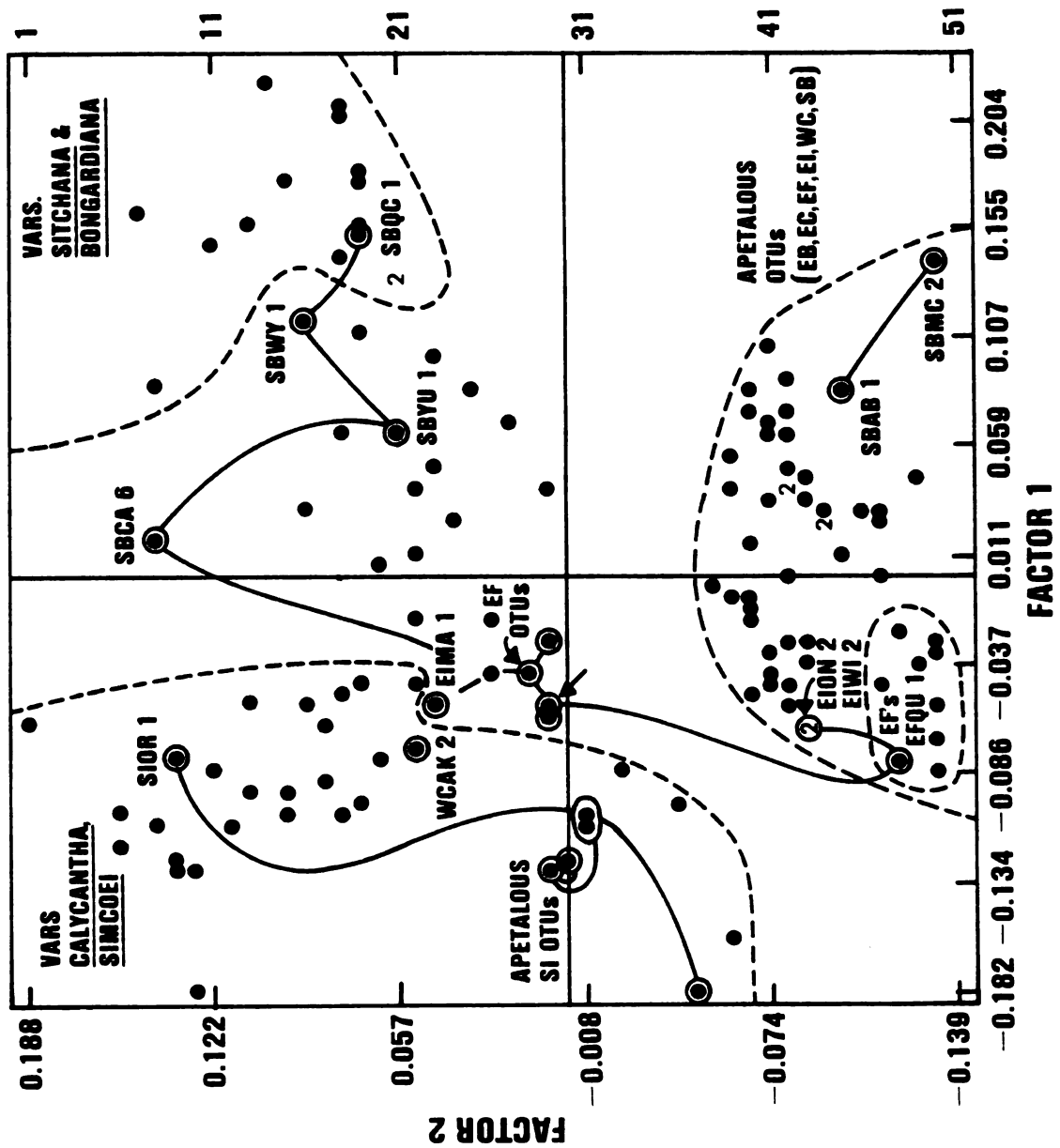


Figure 17

Table 6. Character loadings for three components based on PCA analysis of 125 *S. calycantha* and *S. borealis* OTUs x 33 characters.

Character	Component 1	Component 2	Component 3
Margin of uppermost leaves	.056	-.272	.026
Leaf pubescence	-.013	-.211	.179
Lower leaf midrib pubescence	.117	.157	-.117
Inflorescence type	.014	-.165	.057
Pedicel reflexing	.179	.131	.053
Sepal apex shape	.071	-.011	.008
Sepal nerve presence	-.071	-.242	.007
Sepal nerve length	-.138	-.171	-.244
Petal presence/absence	.028	-.104	.504
Petal length	-.040	.064	-.532
Stem pubescence	-.075	-.104	-.173
Capsule shape	.149	.215	-.136
Seed surface	-.167	-.098	-.153
Number of flowers per stem	-.118	-.177	.141
Number of nodes of flowers	-.186	-.189	.094
Stem length	-.262	-.041	-.035
Leaf length, two nodes below base flower	-.282	-.021	.046
Leaf length, at basal flower	-.277	.065	.106
Leaf length, two nodes above base flower	-.250	.172	.090
Leaf length, at uppermost flower	-.203	.264	.048
Leaf width, two nodes below base flower	-.174	.232	.127
Leaf width, at basal flower	-.171	.268	.145
Leaf width, two nodes above base flower	-.161	.296	.128
Leaf width, at uppermost flower	-.090	.377	.072
Pedicel length	-.213	.096	-.124
Length of sepals at anthesis	-.218	.040	-.263
Length of sepals "in fruit"	-.261	.031	-.167
Style number	.052	.074	.122
Style length	-.202	-.218	-.068
Length of closed capsule	-.254	-.133	-.015
Length of open capsule	-.228	-.164	.060
Seed width	-.171	.019	.131
Seed length	-.209	-.066	.122

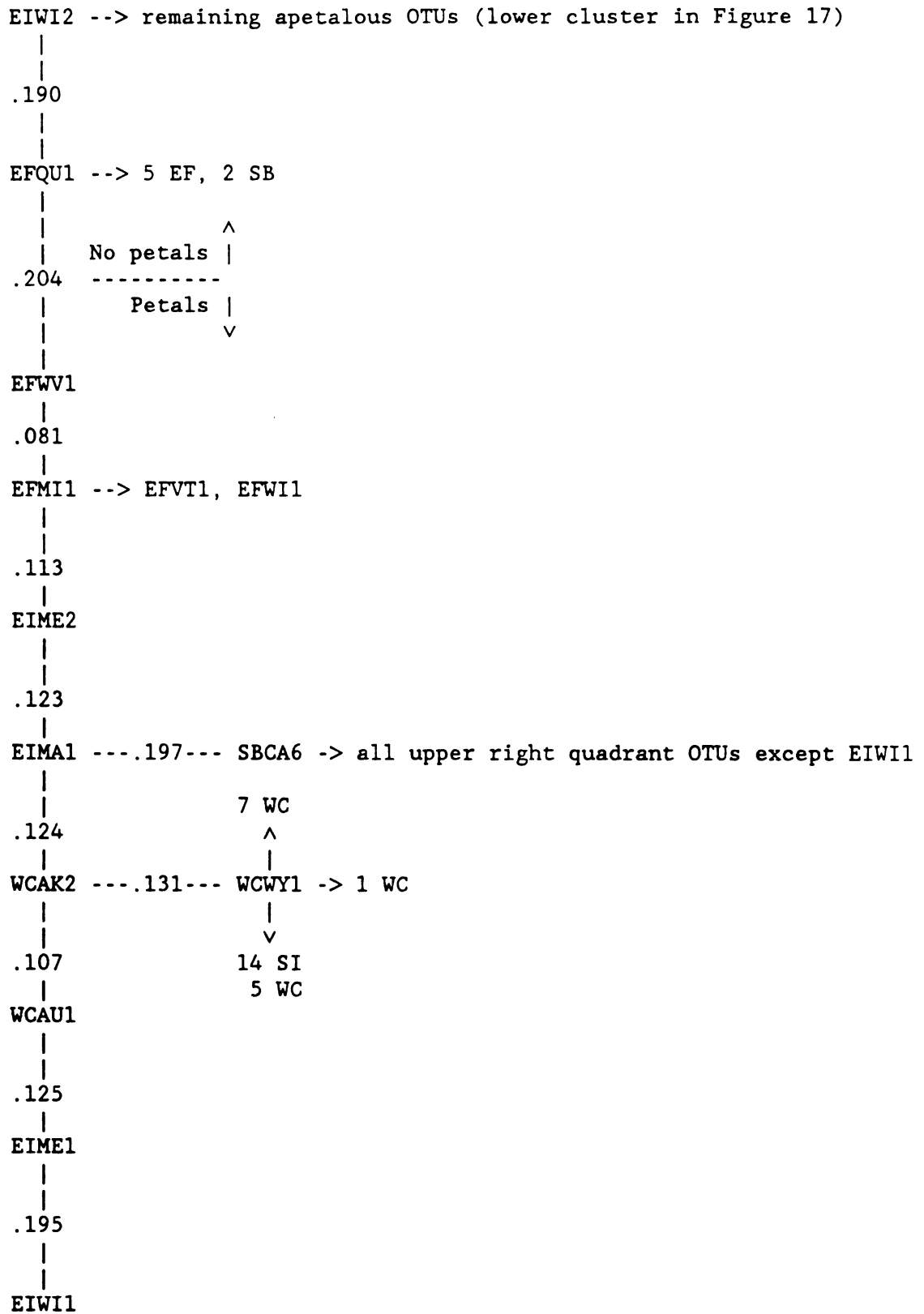


Figure 18. A portion of the MST for the 125 x 33 matrix illustrating the division between petalled and apetalous OTUs.

Figure 19. PCO diagram of factor 1 vs. factor 2, 125 Stellaria calycantha and S. borealis OTUs x 31 characters. Segments connecting OTUs are taken from the MST for this analysis.
* - one OTU, 2 - two OTUs at that location.

Table 7. Character loadings for the third components of PCA analyses of 125 OTUs x 33 characters and 125 OTUs x 31 characters.

	125 x 33 matrix	125 x 31 matrix
Character	Component 3	Component 3
Margin of uppermost leaves	.026	.176
Leaf pubescence	.179	.048
Lower leaf midrib pubescence	-.117	-.382
Inflorescence type	.057	-.204
Pedicle reflexing	.053	.014
Sepal apex shape	.008	-.234
Sepal nerve presence	.007	-.261
Sepal nerve length	-.244	-.420
Petal presence/absence	.504	
Petal length	-.532	
Stem pubescence	-.173	-.302
Capsule shape	-.136	-.275
Seed surface	-.153	-.161
Number of flowers per stem	.141	.002
Number of nodes of flowers	.094	-.008
Stem length	-.035	-.152
Leaf length,		
two nodes below base flower	.046	-.042
Leaf length, at basal flower	.106	-.017
Leaf length,		
two nodes above base flower	.090	-.043
Leaf length, at uppermost flower	.048	-.011
Leaf width,		
two nodes below base flower	.127	-.099
Leaf width, at basal flower	.145	-.012
Leaf width,		
two nodes above base flower	.128	.006
Leaf width, at uppermost flower	.072	.076
Pedicle length	-.124	-.081
Length of sepals at anthesis	-.263	-.069
Length of sepals "in fruit"	-.167	-.055
Style number	.122	.024
Style length	-.068	.088
Length of closed capsule	-.015	.034
Length of open capsule	.060	.034
Seed width	.131	.284
Seed length	.122	.372

Table 8. Major character state changes between OTUs WCWY1 and ECGR1 and trends which merge near these OTUs.

A. Character state changes

Character	WCWY1	ECGR1
Style length	0.62	1.4
Length of closed capsule	2.96	3.95
Leaf pubescence	basal cilia	ciliate to tip
Length of sepals at anthesis	1.77	2.62

B. Character trends	beyond WCWY1	beyond ECGR1
Leaf length	shorter	longer
Leaf shape	ovate	lanceolate
Capsule shape	globose	ovoid

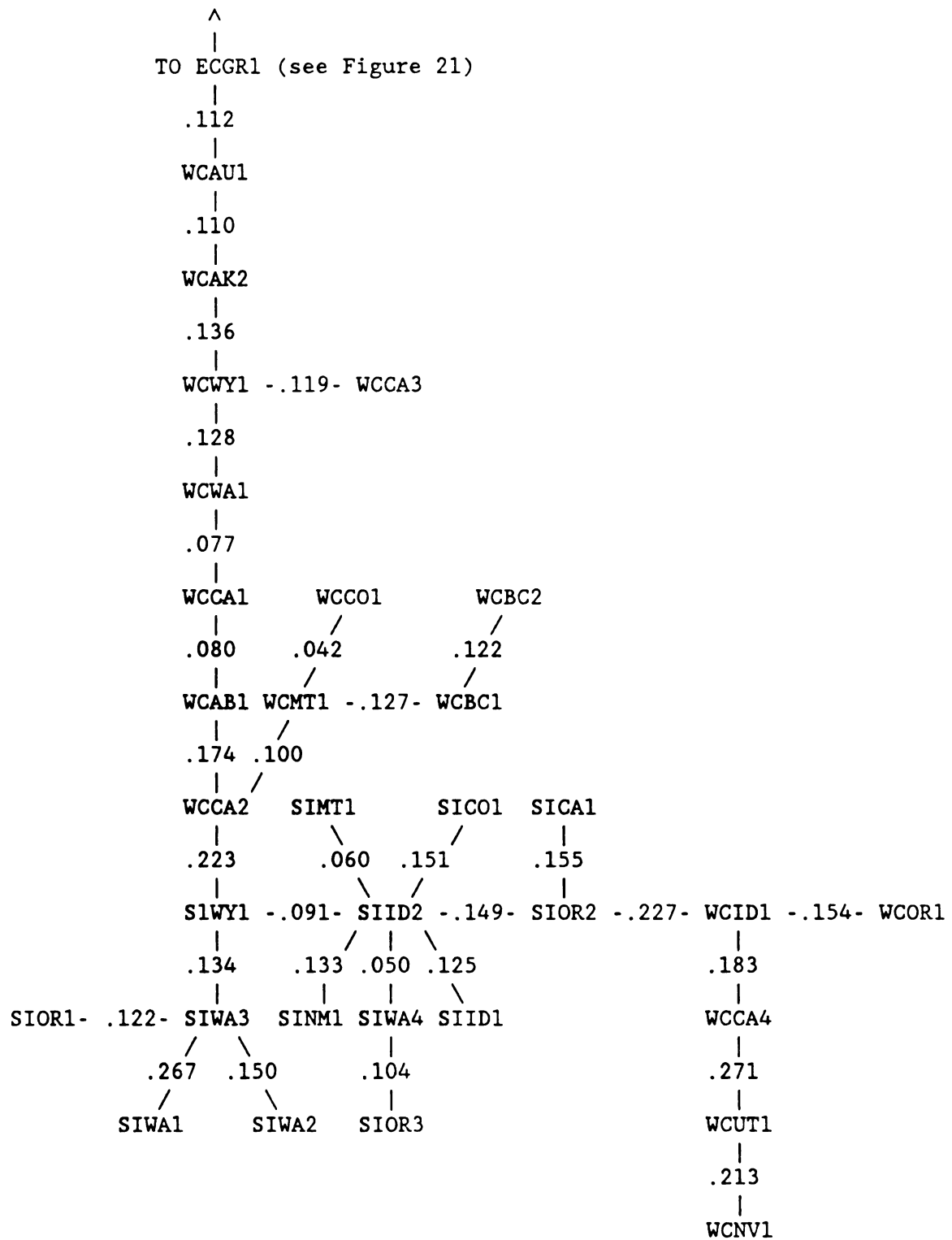


Figure 20. MST for Stellaria calycantha.

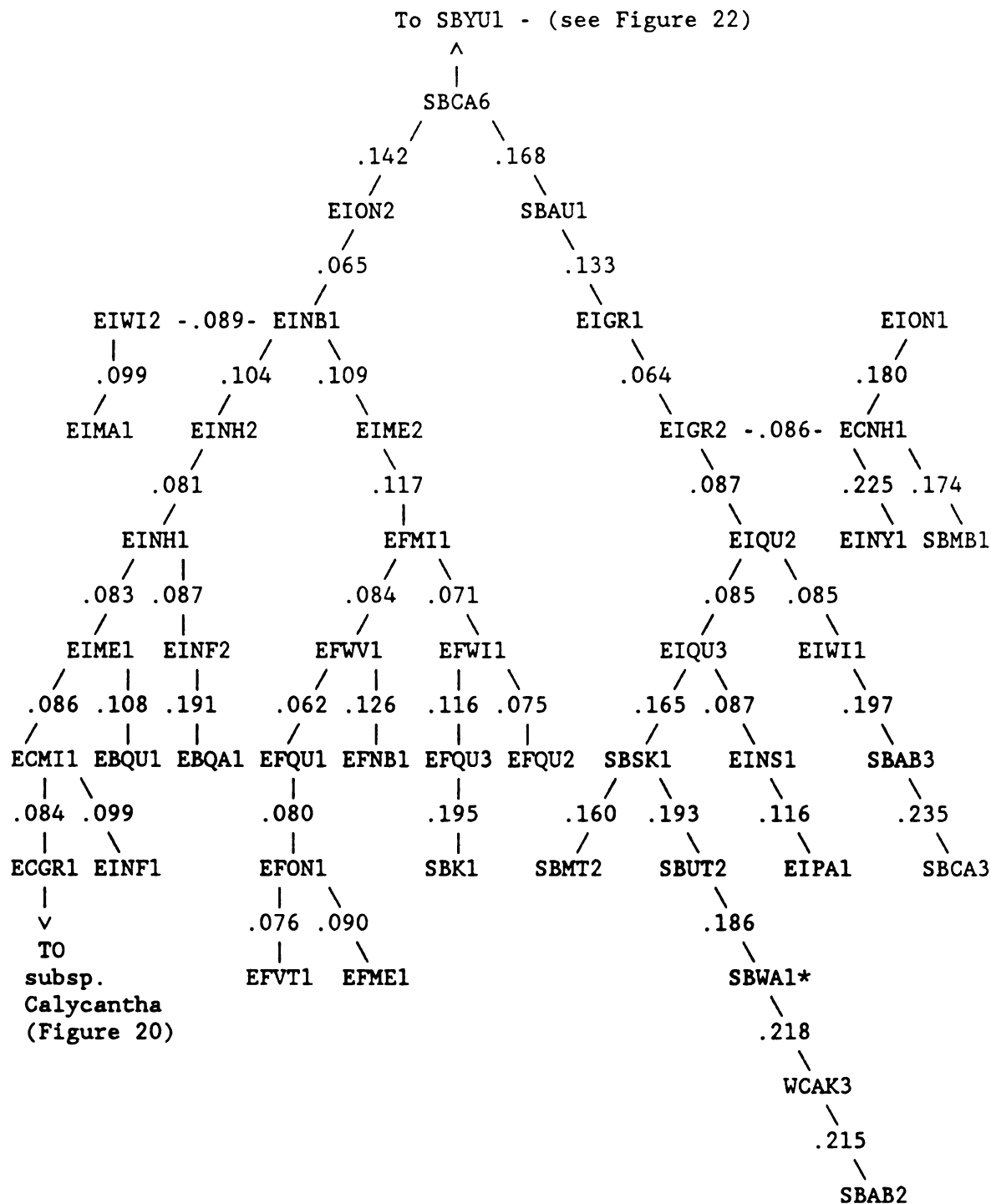


Figure 21. MST for Stellaria borealis - part 1.
Stellaria borealis × S. longifolia hybrids are marked with an asterisk.

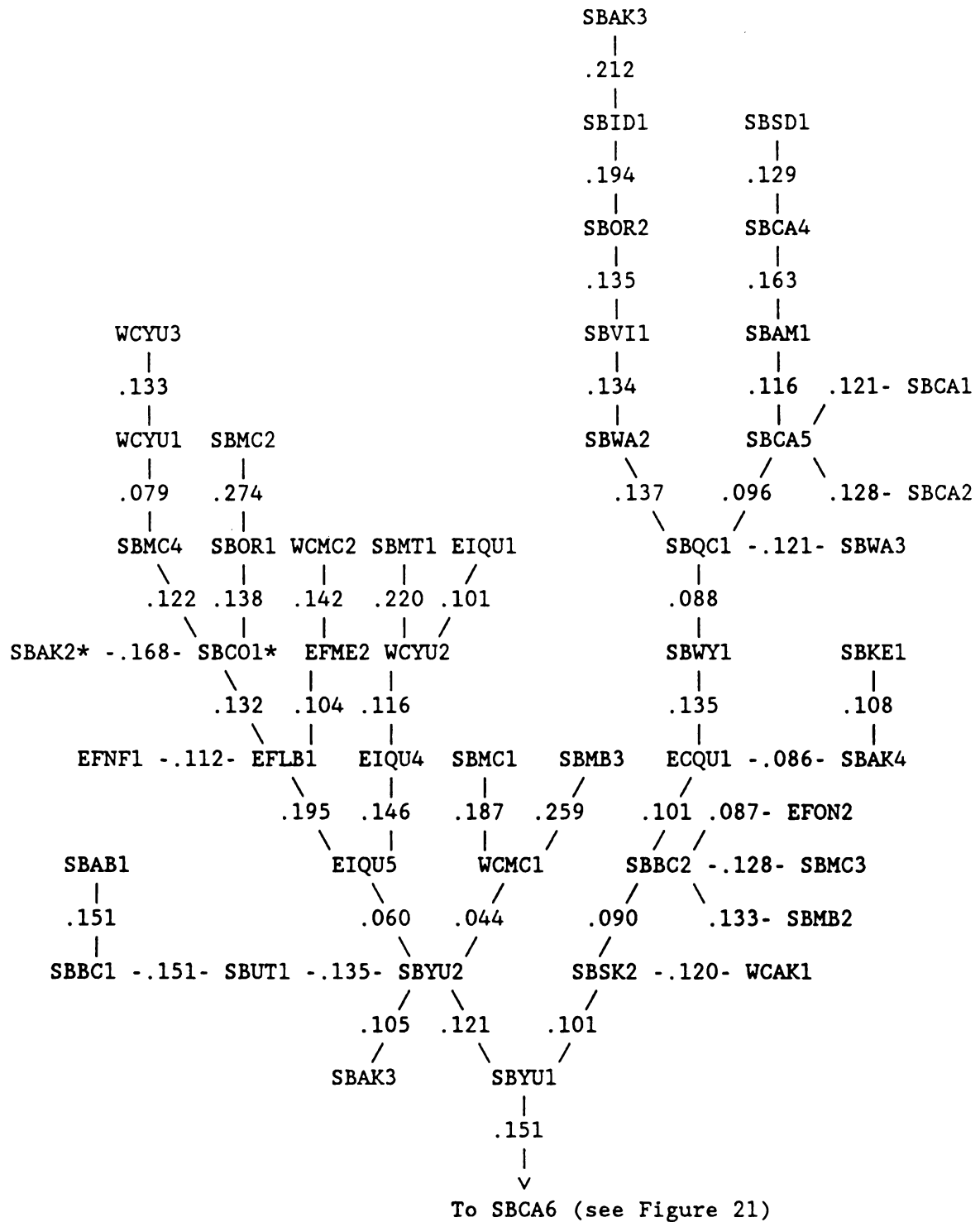


Figure 22. MST for *Stellaria borealis* - part 2.
Stellaria borealis × *S. longifolia* hybrids marked with an asterisk.

Figure 23. UPGMA phenogram of Stellaria borealis, 93 OTUs x 31 characters, illustrating six groups of OTUs. Groups 1 - 5 are included in Stellaria borealis subsp. borealis, group 6 represents S. borealis subsp. sitchana. Level - similarity value of an OTU.

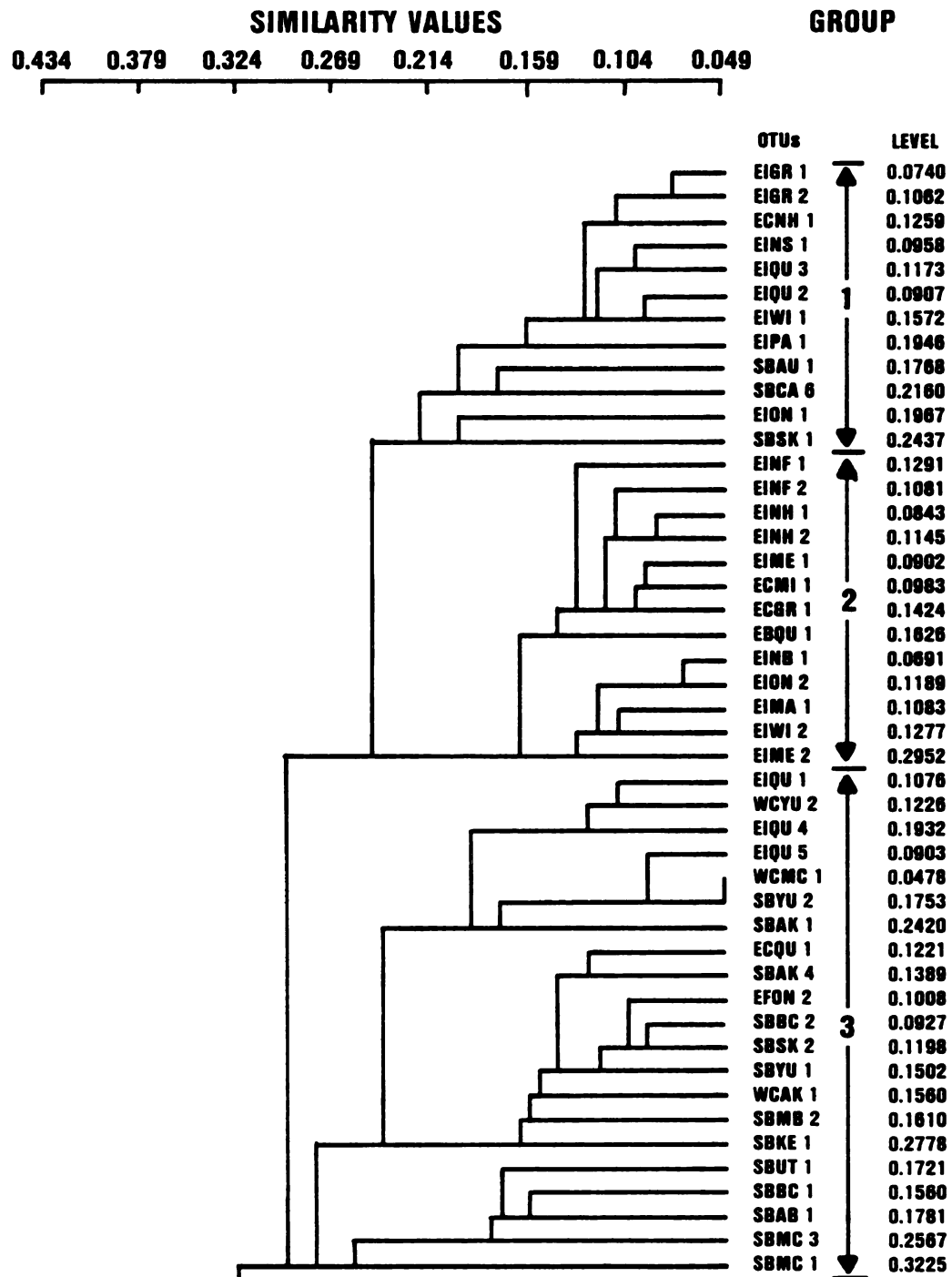


Figure 23

Figure 23 (continued). UPGMA phenogram of Stellaria borealis, 93 OTUs x 31 characters, illustrating six groups of OTUs. Groups 1 - 5 are included in Stellaria borealis subsp. borealis, group 6 represents S. borealis subsp. sitchana. Level = similarity value of an OTU.

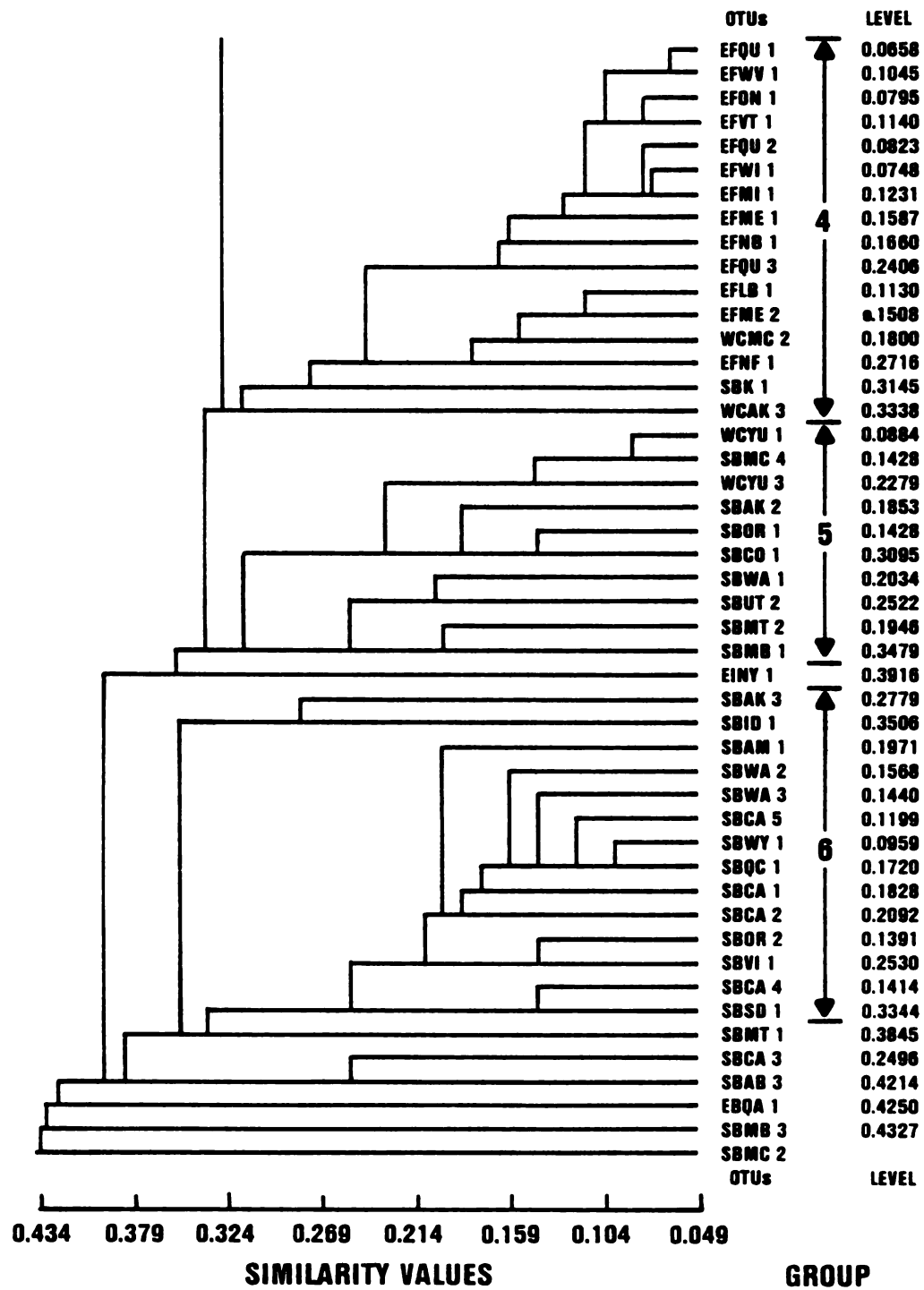


Figure 23 (continued)

Table 9. Discriminant function coefficients and classification results from analysis of matrix of 160 OTUs x 33 characters, 81 OTUs in analysis phase.

A. STANDARDIZED CANONICAL DISCRIMINANT FUNCTION COEFFICIENTS

	FUNC 1	FUNC 2	FUNC 3	FUNC 4	FUNC 5	FUNC 6
LEAFTIP	.72539	-.10849	.80947	.55421	.37709	-.41457
LEAFPUB	-.60831	.20041	-.13859	-.42364	.29283	.44564
INFLTYP	-2.73583	-.39916	-.11014	.05622	-.01747	-.15117
PEDRFLX	-.39131	-.72882	-.19368	.45436	.60674	-.17963
SEPAPEX	-.25518	-.27842	.41947	-.03277	-.63847	.39831
SEPNERV	.31409	-.16704	-.21742	.04988	.31693	.21489
NERVLNTH	.50491	1.53729	-.41850	.43844	-.21802	.28316
PETALS	8.12694	.94903	2.88599	2.84374	.77972	.58687
PETLNTH	7.71551	.53330	2.52860	3.24804	.96352	.75966
STEMPUB	.47784	.58647	.29730	.39943	-1.06228	.04679
CAPSHAP	-.52963	-.35415	-.22531	.45020	.13184	.45759
SEEDSUR	.10062	-1.13358	.38671	.27420	.58712	-.67202
FLWSTEM	-.39015	1.05874	.20821	-.77181	-.35043	-.01933
NODEFLW	.09391	-1.66355	.24914	1.03917	.23664	-.30237
STEMLNTH	.39605	-.44284	-.47250	.42517	.49902	.07796
LF2BLN	.20727	-.84771	.81063	1.00442	1.41677	.62215
LFBLN	-.55358	.68900	.02406	-1.74463	-1.25327	.39535
LF2ALN	4.24386	2.59279	-.07274	-.00866	-.66702	-.52642
LFTPLN	.30214	-2.06274	1.90006	1.54919	.68489	-.83767
LF2BWD	.04741	.77226	-.09677	-.51066	-1.50010	.16639
LFBWD	.75906	-1.19364	-.17208	.48795	1.07734	-.55479
LF2AWD	-4.21911	-1.24183	.13946	.10731	.46937	.86033
LFTPWD	.77896	1.69897	-1.71639	-.53481	-.32784	.33426
PEDLN	-.28278	-.05547	.16622	.08778	.10581	-.30890
SEPANLN	-.24595	.41308	.09881	-.13700	.11260	.70755
SEPFRLN	-.24424	-.97852	.00697	1.15659	.47604	-.27514
STYNO	.67824	.52425	-.11656	.24190	.00178	-.16618
STYLN	-.26941	.88890	.63400	-.45568	.09912	.24468
CAPCLLN	.65524	.98255	-.52565	-.48328	-1.13500	-.23738
CAPOPLN	-.62932	-.04443	.33643	-.30994	.48507	-.16486
SEEDLN	.43667	.20136	.24910	.03623	.01451	.07670
SEEDWD	-1.10563	.15002	-.48675	.08960	-.02684	-.26401

B. CLASSIFICATION RESULTS: # OF OTUs
CORRECTLY ASSIGNED %

<u>S. obtusa</u>	17/17	100
<u>S. crispa</u>	21/21	100
<u>S. calycantha</u> var. <u>calycantha</u>	15/18	83.3
<u>S. calycantha</u> var. <u>simcoei</u>	10/14	71.4
<u>S. borealis</u> subsp. <u>sitchana</u>	9/17	52.9
<u>S. borealis</u> subsp. <u>borealis</u>	41/49	83.7
<u>S. borealis</u> subsp. <u>interior</u>	21/24	87.5

OVERALL PERCENTAGE CORRECTLY ASSIGNED - 83.75

DISCRIMINANT FUNCTION 1

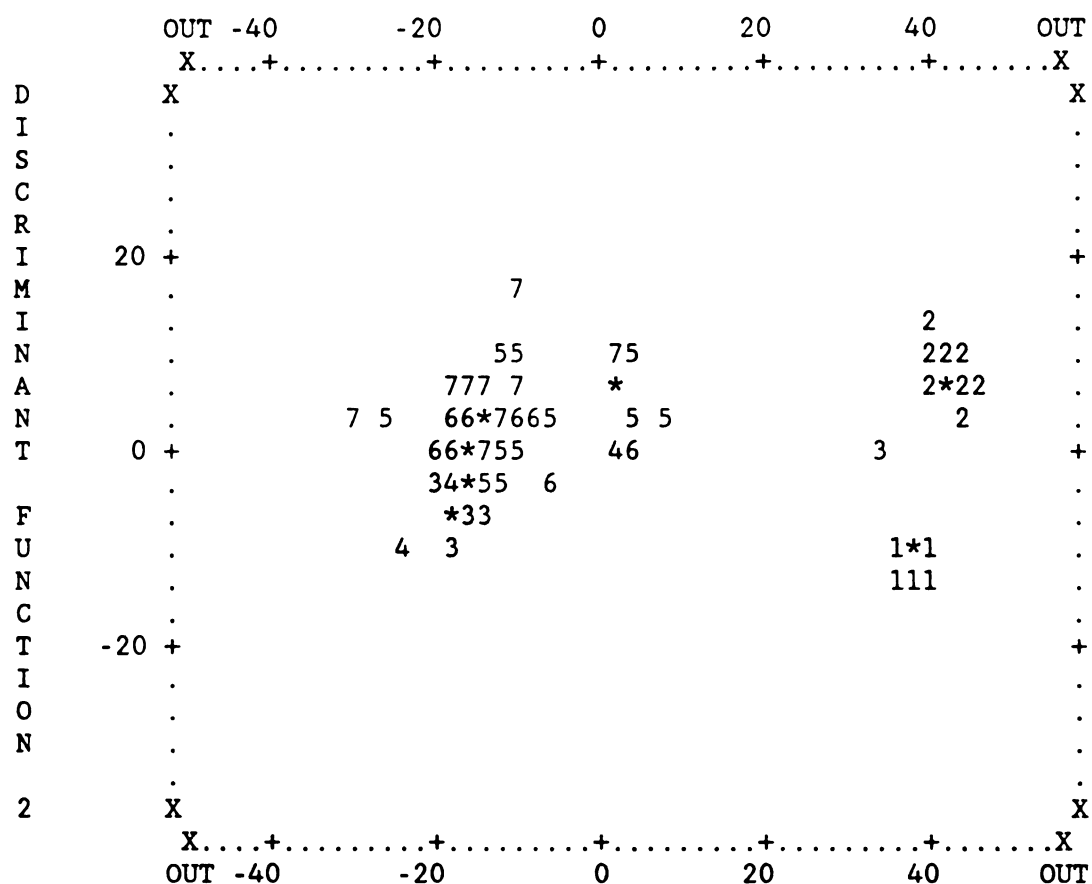


Figure 24. Scatterplot from discriminant analysis of matrix of 160 OTUs x 33 characters, standardized discriminant function coefficients listed in Table 9. 1 - 7 = OTU group numbers as originally assigned, * = a group centroid. Numbers represent one or more OTUs.

Table 10. Discriminant function coefficients and classification results from analysis of matrix of 160 OTUs x 31 characters, 96 OTUs in analysis phase.

A. STANDARDIZED CANONICAL DISCRIMINANT FUNCTION COEFFICIENTS

	FUNC 1	FUNC 2	FUNC 3	FUNC 4	FUNC 5	FUNC 6
LEAFTIP	-.23133	-.00796	.30922	-.04746	.40196	-.23840
LEAFPUB	-.26076	.09248	-.10365	-.46154	.26652	.51343
INFLTYP	-1.72148	-.42512	-.06601	.01774	.04588	-.08224
PEDRFLX	-.16284	-.41514	-.26007	.22561	.52976	-.13665
SEPAPEX	-.09673	-.28180	.51114	.19696	-.48675	.25935
SEPNERV	.20314	.05428	-.41857	-.04560	-.00445	-.13750
NERVLNTH	.03183	1.14661	-.16925	.36438	.00629	.50305
PETALS	2.32555	1.99575	1.76701	.84756	.45931	.18602
PETLNTH	2.28529	1.77674	1.56973	1.34407	.66770	.25419
STEMPUB	.16206	.46074	.38629	.55381	-.94736	-.02784
CAPSHAP	-.27066	-.34662	-.04050	.44709	.23224	.47743
SEEDSUR	.05024	-.79621	.27554	-.01575	.66056	-.52737
FLWSTEM	.34296	.80254	.26250	-.27037	-.41774	-.00929
NODEFLW	-.31824	-1.10407	.20602	.53614	.39554	-.24878
STEMLNTH	.10240	-.18746	-.41398	.02653	.40425	-.00447
LF2BLN	.70923	.63685	.42180	.66160	.81521	.02305
LFBLN	-.55642	-.40980	.21253	-1.11720	-.97660	.75322
LF2ALN	2.30478	1.62272	.32241	.55984	-.08848	-.53947
LFTPLN	-.90965	-1.22178	1.05192	.18877	.70039	-.45023
LF2BWD	-.51681	-.16265	.08001	-.00310	-1.01746	.39538
LFBWD	.83423	-.43670	-.21110	.13284	.90246	-.71676
LF2AWD	-2.36852	-.70633	-.30806	-.11373	.15854	.88972
LFTPWD	.96431	1.00360	-.98044	.18754	-.25050	-.06699
PEDLN	-.10850	.13542	.09866	-.10407	.01406	-.35484
SEPANLN	-.03691	.46897	.16302	.30705	.21837	.37974
SEPFRLN	-.55332	-.54787	-.36549	.18893	.21306	.06773
STYNO	.06305	.35046	-.20718	.12136	-.07481	-.33781
STYLN	-.13063	.71646	.62155	-.31980	.05296	.18754
CAPCLLN	.49489	.27239	.18954	-.01453	-.40889	-.31753
SEEDLN	.08839	.14638	.00921	.02798	-.10510	.02406
SEEDWD	-.41733	.14691	-.23997	.08296	.13121	-.23525

B. CLASSIFICATION RESULTS: # OF OTUs %
CORRECTLY ASSIGNED

<u>S. obtusa</u>	17/17	100
<u>S. crispa</u>	21/21	100
<u>S. calycantha</u> var. <u>calycantha</u>	17/18	94.4
<u>S. calycantha</u> var. <u>simcoei</u>	11/14	78.6
<u>S. borealis</u> subsp. <u>sitchana</u>	10/17	58.8
<u>S. borealis</u> subsp. <u>borealis</u>	42/49	85.7
<u>S. borealis</u> subsp. <u>interior</u>	21/24	87.5

OVERALL PERCENTAGE CORRECTLY ASSIGNED - 86.87

DISCRIMINANT FUNCTION 1

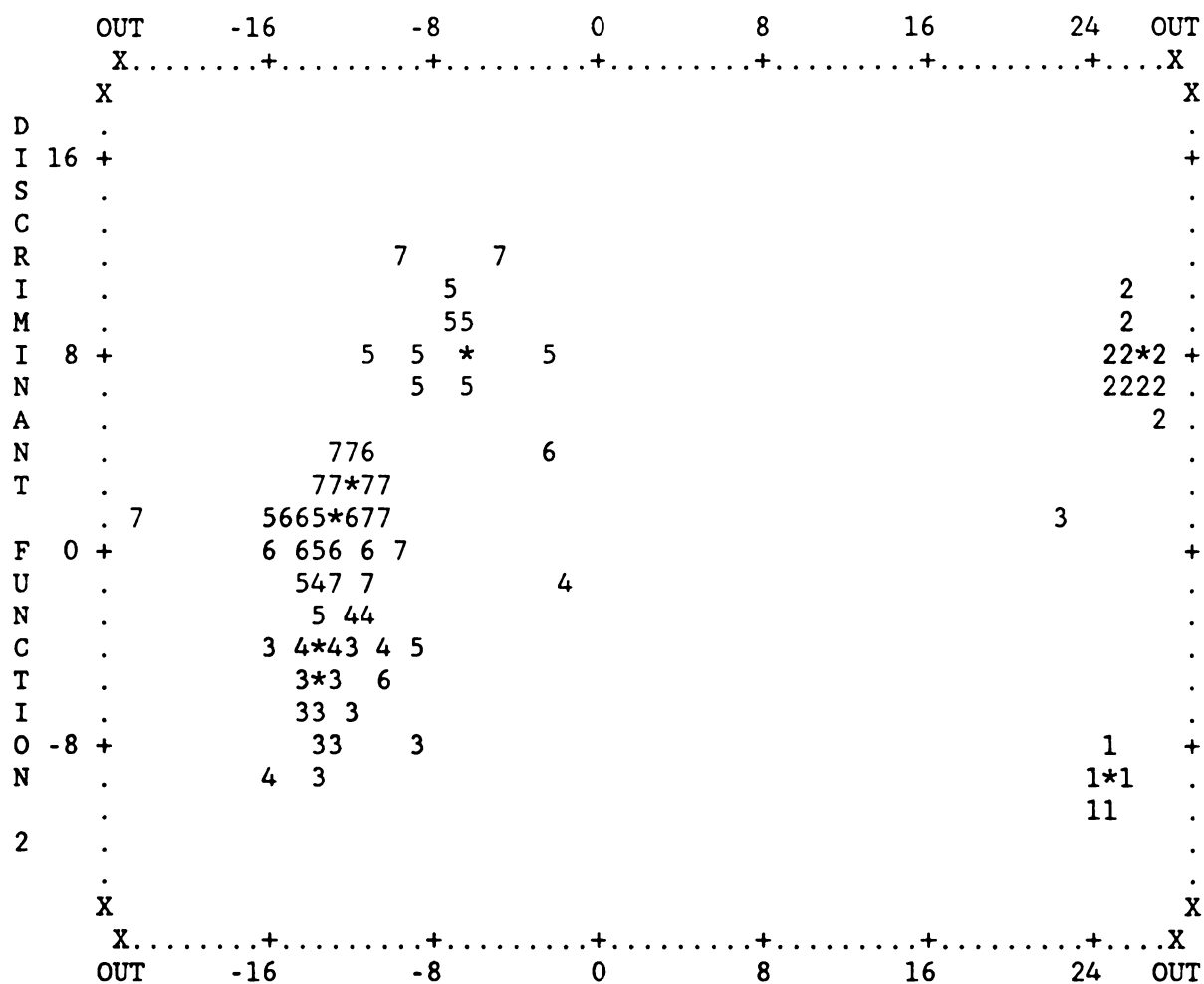


Figure 25. Scatterplot from discriminant analysis of matrix of 160 OTUs x 31 characters, standardized discriminant function coefficients listed in Table 10. 1 - 7 = OTU group numbers as originally assigned, * = a group centroid. Numbers represent one or more OTUs.

Table 11. Discriminant function coefficients and classification results from analysis of matrix of 122 OTUs x 33 characters, 59 OTUs in analysis phase.

A. STANDARDIZED CANONICAL DISCRIMINANT FUNCTION COEFFICIENTS

	FUNC 1	FUNC 2	FUNC 3	FUNC 4
LEAFTIP	1.05203	.93688	.89725	-.52793
LEAFPUB	-.53696	-.48699	.22307	.30310
INFLTYP	-2.57440	-.97315	.44554	-.07006
PEDRFLX	-.76900	.68798	.77890	-.33680
SEPAPEX	-.11286	-.30690	-.50788	.73568
SEPNERV	.10086	.35033	.24540	.17024
NERVLNTH	1.02472	-.44054	-.96271	.16615
PETALS	9.18344	3.92630	.98715	.87996
PETLNTH	8.63737	4.48814	1.09198	1.13202
STEMPUB	.88480	-.19167	-1.16342	.10176
CAPSHAP	-.68222	.30510	.04850	.46650
SEEDSUR	-.33613	1.07514	1.24802	-.91095
FLWSTEM	.24171	-1.45199	-.48717	-.09516
NODEFLW	-.75652	1.57970	.54271	-.16486
STEMLNTH	.45238	1.38913	.69917	-.09038
LF2BLN	.13130	.64745	1.83071	1.17591
LFBLN	-.49463	-2.09326	-1.37913	.07298
LF2ALN	4.91251	.24592	-2.13798	-.53671
LFTPLN	.23620	2.42357	2.32140	-1.13356
LF2BWD	.04680	-.93196	-1.92035	.24421
LFBWD	.38749	1.91746	1.05046	-.20875
LF2AWD	-4.26258	-1.40813	1.76585	.93733
LFTPWD	.65954	-.90361	-1.99179	.26015
PEDLN	-.27656	-.18764	.12419	-.31664
SEPANLN	.06551	-1.04741	-.28613	1.25332
SEPFRLN	-.10578	2.28422	1.56209	-.69381
STYNO	.86665	.33987	-.04037	-.40139
STYLN	.36630	-1.38849	.23347	.33214
CAPCLLN	.54970	-1.13481	-2.49018	.08055
CAPOPLN	-.38139	-.14963	1.29236	-.56222
SEEDLN	.58312	.29592	.14352	-.08210
SEEDWD	-1.16130	-.56452	-.56300	-.32032

B. CLASSIFICATION RESULTS: # OF OTUs %
CORRECTLY ASSIGNED

<u>S. calycantha</u> var. <u>calycantha</u>	13/18	72.2
<u>S. calycantha</u> var. <u>simcoei</u>	10/14	71.4
<u>S. borealis</u> subsp. <u>sitchana</u>	9/17	52.9
<u>S. borealis</u> subsp. <u>borealis</u>	41/49	83.3
<u>S. borealis</u> subsp. <u>interior</u>	20/24	83.3

OVERALL PERCENTAGE CORRECTLY ASSIGNED - 76.23

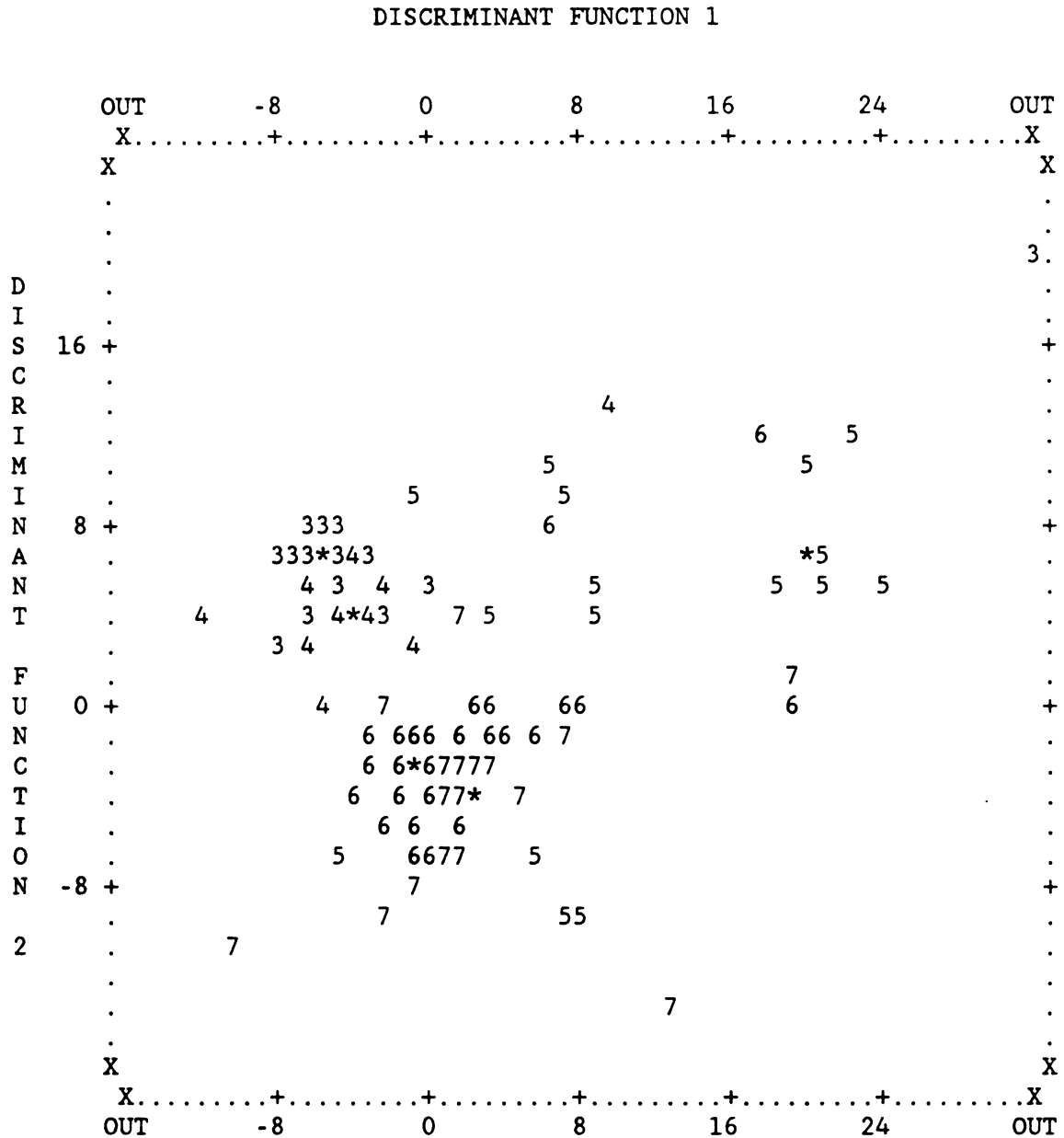


Figure 26. Scatterplot from discriminant analysis of matrix of 122 OTUs x 33 characters, standardized discriminant function coefficients listed in Table 11. 3 - 7 = OTU group numbers as originally assigned, * = a group centroid. Numbers represent one or more OTUs.

Table 12. Discriminant function coefficients and classification results from analysis of matrix of 122 OTUs x 26 characters, 84 OTUs in analysis phase.

A. STANDARDIZED CANONICAL DISCRIMINANT FUNCTION COEFFICIENTS

	FUNC 1	FUNC 2	FUNC 3	FUNC 4
LEAFTIP	.30947	-.09548	.61045	-.05327
LEAFPUB	.27098	-.34023	.02581	.53401
INFLTYP	.04779	-.18920	.07901	-.06412
PEDRFLX	-.14747	.13853	.30749	-.15448
SEPAPEX	.38847	.19267	-.21175	.20857
SEPNERV	-.52437	-.30212	-.26579	-.05306
NERVLNTH	.63649	.61558	.33002	.39209
STEMPUB	.42142	.45363	-.98138	.02525
CAPSHAP	-.12462	.43783	.17233	.32300
SEEDSUR	-.25828	.07346	.36232	-.48451
FLWSTEM	.17868	-.01144	-.37037	.19912
NODEFLW	.13724	.47891	.36738	-.29823
STEMLNTH	.08421	-.02581	.05992	.05870
LFBLN	-.35381	-.65542	.02502	.73650
LF2ALN	.96072	.20783	-.28010	-.82298
LFTPLN	.13255	.04756	.35784	.06853
LFBWD	-.04888	.43598	.19276	-.73040
LF2AWD	-.43021	-.02426	.16146	1.18902
LFTPWD	-.23651	.00997	-.16067	-.22986
PEDLN	-.20839	.06872	.24616	-.35908
SEPANLN	.06311	.03461	.59716	.36672
SEPFRLN	.37103	.63542	-.08780	-.03743
STYLN	.70532	-.54696	.05140	.18171
CAPCLLN	.25287	.11523	-.26960	-.17887
SEEDLN	-.04476	-.16907	.02388	.18976
SEEDWD	.39738	.16031	-.02470	-.46132

B. CLASSIFICATION RESULTS: # OF OTUs
CORRECTLY ASSIGNED

<u>S. calycantha</u> var. <u>calycantha</u>	18/18	100
<u>S. calycantha</u> var. <u>simcoei</u>	9/14	64.3
<u>S. borealis</u> subsp. <u>sitchana</u>	15/17	88.2
<u>S. borealis</u> subsp. <u>borealis</u>	44/49	89.8
<u>S. borealis</u> subsp. <u>interior</u>	22/24	91.7

OVERALL PERCENTAGE CORRECTLY ASSIGNED - 88.52

DISCRIMINANT FUNCTION 1

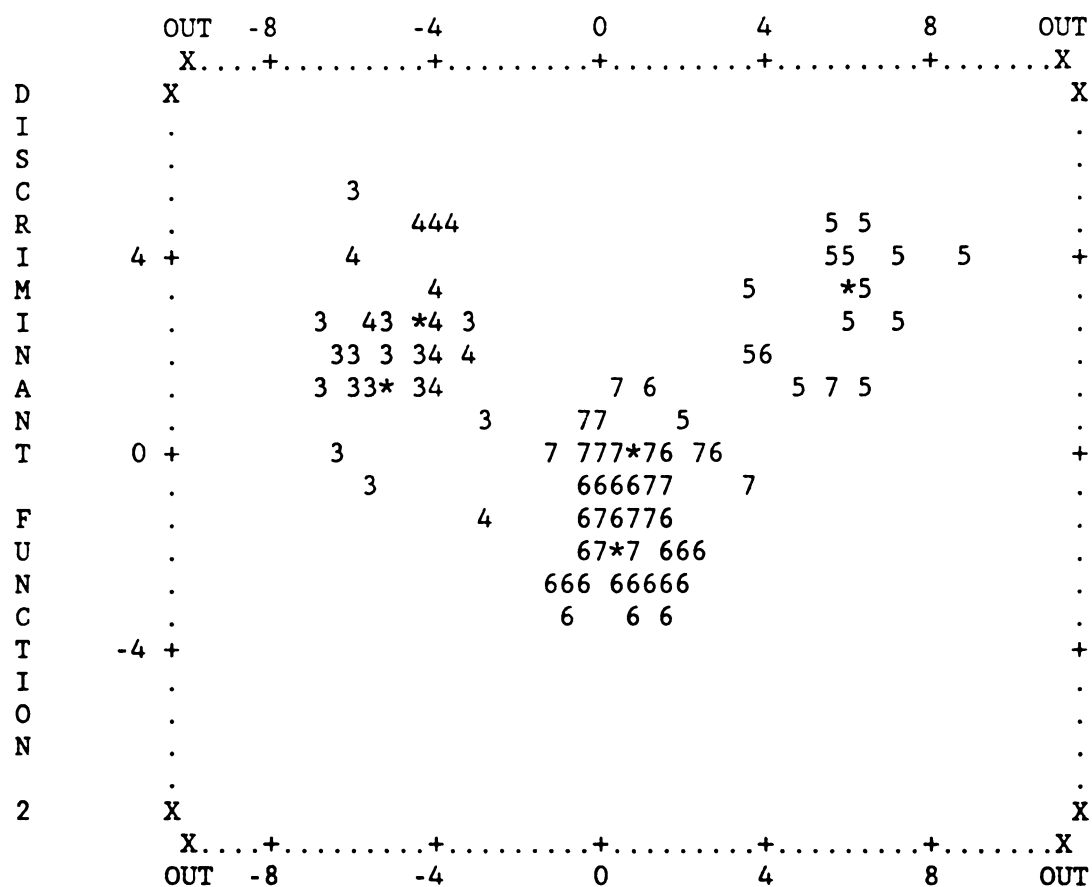


Table 13. Discriminant function coefficients and classification results from analyses of matrix of 32 OTUs x 26 characters, 20 OTUs in analysis phase.

A. STANDARDIZED CANONICAL DISCRIMINANT FUNCTION COEFFICIENTS

1. Analysis including stem pubescence		2. Analysis excluding stem pubescence	
	FUNC 1		FUNC 1
LEAFTIP	-.45979	LEAFTIP	-1.46083
LEAFPUB	-1.98199	LEAFPUB	-.05994
INFLTYP	-7.05272	INFLTYP	.19570
SEPAPEX	9.51683	SEPAPEX	3.19801
SEPNERV	3.00242	SEPNERV	-5.15835
NERVLNTH	5.20199	NERVLNTH	3.94838
STEMPUB	7.54517		
CAPSHAP	2.17539	CAPSHAP	1.74864
FLWSTEM	1.97595	FLWSTEM	-2.02818
NODEFLW	-1.15602	NODEFLW	.48440
STEMLNTH	2.01005	STEMLNTH	1.87943
LFBLN	8.23156	LFBLN	8.84656
LF2ALN	-1.50657	LF2ALN	-4.03859
LFTPLN	2.96499	LFTPLN	-2.90512
LFBWD	-.13538	LFBWD	-1.64480
LF2AWD	-3.48804	LF2AWD	1.89727
PEDLN	-6.82794	PEDLN	-6.23028
SEPANLN	4.16121	SEPANLN	2.25085
		SEPFRLN	-.13172

B. CLASSIFICATION RESULTS:

	# OF OTUs CORRECTLY ASSIGNED	%
1. Analysis including stem pubescence		
<u>S. calycantha</u> var. <u>calycantha</u>	16/18	88.9
<u>S. calycantha</u> var. <u>simcoei</u>	13/14	92.9
OVERALL PERCENTAGE CORRECTLY ASSIGNED - 90.63		
2. Analysis excluding stem pubescence		
<u>S. calycantha</u> var. <u>calycantha</u>	16/18	88.9
<u>S. calycantha</u> var. <u>simcoei</u>	9/14	64.3
OVERALL PERCENTAGE CORRECTLY ASSIGNED - 78.13		

— DISCRIMINANT FUNCTION 1 —

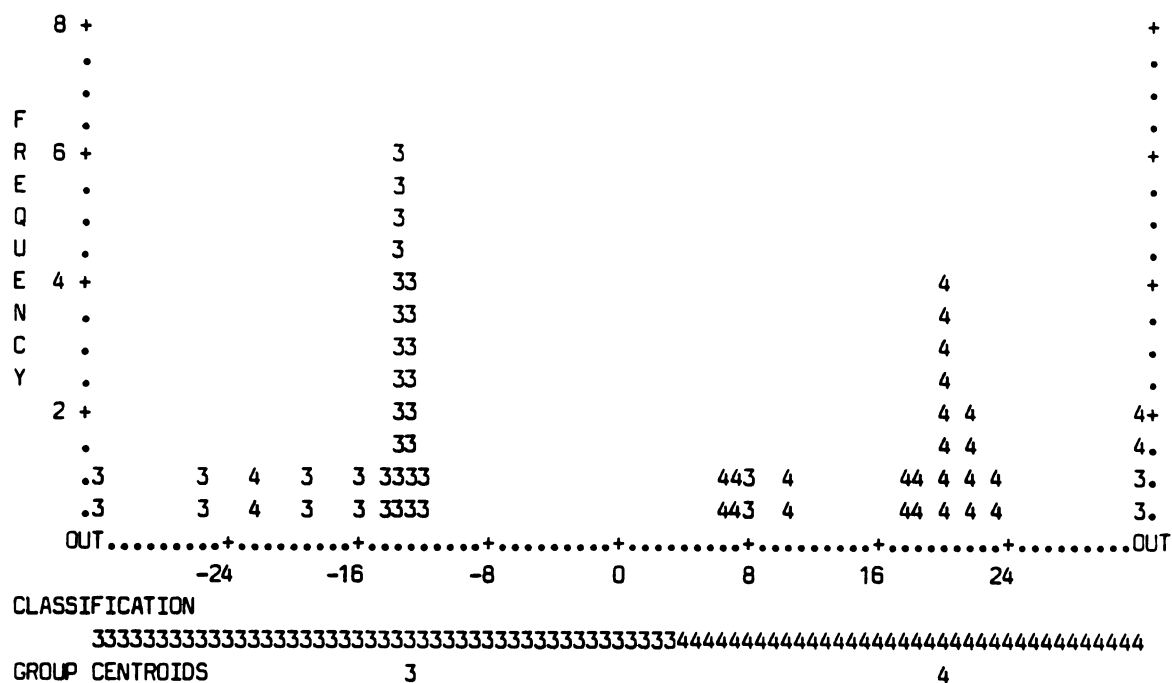


Figure 28. Histogram from first discriminant analysis of matrix of 32 OTUs x 26 characters, STEMPUB included, standardized discriminant function coefficients listed in Table 13. 3 - 4 = OTU group numbers as originally assigned. One OTU - two vertical numbers.

— DISCRIMINANT FUNCTION 1 —

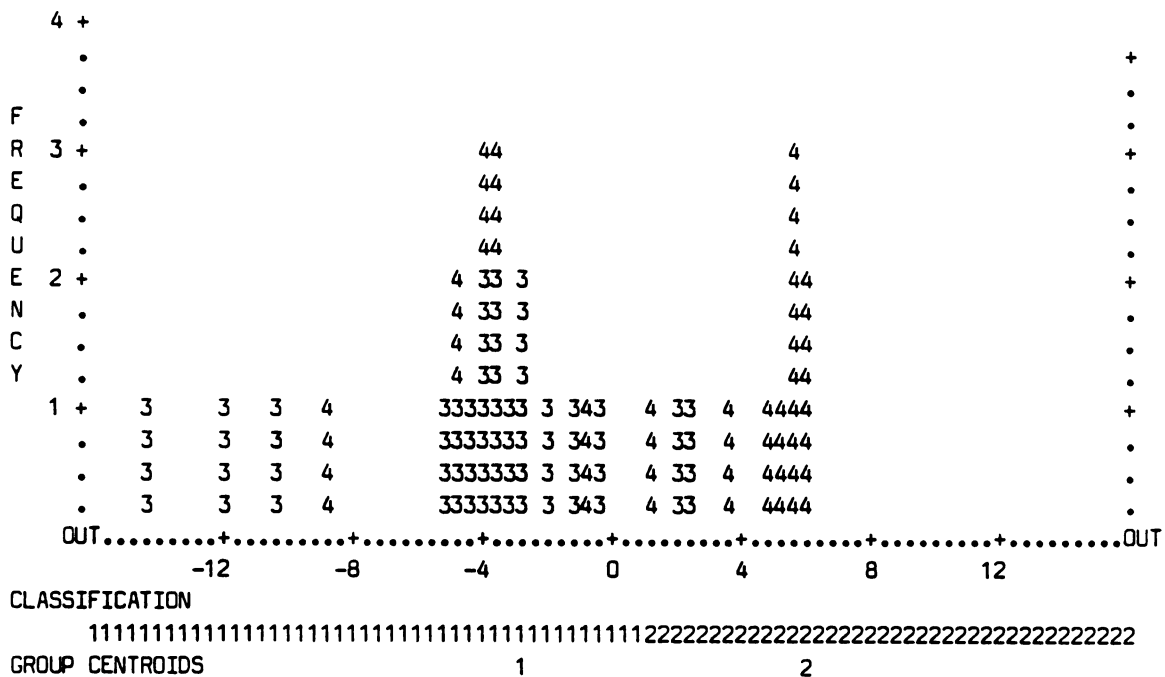


Figure 29. Histogram from second discriminant analysis of matrix of 32 OTUs x 26 characters, STEMPUB excluded, standardized discriminant function coefficients listed in Table 13. 3 -4 = OTU group numbers as originally assigned. One OTU = four vertical numbers.

Table 14. Discriminant function coefficients and classification results from analysis of matrix of 90 OTUs x 26 characters, 64 OTUs in analysis phase.

A. STANDARDIZED CANONICAL DISCRIMINANT FUNCTION COEFFICIENTS

	FUNC 1	FUNC 2
LEAFTIP	.22868	.80832
LEAFPUB	-.11406	.58010
INFLTYP	-.04139	-.06525
PEDRFLX	.24574	.20127
SEPAPEX	.28671	.05953
SEPNERV	-.62251	-.08301
NERVLNTH	.80827	.11270
STEMPUB	.55391	-1.02731
SEEDSUR	.02641	.12332
FLWSTEM	-.17238	-.28102
NODEFLW	.92756	.11804
STEMLNTH	-.25229	.20974
LFBLN	-.96161	.61725
LF2ALN	.75816	-.66188
LFTPLN	.29315	-.12802
LFBWD	.28091	-.62886
LF2AWD	.03323	.53696
LFTPWD	-.21687	.49885
PEDLN	-.03412	.35654
SEPANLN	.23536	.80142
SEPFRLN	.69654	-.22977
STYLN	.14592	.28837
CAPCLLN	.52215	-.38693
SEEDLN	-.21020	.11758
SEEDWD	.32973	.10054

B. CLASSIFICATION RESULTS: # OF OTUs
CORRECTLY ASSIGNED %

<u>S. borealis</u> subsp. <u>sitchana</u>	15/17	88.2
<u>S. borealis</u> subsp. <u>borealis</u>	46/49	93.9
<u>S. borealis</u> subsp. <u>interior</u>	23/24	95.8

OVERALL PERCENTAGE CORRECTLY ASSIGNED - 93.33

DISCRIMINANT FUNCTION 1

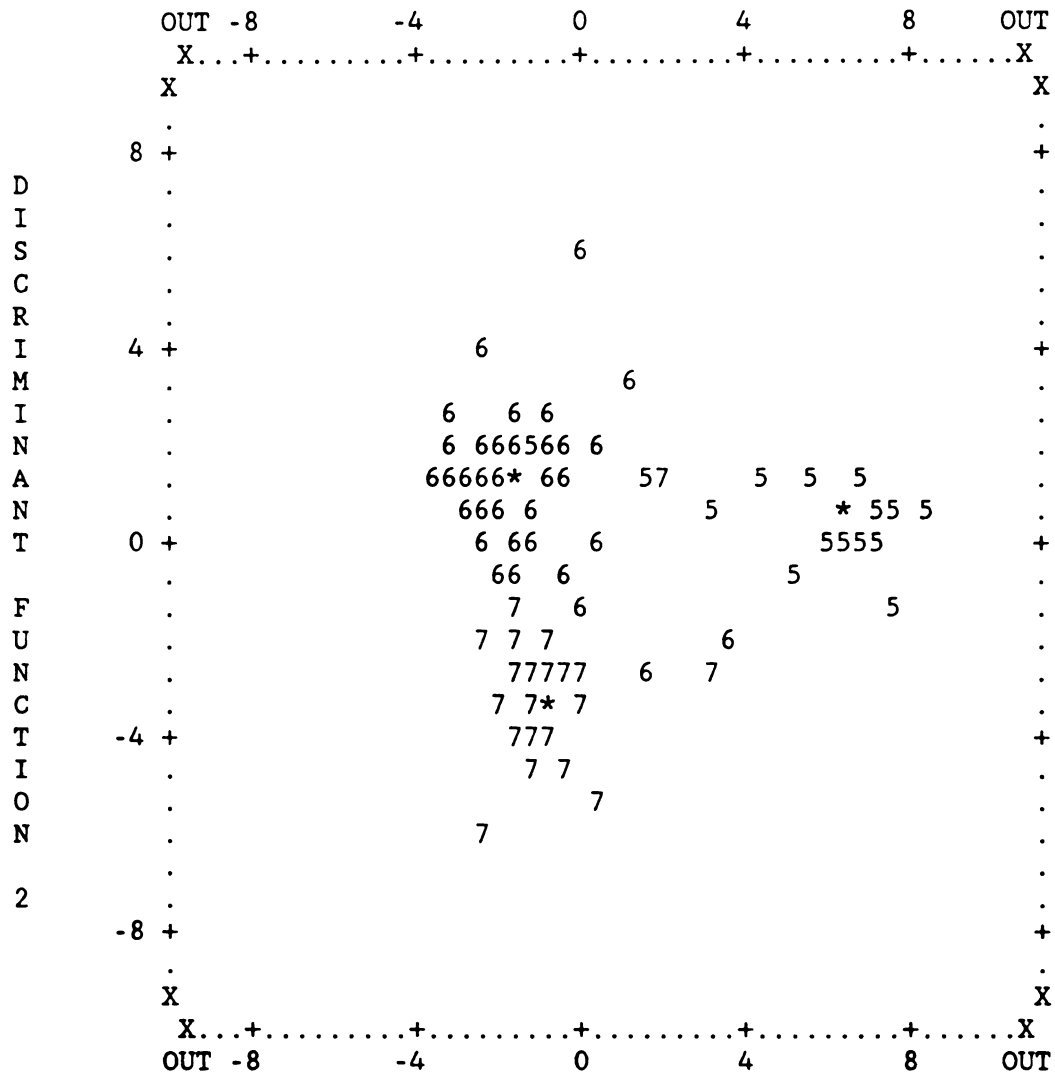


Figure 30. Scatterplot from discriminant analysis of matrix of 90 OTUs x 26 characters, standardized discriminant function coefficients listed in Table 14. 5 - 7 = OTU group numbers as originally assigned, * = a group centroid. Numbers represent one or more OTUs.

Table 15. Discriminant function coefficients and classification results from analysis of matrix of 73 OTUs x 26 characters, 53 OTUs in analysis phase.

A. STANDARDIZED CANONICAL DISCRIMINANT FUNCTION COEFFICIENTS

	FUNC 1
LEAFTIP	.83138
LEAFPUB	.59589
PEDRFLX	.15244
SEPAPEX	.20976
SEPNERV	.11364
NERVLNTH	-.30482
STEMPUB	-1.12980
SEEDSUR	.14019
FLWSTEM	-.52673
NODEFLW	.32381
STEMLNTH	.21090
LFBLN	.43817
LF2ALN	-.96665
LFTPLN	.16374
LFBWD	-.40168
LF2AWD	.85786
LFTPWD	.14593
PEDLN	.24412
SEPANLN	.40941
SEPFRLN	.12571
STYLN	.07289
CAPCLLN	-.61362
SEEDLN	.11345
SEEDWD	.02900

B. CLASSIFICATION RESULTS:	# OF OTUs	%
	CORRECTLY ASSIGNED	
<u>S. borealis</u> subsp. <u>borealis</u>	45/49	91.8
<u>S. borealis</u> subsp. <u>interior</u>	23/24	95.8

OVERALL PERCENTAGE CORRECTLY ASSIGNED - 93.15

— DISCRIMINANT FUNCTION 1 —

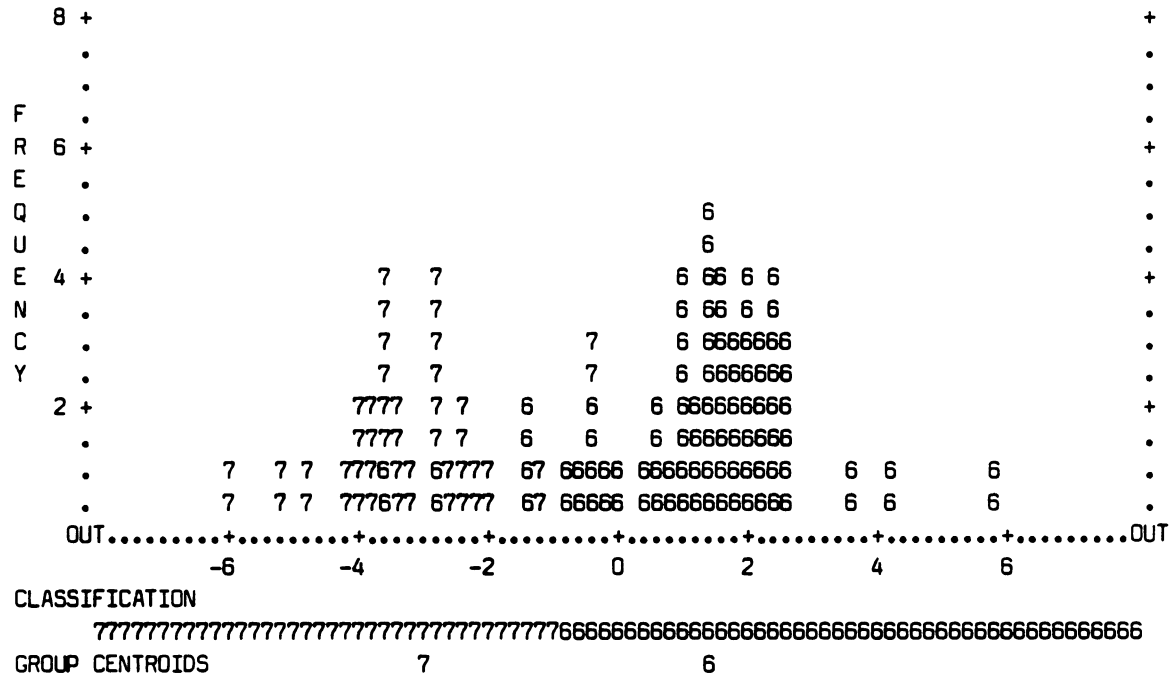


Figure 31. Histogram from discriminant analysis of matrix of 73 OTUs x 26 characters, standardized discriminant function coefficients listed in Table 15. 6 - 7 = OTU group numbers as originally assigned. One OTU = two vertical numbers.

Table 16. Discriminant function coefficients and classification results from analysis of matrix of 42 OTUs x 26 characters, 26 OTUs in analysis phase; EC, EB, group 7 OTUs left as unclassified.

A. STANDARDIZED CANONICAL DISCRIMINANT FUNCTION COEFFICIENTS

	FUNC 1
LEAFTIP	3.94442
LEAFPUB	2.14783
PEDRFLX	3.29031
SEPNERV	-1.13780
STEMPUB	-3.41247
FLWSTEM	-9.40091
NODEFLW	7.39284
STEMLNTH	4.67414
LFBLN	-3.88267
LF2ALN	-3.15156
LFTPLN	7.10717
LFBWD	-1.54865
LF2AWD	.80405
LFTPWD	-4.17154
PEDLN	-.42155
SEPANLN	-2.61723
SEPFRLN	2.93605
STYLN	-2.81728
CAPCLLN	1.50060
SEEDLN	2.39982
SEEDWD	-1.38294

B. CLASSIFICATION RESULTS:	# OF OTUs	%
	CORRECTLY ASSIGNED	
<u>S. borealis</u> var. <u>floribunda</u>	13/13	100
<u>S. borealis</u> var. <u>isophylla</u>	19/19	100

Placement of 6 EC and EB OTUs: 6 to group 6 (100%)

Placement of 23 Group 7 OTUs: 22 to group 6 (95.65%)

1 to group 5 (4.35%)

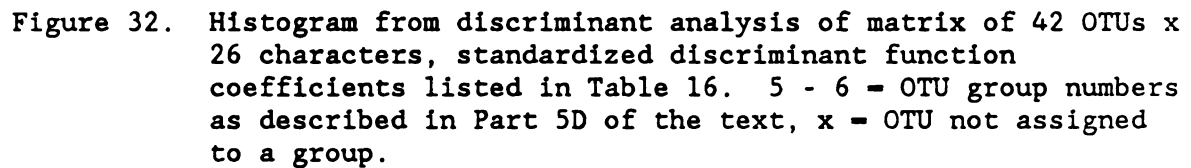


Table 17. Discriminant function coefficients and classification results from analysis of matrix of 122 OTUs x 26 characters, 84 OTUs in analysis phase. Three groups are recognized as described in Part 6 text.

A. STANDARDIZED CANONICAL DISCRIMINANT FUNCTION COEFFICIENTS

	FUNC 1	FUNC 2
LEAFTIP	.34275	.14881
LEAFPUB	.23430	-.37229
INFLTYP	.06869	-.14104
PEDRFLX	-.12902	.25875
SEPAPEX	.35122	.08966
SEPNERV	-.50033	-.37898
NERVLNTH	.56422	.67220
STEMPUB	.52960	.09723
CAPSHAP	-.19165	.45655
SEEDSUR	-.19098	.24418
FLWSTEM	.14322	-.16268
NODEFLW	.15651	.61217
STEMLNTH	.07980	-.00633
LFBLN	-.40528	-.67996
LF2ALN	1.03223	.18800
LFTPLN	.12985	.17027
LFBWD	.02218	.54667
LF2AWD	-.56251	-.08750
LFTPWD	-.21024	-.03097
PEDLN	-.16011	.18610
SEPANLN	.03250	.21840
SEPFRLN	.33416	.56669
STYLN	.72315	-.50408
CAPCLLN	.25752	.03015
SEEDLN	-.05812	-.16914
SEEDWD	.46853	.20419

B. CLASSIFICATION RESULTS: # OF OTUs %
CORRECTLY ASSIGNED

<u>S. calycantha</u>	31/32	96.9
<u>S. borealis</u> subsp. <u>sitchana</u>	15/17	88.2
<u>S. borealis</u> subsp. <u>borealis</u>	71/73	97.3

OVERALL PERCENTAGE CORRECTLY ASSIGNED - 95.90

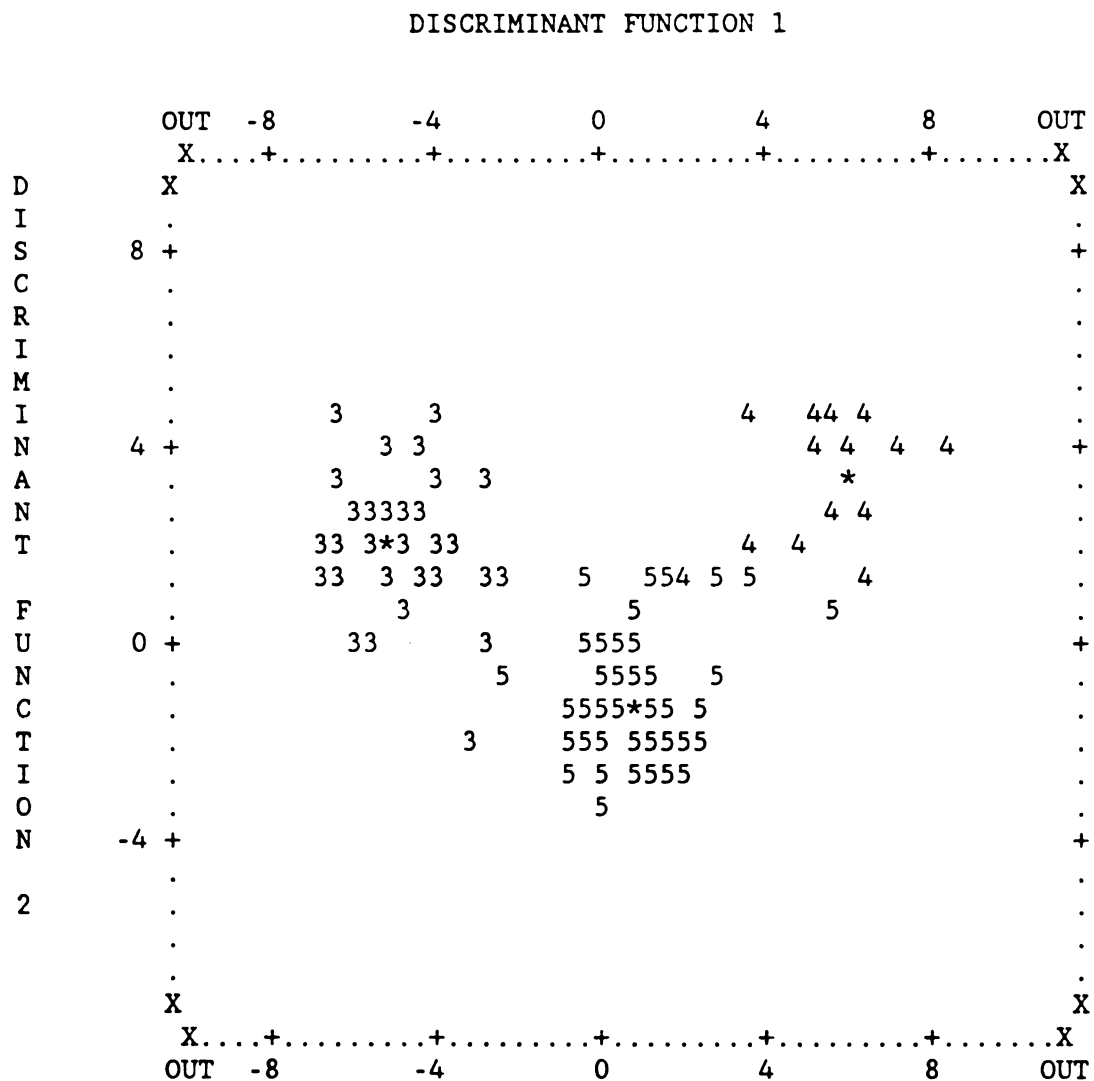


Figure 33. Scatterplot from discriminant analysis of matrix of 122 OTUs x 26 characters, standardized discriminant function coefficients listed in Table 17. 3 - 5 = OTU group numbers as described in Part 6 text, * = a group centroid. Numbers represent one or more OTUs.

Table 18. Discriminant function coefficients and classification results from analysis of matrix of 160 OTUs x 31 characters, 96 OTUs in analysis phase. Five groups are recognized as described in Part 6 text.

A. STANDARDIZED CANONICAL DISCRIMINANT FUNCTION COEFFICIENTS

	FUNC 1	FUNC 2	FUNC 3	FUNC 4
LEAFTIP	-.18065	.06750	.37481	.07329
LEAFPUB	-.21952	.12714	-.21604	-.38423
INFLTYP	-1.71230	-.40010	-.05981	.02629
PEDRFLX	-.09415	-.29330	-.21787	.38883
SEPAPEX	-.16087	-.45730	.42184	.04151
SEPNERV	.19738	.10766	-.37704	-.04948
NERVLNTH	-.01228	1.06684	-.23310	.38387
PETALS	2.33891	1.85429	1.82305	.99557
PETLNTH	2.29964	1.64489	1.60788	1.54903
STEMPUB	-.01954	.33254	.52314	.33583
CAPSHAP	-.25172	-.39953	-.14225	.55162
SEEDSUR	.15278	-.61131	.37898	.16863
FLWSTEM	.27528	.71013	.26501	-.39509
NODEFLW	-.26462	-1.03851	.23795	.63188
STEMLNTH	.16089	-.07636	-.38654	.15549
LF2BLN	.79227	.71223	.48680	.93153
LFBLN	-.60860	-.62783	-.00545	-1.37852
LF2ALN	2.17907	1.56910	.46717	.48506
LFTPLN	-.78659	-1.11112	1.10750	.37616
LF2BWD	-.63159	-.38808	-.05853	-.31054
LFBWD	.94379	-.16705	-.02996	.38473
LF2AWD	-2.26472	-.73493	-.48794	-.01920
LFTPWD	.87869	1.01513	-.92197	.10165
PEDLN	-.11333	.17377	.17170	-.11044
SEPANLN	-.02915	.41757	.10954	.38365
SEPFRLN	-.50863	-.48141	-.37387	.24919
STYNO	.02635	.38506	-.12920	.07927
STYLN	-.12766	.66667	.61229	-.28732
CAPCLLN	.41857	.21691	.23440	-.15861
SEEDLN	.06889	.12051	.00340	-.00563
SEEDWD	-.43975	.22225	-.18701	.11904

B. CLASSIFICATION RESULTS: # OF OTUs %
CORRECTLY ASSIGNED

<u>S. obtusa</u>	17/17	100
<u>S. crispa</u>	21/21	100
<u>S. calycantha</u>	31/32	96.9
<u>S. borealis</u> subsp. <u>sitchana</u>	10/17	58.8
<u>S. borealis</u> subsp. <u>borealis</u>	68/73	93.2

OVERALL PERCENTAGE CORRECTLY ASSIGNED - 91.88

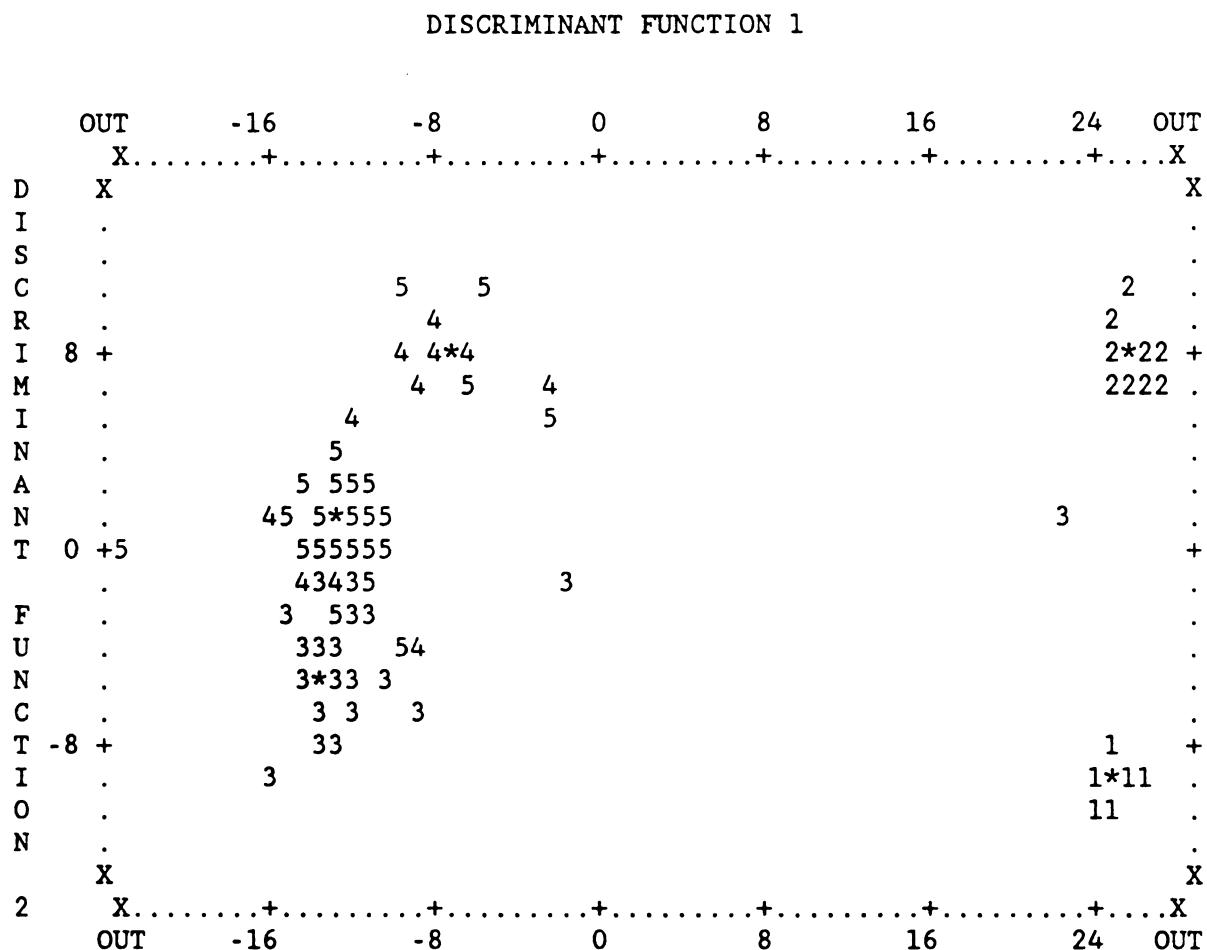


Figure 34. Scatterplot from discriminant analysis of matrix of 160 OTUs x 31 characters, standardized discriminant function coefficients listed in Table 18. 1 - 5 = OTU group numbers as described in Part 6 text, * = a group centroid. Numbers represent one or more OTUs.

Table 19. Discriminant function coefficients and classification results from analysis of matrix of 160 OTUs x 24 characters, 100 OTUs in analysis phase. Five groups are recognized as described in Part 6 text.

A. STANDARDIZED CANONICAL DISCRIMINANT FUNCTION COEFFICIENTS

	FUNC 1	FUNC 2	FUNC 3	FUNC 4
LEAFPUB	.07295	.02771	-.10862	-.41414
PEDRFLX	-.33709	-.35274	-.04938	-.01987
SEPAPEX	-.08334	.65091	.11232	.13081
SEPNERV	.08860	.29316	-.48260	.00990
NERVLNTH	.30440	-1.04469	.39290	.09776
PETALS	-.00372	.70853	.13654	-.09158
PETLNTH	-.09899	1.02604	-.17868	.74822
STEMPUB	.47438	.29632	.18874	.54249
CAPSHAP	-.12651	.03475	-.24277	.63249
SEEDSUR	-.71777	-.02307	.63128	-.32586
FLWSTEM	.42775	.39156	.34575	.32927
STEMLNTH	-.36456	-.63505	.06480	-.11571
LF2BLN	.37525	.76473	.06900	1.01125
LFBLN	.07823	.32008	.12691	-.63267
LF2BWD	-.01839	-.03597	-.53184	-.26745
LFBWD	-.35824	-.00807	-.13850	.44935
PEDLN	.21112	.12757	.19153	.18869
SEPANLN	.44991	.18076	-.06271	.46689
SEPFRLN	-.78182	-.65754	.40179	-.20510
STYNO	.02034	-.22825	-.12184	-.23692
STYLN	.58641	.33344	.34487	-.29242
CAPCLLN	.10253	.14458	.26043	-.03813
SEEDLN	.03321	.09949	-.10788	.24888
SEEDWD	.47834	-.37723	.07609	.07663

B. CLASSIFICATION RESULTS: # OF OTUs
CORRECTLY ASSIGNED

<u>S. obtusa</u>	17/17	100
<u>S. crispa</u>	21/21	100
<u>S. calycantha</u>	32/32	100
<u>S. borealis</u> subsp. <u>sitchana</u>	11/17	64.7
<u>S. borealis</u> subsp. <u>borealis</u>	70/73	95.9

OVERALL PERCENTAGE CORRECTLY ASSIGNED - 94.37

DISCRIMINANT FUNCTION 1

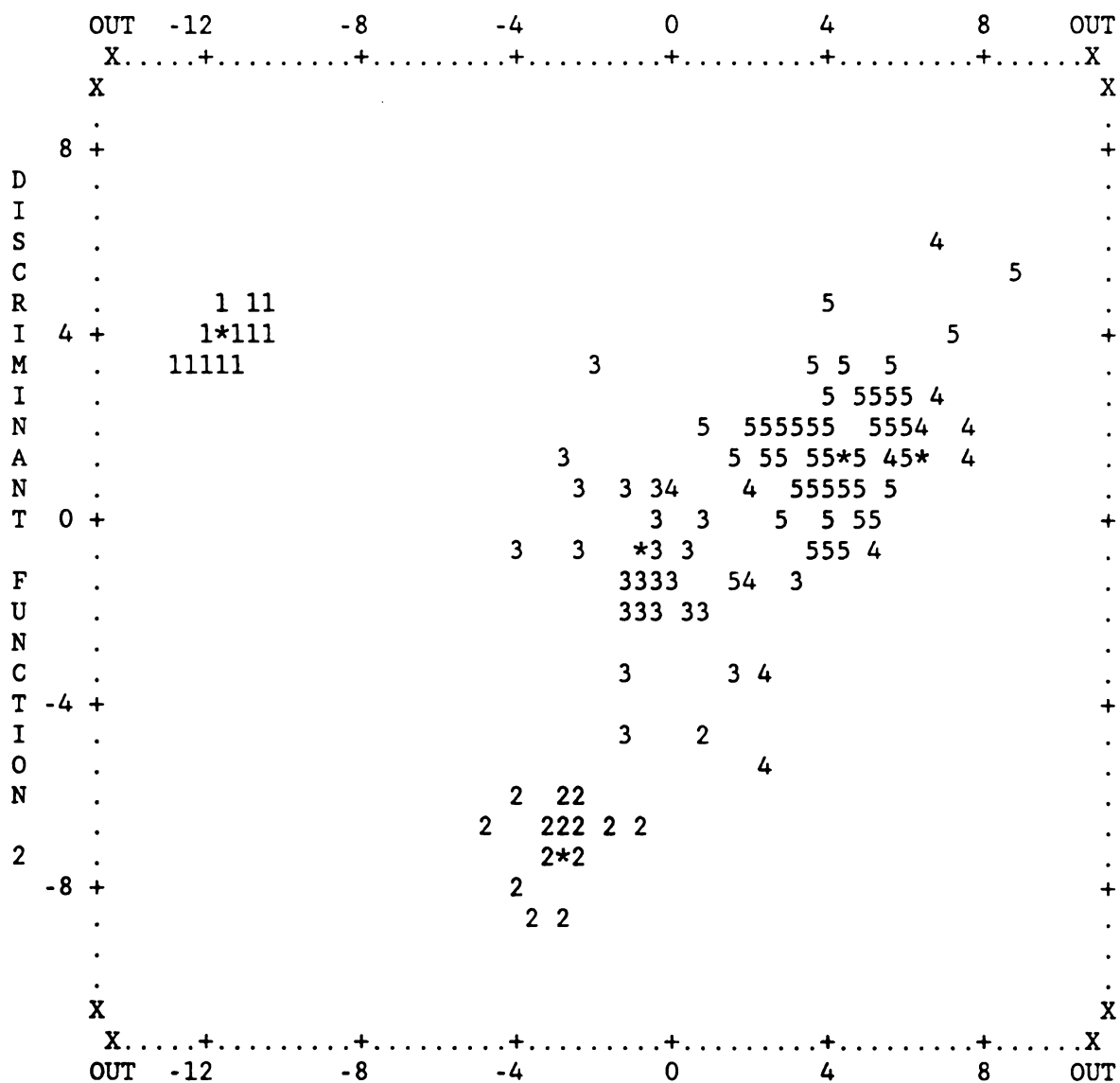


Figure 35. Scatterplot from discriminant analysis of matrix of 160 OTUs x 24 characters, standardized discriminant function coefficients listed in Table 19. 1 - 5 = OTU group numbers as described in Part 6 text, * = a group centroid. Numbers represent one or more OTUs.

Table 20. Chromosome counts and vouchers for the Stellaria calycantha complex: all taxa except S. borealis subsp. borealis.

n	2n	Location	Publication	Collector & No. (Herbarium)
<u>Stellaria obtusa</u>				
	26	Alberta	Morton, unpub.	<u>Morton s.n.</u> (JKM)
	52	Alberta	Morton, unpub.	<u>Morton NA4694</u> (JKM)
	52	Alberta	Morton, unpub.	<u>Morton NA4723</u> (JKM)
	52	Montana	Morton, unpub.	<u>Morton s.n.</u> (JKM)
	65	Oregon	Morton, unpub.	<u>Mason 8900</u> (JKM)
ca	78	Wyoming	Hartman, 1971	<u>Hartman 2914</u> (RM)
<u>Stellaria crispa</u>				
13		Br. Columbia	Taylor & Mulligan, 1968	<u>Calder et al. 34600</u> (DAO)
13		Br. Columbia	Taylor & Mulligan, 1968	<u>Calder et al. 35128</u> (DAO)
	26	Alberta	Morton, unpub.	<u>Morton NA4725</u> (JKM)
	26	British Columbia	Morton, unpub.	<u>Morton & Venn NA13485</u> (JKM)
	52	Alberta	Chinnappa, 1985	<u>Chinnappa CC200</u> (UAC - not seen)
<u>Stellaria calycantha</u>				
13		Br. Columbia	Taylor & Mulligan, 1968	<u>Calder & Taylor 36357</u> (DAO)
13		Washington	Kruckeberg, unpub.	<u>Kruckeberg 5690</u> (WTU)
	26	Colorado	Morton, unpub.	<u>Morton & Venn NA7341</u> (JKM)
	26	Wyoming	Hartman, 1971	<u>Hartman 2911</u> (RM)
	26	Wyoming	Hartman, 1971	<u>Hartman 2926</u> (RM)
	26	Wyoming	Morton, unpub.	<u>Morton & Venn NA7286</u> (JKM)
	26	USSR, Chukotka	Zhukova, 1980	<u>Zhukova 77-47</u> (?)
<u>Stellaria borealis</u> subsp. <u>sitchana</u>				
26		Alaska	Morton, unpub.	<u>Welsh & Moore 8764</u> (JKM)
26		British Columbia	Morton, unpub.	<u>Morton NA3335</u> (JKM)
	52	British Columbia	Chinnappa, 1985	<u>Morton NA3335</u> (JKM)
	52	British Columbia	Morton, unpub.	<u>Morton NA8368</u> (JKM)
ca	52	British Columbia	Morton, unpub.	<u>Morton & Venn NA13536</u> (JKM)
	52	British Columbia	Morton, unpub.	<u>Morton & Venn NA13576</u> (JKM)
	52	British Columbia	Morton, unpub.	<u>Morton & Venn NA13665</u> (JKM)
	52	British Columbia	Morton, unpub.	<u>Morton & Venn NA13669</u> (JKM)
<u>Stellaria borealis</u> X <u>S. longifolia</u>				
39		Canada, ??	Morton, unpub.	<u>Cody 14397</u> (JKM)
39		Alberta	Morton, unpub.	<u>Morton s.n.</u> (JKM)
39		Ontario	Morton, unpub.	<u>Morton & Venn NA10726</u> (JKM)
39		Yukon Territory	Morton, unpub.	<u>Morton NA2170</u> (JKM)
39		Colorado	Morton, unpub.	<u>Morton & Venn NA7326</u> (JKM)
39		Wyoming	Morton, unpub.	<u>Morton & Venn NA7309</u> (JKM)

Table 21. Chromosome counts and vouchers for the Stellaria calycantha complex: Stellaria borealis subsp. borealis.

n	2n	Location	Publication	Collector & No. (Herbarium)
26		Alberta	Morton, unpub.	<u>Morton NA4609</u> (JKM)
26		Quebec	Morton, unpub.	<u>Morton NA4109</u> (JKM)
	44-48	Scandinavia	Peterson, 1936	<u>Sandberg 127</u> (?)
	44-48	Scandinavia	Hara, 1952	cites Peterson, 1936 count
	48	Alaska	Knaben, 1968	<u>Gjaerevoll 685</u> (CAN,S[2], TRH-could not be located)
	52	Canada,??	Morton, unpub.	<u>Cody 14397</u> (JKM)
	52	Alberta	Morton, unpub.	<u>Dumais & Anderson 3376</u> (JKM)
	52	Alberta	Morton, unpub.	<u>Dumais & Anderson 3469</u> (JKM)
	52	Alberta	Morton, unpub.	<u>Morton NA4648</u> (JKM)
	52	British Columbia	Chinnappa, 1985	<u>Chinnappa CC1436</u> (UAC)
	52	British Columbia	Morton, unpub.	<u>Morton NA2000</u> (JKM)
	52	British Columbia	Morton, unpub.	<u>Morton & Venn NA13519</u> (JKM)
	52	British Columbia	Morton, unpub.	<u>Morton & Venn NA13674</u> (JKM)
	52	British Columbia	Morton, unpub.	<u>Morton & Venn NA13684</u> (JKM)
	52	British Columbia	Morton, unpub.	<u>Morton & Venn NA13690</u> (JKM)
	52	British Columbia	Morton, unpub.	<u>Morton & Venn NA14137</u> (JKM)
	52	Manitoba	Löve & Löve, 1982	<u>Löve & Löve S3424</u> (?)
26	52	Newfoundland	Morton, unpub.	<u>Duthie s.n.</u> (JKM)
	52	Newfoundland	Morton, unpub.	<u>Morton & Venn NA12408</u> (JKM)
	52	Northwest Terr.	Morton, unpub.	<u>Morton & Venn NA13866</u> (JKM)
	52	Ontario	Morton, unpub.	<u>Morton NA4536</u> (JKM)
	52	Quebec	Hedberg, 1967	<u>Hedberg 3092b</u> (DAO,UPS?)
	52	Quebec	Morton, unpub.	<u>Morton NA2934</u> (JKM)
	52	Quebec	Morton, unpub.	<u>Morton NA3926</u> (JKM)
	52	Quebec	Morton, unpub.	<u>Morton NA3966</u> (JKM)
	52	Quebec	Morton, unpub.	<u>Morton NA4020</u> (JKM)
26	52	Quebec	Morton, unpub.	<u>Morton NA4059</u> (JKM)
	52	Quebec	Morton, unpub.	<u>Morton NA4073</u> (JKM)
	52	Quebec	Morton, unpub.	<u>Morton NA4091</u> (JKM)
	52	Quebec	Morton, unpub.	<u>Morton & Venn NA8906</u> (JKM)
	52	Yukon Territory	Morton, unpub.	<u>Morton s.n.</u> (JKM)
	52	Yukon Territory	Morton, unpub.	<u>Morton NA2072</u> (JKM)
	52	Yukon Territory	Morton, unpub.	<u>Morton NA2170bis</u> (JKM)
	52	Yukon Territory	Morton, unpub.	<u>Morton & Venn NA13721</u> (JKM)
	52	Yukon Territory	Morton, unpub.	<u>Morton & Venn NA13737</u> (JKM)
	52	Yukon Territory	Morton, unpub.	<u>Morton & Venn NA13762</u> (JKM)
	52	Yukon Territory	Morton, unpub.	<u>Morton & Venn NA14040</u> (JKM)
	52	Yukon Territory	Morton, unpub.	<u>Morton & Venn NA14050</u> (JKM)
	52	Yukon Territory	Morton, unpub.	<u>Morton & Venn NA14087</u> (JKM)
	52	Yukon Territory	Morton, unpub.	<u>Morton & Venn NA14089</u> (JKM)
	52	Iceland	Löve & Löve, 1956	none cited (?)
	52	Alaska	Chinnappa, 1985	<u>Morton NA2116</u> (JKM)
	52	Colorado	Morton, unpub.	<u>Morton & Venn NA7340</u> (JKM)
	52	New Hampshire	Löve & Löve, 1966	<u>Löve & Löve 7562</u> (COLO)
	52	New Hampshire	Morton, unpub.	<u>Morton s.n.</u> (JKM)
	52	Wyoming	Hartman, 1971	<u>Hartman 2862</u> (RM)
	52	Wyoming	Morton, unpub.	<u>Morton & Venn NA7306</u> (JKM)

Character	<u>S. borealis</u>	<u>S. longifolia</u> (<u>S. friesiana</u>)
Stem:		
often smooth,	X	
very rarely scabrous.		X
Leaves:		
often lanceolate	X	
leaf width		intermediate
often basally ciliate	X	
Inflorescence:		
an open panicle		X
bracts all scarious		X
Some have solitary, axillary flowers	X	
Some have scarious as well as herbaceous bracts		X
Some have entirely herbaceous bracts	X	
Petals		
Often small and short-lived	X	
Rarely longer and persistent		X

Figure 36. Morphological features of S. borealis × S. longifolia and their presumed parental origin (translated and summarized from Norman, 1893).

Figure 37. Range of Stellaria calycantha complex, modified from Hultén (1958) and Jalas and Suominen (1983).

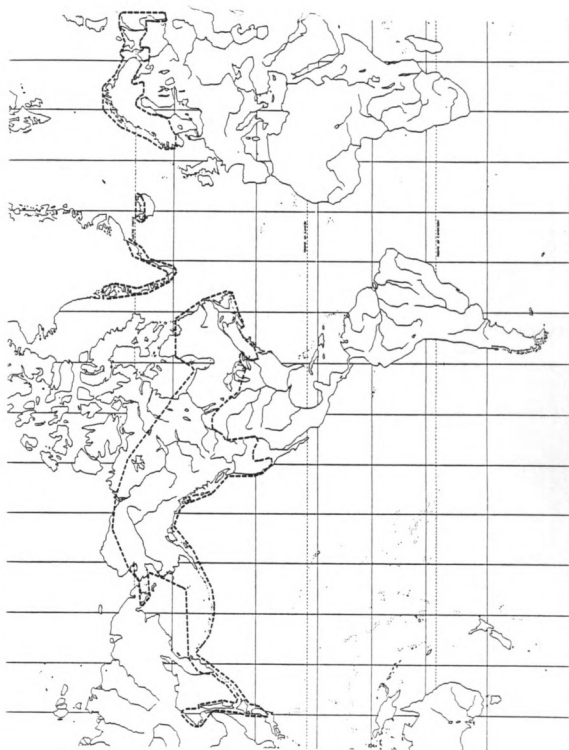


Figure 37

Figure 38. Projected Pleistocene displacement of the Stellaria calycantha complex. Dashed lines, Wisconsin glacial maximum, 22,000 to 15,000 years BP (from Péwé, 1983); Dotted lines, glacial ice boundaries, about 10,000 years BP (from Pewe, 1983). Locations of possible refugia are shown by letters and/or numbers; e = Eastern, w = western. Arrows indicate possible migration routes away from refugia.



Figure 38

Figure 39. Inflorescence form and chronology of flower opening in Stellaria borealis subsp. borealis. Numbers represent flower position; 1 = first flower that opened. Plant cultured in East Lansing, Michigan from seed collected near Thunder Bay, Ontario.

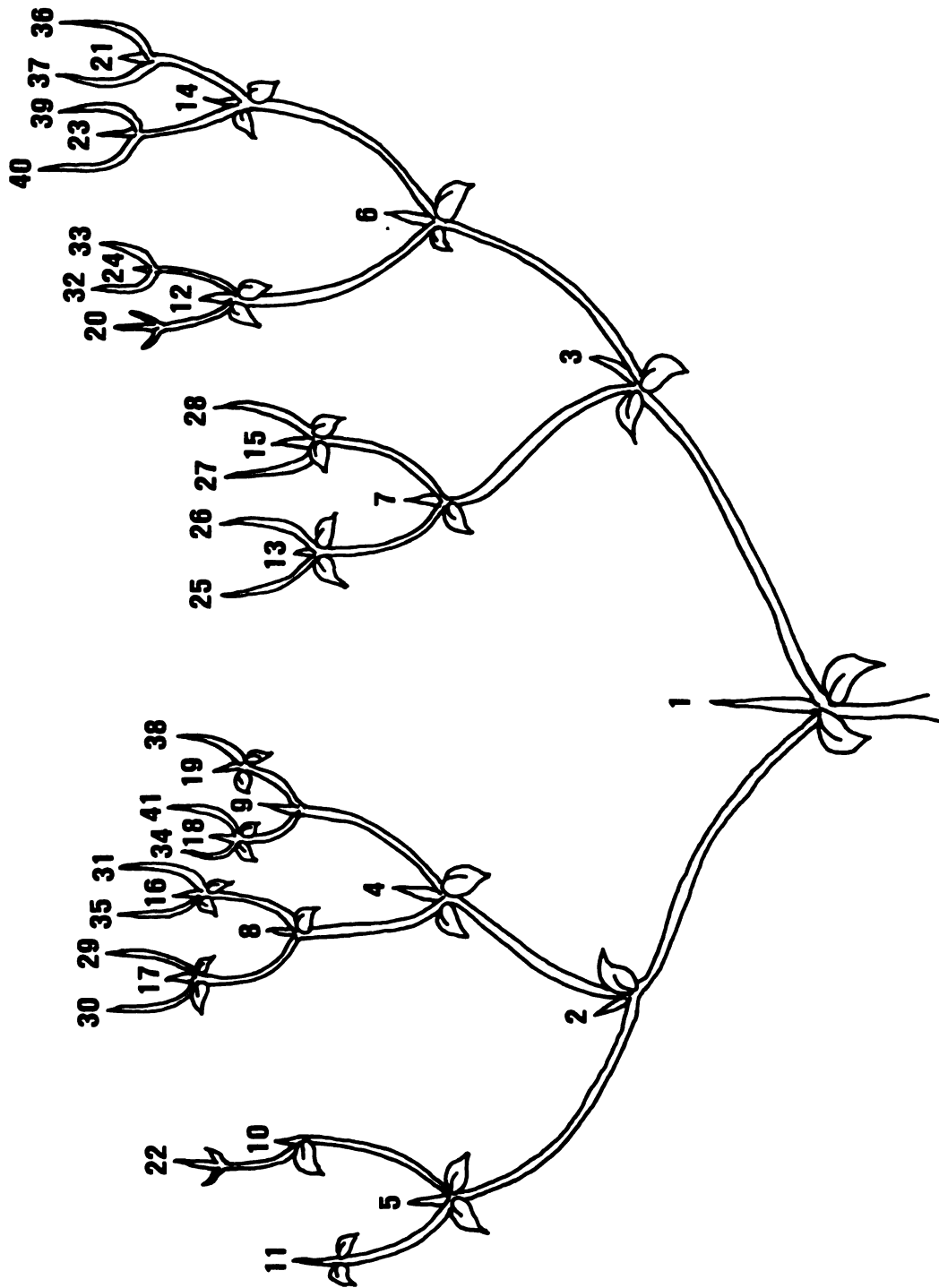


Figure 39

Table 22. A comparison of inflorescence features of wild and cultured Stellaria borealis subsp. borealis for population from Thunder Bay, Ontario.

I. Voucher collected on site: 6 September 1981, Rabeler 649 (MSC).

Habitat: plants in partial shade, on grassy hummocks with Ledum, Picea mariana-Thuja bog, Thunder Bay, Ontario.

Inflorescence bracts	Stem	Number of flowers/stem
Resemble leaves, without	1	1
wide scarious margins;	2	2
bracts gradually reduced in size.	3	15
	4	12

II. Plants cultured at East Lansing, Michigan: 21-1 and 21-2.

Environment: natural May-June light from north-facing window, temperature 15-27°C.

Inflorescence bracts	Stem	Number of flowers/stem
Both plants:		
	Plant 21-1	
	1	40
Mostly leaflike below;	2	25
primarily tiny, mostly	3	32
scarious bracts above.	4	6
	Plant 21-2	
	1	16
	2	3

Table 23. Floral variation in Stellaria borealis subsp. borealis based on cultured material from Ontario.

Total Sample - all stems included

I. Number of petals vs. number of flowers per stem

Plant->	21-1	21-1	21-1	21-1	21-1	21-1	21-1	21-2	21-2	Total	%
Stem #->	1	2	3	4	5	6	7	1	2		
No. of Petals											
0	30	21	21	3	10	1	1	13	3	103	85.72
0.5				1				1		2	1.65
1	6		3					1		10	8.26
1.5			1							1	0.83
2	3									3	2.48
3	1							1		2	1.65
										---	-----
										121	100.00

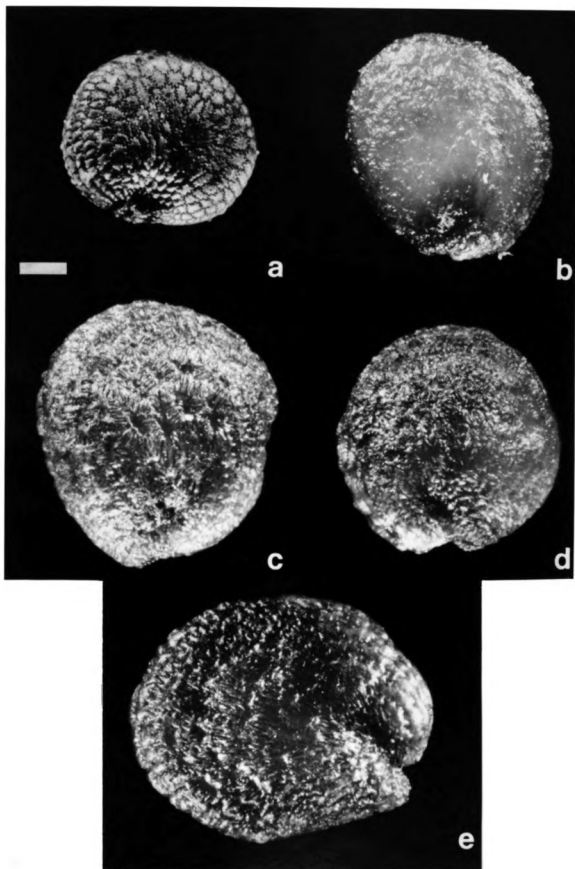
II. Number of sepals vs. number of flowers per stem

Plant->	21-1	21-1	21-1	21-1	21-1	21-1	21-1	21-2	21-2	Total	%
Stem #->	1	2	3	4	5	6	7	1	2		
No. of Sepals											
4	10	1		1				1		13	11.22
5	24	20	25	4	10	1	1	15	3	103	88.78
										---	-----
										116	100.00

III. Styles - 9 recorded - 1 with 3; 4 with 4; 4 with 5.

Figure 40. Seeds of taxa in the Stellaria calycantha complex. Scale in a. = 200 μ ; all seeds illustrated at 64x.

a. S. obtusa, Rabeller 534, Boise Co., Idaho. b. S. borealis subsp. borealis, Rabeller 649, Thunder Bay, Ontario. c. S. crispa, Rabeller 502, Humboldt Co., California. d. S. calycantha, Rabeller 518, Tehama Co., California. e. S. calycantha subsp. sitchana, Rabeller 480, Clatsop Co., Oregon.



- 1 Ground color gray-black, hilum not hidden in a marginal notch, surface reticulate-furrowed

S. obtusa

- 1 Ground color brown or reddish brown, hilum included in a marginal notch, surface smooth to distinctly rugulose

- 2 Surface virtually smooth or at most with a few low, rounded papillae

S. calycantha,
S. borealis subsp. borealis

- 2 Surface rugulose, rows of cells especially evident on the edges

S. crispa
S. borealis subsp. sitchana,
some subsp. borealis

Figure 41. Key to basic seed morphology in the Stellaria calycantha complex.

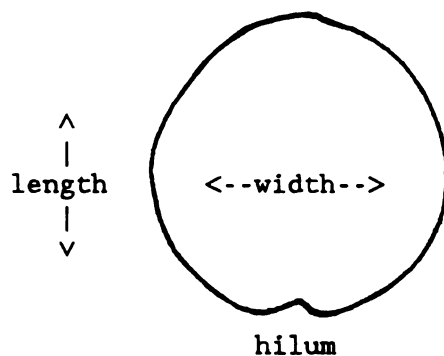


Figure 42. Illustration of seed measurements.

Table 24. Floral Duration in Stellaria borealis subsp. borealis, based on cultured material from Ontario.

Total Sample - all stems included										
Plant-> Stem #->	21-1 1	21-1 2	21-1 3	21-1 4	21-1 5	21-1 6	21-1 7	21-2 1	21-2 2	Total
Number of Flowers tracked	36	10	14	1	2	0	1	8	1	7
Sum of durations in days	151	23	31.5	2.5	4.5	0	1	10.5	3.5	227.5
Mean No. of days	4.19	2.3	2.25	2.5	2.5	-	1.0	1.31	3.5	3.12
Range of duration	1-10	1-4	1-5	2.5	1-3	-	1	1-2.5	3.5	1-10

Table 25. Stellaria borealis and S. obtusa: seeds per capsule.

Plants sampled:

- 21-1 S. borealis from Ontario - capsules collected 8/14/85
 21-2 S. borealis from Ontario - capsules collected 8/14/85
 23-3 S. obtusa from Montana - capsules collected 4/15/85

Plant	Mature/immature seeds per capsule	Range/capsule	Mean/capsule
21-1	3/9, 10/10, 4/26, 6/17, 9/13, 5/21	Mature : 3 - 10 Immature : 9 - 26 Total : (12)22-30	Mature : 6.16 Immature : 16 Total : 22.16
21-2	5/26, 6/28, 4/32, 11/18, 16/17, 3/24	Mature : 3 - 16 Immature : 17 - 32 Total : 27 - 36	Mature : 7.5 Immature : 24.16 Total : 31.66
23-3	9/12, 8/14, 12/11, 12/12, 9/16, 2/14	Mature : (2)8 - 12 Immature : 11 - 16 Total : (16)21-25	Mature : 8.66 Immature : 13.16 Total : 21.82

Table 26. Results of seed flotation experiments with eight species of *Stellaria*.

Species & source	Seed	Length of flotation (Days)										Germination
		0	1	1.5	2	2.5	3	3.5	4	4.5	5	
<u>Stellaria alsine</u>	1		x									
Prince Edward Is.	2			x								
<u>Rabaler 631</u>	3				x							
Avg. = 1.75 days	4					x						
<u>Stellaria calycantha</u>	1				x							
California	2						x					
<u>Rabaler 518</u>	3							x				
Avg. = 3.25 days	4									x		
<u>Stellaria borealis</u>	1		x									
subsp. <u>borealis</u>	2				x							
Quebec	3									sank in 7.5		
<u>Rabaler 637</u>	4									sank in 7.5		
Avg. = 4.5 days												
<u>Stellaria crispa</u>	1		x									
British Columbia	2		x									
<u>Rabaler 426</u>	3					x						
Avg. = 2.38 days	4										x	
<u>Stellaria graminea</u>	1	x										1 germinated
New York	2	x										on day 7
<u>Rabaler 742</u>	3	x										
Avg. = 0 days	4	x										
<u>Stellaria longifolia</u>	1		x									
Minnesota	2						x					
<u>Rabaler 650</u>	3							x				
Avg. = 2.88 days	4								x			
<u>Stellaria media</u>	1			x								All seeds
Michigan	2			x								germinated
<u>Rabaler 749</u>	3				x							on day 3
Avg. = 1.75 days	4				x							
<u>Stellaria obtusa</u>	1			x								
Idaho	2						x					
<u>Rabaler 534</u>	3						x					
Avg. = 2.75 days	4							x				

Fernald (1940)

Stellaria calycantha

var. calycantha
var. simcoei

var. floribunda
var. isophylla
var. laurentiana

var. sitchanavar. bongardiana

Present treatment

Stellaria calycantha

includes:

var. calycantha (p.p.)
var. simcoei

Stellaria borealissubsp. borealis

includes:

S. calycantha

var. floribunda
var. isophylla
var. laurentiana
var. calycantha (p.p.)

subsp. sitchana

includes:

S. calycanthavar. bongardianaStellaria borealis × S. longifolia

Figure 43. Comparison of Fernald's (1940) Stellaria calycantha treatment to the present treatment.

Hitchcock - Scoggan

Present treatment

Stellaria obtusaStellaria obtusa

includes:

S. viridula

includes:

S. viridula (p.p.)S. washingtonianaStellaria crispaStellaria crispaStellaria calycanthaStellaria calycanthavar. calycantha

includes:

var. latifolia

(Scoggan)

includes:

var. calycanthaS. viridula (p.p.)S. simcoeivar. bongardianaStellaria borealissubsp. borealis

includes:

var. floribundavar. isophyllavar. laurentiana

(Scoggan)

includes:

S. calycanthavar. floribundavar. isophyllavar. laurentianasubsp. interiorvar. latifoliavar. sitchanasubsp. sitchana

includes:

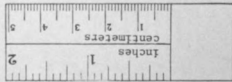
S. calycanthavar. bongardianaStellaria simcoei

includes:

subsp. interiorS. washingtonianaStellaria borealis × S. longifolia

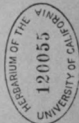
Figure 44. Comparison of the treatment of the Stellaria calycantha complex used by Hitchcock (in Hitchcock & Cronquist, 1964) and augmented by Scoggan (1978), to the present treatment.

Figure 45. Neotype of Stellaria obtusa Engelm.



Part of type

HERB. T. S. BRANDEGEE
FLORA OF NORTH AMERICA
Stellaria obtusa, Ry. n. sp.
B. F. Gayle M. I.,
Antenniock - Ok - Okla
Coll. D. S. B. - 1881



BRANDEGEE HERBARIUM

TYPE OF *Stellaria obtusa* Englemann

Coult. Bot. Gaz., 7:5, 1932

Figure 46. Distribution of Stellaria obtusa Engelm. Collections made since 1960 are indicated by circled dots.

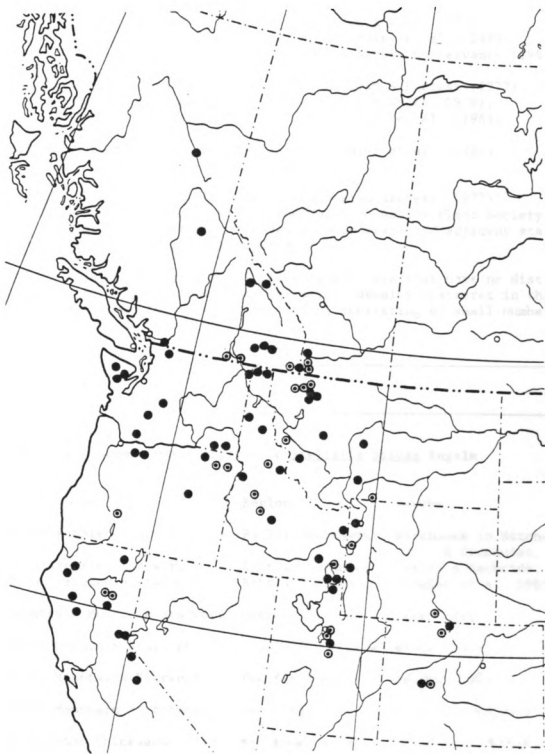


Figure 46

Table 27. Reports of Stellaria obtusa Engelm. as a rare plant.

State/Prov.	Status	Source
Colorado	Special Species*	Kartesz & Kartesz (1977)
	Rare	Argus & White (1978), Straley et al. (1985)
	Not listed	The Nature Conservancy (1986)
Alberta	Rare	Kartesz & Kartesz (1977)
	Rare	Argus & White (1978), Straley et al. (1985)
British Columbia	Rare-R3**	Straley et al. (1985)

*Special Species - fide Appendix A (Kartesz & Kartesz, 1977):
Sensitive Species, listed by the Colorado Native Plant Society as
one which is "rare and/or endemic to Colorado and adjacent states
and which merit(s) further study."

**R3 - Straley et al. (1985) include "plant taxa that have no distinct
geographical range or distribution, usually scattered in the
province, in isolated populations consisting of small numbers of
plants."

Table 28. Common names applied to Stellaria obtusa Engelm.

Common Name	Region	Source
Blunt-sepaled Starwort	Pacific Northwest	Hitchcock in Hitchcock & Cronquist, 1976
Blunt-sepaled Starwort	British Columbia	Taylor & MacBride, 1977
Blunt-sepaled Starwort	British Columbia	Straley et al. 1985
Clustered Mountain Starwort	Oregon	Peck, 1961
Rocky Mountain Starwort	Blue Mtns, Oregon	Mason, 1975
Rocky Mountains Starwort	Pacific States	Abrams, 1944
Rocky Mountain Stitchwort	North America	Kartesz & Kartesz, 1977
Washington Chickweed	Mt. Rainier, WA	St. John & Warren, 1937
Washington Starwort	Pacific States	Abrams, 1944

Figure 47. Lectotype of Stellaria crispa Cham. & Schldl.

ВЕНЕЦИАНСКОЕ
БОТАНИЧЕСКОЕ ОБОЗРЕНИЕ
ВЪЗНИКЛОЕ ПОДЪ
ПРЕДЪЗНАЧЕННЫМЪ



Stellaria media
Lam. 12
Lilacod. 17
Hb. Herb.

Figure 48. Distribution of Stellaria crispa Cham. & Schldl.
Collections made since 1960 are indicated by circled dots.

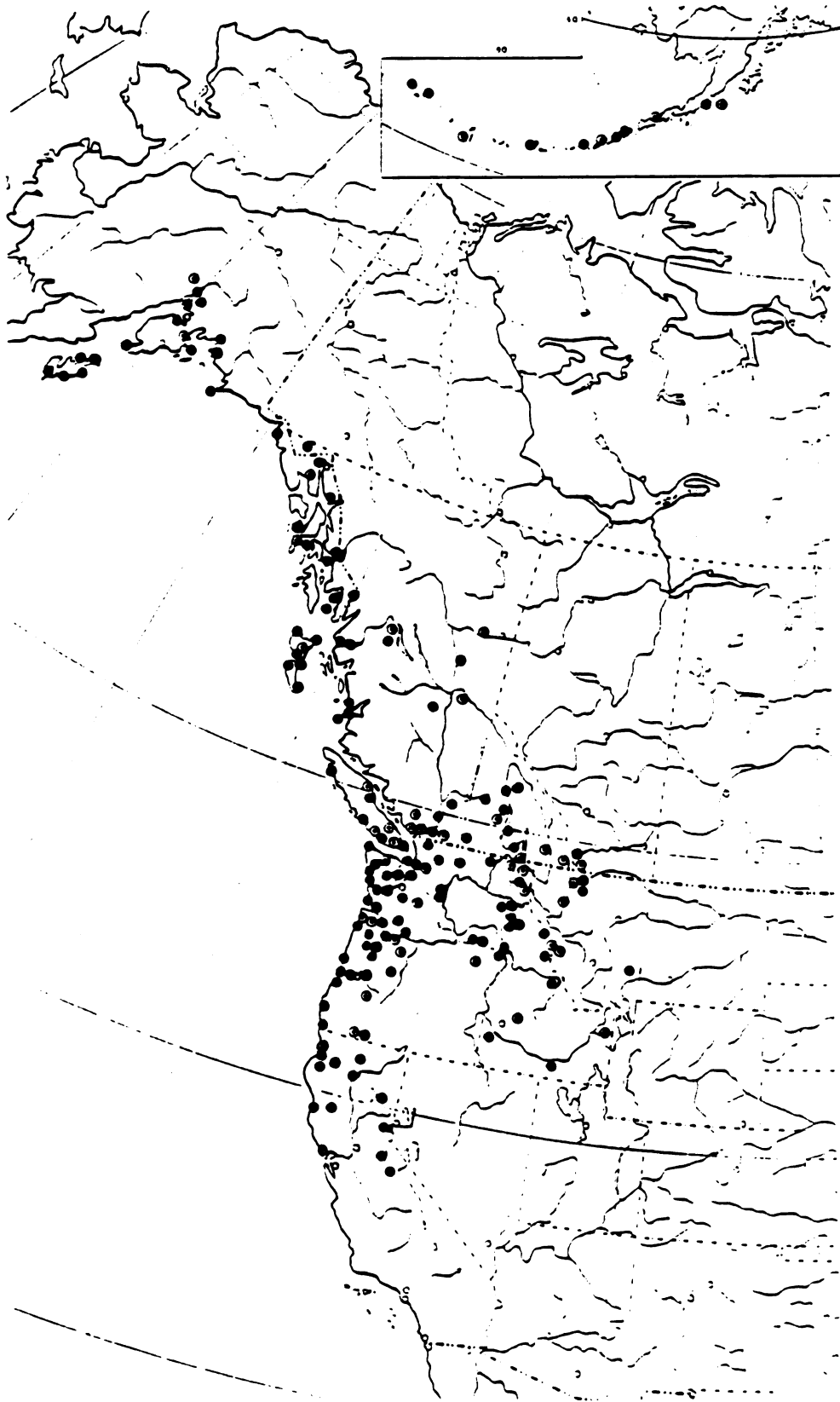


Figure 48

Table 29. Reports of Stellaria crispa Cham. & Schldl. as a rare plant.

State/Prov.	Status	Source
Alberta	Rare	Kartesz & Kartesz (1977) Douglas et al. (1981) -not listed by Argus & White (1978)
Yukon*	Rare	Douglas et al. (1981)

*Based on Anderson 9323 (CAN), a specimen of S. borealis subsp. borealis misidentified as S. crispa.

Table 30. Common names applied to Stellaria crispa Cham. & Schldl.

Common Name	Region	Source
Alpine Chickweed	Mt. Baker, WA	St. John & Hardin, 1929
Chamisso's Starwort	Pacific States	Abrams, 1944
Chamisso's Starwort	Trinity Alps, CA	Ferlatte, 1974
Chamisso's Starwort	Sierras, CA	Niehaus, 1974
Chamisso's Starwort	Sierras, CA	Weeden, 1981
Chickweed	Mt. Rainier, WA	St. John & Warren, 1937
Crimped Stitchwort	North America	Kartesz & Kartesz, 1977
Crisp Starwort	Alaska	Anderson, 1959
Crisp Starwort	Alaska	Welsh, 1974
Crisp Starwort	British Columbia	Taylor & MacBride, 1977
Crisped Starwort	Oregon	Peck, 1961
Crisped Starwort	Pacific Northwest	Hitchcock in Hitchcock & Cronquist, 1976
Crisped Starwort	Pend Oreille Co., WA	Layser, 1980
Ruffled Starwort	Blue Mountains, OR	Mason, 1975

Figure 49. Position of Stellaria crispa within Regel's Stellaria borealis.

Stellaria borealis α apetala Fenzl.; "petalis nullis v. minimis."

(petals absent or minimal.)

Lusus c. crispa; "foliis ovato-lanceolatis, glabris, marginae saepe crispis."

(leaves ovate-lanceolate, glabrous, margin often crisped.)

S. crispa Cham. & Schldl.; sensu Fenzl ex parte.

"Die breitblattrige Form mit am Rande kahlen Blättern und fehlenden oder sehr kurzen Petalen, stellt die St. crispa dar, wie solche Chamisso und Schlechtendahl beschreiben. Der Rand Blätter ist meist kraus, zuweilen aber auch flach. Dieses letztere Verhältniss wechselt bei allen uns vorliegenden Formen der St. borealis."

[The broad-leaved form with glabrous-margined leaves and absent or very short petals represents St. crispa just as Chamisso and Schlechtendal described. The leaf margin is mostly curled, but sometimes also flat. We consider it a form of Stellaria borealis above all for the varying of this last condition.]

β corollina; "petalis calycem dimidium aequantibus v. superantibus."

(petals equal or longer than one-half of the calyx.)

S. crispa sensu Fenzl ex parte.

Lusus a. crispa; "foliis anguste lanceolatis, margine glabris crispis."

(leaves narrowly lanceolate, margin glabrous, crisped.)

"Hierher gehören die schmalblattrige Blumenblätter tragenden Formen, die Fenzl zu St. crispa rechnet."

[Here belong the narrow-leaved petal-bearing forms which Fenzl included with S. crispa.]

Figure 50. Lectotype of Stellaria calycantha (Ledeb.) Bong.



Hortus Botanicus Imperiali

LE



Sp. calycanthra / Koll/Hoy

11/20-1936

Determin. V. Vassiljev.

Posttridachna
leucorhiza calycanthra, n. sp.
Sp. calycanthra, n. sp.
Sep. 19.

Stellaria borealis

Ussuri



Figure 51. Distribution of Stellaria calycantha (Ledeb.) Bong.
Collections made since 1960 are indicated by circled dots.

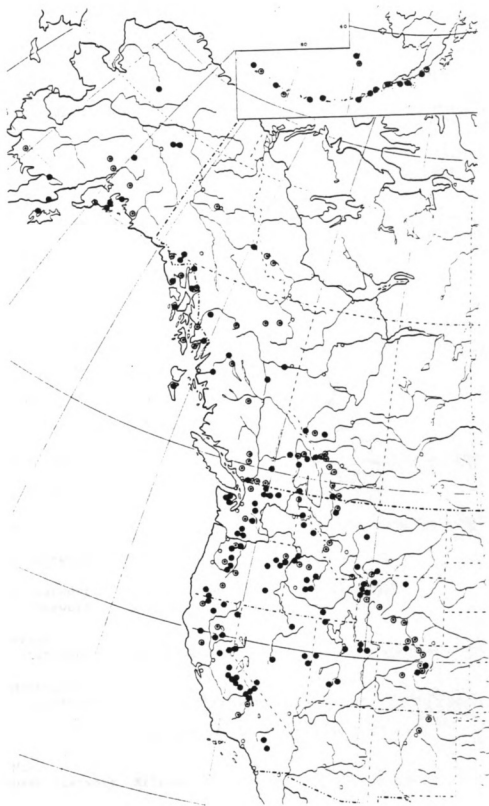


Figure 51

Table 31. Reports of Stellaria calycantha (Ledeb.) Bong. as a rare plant.

Listed Taxon	State/Prov.	Status	Source
<u>S. calycantha</u>	New Mexico	Rare?	The Nature Conservancy (1986)
<u>S. calycantha</u> var. <u>calycantha</u>	Idaho	Rare	The Nature Conservancy (1986)
<u>S. simcoei</u>	Colorado	Special* Species	Kartesz & Kartesz (1977)
	Idaho	Rare	The Nature Conservancy (1986)
	Montana	Rare?	The Nature Conservancy (1986)

*Special species - fide Appendix A (Kartesz & Kartesz, 1977):
Sensitive Species, listed by the Colorado Native Plant Society as
one which is "rare and/or endemic to Colorado and adjacent states
and which merit(s) further study."

Table 32. Common names applied to Stellaria calycantha (Ledeb.) Bong.

Common name	Region	Source
Bog Starwort	Blue Mountains, OR	Mason, 1975
Boreal Chickweed	Mt. Rainier, WA	St. John & Warren, 1937
Calyxeye Starwort	Utah	Arnold, 1980
Chickweed	Idaho & WA	St. John & Warren, 1925
Interior Starwort	Sierras, CA	Weeden, 1981
Northern Starwort	Pacific States	Abrams, 1944
Northern Starwort	Oregon	Peck, 1961
Northwestern Stitchwort	North America	Kartesz & Kartesz, 1977
Simcoe Mountain Starwort	Pacific Northwest	Hitchcock in Hitchcock & Cronquist, 1976
	Pend Oreille Co., WA	Layser, 1980
Simcoe Mtn. Northern Starwort	British Columbia	Taylor & MacBride, 1977

Figure 52. Representative specimen of Stellaria borealis Bigelow subsp. borealis.



Figure 53. Distribution of Stellaria borealis Bigelow subsp. borealis.
Collections made since 1960 are indicated by circled dots.

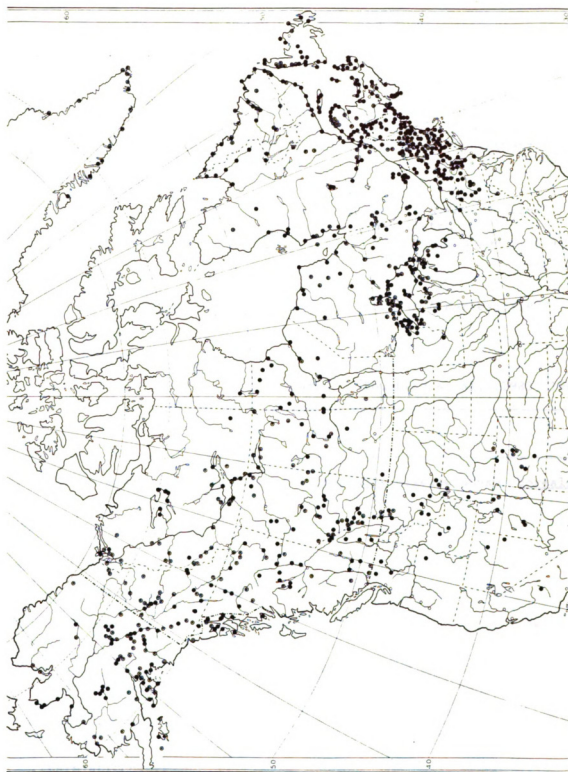


Table 33. Reports of S. borealis Bigelow subsp. borealis as a rare plant.

Listed taxon	State/Prov.	Status	Source
<u>S. calycantha</u>			
	New York	Rare	Kartesz & Kartesz (1977) -not listed in Mitchell & Sheviak (1981)
	New Jersey	Rare	Snyder & Vivian (1981)
		Rare	The Nature Conservancy (1986)
	West Virginia	Rare	The Nature Conservancy (1986)
<u>S. calycantha</u> var. <u>isophylla</u>			
	Manitoba	Rare	Kartesz & Kartesz (1977) -not listed in White & Johnson (1980)
<u>S. calycantha</u> var. <u>laurentiana</u>			
	Quebec	Rare	Kartesz & Kartesz (1977)
<u>S. calycantha</u> var. <u>sitchana</u>			
	Quebec: Anticosti	Rare	Bouchard et al. (1983, 1985)

Table 34. Common names applied to S. borealis Bigelow subsp. borealis.

Common Name	Region	Source
Alpine Stitchwort	New England	Seymour, 1982
Calyxeye Starwort	Utah	Arnold et al. 1980
Mountain Starwort	New Jersey	Snyder & Vivian, 1981
Northern Chickweed	NE Minnesota	Lakela, 1965
Northern Chickweed	Ulster Co., NY	Domville & Dunbar, 1970
Northern Chickweed	Manitoulin Is., ON	Morton & Venn, 1984
Northern Starwort	Wisconsin	Schlising & Iltis, 1962
Northern Starwort	British Columbia	Taylor & MacBride, 1977
Northern Stitchwort	east North America	Britton & Brown, 1913
Northern Stitchwort	North America	Kartesz & Kartesz, 1977
Northern Stitchwort	Delaware Co., NY	Brooks, 1983

Figure 54. Representative specimen of Stellaria borealis Bigelow subsp. sitchana (Steudel) Piper.



"The same collected at Lake Superior
by Dr. Robbins." -Asa Gray.

Ex Herbarium Elihu Hall
Field Museum of Natural History

No. 55.

Stellaria borealis Bickel.
var. *carolinensis* Presl.
(*S. hirsutella* Friss.)

Wet places and thickets, valley of
the Willamette at Salem.
1871.

Figure 55. Distribution of Stellaria borealis Bigelow subsp. sitchana (Stuedel) Piper. Collections made since 1960 are indicated by circled dots.

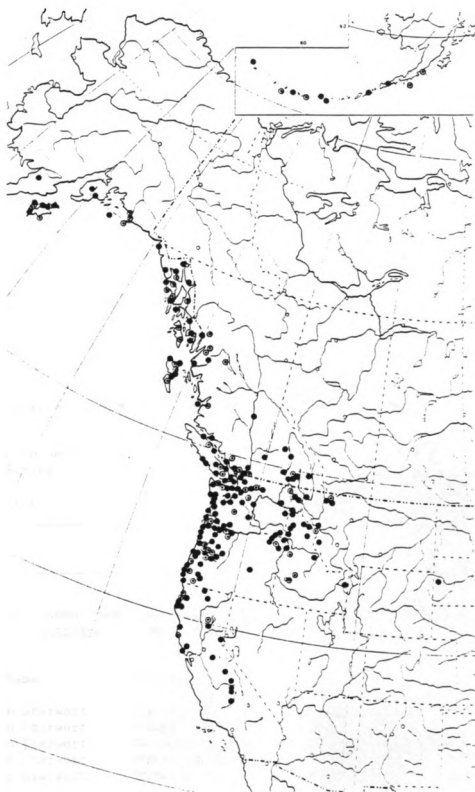


Figure 55

Table 35. Summary of collections of S. borealis subsp. borealis and sitchana infected with Ustilago violacea.

<u>S. borealis</u> subsp. <u>borealis</u>		
State/Province	# of Collections	Collection dates
Canada		
Alberta	1	1980
Manitoba	1	1854
Newfoundland	1	1925
Newfoundland/Labrador	2	1892, 1973
Northwest Territories	2	1939, 1976
Nova Scotia	1	1951
Ontario	1	1937
Quebec	6	1930, 1939, 1944(2), 1960, 1970
Saskatchewan	2	1962, 1975
Yukon	1	1944
Denmark		
Greenland	2	1962, 1967
United States		
Alaska	4	1932, 1941, 1965, 1981
New Hampshire	4	1895, 1901, 1907, 1924

<u>S. borealis</u> subsp. <u>sitchana</u>		
State/Province	# of Collections	Collection Dates
Canada		
British Columbia	1	1967
United States		
Alaska	5	1916(2), 1925, 1977, 1981
Washington	2	1980(2)

Table 36. Common names applied to Stellaria borealis Bigelow subsp. sitchana (Steudel) Piper.

Common Name	Region	Source
Northern Starwort	Pacific States	Abrams, 1944
Northern Starwort	Oregon	Peck, 1961
Northern Starwort	British Columbia	Taylor & MacBride, 1977
Northern Starwort	Pend Oreille Co., WA	Layser, 1980
Northern Starwort	Sierras, CA	Weeden, 1981
Sitka Starwort	Alaska	Anderson, 1959

Figure 56. Representative specimen of Stellaria borealis Bigelow $\times$ S. longifolia Muhlenb. ex Willd.



University of Waterloo

Herbarium

Name *Stellaria calycantha* (Led.) Bong.

Family Caryophyllaceae

Collector J.K. Morton and Joan M. Venn

No. NA 7309 Date 6 July 1974

Locality Medicine Bow Mts., nr. Laramie,
Wyoming, U.S.A. On lower slopes on
E. side at ski area

Remarks In willow swamp. Fls. with petals

2-39

Specimens in: WAT, JKM

Det. JKM

1976

Figure 57. Distribution of Stellaria borealis Bigelow $\times$ S. longifolia Muhlenb. ex Willd. Collections made after 1960 are indicated by circled dots.

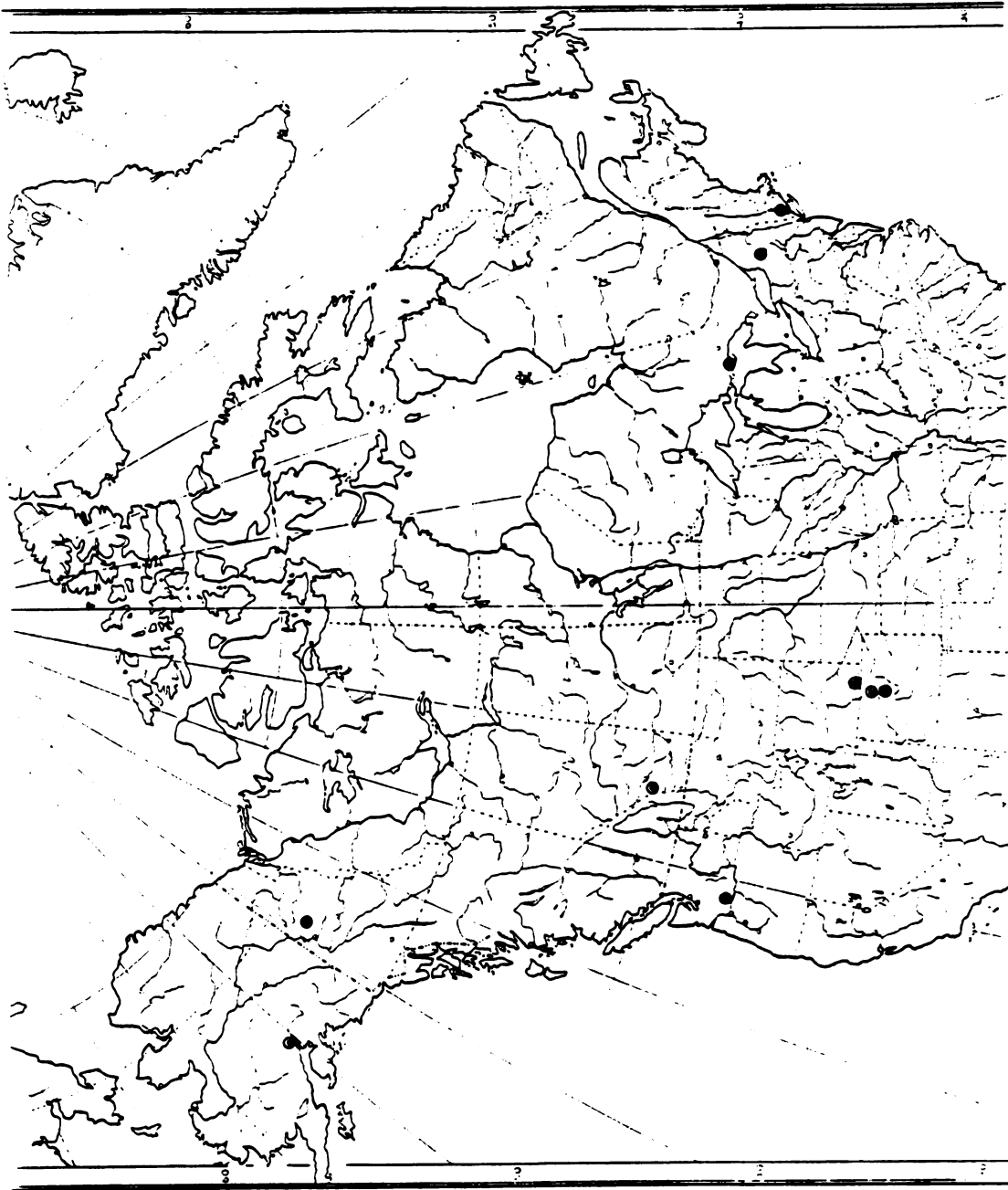


Figure 57

APPENDIX B

Collection data for specimens used in numerical analyses

OTUs are listed alphabetically by OTU Codes which translate as follows:

First two letters - possible taxon identity

CR - S. crispa

EB - eastern S. calycantha var. bongardiana
(S. calycantha var. laurentiana of Fernald)

EC - eastern S. calycantha var. calycantha

EF - eastern S. calycantha var. floribunda

EI - eastern S. calycantha var. isophylla

OB - S. obtusa

SB - S. calycantha vars. sitchana and bongardiana,
some subsp. interior sensu Hultén

SI - S. calycantha var. simcoei

WC - western S. calycantha var. calycantha

Remaining letters - abbreviations for states and provinces.

All are standard Postal Abbreviations except for the following:

AM - Alaska, Middleton Island

AU - Alaska, Aleutian Islands

K - Alaska, Kodiak Island

QA - Quebec, Anticosti Island

QC - British Columbia, Queen Charlotte Islands

VI - British Columbia, Vancouver Island

Number - distinguishes different OTU's from the same state/province.

Identification List

Species and ID Code used in listing		OTU numbers
<u>Stellaria borealis</u>	1	22-33, 35-64, 82, 84-85, 88, 91-92,
subsp. <u>interior</u>		98, 101-111, 116-119, 125-127, 143,
		145, 155-156, 163-165
<u>Stellaria borealis</u>	2	87, 89-90, 93-97, 100, 112-115,
subsp. <u>sitchana</u>		121, 123-124
<u>Stellaria borealis</u>	3	34, 86, 99, 122
× <u>S. longifolia</u>		
<u>Stellaria calycantha</u>	4	83, 128-142, 144, 146-154, 157-162
<u>Stellaria crispa</u>	5	1 - 21
<u>Stellaria longipes</u>	6	120
<u>Stellaria obtusa</u>	7	65 - 81

OTU#	ID Code	Location & habitat, collection date, collector and number, herbarium where specimen is deposited.
1	CRAB1	5 CANADA. ALBERTA. Improvement Dist. 6: Moist thicket along stream, spruce-fir forest, between N Kootenay Mtn and Lynx Creek camp, Carbondale River region, 5000 ft, 16 Jul 1971, <u>Packer & Silberhorn</u> 1971-147 (ALTA).
2	CRAK1	5 USA. ALASKA. Juneau Bor.: Shaded cliff, Funter Bay, 0 ft, 7 Jun 1915, <u>Walker & Walker</u> , <u>RM Herbarium</u> 696 (NY).
3	CRAK2	5 USA. ALASKA. Juneau Bor.: Wet woods, Juneau, 1 Jun 1940, <u>Anderson</u> 6239 (GH).
4	CRAU1	5 USA. ALASKA. Aleutian Islands: In sandy soil near creek, Attu Village site, Chic[h]agof Harbor, Attu Island, 12 Jul 1945, <u>Van Schaack</u> 598 (MICH).
5	CRBC1	5 CANADA. BRITISH COLUMBIA. New Westminster Dist.: Sunny opening adjacent to <u>Thuja-Tsuga</u> forest, 0.1 mi E of jct. of Dewdney Trunk Rd. - 288th St., E of Haney, 17 Jul 1980, <u>Rabeler</u> 426 (MSC).
6	CRBC2	5 CANADA. BRITISH COLUMBIA. Yale Dist.: Sandy roadside bank, edge of coniferous woods, 12 mi W of Ranger Sta. on Hope-Princeton Hwy, Manning Prov. Park, 16 Jul 1953, <u>Calder & Savile</u> 10604 (DAO).
7	CRBC3	5 CANADA. BRITISH COLUMBIA. Coast Range 2 Dist.: Mossy slopes along beach, Spider Island, 10 Jul 1939, <u>McT. Cowan</u> 11668 (CAN).
8	CRCA1	5 USA. CALIFORNIA. Glenn Co.: Canyon of Snow Basin Creek, 12 Aug 1943, <u>Howell</u> 19289 (CAS).
9	CRID1	5 USA. IDAHO. Latah Co.: Along stream in deep woods, N side of Cedar Peak, 2 Jul 1936, <u>Dillon & Dillon</u> 754 (UC).
10	CRK1	5 USA. ALASKA. Kodiak Island Bor.: By roadside, 4 mi N of village through pine wood to Mill Bay, 1 Jul 1936, <u>Hutchinson</u> 181 (MO).
11	CRMT1	5 USA. MONTANA. Lake Co.: In shallow water of stream, along Skidoo Creek about 5 mi up road from Hwy 35, 4000 ft, 13 Jul 1966, <u>Woodland</u> 600 (DS).
12	CROR1	5 USA. OREGON. Lane Co.: On shaded hillside in Douglas Fir forest, Clover Ridge, T17S R11W S5, [Suislaw Nat. Forest], 900 ft, 16 Jun 1938, <u>Detling</u> 2966 (ORE).
13	CROR2	5 USA. OREGON. Washington Co.: Forest Grove, 3 Jun 1893, <u>F. E. Lloyd s.n.</u> (NY).

- 14 CROR3 5 USA. OREGON. Tillamook Co.: Along shore at Wheeler, 14 May 1939, Muenschner & Muenschner 15298 (CU).
- 15 CRQC1 5 CANADA. BRITISH COLUMBIA. Queen Charlotte Dist.: Logged-over area adjacent to Thuja-Tsuga forest, summit on road between Gillatt Arm of Cumshewa & Peel Inlet, Moresby Island, 19 Jun 1964, Calder & Taylor 35211 (DAO).
- 16 CRQC2 5 CANADA. BRITISH COLUMBIA. Queen Charlotte Dist.: On disturbed bank by roadside coniferous woods, Moresby Logging Camp, Cumshewa Inlet, Moresby Island, 28 May 1957, Calder, Savile, & Taylor 20957 (DAO).
- 17 CRVI1 5 CANADA. BRITISH COLUMBIA. Vancouver Island - Barclay Dist.: Dry sandy soil, open area, dense coniferous woods, trail from Bamfield to Bachena Bay, 48°47'N 125°08'W, 11 Jun 1961, Calder & MacKay 30301 (DAO).
- 18 CRWA1 5 USA. WASHINGTON. King Co.: Seattle, 1 Aug 1933, W. J. Eyerdam s.n. (MO).
- 19 CRWA2 5 USA. WASHINGTON. Pierce Co.: Scrambling with Galium in dry soil, N of Tahoma Creek, S of Indian Henry's Camp trail, Mt Rainier Nat. Park, 3120 ft, 31 Jul 1980, Rabaler 471 (MSC).
- 20 CRWA3 5 USA. WASHINGTON. Pierce Co.: Takoma River bars, Mt Rainier Nat. Park, 17 Sep 1919, Flett 3069 (WS).
- 21 CRWA4 5 USA. WASHINGTON. Pierce Co.: Moist woods, upper valley of the Nesqually [Mt Rainier], 12 Jun 1895, Allen 156 (DS).
- 22 EBQA1 1 CANADA. QUÉBEC. Saguenay Co. - Anticosti Island: Anfractuosit  de rocher, T te a la Vache: 2 mi E of Riv re Galiote, 18 Jul 1942, Rousseau 52368 (MT).
- 23 EBQU1 1 CANADA. QU BEC. Gasp -Ouest Co.: Calcareous sea-cliffs and rock-slides, by the Gulf of St. Lawrence, Christie, 25 Jul 1922, Fernald & Pease, Fl. Quebec 25058 (GH). Holotype of Stellaria calycantha var. laurentiana.
- 24 ECGR1 1 DENMARK. GREENLAND. Skjoldungen Dist.: Eqaungmiut (Dronning Maries Dal), 63°28'N 41°55'W, 13 Aug 1970, Astrup & Kliim-Nielsen, G.B.U. 864 (MO).
- 25 ECMI1 1 USA. MICHIGAN. Keweenaw Co.: Boreal forest, Passage Island, Isle Royale Nat. Park, 9 Aug 1975, Voss 14715 (LKHD).

- 26 ECNH1 1 USA. NEW HAMPSHIRE. Coos Co.: Rock crevices at base of WMTW-TV antenna, E exposure, S of Mt Washington summit, White Mtn Nat. Forest, 6250 ft, 13 Aug 1981, Rabeller 642 (MSC).
- 27 ECQU1 1 CANADA. QUÉBEC. Baie James Terr.: Sous les Salix en haut du rivage, Vieux-Comptoir, 52°37'N 78°42'W, 31 Jul 1954, Lepage 32098 (DAO).
- 28 EFLB1 1 CANADA. NEWFOUNDLAND/LABRADOR. Roadsides, near the mouth of Otter Creek, Goose Bay, 20 Jul 1969, Rouleau 11221 (MT).
- 29 EFME1 1 USA. MAINE. Aroostook Co.: Recent clearing, valley of Limestone River, Limestone, 22 Jun 1898, Fernald 2277 (NEBC).
- 30 EFME2 1 USA. MAINE. Penobscot Co.: Wet muddy bank, Lower Penobscot Valley, Veazie, 15 Sep 1897, M. L. Fernald s.n. (NEBC).
- 31 EFMI1 1 USA. MICHIGAN. Delta Co.: In Mnium mat under Alnus on SW shore of Bear Lake, 0.5 mi S of FR 2436, T43N R18W S36 SW1/4, 24 Jun 1980, Rabeller 364 (MSC).
- 32 EFNBI 1 CANADA. NEW BRUNSWICK. Charlotte Co.: Dense mat in shingle at top of beach, S shore of White Head Island, Grand Manan, 5 Aug 1927, Weatherby & Weatherby 5751 (GH).
- 33 EFNFI 1 CANADA. NEWFOUNDLAND. Humber Dist.: Slaty bank, near Curling, Humber Arm, Bay of Islands, 31 Aug 1929, Fernald & Long, Fl. NW Newfoundland 1679 (GH).
- 34 EFNYY 3 USA. NEW YORK. Oneida Co.: Shady flats of a stream around sand bog, Deerfield, 10 Jun 1901, Haberer 2264 (GH).
- 35 EFON1 1 CANADA. ONTARIO. Thunder Bay Dist.: Gravelly shore, N shore of Paradise Island, 20 mi SE of Nipigon, 5 Aug 1956, Garton 2965 (DAO).
- 36 EFON2 1 CANADA. ONTARIO. Kenora Dist.: Rich moist depression between river terrace, junction of the Fawn and Poplar Rivers, 26-28 Jul 1952, Moir 944 (CAN).
- 37 EFQU1 1 CANADA. QUÉBEC. Abitibi Co.: Spirit Lake (Abitibi), 9 Jul 1918, Marie-Victorin 8483 (US).
- 38 EFQU2 1 CANADA. QUÉBEC. Nouveau-Québec: Sandy soil along small stream at camp, Fort Chimo area, 58°07'N 68°23'W, 5 Aug 1948, Calder 2380 (MT).

- 39 EFQU3 1 CANADA. QUÉBEC. Gaspé-Ouest Co.: In moss under Salix and Alnus roadside, ditch S side of QU 132, 1.1 km W of Rivière Ste. Marthe, 10 Aug 1981, Rabeler 637 (MSC).
- 40 EFVT1 1 USA. VERMONT. Orleans Co.: Common in swamp, Willoughby, 15 Jul 1898, G. C. Kennedy s.n. (NEBC).
- 41 EFWI1 1 USA. WISCONSIN. Ashland Co.: Jumble of rock & driftwood over claybank, near boat dock, S end of Devils Island, T53N R3W S15 NW1/4, 30 Jul 1980, Cochrane & Cochrane 9197 (MSC).
- 42 EFWV1 1 USA. WEST VIRGINIA. Tucker Co.: In cold pool at base of cranberry bog, Dolly Sods, 4000 ft, 24 Aug 1984, E. E. Hutton Jr. s.n. (MSC).
- 43 EIGR1 1 DENMARK. GREENLAND. Tunugdliarfik: Majut, 61°04'N 45°35'W, 150 m, 29 Aug 1962, Hansen, Hansen, & Petersen 2171 (DAO).
- 44 EIGR2 1 DENMARK. GREENLAND. Godthaab, 64°11'N, 19 Aug 1936, J. Lagerkranz s.n. (RM).
- 45 EIMA1 1 USA. MASSACHUSETTS. Middlesex Co.: Wet sphagnous meadow, R.F. Root's swamp, Concord, 11 Jun 1921, R. J. Eaton s.n. (NEBC).
- 46 EIME1 1 USA. MAINE. Aroostook Co.: Springy woods in disintegrated volcanic rock, Haystack Mtn, 10 Jul 1902, E. F. Williams, J. F. Collins, & M. L. Fernald s.n. (GH).
- 47 EIME2 1 USA. MAINE. Lincoln Co.: White Island, off Boothbay, 5 Jul 1903, J. R. Churchill s.n. (MO).
- 48 EINB1 1 CANADA. NEW BRUNSWICK. Madawaska Co.: Banks of the Grand River, about 1 mi E of Flemming, 4 Jul 1927, Malte & Watson 244 (CAN).
- 49 EINF1 1 CANADA. NEWFOUNDLAND. St. Barbe Dist.: In moss at base of limestone shelf, E side of NF 430 2km S of road to Bartlett's Harbor, 28 Jul 1981, Rabeler 618 (MSC).
- 50 EINF2 1 CANADA. NEWFOUNDLAND. St. Georges - Port Au Port Dist.: Border of brook, Green Gardens, Cape St. George, 20 Jul 1922, Mackenzie & Griscom 11055 (GH).
- 51 EINH1 1 USA. NEW HAMPSHIRE. Coos Co.: Tuckerman's Ravine, Mt Washington, 30 Jul 1890, J. R. Churchill s.n. (MO).

- 52 EINH2 1 USA. NEW HAMPSHIRE. Cheshire Co.: Open woods, Gap Mtn, Troy, 13 Jun 1898, Rand & Robinson 459 (GH). Holotype of Stellaria calycantha var. isophylla.
- 53 EINS1 1 CANADA. NOVA SCOTIA. Yarmouth Co.: By spring-rill in rocky and gravelly barrens, Tusket, 15 Jul 1920, Long & Linder, GH Exped. to Nova Scotia 21201 (CAN).
- 54 EINY1 1 USA. NEW YORK. Wayne Co.: Arbor-vitae swamp, E of Clyde, 23 Jun 1917, Wiegand, Fl. of New York 8069 (GH).
- 55 EION1 1 CANADA. ONTARIO. Thunder Bay Dist.: Cedar bog, N side of Little Pigeon Bay, Crooks Twp., Lake Superior, 17 Jul 1952, Garton 1878 (DAO).
- 56 EION2 1 CANADA. ONTARIO. Cochrane Dist.: Mossy floor in opening in black spruce, Hudson Bay lowlands, S of Ogoki along Ogoki River, 51°38'N 85°57'W, 9 Aug 1956, Baldwin, Porsild et al. 6760 (LKHD).
- 57 EIPA1 1 USA. PENNSYLVANIA. Lackawanna Co.: Wet sphagnous wooded swamp along US 6, 0.75 mi WSW of Clark Summit, 6 Aug 1946, Glownke 8328 (PENN).
- 58 EIQU1 1 CANADA. QUÉBEC. Nouveau-Québec: Moist willow swamp, 3 mi W of camp, Fort Chimo area, 58°07'N 68°23'W, 23 Aug 1945, Calder 2729 (US).
- 59 EIQU2 1 CANADA. QUÉBEC. Baie James Terr.: Bas de la falaise d'argile, Rupert House, 51°30'N, 11 Jul 1945, Dutilly & Lepage 14134 (CAN).
- 60 EIQU3 1 CANADA. QUÉBEC. Argenteuil Co.: Bois très humide dans les sphaignes, St-Adolphe[-d'Howard], 5 Jul 1947, Rolland-Germain 6212 (MT).
- 61 EIQU4 1 CANADA. QUÉBEC. Saguenay Co.: Grassy shore, Point au Maurier, Charnay, 16 Jul 1915, St. John, Herb. Geol. Surv. Canada 90434 (CAN).
- 62 EIQU5 1 CANADA. QUÉBEC. Duplessis Co.: Sables decapes, chemin de fer mi 146, Jiggs, Petit lac Manicouagan, 23 Jul 1962, M. Maldagne & G. Lemieux s.n. (DAO).
- 63 EIWI1 1 USA. WISCONSIN. Florence Co.: Mossy sedgy seepage in Thuja woods, N-facing slope at S end of Pickerel Lake, T40N R17E S7, 30 Jun 1964, Iltis & Turner 22059 (WIS).
- 64 EIWI2 1 USA. WISCONSIN. Vilas Co.: On mud and debris of old beaver dam, Siphon Creek, T42N R8E S13, 14 Jun 1961, Schlising & Schlising 1950 (UC).

- 65 OBAB1 7 CANADA. ALBERTA. Waterton Lakes Nat. Park: Weed, parking lot at last shelter, Twin Lakes Trail, 49°08'N 114°09'W, 6300 ft, 15 Aug 1969, Kuijt & Blais 2949 (ALTA).
- 66 OBBC1 7 CANADA. BRITISH COLUMBIA. Similkameen Dist.: Cliffs and talus slopes, 40 mi W of Trail, 10 mi N of WA boundary, 5000 ft, 3 Aug 1964, Scoggan 16087 (CAN).
- 67 OBBC2 7 CANADA. BRITISH COLUMBIA. Kootenay Dist.: One clump on sand and gravel bar in creek, 3.5 mi NNE of Galloway beside Sand Creek, 49°24'N 115°11'W, 3400 ft, 29 May 1958, Taylor & Ferguson 922 (DAO).
- 68 OBCA1 7 USA. CALIFORNIA. Placer Co.: Moist soil about rocks, near the Yuba River below Cisco, 5500 ft, 25 Jul 1919, Heller 13298 (GH).
- 69 OBCA2 7 USA. CALIFORNIA. Butte Co.: On gravel bars by Butte Creek, Jonesville, 1500 m, 18 Jul 1931, Copeland, UC Herbarium 636 (GH).
- 70 OBCO1 7 USA. COLORADO. Routt Co.: Wet outlet of beaver dam along trail, between Slavonia & Mica Creek, 30 mi NE Steamboat Springs, Routt Nat. Forest, 29 Jul 1951, Weber 7088 (WS).
- 71 OBID1 7 USA. IDAHO. Boise Co.: In moss on dry soil along two-track, 30m N of turnout E of ID 21, 21 mi SW of Lowman, Boise Nat. Forest, T7N R7E S20 NW 1/4, 6100 ft, 12 Aug 1980, Rabaler 534 (MSC).
- 72 OBID2 7 USA. IDAHO. Caribou Co.: Along a rotting log in grassy meadow, Grays Range, Gravel Creek Campground, 22 mi NNE of Soda Springs, T6S R43 S2, 6700 ft, 19 Jul 1971, Holmgren & Marttala 5518 (UTC).
- 73 OBMT1 7 USA. MONTANA. Gallatin Co.: Bridger Mtns, 7000 ft, 14 Jun 1897, Rydberg & Bessey 4014 (NDG).
- 74 OBMT2 7 USA. MONTANA. Glacier Co.: Many Glaciers, Glacier Nat. Park, 12 Jul 1934, Jones 5338 (GH).
- 75 OBOR1 7 USA. OREGON. Wallowa Co.: Creeping along the ground in moist shady woods, Lostine River Rd., near the Pole Bridge, T2S R43E S16, 4100 ft, 28 Jun 1969, Mason 8199 (ORE).
- 76 OBOR2 7 USA. OREGON. Grant Co.: Frequent in wet soil around springs in Yellow Pine, Indian Springs, Blue Mtns, Malheur Nat. Forest, 5 Aug 1946, Maguire & Holmgren 26892 (UTC).

- 77 OBUT1 7 USA. UTAH. Cache Co.: Marshy ground at margin of Tony Grove Lake Bear River Range, 8000 ft, 4 Aug 1938, Maguire & Snell 16042 (CAN).
- 78 OBUT2 7 USA. UTAH. Salt Lake Co.: Alta, Wahsatch Mtns, 10000 ft, 29 Jul 1879, Jones 1096 (RM). Upper plant only.
- 79 OBWA1 7 USA. WASHINGTON. Whatcom Co.: Forming thick mats on gravel along Slate Creek Barron, Mt Baker Nat. Forest, 23 Jun 1939, Muenschner 10046 (GH).
- 80 OBWA2 7 USA. WASHINGTON. Pierce Co.: Alder woods, upper valley of the Nesqually [Mt Rainier], 18 Jun 1895, Allen 157 (MSC). Isotype of Alsine washingtoniana.
- 81 OBWY1 7 USA. WYOMING. Teton Co.: In great tufts on rather dry ground, West De Lacy Creek, Yellowstone Nat. Park, 4 Aug 1899, Nelson & Nelson 6298 (RM). Upper plant only.
- 82 SBAB1 1 CANADA. ALBERTA. Banff Nat. Park: Boggy ground, foot of Squaw Mtn near Banff, 4500 ft, 22 Jul 1899, McCalla 2407 (WTU).
- 83 SBAB2 4 CANADA. ALBERTA. Banff Nat. Park: Wet meadow by lake, Sunshine Ski Lodge, Fatigue Pass, 7 Aug 1945, Porsild & Breitung 13925 (CAN).
- 84 SBAB3 1 CANADA. ALBERTA. Strathcona Co.: Spruce woods, few rods S of Davis' Lake, 5 mi SE of Fort Saskatchewan, 24 Jul 1945, Turner 4590 (ALTA). Isotype of Stellaria calycantha var. latifolia.
- 85 SBAK1 1 USA. ALASKA. Fairbanks North Star Bor.: Miller House, on Steese Highway, 115 mi N of Fairbanks, 2100 ft, 2-26 Jul 1937, Scamman 750a (GH).
- 86 SBAK2 3 USA. ALASKA. Matanuska Bor.: Matanuska, 10 Jul 1931, J. P. Anderson s.n. (ISC). Left plants only.
- 87 SBAK3 2 USA. ALASKA. Sitka Bor.: Sitka, 6-9 Sep 1904, Piper 4412 (US).
- 88 SBAK4 1 USA. ALASKA. Steppe bluff, Gakona, ca 2 km E of Gakona Junction, 62°18'N 145°20'W, 9 Jul 1981, Khokhryakov, Yurtsev, & Murray 6228 (ALA).
- 89 SBAM1 2 USA. ALASKA. Middleton Island: Roadsides, near airstrip and base, 59°25'N 146°20'W, 2 Aug 1956, Thomas 6278 (CAN).

- 90 SBAU1 2 USA. ALASKA. Aleutian Islands: Disturbed habitat, vic. of naval base, Massacre Bay, SE part of Attu Island, 26 Aug 1949, Miller 1293 (US).
- 91 SBBC1 1 CANADA. BRITISH COLUMBIA. Kamloops Dist.: Alpine slopes of Chipuin Mtn, Marble Mtns [NE of Lillooet], 6000 ft, 21 Jul 1938, Thompson & Thompson 605 (CAN).
- 92 SBBC2 1 CANADA. BRITISH COLUMBIA. Peace River Dist.: Roadside, Alaska Hwy, 30 mi E of Summit Pass, 27 Aug 1943, Raup & Correll 11562 (A).
- 93 SBCA1 2 USA. CALIFORNIA. Humboldt Co.: Moist places, Eureka, 0 to 200 ft, 22 May 1900, Tracy 795 (UC). Left plant.
- 94 SBCA2 2 USA. CALIFORNIA. Humboldt Co.: Moist places, Eureka, 0 to 200 ft, 22 May 1900, Tracy 795 (UC). Right plant.
- 95 SBCA3 2 USA. CALIFORNIA. Mariposa Co.: Bridal Veil Meadows, Yosemite Nat. Park, 4000 ft, 13 Jul 1911, Hall 9105 (UC).
- 96 SBCA4 2 USA. CALIFORNIA. Mariposa Co.: Wawona, 4000 ft, 20 Jun 1924, Howell 428 (CAS).
- 97 SBCA5 2 USA. CALIFORNIA. Sonoma Co.: Open marshy ground, N half of Lower Pitkin Marsh, 9 Jun 1951, Rubtzoff 153 (DS).
- 98 SBCA6 1 USA. CALIFORNIA. Tulare Co.: Moist places, nr Middle Tule River, 7000-8000 ft, Apr-Sep 1897 [May fide B. Ertter], Purpus 5131 (US).
- 99 SBCO1 3 USA. COLORADO. Clear Creek Co.: Along shaded Little Bear Creek, Idaho Springs, 13 Aug 1942, Degener & Peiler 16815 (MO). Right plant.
- 100 SBID1 2 USA. IDAHO. Bonner Co.: Overflow meadows at mouth of Pack River on Lake Pend Oreille, 16 Jun 1940, Christ 11190 (NY).
- 101 SBK1 1 USA. ALASKA. Kodiak Island Bor.: Sturgeon River, 19 Jul 1899, Coville & Kearney 2237 (US).
- 102 SBKE1 1 CANADA. NORTHWEST TERRITORIES. Keewatin Dist.: On sphagnum in spruce muskeg, NW extremity of Nueltin Lake, mouth of Windy River, 6 Aug 1947, Harper 2388 (MICH).
- 103 SBMB1 1 CANADA. MANITOBA. Moist gravel by stream, Hwy 10, 3 km S of N gate of Riding Mtn Nat. Park, 50°49.7'N 100°04'W, 9 Jul 1979, Cody 24376 (DAO).

- 104 SBMB2 1 CANADA. MANITOBA. W bank of Townsite Slough, Churchill, 23 Jul 1954, Beckett M-28-6 (MIN).
- 105 SBMB3 1 CANADA. MANITOBA. Roadside in sandy clay, Lynn Lake, 1 Oct 1957, Krivda L.L. 39 (NY).
- 106 SBMC1 1 CANADA. NORTHWEST TERRITORIES. Mackenzie Dist.: Disturbed roadside soil, Mackenzie River - Yellowknife Hwy Mile 68.2 N, 12 Jul 1961, Thieret & Reich 7639 (DAO).
- 107 SBMC2 1 CANADA. NORTHWEST TERRITORIES. Mackenzie Dist.: Moist bank of Little Buffalo River, 32 mi W of Fort Smith, 60°02'N 112°48'W, 25 Jul 1950, Cody 4730 (DAO).
- 108 SBMC3 1 CANADA. NORTHWEST TERRITORIES. Mackenzie Dist.: Lakeshore, peat bog, area of Mackenzie Delta, Inuvik, 67°58'N 133°41'W, 23 Jul 1966, Owen-Larsen 247 (UBC).
- 109 SBMC4 1 CANADA. NORTHWEST TERRITORIES. Mackenzie Dist.: Moist sand of roadside, Seven Mile Lake, 27 mi W of Fort Smith, 60°02'N 112°38'W, 22 Jul 1950, Cody & Loan 4650 (DAO).
- 110 SBMT1 1 USA. MONTANA. Glacier Co.: Damp sand along N bank of Two Medicine Creek, 1.2 mi W of Two Medicine Entrance Sta., Glacier Nat. Park, 4880 ft, 16 Aug 1980, Rabaler 551 (MSC).
- 111 SBMT2 1 USA. MONTANA. Flathead Co.: Damp soil along W bank of Avalanche Creek, 10 m NW of Avalanche Lake, 2.2 mi SW of Hwy 1, Glacier Nat. Park, 3930 ft, 15 Aug 1980, Rabaler 547 (MSC).
- 112 SBOR1 2 USA. OREGON. Benton Co.: In marsh around Frazier Creek, W of Canterbury Circle, NE Corvallis, T11S R5W S24, 67.5 m, 15 Jun 1980, Halse 2238 (OSC).
- 113 SBOR2 2 USA. OREGON. Clatsop Co.: Near bank of Necanicum River, S side US 26 at Saddle Mtn St. Park Rd., 45°52'N 123°45'W, 2 Aug 1980, Rabaler 479 (MSC).
- 114 SBQC1 2 CANADA. BRITISH COLUMBIA. Queen Charlotte Dist.: Logged-over woods at margin of village, Alliford Bay, Moresby Island, 27 Jun 1957, Calder, Savile, & Taylor 21857 (DAO).
- 115 SBS D1 2 USA. SOUTH DAKOTA. Lawrence Co.: Wet rocky ground along creek, near Deadwood, 28 Jun 1929, Palmer 37610 (GH).

- 116 SBSK1 1 CANADA. SASKATCHEWAN. Marshy E shore of Little Amyot Lake, 12 mi NW of Beauval, Hwy 155 mile 70. 55°11'N 107°50'W, T71N R13W, 19 Jul 1970, Harms 16950 (DAO).
- 117 SBSK2 1 CANADA. SASKATCHEWAN. Damp shaded ground, Wallwort, 14 Jul 1940, Breitung 652 (ALTA).
- 118 SBUT1 1 USA. UTAH. Summit Co.: Fish Lake, 9000 ft, 3 Aug 1894, Jones 5730 (RM).
- 119 SBUT2 1 USA. UTAH. Beaver Co.: Beaver City [fide GH label], 1877, Palmer 55 (NY).
- 120 SBUT3 6 USA. UTAH. Iron Co.: [Bear Valley fide Welsh (1982) and GH label], 1877, Palmer 54 (NY). Isotype of Stellaria palmeri.
- 121 SBVI1 2 CANADA. BRITISH COLUMBIA. Vancouver Island - Alberni Dist.: Thickets, bottom land, Prairie Farms Alberni, 10 Jul 1917, W. R. Carter s.n. (GH).
- 122 SBWA1 3 USA. WASHINGTON. Skamania Co.: Little White Salmon River below Berry Creek, 26 Jun 1895, Suksdorf 2438 (WS).
- 123 SBWA2 2 USA. WASHINGTON. Pierce Co.: Gravel, W shore of Fish Creek, 3.6 mi N of main park road (E of Nisqually Sta.), Mt Rainier Nat. Park, 2950 ft, 31 Jul 1980, Rabaler 473 (MSC).
- 124 SBWA3 2 USA. WASHINGTON. Thurston Co.: Moist places along fence rows, head of Elds Inlet (Mud Bay), 5 mi W of Olympia, 11 Jun 1940, Meyer 1779 (GH).
- 125 SBWY1 1 USA. WYOMING. Teton Co.: Little Firestone River, 21 Jul 1919, J. Bright s.n. (CM).
- 126 SBYU1 1 CANADA. YUKON. On bog hummocks, Upper Ross River valley, Canol Road Mile 95, 3600 ft, 11 Jul 1944, Porsild & Breitung 10366 (CAN).
- 127 SBYU2 1 CANADA. YUKON. Bonanza Creek, Dawson, 12 Jun 1914, Eastwood 196 (CAN). Isotype of Stellaria calycantha subsp. interior.
- 128 SICA1 4 USA. CALIFORNIA. Fresno Co.: Huntington Lake, 20 Jul 1943, H. M. Pollard s.n. (CAS).
- 129 SICO1 4 USA. COLORADO. Pitkin Co.: In willow thickets of a spruce bog, above hwy between Lincoln Gulch & Lost Man Camp, Roaring Fork River, 9500 ft, 9-13 Jul 1963, Weber 12085 (COLO).

- 130 SIID1 4 USA. IDAHO. Kootenai Co.: Springy places in cañ[ny]ons, S from Wiessner's Peak, 1700 m, 25 Jul 1895, Leiberg 1396 (ORE).
- 131 SIID2 4 USA. IDAHO. Valley Co.: Stibnite area along West End Creek, tributary to Sugar Creek, T18N R9E S2 NE1/4, 6500 ft, 11 Jul 1980, Grimes & Packard 1792 (NY).
- 132 SIMT1 4 USA. MONTANA. Beaverhead Co.: Moist shores, Blair Lake, T15S R1E S2 NW 1/4, 8130 ft, 25 Jul 1979, Lowry 2630b (MO).
- 133 SINM1 4 USA. NEW MEXICO. Colfax Co.: On jeep trail roadcut, 1 mi S of Clear Creek Camp, Philmont Scout Ranch, Cimmaron, 10200 ft, 27 Jul 1968, Hartman 2496 (RM).
- 134 SIOR1 4 USA. OREGON. Klamath Co.: Along banks of tributary of Munson Creek, near Castle Crest Wildflower Garden, Crater Lake Nat. Park, 6475 ft, 5 Aug 1980, Rabeler 494 (MSC).
- 135 SIOR2 4 USA. OREGON. Deschutes Co.: Among moss on log fragment in sun near S bank of Paulina Creek, E of top of Paulina Creek Falls, 6300 ft, 4 Aug 1980, Rabeler 490 (MSC).
- 136 SIOR3 4 USA. OREGON. Deschutes Co.: Wet bank of creek, Park Meadow, E fork of Park Creek, Three Sisters Wilderness, W of Bend, 6150 ft, 14 Aug 1953, Ireland 3274 (ORE).
- 137 SIWA1 4 USA. WASHINGTON. Whatcom Co.: Below glaciers on Heliotrope Ridge, Mt Baker, 7500 ft, 11 Aug 1934, Thompson 11247 (US).
- 138 SIWA2 4 USA. WASHINGTON. Yakima Co.: Streambanks, Mt Paddo, 6000-7000 ft, 17 Sep 1894, Suksdorf 2303 (WS).
- 139 SIWA3 4 USA. WASHINGTON. Chelan Co.: Stevens Pass, Cascade Mtns, 4000 ft, 26 Jul 1934, Jones 5700 (GH).
- 140 SIWA4 4 USA. WASHINGTON. Klickitat Co.: Simcoe Mtns, Jun 1880, T. Howell s.n. (ORE). Isolectotype of Alsine simcoei.
- 141 SIWY1 4 USA. WYOMING. Teton Co.: East De Lacy's Creek, Yellowstone Nat. Park, 7500 ft, 10 Aug 1897, Rydberg & Bessey 4013 (NY).
- 142 WCAB1 4 CANADA. ALBERTA. Improvement Dist. 6: Along streamlet, Carbondale River, Crowsnest area, 5000 ft, 17 Jul 1961, R. T. Ogilvie s.n. (UBC).

- 143 WCAK1 1 USA. ALASKA. Fairbanks North Star Bor.: Fairbanks, 15 Jul 1961, E. Hultén s.n. (A).
- 144 WCAK2 4 USA. ALASKA. Mountains, NW of Walker Lake, upper Kopuk River, Brooks Range, 16 Aug 1950, Jordal 3991 (MICH).
- 145 WCAK3 1 USA. ALASKA. Nome, 26 Jun 1938, Anderson 3641 (GH).
- 146 WCAU1 4 USA. ALASKA. Aleutian Islands: Bare rock in the tundra, near Infantry Road and Cyril Cove, Amchitka Island, 11 Aug 1966, Shacklette 7443 (MICH).
- 147 WCBC1 4 CANADA. BRITISH COLUMBIA. New Westminster Dist.: Glacial moraines, Sphinx Glacier foreland, Garibaldi Park, 5000 ft, 26 Jul 1965, B. Fraser s.n. (UBC).
- 148 WCBC2 4 CANADA. BRITISH COLUMBIA. Kootenay Dist.: Asulkan Valley, near 51°30'N, 5000 ft, 17 Aug 1904, Petersen 509 (PH).
- 149 WCCA1 4 USA. CALIFORNIA. Tehama Co.: Along cold spring drainage into ditch, W side of CA 89, S of Sulphur Works Entrance, Lassen Volcanic Nat. Park, 6550 ft, 10 Aug 1980, Rabaler 518 (MSC).
- 150 WCCA2 4 USA. CALIFORNIA. Siskiyou Co.: Sunny gravelly edge of streamlet, Jaynes Canyon, Siskiyou Mtns, T47N R10W S12, 6400 ft, 26 Jul 1935, Wheeler 3697 (US).
- 151 WCCA3 4 USA. CALIFORNIA. San Bernardino Co.: Wet place along stream, High Creek, San Bernardino Mtns, 23 Aug 1923, Peirson 4158 (JEPS).
- 152 WCCA4 4 USA. CALIFORNIA. Fresno Co.: Bubbs Creek Canyon, in vic. of Vidette Meadows, 9500-10000 ft, 21 Jul 1948, Howell 24815 (CAS).
- 153 WCCO1 4 USA. COLORADO. Larimer Co.: Headwaters of Beaver Creek, 50 mi W of Fort Collins, 9500-10000 ft, 19-20 Jul 1898, C. S. Crandall s.n. (MSC).
- 154 WCID1 4 USA. IDAHO. Elmore Co.: Very wet and springy places, near Big Roaring River Lake, 20 mi N of Pine, 8000 ft, 25 Aug 1947, Meyer & Meyer 2345 (UC).
- 155 WCMC1 1 CANADA. NORTHWEST TERRITORIES. Mackenzie Dist.: Moist soil along roadside ditch, near Giant Mine, Yellowknife, 62°27'N 114°22'W, 30 Jun 1949, Cody & McCause 2335 (DAO).

- 156 WCMC2 1 CANADA. NORTHWEST TERRITORIES. Mackenzie Dist.: Disturbed sandy soil along road, E to ford over Kakisa River, Enterprise - Mackenzie River Hwy, 1 Jul 1959, Thieret & Reich 4905 (CAN).
- 157 WCMT1 4 USA. MONTANA. Madison Co.: Spanish Basin, Madison Range, 6000 ft, 18 Jul 1896, Flodman 430 (US).
- 158 WCNV1 4 USA. NEVADA. Elko Co.: Wet places among Veratrum californicum, upper basin meadow, Hayes Creek, Independence Mtns, 11 Aug 1943, Maguire & Holmgren 22452 (UTC).
- 159 WCOR1 4 USA. OREGON. Wallowa Co.: Wet bank, Ice Lake, Wallowa Mtns, 14 Jul 1934, Peck 18525 (WILLU).
- 160 WCUT1 4 USA. UTAH. Summit Co.: In dense mats, streamside in deep ravine, Henrys Forks Basin, Uinta Mtns, 10900 ft, 12 Aug 1936, Maguire, Hobson, & Maguire 14591 (WTU).
- 161 WCWA1 4 USA. WASHINGTON. Yakima Co.: Along streams, Mt Paddo, 6000-7000 ft, 17 Sep 1894, Suksdorf 2302 (GH).
- 162 WCWY1 4 USA. WYOMING. Carbon Co.: Ferris Mtns, 25 Jul 1898, Nelson 4973a (RM).
- 163 WCYU1 1 CANADA. YUKON. Dry earth bank, N side of Dempster Hwy Mile 22, 16 Jun 1969, Packer 1969-229 (ALTA).
- 164 WCYU2 1 CANADA. YUKON. Lush area about cabin, near 31 Mile cabin on 60 Mile Road, 64°15'N 140°18'W, 14 Aug 1949, Calder & Billard 4494 (DAO).
- 165 WCYU3 1 CANADA. YUKON. Independence Creek, 1 Aug 1902, J. Macoun, Herb. Geol. Surv. Canada 58410 (CAN).

APPENDIX C

Methods for culturing Stellaria plants

1. Germination

- A. Seeds were placed on damp Whatman #1 filter paper in glass petri plates and then placed in the dark on trays under cloth toweling. Distilled water was used exclusively during this phase.
- B. The micropylar end near the future root (hopefully) of the seedling was chipped with a razor blade 3-5 days after first placing the seeds in the petri plates. The chipping was done to "assist" growth - tests done on a small number of seeds showed that no germination occurred without such action.
- C. Germination occurred in (2)7-11(53) days after chipping. Seeds not germinating after approximately three weeks were rechipped; some germinated and grew normally within a week of this second treatment. Only occasionally did the root not appear first, this phenomenon occurring in some seeds of Stellaria crispera and Stellaria obtusa.

2. Further Growth - Year 1:

- A. Plates were left in the dark until the cotyledons appeared, at which time they were moved so as to receive indirect light from GE Watt-Miser 35 fluorescent lights timed to simulate "natural" lighting. During winter months, a minimum of 9 hours of light was provided, similar to that available if the plants were growing outside.

(Exception: Three plants were started under a manually-controlled fluorescent desk lamp also regulated to approximate available outside light).

- B. With further expansion of the cotyledons, individual seedlings were placed, along with a small piece of filter paper to minimize transplant disturbance, into Jiffy-7 Peat Pots. The plants were returned to the same light regime and covered with a glass beaker to maintain the humidity levels the seedlings had experienced within the petri plates and protect them from the inherent dryness of the growth area. Watering regime was changed to a blend of 1 part distilled water, 1 part tap water.
- C. After 2-5 days in peat pots, the peat pots were "planted" into 3 1/4" clay pots, filler composed of 1 part commercial potting soil and one part VSP Peat Lite Mix (exception: pots 32-2, 33-2, 37-1 had 1 part potting soil to 1.5 parts VSP). In addition to the fluorescent lighting described above, the plants are adjacent to a north-facing window, providing "access" to a very indirect form of sunlight.

Fluorescent lighting was disconnected on 1 May, partially in an attempt to counter the signs of drought stress exhibited by several plants by reducing heat at the tray level. Most plants exhibited increased growth, suggesting that the indirect window lighting available at that time was sufficient for growth.

- D. A controlled temperature regime could not be maintained in the available facilities. Daytime temperature as measured at tray level ranged between 20 and 27 (32 in summer)°C, while night temperatures ranged roughly between 10 and 16 (18-20+ in summer)°C.
 - E. Insect damage was a continual threat to all of the plants. A minimal number of chemical control methods were used in an attempt to reduce any adverse effects on cellular chemistry of the plants. The following measures were used during the study: Spraying affected foliage with Safir's Insecticidal Soap and insertion of Bag-A-Bug Insecticide Sticks.
3. Growth condition modifications - year 2:
- A. Plants surviving after the first year and several additional individuals started from seed were kept in the same facilities as described above, but lighting was changed from timed fluorescent lamps to total dependence on natural sunlight from the north-facing window.
 - B. Individual pots were enclosed in plastic bags in an attempt to reduce both water stress from low relative humidity and insect damage (i.e., making foliage less accessible).

APPENDIX D

List of Species of Stellaria

Species names listed below are either accepted in at least one modern flora or are names that I cannot discount as synonyms, etc. Names occasionally used but better treated as synonyms are listed under the appropriate recognized species. Intraspecific taxa are listed only if chromosome information is available. Sources are listed at the end of the Appendix.

All available chromosome counts for Stellaria are summarized below. If all counts are the same for a species, only the most recent report is listed. Sources for all cited chromosome number information are also listed after the species list. Unusual counts are placed in parentheses. Several unpublished counts furnished by Dr. John K. Morton are reported, each marked with an asterisk, one by Dr. Arthur Kruckeberg with a double asterisk.

Total species: 203 Species with known chromosome counts: 50

Source	Species	Chromosome Counts	Source
NSW	1 undescribed species of <u>Stellaria</u>		
- A -			
IK	<u>S. abortiva</u> Gay - Chile		
PH	<u>S. aetensis</u> Lojac. - Sicily		
CH	<u>S. alaschenica</u> Y.Z. Zhao		
NA	<u>S. alaskana</u> Hultén	2n = 46-48	11
RU1	<u>S. alexeenkoana</u> Schischkin		
MED	<u>S. alsine</u> Grimm	n = 12	17
		2n = 24,	5
		26	6
	var. <u>undulata</u> (Thunb.) Ohwi	2n = 46	6
AF1	<u>S. alsinoides</u> Boiss. & Buhse		
RU1	<u>S. ambylosepala</u> Schrenk		
NA	<u>S. americana</u> (Porter ex Robinson) Standley **		
RU1	<u>S. anagalloides</u> C. Meyer in Rupr.		
RU3	<u>S. angarae</u> Popov		
	var. <u>baicalensis</u> Popov	2n = 26	5
CH	<u>S. anhweiensis</u> Migo		
PH	<u>S. antillana</u> Urban - Antilles		
AR2	<u>S. aphanantha</u> Griseb.		
IK5	<u>S. aphananthoidea</u> Muschler - Peru		
CH	<u>S. arenaria</u> Maxim.		
TA	<u>S. arisanensis</u> (Hayata) Hayata	n = 10	11
IK	<u>S. aristata</u> Ser. in DC. - Mexico		

- CL S. arvalis F. Philippi
 JV S. australis Zoll. & Moritz

- B -

- PH S. blatteri Mattf. - Afghanistan
S. borealis Bigelow
 subsp. borealis n = 26*
 (incl. S. calycantha 2n = 52, 6
 var. isophylla (Fern.) Fern., (48) 11
 var. floribunda (Fern.) Fern.,
 var. laurentiana Fern.,
 subsp. interior Hultén)
 subsp. sitchana (Steudel) Piper n = 26
 (incl. S. calycantha 2n = 52*
 var. bongardiana (Fern.) Fern.)
S. borealis X S. longifolia 2n = 39*
 (incl. S. hybrida Doerfler non Rouy & Fouc.)
 CH S. brachypetala Bunge in Ledeb.
 IK S. brauniana Fenzl - Afghanistan
 EU S. bungeana Fenzl

- C -

- S. calycantha (Ledeb.) Bong. n = 13 11
 (incl. S. yesoalpina Nakai?) 2n = 26 5
 (incl. S. simcoeii (Howell) C. Hitchc.)
 CH S. chereriae (Fischer ex Ser.) F. Williams
 var. alpina (Bunge) Schischkin
 var. intermedia (Turcz.) Kozhevnik.
 var. uniflora Fischer
 CL S. chilensis Pedersen
 CH S. chinensis Regel
 MED S. cilicica Boiss. & Bal.
 HM2 S. congestiflora H. Hara
 IK S. cordata Willd. - S. America
 NA S. corei Shinn. 2n = 60 14
 EU S. crassifolia Ehrh. 2n = 26 4
 RU3 S. crassipes Hultén 2n = 72, 11
 104-106 5
 NA S. crispa Cham. & Schldl. n = 13 11
 2n = 26*
 PH S. crispata Benth. ex Don - Himalayas n = 18 4
 AR2 S. cryptopetala Griseb.
 CH S. cuonaensis L.H. Zhou
 EU S. cupaniana (Jordan & Fourr.) Bég. 2n = 22 8
 (incl. S. media subsp. postii Holmboe)
 NA S. cuspidata Willd. n = 26 1
 (incl. S. leptosepala Weberb.;
 S. leptopetala Benth.,
 S. ciliata Vahl ex Pers.)

- D -

RU2	<u>S. dahurica</u> Willd. ex Schldl. var. "pubicalyx" Popov - descr. ross.	2n = 78	5
RU5	<u>S. darvasievii</u> Kamelin		
AR2	<u>S. debilis</u> Urv. (incl. <u>S. axillaris</u> Philippi, <u>S. chubutensis</u> Speg., <u>S. debilis</u> var. <u>condensata</u> Gray, <u>S. stenopetala</u> Philippi, <u>S. xanthospora</u> Chodat & Wilczek)		
NZ	<u>S. decipiens</u> J.D. Hook. - New Zealand	2n = 90	2
CH	<u>S. decumbens</u> Edgew.		
CH	<u>S. delavayi</u> Franchet		
IK	<u>S. depauperata</u> Edgew. - Himalayas		
AS	<u>S. depressa</u> Schmid		
PH	<u>S. diandra</u> Maxim. - Japan		
CH	<u>S. dianthifolia</u> F. Williams		
PH	<u>S. dichasioides</u> F. Williams - China		
CH	<u>S. dichotoma</u> L.		
NA	<u>S. dicranoides</u> (Cham. & Schldl.) Fenzl in Ledeb.	2n = 26	11
CH	<u>S. discolor</u> Turcz.		
JP2	<u>S. diversiflora</u> Maxim. (incl. <u>S. diandra</u> Maxim.)	2n = 44	6
AS	<u>S. divnogorskajae</u> Kozhevn.		
PH	<u>S. drymarioides</u> Thwaites - Ceylon		
QU	<u>S. dulcis</u> Gervais		

- E -

RU1	<u>S. ebracteata</u> V. Komarov		
NA	<u>S. edwardsii</u> R. Br. (incl. <u>S. ciliatosepala</u> Trautv., <u>S. arctica</u> Schischkin)	2n = 36, ca 52, 72, 78, 80+, 90+, 91, 100, 100+, 104	2 17 5 6 4 2 13 4 4
NZ	<u>S. elatinoides</u> J.D. Hook.		
PH	<u>S. emirnensis</u> Danguy - Madagascar		
PH	<u>S. erlangeriana</u> Engl. - France?		
RU1	<u>S. eschscholtziana</u> Fenzl in Ledeb.		

- F -

EU	<u>S. fennica</u> (Murb.) Perf.		
JP3	<u>S. fenzlii</u> Regel (incl. <u>S. sachalinensis</u> Takeda)	2n = ca 40	2
CH	<u>S. filicaulis</u> Makino (incl. <u>S. jaluana</u> Nakai)		

RU3	<u>S. filipes</u> Popov		
PH	<u>S. fischeri</u> Pax - West Africa		
RU1	<u>S. fischeriana</u> Ser. in DC.	2n - 26,	5
		72	11
RU3	<u>S. florida</u> Fischer		
PH	<u>S. flaccida</u> Hook. - Australia		
RU1	<u>S. fontana</u> Popov		
NA	<u>S. fontinalis</u> (Short & Peter) Robinson	2n - 26*	

- G -

IK	<u>S. glandulifera</u> Klotzsch - India		
RU6	<u>S. glandulifera</u> Zolutchin, non Klotzsch - Russia		
NZ	<u>S. gracilenta</u> J.D. Hook.		
EU	<u>S. graminea</u> L.	n - 13,	18
		26	15
		2n - 26, 39	3
		52,	3
		(104)	10
	var. <u>brevifolia</u> Walther	2n - 26?, 52?	3
	var. <u>latifolia</u> Godron	2n - 26, 52	3
	var. <u>macropetala</u> Wiesb.	2n - 26, 52	3
PH	<u>S. gyangtsensis</u> F. Williams		
AS	<u>S. gypsophiloides</u> Fenzl		

- H -

EU	<u>S. hebecalyx</u> Fenzl in Rupr.		
	(incl. <u>S. ponojensis</u> Arrh.)		
CH	<u>S. henryi</u> F. Williams		
EU	<u>S. holostea</u> L.	2n - 26	5
DR	<u>S. howardii</u> Maguire		
IK11	<u>S. hsinganensis</u> Kitagawa - China		
EU	<u>S. humifusa</u> Rottb.	n - 13	13
		2n - ca 24,	17
		26,	5
		ca 91	11

- I -

RU1	<u>S. imbricata</u> Bunge
CH	<u>S. infracta</u> Maxim.
RU3	<u>S. inundata</u> Vorosch.
CR	<u>S. irazuensis</u> J.D. Smith
NA	<u>S. irrigua</u> Bunge

- J -

RU3	<u>S. jacutica</u> Schischkin	2n - 26	12
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- L -

- M -

PH	<u>S. madagascarensis</u> Bég. - Madagascar		
IK	<u>S. manniif</u> J.D. Hook. - Tropical Africa		
RU1	<u>S. martjanovii</u> Krylov		
AS	<u>S. maximowiczii</u> Kozhevnik.		
MED	<u>S. media</u> (L.) Villars	n - 20,	15
	(incl. <u>S. apetala</u> Ucria,	22	5
	<u>S. octandra</u> Pobed.,	2n - (28),	2
	<u>S. wallichiana</u> (Benth.) Haines,	(38-)40	7
	<u>S. xanthanthera</u> Pobed.)	40,	6
		42,44	5
AS	<u>S. merzbacheri</u> Kozhevnik.		
VE	<u>S. micrantha</u> Spruce ex. Rohrb.		
NZ	<u>S. minuta</u> Kirk		
DR	<u>S. minutifolia</u> Maguire		
IK	<u>S. modesta</u> Fenzl - Malaya		

NA	<i>S. monantha</i> Hultén	2n = ca 26, 17 ca 38, 17 52, 5 104 6
CH	<i>S. monosperma</i> Buch.-Ham. ex D. Don. var. <i>japonica</i> Maxim. (incl. <i>S. paniculigera</i> Makino)	n = 26 4 2n = 44 6
AS	<i>S. monosperma</i> (F. Williams) Kozhevnik. - non Buch.-Ham. ex D. Don.	
MED	<i>S. montana</i> Pierrat (incl. <i>S. glochidosperma</i> (Murb.) Freyn)	2n = 26 11
PH	<i>S. montana</i> Rose non Pierrat- Mexico	
IK15	<i>S. mukerjeeana</i> Majumdar - Nepal	
PH	<i>S. multiflora</i> Hook. - Australia	
NA	<i>S. muscorum</i> Fassett	

- N -

MED	<i>S. neglecta</i> Weihe in Bluff & Fingerh.	n = 11 16 2n = 22, 44 6
MED	<i>S. nemorum</i> L. (incl. <i>S. neogaea</i> Bég.)	n = 13 18 2n = 26 5
IK11	<i>S. neo-palustris</i> Kitagawa - Manchuria, Korea	
CH	<i>S. nepalensis</i> Majumdar & Vartak (incl. <i>S. neotomentosa</i> Mizush. ex H. Ohba)	
JP3	<i>S. nipponica</i> Ohwi (incl. <i>S. pterosperma</i> Ohwi?)	2n = 26 6
NA	<i>S. nitens</i> Nutt. (incl. <i>S. praecox</i> Nels.)	2n = 40*
CRI	<i>S. nubigena</i> Standley	
PH	<i>S. nutans</i> F. Williams - China	

- O -

NA	<i>S. obtusa</i> Engelm.	2n = 26*, 52*, 65*, ca 78 11
IK	<i>S. oligosperma</i> Rohrb. - Chile	
CH	<i>S. omeiensis</i> C.Y. Wu & Y.W. Tsui	
CR	<i>S. ovata</i> Willd.	
HM1	<i>S. ovatifolia</i> (Mizush.) Mizush.	
PH	<i>S. oxycoccoides</i> Komarov - China	

- P -

MED	<i>S. pallida</i> (Dumort.) Piré	n = 11 16 2n = 22, 4 (40) 5
EU	<i>S. palustris</i> Retz. (incl. <i>S. barthiana</i> Schur, <i>S. dilleniana</i> Moench, <i>S. glauca</i> With.)	2n = ca 100, 9 ca 130, 9 174-188 11
PH	<i>S. paniculata</i> Edgew. - Himalayas	

AR2	<u>S. parva</u> Pedersen		
NZ	<u>S. parviflora</u> Banks & Sol. ex J.D. Hook. (incl. <u>S. oligosperma</u> Colenso, <u>S. pellucida</u> Colenso)		
HM1	<u>S. patens</u> Don.	n = 13 2n = 26	4 4
IK11	<u>S. patentifolia</u> Kitagawa - China		
JV	<u>S. pauciflora</u> Zoll. & Moritzi		
RU2	<u>S. peduncularis</u> Bunge (in <u>longipes</u> ?) (incl. <u>S. "pseudopeduncularis"</u> Popov-descr.ros)	2n = 72, 78	4 13
AF2	<u>S. perfoliata</u> K.H. Rech.		
MED	<u>S. persica</u> Boiss.		
IK11	<u>S. petiolaris</u> Hand.-Mazz. - China(?)		
RU1	<u>S. petraea</u> Bunge in Ledeb.		
CH	<u>S. pilosa</u> Franchet		
AF1	<u>S. platyphyllum</u> K.H. Rech.		
NA	<u>S. prostrata</u> Baldwin	2n = 26*	
CH	<u>S. pseudosaxatilis</u> Hand.-Mazz.		
NA	<u>S. pubera</u> Michaux	n = 15 2n = 30	14 14
MON	<u>S. pulvinata</u> Grubov		
PH	<u>S. pungens</u> Brongn. - Australia		
PH	<u>S. pusilla</u> Schmid - Tibet		

- R -

CH	<u>S. radians</u> L.	2n = 24	11
IK	<u>S. recurvata</u> Willd. - S America		
CH	<u>S. reticulivena</u> Hayata		
PH	<u>S. rotundifolia</u> Poirer - Chile		
NZ	<u>S. roughii</u> J.D. Hook.		
IK11	<u>S. rugugensis</u> Engl. - Africa		
NA	<u>S. ruscifolia</u> Pallas ex Schldl.	2n = 26, ca 50	2 2

- S -

CH	<u>S. salicifolia</u> Y.W. Tsui & P. Ke		
AF1	<u>S. sarcophylla</u> K.H. Rech.		
FZ	<u>S. saxifraga</u> Fenzl - location ?		
IR	<u>S. scaturiginella</u> K.H. Rech.		
RU4	<u>S. schischkinii</u> Peschk. (incl. <u>S. palibinii</u> Schischkin, <u>S. angarae</u> var. <u>baicalensis</u> p.p)		
PH	<u>S. schimperii</u> Engl. - Abyssinia		
RU1	<u>S. schugnanica</u> Schischkin		
IK	<u>S. semivestita</u> Edgew. - India		
IK10	<u>S. sennii</u> Chiov. - Abyssinia	2n = ca 52	4
PE	<u>S. serpyllifolia</u> Willd.		
JP2	<u>S. sessiliflora</u> Yabe (incl. <u>S. japonica</u> Makino)	2n = 56	6
RU1	<u>S. sibirica</u> (Regel & Tiling) Schischkin		
HM1	<u>S. sikkimensis</u> J.D. Hook.		

- CH S. soongorica Rosch.
 CH S. souliei F. Williams
 CH S. subumbellata Edgew. in J.D. Hook.

- T -

- CH S. tibetica Kurz
 JP1 S. tomentella Ohwi
 (incl. S. iinumae Ohwi,
 S. tomentosa Maxim.)
 PH S. triangularis Sessé & Mocino - Mexico
 PH S. trimorpha Nakai - Korea
 RU1 S. turkestanica Schischkin

- U -

- JP3 S. uchiyamana Makino 2n = 26 6
 CH S. uda F. Williams
 NA S. umbellata Turcz. ex Karelin & Kir. 2n = 26 5
 (incl. S. gonomischa J. Boivin,
 S. weberi J. Boivin)

- V -

- VE S. venezuelana Steyerm.
 CH S. vestita Kurz n = 12,13, 4
 (incl. S. laxa Merr., 14 4
 S. saxatilis Kurz 2n = 26 4
 S. stellato-pilosa Hayata)
 AS S. viridescens (Maxim.) Kozhev.
 IK7 S. viridiflora Pax & K. Hoffm. - China

- W -

- IK S. wagneriana Rohrb. - Ecuador
 CL S. weddellii Pedersen
 RU1 S. winkleri (Briq.) Schischkin
 CH S. wushanensis F. Williams
 CH S. wutaica Hand.-Mazz.

- Y -

- CH S. yunnanensis Franchet

- Z -

- CH S. zangnanensis L.H. Zhou

** - R. L. Hartman (pers. comm.) noted that further study of Stellaria americana may reveal it to be a species of Pseudostellaria.

Sources for chromosome counts:

- | | |
|----------------------------------|----------------------------------|
| 1 - Cave, 1962. | 12 - Moore, 1974. |
| 2 - Federov, 1969. | 13 - Moore, 1977. |
| 3 - Gadella, 1977. | 14 - Morton, 1984a. |
| 4 - Goldblatt, 1981. | 15 - Mulligan, 1984. |
| 5 - Goldblatt, 1984. | 16 - Ornduff, 1967. |
| 6 - Goldblatt, 1985. | 17 - Ornduff, 1968. |
| 7 - Halkka, 1985. | 18 - Rohweder, 1939. |
| 8 - Jalas & Suominen, 1983. | 19 - Zhukova, 1977. |
| 9 - Löve & Löve, 1975. | * - unpublished: Dr. J.K. Morton |
| 10 - Lovkvist in Weimarck, 1963. | |
| 11 - Moore, 1973. | |

Sources for usage of species:

- AF1 - Afghanistan - Kitamura, 1960.
 AF2 - Afghanistan - Rechinger, 1981.
 AR1 - Argentina - Martinez-Crovetto, 1967.
 AR2 - Argentina - Volponi, 1983.
 AS - Central Asia - Kozhevnikov, 1983.
 CH - China - Ke, 1985.
 CL - Chile - Pedersen, 1983.
 CR - Costa Rica - Baker & Burger, 1983.
 DR - Dominican Republic - Maguire, 1958.
 EU - Europe - Jalas & Suominen, 1983.
 FZ - Fenzl in Endlicher, 1840.
 HM1 - Himalayas - Mizushima in Hara, 1966.
 HM2 - Himalayas - Hara, 1977.
 IK - Index Kewensis, volume 2: Jackson, 1895.
 IK# - Index Kewensis, supplement #
 5: Prain, 1921. 11: Salisbury, 1953.
 10: Hill & Salisbury, 1947. 15: Heslop-Harrison, 1974.
 IR - Iran - Rechinger, 1985.
 JP1 - Japan - Ohwi, 1965.
 JP2 - Japan - Mizushima, 1965a.
 JP3 - Japan - Mizushima, 1965b.
 JV - Java - Backer & van der Britt, 1963.
 MED - Mediterranean region - Greuter et al., 1984.
 MON - Mongolia - Grubov, 1972.
 NA - North America - Rice et al., 1982.
 NSW - New South Wales - Cunningham et al., 1981.
 NZ - New Zealand - Allan, 1961.
 PE - Peru - MacBride, 1936.
 PH - World - Pax & Hoffman treatment, 1934.
 QU - Quebec - Gervais, 1982.
 RU1 - Russia - Schischkin in Komarov & Shishkin, 1936.
 RU2 - Russia - Popov, 1957.
 RU3 - Russia - Czerepanov, 1973.
 RU4 - Russia - Peschkova, 1975.
 RU5 - Russia - Kamelin, 1976.
 RU6 - Russia - Zolotuchin, 1984.
 TA - Taiwan - Liu & Ying, 1976.
 VE - Venezuela - Steyermark, 1951.