

AN ABSTRACT OF THE THESIS OF

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Title: Ecology and reproduction in *Collomia macrocalyx* Brand  
(Polemoniaceae)

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Abstract approved:

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Populations of *Collomia macrocalyx* Brand were located and observed in order to determine the distribution, ecology, and reproductive biology of this species and probable relationships to other members of the genus. The purpose of the study was to obtain information that would explain the restricted range of the species and would guide in making recommendations for management and conservation.

*Collomia macrocalyx* is endemic to eastern Oregon "scablands." Until recently it was known from only a few widely disjunct sites, and it had been proposed as an "endangered species." A total of 13 extant populations have now been identified. These are all in sites that are fairly uniform in climate, soils, and associated vegetation. The usual habitat for the species is in deep rock crevices on south-facing slopes or ridgetops.

*Collomia macrocalyx* is morphologically the most advanced and biochemically the most distinct species within the genus. It is an annual with a chromosome number of  $n=8$ . Vegetatively *C. macrocalyx* most closely resembles *C. tinctoria*, while its

floral morphology is more like that of C. linearis. Plants grown under greenhouse conditions have vegetative parts which are larger than those of native populations, and they differ in the frequent occurrence of toothed leaves. A new species of Collomia, discovered during the course of this study, appears to be related to both C. macrocalyx and C. tinctoria.

The seeds of C. macrocalyx require a two to three month dormancy but germinate readily in nature after autumn rains begin. The plants remain vegetative through the winter months. Many individuals die at the onset of renewed growth in the early spring. Larger individuals are encountered more frequently in deep rocky areas than in open soil. These sites may be cooler and moister, and may offer less competition from other species. Flowering begins in mid-April; the flowers are autogamous, and seed-set is rapid. Most individuals die at the onset of summer drought.

Although no pollinators were observed, the presence of some exerted stigmas would allow for occasional out-crossing. Seeds are actively ejected from their capsules upon maturation, the dispersal distance being usually less than 10 cm. Most seeds fall into crevices among rocks where they are unavailable for long-distance dispersal. Mucilaginous seed-coats may assist in their dispersal to a new site. Predation and disease have a minimal effect on survival and reproduction.

The restricted range of C. macrocalyx is explained by its low dispersal rate away from the parental sites, and its

inability to establish itself in habitats where it must compete with other plant species. Though some populations are threatened by human activities, several sites are well protected and the species does not warrant listing as "endangered." Collomia macrocalyx should, however, be monitored to guard against the threats which do exist at some sites.

Ecology and reproduction in Collomia macrocalyx Brand  
(Polemoniaceae)

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Ecology and reproduction in Collomia macrocalyx Brand  
(Polemoniaceae)

INTRODUCTION

Collomia macrocalyx Leiberg ex Brand is a diminutive annual member of the Polemoniaceae. It is endemic to eastern Oregon where it inhabits the "scablands" scattered across the high desert country. Until recently C. macrocalyx had been collected at only a half-dozen widely disjunct sites, and little was known of its biology or the details of its geographical and ecological distribution. The rarity of this species resulted in its being proposed as "endangered" or "sensitive" on federal and state lists of threatened and endangered species.

This study was undertaken to locate and observe populations of C. macrocalyx in order to learn more of its distribution, ecology, reproductive biology and probable relation to other members of the genus. With this information it might be possible to offer explanations for the restricted range of the species and make recommendations for its future management.

The phenology of C. macrocalyx was studied in plants growing both in the wild and under greenhouse conditions. Observations were made of germination, seedling establishment, vegetative and floral development, pollination, seed set and seed dispersal. Predators and diseases were noted as they were encountered. Known sites of former occurrence were visited and additional sites were

searched for. The plant communities and physical characteristics of the different sites were compared in order to understand some of the ecological aspects of the species and to aid in the search for additional populations.

## TAXONOMIC RELATIONSHIPS

The Polemoniaceae are a relatively small angiosperm family composed of approximately 18 genera and 316 species. They are best developed in the western United States, and all but two genera are native to this country (Grant, 1959).

The first recognition of the family as a distinct taxon came in the late eighteenth century. Shortly thereafter, in 1805, de Candolle provided the group with its present status as a "family" and the proper name Polemoniaceae. In some modern phylogenetic systems the Polemoniaceae are placed between the Convolvulaceae and the Hydrophyllaceae, in the order Polemoniales. The derivation of the family from possible ancestral groups has been subject to much debate. In the most recent monograph of the family, Grant (1959) discounts putative origins in the Caryophyllales, Primulales or Geraniales (Dawson, 1936). He hypothesizes,

an evolution of woody plants in a tropical setting from a Ranalian ancestor through successive stages of floral and vegetative development marked by the characters of the present Theales and Ebenales (or Ericales) to the common beginnings of the Contortae and Tubiflorae.

Herbaceous forms would have developed independently within the various Tubiflorae families at a later time. Cronquist (1981), on the other hand, places the Polemoniaceae closest to the Hydrophyllaceae and near the Convolvulaceae in the Solanales (the older and therefore correct name for the Polemoniales). Noting its anatomical similarity to the Gentianales, he adds that this is indicative of the close linkage among the families of Asteridae.

Whatever its origins and phylogenetic placement may be, the family is generally regarded by taxonomists as being a natural and well-defined taxon. The pentamerous flowers are mostly regular, sympetalous, hypogynous and perfect, with five epipetalous stamens alternating with the corolla lobes and often inserted unequally within the corolla tube. The pistil is tricarpellate with axile placentation. The fruit is a loculicidal capsule with three to many seeds. Most species are herbs or low shrubs. The family is differentiated from other members of the order by its gamosepalous calyx, typically tricarpellate ovary, usually numerous ovules and seeds, and the absence of milky latex (Lawrence, 1951).

Many taxonomic problems exist when one tries to define distinct groups below the family level. Several efforts have been made to delimit tribes and subfamilies within the family, and generic circumscriptions have likewise been subject to differing interpretations (Mason, 1945; Grant, 1959). A fair proportion of the polemoniaceous species have been transferred from one genus to another as generic limits are studied and redefined. The problem as stated by Dawson (1936) is that,

the entire group is so closely interrelated that absolute characters, which could serve as a basis to separate genera and species taxonomically, are lacking.

Early workers based their taxa on morphological traits observable on dried herbarium specimens. In this family ecological and genetic characteristics are as essential as morphological traits for determining taxa. Modern taxonomic

methods have greatly improved our understanding of tribal, generic and species relations, however.

Grant (1959) recognized that the tropical genera share a number of common characteristics, and he placed them in three related tribes, Cobaeae, Cantueae, and Bonplandieae. He identified two main lines of evolution within the temperate, herbaceous Polmoniaceae, which he separated as the tribes Polemonieae (including Collomia) and Gilieae.

The Polemonieae are predominately perennial herbs with leaves of simple or no dissection; the calyx is usually herbaceous; the corolla is regular; and the point of insertion of the stamens, if uneven at all, is usually very strongly so. (Grant, 1959).

The center of distribution of the tribe is in cool temperate North America.

The tropical genera are fairly distinct, as are Polemonium and Phlox; however, Gilia and the remaining genera have not been so easily dealt with. At one time or another taxonomists have used Gilia as a repository for almost all of the temperate species outside of Polemonium and Phlox. In the last several decades the favored approach has been to separate several genera from Gilia so that the resulting genus, though still large and heterogenous, is less variable and hence more manageable. Collomia was one of the genera excluded from Gilia by Greene (1887) after its inclusion by Gray (1882).

The genus Collomia, currently consisting of three sections and 14 species, was erected by Nuttall in 1818 based on the type species C. linearis. Two of the species

are found in temperate South America; the remainder are native to the western United States, though the weedy C. linearis is naturalized in eastern North America, Russia and Australia, and C. grandiflora is established in central Europe (Grant, 1959).

The generic name is taken from the Greek "kolla", meaning glue, in reference to the mucilaginous seed coat common in the genus. The species are annual or perennial herbs; the leaves are alternate, mostly simple and entire, sometimes lobed or dissected; the calyx is herbaceous with carinate sinuses, enlarging with the fruit and not rupturing with age; the corolla is funnelform to salverform; the stamens may be inserted regularly or irregularly and may be equal or unequal in length; the carpels each produce one seed, or occasionally two; the seeds are large, dark, lenticular and usually mucilaginous when wet; and the chromosome number is uniformly  $x=8$  (Grant, 1959).

For several decades after Nuttall's publication Collomia was accepted by other taxonomists as a distinct genus (Bentham & Hooker, 1876). Gray (1870) originally considered unequal stamens, mucilaginous seed coats and solitary ovules to be important generic characters for Collomia. He identified 11 species which fitted his early concept of the genus, half of which have since been transferred to other genera. As Gray continued his studies of the group and attempted to place more species within it, its generic boundaries grew hazier. Unable to deal with the

problem of ambiguous traits in any other manner, Gray finally "remanded" the entire genus to Gilia and then placed the questionable species in his section Collomia of Gilia (1882,1886).

Greene (1887) emphasized that the calyx, especially as it developed in fruit, possessed important characters which could be used successfully to segregate Collomia from Gilia. This use of calyx characters has been followed by most students of the family ever since (Brand, 1907; Cronquist, 1959; Grant, 1959; Munz, 1959; Milliken, 1904; Payson, 1924; Wherry, 1944).

Brand (1907) segregated nine species of Collomia into two sections on the basis of whether their seed coats contain mucilage (sect.I: Eucollomia) or do not (sect.II: Collomiastrum). When he later described C. macrocalyx (1921) he failed to note its mucilaginous seed coat and thus erroneously placed it near C. debilis in sect. Collomiastrum. Equal or unequal insertion of the stamens was the second important key character used by Brand to separate species within both sections. Nelson and MacBride (1916) did not agree entirely with Brand's maintenance of Collomia separate from Gilia, and they transferred two Collomia species to Gilia.

Payson (1924) studied C. debilis and its related species when describing a few new varieties. While acknowledging that prior authors had had difficulties with the genus, Payson noted that the group was fairly large, homogenous, and

possessed distinctive calyx characters, so much so that it "it seemed to him more readily distinguished from Gilia than is Phlox itself." Payson therefore concurred with Brand and Peter (1891) in retaining generic rank for Collomia.

Jepson (1943) thought that Collomia "seems in some respects artificial," but he recognized the genus in his flora largely on the basis of recent cytological evidence which supported this division from related genera.

There are many examples of minor genera paired to major genera in the Polemoniaceae. This relationship holds for the pairing of Gymnosteris Greene with Collomia. Wherry (1944) reviewed these two genera together, noting that Gymnosteris had originally been described as a species of Collomia and had subsequently been referred to Gilia, Navarettia, and Linanthus. Greene gave Gymnosteris independent status at the turn of the century (1898), 58 years after its type species was first described. Wherry placed Gymnosteris near Collomia. He believed that though Gymnosteris may not have arisen directly from any extant species of Collomia, the two genera are close and may well share a common ancestor.

Wherry recognized 13 species of Collomia and divided them among three sections. His section Collomiastrum contained the four perennial species that lack mucilaginous seed coats, whereas Brand had based the section on seed coat characters alone, without reference to the perennial habit of the species. Wherry created the section Courtoisia, separating it from Brand's section Eurollomia on the basis of

leaf shape and ovule number. Sect. Courtoisia contains two species, which have lobed or dissected leaves and pluriovulate locules, as opposed to the seven species of sect. Eurollomia's with their simple, linear to lanceolate leaves and predominately uniovulate locules. Wherry rejected Brand's placement of C. macrocalyx near C. debilis and placed it close to C. tinctoria, in sect. Eurollomia.

Grant, in his monograph of the Polemoniaceae (1959), followed Wherry in his treatment of Collomia, adding one additional species (C. trayi) to his sect. Eurollomia. He included data on chromosome numbers that further reinforced the segregation of Gymnosteris (x=6) from Collomia (x=8), and of Collomia from Gilia (x=9).

Taylor and Levin (1975) studied the pollen from each genus and section of Polemoniaceae using scanning electron microscopy. Pollen size, ornamentation, aperture number and type were compared. Four basic pollen types were recognized for the family. Pollen data support some previously proposed intergeneric relationships but suggest other possible interpretations for a few genera. The pollen of Collomia is small (30-60 $\mu$ ), zonocolporate, striato-reticulate, and contains few apertures (7-15). Collomia is in these respects more closely allied with the Gilieae and perhaps should be removed from Grant's placement near Phlox and Gymnosteris in the Polemonieae. On the basis of pollen morphology combined with chromosome number, Collomia (x=8) was thought by the authors to be intermediate in the family (x=9 was taken to be

primitive, with lower numbers derived by descending aneuploidy), a view which is consistent with Grant's proposed phylogeny.

Collomia macrocalyx was first described by Brand (1921) from collections made by John B. Leiberg in eastern Oregon. The lectotype (see Mason , 1951) is from "near Lonerock in Gilliam County, May 25, 1894." Additional collections were made by Leiberg northwest of Lonerock, "near the forks of Cottonwood Canyon," and from "12 miles south of Fossil, Wheeler County," in the same year. Forty-nine years elapsed before C. macrocalyx was recollected, this time by Morton Peck. He found it growing 24 km north of McDermitt in Malheur County, 270 km southeast of the original collections. Ripley and Barneby recollected C. macrocalyx from the same area in 1948. In 1955, C. Leo Hitchcock made two collections in the Lonerock area. Beery located yet another widely disjunct population in the 1960's east of Sparta in Baker County; no voucher specimen was collected and the population was destroyed by road construction in 1967. Since the mid-1970's the Lonerock and McDermitt sites have been verified, and new populations have been discovered in Crook, Jefferson, Wasco and Wheeler counties (see site descriptions, Table 4).

The specific epithet "macrocalyx", translated as "large calyx," aptly depicts the distinctive calyx in the species, which becomes prominent as the fruit matures (Figure 1). Collomia macrocalyx is annual, 2-5 (10) cm tall, branching

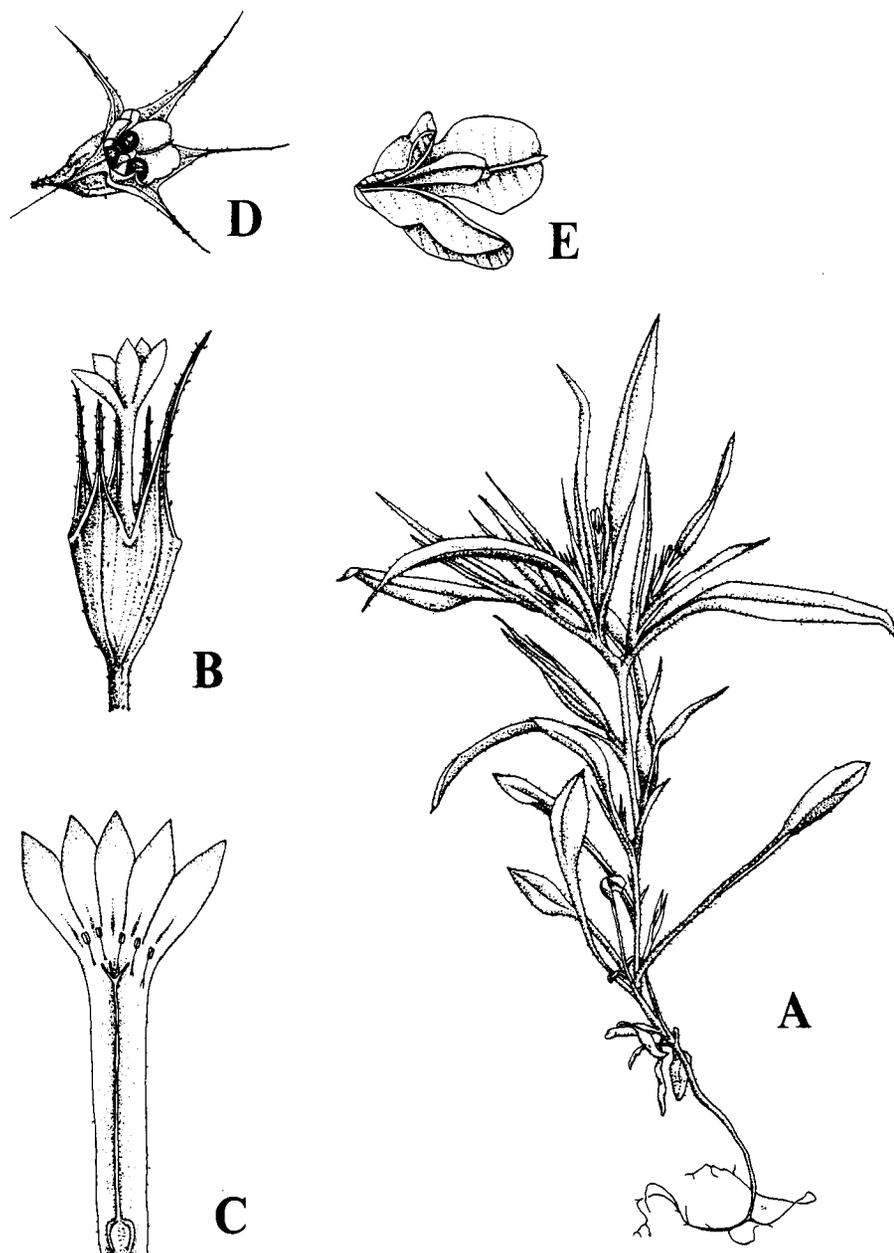


Figure 1. *Collomia macrocalyx* Brand ex Leiberg. A) habit (X 1); B) flower and calyx (X 5); C) flower (X 10); D) capsule (X 3); E) placenta (X 6). Joyal 303; North of Lonerock, Gilliam Co., Oregon.

when well developed; the main stem and branches terminate in dense leafy-bracteate flower clusters; the leaves are entire and few, the lower petiolate and spatulate; the bracts subtending the flowers are linear, 1-3 cm long, 1-2 mm wide, tapering to a slender point; the calyx teeth are narrow, firm, aristate-attenuate, unequal, the longer ones 5-11 cm long in fruit; the corolla is blue, white in the throat, about 1 cm long, the lobes 2-2.5 mm long; the filaments are less than 1 mm long, somewhat unequally inserted a little below the sinuses; and the locules each produce a single seed (description after Cronquist, 1959).

Infrequently collected and a fairly distinct taxon, with no close relatives, C. macrocalyx has not posed much of a taxonomic problem in the 90 years since Leiberg first discovered it. All monographers and floristic compilers have been working from the same few herbarium specimens. They have not examined C. macrocalyx in detail, and it is thus a poorly known species. Brand (1921) placed it near the perennial C. debilis, stating erroneously that it lacked a mucilaginous seed coat ("sub aqua immutata"). Perhaps he had only immature seeds for study and interpreted them incorrectly. Payson (1924) was not aware of the existence of C. macrocalyx when he studied the C. debilis group. Wherry (1944) cited C. macrocalyx as a "rare, endemic species" and correctly removed it from near C. debilis in sect. Collomiastrum of Brand, placing it close to C. tinctoria in his sect. Eurollomia. In his treatment of the Polemoniaceae for the Flora of Idaho,

however, Wherry (1952) inaccurately stated that the corolla color was "yellow suffused with purple." He gave the habitat and range of the species as "open, rocky slopes; in central and eastern Oregon, possibly ranging into Idaho."

Morton Peck was one of the few people who wrote about C. macrocalyx himself having observed and collected it in the field. In the first edition (1941) of his Manual of the Higher Plants of Oregon, Peck erroneously cited Eastwood as the author of the species, but he corrected himself in the second edition (1961). Peck (1941) stated that the species was little known and said nothing of its habitat, giving the range as "Malheur Co." In 1961, he modified the range to "dry hills, Gilliam and southern Malheur Cos." It is curious that Peck did not mention Leiberg's original localities in his earlier work. A 1943 collection from southern Malheur County is the only specimen of C. macrocalyx in Peck's own herbarium (WILLU). One wonders if Peck was more familiar with the species than this one collection indicates. The Malheur County population, "15 miles north of McDermitt," was recollected in 1948, and then not again until 1982.

Arthur Cronquist treated the Polemoniaceae in the Vascular Plants of the Pacific Northwest (Hitchcock et al., 1959). His species description is not appreciably different from those published previously. Cronquist mentioned specifically that the plants are "branched when well-developed," which accurately describes the phenotypic response of the species to optimum growing conditions. In

field populations, one observes that the plants range from tiny, one-flowered individuals early in the spring to robust, well-branched plants with up to 50 flowers on better sites late in the season. The corolla color is also reported more accurately by Cronquist than by Peck and Wherry. Hitchcock had recollected C. macrocalyx near the type locality in 1955 and it is likely that he supplied Cronquist with information about live plants that he had observed. Cronquist gives the habitat and range as, "dry, open places at low elevations; local in Gilliam Co., May-June." Meinke reviewed the species for the Threatened and Endangered Vascular Plants of Oregon (1982). As he had been in communication with the author, he included the most recent geographical information; he used Cronquist's species description and did not attempt a lengthy evaluation of the species.

It becomes evident from a survey of the literature that monographers and floristic compilers have studied and restudied the same half-dozen herbarium collections and have developed little new information about the species. Field studies are essential for a good understanding of the biology of any species, and especially a polemoniaceous one. In the remaining sections, C. macrocalyx will be examined in greater detail. The land it inhabits; its manner of growth and development; how it survives in a harsh environment; how it might have come to occupy its particular habitat and range; and whether it is only marginally successful or rather a

well-established but small, obscure and overlooked species are topics that will be addressed.

## GEOGRAPHY OF THE AREA STUDIED

Geology and geomorphology

Volcanism dominates the geologic history of Oregon. This is due to the region's position on the continent's western edge along an active subduction zone. The state was covered by open sea in the Paleozoic and well into the Mesozoic (Baldwin, 1968). Beginning in the Jurassic, the Nevadan orogenic belt developed as a broad arc of mountains, open to the Pacific Ocean to the west. The center of the arc gradually filled with sediments and became uplifted in the early Cenozoic (Detling, 1968). Through most of the Tertiary the Cascade Range slowly grew to its current height. Extensive Miocene lava flows blanketed much of the land to the east of the Cascades with thick basalts, capping the sediments laid down in prior eras. By the Pliocene, the Cascades became elevated enough to intercept much of the moisture borne on the prevailing westerly winds. The interior regions became drier, and marked extremes in temperatures developed. Though the continental ice sheets of the Pleistocene did not reach Oregon, the higher mountains were subject to extensive glaciation. The glaciers receded in the Holocene. About 6,000 years B.P. the eruption of Mt. Mazama deposited a conspicuous layer of ash in central and southeast Oregon. Many new lava flows also occurred at this time. These events mark the middle Holocene, a period of hot, dry weather known as the Hypsithermal Interval (Baldwin, 1968; Reveal, 1979).

These various major geologic events not only altered the climate significantly but also established distinctive patterns of plant migration. The north-south trending mountains have contrasting extremes of precipitation and temperature on their opposite slopes. They provide nearly unbroken migration routes, which were very important during the alternating warm-dry and cool-dry climatic cycles. Basalt and ash substrates likewise played a major role in determining what vegetation developed in the region.

Within eastern Oregon, several geographic provinces have been recognized. Those of concern to this thesis are the Columbia River Plateau, the Blue Mountains, and the Basin and Range Provinces.

The Columbia River Plateau of Oregon is bordered on the west by the Cascades, to the north by the Columbia River, and to the south and east by the Ochoco and Blue Mountains. Gentle, rolling hills characterize the province. These average 300-600 m in elevation, being higher at the region's periphery and gradually lowering toward the Columbia River. Where major rivers flow through the plateau they have cut deeply to create steep-sided canyons. The province's single most important geologic event occurred in the Miocene when a "vast outpouring of lavas" covered the region with basalts 600-1500 m thick (Franklin and Dyrness, 1973). Plio-Pleistocene deposits overlie the basalt in some areas. Pleistocene deformation produced the present ridges and hills. It is along the exposed southern rim of the Columbia

River basalts that half of the known populations of C. macrocalyx are located, and nearly all the known sites for the species occur within the province.

The Blue Mountain Province is composed of several ranges, with minimum elevations at approximately 750 m in the western valleys of the Ochoco Mountains up to 2900 m in the Wallowa Mountains to the east. Columbia River basalts occupy large areas in the western half of the province and to the north and south of the Wallowas. Pleistocene glaciation was widespread at higher elevations in the Blues and Wallowas. Volcanic ash was subsequently deposited though erosion has removed this layer from most of the south-facing slopes. The area is geologically complex and contains some of the oldest rocks exposed in Oregon.

The Basin and Range is a vast area extending from the Blue Mountains south into Nevada and Utah. The province is defined by a series of fault-block mountains enclosing basins with internal drainage. These are aligned principally along north-south axes. Elevations begin at 1200 m in the lower basin bottoms and reach 2900 m in the higher ranges. Relief is generally low and rolling except for the steep slopes of fault-block mountains. Most streams are intermittent and numerous shallow lakes which occupy the basin floors are saline due to the scant precipitation. Though small outcrops of Paleozoic and Mesozoic rock formations are present in the Pueblo and Trout Creek Mountains, virtually all rocks in the province date from the Miocene or later and are basalt.

## Climate

Oregon's climate east of the Cascades is continental, and the semi-arid landscape is variously referred to as desert, high desert or steppe. In comparison to the maritime areas to the west, the winters are colder, the summers are hotter, and the frost-free season is much shorter. Diurnal temperature fluctuations are typically 10° to 16°C (U.S.D.A. Weather Bureau, 1930). The Rocky Mountains to the east lessen the severity of the continental air masses, resulting in temperatures that are milder than those of the Great Plains.

Annual precipitation ranges from 180 to 500 mm; 55-75 percent of precipitation falls between October 1 and March 31. Summers are very dry (30-70 mm). What little rain does fall then is usually associated with local thunderstorms which are especially frequent in and around the mountains. Winter precipitation is most often in the form of snow. Precipitation, or the lack thereof, is the key factor determining whether land east of the Cascades is forest or grassland, and the quantity of rainfall is strongly correlated with increasing elevation. Table 1 summarizes climatic data from several weather stations located near C. macrocalyx sites (U.S.D.A. Weather Bureau, 1930); locations of these stations are indicated in figure 2.

## Soils

Though many different soil types are found in the three provinces, sites supporting C. macrocalyx populations are mostly basalt-derived and were formed under grassland or

Table 1. Climatic data for selected weather stations near Collomia macrocalyx sites.

Station Name & Elev. (m)	Precipitation Averages (mm)				Days w/ yield >0.25 mm Precip.	Temperature Averages (°C)				Number Years Data Collected
	Annual	January	July	Snow		January	July	January Minimum	July Minimum	
Antelope 802	282.7	35.1	1.5	492.8	91	-2.1	20.1	-6.8	30.7	7
Condon 878	308.6	34.0	10.2	828.0	71	-2.1	19.4	-6.3	29.3	26
Fossil 823	336.0	40.4	7.1	-	54	-	-	-	-	8
Lonerock 949	366.8	37.1	13.0	886.5	17	-0.2	16.7	-5.8	26.9	17
Ochoco Creek 1158	387.1	50.8	16.5	1051.6	73	-	-	-	-	9
Prineville 878	226.6	23.9	7.9	348.0	51	-0.2	18.7	-6.2	30.4	32
Sparta 1256	532.6	79.5	15.2	3131.8	81	-4.1	19.7	-8.8	29.2	34
McDermitt, NV 1433	288.0	40.1	6.9	977.9	49	-2.8	20.3	-9.7	30.6	10

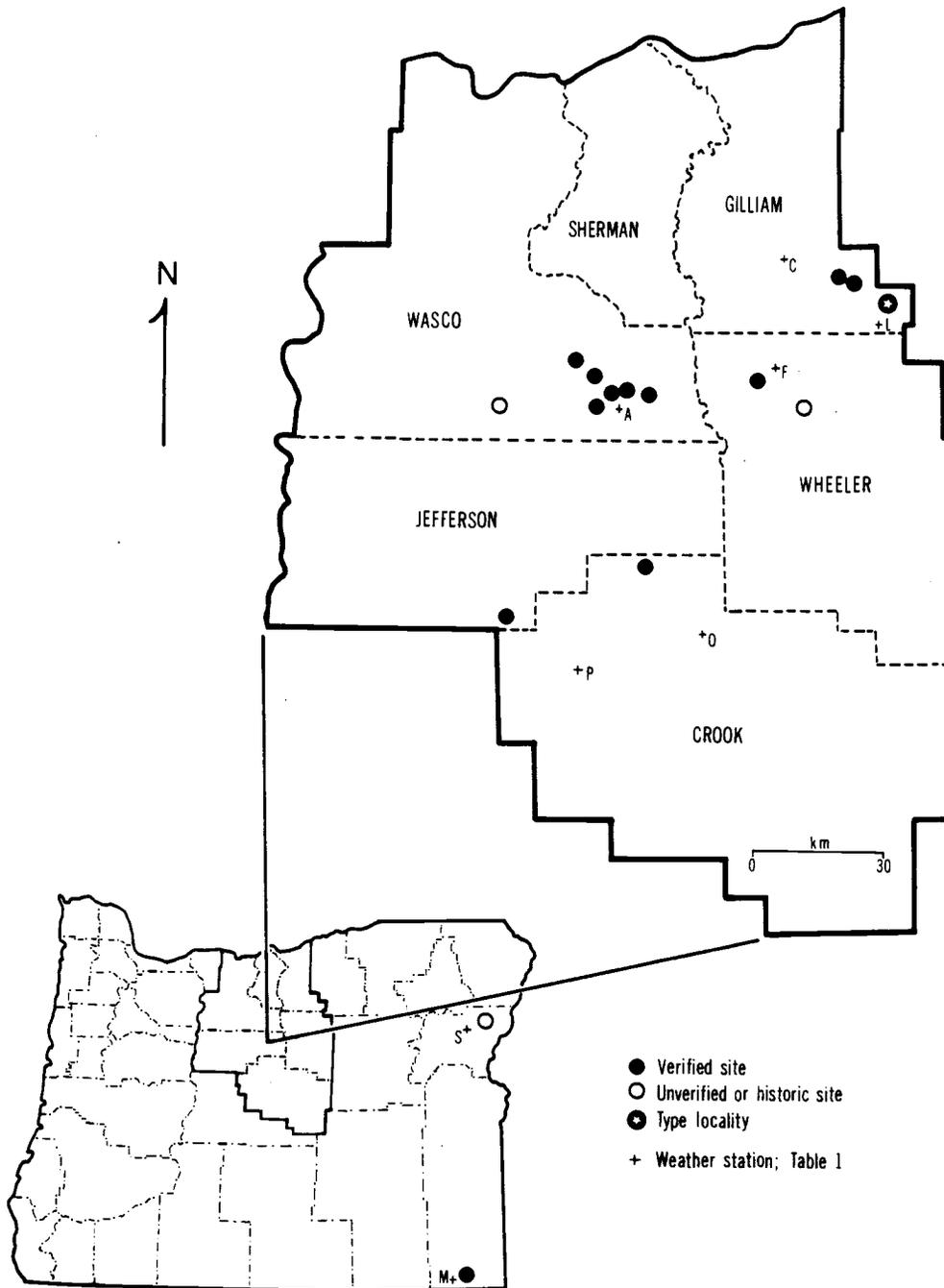


Figure 2. Distribution of Collomia macrocalyx in Oregon.

shrub-grassland vegetation. All are classified as lithosols by Daubenmire (1970). Lithosols are particularly sensitive to summer heat and drought and to intense frost action during the winter (Franklin and Dyrness, 1973). "Frost boils" are conspicuous in the spring. The coarse, unstable substrates are derived from hydrothermally-altered basalts; the resulting soils are extremely shallow and stony. Some of these soils have been formed by glacial-fluvial erosion; others have been formed by the exposure of ridgetop basalts to wind and rain. No significant differences have been found among the soils formed by the two processes. A wide gap in size-class distribution of particles which generally exists between large rocks and sandy loam produces various types of patterned ground. "Rock strips" and talus are found on slopes; on flatter surfaces hexagonal "pebble nets" are common. Near the southern edge of continental glaciation, "periglacial phenomena" have formed huge inactive stone nets.

Selected soil characteristics for five C. macrocalyx sites are given in table 2; sites are identified in table 3. All soil tests were run at the O.S.U. Soil Testing Lab. The pH measurements are fairly normal for eastern Oregon (6.4-6.8). McDermitt is drier; therefore a higher pH is not unusual. 10-15 ppm phosphorus is considered normal and the minimum acceptable level for agricultural lands in eastern Oregon. 1-2% organic matter is typical for eastern Oregon agricultural lands, assuming a homogenized top-soil of 150-200 mm. Samples for this study were taken from only the upper

Table 2. Selected soil characteristics for five Collomia macrocalyx sites.

Site name	pH	Phosphorus (ppm)	% Organic matter*	Soil particle size distribution**				Textural class
				%Gravel >2mm	%Sand 2.0- .5 mm	%Silt 0.05- .002 mm	%Clay <0.002 mm	
Antelope	6.6	11.0	2.5	11.5	36.3	37.3	14.9	loam
Fossil	6.6	10.0	3.1	32.2	35.2	24.1	8.5	gravelly loam
Lonerock	6.2	8.0	1.3	15.3	24.1	39.0	21.6	loam
McDermitt	7.0	5.0	1.7	30.6	25.3	32.6	11.7	gravelly loam
Trout Creek	6.6	5.0	1.5	45.2	30.9	19.8	4.1	gravelly sandy loam

\* Only the top 50-80 mm were sampled; standard soil tests are 150-200 mm deep.

\*\* Rocks greater than 20 mm dia were common on all sites but are not included in the above calculations.

50-80 mm of soil and from untilled lands. As such the soils from Antelope and Fossil would be considered average for the region whereas Lonerock, McDermitt and Trout Creek have a low percentage of organic material.

### Vegetation and vegetation history

Physical substrate, topography and climate are important factors in determining what type of vegetation can occur in a given area. Vegetation history also contributes to the development of the plant communities which occupy a given area. The theory of "geofloras" is now widely accepted by botanists as a partial explanation of how modern floras have developed. Simply stated, by reconstructing fossil floras and comparing them with present day floras, scientists have traced the migration of floristic elements in response to changing climatic conditions. Within the mountain and valley mosaic of the intermountain region routes of migration have been principally determined by latitude and altitude. Migrational patterns have led to the isolation of plant communities which have then been subject to further evolutionary modification. The two major geofloras of importance to this region are the Arcto-Tertiary and the Madro-Tertiary; the former consists of boreal species whereas the latter is derived from austral species.

The earliest reconstructed Eocene forest in the study area was sub-tropical, mesophytic and broad-leaved, reflecting the warm, wet climate of that epoch. Cooling and drying in the Oligocene resulted in this vegetation being

replaced by more temperate forest species. Precipitation declined further and seasonal fluctuations increased subsequent to the Cascade uplift of the Miocene. It was about this time that herbaceous life forms, especially the annuals, increased in numbers and significance compared to the earlier woody angiospermous floras (Daubenmire, 1978). A culmination of the xeric trend and the spread of the Madro-Tertiary geoflora into the region dominated Pliocene events in Oregon (Detling, 1968). The cooling trend which peaked with Pleistocene glaciations halted the further development and advance of this floristic element.

The principle vegetation patterns of the present intermountain region were well established by the Pleistocene (Reveal, 1979). Though some species were exterminated as boreal forests and austral communities shifted in response to the alternating warm-dry and cool-moist periods, the floras remained essentially intact. The Hypsithermal Interval (6,000 B.P.) was the last major warm-dry climatic extreme allowing Madro-Tertiary species to advance northward and upslope. A somewhat cooler-moister period has existed during the past 4,000 years resulting in a downslope and southern migration of some Arcto-Tertiary species. The region now supports a diverse assemblage of plant species with vegetation ranging from true desert to steppe/shrub-steppe to mesic boreal forests.

Herbaceous, perennial "bunchgrasses" characterize steppe vegetation. Shrub-steppe is the term applied when shrubs

(mostly Artemisia species in Oregon) contribute substantially to steppe stand composition. Steppe and shrub-steppe are found at low and mid-elevations throughout the region. Daubenmire (1978) labels the Columbia Plateau and northern Great Basin steppe the Agropyron spicatum Province. Though many different plant associations comprise this floristic province, some generalizations are possible. Summers are hot and dry and winters are cold; maximum vegetative growth and flowering activity occur in the spring. During the summer, annuals die, perennial herbs aestivate, and only deep-rooted shrubs remain green. Artemisia tridentata/Agropyron spicatum and Artemisia tridentata/Festuca idahoensis are the prevalent plant associations in both areas. In contrast with the Columbia Plateau, southeast Oregon has higher average elevations; it has few deep, loamy soils and supports many desert communities. Juniperus occidentalis and Cercocarpus ledifolius occur in association with shrub-steppe, and moist meadow-steppes are rare. Since European contact most pristine steppe has either been destroyed by cultivation and water impoundment or modified by the change in fire regime, increased grazing and introduction of weedy species.

Collomia macrocalyx is largely restricted to the lithosolic associations which are scattered throughout the Agropyron spicatum Province. The bedrock on these sites characteristically lies just below the thin, stony soil. As a result the effects of summer heat and drought, along with winter wetness and frost action, are intensified, producing

an extremely rigorous environment for vascular plants. Vegetation is sparse. Species diversity nevertheless ranges from poor, as might be expected, to as great as that of adjacent habitat types. Poa sandbergii is the most prevalent vascular plant and a moss/lichen crust usually covers the rocks and bare soil. Allium, Eriogonum, Lomatium, the Brassicaceae, and suffrutescent shrubs have their best steppe representation here (Franklin and Dyrness, 1973). A taller shrub layer is often present; here dominance may be by one species, but it is more frequently shared by several species. Daubenmire (1970) studied the different lithosolic shrub/herb associations and could not satisfactorily correlate them with soil or macroclimate. Artemisia rigida/Poa sandbergii was the most widespread type encountered. Daubenmire conjectured that the fracture system of the underlying basalt might hold the key to explaining the variation in shrub dominants.

These areas are less subject to modification by grazing and fire than the surrounding zonal associations. Excessive sun, wind and frequent soil drought produce perennial grasses that are stunted and therefore less palatable. This factor, combined with the difficulty that large herbivores have in walking across rocky surfaces, results in the area not being grazed significantly until other nearby forage has been severely depleted. Fire does not carry well nor burn hotly in sparse vegetation. Weedy species are present, but no studies have examined their impact on these sites. Showy-flowered species make many of these areas conspicuous in the spring.

A list of associated species (Table 3) was compiled in order to compare the different sites on which C. macrocalyx populations occur. Because these sites are not readily accessible from western Oregon, travel time and expenses were a limitation on field studies. As a result most sites were not rigorously collected, and some species have undoubtedly been missed. Malheur County was visited only in early June, and several other sites were visited on two or three occasions. A thorough inventory would have required more frequent visits to all sites beginning in early spring and continuing to at least mid-summer. The identification of some species are tentative due to the unavailability of flowers and mature fruit. Taxa in certain problematic genera or species complexes likewise were difficult to name.

#### Site descriptions

Search methods. Herbarium records and the Oregon Rare, Threatened and Endangered Vascular Plant files at the Oregon State University herbarium (OSC) were consulted for reported localities of C. macrocalyx. Label information was often vague. Dr. Janet Hohn, Endangered Species Office, U.S. Fish & Wildlife Service, Portland, Oregon, and a Collomia specialist, Dr. Dieter Wilken, curator of the herbarium at Colorado State University, Fort Collins, also provided distributional information.

A search was made for C. macrocalyx sites in the spring of 1981 (table 4; figure 1). By comparing the similarities shared by these sites and contrasting them with adjacent



Table 3 continued	Antelope				CRNG	Fossil	LG	Lonerock	McD	SC	TC
	I	II	III	IV							
<i>Astragalus curvicarpus</i>											
var. <i>subglaber</i>			x								
<i>A. howellii</i>											
var. <i>aberrans</i>					x	x					
<i>A. lentiginosus</i>									x		
<i>A. purshii</i>											
var. <i>purshii</i>							x		x		x
<i>A. reventus</i>											
var. <i>conjunctus</i>							x	x			
<i>A. whitneyi</i>						x					x
<i>Balsamorhiza careyana</i>											
var. <i>intermedia</i>					x					x	
<i>B. serrata</i>	x					x				x	
<i>B. sp.</i>			x								
<i>Calochortus macrocarpus</i>											x
<i>Castilleja chromosa</i>	x										
<i>Chaenactis douglasii</i>											
var. <i>douglasii</i>			x								
var. <i>achilleaefolia</i>						x				x	
<i>Claytonia umbellata</i>		x						x			x
<i>Crepis acuminata</i>						x				x	
<i>C. intermedia</i>										x	
<i>C. sp.</i>								x			
<i>Cymopterus watsonii</i>										x	
<i>Delphinium andersonii</i>											x
<i>D. burkei</i>								x			
<i>D. nuttalianum</i>	x				x	x	x	x			x
<i>Erigeron chrysopsidis</i>											
ssp. <i>chrysopsidis</i>			x	x	x		x	x			x
<i>E. linearis</i>	x	x			x					x	
<i>E. poliospermus</i>											
var. <i>poliospermus</i>		x			x					x	
<i>E. sp.</i>			x								
<i>Eriogonum compositum</i>											
var. <i>compositum</i>										x	x
<i>E. douglasii</i>											
var. <i>douglasii</i>				x							
var. <i>tenue</i>	x										
<i>E. heracleoides</i>											
var. <i>angustifolium</i>										x	
var. <i>heracleoides</i>		x									
<i>E. ovalifolium</i>											
var. <i>ovalifolium</i>									x		
<i>E. sphaerocephalum</i>											
var. <i>sphaerocephalum</i>					x						
<i>E. strictum</i>											
ssp. <i>proliferum</i>											
var. <i>flavissimum</i>					x						
var. <i>proliferum</i>	x	x									x
ssp. <i>strictum</i>							x	x			
<i>E. sp.</i>			x	x							
<i>Eriophyllum lanatum</i>											x
<i>Fritillaria pudica</i>		x						x			
<i>Grindelia nana</i>			x								
<i>Hieracium scouleri</i>											x
<i>Hydrophyllum capitatum</i>											
var. <i>capitatum</i>			x	x		x	x	x		x	
<i>Lewisia rediviva</i>	x	x	x	x	x	x		x	x	x	x
<i>Lithophragma bulbifera</i>						x					
<i>L. parviflora</i>			x	x			x		x		x



Table 3 continued	Antelope				CRNG	Fossil	LG	Lonerock		McD	SC	TC
	I	II	III	IV				NW	N			
<i>Collinsia parviflora</i>	x	x	x	x	x		x	x				x
<i>Collomia grandiflora</i>			x	x						x		x
<i>Crocidium multicaule</i>	x	x			x		x					
<i>Cryptantha circumscissa</i>										x		
<i>C. flaccida</i>										x		
<i>Descurania pinnata</i>												
var. <i>filipes</i>												
<i>D. richardsonii</i>		x	x				x			x		
var. <i>sonnei</i>					x							
var. <i>viscosa</i>								x				
<i>D. sp.</i>				x								
<i>Draba verna</i>		x	x		x		x	x	x	x		x
<i>Epilobium minutum</i>					x			x	x			x
<i>Eriogonum vimineum</i>												
var. <i>vimineum</i>		x										
<i>Erodium cicutarium</i>	x		x	x	x		x	x	x		x	x
<i>Euphorbia sp.</i>					x							
<i>Galium aparine</i>					x			x				x
<i>Idahoia scapigera</i>	x	x			x							
<i>Lepidium perfoliatum</i>						x						
<i>Lesquerella cf. kingii</i>												
var. <i>sherwoodii</i>						x						
<i>Lotus purshianus</i>			x									
<i>Lupinus uncialis</i>										x		
<i>Melilotus officinalis</i>												x
<i>Mentzelia albicaulis</i>			x			x				x		
<i>Microsteris gracilis</i>			x	x	x	x		x	x	x		x
<i>Montia linearis</i>								x	x			
<i>M. perfoliata</i>						x		x				
<i>Phacelia linearis</i>			x	x	x							
<i>Plectritis macrocera</i>					x			x		x		x
<i>Ranunculus testiculatus</i>				x		x		x	x			
<i>Sisymbrium altissimum</i>		x	x	x								
<i>Stellaria nitens</i>						x						
<i>S. sp.</i>				x								
<i>Thysanocarpus curvipes</i>				x								

\* Dates on which species were recorded were:

Antelope: May 9, 1981

Antelope II: May 30, 1981; July 24, 1981; April 11, 1982; May 8, 1982

Antelope III: June 17, 1981; July 24, 1981

Antelope IV: May 16, 1982

CRNG: June 13, 1982; May 7, 1983

Fossil: August 14, 1982; May 7, 1983

Lawrence Grassland: May 30, 1982; July 11, 1982

Lonerock NW: May 30, 1981; May 6, 1983

Lonerock N: May 6, 1983

McDermitt: June 11, 1982; June 10, 1983

SnoCap: June 18, 1981

Trout Creek: May 10, 1981; June 16, 1981; June 1, 1981; July 27, 1981; May 29, 1982.

Table 4. Reported locations of Collomia macrocalyx in Oregon.

Site	County	T	R	Sec	Location	Elev. (m)	Aspect	Slope & position on hill	Years	Ownership
Antelope I	Wasco	7S	17E	19	5 km N of Antelope W of hwy #218	1055	S/SE	20°-30° middle 1/3	1981-2 Joyal	private
Antelope II	Wasco	7S	17E	29	5 km N of Antelope E of hwy #218	1060	S/SW/W/E/SE	0°-20° ridgetop	1981-2 Joyal	private
Antelope III	Wasco	8S	18E	6	8 km E of Antelope N of hwy #218	1235	S/SW (slight)	0°-10° ridgetop	1981-2 Joyal	private
Antelope IV	Wasco	8S	16E	2	5 km W of Antelope N of hwy	995	S/SW (slight)	0°-10° ridgetop	1982 Joyal	private
Cow Canyon	Wasco	8S	15E	21	32 km W of Antelope W of hwy #97	ca.850	E/SE?	?	1981 Lewis	private?
Crooked River Natl Grasslands	Jefferson	13S	14E	35	16 km NW of Prineville 1.5 km W of hwy #26	1125	S/SE	0°-10°	1982-3 Joyal	U.S.F.S.
Fossil I	Wheeler	8S?	22E?		"12 miles S of Fossil"	1000?	?		1894 Leiberg	
Fossil II	Wheeler	7S	21E	19	9 km SW of Fossil N of hwy #218	1125	S/SE & E/SE	0°-10° upper 1/3	1982 Joyal	private
Lawrence Grasslands	Wasco	7S	16E	16	5 km SW of Shaniko	990	E/SE	10°-30° upper 1/3	1982 Joyal & Mauer	Nature Conservancy
Lonerock I	Gilliam	5S	24E	19	"near Lonerock" 5 km N of Lonerock	1190	S/SW	0°-10° ridgetop	1894 Leiberg 1983 Joyal	private
Lonerock II	Gilliam	5S	23E	6	14 km NW of Lonerock N of road	1040	S/SW	0°-10° hilltop	1894 Leiberg 1955 Hitchcock 1981-3 Joyal	private
McDermitt	Malheur	38S	42E	36	24 km N of McDermitt 1.5 km E of hwy #95	1525	N (slight)	0°-10° hilltop	1943 Peck 1948 Ripley & Barneby 1982-3 Joyal	state (BLM)
SnoCap	Wasco	6S	16E	32	5 km W of Shaniko N of hwy #97	1070	S/SW	10°-30° middle 1/3	1981-2 Joyal	private
Sparta	Baker	8S?	44E?		E of Sparta	1200?	?	?	1966 Beery	?
Trout Creek	Crook	12S	18E	9	43 km N of Prineville	1370	S/SW	0°-20° upper 1/3	1978 Kemp 1981-2 Joyal	U.S.F.S.

areas that did not support C. macrocalyx, a set of site characteristics was developed. In the early part of the study, sites thought to contain C. macrocalyx as well as areas thought to be poor candidates were examined. Though many areas were searched, only a few new sites were found. Steep slopes, large rock nets and strips where individual rocks averaged greater than 20-30 cm across, and severely disturbed sites were never found to contain C. macrocalyx. In 1982, I revisited all of the 1981 C. macrocalyx sites and relocated the site north of McDermitt. The Sparta site was reportedly destroyed in 1967 so, as travel time was limited, I did not search in that area south of the Wallowas. While employed by the Ochoco National Forest during the summer of 1982, I was able to visit many of the "scab flats" in the western Ochocos and in the Maury Mountains. Other than the site at Trout Creek, no other C. macrocalyx was found there. Two populations of the related C. tinctoria were located, as well as plentiful material of C. linearis and C. grandiflora. Outside of the Ochocos, I observed only three sites whose characteristics appeared suitable for C. macrocalyx, and populations were indeed found at these localities.

Table 4 contains the following information: site name; county; geographical coordinates (township, range, and section); location; elevation in meters; aspect; slope and position on hill; years the site was visited and by whom; and land ownership. Most of the sites occur within a contiguous five county area composed of SE Gilliam, NW Wheeler, SW

Wasco, NW Crook, and south-central Jefferson Counties (figure 1). These localities fall within a 110 km strip with the Crooked River National Grassland site (Jefferson Co.) at the southwest corner and Lonerock (Gilliam Co.) at the northeast end. The populations in Baker and Malheur counties are disjunct from each other by approximately 270 km and from the main populations by 210 and 350 km respectively. Elevations range from 850 to 1525 m. C. macrocalyx is generally found on gentle, south-facing slopes (less than 30°) occupying the upper third of hillsides, hilltops and ridgetops. It is restricted to rocky soils, frequently growing in rock strips and nets and along small rock outcrops, which are common in some areas of eastern Oregon. Nine out of the fifteen sites are recent discoveries within the five county area; six are located within a 15 km radius of the town of Antelope. Ownership is largely private; two sites are on U.S. Forest Service lands, one is state-owned and in the process of being transferred to the Bureau of Land Management, and another is on Nature Conservancy property. All sites are currently open to cattle grazing or have been grazed in the past, except for two sites which are inaccessible to cattle.

The "Shaniko Surface" basalt, the southern edge of which crops out in a prominent northeast to southwest-trending rim called the "Antelope Scarp," terminates north of the town of Antelope (Baldwin, 1968). It is along this rim that the four Antelope sites occur. Sites I and II are on hills on opposite sides of Highway # 218 as it cuts through the rimrock toward

Shaniko. At site I, C. macrocalyx is found in rock strips within fenced rangeland; at site II it is scattered in the deep rock in and along a gravel road giving access to a television tower. The road receives little traffic, but recent activity at a gravel pit near the road entrance has been substantial. Sites III and IV are on isolated ridgetops surrounded by steep, unstable basalt talus.

Collomia macrocalyx has been reported from Cow Canyon by George Lewis, Jr., of Portland, Oregon. This is the lowest elevation reported (850 m) and the area, as viewed from the road, looks steeper than other sites. Time was not available for me to verify the site, and no voucher specimens have been collected there. The Crooked River National Grasslands site slopes gently southward down to the head of Japanese Creek with an abrupt drop-off to the north. Collomia macrocalyx is located in the lattice-work of deep rocks which runs along the edge of the cliff. Access is possible directly onto the site by U.S.F.S. road # 900 and an unmaintained dirt and boulder road.

Fossil I is an original Leiberg locality, described by him as "12 miles south of Fossil." I have searched the area but have been unsuccessful in finding C. macrocalyx there. Pinus ponderosa-Pseudotsuga menziesii forests are dominant in the area, but some of the hilltops are open and could conceivably support C. macrocalyx. At Fossil II the vegetation is sparse, rock outcrops few, and the soils extremely thin and rocky. Selaginella and mosses grow

plentifully among the rocks. A gravel pit and an unmaintained dirt road are adjacent to the site. The Lawrence Grassland population is located along the edge of eroded rimrock above a feeder stream into Ward's Creek. Collomia macrocalyx is present on the rock outcrops as well as in a few rock strips.

Most collections made since 1894 in the Lonerock area have been from an area 14 km northwest of Lonerock; these are approximately where Leiberg's second collection was made. His first collection came from "near Lonerock;" a population which was recently discovered (1983) in the hills north of Lonerock matches this description well and should be considered the topotype. The area is privately owned rangeland at the southern edge of the wheat-growing region of the Columbia Plateau. The McDermitt site is a rocky, thin-soiled gentle hilltop at the western edge of a series of low, rolling hills, on the east side of Oregon Canyon. This is the most widely disjunct site discovered thus far.

The SnoCap Identifier, a public parking area with a display indicating the positions of major Cascade peaks, is immediately adjacent and to the south of a C. macrocalyx population. Rock outcrops and strips which ribbon the hillside provide suitable habitat for C. macrocalyx. Sparta is the second disjunct site for the species. It had been monitored by Gene Beery and reportedly "destroyed by road-building construction" in 1967. Trout Creek is a high-elevation site occurring in a south-facing opening surrounded by Pinus ponderosa-Pseudotsuga menziesii forest in the Ochoco

National Forest. Collomia macrocalyx grows in rock outcrops and in the rocky soil nearby.

## MORPHOLOGY AND LIFE HISTORY

Morphology of the species

Materials and methods. Specimens were examined of C. macrocalyx, C. tinctoria Kell., C. linearis Nuttall and a fourth related taxon not yet named. Twenty-four vegetative and 28 floral characters were studied in each. In collections that contained a single individual, the measurements represent that specimen alone. When the collection was composed of more than two individuals, the smallest and the largest ones were measured. No more than one flower was removed from each sheet, due to the rarity of the collections. The bracts selected for measurement were always the ones immediately subtending a flower.

Plants were grown in greenhouses at Oregon State University in the spring of 1982 and the fall and winter of 1982-83; additional plants were cultivated in flowerpots outdoors in Prineville, Oregon, from June through October of 1982. The greenhouses were maintained at 18°C day and 15°C night. Light was the natural photoperiod for 45°N latitude, without supplementary illumination, except for extraneous light from adjacent greenhouses. Lights ("Gro-lights"), 24 hours per day, were used to initiate flower production in February 1983.

Vegetative traits. A detailed morphological comparison of C. macrocalyx with its close relatives, C. linearis, C. tinctoria, and a fourth as yet undescribed taxon, is given in

Figures 3 and 4; a synoptical key to these four species follows:

- A.1. Calyx tube urn-shaped, teeth slightly to very unequal in length, the longest usually greater than 4 mm in fruit; filaments 0.5 mm long, unevenly inserted slightly below corolla throat; corolla funnelform; bracts linear, the lower margins ciliate or not .....B.
- A.2. Calyx tube flared, teeth more or less equal and usually less than 3 mm in fruit; filaments evenly or unevenly inserted, the three shorter ones 0.5 mm, the two longer ones 1-2 mm; bracts linear to linear-lanceolate, the lower margins ciliate.....C.
- B.1. Calyx teeth very unequal in fruit, the longest tooth 1.5-2 times the calyx tube length, with glandular-puberulent hairs; corolla tube sparsely pubescent; bracts and leaves puberulent to glandular-puberulent; peduncles and petioles densely glandular pubescent; stems slightly to thickly puberulent or glandular.....C. macrocalyx
- B.2. Calyx teeth more or less regular, the longest tooth usually less than 1.5 times the calyx tube, with non-glandular, puberulent hairs; corolla tube essentially glabrous; bracts and leaves puberulent, non-glandular, ciliate on lower margins; peduncles and petioles densely villous and non-glandular; stems puberulent.....  
.....C. sp. nov. ined.
- C.1. Corolla salverform; filaments inserted more or less evenly at corolla throat, the two longer ones 2.0 mm;

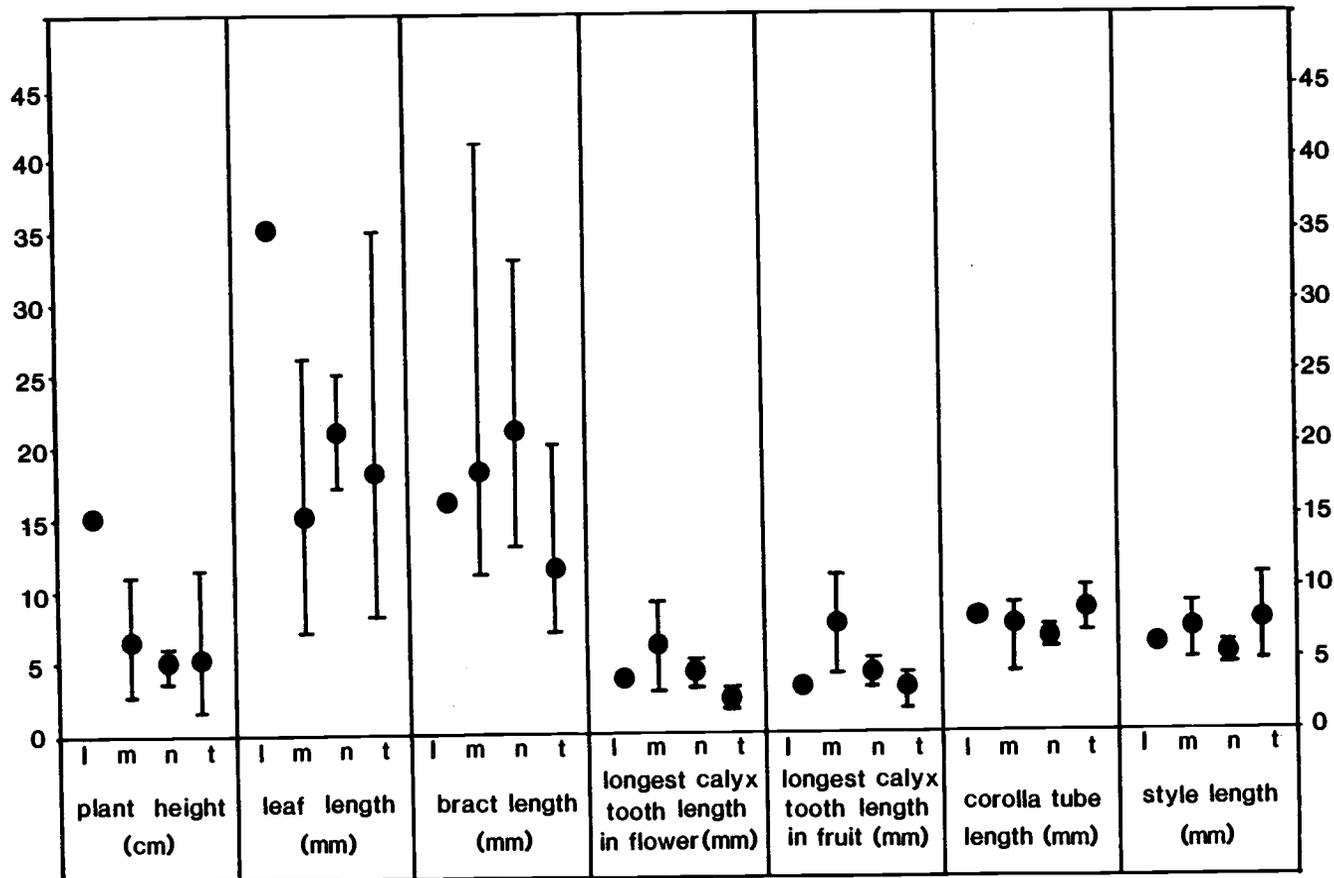


Figure 3. Comparison of morphological traits of Collomia macrocalyx and three related taxa. a. Mean (dot) and range (bar) for seven characters. l = C. linearis; m = C. macrocalyx; n = C. sp. nov. ined.; t = C. tinctoria.

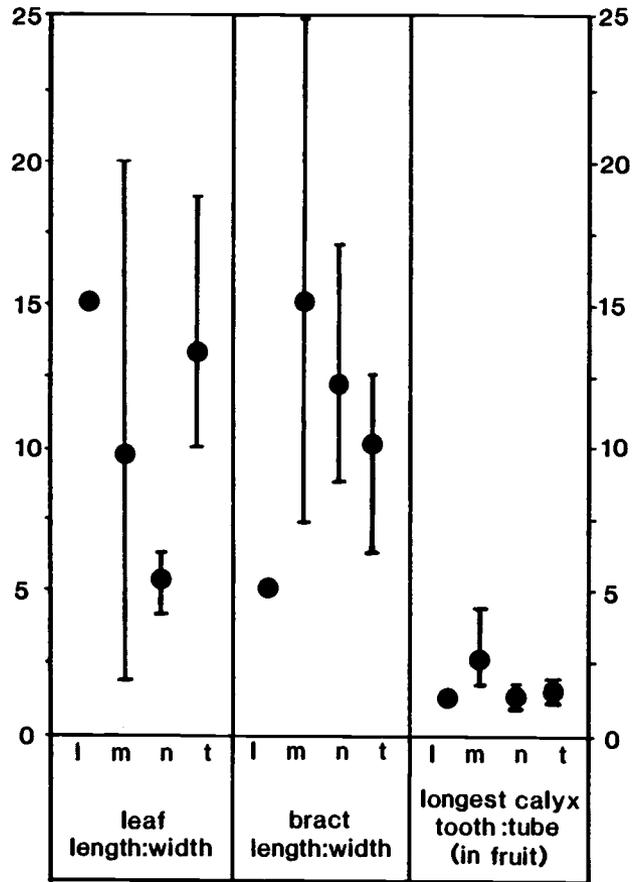


Figure 3. Comparison of morphological traits of Collomia macrocalyx and three related taxa. b. Mean (dot) and range (bar) for three ratios of characters. l = C. linearis; m = C. macrocalyx; n = C. sp. nov. ined.; t = C. tinctoria. Continued



glandular-puberulent to glandular-villous throughout, often unevenly so; bracts linear-lanceolate, 6-10 times longer than wide; cauline leaves few and mostly opposite....C. tinctoria  
 C.2. Corolla funnelform; filaments inserted unevenly, the lowest well down the corolla tube and 0.5 mm long, the upper two at the throat and 1-2 mm long; finely and evenly puberulent throughout or glabrous, with many glandular hairs restricted to and abundant in the inflorescence (bracts, calyx and petioles); bracts lanceolate, 4 times longer than wide; cauline leaves numerous and alternate.....C. linearis

Collomia macrocalyx is a tiny annual, seldom exceeding 10 cm in height or width. The ratio of plant height above the hypocotyl to the length of the hypocotyl itself is usually small; a markedly elongated hypocotyl is necessary in many instances to raise the epicotyl of the plant to the surface from the point of seed germination deep in the rocky substrate. Usually one to three pairs of opposite, spatulate leaves are produced below the inflorescence. As the inflorescence forms, a few alternate, spatulate to linear, leafy bracts are produced. Later-formed bracts are entirely linear, the smallest ones being immediately beneath a flower.

In robust individuals, six or seven branches develop. Branching may occur three or four times before terminating in dense, leafy-bracteate flower clusters. Flowers and bracts are produced indeterminately until the plant senesces in response to summer drought.

Anthocyanin pigments color the stem and peduncles as

well as the mid-veins and tips of the leaves and bracts. The entire plant is covered with a fine puberulence, although the distribution of pubescence and glandular hairs is not uniform. Near the cotyledons, the stem has a sparse, simple puberulence, which increases up the stem toward the inflorescence. Peduncles and petioles are moderately to thickly puberulent and contain a few glandular hairs. Leaves and bracts are slightly to moderately puberulent; a few glandular hairs can sometimes be found thinly scattered over the leaf surface, but they are usually present and denser on the bracts.

These pubescence patterns differ in the three other taxa related to C. macrocalyx (Figure 4). In C. linearis, the puberulence can vary from essentially absent to dense but it is always evenly spread throughout the plant. Glands, which are conspicuous, are restricted to the inflorescence bracts and calyces. The pubescence of C. tinctoria more closely resembles that of C. macrocalyx except that it is everywhere more glandular. The pubescence of the unnamed taxon, C. sp. nov. ined., is similar to C. macrocalyx but lacks glandular hairs. Unlike C. macrocalyx, the latter three taxa all have ciliate hairs on the lower margins of their leaves and bracts.

Under cultivation, a few morphological characters of C. macrocalyx display phenotypic plasticity. Anthocyanins develop less vividly under low light intensities though pubescence patterns do not change measurably. Major

differences occur in the size of cultivated plants: individuals are more robust; five to ten branches per plant are common; flowers may number 25-50; and leaves are larger (43 X 5 mm vs. 15 X 2 mm in native populations). Wilken (1977) found similar responses in C. linearis growing in meadow versus disturbed sites in Colorado. Such observations reinforce the use of floral characters instead of vegetative characters (quantitative) in defining specific limits. One curious change noted in greenhouse specimens of C. macrocalyx is that the margins of the bracts frequently bear one to four teeth, a feature which has not been observed in native populations. Serrate leaves are the rule in sects. Collomiastrum and Courtoisia but not in sect. Collomia, which has entire, linear to lanceolate leaves. Wherry (1944) considered entire leaves to be the derived trait and leaf serration to be the primitive condition. Toothed bracts in cultivated C. macrocalyx may be the expression of an ancient character which usually is developmentally suppressed in native populations.

Inflorescence. The first flower is initiated in the axil of the uppermost bract. When only a few flowers are produced on a plant, they are tightly clustered at the stem apex, each flower having a subtending bract. If more flowers are produced, the first will be in the axil of the bract immediately below the terminal inflorescence. Further flower buds are initiated in descending order down the stem in axils of remaining bracts. Branches are produced in a similar,

basipetal order. Each branch generally elongates 1 cm or more before producing another densely packed, leafy-bracteate flower cluster. This pattern is repeated indefinitely, if conditions are favorable.

In contrast with C. macrocalyx, C. linearis has a tall, leafy stem, usually with a single, tightly-packed, terminal, bracteate inflorescence. Additional inflorescences, if any, are sessile in the upper leaf axils, decreasing in size down the stem. In more robust individuals, these may be supported on peduncles or longer side branches. Collomia tinctoria has a more nearly dichotomous branching pattern and smaller flower clusters with fewer bracts. The unnamed new taxon has a branching pattern and inflorescence structure similar to C. macrocalyx. In cultivation the inflorescence of C. macrocalyx loses the tight compactness of the terminal flower clusters, but it does not display the regular dichotomy of C. tinctoria.

Calyx. Collomia macrocalyx is readily separated from related species by its distinctive calyx (Figure 1 and 3). The tube is more urn-shaped than flared, though the edges of the sinuses flare somewhat. The teeth are aristate-attenuate and uneven in length. The calyx tube is white and sparsely puberulent, with few or no glandular hairs. The teeth are green with anthocyanic tips and are moderately puberulent; glandular hairs are often present. In contrast, C. linearis has more numerous glandular hairs throughout the calyx, with a thick, almost villous, pubescence on the teeth. The calyx

tube of Collomia tinctoria has pubescence similar to that of C. macrocalyx, but the teeth are more glandular. The unnamed taxon has no glandular hairs but has a thick pubescence on the margins of the teeth.

Corolla. The funnelform corolla of C. macrocalyx has a white throat with clear blue-purple lobes. The five filaments are about 0.5 mm long and unevenly inserted (2,2, and 1 pattern) slightly below the throat. The anthers are pale blue, as in the other three related taxa. Collomia linearis has three short filaments inserted unevenly down the tube and two longer filaments inserted just below the throat. Collomia tinctoria has three short and two long filaments inserted more or less equally just below the throat. The unnamed taxon is similar to C. macrocalyx in filament length and placement.

The three stigmas of C. macrocalyx are usually level with the anthers or slightly below, but they are exerted in 10-15% of the flowers. Under cultivation, the styles more frequently elongate to produce exerted stigmas (50% of flowers examined, see Table 5). The other taxa generally have stigmas inserted below the stamens. Collomia tinctoria has exerted stigmas with about the same frequency (20%) as C. macrocalyx.

The tricarpellate, loculicidal capsule, including its septa, become chartaceous as it matures. Each seed is attached longitudinally to the center of the placental septum within its cavity. The septa detach from the base of the ovary assisting in the active ballistic dispersal of the

Table 5. Style placement in cultivated Collomia macrocalyx.

<u>Seed source</u>	Number <u>exserted</u>	Number <u>inserted</u>	Percent <u>exserted</u>
Antelope I	39	13	75.0
Antelope II	28	7	80.0
Antelope III	45	42	51.7
Lonerock	3	9	25.0
Trout Creek	35	77	31.3
	<hr/>	<hr/>	<hr/>
Total	150	148	50.3

seeds. After the seeds have been dispersed, the septa are blown away.

Chromosome number. Materials and methods. Flower buds of several different ages were collected from native populations and from plants grown in cultivation. They were immediately placed in a 6:3:1 mix of 95% ethanol, chloroform and glacial acetic acid to fix meiotic activity. The medium was prepared on the same day of use and the buds stored in the mix for 24 hours or longer. They were then drained and and stored at 4°C in 70% ethanol. Prior to use, the ethanol was drained and Snow's aceto-carmine stain (1963) added. The samples were incubated overnight at 69°C. Excess stain was then drained and buds rinsed two to three times in 70% ethanol, and stored in 70% ethanol at 4°C until use.

Stamens were extracted from flower buds, mounted in 45% acetic acid and Hoyer's medium, and examined with a Zeiss microscope for meiosis. No meiotic activity was observed in any of the prepared buds though some of the ovary walls had visible chromosomes. All appeared to be  $2n=16$  but it was not possible to obtain a clear count from these. Therefore we found it necessary to repeat the procedure with root-tips. For this seeds from several populations were germinated. When the hypocotyls were approximately 1 cm long the seedlings were placed in distilled water at 4°C overnight. They were fixed in a 3:1 95% ethanol:glacial acetic acid mixture for 24 hours, drained, rinsed with 70% ethanol, placed in Snow's aceto-carmine stain and incubated for 24 hours.

A count of  $2n=16$  was obtained from the McDermitt population. Chromosome numbers have not been obtained for C. sp. nov. ined. Aside from this species, the remaining 13 Collomia species are  $2n=16$  except for one tetraploid ( $2n=32$ ) in temperate South America.

Summary of morphological studies. Collomia macrocalyx shares many morphological similarities with both C. linearis and C. tinctoria. If floral traits are emphasized it is allied more closely with C. linearis, whereas focus on vegetative characteristics place it nearer to C. tinctoria. Inflorescence form is intermediate and the calyx is different in all three taxa. Recent studies have shed new light on the purported relationship of C. macrocalyx to these two species and to the remainder of the genus. These studies will be discussed in the section on evolutionary trends.

On the basis of vegetative and floral morphology, the undescribed taxon appears intermediate between C. macrocalyx and C. tinctoria. As with C. macrocalyx's relationship to C. linearis and C. tinctoria, the undescribed taxon can be placed closer to C. macrocalyx or C. tinctoria depending upon which traits are emphasized. Its flower and inflorescence are closer to C. macrocalyx; its vegetative parts are more like C. tinctoria, and its calyx and pubescence pattern are somewhat intermediate.

## Life history

### Germination of seeds

Seeds are important in the life cycle of many angiosperms; they are vital to annual species which must reproduce from seed at the beginning of each growing season. Seeds of desert annuals are specially adapted to survive the vagaries of weather encountered in this harsh environment. A proper understanding of Collomia macrocalyx's biology, particularly since it is a rare desert annual, therefore necessitates a study of germination requirements. Preliminary quantitative studies have been done, but were necessarily limited by the small number of seeds available.

Seeds were collected at most study sites in 1981-82 and from plants grown in cultivation. Initially, some of the seeds that ripened on C. macrocalyx transplanted to clay pots from the wild, were left where they fell on the soil. They were watered regularly until the plants senesced, about one month after seed dispersal. Pots and seeds were then air-dried and stored at room temperature (22°C). Four months later, pots were resaturated, given a 15-hr photoperiod, and maintained at room temperature. Whereas freshly fallen seeds did not germinate, seeds treated to an after-ripening period germinated within six days. Though no stratification was required, a period of dormancy seemed to be necessary prior to germination.

Seeds ranging in age from ten to twenty weeks were tested to delimit an after-ripening period. The seeds were

placed on filter paper in Petri plates and kept moist at room temperature with a 15-hr photoperiod. Seed of different ages all showed some germination, but the amounts were uniformly low (13.4% overall; range 3.8% to 30.8% n = 217). The only generalization possible from this small test is that seeds as young as ten weeks old can germinate under these particular experimental conditions.

Because C. macrocalyx flowers early in the spring, seeds must germinate very early, possibly at the time of the first autumn rains. As this would require germination at low temperatures, a second set of seeds (n = 217) was tested for germination at a range of temperatures, both in darkness and in light. Ten- to twelve-month-old seeds were used. Seeds were placed on filter paper in Petri plates, saturated with water, and placed at room temperature (22°C) and in Percival growth chambers at four different temperatures (5°, 10°, 15°, and 20°C) with a 15-hr photoperiod or with light excluded by aluminum foil. Germination occurred under all conditions, averaging 43% overall. Germination rates were higher at lower temperatures. The light and dark pooled percentages were: 72.7% at 5°C; 56.9% at 10°C; 46.9% at 15°C; 23.9% at 20°C; and 30.6% at 22°C. Rates were similar in both darkness and light. However, they fell rapidly in light at temperatures greater than 10°C (37.0% average total; 75.0% at 5°C down to 4.5% at 22°C) but only slowly in the dark (48.7% average total; 71.9% at 5°C down to 33.3% at 22°C). These trends in response to temperature and light can not be substantiated

until adequate seed is available.

Finally, seeds which matured on cultivated C. macrocalyx in late August and early September, 1982, were left unharvested. The parental plants and seeds, which were maintained in pots at Prineville, in Crook County, were exposed to frequent freezing and thawing during the month of September. In October, they were moved to a greenhouse and kept at 18°C day and 15°C night. Although the last plants died in early October, the pots were kept watered. The seeds germinated at a rate of 80-90% during the second week of January, after four to five months of dormancy in moist soil.

Seedlings of C. macrocalyx were observed in early December 1982 at the Crooked River National Grasslands (CRNG) site. Individuals were plentiful among the rocks; reinspection of the same area in February 1983 disclosed that most of the seedlings had not survived the winter.

Though not conclusive, the above results are informative. It appears that stratification is not required, although an after-ripening period is; the species is a winter annual; and no particular light or dark period is necessary for germination.

Collomia macrocalyx seeds apparently require after-ripening following seed dispersal, which inhibits germination for ten to twenty weeks. This period coincides with a drought-induced dormancy. An innate dormancy is important nonetheless. Summer thunderstorms, which briefly moisten the parched desert soil, are common. If seeds germinated then,

most plants would die before flowering and setting seeds. After the autumn rains begin, the soil is resaturated and remains so, excluding the effects of freezing, until early summer. By germinating in the fall, winter annuals get a head start on spring growth, producing an optimum number of flowers and seeds before summer drought kills them. The absence of any special need for stratification is not surprising. This would be of little benefit to a species that can delay germinating until after summer drought but then take advantage of a longer, cool wet season.

Seed size and shape, and in this species the presence of a mucilaginous seed coat, are important in determining germination success. Considering the diminutive size (4-10 cm) of the plants, a relatively large amount of energy is allocated to seed production. The flattened, oval seeds average 2-2.5 X 1 mm and contain plentiful endosperm. A 10- to 15-cm hypocotyl must often be produced to elevate the cotyledons to the surface from deep in rocky crevices. Seed shape determines the area of contact with the substrate. The greater contact a seed makes with its substrate, the better it absorbs moisture. The presence of a mucilaginous seed coat markedly increases the area of seed-to-soil surface contact, and decreases the minimum soil water tension needed for moisture uptake and germination (Harper, 1977). Thus mucilaginous seeds are less sensitive to variation in water supply. Although C. macrocalyx seeds occur in thin, rocky soil in highly variable microsites, the mucilaginous seed

coat acts to homogenize the environment and provide more "safe sites". In summary, the morphological characteristics and germination behavior of the seeds of C. macrocalyx indicate that this species inhabits a fairly predictable, though restricted, environment.

#### Establishment of seedlings

Collomia macrocalyx seeds germinate after autumn rains saturate the soil in late September or early October. Individuals that germinate in deep rocks must produce long hypocotyls from food reserves stored in their relatively large seeds. The slender roots make contact with only a thin layer of soil that lies on or below the rocks. No more than one or two pairs of true leaves develop through the winter. In middle to late April, leafy bracts and, shortly thereafter, flower buds form in response to increasing day length. More bracts and flowers, along with branches in more robust individuals, are produced in late May and early June as the weather warms. Seeds are set and mature rapidly. By mid-June, the cloudy, wet spring gives way to clear, dry summer weather, and hot days alternate with chilly desert nights. The soil dries quickly and plants begin to senesce. By the end of June most individuals have died. Only a few of the larger C. macrocalyx plants at Antelope II were still producing flowers in late July, 1981. In 1982, most plants had died by late June, but mild, moist weather prevailed for most of July and August and the remaining plants persisted late into the season.

Collomia macrocalyx seeds usually are not deeply buried and frequently are visible lying on the soil surface or among rocks. Moisture from scattered summer thunderstorms may swell the mucilage in the seed coats and attach them to the rocky substrate or to an animal which may serve as a dispersal agent. Seedlings at a frequency of 100-200 per m<sup>2</sup> were observed in the first week of December 1982 at the CRNG site. Most were in the deep rock of the "rock nets" rather than in the soil and rock areas in between. Only about 10-20% survived through the winter of 1982-83. The winter was mild and wet, and several of the early spring annuals, including Lomatium canbyi Coult. & Rose, L. hendersonii Coult. & Rose, and Phlox hoodii Rich. were flowering at the time of the field check in late February. Beatley (1967) found high mortality in desert winter annuals in southern Nevada, with death occurring mostly in the early spring at the time of physiological change from slow winter growth to rapid spring growth.

#### Relationship to substrate

A partial survey of C. macrocalyx at the CRNG site was completed in August, 1982 (Table 6). A second survey there, and at Trout Creek and Antelope II, was also done concurrently. The purpose of the survey was to estimate the size of the populations, to determine the size class distribution and density of individuals within the populations, and if possible, to correlate the latter with substrate and associated vegetation. By conducting the survey

Table 6. Size class distribution of Collomia macrocalyx individuals in relation to substrate at three sites. August 1982.

SUBSTRATE and SIZE CLASS	SITE							
	<u>CRNG</u> (10 X 20 m grid) n = 211		<u>CRNG</u> n = 200		<u>Antelope II</u> n = 200		<u>Trout Creek</u> n = 200	
	<u>#</u>	<u>%</u>	<u>#</u>	<u>%</u>	<u>#</u>	<u>%</u>	<u>#</u>	<u>%</u>
<u>Rocks</u>								
I	44	42.3	70	43.2	128	83.1	44	35.5
II	34	32.7	58	35.8	23	14.9	64	51.6
III	23	22.1	31	19.1	3	1.9	16	12.9
IV	3	2.9	3	1.9	0	.0	0	.0
	<u>104</u>	<u>100.0</u>	<u>162</u>	<u>100.0</u>	<u>154</u>	<u>99.9</u>	<u>124</u>	<u>100.0</u>
<u>Soil &amp; rocks</u>								
I	50	46.7	29	76.3	42	91.3	24	49.0
II	33	30.8	7	18.4	4	8.7	20	40.8
III	18	16.8	2	5.3	0	.0	5	10.2
IV	6	5.6	0	.0	0	.0	0	.0
	<u>107</u>	<u>99.9</u>	<u>38</u>	<u>100.0</u>	<u>46</u>	<u>100.0</u>	<u>49</u>	<u>100.0</u>
<u>Sand</u>								
I	0	.0	0	.0	0	.0	6	22.2
II	0	.0	0	.0	0	.0	9	33.3
III	0	.0	0	.0	0	.0	7	25.9
IV	0	.0	0	.0	0	.0	5	18.5
	<u>0</u>	<u>.0</u>	<u>0</u>	<u>.0</u>	<u>0</u>	<u>.0</u>	<u>27</u>	<u>100.0</u>
<u>Total</u>								
I	94	44.5	99	49.5	171	85.5	74	37.0
II	67	31.8	65	32.5	26	13.0	93	46.5
III	41	19.4	33	16.5	3	1.5	28	14.0
IV	9	4.3	3	1.5	0	.0	5	2.5
	<u>211</u>	<u>100.0</u>	<u>200</u>	<u>100.0</u>	<u>200</u>	<u>100.0</u>	<u>200</u>	<u>100.0</u>

at the end of the season, it was possible to measure the plants when they had attained their maximum size.

After the limits of the C. macrocalyx at the CRNG site were determined, a 10 X 20 m grid was laid through the center of the population. The grid was divided into plots 1 m<sup>2</sup> in size. A diagram of the rock nets was overlain on the base map. The number of C. macrocalyx in each size class were recorded for each plot. Size classes used were as follows: class I, one to five flowers; class II, six to ten flowers; class III, 11-20 flowers; and class IV, more than 20 flowers. I also recorded the predominant substrate for each plot (deep rocks vs. soil-rock mixture), average size of rocks, and percent cover of Artemisia rigida (Nutt.) Gray, the only shrub present, and bunchgrasses (mostly Poa sandbergii) Vasey. Artemisia rigida and bunchgrasses persist through the season and are easy to measure in late August, whereas most forbs have disappeared by this time. This method was time-consuming for one person working alone. Another problem was that exact locations of C. macrocalyx individuals relative to each other and to shrubs, bunchgrasses, and substrate were not recorded. A second method for surveying the CRNG population, as well as the populations at Trout Creek and Antelope II, was therefore devised. A one meter wide belt transect was drawn through the center of each population, passing through areas both of deep rocks and of mixed soil and rock. Each C. macrocalyx encountered was assigned to a size class and circles of 10 cm and 25 cm radii drawn around

each individual. The substrate and number of other C. macrocalyx individuals within each circle were recorded. The presence of A. rigida, bunchgrasses, and cheat grass (Bromus tectorum L.) were recorded for the smaller circle. At the edge of the population, I repeated the procedure with a second belt transect parallel to the first in the opposite direction.

A chi-square test for homogeneity was used to determine if estimates of the numbers in each size class by the two different surveying methods at the CRNG site were similar. Results indicate that classes I, II, and III are not significantly different ( $X^2 = 1.046$ , d.f. = 2,  $p = .640$ ). If size class IV is included, the  $X^2 = 3.662$  (d.f. = 3) and  $p$ -value = .200 signify that a significant difference exists in the results from the two methods, and that this difference is present in the estimates for size class IV. The belt-transect method appears to underestimate the presence of larger individuals (see Table 6).

With respect to the relationship of C. macrocalyx to different types of substrates (Table 6), the belt-transect method for surveying the populations gave more precise data. In the grid survey (Table 6, first column), only the dominant substrate was recorded for each plot at CRNG although both types (rock vs. mixed rock and soil) may have been present. The belt-transects more accurately show that many more plants grow in deep rock than in the soil and rock areas, and that larger individuals are generally found in rocky areas. An

exceptional situation existed at Trout Creek where the largest plants observed grew in a sandy area devoid of rocks and of other vegetation. Collomia macrocalyx established in these open areas and perhaps, without competition and with adequate water through the winter, and good root development grew well. Possibly there is less competition in rocks and in sandy open places than in soil and rock areas, which usually have a greater cover of herbs, mosses and lichens.

In general, individuals occupying the best microsites are more protected, have more moisture available to them, and develop better root systems; they grow larger, produce more flowers and set more seed. They are thus better equipped to withstand potential factors of mortality (Cook, 1979).

Most of the C. macrocalyx sites are on south-facing slopes or ridgetops (Table 4) which are subject to greater diurnal temperature fluctuations than adjacent areas. All are windy, so that surface drying is rapid. The shallow soil further increases the extremes in temperature and drought. It is the long winter period during which the soil is waterlogged, frozen, or both, that C. macrocalyx exploits so well.

If the five to six winter months are critical in the life history of C. macrocalyx, the principal causes of mortality must be evaluated. Beatley (1967) and Burk (1982) found that mortality is high in winter annuals in the southern Nevada desert. Predation and drought are the two

major causes of seedling mortality (Cook, 1979). Demographic studies have shown that the highest risk of death occurs early in the life of a plant; survivorship increases with age as better roots are developed and plants depend less on surface moisture (Cook, 1979). Collomia macrocalyx survives through the initial establishment phase by germinating at a time when the ground is saturated and remains so for a long time.

Because more individuals grow in rocks, more seeds drop there. Assuming, also, that dispersal is less from deep rocks than from soil and rock areas, more seeds remain available to germinate in the deep rocks. Though many of the seedlings that grow there do not survive, many more seem to survive there than in adjacent soil and rock areas. Alternatively, deep rocks may provide a "safer" site for seedling establishment than the more exposed soil and rock areas. Factors to consider include protection from foraging predators, drought, and competition.

Seedlings that become established in deep rocks are protected from grazing and trampling of herbivores. The plants are still vulnerable to small animals and insects that can move between the rocks. Most insects are dormant during the winter, but mice and other rodents which are active may eat the shoots of winter annuals. Water relations are often the most important factor to consider in successful seedling establishment. Seedling mortality is highest immediately after germination and is correlated with decreasing soil

moisture (Cook, 1979). Persistent winds, dry air, large annual extremes in air temperature, and sandy to gravelly soils are common in arid regions such as eastern Oregon. Stark and Love (1969) note that the scarcity of silt and clay make it difficult for water in the soil to establish capillary action. As a result, little moisture is lost by evaporation from the soil surface, except shortly after rainfall. Shallow-rooted plants likewise cannot draw water up through the soil if little movement of water occurs. Though many desert annuals germinate in sand immediately after a good soaking rain or in the shade of shrubs, few seem able to exploit deep sources of water. Stark and Love (1969) found that water condensation on rocks in Death Valley was a major source of water for plants, and that the roots of many desert shrubs were concentrated under rocks. Perhaps, by exploiting the deep rock microsite, C. macrocalyx is able to use the extra moisture, as well as cooler temperatures, among the rocks.

Several deep-rooted perennials (Claytonia umbellata Wats., Lomatium minus (Rose) Math. & Const., and Hydrophyllum capitatum Benth.) and one shrub (Artemisia rigida) inhabit the deep rocks where C. macrocalyx appears to grow best. The only other annual regularly encountered in the deep rocks is the weedy cheatgrass, Bromus tectorum, although it is not very common there. The paucity of species in this microsite may be advantageous for C. macrocalyx if it is not a good competitor. In a desert environment with much open space and

adequate moisture for five to six months, the probability of germination may be high initially because competition for resources is minimal. Off the rocks, as the soil dries out in late spring, competition may become more important to C. macrocalyx's vigor and survivorship. In open areas, competition is not for above-ground space as much as it is for below-ground water and nutrients. This aspect of competition has not been studied for C. macrocalyx; most sampling methods would be too destructive for a rare plant study. It should be noted, however, that C. macrocalyx plants in greenhouses, where water is plentiful and competition is minimal, grow easily and are much larger than their parents.

#### Flowering and pollination

Collomia macrocalyx plants that were four- and 15-weeks old, germinated in the Oregon State University greenhouses, and transplants taken in December, 1982, from the CRNG site (ca. 15-weeks old) remained vegetative under short days in the winter. In February, 1983, plants were placed under 24 hrs of light per day ("Gro-lights"). Both groups of older plants produced bracts and flower buds within one week, and the first flowers opened after 10 days. The four-week old plants had produced bracts but no flower buds after 6 weeks of long-day photoperiod.

Flowers of C. macrocalyx open in midmorning and close in the late afternoon, each flower lasting for a single day. The anthers contain 100-150 pollen grains each and are positioned at the throat of the corolla. The stigmas are at the same

level or about one mm below. Self-fertilization occurs through the release of pollen directly onto the stigmas, and there is little chance of out-crossing. Fresh pollen was stained with cotton-blue in lacto-phenol to check for viability. All grains appeared full and normal. Pollen-tube formation is rapid; although the style is shed with the shriveled corolla, often within 24 hrs after pollination, seeds develop normally. No pollinators have been observed at any time in native populations or on cultivated plants. Small beetles (Bombyliidae) pollinate some members of the genus Collomia (Grant and Grant, 1965) and similar insects may occasionally visit C. macrocalyx. The combination of small, inconspicuous flowers, anthers directly above the stigma, and a good seed-set without insects is a well-known indicator of autogamy (Pijl, 1980), and autogamy is well developed in the genus Collomia (Grant and Grant, 1965; Wilken, 1982).

In occasional flowers of C. macrocalyx growing in nature, the stigmas are exerted well above the stamens. This was observed in two out of 15 flowers (13.3%) dissected from dried Fossil and Lonerock specimens. When brought into cultivation in Prineville, C. macrocalyx from five sites produced exerted stigmas 50.3% of the time, ranging from 25.0% to 80.0% in different populations (Table 5). Flowers with exerted and inserted stigmas were sometimes observed on the same plant under cultivation.

Baker's Law (1955) predicts that disjunct populations self-pollinate more than populations in the central region of

a species' range. Lewis (1963) states that most autogamous species have measurable rates of out-crossing. Exserted stigmas would be expected to promote out-crossing, but how often this happens with the occasional exserted-stigma flowers in C. macrocalyx is unknown. The probability of out-crossing is usually greater in more hospitable environments. The ability to respond phenotypically to better growing conditions under cultivation, expressed in the production of more exserted stigmas, may increase out-crossing possibilities in nature. The cultivated plants that continued to produce predominantly inserted stigmas (Trout Creek and Lonerock) are from populations that are located farthest from the present C. macrocalyx population center. Antelope I and II are on ridges within sight of each other and at the center of known localities for C. macrocalyx; both have exserted stigmas predominating in cultivated plants. Antelope III is 8 km east of the first two Antelope sites and has an equal number of inserted and exserted stigmas. Results of a chi-square test for homogeneity for the five sites indicated that the stigma insertion data vary significantly among the five sites, though Antelope I and II, and Trout Creek and Lonerock, are pairs which are similar (Table 5). The peripheral populations may be genetically programmed to be stronger selfing, and therefore, pioneering, species than the central populations near Antelope and Shaniko.

### Seed-set and dispersal

Capsules ripen one to two weeks after fertilization. In the field, seed-set is better early in the season. One of the three seeds sometimes aborts, with the shriveled seed remaining attached to the placenta after the other two seeds have been dispersed. Failures in pollination, pollen-tube formation, or fertilization may be responsible. The development of autogamy in the species makes pollination failure unlikely; the second and third factors are perhaps more probable, but they have not been investigated. A more likely explanation is that seeds abort soon after fertilization because physiological stress limits resource allocation to the third seed. With the onset of summer drought, more seeds, and even entire capsules abort as a prelude to general senescence.

Seed-set in cultivated plants grown in Prineville during the summer of 1982 was studied (Table 7). These plants were never subject to severe drought although they were regularly allowed to dry to the point of incipient wilt. Of the 267 capsules examined, all three ovules developed into apparently good seed in 59.5% of the individuals and one seed aborted in 23.2% of the cases. Exserted- and inserted-stigma flowers appeared to have similar seed-set, although seed-set data (Table 7) were not separated by stigma placement in flowers.

When seeds ripen, the capsules dehisce loculicidally, taking about 24 hours from the time the suture first splits until the seeds are fully exposed. The placental septum detaches

from the base of the capsule. As it dries, it pushes up and out, and in the process the seeds are ejected from the capsule as active ballists (Pijl, 1982). Seeds observed at Antelope III and Trout Creek and in cultivated plants in Prineville were usually deposited within 10 cm of the parent plant. In capsules that abort only one seed, the placenta detaches from the calyx and the loosened placenta is eventually blown away. Capsules that abort two or all three seeds have a placenta that remain attached.

Because most seeds fall close to their parents, usually deep into a rocky substrate, the probability of long-distance dispersal is low. Small mammals, birds, or large insects may conceivably carry seeds out and away from the rocks. Surface run-off does not appear to be great. The land is water-logged or frozen from October through May, but lateral movement of water is usually minimal. I found fewer seeds than expected around isolated C. macrocalyx plants in midsummer, in comparison to the number presumed to mature on a given individual; insects, birds, or rodents may be harvesting them.

When adequate moisture is present, mucilage in the seed coats causes the seeds to adhere to the soil or rocks where they have fallen (atelochoy), or to a dispersal agent that transports them away (epizoochoy) from the parental site. Calculations have been made of seed production based on seed-set (Table 7), size and density of plants at three sites (Table 6) have been made (Table 8, 9). At the CRNG site, the

Table 7. Seed development in cultivated Collomia macrocalyx.  
Proportion of capsules with different numbers of normal seeds.

<u>Seed source</u>	<u>Number seeds developing per capsule</u>								total per site
	3	%	2	%	1	%	0	%	
Antelope I	21	65.6	8	25.0	1	3.1	2	6.3	32
Antelope II	41	75.9	4	7.4	2	3.7	7	13.0	54
Antelope III	39	55.7	14	20.0	0	.0	17	24.3	70
Lonerock	12	85.7	1	7.1	1	7.1	0	.0	14
Trout Creek	47	48.5	35	36.0	8	8.2	7	7.2	97
Total Numbers	160		62		12		33		267
Percent of total		59.9		23.2		4.5		12.4	100

Table 8. Flower and seed production by Collomia macrocalyx at three sites.  
August 1982.

Size classes*	CRNG (10 X 20 m grid)		CRNG		Antelope II		Trout Creek	
	# pls	%total	# pls	%total	# pls	%total	# pls	%total
I (1-5 fls)	94	44.5	99	49.5	171	85.5	74	37.0
II (6-10 fls)	67	31.8	65	32.5	26	13.0	93	46.5
III (11-20 fls)	41	19.4	33	16.5	3	1.5	5	2.5
IV (>20 fls)	9	4.3	3	1.5	0	.0	5	2.5
	<u>211</u>	<u>100.0</u>	<u>200</u>	<u>100.0</u>	<u>200</u>	<u>100.0</u>	<u>200</u>	<u>100.0</u>
<u>Estimated average flower production**</u>								
	<u># fls</u>	<u>%total</u>	<u># fls</u>	<u>%total</u>	<u># fls</u>	<u>%total</u>	<u># fls</u>	<u>%total</u>
I X 2.5	235	14.2	247.5	18.1	427.5	62.5	185	12.3
II X 8.0	536	32.4	520	37.9	208	30.4	744	49.5
III X 16.0	656	39.7	528	38.5	48	7.0	448	29.8
IV X 25.0	225	13.6	75	5.5	0	.0	125	8.3
	<u>1652</u>	<u>99.9</u>	<u>1370</u>	<u>100.0</u>	<u>683.5</u>	<u>99.9</u>	<u>1502</u>	<u>99.9</u>
Seeds/fl if perfect set	x 3		x 3		x 3		x 3	
Total estimated seed production	4956		4111.5		2050.5		4506	
Average pl size (# fls/pl)	7.8 x 3		6.9 x 3		3.4 x 3		7.5 x 3	
Average seed set/pl if perfect set	<u>23.4</u>		<u>20.7</u>		<u>10.3</u>		<u>22.5</u>	

\* Data from table 6.

\*\* Numbers used are the median for each size class above.

Table 9. Estimated seed production under idealized conditions of little or no water stress.

<u>Site</u>		<u>CRNG grid</u>	<u>CRNG</u>	<u>Antelope II</u>	<u>Trout Creek</u>
Total fls per 200 pls*		1565.9	1370.5	683.5	1502.0
<u>Seeds per capsule</u>	<u>Theoretical proportion of seed produced**</u>				
3/3	.599	2813.9	2462.8	1228.2	2699.1
2/3	.232	726.6	635.9	317.1	696.9
1/3	.045	70.5	61.7	30.8	67.6
0/3	.124	.0	.0	.0	.0
Total seeds per 200 pls	1.000	3611.0	3160.4	1576.1	3463.6
Average seeds per pl		18.1	15.8	7.9	17.3
Average seeds per pl if seed-set were 3/3		23.4	20.7	10.3	22.5

\* from table 6; CRNG grid adjusted to 200 pls.

\*\* from table 7.

211 individuals scattered in a 10 X 20 m grid produced an estimated 1652 flowers. If seed set were perfect, these would yield 4956 seeds, or 23.4 seeds per plant on the average. When actual rates from seed abortion are calculated (Table 7), the estimated number of seeds produced by the 211 plants in the grid at CRNG (Table 6) falls to 3809 (Table 9) or an average of 18 seeds per plant. Because of the limited area sampled by the grid this figure should be doubled or tripled to estimate the entire population at this particular site.

Within the grid, only about 5% of the potential seed source (3809) became established as mature plants (211). Possible explanations could be: 1) seeds are being dispersed away from the site; 2) seeds are being eaten or otherwise destroyed; 3) seeds are not viable; or, 4) seedlings are not becoming established after successful germination on site. Many seeds are found in the rocks, but seeds shed off the rocky sites soon disappear. No dispersal agents have been identified, although mucilaginous seeds have been implicated in long-distance dispersal (Grant, 1959; Hsiao and Chuang, 1981). Although I have not seen seeds being eaten, Corimelid bugs, which are known to eat developing seeds, are present at Trout Creek. Some predation by insects such as the seed bugs (Lygaeidae) is also likely. Lack of seed viability is probably responsible for some loss. Failure of seedlings to become established probably accounts for a major portion of seed loss, at least in the rocks.

### Predation and disease

Observed predation on C. macrocalyx included partially eaten bracts and severed stems, inflorescences bound together by leaf-roller insect larvae, and bract deformation by eriophyid mites. Three insect taxa have been found in association with C. macrocalyx.

Leaf-roller larvae were present at Trout Creek and Antelope II in 1981 and again at Antelope II in 1982. No more than a dozen larvae or cocoons were observed at either site at any one time. Larvae which pupate in small- to average-sized plants (1-10 flowers) of C. macrocalyx construct their cocoons in a manner that seriously impairs flowering. This effectively curtails seed production by the host plant unless it can produce a new inflorescence on a side branch. The larvae were reared on the more abundant Willamette Valley taxon, Collomia heterophylla Hook., on which they pupated and emerged as adult moths. The moths, submitted to the Oregon State University Entomology Museum for identification, were assigned to family Tortricidae, Order Lepidoptera, but could not be identified to genus and species. The tortricids are a large family, and it is not known whether the taxon found in association with C. macrocalyx is a generalist or if it is specially adapted to this particular host taxon.

Corimelaena extensa Uhler, "Negro bugs" (family Corimelaenidae, order Hemiptera), were present at Trout Creek in June and July, 1981. Collections were made, and identification was provided by Dr. John D. Lattin, O.S.U.

Entomology Museum. Members of the group are usually generalists, common on vegetation and flowers, and are known to eat developing seeds. I could not be sure that the bugs were actually feeding on any part of the C. macrocalyx plants, though some bracts had been chewed. The bugs were plentiful on C. macrocalyx and absent from nearby unrelated taxa.

The bracts of several plants found at Lonerock were infested by eriophyid mites (family Eriophyidae, order Actinedida) in 1981 and 1982. Infested bracts are fleshy, toothed at the tip, and their sides are sealed together. Flowers that would normally develop at the base of the bracts are inhibited, and seed production is reduced.

Leaves at the Lonerock site showed evidence of insect damage, but no herbivorous insects were encountered during my visits there. Plants whose stems had been severed were found occasionally at several sites.

The three insect taxa which were observed on C. macrocalyx have a minor impact on the species and do not constitute a serious threat to the affected populations. Browsing damage by large mammals was not evident.

No symptoms of disease were detected on C. macrocalyx at any of the sites visited during the 1981 and 1982 field seasons.

## DISCUSSION AND CONCLUSIONS

Evolutionary trends

Grant (1959) places the origin of the Polemoniaceae in Mexico at a time when warm, moist tropical climate prevailed over an extensive area. A subsequent split between early members of the group resulted in the eventual development of the Gilia tribe to the south and the Polemonium tribe to the north. The Gilieae were well-adapted to warm climates, developed a tolerance to drought, and were eventually incorporated into the Madro-Tertiary geoflora; the Polemonieae retained their requirement for high moisture but adapted to cooler temperatures, becoming an element of the Arcto-Tertiary geoflora. Much intermingling of the tribes has taken place since, and some of the most abundant and characteristic members of the spring flora of North America are in the family Polemoniaceae.

The Great Basin is not an area of high endemism but rather a meeting place for Rocky Mountain (Arcto-Tertiary), Southwest (Madro-Tertiary), and Pacific coastal floras. Climatic fluctuations associated with Pleistocene glaciation resulted in major environmental changes. Migrations north and south, as well as altitudinally, fragmented plant communities and isolated species. High rates of speciation are common under such extreme environmental change (Axelrod, 1967). The change in adaptation of a species from mesic to xeric conditions would lead to preferential expansion of its range once it had acquired the potential for desert survival. In

the Great Basin, widespread species are commonly found at lower elevations with related endemics restricted to higher elevations. Most of the low-elevation flora has become established within the last 10,000 years (Grant, 1959; Reveal, 1979). Migration of the Madro-Tertiary geoflora has mostly been from south to north and up in elevation. East of the Sierra-Cascade axis, the majority of mid- to high-elevation migrations have been from east to west, from the Rocky Mountains, and southward into Nevada via southwest Idaho and southeast Oregon.

Determination of evolutionary trends for the Polemoniaceae has been based entirely on the study of extant taxa, because no good fossil record exists for the family. According to Grant (1959) and Wherry (1944), primitive and derived traits are held to be:

<u>Primitive</u>	<u>Derived</u>
mesic habitat	*xeric habitat
rhizomatousperennials	*non-rhizomatous perennials and annuals
x=9	x=6
alternate, pinnate leaves	*opposite, linear leaves
bracts absent	*bracts present
herbaceous calyx	*membranous calyx
regular calyx teeth	*irregular calyx teeth
campanulate corolla	*funnelform to salverform corolla
large, xenogamous flowers	*small, autogamous flowers

equally inserted stamens	*unequally inserted stamens
septicidal capsule	*loculicidal capsule
*dehiscent capsule	indehiscent capsule
many-seeded carpels	*one-seeded carpels
non-mucilaginous seed-coat	*mucilaginous seed-coat

The species of Collomia range from those having traits mostly in the first column, to Collomia macrocalyx (\*) which possesses traits that are almost entirely in the second column. The genus is assumed to be of Arcto-Tertiary origin, with the majority of species presently centered in the northern Rockies and the Pacific Northwest (Grant, 1959). Twelve of the 14 species in the genus, including all of the primitive members, are native to this region. The genus contains good examples of speciation following range expansion and displacement (Daubenmire, 1978) and long-distance dispersal (Grant, 1959). A primitive ancestor may be hypothesized to have expanded its range and migrated south and down in elevation in response to Pleistocene cooling, invading the Great Basin from the north. As the glaciers receded, migration reversed. As temperatures warmed the species moved upslope to their present positions at higher elevations. The perennials with long tap-roots and large xenogamous flowers were well-adapted to rocky, alpine habitats left behind by the glaciers. The populations became isolated in the Rockies and along the Sierra-Cascade axis and eventually differentiated into four distinct species. These taxa are closely related morphologically, palynologically and

biochemically. They retain many of the hypothesized traits of the primitive ancestral type and together comprise the section Collomiastrum. Collomia mazama, a member of this section, is close to Polemonium in both morphology and flavanoids and may represent a link to that more "primitive" genus.

Warming and drying in the Hypsithermal Interval, 6,000 B.P., forced many montane species higher upslope (Detling, 1968; Reveal, 1979). Collomia taxa which persisted at lower elevations on both sides of the Sierra-Cascade crest eventually differentiated into several species. They are more widely adapted than sect. Collomiastrum, possess many derived characteristics and fall into two distinguishable taxonomic sections. On the wetter, oceanic side of the mountains, two of the annual taxa that evolved are now placed in sect. Courtoisia. Collomia heterophylla is a widespread species of mesic sites from British Columbia south to central California; C. diversifolia is restricted to serpentine soils in the southern part of C. heterophylla's range. The two taxa are morphologically similar. Collomia heterophylla's pollen is similar to that of C. tinctoria and C. tracyi in sect. Collomia, and these three differ significantly from the rest of the genus. The flavanoid pattern of C. heterophylla is closer to C. grandiflora and C. linearis in sect. Collomia than it is to C. diversifolia, though all of the taxa in these two sections show a large amount of flavanoid variation (Wilken et al., 1982). Sect. Courtoisia is somewhat

intermediate between the primitive sect. Collomiastrum and the more advanced members of sect. Collomia.

Though they are all closely related morphologically two distinct groups can be recognized among the species of sect. Collomia. The first group is composed of C. tinctoria, C. tenella and C. tracyi; the second contains C. linearis, C. grandiflora, C. macrocalyx, and two South American species, C. biflora and C. cavanillesii. All of the North American species except C. tracyi are native to the northern edge of the Great Basin. The C. tinctoria group is adapted to more mesic, mid-elevation sites while the C. linearis group is better adapted to xeric conditions at lower elevations. The former are morphologically the most specialized in the genus and contain the most flavanoids. Collomia tinctoria represents a highly variable complex throughout its range. In the C. linearis group, the two South American species have similar floral, vegetative, and pollen morphology, and flavanoid composition. Collomia cavanillesii is the only polyploid reported in the genus, and Wilken (pers. comm.) believes that it may prove to be conspecific with C. biflora, with both related to C. linearis of North America. Collomia linearis is intermediate among the taxa of Collomia in leaf, floral and inflorescence morphology, and in flavanoid composition, placing it at a point of evolutionary divergence between the perennial and annual taxa (Wilken et al., 1982). Collomia grandiflora's floral and pollen morphology exhibit similarities with the primitive sect. Collomiastrum. It is

the only xenogamous species in sect. Collomia in North America.

Collomia macrocalyx has the most advanced morphology and the most distinctive flavanoid profile in the genus. It is morphologically related to both C. linearis and C. tinctoria and can be fitted into either group depending upon which characteristics are stressed (Table 10). Floral traits show affinities with C. linearis while vegetative traits suggest relationship to C. tinctoria. Pollen (Chuang, 1978) and flavanoid studies (Wilken et al., 1982) reinforce its placement closer to C. linearis. Collomia macrocalyx probably originated sometime between the late Pleistocene and the Hypsithermal from a primitive relative similar to a present-day member of sect. Collomiastrum. It may be that C. macrocalyx, C. tinctoria, and C. linearis diverged about the same time. Of these taxa, C. linearis became the most widely-adapted, xeric species, C. tinctoria occupied mid-elevations, where it favored a habitat similar to C. linearis, though more mesic, and C. macrocalyx remained at low elevations where it retreated to the physiologically most stressful but less competitive rocky, thin-soiled areas. Collomia macrocalyx and C. tinctoria are a good example of related species separated temporally and elevationally within the same geographical range (Figure 5). Neither is common, though C. tinctoria has a wide geographical range.

The discovery of a new taxon, still only poorly studied

Table 10. Comparison of seven species of section Collomia with representative species of sections Collomiastrum and Courtoisia.

Sect. <u>Collomia</u>	Leaves	Bracts	Corolla	Filament	Range	Flowering
<i>C. grandiflora</i>	linear/ lanceolate	lanceolate	funnelform showy	uneven, 4 long & 1 long	widespread E Cascades	June- August
<i>C. linearis</i>	lanceolate	lanceolate	funnelform	uneven, 2 long & 3 short	widespread E Cascades	May- August
<i>C. macrocalyx</i>	spatulate	linear	funnelform	uneven, 5 short	central, NE & SE OR	April- June
<i>C. tenella</i>	linear or lanceolate	linear & few	funnelform?	even, 2 long & 3 short	central WA, central ID, NE OR, NV, UT, NW WY	June- July
<i>C. tinctoria</i>	linear	linear & few	salverform	even, 2 long & 3 short	central WA, central ID, E OR, N NV Sierras	June- August
<i>C. tracyi</i>	linear	linear	funnelform	uneven	Siskiyou	July
<i>C. sp. nov. ined.</i>	linear?	linear	funnelform	uneven, 5 short	SE OR, NE NV	May- June
sect. <u>Collomiastrum</u>						
<i>C. debilis</i>	toothed	toothed & few	funnelform showy	even, 5 long	alpine, NE OR, WA Cascades & Olympics	July
sect. <u>Courtoisia</u>						
<i>C. heterophylla</i>	toothed	entire to toothed	funnelform	uneven	W Cascades BC to N CA; N ID	May- July

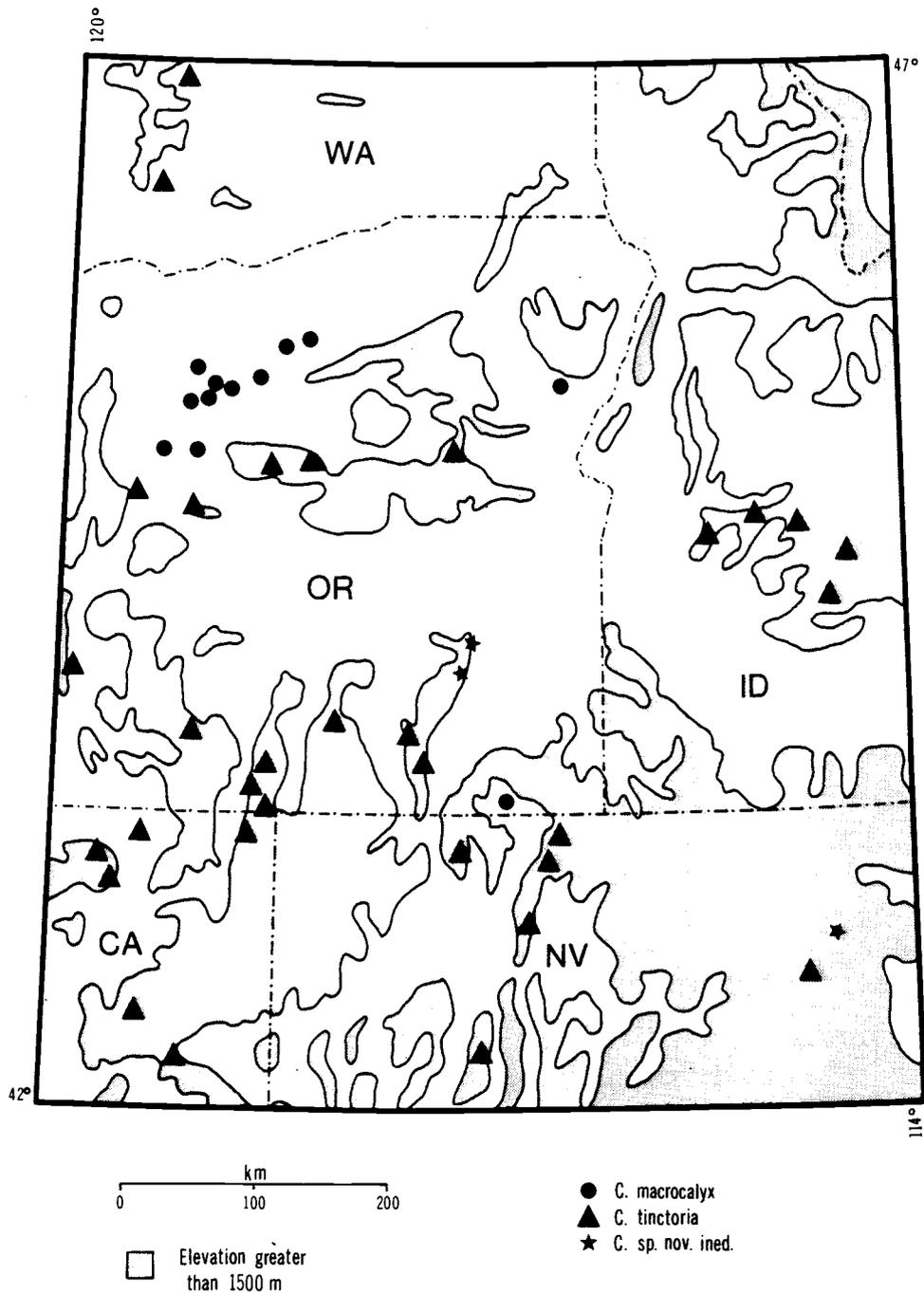


Figure 5. Distribution of *Collomia macrocalyx* and related taxa in the northwestern Great Basin. (*C. linearis*, which is not illustrated, is found throughout the range of the species illustrated.) All points are plotted from herbarium records.

but apparently intermediate morphologically between C. macrocalyx and C. tinctoria, raises new questions about the purported relationship between the latter two species. As in the case of C. macrocalyx's relationship to C. linearis and C. tinctoria, the undescribed taxon can be placed closer to either C. macrocalyx or C. tinctoria, depending upon which characteristics are emphasized. The pollen of the newly-discovered species is similar to that of C. macrocalyx. It is found on the edge of the range of both species where the two overlap (Figure 5). Whereas the known elevational distribution is similar to that of C. tinctoria, the taxon flowers in the spring like C. macrocalyx, whereas C. tinctoria flowers from mid- to late summer. It may be that the undescribed taxon is an evolutionary offshoot from either C. macrocalyx or C. tinctoria. Alternatively, it may be of hybrid origin, though the high degree of autogamy in both related taxa and the rarity of hybrids in the genus, make this a less likely possibility.

Because C. macrocalyx has such widely disjunct populations, it has been thought to be a relict species that formerly occupied a larger, more contiguous range. It is believed to have lost range, its populations having become separated in response to changing climatic conditions. An alternative hypothesis is that C. macrocalyx evolved relatively recently within a restricted geographical area and has not expanded its range except for a couple of successful long-distance events. It frequently occupies a rocky

habitat not unlike the perennial species of Collomia found at higher elevations.

The Polemoniaceae are well suited to long-distance dispersal (Grant, 1959). Given the widespread distribution of closely related taxa, all having mucilaginous seed coats, the chance dispersal of C. macrocalyx seeds is highly probable. Collomia macrocalyx, however, has difficulties in establishment after germination, and it is probably a poor competitor. The probability of successful establishment in a new site is thus a major obstacle, the result being a species with a restricted distribution. The two known disjunct populations may be the product of successful establishment after long-distance dispersal to a favorable site.

If the first hypothesis is favored, the presence of a well-defined community of associated species at the different sites, especially the widely disjunct sites, would strengthen the argument; the occurrence of C. macrocalyx in different communities would weaken the hypothesis. Several community types have been described for lithosolic associations (Daubenmire, 1970). The associated species found on C. macrocalyx sites are mostly much more widespread than is C. macrocalyx itself. Without more detailed study of the sites and of the lithosolic plant communities of eastern Oregon, it is not possible to determine if C. macrocalyx is a component of a "well-defined" community type. Whether it is an ancient relict or neo-endemic with some successful long-distance dispersals thus can not be readily answered.

### Species status and recommended management

Collomia macrocalyx is a rare annual endemic to eastern Oregon. Reasons for its restricted range are probably innate to the species rather than the product of recent habitat modification. The species has been variously listed as "proposed endangered" (Federal Register, 1980; Ayensu and de Philipps, 1974), "sensitive" (U.S. Forest Service, Ochoco National Forest, unpubl.), and "very rare and endangered" (Siddall et al., 1979) by federal and state agencies. In order to make recommendations for listing, categories established by these agencies must first be reviewed. The biology of the species and perceived threats to its continued existence must be evaluated before it is assigned to the most appropriate category. On the federal level, a taxon can be proposed endangered or threatened, or it may be deleted for one of several reasons; the U.S. Fish & Wildlife Service assigns taxa to final listing after research shows that the taxa warrant assignment to their respective categories. Federal agencies are directed to manage public lands so that the possible impact on endangered and threatened species is minimal. Environmental Impact Statements must be prepared when any major action is proposed which may alter the habitat of an endangered species. The categorical listing of taxa frequently changes as new knowledge is gained concerning their biological range or ecological requirements. Successful management has as one of its goals the eventual deletion of a taxon from listing, after its populations are stabilized and

threats are eliminated.

New species evolve and old ones become extinct as part of the natural processes of evolution. The concern today is that the rate of species extinction has been unnaturally accelerated by human activities. To be listed as "endangered" a species must be threatened with extinction in all or a substantial portion of its range in the future. Reasons for endangerment may be man-made (e.g., loss of habitat, over-collecting) or may be due to natural changes in the habitat of the species to which it can not readily adapt. Threats may be man-made or natural, but the threat of extinction is not imminent. If a species is restricted in distribution and habitat, but has no perceivable threats to its survival, it is rare but does not warrant protection under the U.S. Endangered Species Act. "Threatened" or rare taxa are frequently retained on state "watch lists" whose purpose is to monitor small populations which may require listing and/or management in the future. One example that has been used to illustrate the difference between endangerment and threat or rarity states that if a bulldozer could destroy the only population of a species in a day, then a listing as endangered is warranted. The important points here are: 1) the populations are small and restricted, and 2) they are readily accessible.

Two years ago, C. macrocalyx had only two known extant sites and five that were unverified or had been destroyed recently. One of the extant populations was in fenced

rangeland at the southern edge of the wheat-growing region of the Columbia Plateau. The second was in a forest opening, with a helispot located on a flatter part of the same ridge. Given the paucity of sites and their relatively easy access, the species was proposed as "endangered" by the U.S. Fish & Wildlife Service (Federal Register, U.S.F.W.S., 1980). Field studies during the past two years have resulted in the rediscovery of two old localities and identification of nine additional sites. I have little doubt that several more localities could be found if the remainder of the "Antelope Scarp" north of Antelope were searched in detail. The sites vary in population size and possible threats (table 4 and section III.5., site descriptions).

Collomia macrocalyx is restricted to a specific habitat; its rarity is due more to its narrow ecological amplitude than to habitat modification. Specifically, poor establishment and competitive abilities coupled with low dispersal to suitable areas away from established sites are the major reasons for its rarity. Whether these factors constitute a real threat of extinction in the future hinges on the balance between its stable but precarious existence and perceivable increased habitat modification.

Areas occupied by C. macrocalyx are not prime agricultural lands though most are open to grazing. The generally rocky surface and poor forage produced on lithosolic sites make them unattractive to cattle (Daubenmire, 1970). Thus these areas are not heavily grazed

until adjacent grasslands have been severely depleted. One of the reasons that C. macrocalyx does not expand out of the rocky areas, however, may be that it can not take much trampling. Because the area is not intensely cultivated, the effects of agricultural spraying of chemicals are probably minimal. Isolated ridgetops along the Columbia River Plateau are neither tilled nor grazed by cattle and support some of the last undisturbed native grassland vegetation in the area (Rickard et al., 1978).

Rocky areas along highways are a source of gravel for local road construction. High ridges are prime locations for television transmitter stations; their structures, and the access roads to them are another disturbance on these sites. "Scab flats" in forest openings are not heavily grazed, but many are designated "helispots" for landing fire-fighting supplies, and such activity can seriously disturb vegetation during their brief periods of use. These are the major threats to native vegetation on these sites; each applies to one or more of the C. macrocalyx populations.

Sparta was "destroyed by road-building construction" in 1967. Part of Antelope II was destroyed by regrading of a road around a gravel pit in 1982; a substantial portion of the C. macrocalyx population is also along the gravel road which leads to a television tower. Fossil II is likewise situated along the edge of a gravel pit. There is a designated helispot at Trout Creek. The U.S. Forest Service has been notified of the presence of C. macrocalyx and

another proposed endangered species, Oryzopsis hendersonii Vasey, on the site.

The U.S. Forest Service and The Nature Conservancy have been informed of C. macrocalyx on their lands (Trout Creek and Crooked River National Grasslands, and Lawrence Grasslands, respectively). The McDermitt site is owned by the state of Oregon but is part of a large land exchange currently being negotiated with the Bureau of Land Management to consolidate holdings by the two agencies. The B.L.M. has been notified of the recent rediscovery of C. macrocalyx. Among privately owned sites, Lonerock was recently sold; the property was well-managed rangeland and The Nature Conservancy had been interested in acquiring the property prior to its sale to another rancher. During the winter of 1983, baled hay was fed to cattle at the center of the C. macrocalyx population. It is not known what the response of land owners would be if they were informed of the existence of an "endangered" species on their properties, as this could conceivably alter land use practices. Access is fairly easy to all sites except Antelope III and IV, which are on the tops of isolated ridgetops that cattle, and off-road vehicles, have extreme difficulty reaching.

When C. macrocalyx is evaluated throughout its known range, it becomes obvious that several populations face the threat of adverse human activities. Likewise, at least two sites are so well-protected that man-made threats to the populations are extremely low. The remaining sites appear to

be fairly stable; federal agencies are aware of the location and status of these populations and are not likely to undertake actions which might adversely affect C. macrocalyx. Privately owned properties could conceivably be modified in a manner which would threaten C. macrocalyx. However, given the current economic base of the area, the relatively poor soil quality, and the lack of mineable resources, a change of land use is not anticipated in the near future.

In summary, the relative rarity of C. macrocalyx, taken together with the perceived threats to its continued existence in some of its range, lead me to conclude that it should not be listed as "endangered" at this time, but that it does fit the federal category of "threatened" in all or part of its range.

Management: Collomia macrocalyx has little or no reserve of stored seeds in the soil. Its populations are thus particularly vulnerable to extermination if a severe winter were to result in the death of too many seedlings or if an early drought produced a very low seed set. One or more of the sites should be monitored to determine the response of populations to climatic fluctuations. Moderate grazing does not appear to be detrimental to the species. Some trampling may be beneficial if it produces openings in the cover of lichens and mosses in which C. macrocalyx might become established. This is probably not as beneficial to a poorly competitive annual as it might be to a weedy annual or a perennial species, which needs an opening for initial

establishment. Collomia macrocalyx has not been found in seriously over-grazed areas and probably could not take heavy trampling. If enough seed could be produced from greenhouse plants, an experiment might be designed to sow seeds along a gradient of rock to soil, and from dense vegetation cover to open ground. It could then be determined whether competition, water relations, a combination of the two, or some other factor is responsible for C. macrocalyx's restricted distribution.

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## APPENDIX

Appendix

## Specimens cited:

Collomia macrocalyx Leiberg. OREGON: Crook Co.: Trout Creek, Ochoco National Forest, 1370 m, Joyal 2, 198 (OSC). Gilliam Co.: Near Lonerock, 1240 m, Leiberg 113 (GH, ORE, isolectotype); near forks of Cottonwood Canyon, 1290 m, Leiberg 153 (GH, paratype); ca. 9 miles NW of Lonerock, Hitchcock 20588 (UW, NY); ca. 8 miles NW of Lonerock, Hitchcock 20501 (UW); 8.8 miles (14 km) NW of Lonerock, 1040 m, Joyal 42 (OSC). Jefferson Co.: ridge N of Japanese Creek, Crooked River National Grassland, 1125 m, Joyal 143 (OSC). Malheur Co.: 15 miles N of McDermitt, 1525 m, Peck 21721 (WILLU, CAS), Ripley & Barneby 9368 (NY), Joyal 144 (OSC). Wasco Co.: 3 miles (5 km) N of Antelope, 1055 m, Joyal 22 (OSC); 3 miles (5 km) N of Antelope, 1060 m, Joyal 23, 197 (OSC); 5 miles (8 km) E of Antelope, 1235 m, Joyal 73 (OSC); 3 miles (5 km) W of Antelope, 995 m, Joyal 130 (OSC); 3 miles (5 km) W of Shaniko, 1070 m, Joyal 88 (OSC); 3 miles (5 km) SW of Shaniko, 990 m, Joyal 142 (OSC). Wheeler Co.: 12 miles (19 km) S of Fossil, Leiberg s.n. (WSU, paratype).

C. sp. nov. ined. OREGON: Malheur Co.: Barren Valley, Leiberg 2189 (DS), Joyal 376 (OSC). NEVADA: Elko Co.: Pequop Mtns, 2070 m, Ripley & Barneby 4606 (CAS), Joyal 402 (OSC).

C. tinctoria Kell. OREGON: Crook Co.: Lookout Mtn., Ochoco National Forest, 2100 m, Joyal 181 (OSC). Harney Co.: Canyon of Wild Horse Creek, Steens Mtn, 1200 m, Peck 14103 (WILLU).

Lake Co.: NE of Lakeview, 1630 m, Ripley & Barneby 6060 (CAS). CALIFORNIA: Modoc Co.: Between Mill Creek Public Camp and Clear Lake, 1770 m, Hammerly 41 (CAS). IDAHO: Elmore Co.: Atlanta, Boise National Forest, 1980 m, MacFadden 15793 (CAS). NEVADA: Humboldt Co.: Buckskin Mtn, Santa Rosa Range, Ownbey & Ownbey 2794 (CAS); Jackson Mtns, 2165 m, Tiehm et al. 5017 (CAS). WASHINGTON: Klickitat Co.: Klickitat River, Suksdorf s.n. (DS).