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DISJUNCTION AND ENDEMISM IN THE FLORA OF THE CENTRAL WESTERN CASCADES OF OREGON: AN HISTORICAL AND ECOLOGICAL APPROACH TO PLANT DISTRIBUTIONS

by

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INTRODUCTION

The Western Cascades of central Oregon comprise a unique area of great floristic diversity. Included in the flora of the area are numerous species with disjunct distributions. About 95 percent of this region supports some phase of the broadly-defined mesic conifer forest (Detling, 1968), a low diversity floristic unit dominated by *Pseudotsuga menziesii* and species of *Abies* and *Tsuga*. Occurring in clearings, meadows, bogs, and on scree slopes and outcrops are numerous additional species many of which are typical of this region of the Cascades. However, approximately 20 percent of the flora of the region consists of species characteristic of other regions. These species are disjunct, often markedly so, in their Western Cascade occurrences. They are concentrated in, but not restricted to, the non-forest habitats. Disjunct elements in the Western Cascade flora include boreal, high alpine, Siskiyou-Klamath, Great Basin, and lowland valley species. Three species are endemic to the study region and its immediate environs. The study of the distributions of these disjunct and endemic species is the subject of this work.

Two distinct approaches have been taken in previous work on disjunctions. One, exemplified by the studies of Baker (1955, 1959a, 1959b, 1961) and Carlquist (1966a, 1966b), emphasizes the biological and evolutionary mechanisms which adapt plants for long-distance dispersal. Thus the role of invasion of new areas by plants is stressed, and disjunct segments are likely to be considered outliers of expanding populations. At the other extreme, the studies of Gleason (1922), Fernald (1925), Marie-Victorin (1938), and Detling (1953, 1954, 1958, 1961, 1966, 1968) are concerned with the historical aspects of disjunctions. These workers have tended to focus exclusively on the relictual concept (Fryxell, 1962) and to hypothesize retreating migration or incipient extinction to explain disjunct populations. Such studies normally center around the climatic changes of the Pleistocene and Recent epochs. A special case involves the study of nunataks, or isolated mountain peaks which were ice-free during the Pleistocene but surrounded by glacial ice. Such mountain peaks often support relics from the Wisconsin and previous glaciations, often far to the south of their normal ranges (Marie-Victorin, 1938; etc.).

In studies with both biological and historical hypotheses, several assumptions are made concerning the nature of disjunctions. Biological studies often consider geographical disjunction only, completely disregarding the time factor; while historical studies typically concentrate on large changes through time and often fail to consider important biological differences between species of similar geographic affinity. In addition, the historical approach normally assumes that at some time plants of a relict species occupied all areas between each locality of present occurrence. Inherent in both approaches is the assumption that the habitats of disjunct species, wherever they occur, are generally similar.

The Western Cascade Range bears significantly on the general problem of disjunctions in several ways. First, a large number of more or less discrete islands of disjunct species occur in the area. Second, the boreal, austral, cold desert, and high and low altitude species are found together, often in the same association type and occasionally so physically close that they are probably in competition with one another during certain seasons. Thus it seems that the general assumption that disjunct organisms are found in habitats generally similar to those of their parental populations is here violated. Such considerations show the Western Cascades to be an ideal area for studying the history and biology of disjunct species.

REVIEW OF THE LITERATURE

There is a paucity of published work that pertains directly to the geology or floristics of the Western Cascade Range. A summary of the existing literature in these two areas is given below.

Geology and Physiography

While Dicken (1955) and Baldwin (1964) present brief discussions of the physiography and geology of the Western and High Cascades, neither treats them in detail and both rely primarily on the findings of other workers.

Williams (1942, 1944, 1953) presents, in semi-popular form, the geologic history of these ranges together with considerations of the origins, products, and forms of volcanic eruptions. According to Williams (1953), the Western Cascades are the result primarily of fissure eruptions in a broad downwarping area. Small cones may have developed locally, but no evidence of their original forms remains. Eruptions began to the west, perhaps in what is now the Willamette Valley, during the Eocene and migrated eastward to the present crest of the High Cascade Range by the middle of the Pliocene. There were several periods of intense volcanism during the Tertiary, the most extreme of which included middle and late Miocene times. Between these periods of volcanism, erosion degraded the mountains and subsequent eruptions tended to fill the topographic lows. At the end of the

Miocene the older flows were uplifted and thrown into broad gentle folds. Although there was still some activity in Western Cascade vents by the beginning of the Pliocene, most volcanism by this time was localized in the present High Cascade Range, a north-south trending line of impressive composite volcanoes. Volcanic activity in the High Cascades has continued at lower rates into the present century.

The work of Thayer (1936, 1939) has elucidated the geology of the North Santiam River drainage, which extends from the Willamette River Valley to the crest of the High Cascades. Thayer describes the stratigraphy, structure, and glacial and erosional history of this diverse region, which forms the northern border of the area under consideration here. In his stratigraphic work, Thayer distinguishes as discrete formations any flows separated by a recognizable unconformity and groups the formations into "series" such as the Breitenbush, Mehama, and Sardine. Of particular interest are Thayer's ideas concerning the putative presence of the "Cascade fault scarp," which is considered (Thayer, 1936) to be a structural boundary between the Western and High Cascades. Thayer and previous workers had noted the sharp line physiographically delimiting the two ranges essentially throughout their length in Oregon. To the west the older range rises steeply to dissected ridges often over 1000 m above the floor of the line of valleys marking the boundary. To the east the High Cascade plateau slopes gently up to Recent cinder cones and finally to the high peaks which range from 2400 to 3500 m in elevation. After a reconsideration of some as yet unresolved stratigraphic problems, Thayer (1939) modifies his original opinion by observing that, at least in the North Santiam region, a fault need not be invoked to explain the observed stratigraphic relations. Of critical concern in this decision is the presence of a topographic and stratigraphic bridge between the two ranges which includes Outerson Mountain and related peaks. Such bridges are exceptional in the central Cascades.

Thayer (1939) calls attention to glacial moraines and reworked tills in the valley of the North Santiam River. The large alpine valley glaciers which deposited this debris had their origin high on the slopes of Mt. Jefferson, as much as 58 air km to the east. The Wisconsin glaciers, however, came barely into the Western Cascades from the higher mountains if Thayer's interpretations are correct. He also notes the presence of many small cirques and associated features in the more completely dissected portions of the Western Cascades. It is likely that some of these lower glaciers acted as tributaries to the larger valley glaciers. Hopson (1946) notes morainal features in the McKenzie River Valley, extending as far west as Blue River, or to an approximate elevation of 300 m.

Maps of numerous mining claims and petrographic and economic aspects of propylitically altered regions scattered through the Western Cascades are presented by Callaghan and Buddington (1938). Such areas of alteration are closely associated with small dioritic intrusive bodies, although the mineralization which makes them of economic value occurred later than the intrusions themselves--perhaps in the late Miocene. This is evidenced by mineral veins which cut through both altered country rock and the intrusive bodies, but are thought to be genetically related to the latter. Due to the extreme chemical complexity of the substrate in altered areas and possible subsequent effects on the vegetation patterns, such regions were excluded from the present study area.

The most recent and comprehensive studies of Western Cascade geology have been made by Peck (1960), Wells and Peck (1961), and Peck and others (1964). The last paper contains data on the stratigraphy, structure, and petrology of the region. Peck and others also discuss the intrusions and the concurrent and subsequent alterations of the country rock. A very large area is covered in this work, and a great deal of new information is presented. However, it is a pilot study needing extensive further documentation. Peck lumps the Mehama and Breitenbush Series of Thayer (1936) into the Little Butte Series of Wells (1956) and Wells and Peck (1961). He also treats the Sardine Series as a single formation. This conservative treatment is more in keeping with present lack of knowledge of the correlations of the beds in these groups of flows. The Little Butte is an important Western Cascade series to the west and south of the study area, but within the area it comprises only about 17 percent of the total surface (Peck and others, 1964). This dominantly tuffaceous series weathers rapidly and except for recent roadcuts and occasional brecciated vents has not been found to crop out in the study area. Peck dismisses Thayer's (1936) proposal of a series of faults between the Western and High Cascades with the observation that a linear scarp is not topographically evidenced at all localities.

Three geologic maps are available for the portion of the Western Cascades considered here. The first (Williams, 1957) is a reconnaissance map of the central portion of the High Cascades but includes the proposed western limit of the Plio-Pleistocene volcanic rocks of that range, which occur irregularly well into the physiographically-defined Western Cascades. According to the most recent map, Plio-Pleistocene flows cover about 44 percent of the present study area. However, proposed contacts between Miocene and Plio-Pleistocene flows were visited by the mappers in only a small number of instances, and these were confined to the most heavily forested areas of the Western Cascades, where good outcrops are extremely rare. Peck does demonstrate overlapping but probably statistically significant differences between the chemistries of Miocene and Plio-Pleistocene volcanics of the Cascade Ranges, but it appears that none of the reputed Pliocene rocks from the Western Cascades were included in these samples. Thus, the extent of Plio-Pleistocene rocks in the Western Cascades and the locations of contacts between them and older flows are still open to considerable question.

In summary, the basic history, structure, and stratigraphy of both Western and High Cascade Ranges is relatively well known and documented, but detailed information on any portion of the study area is lacking.

Phytogeography

The first published note of extra-limital species in western Oregon was made by J. C. Nelson in 1918. Using terms striking in their immediacy, Nelson (p. 23) states that

> . . . species which have been regarded as distinctively Californian are pressing steadily northward . . . . In the same way, species that have been considered as belonging to the flora of the interior are continually being transported down the Columbia, and even travelling over the low summits of the Cascades.

Although Nelson discusses only two species which are here considered important Western Cascade disjuncts (Gilia aggregata and Silene campanulata glandulosa), his early recognition of the major pathways by which disjunct species have arrived in western Oregon is noteworthy.

Two papers by Detling deal directly with floristics and phytogeography in the study area (1953, 1968). In a paper calling attention to the existence of dry-adapted species in "xeric islands" in Oregon west of the Cascade crest, Detling (1953) describes the general nature of the islands and discusses the present and postulated past distributions of the various "xeric" plant species. "Xeric" literally means "dry." Detling evidently uses the term only in a general sense, to denote plants found under conditions of low moisture availability. Seasonal changes in moisture in the Western Cascades render such a general definition of little use for more detailed ecological or physiological studies.

Detling (1953) plots the ranges of 32 "xeric species" on 8 mountain summits of the Coast and Western Cascade Ranges. Three of these islands (Castle Rock, Horsepasture Mountain, and Rebel Rock) are in the present study area and now have been sampled more completely. Of Detling's 32 xeric species, only 13 are considered of critical importance here. These are Allium crenulatum, Arabis holboellii retrofracta, Arenaria capillaris americana, Arnica parryi, Artemisia tridentata, Collomia linearis, Erigeron foliosus confinis, Gilia aggregata, Linum perenne lewisii, Lupinus arbustus neolaxiflorus, Phacelia linearis, Sedum stenopetalum, and Silene douglasii. Of the remaining, four were misidentified (Delphinium depauperatum = D. menziesii pyramidale;

Hackelia diffusa = *H. jessicae*; *Hieracium cynoglossoides nudicale* = *H. scouleri scouleri*; *Madia minima* = *M. exigua*); three are not xeric species, but are annuals or perennials of short growing season adapted to either snowbed or seep-slope environments (*Claytonia lanceolata*, *Crocidium multicaule*, *Erythronium grandiflorum pallidum*); and five are not found within the study area (*Lupinus lepidus medius*, *Poa scabrella*, *Sidalcea asprella*, *Sisyrinchium douglasii*, *Viola sheltonii*). Finally, seven of Detling's species, while basically "xeric" and restricted to rather specialized environments within the area, have proved quite widespread and common in surrounding regions and cannot be considered disjunct in the Western Cascades, although their presence there is notable and supports conclusions about more disjunct dryland species. The seven species are *Bromus polyanthus*, *Eriogonum compositum*, *Eriogonum umbellatum*, *Microsteris gracilis*, *Polygonum douglasii*, *Prunus emarginata*, and *Sanicula graveolens*.

Concerning the islands themselves, Detling notes rapid erosion as being responsible for the shallow soil depth and subsequent rapid drainage and desiccation by wind and sun. He suggests that the dark color of the igneous rock and associated higher heat-holding capacity result in a longer growing season in these habitats.

Detling uses the bog-pollen data of Hansen (1947) in discussing the warm dry climatic maximum of about 6000 years ago and concludes that his xeric species

> are relicts of a once widespread xeric flora which originated first, in the Rogue River Valley, and secondly, on the plateaus of east-central Oregon. They have persisted on the mountain summits because of the arid and relatively warm conditions of

> the shallow soil and exposed dark rocks, and the consequent freedom from competition with the surrounding mesic forest types. (p. 46-47)

He makes no note in this paper of the boreal and arctic-alpine species which occur with the xeric species.

In the larger context of the history of the vegetation of the Pacific Northwest, Detling (1968) reaffirms, without major change, portions of the Xeric Island Hypothesis. Here he summarizes the paleobotanical work of Axelrod, Hansen, and Heusser, discusses the migrational history of western North American angiosperms from their first appearances in the Cretaceous to the present, and describes the major extant vegetation units.

An unpublished dissertation reporting comprehensive natural history studies of the McKenzie River drainage has been presented by Hopson (1947). Her lists of the major plants and vertebrates and some of her comments on the geology of this region are helpful in understanding the general nature of the Cascade Ranges. Hopson reports several disjunct plant and animal species, mostly from the Western Cascades. The area encompassed by her work extends from the mouth of the McKenzie River near Coburg to the summits of the Three Sisters and covers an elevational range of over 3000 m.

Two workers have completed floristic studies in other portions of the Western Cascades. Baker (1949a, 1951) studied the flora of Fairview Mountain in southern Lane County where he noted a number of disjunct xeric and a few disjunct boreal species. Unfortunately, a significant number of Baker's species were misidentified, and voucher specimens of many others have not been located. In addition, Baker

(1951) claimed numerous "range extensions," although many of the species concerned had been collected previously either from the Fairview-Bohemia region or from localities still more distant from the presumed parental populations. Despite these limitations, however, his work was the pioneer floristic study in the Western Cascades and is of continuing value as the most comprehensive study of this highly diverse mountain peak.

In a more recent study of the flora of Monument Peak, Aller (1956) defines the major community types, hypothesizes on their origins and ecological requirements, and lists the plant species found on the mountain. Of particular interest to the present study are his comments on the wet Acer-Alnus community, which is a widespread feature of the north and east-facing slopes of the Western Cascades. Aller concludes that the factors responsible for its existence on Monument Peak include some type of disturbance of the dominant mesic forest coupled with only moderately steep slopes and abundant soil moisture. Aller emphasizes the dynamism of the various Monument Peak plant communities.

Several published and unpublished papers concern the floristics or ecology of the High Cascade Range adjacent to the area of present interest. Roach (1952) analyzes the phytosociology of the Nash Crater lava flows abutting the eastern side of the study area, naming and describing various associations according to the European system (Braun-Blanquet, 1932). An interesting outcome of Roach's work was documentation of the much greater diversity of the plant species of mesic and hydric habitats than in drier sites in the lava flows, some of which, according to Roach, may be as young as 400 years. The contrary is true in the Western Cascade flora, in that more species are adapted to habitats that are at least seasonally dry than to all other habitats combined.

In addition, three botanical studies have been completed in the region of the Three Sisters. Van Vechten (1960), in an unpublished dissertation, describes the timberline and alpine vegetation of the area. His work is of value in relating plant communities to the glacial processes which are so marked at high elevation in this region. Pechanec (1961) sampled the mosses of the High and Western Cascades in the latitude of the Three Sisters and found correlations between the moss communities and the trees and other plant species of the sample areas. Ireland (1968) published an illustrated flora with keys to the vascular plants he found within the region.

Several papers, while not concerned directly with the study area or its immediate environs, report studies of floristically allied areas. Publications by Detling (1954, 1958, 1961) discuss the floras of Saddle Mountain, Clatsop County, and the Columbia Gorge; and the ecology and history of the chaparral formation of southwestern Oregon. In each of these studies, species are divided into groups of geographic affinity, which are then discussed as migrational units. The areas discussed are among the most interesting regions in the Pacific Northwest, and numerous species occur in them which are found again, as disjuncts, in the Western Cascades.

Of minor importance to floristic considerations within the study area are the treatments of broad vegetational units or biotic zones such as those given in various manuals and short papers (Peck, 1925a, 1925b, 1961; Larrison, 1946). A large number of species which Peck (1925a, 1925b) suggests are characteristic of the valleys of southwestern Oregon or of the diverse areas of Eastern Oregon also occur in the Western Cascades.

OBJECTIVES OF THE STUDY

The objectives of the present work can be briefly stated as follows:

1. to elucidate the ranges of disjunct species occurring in the Western Cascades by analyzing the geographical, geological, historical, ecological, and biological patterns of the species and areas;

2. to examine the processes leading to and maintaining these disjunctions;

3. to test experimentally Detling's "Xeric Island Hypothesis" concerning the origin of Western Cascade disjunctions;

4. to investigate the role of disjunctions in the evolutionary history of the larger groups which have disjunct species in the Western Cascades;

5. to arrive at a better understanding of the nature of disjunctions in general.

INVESTIGATIONS UNDERTAKEN

Observations were made and experiments were conducted on several of the variables that might influence the distribution of Western Cascade disjunct species. An attempt was made to follow a more synthetic line of investigation than has previously been used.

Physical environments and vegetation units have been approached in a primarily descriptive manner, although some experiments were performed involving both. Other investigations centered on the various species showing extraordinary distribution ranges. Aspects studied include systematics, geographical and ecological distributions, dispersibility, pollinators, breeding systems, moisture regimes, and phenology. Experimental studies on germination and establishment were performed in the field and in the laboratory and included studies of inhibition of germination and growth by soils of differing parent materials.

PHYSICAL ENVIRONMENTS

Introduction

The area of the Western Cascades in which this study has concentrated is shown in Appendix B, p. 162. It is irregular in shape, and the north-south axis is elongated. The latitudinal boundaries approximately coincide with N 43° 58' and N 44° 40'; while longitudinal boundaries are W 122° 0' and W 122° 22'. The region is characterized geologically by primarily horizontal flows of andesites and basalts which have been locally intruded by dikes and plugs. Oligocene and Miocene flows have been gently warped, but more recent volcanic rocks have retained their original dips (Thayer, 1939). Erosion has produced a maturely dissected topography with numerous valleys and steep ridges, the peaks of which stand at a remarkably uniform height of 1500 to 1700 m. Average annual precipitation ranges from 1525 mm to 1900 mm. This is comparable to the rainfall on the immediate coast and is exceeded in Oregon only in isolated spots in the high Coast Range or the Cascades (Detling, 1948a, 1948b). Spring rainfall may be considerable, but little or no precipitation falls during the summer months. In winter the snowpack in the area may become quite deep (up to 4 m), but on south-facing slopes and ridgetops the snow frequently melts or is blown away. Winter air temperatures average well below freezing, although temperatures under or within the snowpack are consistently near 0° C.

Physiography and Geology

Several types of observations were made on the peaks themselves. Rock types were observed, and fresh samples were collected wherever possible. Field relations between flows, attitudes of flows, and evidences of faulting were noted but not quantified. Erosional features were noted together with physiographic effects on the composition of plant communities. The most significant of these findings are reported in the following paragraphs.

Relationships of Vegetational Units to Physiography

Several vegetational units were found to be closely associated with repeated physiographic features of Western Cascade peaks. Many of the south or west-facing slopes have thin, easily erodable soils. In addition, they are swept relatively clear of snow during winter and are the first habitats to melt free of snow in spring. These slopes support meadows which vary in cover and species composition with the amount of runoff available through the growing season and the depth of the soil. Such meadows were later used to help deduce erosional patterns and patterns of snow accumulation.

Snowpocket areas were found frequently on the north or east sides of ridges and in gentle depressions on the south-facing slopes. Such areas support a characteristic flora regardless of exposure direction. The presence of species such as *Orogenia fusiformis* and *Dicentra uniflora* indicate heavy accumulations of snow.

Certain species were found only in association with glacial physiographic features. *Ivesia gordonii*, *Polemonium pulcherrimum*, and *Douglasia laevigata*, all highly restricted species in the area, are found on vertical walls or in the derived fine scree around the headwalls of old cirques. These are all species of arctic or high alpine derivation.

Erosional Features

Various aspects of erosional processes were investigated. Isolation of various peaks was considered as a possible factor influencing the number of disjunct species supported. Problems both of dispersal and of reduced habitat size are greater on isolated peaks. The dominant ridge and valley structure of the Western Cascades results in few truly isolated mountain masses, but regions where several ridges come together can be compared with the few peaks which do not connect with any other by a high ridge. Three Pyramids, Crescent Peak, and Carpenter Mountain, isolated peaks of markedly differing aspect, support 19, 14, and 13 disjunct species respectively. On the other hand, Iron Mountain, Horsepasture Mountain, Lowder Mountain, and Rebel Rock, all at or near the junctions of major ridges, support 42, 30, 25, and 41 disjunct species respectively. Although other factors are also important, this evidence points toward isolation as one factor influencing the concentration of distributionally interesting species.

Numerous small Pleistocene glaciers were an important factor in the erosion of the Western Cascades. Steep headwalls of cirques and associated tarns occur for example on Three Pyramids, North Peak, Echo Mountain, Cone Peak, Browder Ridge, Lowder Mountain, and Indian Ridge.

The largest cirques are confined to the northern or eastern slopes of these mountains.

Certain other typical glacial features have not been observed in the Western Cascades. Many of the glacial valleys have been deepened by stream action since retreat of the ice, and V-shaped valleys are predominant in the Western Cascades except for the major river valleys, which contained valley glaciers from the High Cascades. In addition, no primary evidence of abrasion such as glacial striations have been found in the Western Cascades.

These findings may support Thayer's (1939) proposal that the Wisconsin ice did not advance as far in this region as did glaciers of earlier maxima. Hopson (1946) invoked a sudden melting of glacial ice to sluice away the striated rocks in the U-shaped White Branch Valley. Such sluicing would, however, produce a V-shaped valley, and this hypothesis does not appear tenable. In this instance, striations (if persistent) may well be buried beneath morainal deposits and talus. Another alternative to Thayer's proposal is that at these low elevations the Wisconsin ice would have melted much earlier than ice in higher alpine regions to the east, allowing more time and better conditions for weathering and erosion of the less durable glacial features.

Since many of the slopes supporting disjunct species seem to be in rapid movement, experiments were conducted on the rates of erosion of various types of slopes on Iron Mountain. In October, 1966, iridescent yellow spray paint was applied in horizontal and vertical lines at a height of about 1.2 m to two vertical scoriaceous outcrops of different freshness and to two slopes of unconsolidated material. One of the latter was a creep-slope of fragments averaging over 3 cm in diameter, and the other was composed of fine scoria averaging less than 5 mm in diameter. All slopes were examined after nine months and after one year. After nine months, only occasional pieces of paint-flecked gravel and sand were evident on the fine scoria slope. Some of these fragments had migrated 3 m or more downslope from the original line. At the end of one year, a thorough search recovered no painted rocks in the area.

Other surfaces did not erode so rapidly. The line on the slope of larger unconsolidated material was still evident after one year; the most distant pieces were found about 1 m downslope. After 21 months, painted fragments were aligned parallel to the slope in a drainage furrow. This spot was found later to be covered continually with snow from early winter until July. Lines on the vertical outcrops were still quite fresh, except that the paint had flaked off the rock in several spots, perhaps indicating that the rock was not covered by snow during the winter and was alternately heated and cooled. The more weathered outcrop had lost several small chunks of rock, amounting to approximately five percent of the total line area. Evidently all loss of paint from the less weathered face was due to flaking. These results demonstrate a wide range in stability of closely proximate habitats on the same slope. Similar results were obtained using allied techniques in British Columbia by Brink (1964).

Stratigraphic and Structural Geology

Structural and stratigraphic investigations in the Western Cascades are difficult for the following reasons: (1) the percentage of unweathered outcrops is very small; (2) the individual flows seem to be of limited extent and cannot ordinarily be followed from peak to peak; (3) the lithology of the volcanic rocks can vary considerably, even within a single flow, while the chemistry may remain essentially the same; (4) the orientation of flows is difficult to determine; (5) absolute dates for the rocks are not obtainable with any degree of accuracy. Each of these points merits further consideration.

In only one instance was a single flow observed in two separate localities. An outstanding bright red band of scoriaceous basalt of approximately 2 m thickness on Iron Mountain was also found, much reduced in thickness, on the lower slopes of Browder Ridge about 1.6 km distant. The andesitic basalts in the region of Iron Mountain are strongly flow-banded. According to three-point determinations they dip to the east-southeast at 5-8°. Peck and others (1964) map these flows as a vent in the Plio-Pleistocene High Cascade volcanic rocks, but flows throughout this area are nearly parallel and show no brecciation. Furthermore, according to both Peck and others (1964) and Thayer (1939), Plio-Pleistocene flows are not deformed but retain their original dips. No Plio-Pleistocene volcano of the magnitude required to have produced all these parallel flows can be postulated for this deeply dissected area; and the attitudes correspond to those reported for the eastern limb of the Breitenbush Anticline (Peck and others, 1964; Thayer, 1939). Thus it seems likely that much or all of this region is actually composed of the youngest flows of the Miocene Sardine Formation, which are presumably the most recent rocks included in the general period of deformation which produced the Breitenbush Anticline. It is also possible that contrary to the opinions of Peck and Thayer, some of the early Pliocene flows may have been warped together with the Miocene and older rocks. An angular unconformity of less than 10^{o} between flows exposed on the "nigger baby," an erosional remnant on the southeast face of Iron Mountain, may suggest that these flows are contemporaneous with the uplift and folding of the Western Cascades. The origin of the flows is unknown, but the latter hypothesis indicates a source area to the southwest.

Volcanic rocks of the Western Cascades range from olivine basalts to rhyodacites, but the few samples analyzed from the more recent flows are primarily basaltic andesites (Peck and others, 1964). The appearance of these rocks is highly variable, especially regarding color, texture, and the presence of phenocrysts, while the chemical compositions seem, from the little work yet completed, to remain rather constant. Hand specimens are thus difficult to identify to type.

Flows where banding is not obvious are most common and are typically exposed for only short distances, making determinations of their orientations extremely difficult.

Some dating of Western Cascade rocks has been attempted using fossil floras and lead radioactivity determinations (Peck and others, 1964). Fossil leaves are known from a number of localities in the Western Cascades, but dating by this method is highly restricted and imprecise. Lead radioactivity dates are possible only from the dioritic intrusives. These methods have indicated ages of more than 35 ± 10 million years for portions of the Little Butte Series and of more than 25 ± 10 million years for the Sardine Formation (Peck and others, 1964,

p. 40). Extrapolations from the sites where dates have been obtained to other areas should be made only with great care. It is unlikely that either of these techniques will aid in discovering the contact between Miocene and Pliocene volcanic rocks in the Western Cascades, or the contact between Western Cascade flows and those of the High Cascades. Intensive field work in the area will be necessary before these problems can be solved.

A striking physiographic feature noted in the course of this study is the "valley-in-valley" effect found along the western margin of the area, especially in the valleys of Blue River, Tidbits Creek, Canyon Creek, and Squaw Creek. In these areas the higher mountainsides show a uniform gentle slope with a break where uniformly steeper lower slopes begin. This effect has been caused by more rapid erosion of the lower parts of the valleys. This rapid erosion could in turn have several causes. Uplift, either regional or through faulting along the eastern edge of the range as proposed by Thayer (1936), would result in increased stream gradients and more rapidly incised valleys. Also, the region where this effect is most striking is near the axis of the Breitenbush Anticline, where the Sardine Formation and the Little Butte Series are in contact over large exposed areas. The rapid erosion of the tuffaceous Little Butte pyroclastics indicates that the break in the steepness of these slopes may approximate the contact between the Little Butte and the more resistant overlying flows. The last hypothesis seems most likely.

Classification of Peaks

Methods

Forty-two peaks were sampled, of which 28, ranging from maximum elevations of 1150 m to 1800 m, fall within the boundaries of the study area. Five other Western Cascade peaks to the north, south, and west were sampled for comparative purposes, as were seven lower peaks of the High Cascade Range (1250 m to 1900 m), the Three Sister region, and Crater Lake National Park.

For ease of presentation, these peaks have been grouped into classes according to a set of four physiographic characteristics which are important influences on floristic composition and vegetational patterns (see Table I). The criteria chosen include the following: (1) texture of parent rock; (2) proportion of peak on which outcrops are found; (3) direction of exposure of outcrops; and (4) slope steepness, with outcrop slope emphasized.

Non-rigorous manipulations of the data have shown that any given character state is highly correlated with particular states of the other characters, and in large part, division of the peaks into two large classes was easy. However, since this is an artificial classification system using only a small number of characters, certain peaks had to be considered intermediate. The system was also used for peaks outside the Western Cascades, although under such conditions it occasionally proved to be misleading.

Table I. Physiographic Features, Classification, and Number of Disjunct Species on 42 Western and High Cascade Mountain Peaks. (Peaks are arranged from north to south within groups.)

<u>Key to Symbols</u>:

Rock Texture

0	pumice or scoria gravel
1	highly scoriaceous andesite or basalt
2	scoriaceous andesite or basalt
3	slightly scoriaceous andesite or basalt
4	moderately dense blocky andesite
5	dense blocky andesite

Outcrop Size

s	small
m	medium
l	large

Outcrop Exposure

0	outcrops facing various directions
1	outcrops facing mostly north
2	outcrops facing mostly east
3	outcrops facing mostly south and/or west

Outcrop Steepness

1	slopes relatively gentle
2	slopes moderately steep
3	slopes precipitous

Peak	Rock Texture	Outcrop Size	Outcrop Exposure	Outcrop Steepness	Class	Disjunct Species
Bachelor Mt.	3	m	3	2	int.	26
Three Pyramids	2	l	3	3	1	19
Crescent Mt.	5	s	0	1	2	14
North Peak	1	m	3	3	1	17
Echo Mt.	2	m	3	2	1	33
South Peak	1	m	3	2	1	30
Cone Peak	1	m	3	2	1	37
Iron Mt.	1	l	3	3	1	42
Browder Ridge	2	l	3	3	1	34
Jumpoff Joe	3	l	1	2	int.	5
Squaw Peak	5	s	0	3	2	(3)
Twin Buttes	3	s	0	2	2	15
Carpenter Mt.	4	s	0	3	2	13
Tidbits Mt.	5	m	0	3	2	15
Lookout Mt.	5	s	0	2	2	(9)
Frissell Point	5	s	0	2	2	17
Castle Rock	4	s	0	3	2	12
O'Leary Mt.	3	m	3	3	1	23
Horsepasture Mt.	3	s	0	2	2	30
Lamb Butte	5	s	0	3	2	4
English Mt.	3	s	0	2	2	14
Lowder Mt.	3	m	0	3	int.	25
Yankee Mt.	4	m	3	2	2	(9)
Tipsoo Butte	5	m	3	2	2	17
Olallie Mt.	5	s	0	2	2	18
Indian Ridge	5	m	2	2	2	12
Sardine Butte	5	s	0	2	2	5
Rebel Rock	3	l	3	3	1	41
Monument Peak	4	s	0	2	2	10
Huckleberry Mt.	5	s	2	2	2	(5)
Fairview Peak	3	l	3	2	1	33
Bohemia Mt.	2	l	0	3	1	37
Hershberger Mt.	3	m	3	3	1	23
Grizzly Peak	3	m	0	2	2	7
Maxwell Butte	1	m	0	1	0	10
Little Nash Cr.	0	l	0	2	0	1
Hogg Rock	5	l	3	3	1	1
Hoodoo Butte	0	m	3	1	0	1
Sand Mt.	0	l	0	1	0	1
Steptoes	0	l	3	1	0	5
Three Sisters	2	l	0	3	1	28
Crater Lake	1	l	0	2	0	32

Results

Class 1 mountains include those composed of moderately to highly scoriaceous basalt or andesite flows, and with relatively large, south or west-facing, precipitous outcrop areas. The upper portions of these peaks are dominated by open meadow or scree habitats rather than forest. Class 2 mountains, on the other hand, are defined as those composed of dense volcanic material with small, moderately steep or gently sloping outcrops which face in a variety of directions. Class 2 peaks are usually forested, except for summit and ridgetop outcrops.

Good examples of Class 1 mountains are Three Pyramids, Iron Mountain, Browder Ridge, and Rebel Rock. Also included in this class are peaks which differed in one criterion by one or two of the relative units, or in two criteria by only one unit. Such peaks are North Peak, Echo Mountain, South Peak, Cone Peak, O'Leary Mountain, Fairview Peak, Bohemia Mountain, and Hershberger Mountain.

Exemplary Class 2 mountains include Crescent Mountain, Twin Buttes, Lookout Mountain, Frissell Point, Horsepasture Mountain, English Mountain, Olallie Mountain, Sardine Butte, Monument Peak, and Huckleberry Mountain. Peaks included in this class which differ slightly in one or two characters are Squaw Peak, Carpenter Mountain, Tidbits Mountain, Castle Rock, Lamb Butte, Yankee Mountain, Tipsoo Butte, and Indian Ridge.

Three peaks had to be considered intermediate in this classification. Bachelor Mountain, while having south and west-facing outcrops of moderately scoriaceous texture, has only an average outcrop area of moderate steepness. Lowder Mountain, a flat-topped peak perhaps representing an old flow surface, has precipitous outcrops of moderately scoriaceous texture, but the cliffs encircle essentially the entire top of the mountain and are of only moderate extent. Jumpoff Joe is a low elevation vent in the Little Butte Series near the axis of the Breitenbush Anticline. It is composed of a friable breccia which weathers in similar fashion to more scoriaceous rocks. The vent has been exposed on the north by stream or glacial action in the otherwise rapidly weathering Little Butte pyroclastics, accounting for the large expanse of nearly vertical north-facing outcrop. Jumpoff Joe, with a summit at only 1300 m, is the only peak in the study area composed entirely of Oligo-Miocene Little Butte Series (Peck and others, 1964), which perhaps explains its unusual erosional behavior.

Most of the lower mountains of the High Cascade Range are cinder cones composed of pumice and clinkery volcanic ash rather than flows of consolidated material. Such peaks are considered "Class 0" in this work. Included in this category is the region of Mount Mazama surrounding Crater Lake, since the denser flows of the ancient mountain have been deeply covered with a mantle of pumice.

Table I also lists the number of distributionally interesting species found on each mountain. Those numbers appearing in parentheses indicate peaks which were inadequately sampled. Numbers of disjunct species are highly correlated with peak classes. The mean number of disjunct species on Class 1, intermediate, Class 2, and Class 0 peaks are 29, 19, 12, and 8 respectively. With the present data Class 1 mountains are separated from those of Class 2 at the level of 17 disjunct species.

Horsepasture Mountain, a Class 2 peak, is the only exception to this statement. It supports at least 30 disjunct species and is one of the most floristically diverse areas in the Western Cascades. Unlike other such centers of diversity, Horsepasture Mountain has numerous, small, widely-scattered outcrop and meadow areas offering a variety of habitats. Although it must be placed with much less diverse peaks according to the system used here, these unique aspects perhaps explain why it is floristically more closely related to Class 1 mountains.

VEGETATION DESCRIPTION

All species of vascular plants except members of the Gramineae and Cyperaceae were recorded in the field from each major habitat on each peak. A checklist of the species found on each of the sampled peaks, including both those within the study area and from adjacent regions is presented as Appendix A.

Associated groups of plants became obvious with extensive observations, but no quantitative sampling was undertaken. The vegetation units described below consist of groups of species which recur wherever certain physical conformations are found. The environment is thus of great importance in defining the units, which are not "communities" in the standard phytosociological sense. The associations intergrade, often to a marked degree, but are the result of careful study in many different localities within the study area.

Mesic Conifer Forest

The mesic conifer forest is most important. It covers as much as 85 percent of the land area in the Western Cascades and is responsible for most of Oregon's timber production. Although generally found under 1350 m elevation, under certain conditions it may extend much higher. It is dominated by *Pseudotsuga menziesii*. Important associated species include *Abies grandis*, *Tsuga heterophylla*, *Cornus canadensis*, *Pedicularis racemosa*, *Chimaphila umbellata*, *Pyrola asarifolia*, *Pyrola* *picta*, *Listera caurina*, *Anemone deltoidea*, *Montia sibirica*, *Senecio harfordii*, *Viola glabella*, *Synthyris reniformis*, *Vaccinum parvifolium*, *Streptopus curvipes*, *Sedum oreganum*, *Galium oreganum*, *Polystichum munitum*, *Berberis nervosa*, *Gaultheria shallon*, *Rosa gymnocarpa*, *Tiarella unifoliata*, *Clintonia uniflora*, *Smilacina sessilifolia*, *Arenaria macrophylla*, *Dicentra formosa*, and *Ribes lacustre*.

Dry Mixed Conifer Forest

Dominant tree species in this broadly defined vegetational unit vary with elevation. *Abies amabilis* and *Pinus monticola* are co-dominants in all stands. At lower elevations (about 900 m) the unit is apparently subclimax to re-establishing Mesic Conifer Forest following fire. Here other important tree species are *Pseudotsuga menziesii* and occasionally *Tsuga heterophylla*. On forested ridgetops at about 1500 m elevation, *Abies procera* and *Tsuga mertensiana* occur with *Abies amabilis* and *Pinus monticola*. This facies of the unit appears to be climax.

Both subdivisions contain a strikingly similar understory flora, which includes *Xerophyllum tenax*, *Rubus lasiococcus*, *Coptis laciniata*, *Hypopitys monotropa*, *Allotropa virgata*, *Rhododendron macrophyllum*, *Gaultheria ovatifolia*, and *Eburophyton austinae*. It is the similarity in non-tree species that warrants the fusion of these otherwise distinct units.

Xeric Conifer Forest

This unit intergrades completely with the last. It is found primarily on south-facing slopes where extensive ground fires have burned within the last century. Living trees show a bimodal age distribution, with large old trees (mostly *Pseudotsuga menziesii*) having thick fire-blackened bark on the lower portion of the trunk. Trees of intermediate ages were evidently killed by the fire. Younger post-fire vegetation also includes douglas fir together with many species which are characteristic of the dry hillsides within the major valleys of western Oregon or are characteristic fire-following species. They include *Libocedrus decurrens*, *Abies grandis*, *Castanopsis chrysophylla*, *Arbutus menziesii*, *Ceanothus velutinus*, *Ceanothus integerrimus*, *Quercus garryana*, *Rhus diversiloba*, *Rhododendron macrophyllum*, *Arctostaphylos columbiana*, *Rubus ursinus*, *Penstemon cardwellii*, and *Hieracium albiflorum*.

Lowland Xeric Meadow

Especially in the region of the South Fork of the McKenzie River, clearings and meadows associated with the Xeric Conifer Forest contain a large number of species characteristic of the dry hills and fields within the Willamette Valley and other major valleys in western Oregon. Although their occurrences in the Western Cascades are disjunct and noteworthy, most of the components of this association do not occur with those disjunct species found at higher elevations and have not been treated in detail in this study. This grassy meadow association is not found above 600 m, except on Castle Rock, where it reaches 1000 m and is confined to dry south-facing slopes. Such areas often support scattered trees of *Quercus garryana*, *Arbutus menziesii*, and *Philadelphus gordonianus lewisii*; and shrubs such as *Rhus diversiloba*, *Ceanothus sanguineus*, and *Ribes sanguineum*. The dominant perennial herbs include *Brodiaea* *hyacinthina*, *Brodiaea pulchella*, *Berberis aquifolium*, *Psoralea physodes*, *Convolvulus nyctagineus*, and *Apocynum androsaemifolium*. Annuals are abundant, including many species of grasses, *Polygonum spergulariaeforme*, *Clarkia rhomboidea*, *Clarkia amoena*, *Linanthus bicolor*, *Orthocarpus attenuatus*, *Githopsis specularioides*, *Conyza canadensis*, *Madia gracilis*, and *Madia exigua*.

Boreal Forest

The above name is borrowed from Detling (1968) and is here defined as that phase of the forest vegetation that is typically found at high altitudes (over 1500 m) on north-facing slopes, where dense stands of small trees are often encountered. Dominant tree species include *Tsuga mertensiana*, *Abies lasiocarpa*, and *Chamaecyparis nootkatensis*, with a sparse herbaceous flora of *Arnica latifolia*, *Pedicularis bracteosa flavida*, *Valeriana sitchensis*, and *Viola orbiculata*. Snow cover in such communities is always heavy and lasts until midsummer or later.

Snowbed

Beneath north-facing outcrops or on steep open slopes, as well as in certain wind-protected sites on south or east-facing slopes, snow accumulates to great depths in the winter, often exceeding 8 m. Numerous species, mostly of high alpine or boreal affinity, flower and rapidly set seed and desiccate at the edge of these snowbanks as they melt. Such species include *Orogenia fusiformis*, *Dicentra uniflora*, *Claytonia lanceolata*, *Erythronium grandiflorum pallidum*, *Luetkea pectinata*, *Mertensia bella*, and occasionally wider-ranging species such as *Trillium* *ovatum*, *Senecio triangularis*, and *Hydrophyllum occidentale*.

Peaty Melt Seep

A continually wet habitat of gentle or level slope where snowmelt or spring water trickles throughout most of the supper supports several species characteristic of true sphagnum bogs, which are rare in the Western Cascades. A similar environment has been found on the sedge mat surrounding small tarns at elevations above 1600 m. Characteristic species of this habitat include *Dodecatheon jeffreyi*, *Pedicularis groenlandica*, *Trifolium longipes*, *Boykinia major*, *Caltha biflora*, *Habenaria dilatata*, *Stenanthium occidentale*, *Ranunculus alismaefolius alismellus*, *Drosera rotundifolia*, *Kalmia polifolia*, and *Tofieldia glutinosa*.

Rocky Melt Seep

Occasionally snowmelt trickles over outcrops, especially on south-facing slopes where the thin soil characteristic of non-forest habitats in the Western Cascades has eroded away in response to fires and frost action. Unlike Peaty Melt Seeps, these habitats typically desiccate shortly after midsummer, and plants found here tend to be ephemeral annuals or stoloniferous perennials with ephemeral aboveground parts. Such plants can survive the dry season in dormant condition. Prominent species include *Dodecatheon jeffreyi*, *Romanzoffia sitchensis*, *Lewisia triphylla*, *Mimulus breweri*, *Mimulus guttatus*, *Polygonum kelloggii*, *Linanthus harknessii*, *Allium amplectens*, *Saxifraga integrifolia*, *Saxifraga occidentalis rufidula*, and *Gayophytum humile*.

Wet Meadow

Open areas, frequently on east-facing slopes, which have relatively constant sources of moisture and sufficiently gentle slopes to build up a relatively deep organic soil support a characteristic wet meadow flora. Dominated by *Veratrum viride*, *Senecio triangularis*, and *Valeriana sitchensis*, this association also includes *Ribes bracteosum*, *Rubus spectabilis*, *Mitella breweri*, *Ligusticum grayi*, *Mertensia bella*, *Hydrophyllum fendleri albifrons*, and *Hydrophyllum tenuipes*. Much of this association is repeated around the borders of larger boggy areas, such as Quaking Aspen Swamp or the Potholes. This phase grades into the Peaty Melt Seep community discussed above. Another phase of this association is dominated by *Acer circinatum* and *Alnus sinuata*, which frequently form dense thickets of small tangled trunks and branches on the steeper wet slopes throughout the Western Cascades. Most of the species mentioned above can be found around the edges of a maple or alder thicket or under its canopy. It is notable that these two tree species are also found in much less abundance on open slopes supporting Mesic or Xeric Meadow communities.

Mesic Meadow

The factors responsible for the maintenance of the remarkable open meadow slopes in the Western Cascades are not clear but doubtless include fire, heavy snowpack, occasional snow- and landslides, rapid downslope creep of the light loamy soil, and the churning and cutting action of rodents, especially *Aplodontia rufa*. Occasionally saplings seem to be establishing in these habitats, but not in sufficient numbers to allow the conclusion that succession is returning such areas to forest. This community, while normally encountered on south or west-facing slopes, has an adequate supply of moisture until shortly past midsummer when the drier patches begin to desiccate. Most of the associated species are herbaceous perennials which have adequate time to set seed during the warm moist part of the early summer. The stems of many of them are brown and withered by August. Mesic Meadows are dominated by Rubus parviflorus, Pteridium aquilinum, and Rudbeckia occidentalis but also include such herbaceous perennials as Aquilegia formosa, Erigeron aliceae, Lupinus latifolius columbianus, Ribes binominatum, Ribes viscosissimum, Polygonum phytolaccaefolium, Cirsium centaurea, Mertensia paniculata, Dicentra formosa, Vicia americana truncata, and Epilobium angustifolium, together with occasional ephemeral annuals such as Galium bifolium and Gayophytum humile, which grow in the shade of the taller perennials.

Subalpine Xeric Meadow

Between the Mesic Meadows and dry, rocky, surrounding areas, especially on Class 1 peaks, is found a loose association of species many of which have disjunct ranges. In this habitat soils are much thinner and rockier than those of the Mesic Meadow, and moisture stress increases earlier in the season. Few of these species are ephemeral; rather they are capable of sustaining high moisture tensions in their stems until very late in the summer. Other species, mostly herbaceous perennials, die back earlier in the season. Representative species are Gilia aggregata, Collomia linearis, Gayophytum diffusum parviflorum, Orthocarpus imbricatus, Luina stricta, Polygonum minimum, Polygonum douglasii, Polygonum cascadense, Navarretia divaricata, Lupinus arbustus neolaxiflorus, Linum perenne lewisii, Eriogonum nudum, Microsteris gracilis, Collinsia parviflora, Potentilla glandulosa, Cerastium arvense, Artemisia ludoviciana latiloba, Calochortus lobbii, Rumex acetosella, Pachystima myrsinites, Amelanchier alnifolia semiintegrifolia, and Phacelia heterophylla.

Fine Gravel Scree

This community is continuous with the Xeric Meadow on Class 1 mountains and supports, in lower densities, many of the species that are common in that habitat, as well as others such as Lotus nevadensis douglasii, Chrysothamnus nauseosus albicaulis, Allium crenulatum, Ivesia gordonii, Trifolium productum, Aster gormanii, Crepis occidentalis, Sedum oregonense, and Sanicula graveolens. In this community plants are characteristically widely dispersed with much intervening bare substrate which is in rapid movement downslope. The community, consisting primarily of disjunct species, is confined to ridges of rapidly weathering scoriaceous material which are oriented nearly perpendicular to the prevailing northwesterly winds.

Boulder Creep Slope and Outcrop Ridge

Although these two habitats are physically different, they support many of the same species and so are considered together in this treatment. The Boulder Creep Slope is normally south or west-facing and consists of weathered rock fragments in a fine loamy matrix, the whole moving downslope at moderate speed. Drainage is good, and the soils are typically quite dry through the first 10 cm but may be moister below that level. The Outcrop Ridge habitat is also found on south or west-facing slopes, where mass wasting of small fragments results in cropping out of small patches of parent rock which are barely exposed and eroded parallel to the general slope of the area. Many species are able to root in the weathered cracks of the outcrops or in occasional small pockets of finer material. Included are *Delphinium menziesii pyramidale*, *Castilleja hispida*, *Penstemon procerus brachyanthus*, *Sedum stenopetalum*, *Sedum divergens*, *Eriophyllum lanatum*, *Arctostaphylos nevadensis*, *Haplopappus hallii*, *Silene douglasii*, *Cheilanthes siliquosa*, *Cheilanthes gracillima*, *Comandra umbellata*, *Lomatium martindalei*, *Sanicula graveolens*, *Eriogonum umbellatum*, *Eriogonum compositum*, *Juniperus communis saxatilis*, *Erigeron foliosus confinis*, *Penstemon deustus*, *Arenaria capillaris americana*, *Erysimum asperum*, *Antennaria rosea*, *Phacelia heterophylla*, *Anaphalis margaritacea*, and *Penstemon cardwellii*. Occasionally these plants are found on ridgetop deflation armor flats where frequent high winds carry away finer soil particles, leaving an impervious pile of weathered rock fragments.

Blocky Talus

Below cliffs on high north-facing slopes of Class 2 mountains, Western Cascade andesites weather into large rectangular blocks which form extensive talus piles. This phenomenon has been found only on the north sides of peaks composed of relatively dense parent rock. Vegetation is sparse in these areas, but it is quite constant. Plant species include *Sambucus racemosa pubens arborescens*, *Acer circinatum*, *Thalictrum occidentale*, *Aquilegia formosa*, *Cardamine integrifolia sinuata*, and *Campanula rotundifolia*.

Vertical Outcrop

On dikes, cirque headwalls, or other erosional surfaces that are steep or vertical, slow weathering produces crevices and pockets that provide some protection from excessive wind and heat. Adapted to these exposed environments are *Saxifraga bronchialis vespertina*, *Penstemon rupicola*, *Selaginella wallacei*, *Erigeron cascadensis*, *Polemonium pulcherrimum*, *Douglasia laevigata*, *Castilleja rupicola*, *Saxifraga cespitosa*, *Heuchera micrantha*, and *Polypodium hesperium*. Certain of these species, such as *Saxifraga bronchialis verpertina*, *Douglasia laevigata*, and *Castilleja rupicola*, are found only on the windward sides of the outcrops. If the outcrop is oriented 60 degrees or more to the prevailing winds, they are not likely to be found at all. This association is restricted to Class 1 peaks.

INVESTIGATIONS ON SPECIES WITH UNUSUAL DISTRIBUTIONS

Systematics

Since determination of the range of a taxon requires an uncompromisingly distinct impression of the range of variation allowable within that taxon, detailed studies of herbarium specimens and comparisons with the available taxonomic literature were undertaken in a number of instances. In even the most ambitious of these studies, the results are not monographic in scope but represent better syntheses of the taxonomic and evolutionary knowledge of these species than is available in present literature. These studies have shown that many of the Western Cascade disjuncts are characterized by complex and poorly understood intra- and interspecific relationships. More detailed information on materials and methods and taxonomic treatments of the species are given in Appendix B.

Geographical Ranges

With the discovery of a number of species new to the Western Cascades, it was considered desirable to document thoroughly the known ranges of all these species and to attempt to locate all populations of these plants within the study area. Nine West Coast herbaria were sampled, and the study area was sufficiently traversed to locate by far the largest portion of the interesting populations. In the herbarium sampling label information was copied from all Oregon Cascade specimens and others representing the complete range of documented localities. Voucher specimens from new and previously known localities collected during the course of this study have been deposited in the Herbarium of the University of Oregon. They were taken for all species showing unusual distribution patterns from all their major habitats on all the peaks sampled. In addition, range information was gathered from monographic treatments and from local and regional floras. The herbaria sampled and the completed dot distribution maps are found in Appendix B. Table II contains a summary of the geographical information found in Appendix B.

Also given in Table II for reference is the number of localities for each of the disjunct species now known from the entire Western Cascade Range and the number of these localities visited during the present study. These numbers show that the area has been poorly botanized over the last 100 years: 87 percent of the known disjunct species localities are ones discovered or visited during this study.

Ecological Ranges

Also presented in Appendix B are qualitative observations on the ecology of the distributionally interesting species both in the Western Cascades and, insofar as could be determined, in their more typical associations. Field observations were the most important source of information, but studies of floristic literature and herbarium labels were of some help, especially in determining the nature of typical habitats for the species in other regions. In the study area observations were made on aspects of the environment and the relationships of interesting

Table II. Aspects of the Distribution and Ecology of Western Cascade Disjunct and Endemic Species.

<u>Key to Symbols</u>:

Associations (listed in order of importance for each species)

MF	Mesic Forest
CF	Dry Mixed Conifer Forest
LXM	Low Elevation Xeric Meadow
WM	Wet Meadow
MM	Mesic Meadow
SXM	Subalpine Xeric Meadow
GS	Fine Gravel Scree
OR	Outcrop Ridge
BC	Boulder Creep Slope
RMS	Rocky Melt Seep
S	Snowbed
BT	Blocky Talus
VO	Vertical Outcrop

(see p. 31-40 for more complete descriptions)

Growth Form

EA	ephemeral annual
PA	persistent annual
LA	late-blooming annual
EP	ephemeral perennial
PP	persistent herbaceous perennial
S	shrub
T	tree

	Associations	Growth Form	No. Western Cascade Populations Observed	Total Known Western Cascade Populations (Wash. to Cal.)
Southern and Eastern Element				
Selaginella scopulorum	OR	EP	13	13
Pinus ponderosa	GS	T	2	2
Arabis platysperma howellii	S,OR	PP	3	3
Linum perenne lewisii	SXM,OR	PP	6	7
Gayophytum humile	RMS,MM	EA	27	28
Linanthus harknessii	GS,SXM,RMS	EA	8	9
Navarretia divaricata	GS,SXM,RMS	PA	20	21
Monardella odoratissima	BC,SXM,OR	PP	4	4
Penstemon deustus	BC,OR	PP	7	8
Mimulus breweri	RMS,GS,MM,SXM	EA	30	32
Castilleja pruinosa	OR,BC	PP	5	11
Galium bifolium	MM	EA	22	22
Lonicera conjugialis	CF,SXM,BC	S	2	2
Chrysothamnus nauseosus albicaulis	GS,OR	S	3	4
Nothocalais alpestris	MM,SXM	PP	1	1
Southern Element				
Cheilanthes siliquosa	BC,OR,SXM	PP	20	22
Allium crenulatum	GS	EP	10	12
Arenaria pumicola	OR,BC	PP	2	5
Silene campanulata glandulosa	OR	PP	10	13
Cardamine integrifolia sinuata	BT	PP	3	6
Ribes binominatum	MM,MF	S	25	26
Ribes erythrocarpum	MF,S	S	4	6
Trifolium productum	GS,OR	PP	5	6
Trifolium howellii	MF,WM	PP	4	6
Mimulus pulsiferae	RMS,GS,OR	EA	4	5
Erigeron foliosus confinis	OR,BC	PP	19	21
Crepis occidentalis	GS	PP	5	5
Eastern Element				
Populus tremuloides	MM	T	1	1
Polygonum kelloggii	RMS,OR	EA	5	5
Lewisia triphylla	RMS,S	EP	13	13
Arabis holboellii retrofracta	OR,BC	PP	24	26
Horkelia fusca	SXM,S	PP	1	1

Table II - continued

	Associations	Growth Form	No. Western Cascade Populations Observed	Total Known Western Cascade Populations (Wash. to Cal.)
Lathyrus lanszwertii aridus	GS,OR,CF	PP	4	4
Gayophytum diffusum parviflorum	SXM	LA	10	11
Gilia aggregata	SXM,GS,OR	PP	18	19
Collomia linearis	SXM	PA	7	9
Gentiana calycosa n. subsp.	MF,WM	PP	4	4
Pterospora andromedea	MF,CF	PP	1	2
Cryptantha affinis	SXM,MM	PA	1	1
Helianthus cusickii	OR,MM,CF	PP	1	1
Artemisia ludoviciana latiloba	SXM	PP	16	17
Artemisia tridentata	SXM,CF,OR,BC	S	2	2
Arnica parryi	SXM,CF	PP	8	9
Microseris nutans	SXM,GS	PP	14	14
Crepis acuminata	OR	PP	2	2
Northern Element				
Polystichum andersonii	WM	PP	2	2
Chamaecyparis nootkatensis	OR,MF	T	23	26
Arenaria capillaris americana	OR,BC	PP	17	17
Sedum divergens	BC,OR,GS	PP	14	16
Hydrophyllum fendleri albifrons	WM,MM	PP	13	14
Orogenia fusiformis	S	EP	15	18
Rhododendron albiflorum	MF,WM	S	3	4
Menziesia ferruginea	MF,MM	S	2	3
Douglasia laevigata	VO,OR	PP	5	5
Mertensia bella	WM	EP	19	20
Castilleja rupicola	VO,OR	PP	5	5
Lonicera utahensis	RMS,S	S	2	3
Haplopappus hallii	OR,BC	PP	19	21
Luina stricta	MM	PP	12	12
Alpine Element				
Polygonum newberryi	S,GS	PP	8	9
Spraguea umbellata	GS,S	PP	3	7
Arenaria rubella	VO	PP	6	6
Luetkea pectinata	S,GS	PP	2	3

Table II - continued

	Associations	Growth Form	No. Western Cascade Populations Observed	Total Known Western Cascade Populations (Wash. to Cal.)
Ivesia gordonii	GS,OR	PP	2	2
Polemonium pulcherrimum	VO	PP	1	1
Linanthastrum nuttallii	OR,VO,GS	PP	3	3
Erigeron compositus	OR,GS,BC	PP	1	2
Valley Element				
Populus trichocarpa	BT	T	4	4
Quercus garryana	LXM,OR	T	4	4
Polygonum spergulariaeforme	LXM	LA	3	4
Convolvulus nyctagineus	LXM,GS,BC	PP	3	7
Plagiobothrys scouleri	GS,SXM	PA	1	1
Widespread Element				
Polygonum douglasii	SXM,GS	PA	28	30
Polygonum minimum	SXM,GS	PA	30	36
Silene douglasii	OR,BC	PP	22	22
Sedum stenopetalum	BC,OR,GS,SXM	PP	16	18
Lupinus arbustus neolaxiflorus	SXM,GS	PP	27	30
Lotus nevadensis douglasii	GS,OR,BC	PP	16	22
Phacelia linearis	OR,GS,SXM	PA	2	3
Endemic Element				
Polygonum cascadense	SXM,GS	PA	17	19
Aster gormanii	GS,OR	PP	1	1
Erigeron cascadensis	VO,OR,GS	PP	9	10

species to the rest of the vegetation. Some of these findings are presented in the preceding section on vegetation as well as in Appendix B. Table II presents growth forms of the species and the associations in which they have been found in the Western Cascades.

Dispersibility, Pollinators, and Breeding Systems

Since breeding systems have been shown to be important in establishing (Baker, 1956) and maintaining (Carlquist, 1966a) species populations after long-distance dispersal, observations were made in the field on various mechanical adaptations for dispersal, on pollinators noted visiting the various species, and on floral morphology, size, color, and display to possible pollinators. The results are presented in Table III, together with the kind of breeding system suggested by the behavior of each species. It should be stressed that the proposed breeding systems are not supported by experimental evidence but are deductions from the trends compiled by numerous other workers. In general, small-flowered species which always set seed are presumed to be self-fertilizing, while large-flowered forms which are regularly visited by animal pollinators are concluded to be at least partially outcrossing. Because modal apomixis is often a difficult reproductive method to deduce, it is suggested in Table III only for forms which produce little or no pollen.

Among the dispersal adaptations noted were vegetative reproduction by fragmenting stems which root at the nodes; prickly, bur-like leaves; tumble-weed-like, disarticulating flower heads that are blown by the wind, scattering seed; winged, disarticulating flowers that

Table III. Dispersal Adaptations, Pollinators, Seed Set, Floral Morphology and Exposure, Probable Breeding Systems, and Number of Western Cascade Localities of Disjunct and Endemic Species.

Key to Symbols

Dispersal Adaptations

1	vegetative reproduction: fragmenting stems
2	prickly, bur-like leaves
3	tumbleweed inflorescences
4	winged, disarticulating flowers
5	spiny, bur-like calyces
6	explosive fruits
7	spiny berries
8	bird-eaten berries
9	fruits with hooked spines
10	pappus or coma: wind-blown fruits
11	wind-blown spores
12	spiny-tuberculate seeds
13	winged seeds
14	light, minute seeds
15	large, heavy seeds
16	glutinous seeds

Spopophyll Exsertion

0	no perianth
CL	flowers cleistogamous
IN	stamens and style completely included
SI	stamens and style slightly included
EX	stamens and style exserted

Proposed Breeding Systems

A	apomictic
SF	probably self-fertilizing
SC	probably self-compatible, but partially out-crossing
OC	probably mostly out-crossing
SI	probably self-incompatible

Pollinators

0	none
W	wind
D	Diptera
L	Lepidoptera
H	Hymenoptera
C	Coleoptera
B	hummingbirds

Flower Exposure

CC	completely concealed
PC	partly concealed
EX	fully exposed

Flower Color

G	green
GW	greenish-white
GP	greenish-pink
W	white
P	pink
L	lavender
V	violet
BL	blue
Y	yellow
S	salmon
R	red
M	maroon
BR	brown

Flower Size

d	diameter
h	diameter of head
L	length

(all measurements in mm)

	Adaptations for Dispersal	Pollinators	Exposure of Flowers	Sporophyll Exsertion	Flower Color	Flower Size (mm)	Flowers Setting Seed (%)	Probable Breeding System
Southern & Eastern Element								
Selaginella scopulorum	1,2	-	-	-	-	-	-	SC
Pinus ponderosa	13	W	-	-	-	-	-	OC
Arabis platysperma howellii	13	0	EX	EX	V	5d	80-	SC
Linum perenne lewisii	15	D,L,H	EX	EX	BL	35d	90+	SI
Gayophytum humile	0	0	EX	EX	W	2d	100	SF
Linanthus harknessii	0	0	EX	IN	W	1d	80+	SF
Navarretia divaricata	16	0	EX	EX	W	1d	80+	SF
Monardella odoratissima	0	H	EX	EX	L	14h	?	OC
Penstemon deustus	0	0	EX	IN	L	12L	90+	OC
Mimulus breweri	14	0	EX	IN	V	3d	100	SF
Castilleja pruinosa	13	0	EX	IN	R	23L	?	OC
Galium bifolium	9	0	CC	EX	G	1d	100	SF
Lonicera conjugialis	8	0	PC	IN	M	7L	80+	SC
Chrysothamnus nauseosus albicaulis	10	L	EX	EX	Y	9L	60+	SI
Nothocalais alpestris	10	0	EX	EX	Y	30h	90+	OC
Southern Element								
Cheilanthes siliquosa	11	-	-	-	-	-	-	SC
Allium crenulatum	3	0	EX	EX	P	12h	90+	SC
Arenaria pumicola	0	0	EX	EX	W	8d	?	OC
Silene campanulata glandulosa	12	H,C	EX	IN	GW	11d	?	OC
Cardamine integrifolia sinuata	6	0	EX	EX	L	10d	80-	SC
Ribes binominatum	7	0	PC	SI	GW	6d	80+	SC
Ribes erythrocarpum	8	0	EX	EX	S	5d	30+	OC
Trifolium productum	4	0	EX	IN	L	10L	50	SC
Trifolium howellii	4	0	EX	IN	W	10L	?	SC
Mimulus pulsiferae	0	0	EX	IN	Y	5d	?	SC
Erigeron foliosus confinis	10	L,H	EX	EX	V	20h	80+	OC?
Crepis occidentalis	10	L	EX	EX	Y	22h	70+	A

Table III - continued

	Adaptations for Dispersal	Pollinators	Exposure of Flowers	Sporophyll Exsertion	Flower Color	Flower Size (mm)	Flowers Setting Seed (%)	Probable Breeding System
Eastern Element								
Populus tremuloides	10	W	PC	0	G	7L	0?	OC
Polygonum kelloggii	0	0	PC	EX	P	2d	100	SF
Lewisia triphylla	3	D,C	EX	EX	P	6d	100	SC
Arabis holboellii retrofracta	6	C	EX	EX	L	5d	90+	SC
Horkelia fusca	0	D,C	EX	EX	W	8d	?	OC
Lathyrus lanszwertii aridus	0	0	PC	IN	L	10L	?	?
Gayophytum diffusum parviflorum	0	0	EX	EX	W	3d	100	SC
Gilia aggregata	16	B	EX	EX	R	20L	90+	SI
Collomia linearis	0	0	EX	SI	P	12L	?	SC
Gentiana calycosa n. subsp.	0	0	EX	SI	BL	50d	90+	OC
Pterospora andromedea	13	0	EX	IN	BR	6d	100	SF
Cryptantha affinis	5	0	PC	IN	W	1d	100	SF
Helianthus cusickii	0	L	EX	EX	Y	65h	?	SI?
Artemisia ludoviciana latiloba	0	W?	EX	EX	Y	4h	?	SI?
Artemisia tridentata	0	W?	EX	EX	Y	4h	?	SI
Arnica parryi	10	0	EX	EX	Y	10h	100	A?
Microseris nutans	10	L	EX	EX	Y	20h	80+	OC
Crepis acuminata	10	L	EX	EX	Y	16h	?	SI
Northern Element								
Polystichum andersonii	11	-	-	-	-	-	-	SC
Chamaecyparis nootkatensis	0	W	-	-	-	-	-	OC
Arenaria capillaris americana	0	D,C	EX	EX	W	10d	?	OC
Sedum divergens	1,14	L,H	EX	EX	Y	9d	90+	OC
Hydrophyllum fendleri albifrons	15	0	PC	EX	GW	9d	20+	SC
Orogenia fusiformis	0	C	PC	EX	W	12h	80+	SC
Rhododendron albiflorum	0	0	EX	EX	W	25d	?	OC

Table III - continued

	Adaptations for Dispersal	Pollinators	Exposure of Flowers	Sporophyll Exsertion	Flower Color	Flower Size (mm)	Flowers Setting Seed (%)	Probable Breeding System
Menziesia ferruginea	0	O	PC	IN	GP	6d	90+	SC
Douglasia laevigata	0	O	EX	IN	V	16d	60+	OC
Mertensia bella	12	H	PC	IN	BL	6d	80+	SC
Castilleja rupicola	13	O	EX	IN	R	30L	?	OC
Lonicera utahensis	0	C	PC	IN	GW	10L	?	SC
Haplopappus hallii	10	O	EX	EX	Y	14h	60+	OC
Luina stricta	10	L,C	EX	EX	Y	18L	80+	SI
Alpine Element								
Polygonum newberryi	0	O	PC	IN	GW	3d	?	SF
Spraguea umbellata	4	O	EX	IN	P	30h	?	SF
Arenaria rubella	0	D	EX	EX	W	4d	?	SC
Luetkea pectinata	0	O	EX	EX	W	7d	?	OC
Ivesia gordonii	3	L	EX	EX	Y	6d	50-	OC
Polemonium pulcherrimum	0	H,C	EX	EX	BL	15d	20-	OC
Linanthastrum nuttallii	0	O	EX	IN	W	12d	?	OC
Erigeron compositus	10	O	EX	EX	W	14h	80+	OC?
Valley Element								
Populus trichocarpa	10	W	PC	O	G	6L	?	OC
Quercus garryana	0	W	CC	O	G	(5)	?	OC
Polygonum spergulariaeforme	0	D	PC	EX	P	4d	?	SC
Convolvulus nyctagineus	0	D,C	EX	SI	W	40d	?	OC
Plagiobothrys scouleri	5	O	EX	IN	W	1d	?	SF
Widespread Element								
Polygonum douglasii	0	O	PC	CL	GP	4d	100	SF
Polygonum minimum	0	O	PC	EX	P	2d	100	SF
Silene douglasii	12	L,H,C	EX	IN	W	14d	90+	OC
Sedum stenopetalum	1	L,H	EX	EX	Y	11d	0	A
Lupinus arbustus neolaxiflorus	0	H	EX	IN	BL	11L	90+	OC
Lotus nevadensis douglasii	0	H	EX	IN	Y	10L	90+	SC
Phacelia linearis	0	O	EX	EX	W	10d	?	OC
Endemic Element								
Polygonum cascadense	0	O	PC	EX	P	2d	100	SF
Aster gormanii	10	O	EX	EX	W	20h	40+	?
Erigeron cascadensis	10	L	EX	EX	W	14h	80+	OC?

might be wind dispersed; spiny, bur-like calyces; somewhat explosive siliques; spiny, bur-like berries; red, bird-eaten berries; bur-like nutlets with hooked spines; fruits or seeds with plumed appendages such as pappus or coma for wind dispersal; windblown spores or light minute seeds; and spiny-tuberculate, winged, or glutinous seeds. Several species showed the evidently negative dispersal adaptation of large, heavy, unpalatable seeds. This characteristic is also noted in Table III.

Some species of quite limited distribution could not be observed long enough in the field to see visits by pollinators. Such species include Arabis platysperma, Luetkea pectinata, Rhododendron albiflorum, Douglasia laevigata, Gentiana calycosa n. subsp., Linanthastrum nuttallii, Phacelia linearis, Castilleja pruinosa, Castilleja rupicola, and Nothocalais alpestris. Insect visitors are reported here only to order although more specific identifications were made for some Lepidoptera, Hymenoptera, and Diptera. All major groups of temperate pollinators were encountered, but the most abundant and frequently seen were unidentified small beetles, which spend considerable time within a single flower and are often found in rather large numbers. The only evidently obligate relationship between a disjunct plant and pollinator involved Gilia aggregata, a polemoniaceous species with scarlet tubular flowers, and the rufous hummingbird, Selasphorous rufus. Females of other hummingbird species may also visit G. aggregata in the Western Cascades, but they could not be differentiated from S. rufus in the field. G. aggregata ranges throughout most of the Western United States and undoubtedly is pollinated by other species of hummingbirds in other parts of its range. It has not been shown conclusively in this study that any of the observed visitors actually effect either cross or self-fertilization, although at least in the case of the larger more attractive visitors a considerable amount of cross pollination can be assumed.

The most striking feature of Table III is the evident range in breeding systems represented by Western Cascade disjunct species. The range in adaptations for dispersal, pollinators, and breeding systems for disjunct species seems to be quite comparable with that of the Western Cascade flora as a whole. The presently available evidence thus indicates that type of breeding system has been of no general significance either in establishing or maintaining Western Cascade disjunct populations. This may in turn argue for relatively easy, repeated dispersal to the area. Sixty percent of the species have specific adaptation for such dispersal.

Moisture Regimes and Phenology

The present hypotheses concerning the presence of disjunct species in the Western Cascades implicate the moisture tolerances of the disjunct plants or the cycle of moisture availability in the areas where these species are concentrated. An attempt was made to gather biologically significant data, using a sap-tension pressure-chamber, from a number of species that might help test these ideas, especially Detling's "Xeric Island Hypothesis." Iron Mountain was chosen to sample intensively, because of its diversity of habitats and disjunct species and its accessibility. Some additional corroborative information was collected on Sardine Butte and in Crater Lake National Park. A great deal of information on variability within species, among species, among habitats, and with time was obtained from these studies. The results have elucidated the range of stresses encountered under various conditions and have indicated different kinds of adaptation to seasonally increasing moisture stress. In addition, it has been shown that there is no reasonable *a priori* way of defining xeric and mesic localities or xeric and mesic species. Such definitions must always refer to the functional environment of the individual plant or at most to members of a species population within a given habitat.

Literature Review and Methods

Moisture stress data were obtained using the sap-tension pressure-bomb devised by Scholander and others (1965) to measure in an almost direct fashion the water tension in the xylem cells of plants. Scholander's simple but elegant technique involves cutting the stem to be measured, sealing it in a pressure-chamber with the cut end exposed to the atmosphere, and opposing the original tension in the stem with a positive gas pressure applied through the stomata of the leaves. When the applied pressure is equal to the original tension, an equilibrium state is produced, and sap reappears at the cut surface of the stem. Scholander and his colleagues performed studies on the sap tension of various plants as related to habitat, height, and parasitism, finding low tensions in all herbs and ferns (those measured were confined to damp forest or fresh water environments) and high tensions in the trees and shrubs of desert and seashore environments. Tensions in trees increase with height, and parasites of the genera *Phoradendron* and *Phrygilanthus* were found without exception to have higher tensions than those found in their hosts. In addition, Scholander presents a theoretical model showing that the equilibration pressure is, in fact, equal and opposite to the hydrostatic pressure in the xylem of the intact stem.

The data of Boyer (1967) support Scholander's model. Boyer compares the water potential of leaves as measured by a thermocouple psychrometer with the water potential of the xylem cells as measured with a pressure-chamber. He used greenhouse cultures of *Taxus cuspidatus*, *Helianthus annuus*, and *Rhododendron roseum*. Although Boyer found that configuration of the tissues in the stem may be responsible for considerable error in some cases, as in *Rhododendron*, he reports accuracy of the pressure-bomb technique within about two atmospheres.

Boyer states that the pressure-chamber technique actually measures leaf water potential and not tension in the xylem. However, if the various tissues of the leaf are in equilibrium with regard to diffusion pressure deficits, the two measures will be identical. There is no theoretical reason to assume that mesophyll cells and vascular tissue in the leaf would not be in moisture equilibrium, and Boyer found no differences, even in rapidly transpiring material. Thus, it can be assumed reasonably that pressure-bomb readings are measurements of negative hydrostatic pressure within the water conducting tissues.

Scholander and others (1965) have shown that initial xylem exudates from a wide variety of species, including extreme halophytes, are almost pure water, leaving hydrostatis tension as the only component of the xylem diffusion pressure deficit. Boyer (1967) found somewhat higher osmotic potential in the xylem sap, but he used exudate from tissues which had previously been pressurized. It is possible that some damage was incurred by mesophyll cells during the first pressurization and that later exudate actually represents a mixture of xylem and cell saps.

Waring and Cleary (1967) found good correlation between water stress in twigs of douglas fir as measured by the pressure-bomb and the water potential of associated leaves determined by a vapor equilibration technique. These findings add experimental support to Scholander's model. Waring and Cleary also report on field studies of coniferous species in southwestern Oregon. A moisture gradient responsive to exposure and soil type is described. Reported differences among the various coniferous tree species in the same stand are small once root systems are well established.

A portable model of Scholander's pressure-bomb was used in this study. The model was designed by B. D. Cleary at the Oregon State Forest Research Laboratory, Corvallis.

Over 1000 readings were made with the instrument during the summer of 1967. No rainfall was recorded in the study area during this time, and almost every day was clear and sunny, resulting in unusually high and continued water stresses and accompanying extreme fire danger. Since a large number of readings was desired, specimens were cut and sealed immediately in plastic bags, kept out of direct sunlight, and returned to a convenient location to be measured using standard large cylinders of compressed nitrogen. After the initial cutting, stems were not recut, but phloem was trimmed (except for small annuals), the stems were fitted into slits in rubber stoppers and sealed into the pressure-chamber with one cm or less of the stem protruding into a normal atmosphere. Pressure in the chamber was slowly raised, at a rate of about 0.6 atmospheres per second. Gas flow was stopped and the gauge pressure read when the cut xylem darkened as the tracheids or vessels filled with sap. The pressure was then released and the measured stem was discarded. A broad ecological and taxonomic spectrum of plant species was studied using the pressure-bomb method, and several more or less distinct sources of variation in readings were encountered. They are described and exemplified below.

Variation with Time after Cutting

Since the above method required occasional long intervals between cutting the stems and measuring the sap tension, the error introduced by this delay was determined for several species of different growth habit (Figure 1). In the first such experiment, 20 stems from one large tree of Pseudotsuga menziesii were cut, divided into four groups, and sealed into one-pint plastic bags with most of the air expressed. Each group of stems was measured at approximate half-hour intervals, the first being read about 15 minutes after cutting. F tests between the means demonstrate no significant differences in readings taken immediately and two hours after cutting.

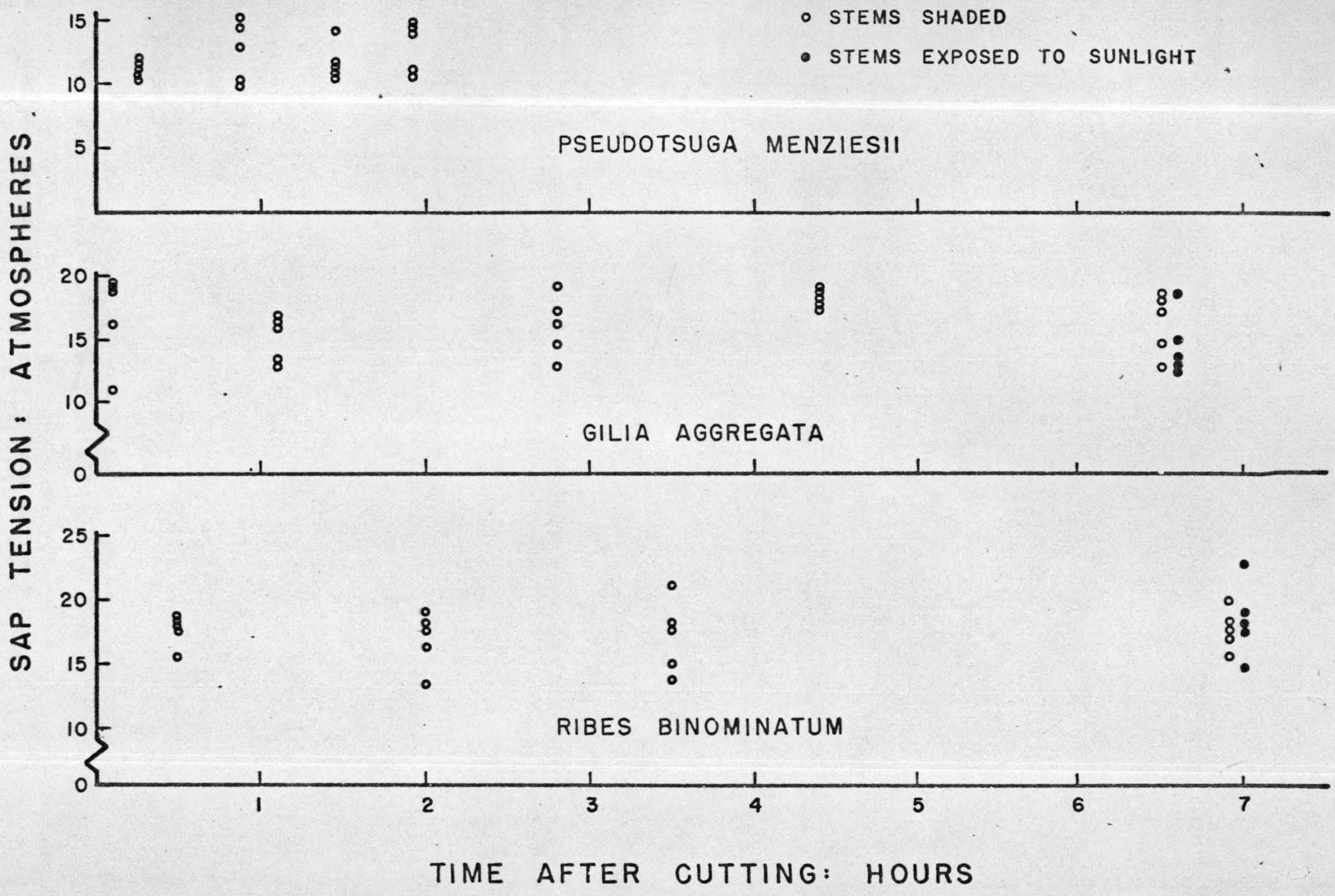

Figure 1. Variation in Maximum Sap Tension with Time after Cutting: Stems Stored in Plastic Bags.

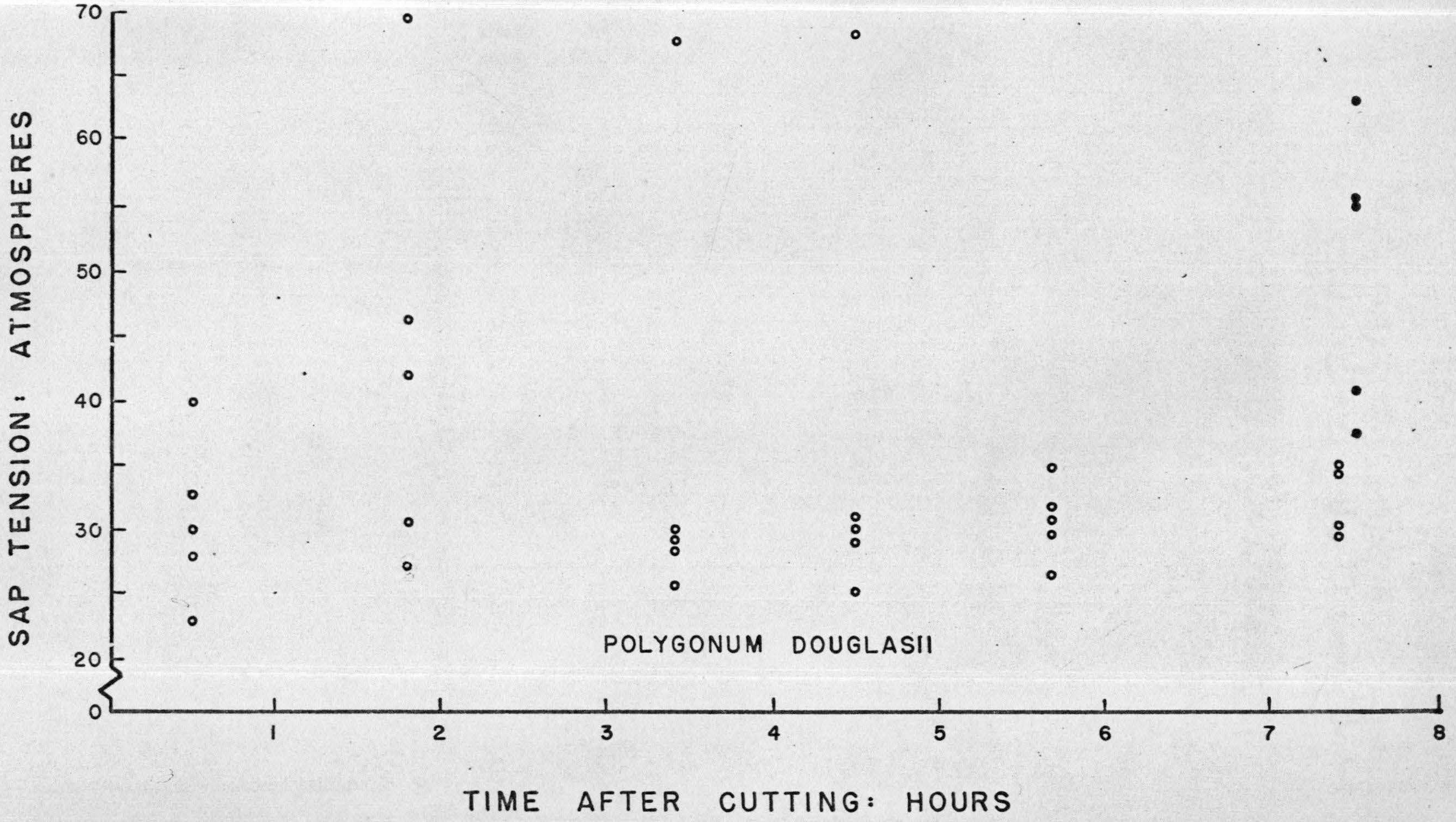

Figure 1 (cont). Variation in Maximum Sap Tension with Time after Cutting: Stems Stored in Plastic Bags.

After discovering that the bagging method would often entail delays of longer than two hours, additional experiments were performed. Stems representing populations of *Ribes binominatum*, a perennial shrub; *Gilia aggregata*, a biennial herb; and *Polygonum douglasii*, a small annual, were collected in a similar manner in the early afternoon of a sunny day. Four bags of stems were kept shaded at ambient temperature, and one was left on open ground in full sun until sunset. Shaded bags were measured at irregular intervals averaging longer than one hour, and the last shaded bag and that left in the sun were measured together about seven hours after they were collected--a much longer delay than was necessary in other experiments.

In groups of stems left in the shade, differences between initial and final samples were not significant as determined by an F test between the means. Bags of stems left in the sun were coated internally with condensed moisture, but for *Ribes binominatum* and *Gilia aggregata* pressure bomb readings fell well within the range of the shaded samples. Only in *Polygonum douglasii* did treatment of the cut and sealed stems result in obviously different readings. Although the highest readings for the experiment came from shaded stems measured early in the experiment, the moisture tension in sun-treated stems averaged much higher, indicating that they had lost considerable water. It seems likely that the difference between the two perennials and the annual resulted from the relative masses of the stem pieces, indicating that *Polygonum douglasii* lost relatively more moisture to the air which remained in the plastic bag. Also pertinent is the fact that the annual showed greater stress at the beginning of the experiment, indicating a lower water to dry weight ratio than in the other species. This series of experiments demonstrates clearly that with reasonably careful treatment, sap tensions, even in small annuals, remain remarkably constant for long periods after cutting. The plastic bag storage technique was used for all subsequent measurements.

An interesting result of this large-scale sampling of populations was the range in variance from one population subsample to another. This is particularly marked in *Gilia aggregata* and *Polygonum douglasii*.

Diurnal Variation

Scholander and others (1965) report marked diurnal variation in sap tension in various plants. Waring and Cleary (1967) note that equilibration between plant and soil occurs by early evening but present measurements indicate that it continues at lesser rates throughout the dark hours. Due to this fact and to field sampling problems after dark, minima in this study are represented by cuttings taken before full light in the morning. Maxima were found to occur between about 1300 and 1700 hours on cloudless days with little haze.

In Figure 2 diurnal curves are compared for three species. Each point in this graph represents a single measurement. Later studies showed that sap tensions in phenologically similar populations of *Polygonum cascadense* ranged over about 8 atmospheres at minimum tension and 11 atmospheres at maximum tension. *Lotus nevadensis douglasii* and *Luina stricta* are herbaceous perennials and show considerably less variability than the annual knotweed. In the two perennials

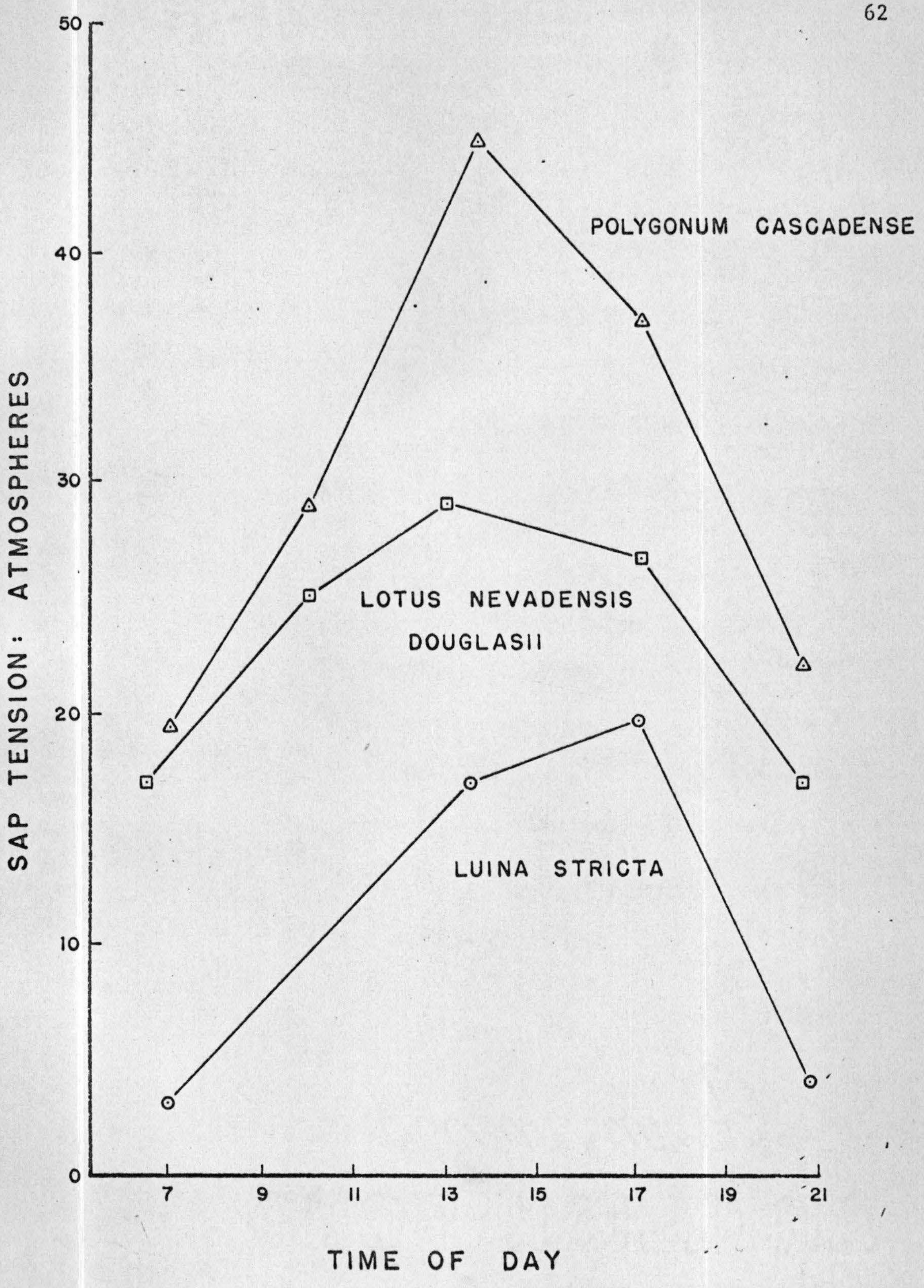

Figure 2. Diurnal Variation in Sap Tension in Three Species on Iron Mountain, July 23, 1967.

population variation was within 3 atmospheres at minimum tension and within 5 atmospheres at maximum.

The most symmetrical curve is that for *Lotus nevadensis douglasii* taken from a south-facing scree slope. *Luina stricta*, confined to more westerly meadow slopes, reaches maximum tension later in the evening, due evidently to its direction of exposure. *Polygonum cascadense* shows both the highest minimum tension and the greatest diurnal variation. It is dependent on moisture near the soil surface, unlike the deeper-rooted perennials. The *Polygonum* population grew in dry rocky loam on a southwest-facing slope. In these studies actual minimum tensions probably were not obtained, since the sun had risen (although not on the slopes sampled) when the stems were cut.

Variation within Individual Plants

It might be expected from the anatomical and molecular arrangement of water in plant stems that equilibration of diffusion pressure deficits would be rapid and that differences in sap tension measurements within a single plant would be due to experimental error. However, Vité and Rudinsky (1959) have demonstrated that in conifers, even without the more continuous water columns provided by angiosperm vessels, sap migrates up the trunk in definite spiral patterns and does not diffuse through the entire stem. Water from one sector of roots will therefore supply only a portion of the branches, but all roots supply the crown tip. Using injected dyes, Vité and Rudinsky characterized a variety of patterns of water movement, the most restricted of which were characteristic of *Pseudotsuga menziesii* and *Chamaecyparis* *lawsoniana*. These findings indicate that sap tensions in portions of a single plant occupying different micro-environments might be markedly different. This phenomenon has been demonstrated in *Pseudotsuga menziesii* (Figure 1) and *Vaccinium membranaceum* (Figure 3).

In general, however, when measurements were taken from several stems of a single individual, the readings were tightly clustered and spanned less than one atmosphere (Figure 3). These measurements demonstrate the repeatibility and precision of pressure-bomb measurements.

Variation among Parts of a Plant

An attempt was made to determine the reliability of extrapolating from one portion of a single plant to another, as well as to determine how small a plant part might be used to produce a reliable measurement. A large plant of *Ivesia gordonii*, a cespitose perennial herb, was dug; and individual leaves, flowering stems having a single bract, and portions of the branching rootlike caudex were sealed in plastic bags and measured. The results are shown in Figure 4. Measurements for all three plant parts overlap, and differences between the means are insignificant at the 5 percent level as determined by the F test. Flowering stem and caudex measures showed low variance, but that of the leaves was considerably greater. Since the leaves are small and had to be carried in a knapsack for most of a hot afternoon, the greater variance may in part be the result of loss of water to air in the plastic bag. These findings do indicate that virtually any measurable part of the plant can be used with considerable reliability.

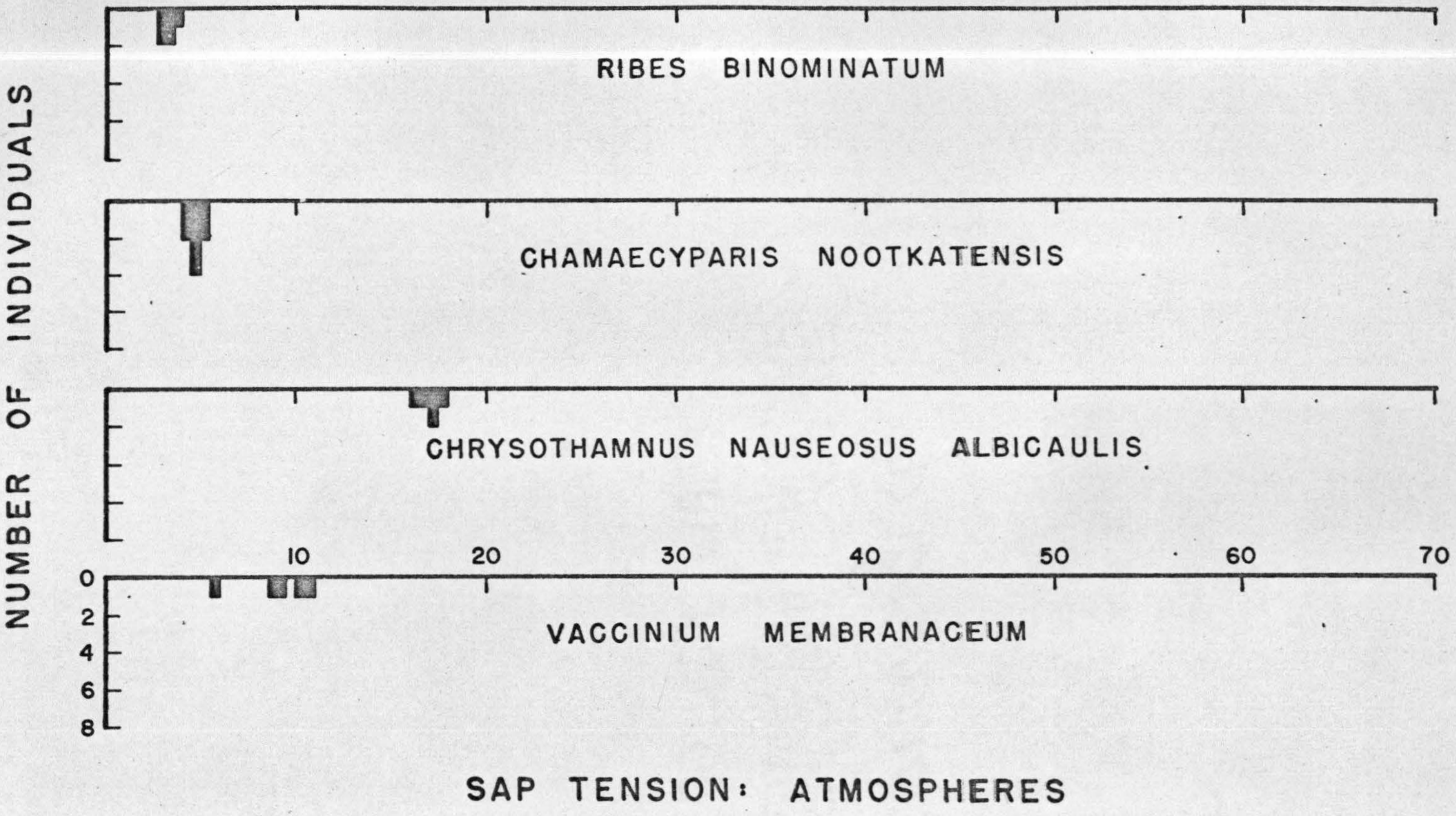

Figure 3. Variation in Minimum Sap Tension within Single Plants on Iron Mountain, August 1967.

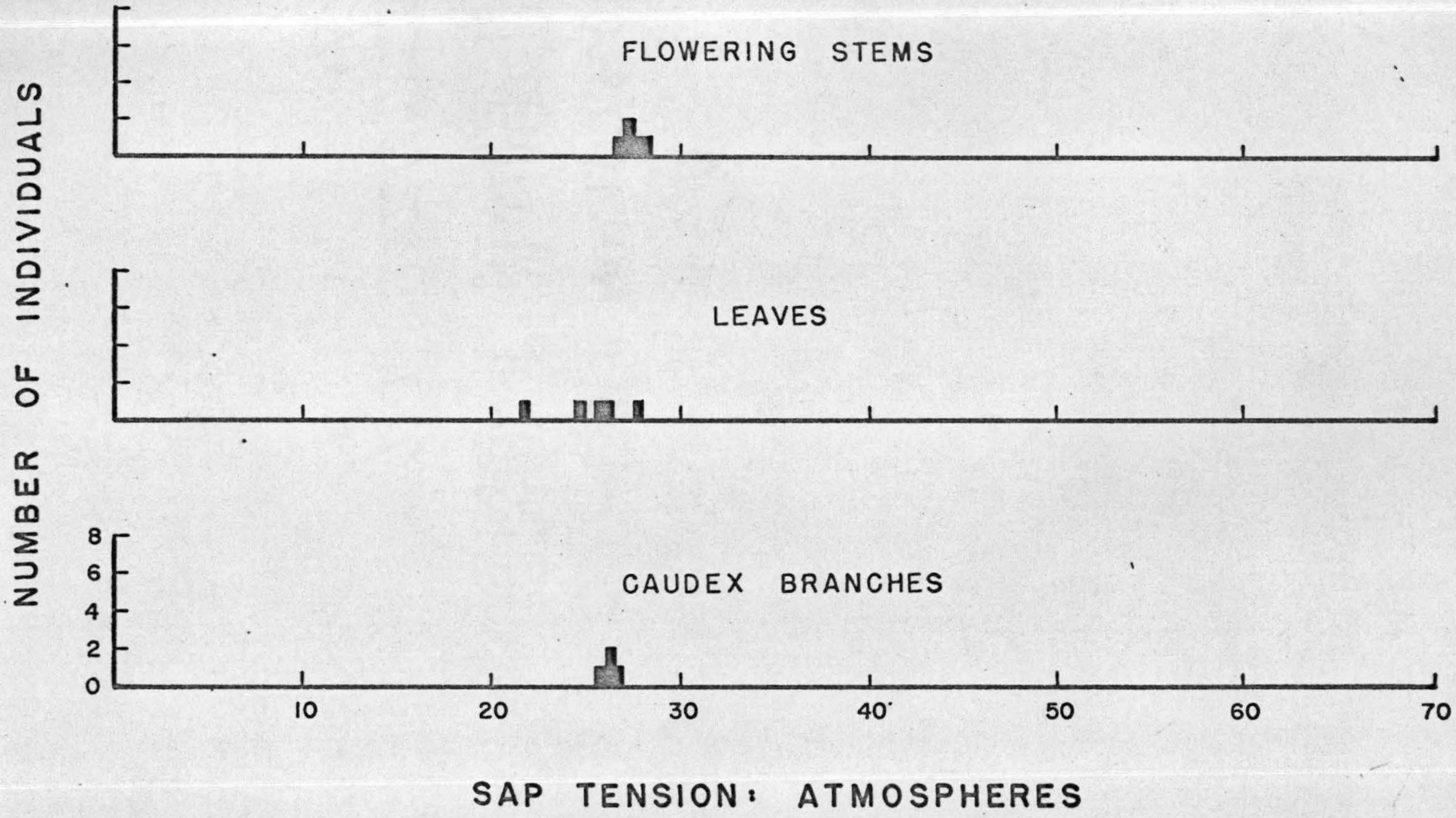

Figure 4. Variation in Maximum Sap Tension among Plant Parts in <u>Ivesia gordonii</u> (Cone Peak, 3 August 1967).

Variation within a Population

Figure 5 shows that minimum sap tensions are quite constant within populations growing in more mesic habitats (*Chamaecyparis nootkatensis*, *Ribes binominatum*, *Lupinus arbustus neolaxiflorus*), but that in areas where moisture stress is generally higher, even minimum tensions show large variances within small populations (*Chrysothamnus nauseosus albicaulis*, *Gilia aggregata*).

The *Chamaecyparis nootkatensis* population measured is actually a clone of individuals beneath the Mesic Forest canopy. Many new trunks have been added by self-layering of branches. These trunks are still interconnected, but each has a well-established root system of its own. The remarkable clustering of readings, as well as showing the reproducibility of results with this technique, indicates that such clones should be considered single individuals for physiological purposes.

Population Variation Correlated with Plant Size

It was noted early in the sap tension determinations that in a variety of small annuals growing in drier sites, high measurements were strongly correlated with small plant size. This phenomenon has been demonstrated in trees by Waring and Cleary (1967) but is best exemplified in annuals such as *Polygonum douglasii*, as shown in Figure 6. A sample of nine plants showing the range of sizes present within 2500 square cm was ordered by size of plant and measured. Without exception sap tension increased with decreasing plant size.

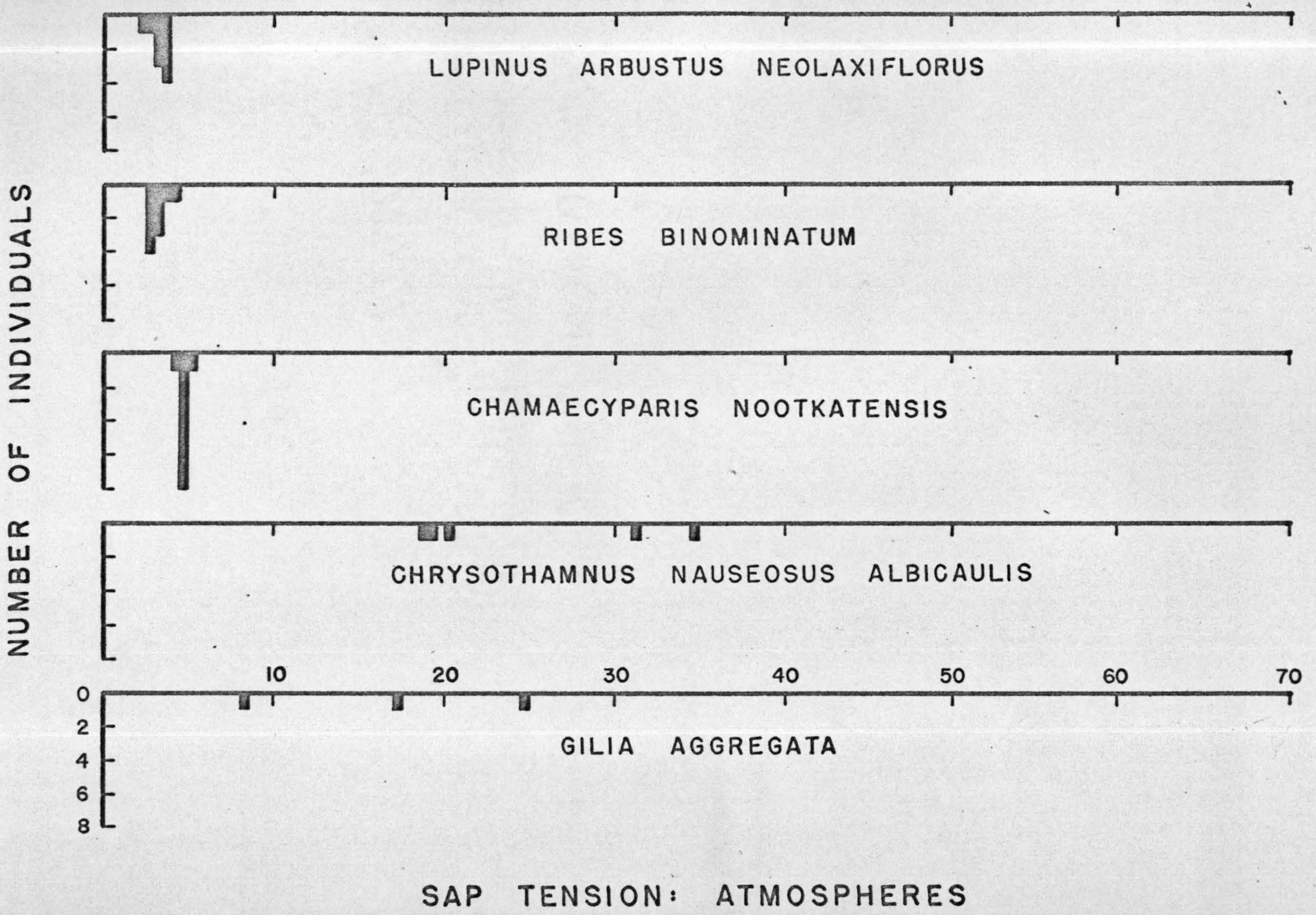

Figure 5. Variation in Minimum Sap Tension within Species Populations on Iron Mountain, August 1967.

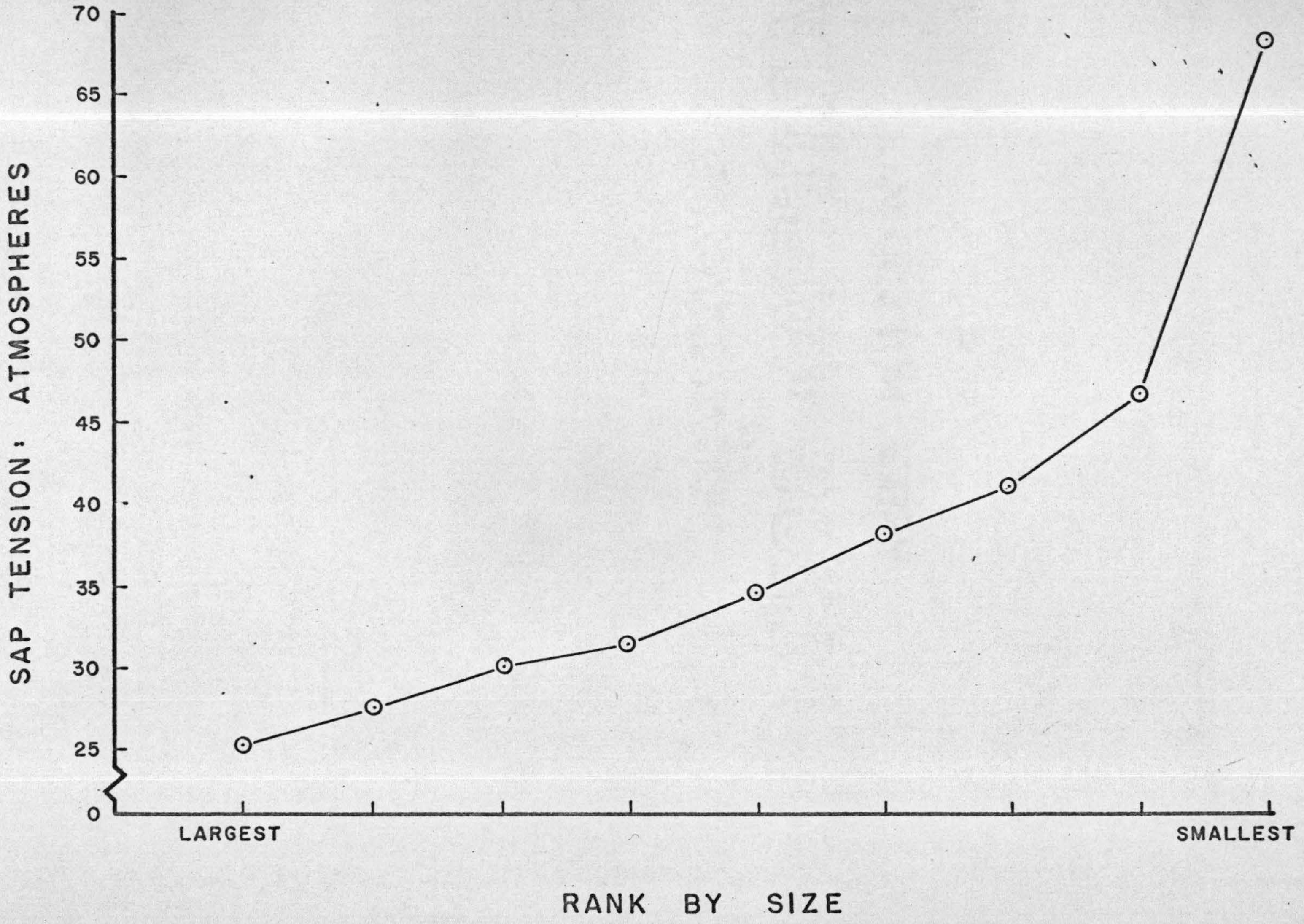

Figure 6. Maximum Sap Tension as Related to Plant Size in Polygonum douglasii (Iron Mountain, 2 August 1967).

These annuals have shallow root systems and almost certainly compete for water near the surface of the soil. Digging numerous plants has demonstrated that depth of root penetration is correlated with plant height. It is thus likely that high sap tension is to some extent both cause and effect of small plant size, since small plants are poor competitors for soil moisture, which is probably limiting, and therefore remain of lesser stature.

Population Variation at Minimum and Maximum Tension

Waring and Cleary (1967) note that sample variation is greater at maximum tension than at minimum tension. This has been confirmed in a number of Western Cascade species, exemplified in Figure 7 by *Collomia linearis*, an annual. While minimum tensions span only 2.5 atmospheres, maximum tensions range over at least 43 atmospheres, the highest reading being over 68 atmospheres. In this, as in other annuals, variation in depth of root penetration is probably of major significance to variation in maximum tension. Even at these high maximum tensions, individuals of *C. linearis* seem capable of completely equilibrating with the soil during the night.

Variation with Habitat

A number of Western Cascade disjunct species are found in more than one habitat type. They are of major importance in comparing the moisture regimes in the various sites where they occur. *Chamaecyparis nootkatensis* is found as a forest tree among similar-sized specimens of *Tsuga mertensiana* and *Abies lasiocarpa* on north-facing slopes near

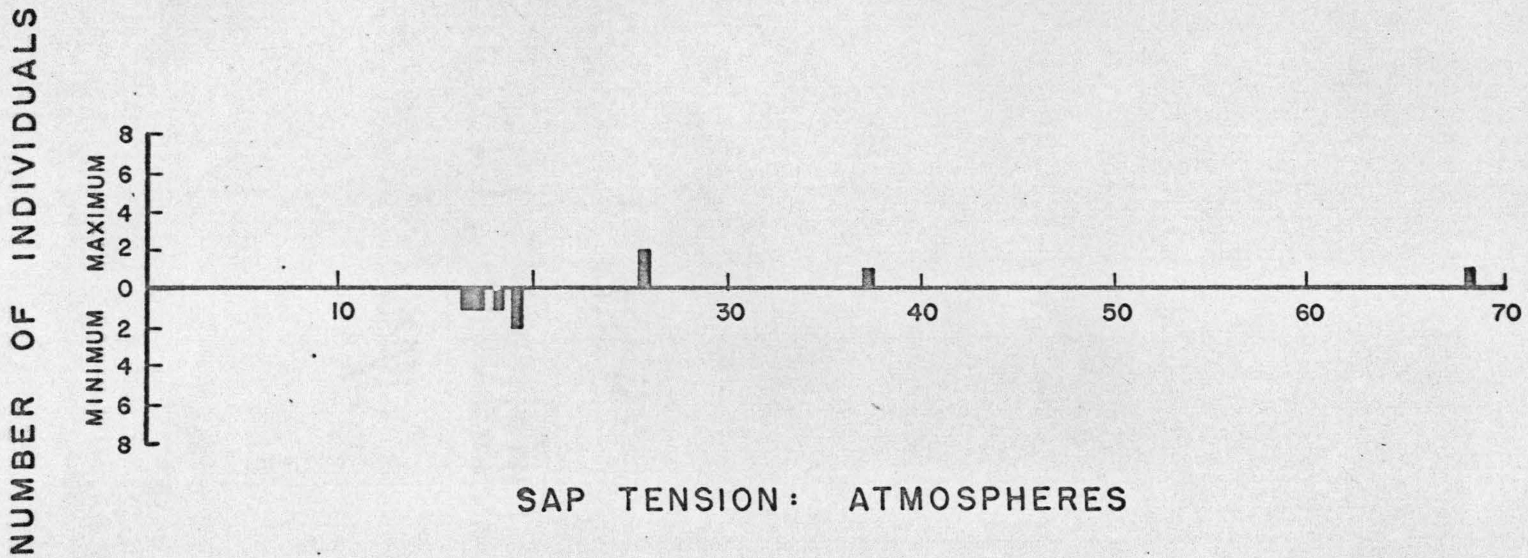

Figure 7. Population Variation at Minimum and Maximum Sap Tension in <u>Collomia linearis</u> (Iron Mountain, 23 August 1967).

the summits of some Western Cascade peaks and as occasional understory clones beneath less dense but more mature Pseudotsuga menziesii - Abies amabilis forests on lower slopes. It also occurs in very shallow soils, sometimes rooted in rock crevices on exposed ridges of various exposures. Four such habitats were compared using pressure-bomb techniques, but only two are reported here since the two forest localities were found to be nearly identical, as were the two ridge localities. Figure 8 shows that the forest populations had considerably lower tensions, both at maximum and minimum tension, than the ridge populations.

Specimens of Ribes binominatum from the same shaded forest locality, however, had significantly higher minimum tensions than comparable populations in open, southwest-facing meadows. Maxima were nearly the same. This indicates that the hot open meadows actually comprise a less stressful environment for Ribes binominatum than does the shaded forest. This is probably due to the heavy dew in the meadows, resulting in less nighttime transpiration and consequently more rapid equilibration with the soil. Nightly dew may also add a considerable amount of moisture to the surface soil during a prolonged drought.

Stems of Pachystima myrsinites were taken from three different habitats on Sardine Butte. The first was a dense forest with much coniferous litter and little ground-cover, the second a moderately steep east-facing rockfall slope, and the third the rocky exposed summit of the east spur of the peak. Figure 8 shows the expected relationships between the moisture regimes of the three habitats for this species: increasingly high tensions were recorded from the forest, rockfall slope, and exposed summit habitats.

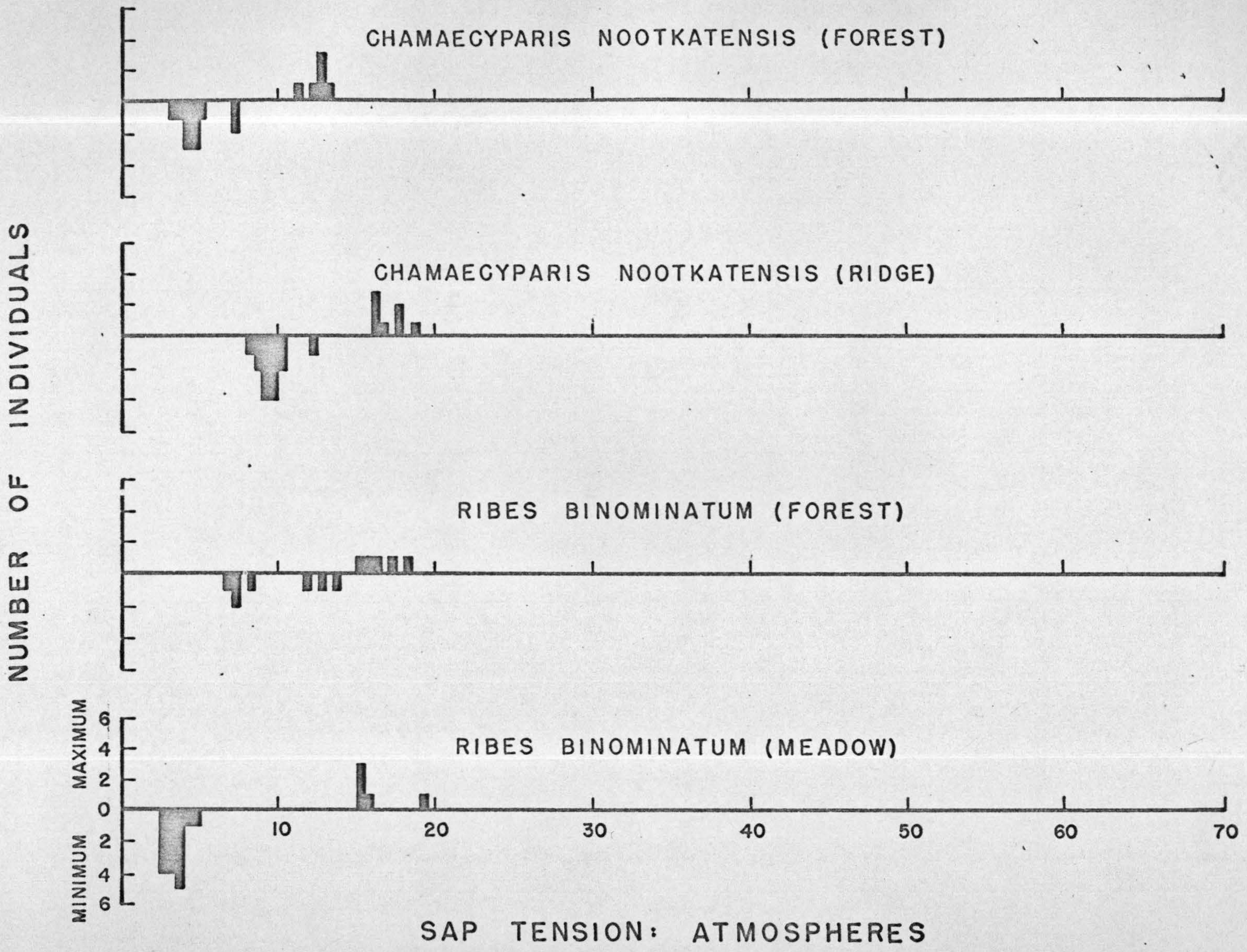

Figure 8. Variation in Sap Tension with Habitat (Iron Mountain, 2 August 1967).

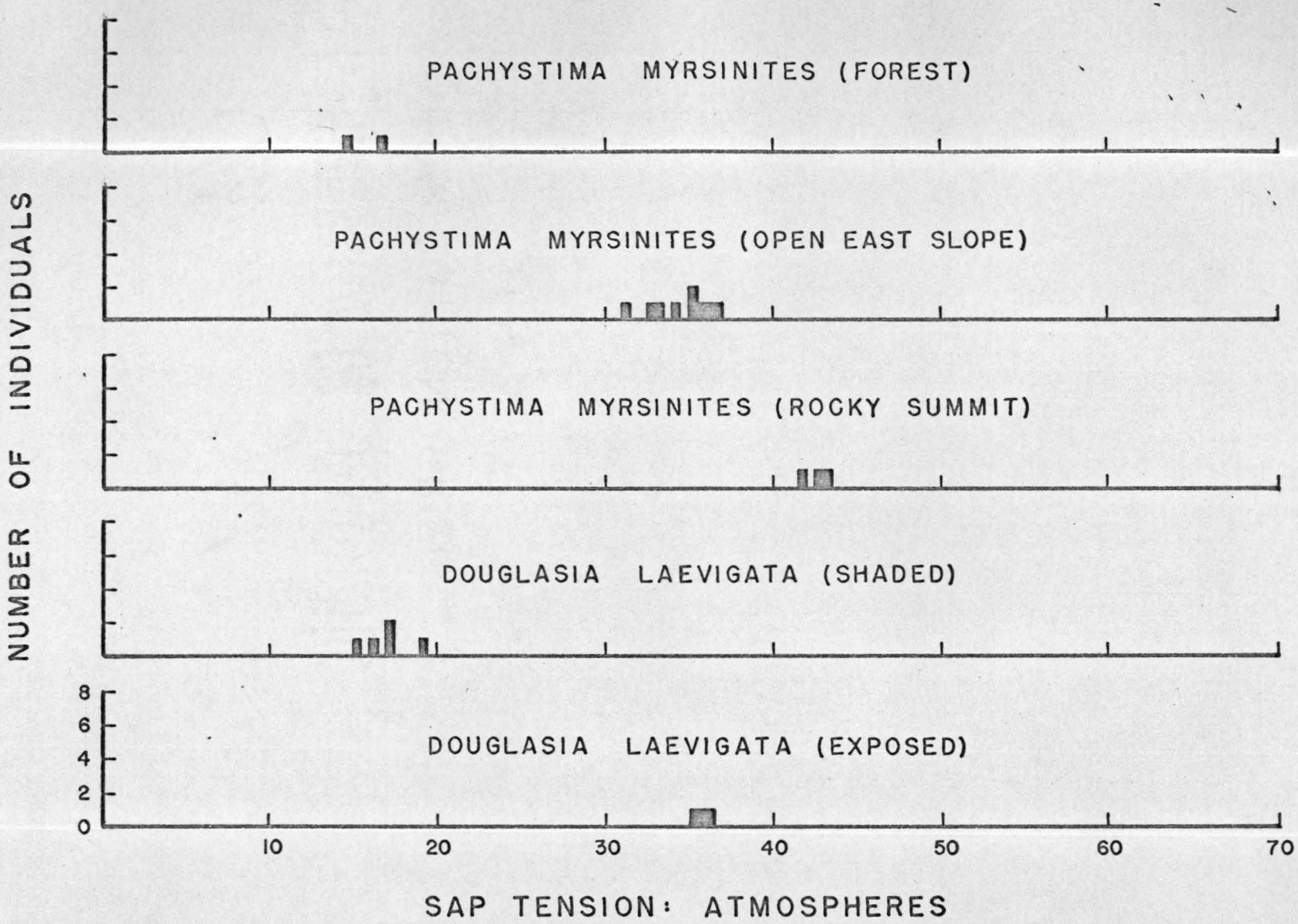

Figure 8 (cont.). Variation in Sap Tension with Habitat (Sardine Butte, 27 July 1967; and Cone Peak, 3 August 1967).

Douglasia laevigata is a highly restricted species in the Western Cascades, being found only on certain west or north-facing vertical basaltic outcrops exposed to the prevailing winds. On one such rock wall on Cone Peak, specimens were sampled from a rather deep protected crevice and from a more exposed crevice less than a meter away. The more protected plants were etiolated, had very large leaves for the species, and did not flower abundantly compared with close neighbors but exhibited sap tensions lower by more than 16 atmospheres (Figure 8). Such major differences in moisture regimes over small distances illustrate the difficulty in attempting to describe a species or a region, no matter how small, as "xeric" or "mesic."

Variation with Habitat and Phenological Stage

Especially in annuals, it is difficult or impossible to separate habitat differences from phenological differences, since as the plant matures and dies during a single season, it exhibits a distinct progression of sap tensions. A moister habitat may simply prolong this characteristic progression. Such problems are illustrated well by populations of *Polygonum cascadense* on Iron Mountain. On 2 August plants were measured from three habitats of differing insolation, exposure, and soil type (Figure 9). The highest population was found on a steep south-facing scree slope; the population of intermediate elevation on partly-shaded, more gently-sloping fine gravel scree near xeric meadow species; and the lowest population in the shade of robust meadow species. The apparent age of the individuals became less with decrease in altitude, and sap tensions decreased correspondingly. On

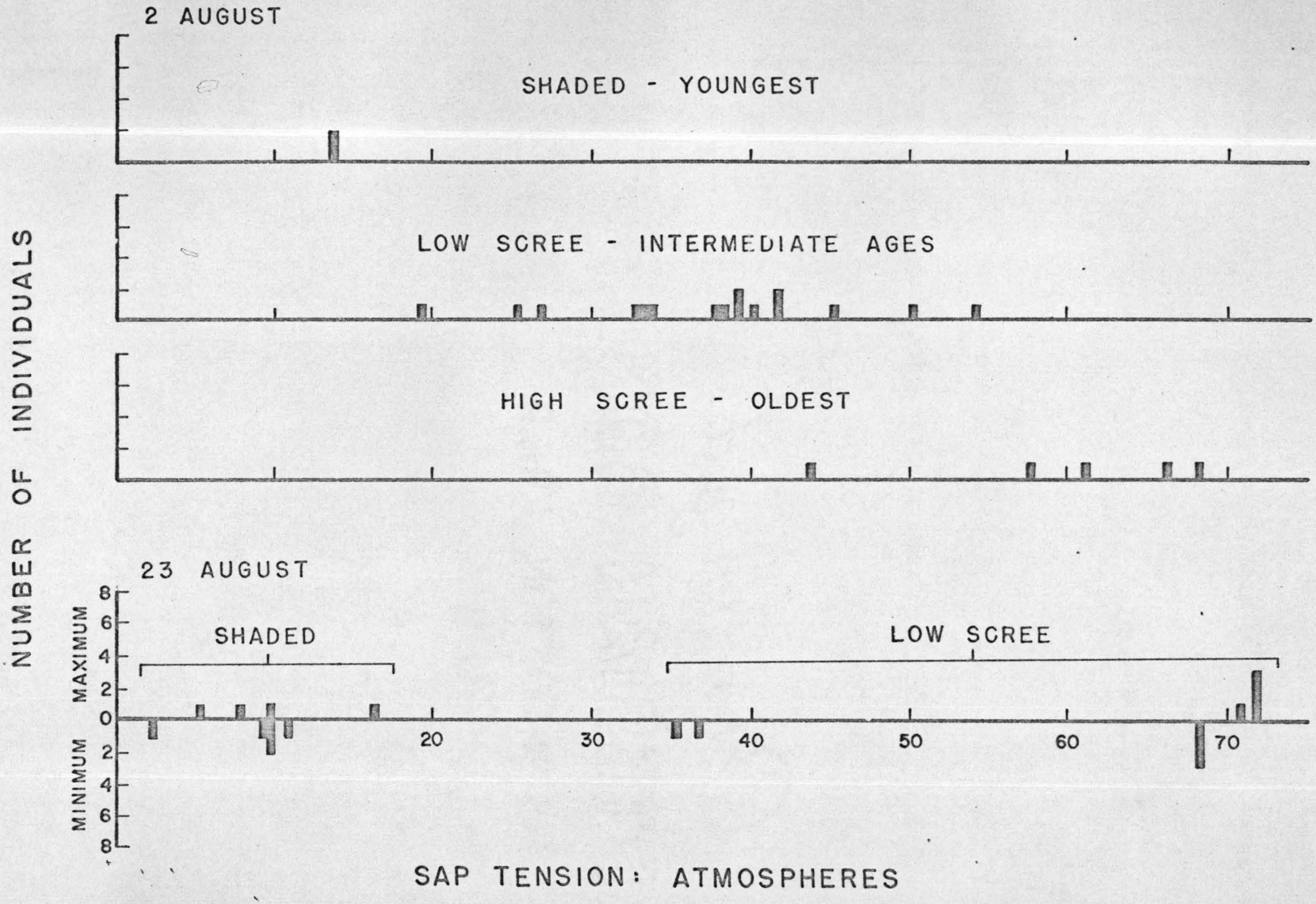

Figure 9. Variation in Sap Tension with Habitat and Phenological Stage in *Polygonum cascadense* (Iron Mountain).

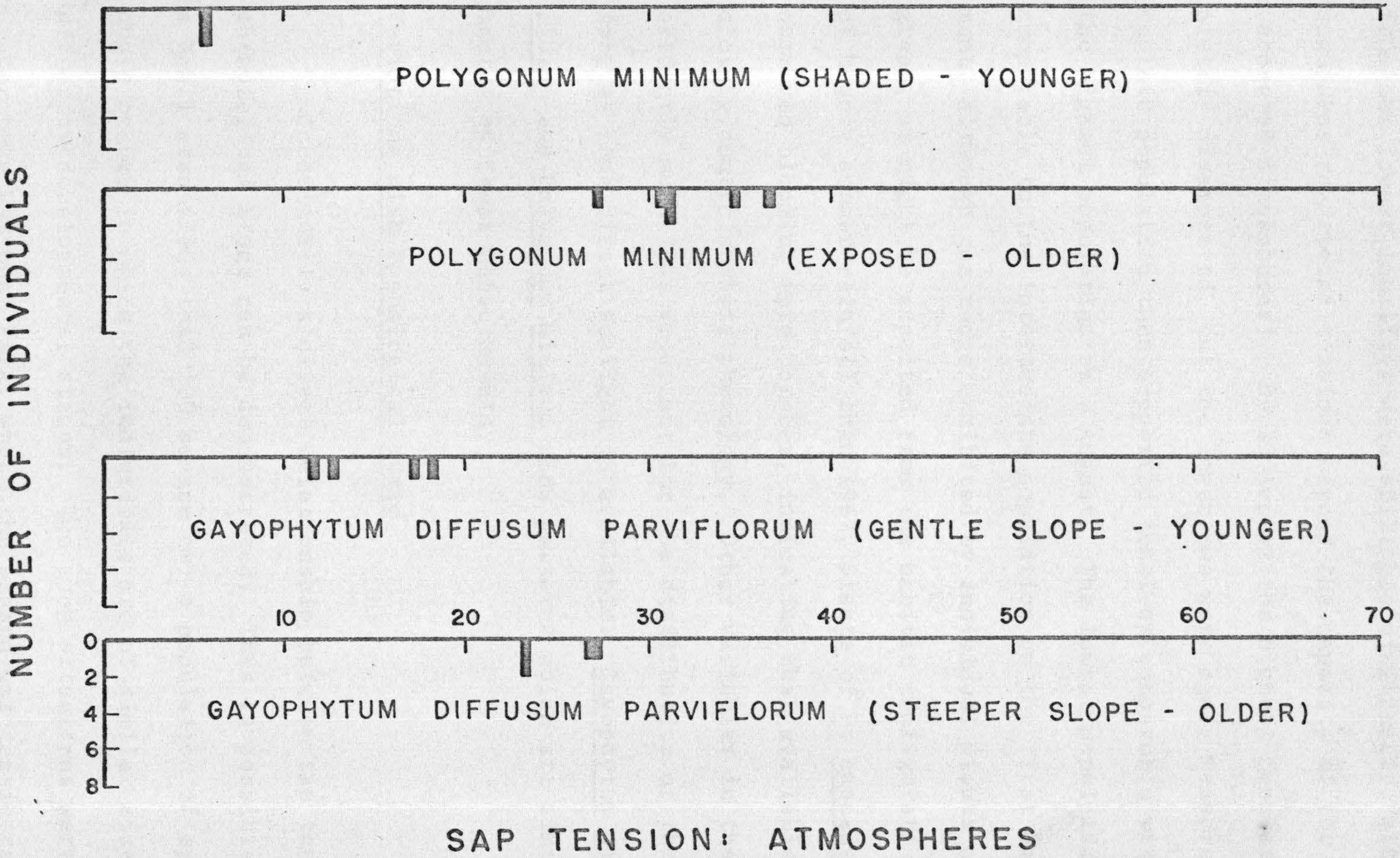

Figure 9 (cont.). Variation in Sap Tension with Habitat and Phenological Stage in Polygonum minimum (Iron Mountain, 2 August 1967) and Gayophytum diffusum parviflorum (Iron Mountain, 23 August 1967).

2 August plants at the highest locality (separated by 60 vertical m from the lowest locality) were still blooming freely, although some specimens registered tensions beyond the capacity of the instrument (above 68 atmospheres). By 23 August the highest population had completely disappeared, but the lower two were again measured. The intermediate population then supported tensions comparable with those of the highest population on 2 August. The lowest population was in turn comparable to the intermediate population on the first date of measurement, although the range exhibited by individual plants was not as great, as might be expected from the habitat configuration. In years of higher summer rainfall than 1967, plants of *P. cascadense* have been observed blooming into October, indicating that available moisture closely controls their phenology. Other variables in the habitat are evidently much less important for the distribution of the species, as long as some direct sunlight is available. *Gayophytum diffusum parviflorum* and *Polygonum minimum* show patterns which are similar but documented by fewer measurements.

Variations with Phenological Stage

Occasionally a direct relationship between sap tension and phenological stage can be demonstrated. This is possible where within a small area (less than 100 square cm) a population of ephemeral annuals occurs in which the individuals are of similar sizes but are at different developmental stages. Two such situations were observed at Crater Lake National Park, where the season was considerably delayed over that on Iron Mountain, and earlier phenological stages of many species were available for study.

Specimens of Polygonum kelloggii exhibited uniform minimum tensions, even though a complete progression of phenological stages was represented in the population (Figure 10). When measured at maximum tension, the phenologically oldest specimens (not necessarily the smallest individuals) had sap tensions almost 30 atmospheres higher than the youngest. It is obvious that moisture was beginning to be limiting for some members of the population and that within a few days at most the population would be entirely gone.

An even more striking example of rapid desiccation was illustrated by a population of Mimulus breweri from the same meadow, although age differences among the individuals were less obvious than in Polygonum kelloggii. Minimum tensions were consistently low except in one individual which represented a slightly more advanced phenological stage. This specimen registered above 68 atmospheres on the pressure-bomb apparatus (Figure 10). Maximum tensions were only slightly higher than minima except, again, for the oldest individual, which measured 18 atmospheres higher than any other. Within the population there are never more than a few plants with intermediate sap tensions. The sap tension measurements corroborate the morphological evidence that when water begins to become limiting for these plants, they desiccate rapidly and die. Unfortunately, it is impossible to take repeated measurements on a single individual, and this rapid progression cannot be completely followed with the pressure-bomb apparatus.

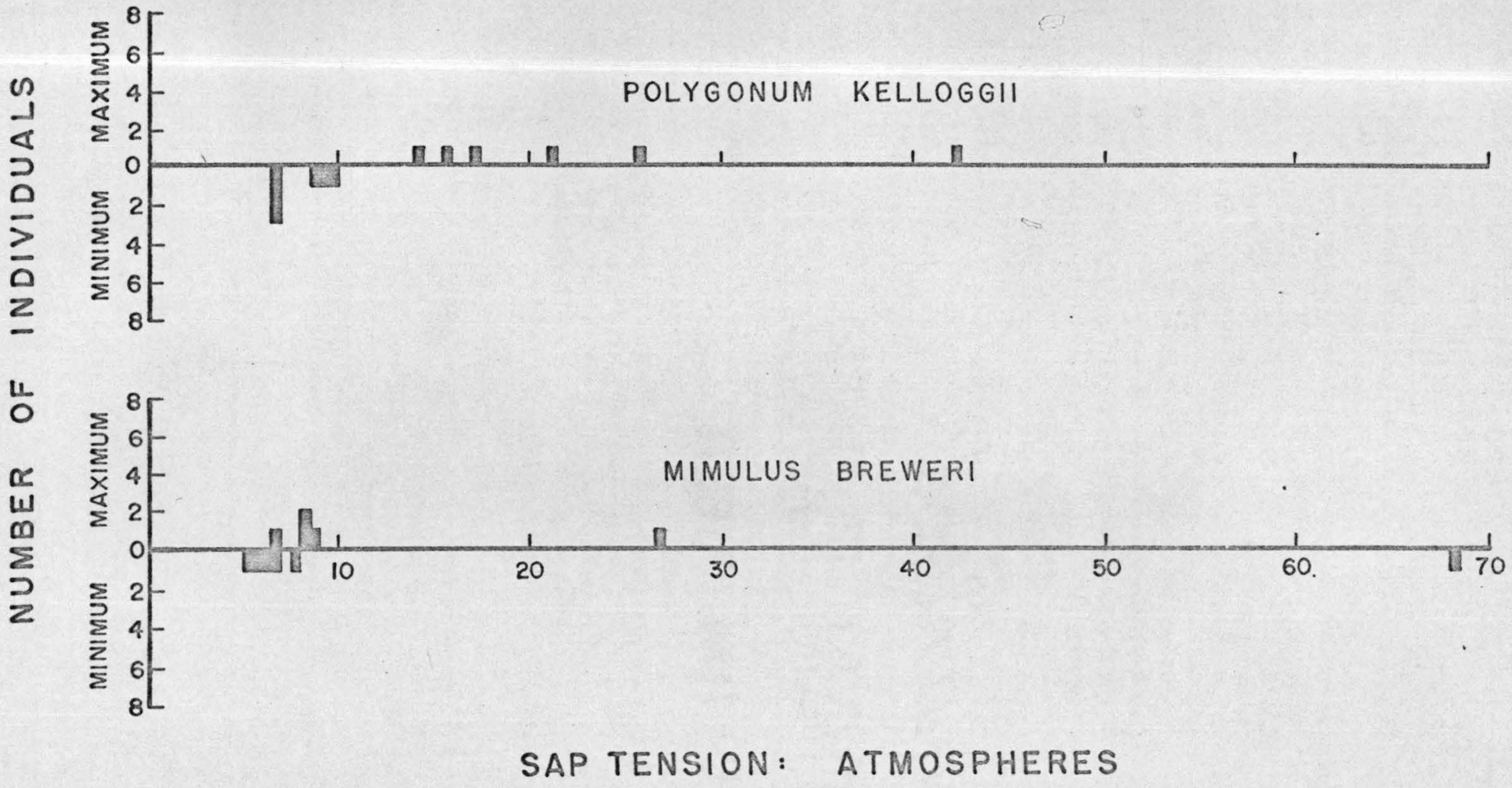

Figure 10. Variation in Sap Tension with Phenological Stage (Crater Lake, 13 August 1967) see text for explanation.

Xeric Indicators

Sap tensions were measured in seven of the species termed "xeric indicators" by Detling (1953): *Lupinus arbustus neolaxiflorus*, *Collomia linearis*, *Gilia aggregata*, *Linum perenne lewisii*, *Polygonum douglasii*, *Sedum stenopetalum*, and *Silene douglasii*. Sap tensions ranged from the lowest registered by any species (*Lupinus arbustus neolaxiflorus*: 2 atmospheres) to readings above 68 atmospheres (*Collomia linearis*, *Linum perenne lewisii*, *Polygonum douglasii*, and *Sedum stenopetalum*). No general conclusions are possible from these observations except that these species encompass a wide range of adaptations to a progressively decreasing water supply. It is clear, as discussed by Thoday (1933), that many meanings might be attached to such a term as "xeric species," and that investigators must take care to define usage of such terms in as strict a sense as possible.

Maximum Recorded Stresses

Twelve Western Cascade species were found to have sap tensions above 68 atmospheres before seeds were entirely ripe. Most of these species were annuals, such as *Polygonum douglasii*, *Polygonum minimum*, *Polygonum cascadense*, *Gayophytum diffusum parviflorum*, *Linanthus harknessii*, *Collomia linearis*, *Orthocarpus imbricatus*, *Mimulus breweri*, and *Galium bifolium*. The last two species are spring ephemerals, and it is likely that their seeds would have matured rapidly even if detached from the desiccating plants. *Linanthus harknessii* exhibits modified ephemeral tendencies even at these high sap tensions. The highest measured tension, exceeding 71.5 atmospheres, was recorded in *Polygonum cascadense*.

Sedum stenopetalum and *Linum perenne lewisii*, herbaceous perennials, and *Arctostaphylos nevadensis*, a woody perennial, also exhibited tensions above 68 atmospheres. This is particularly noteworthy in *Arctostaphylos*, a typically high-montane species, which showed no dieback of stems sustaining these extreme tensions.

Tensions in an annual, *Navarretia divaricata*, and two woody perennials, *Juniperus communis saxatilis* and *Pachystima myrsinites*, measured greater than 50 atmospheres. The perennials again showed no ill effects from the moisture stress.

A number of species (including only one annual) characteristic of diverse geographic regions were found to have sap tensions above 40 atmospheres. They are *Polygonum kelloggii*, *Ivesia gordonii*, *Lotus nevadensis douglasii*, *Gilia aggregata*, *Penstemon deustus*, *Haplopappus hallii*, *Chrysothamnus nauseosus albicaulis*, and *Artemisia ludoviciana latiloba*.

Laboratory Germination Experiments

Germination experiments in sub-irrigated peat pots using a variety of volcanic Western Cascade soils, serpentine soil from the Illinois Valley, Josephine County, and greenhouse rotted leaf mold indicated no restriction of germination or establishment among those species tested. The volcanic soils used were derived from all three major volcanic units in the Western Cascades. The Little Butte Series was represented by soil from Jumpoff Joe, the Sardine Formation by soil from the lower slopes of Iron Mountain, and Plio-Pleistocene volcanics by soils from Rebel Rock and Sand Mountain. Species used had previously been shown to germinate on wet sterilized filter paper in light without previous stratification. Replicate pots were autoclaved to destroy the original microflora. The autoclaved soils, however, broke down physically and became sufficiently hydrophobic that capillary water would not rise five cm. No species germinated on such soils, but all did readily on unautoclaved counterparts. Difference in growth rate was the only notable outcome of this experiment. All species persisted but grew slowly on serpentine soil. The Western Cascade soils produced a range of growth rates, correlated with the texture and amount of organic matter in the particular soil. All species were most robust on greenhouse soil. These results indicate that such factors as secondary organic nutrients and water availability are more important to germination and growth in these species than the chemical composition of the parent rock from which the soils were derived.

Germination and Establishment in the Field

Plots were sown with seed of disjunct species at several localities in the Western Cascades in an attempt to establish them in sites where they had not previously been found. Experiments of this type, which are similar to those reported by Cavers and Harper (1967a, 1967b), test the acceptibility of the various habitats to the propagules of the disjunct species. With the addition of proper controls, information can be gathered on the degree of past dispersal of the species as well as on competitive exclusion by existing vegetation.

Methods

Seeds of 22 disjunct or endemic Western Cascade species were collected during the late summer and fall of 1966. They were cleaned, counted, and bagged in equal numbers depending on the availability of good seed. Field sites were chosen on Iron Mountain, Rebel Rock, and Sardine Butte. The first peak, because of its easy access and great number of disjunct species, supplied much of the seed used in the experiments. Since some seeds were resown at or near their sites of collection, Iron Mountain acted as a partial control in the establishment studies. Rebel Rock also supports a large number of disjunct species, but the disjunct flora is of a different composition. Six of the species tested in these experiments do not occur naturally on Rebel Rock, and three of them have not been found on Iron Mountain. Sardine Butte, which lies farther to the west and has only a small outcrop area at the summit, supports five of the disjunct and endemic species including only two of those utilized in the experiments.

Representative habitats were chosen on each of these peaks. Three were selected from Iron Mountain including a mesic meadow dominated by Rubus parviflorus and Pteridium aquilinum, with frequent occurrences of Ribes binominatum, Luina stricta, Gilia aggregata, Artemisia ludoviciana latiloba, Lupinus latifolius, Vicia americana, Eriophyllum lanatum, and Cirsium centaurea. This site is on a moderately steep, southwest-facing slope, partially shaded to the west by several large, free-standing douglas fir trees. The soil is a deep light loam, rich in organic matter, which, judging from spring slumping and observable creep of cleared areas, undergoes considerable movement downslope during those seasons when it is not covered by snow or dense herbaceous vegetation. The second habitat is a considerably less steep, southwest-facing slope of fine scoriaceous material which presumably creeps at a rate at least comparable with that of the meadow soil. There is little or no organic matter in the "soil" of this slope; the only cover consists of widely dispersed small annuals. The third and most severe habitat is a flat but rough area of scoriaceous rock which crops out at the brink of the south-facing precipice on Iron Mountain. Fine mineral soil collects only in small pockets of the scoria, and the site supports only mosses and mats of *Selaginella wallacei*, both of which desiccate during the dry portion of the summer.

Habitats on Rebel Rock include forest, dry meadow, and cliff-brink sites. The most protected site is under a moderately dense canopy of mature *Abies lasiocarpa* and *Pseudotsuga menziesii*. The dominant species growing in the damp, rich, loamy, black soil are *Valeriana sitchensis*, *Galium oreganum*, *Viola orbiculata*, *Hieracium albiflorum*, *Aquilegia formosa*, and *Aster ledophyllus*. A small patch of *Mertensia bella* occurs in a slightly more exposed area only a few meters away. The second habitat is a dry ridgetop meadow dominated by an unidentified species of *Carex*. Also abundant are *Viola nuttallii bakeri*, *Calochortus lobbii*, *Lupinus sericeus*, and *Cirsium centaurea*. The ridge at this point slopes slightly to the southwest, and the soil is a well-drained peaty loam with numerous included fragments of andesite. The soil is not as deep as that in the forest habitat or in the meadow site on Iron Mountain; the numerous rocks preclude accurate measurements of depth. Two parallel but slightly different sites were chosen at the top of the south-facing precipitous slope that runs the length of the Rebel Rock ridge. One site, in a pocket of outcropping scoriaceous rock, contains an accumulation of reddish rocky loam and supports a moderately dense growth of *Arctostaphylos nevadensis*, *Eriophyllum lanatum*, *Eriogonum umbellatum*, *Antennaria rosea*, and such annuals as *Polygonum douglasii*, *Polygonum minimum*, and *Navarretia divaricata*. The neighboring plot has considerably less soil development and supports mosses, *Selaginella wallacei*, *Calochortus lobbii*, *Eriophyllum lanatum*, and *Polygonum minimum*. The soil-pocket plot was cleared following the method described below, and the plot having less soil was left undisturbed. The area is flat, and exposure to the sun in both plots is complete.

Only one site was chosen on Sardine Butte because of the paucity of habitats available. This site is located at the summit of the east spur of the mountain in a flat area of blocky andesite. Light mineral soil has accumulated between the large blocks of parent material, giving the entire area a well-drained surface of uneven depth. Drought-tolerant species such as *Arctostaphylos nevadensis*, *Juniperus communis saxatilis*, *Comandra umbellata*, *Hieracium scouleri*, and *Pachystima myrsinites* are mixed with a few "ephemeral" perennials, especially *Selaginella wallacei* and *Allium amplectens*.

Sites were visited in early October, 1966, and pairs of square meter plots were chosen in each habitat. Plot pairs were as uniform in soil and vegetative cover as possible. One of the plots was cleared of vegetation and the soil cleaned of most of the roots and rhizomes. Both plots were divided into 400 square cm subplots onto which the seeds were scattered. They were then pressed gently into the soil to minimize downslope movement. Such variables as inequalities in the vegetation within the undisturbed plots and edge effects in the cleared plots were ignored.

All plots were visited at least twice during the growing season of 1967--in the early spring and early fall. Observations were made on the number, size, and phenological stage of seedlings of each of the species as well as the rates of recolonization of the cleared plots by native vegetation.

Results

The information gained from the seed plots is summarized in Tables IV, V, VI, and VII. Several interesting features of these tables are discussed below.

In the Rebel Rock plots only one species showed no germination at all--*Chamaecyparis nootkatensis* (Table V). It did not germinate either in the field or in subsequent laboratory tests, and the seed can probably be considered inviable. Four species germinated but failed to live in any of the plots throughout a single summer. These include *Allium crenulatum*, *Lewisia triphylla*, *Sedum divergens*, and *Castilleja rupicola*. All 17 other species were still living in the establishment plots by late August, 1967. Sixteen species established themselves in the cleared forest plot, far more than in any other habitat, although it is almost certain that most of these will be

Table IV. Numbers of Seeds Sown, Germinated, and Established in Cleared and Uncleared Plots in One Habitat on Sardine Butte.

Species	A	Outcrop					
		Cleared			Uncleared		
		1	2	3	1	2	3
Chamaecyparis nootkatensis	10	0	0	0	0	0	0
Allium crenulatum	25	0	0	0	5	0	0
Polygonym douglasii	8	7	0	0	0	0	0
Polygonum minimum	15	2	0	0	0	0	0
Polygonum cascadense	25	1?	0	0	0	0	0
Polygonum kelloggii	50	1	1	1	0	0	0
Lewisia triphylla	50	0	0	0	0	0	0
Arabis holboellii retrofracta	50	0	0	0	0	0	0
Sedum divergens	50	0	0	0	0	0	0
Ivesia gordonii	13	1?	0	0	4	0	0
Trifolium productum	16	2	0	0	2	0	0
Linum perenne lewisii	50	27	18	0	17	0	0
Douglasia laevigata	13	0	0	0	0	0	0
Gilia aggregata	25	0	0	0	11	7	0
Linanthus harknessii	50	26	9	9	11	4	4
Navarretia divaricata	50	9	4	4	3	1	1
Mertensia bella	25	0	0	0	0	0	0
Penstemon deustus	30	0	0	0	0	0	0
Castilleja rupicola	25	0	0	0	0	0	0
Castilleja pruinosa	50	0	0	0	0	0	0
Galium bifolium	13	2	2	2	4	4	4
Luina stricta	10	0	0	0	0	0	0

Explanation:

A: Number of seeds sown per plot
1: Number of germinated seeds
2: Number of seedlings surviving one year
3: Number of plants setting some seed
*: Species which were abundant both in and around the sown plots

Table V. Numbers of Seeds Sown, Germinated, and Established in Cleared and Uncleared Plots in Three Habitats on Rebel Rock. (See Explanation, Table IV.)

Species	A	Forest						Meadow						Outcrop					
		Cleared			Uncleared			Cleared			Uncleared			Cleared			Uncleared		
		1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Chamaecyparis nootkatensis	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Allium crenulatum	25	11	0	0	9	0	0	7	0	0	0	0	0	3	0	0	0	0	0
Polygonum douglasii	8	2	2	1	0	0	0	0	0	0	0	0	0	14*	14*	14*	1*	0	0
Polygonum minimum	15	2	2	2	1	0	0	10	4	4	7	0	0	14*	14*	14*	71*	50*	50*
Polygonum cascadense	25	8	8	8	0	0	0	7	7	7	2	0	0	6	5	5	0	0	0
Polygonum kelloggii	50	0	0	0	0	0	0	0	0	0	0	0	0	19	19	19	0	0	0
Lewisia triphylla	50	8	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0
Arabis holboellii retrofracta	50	13	13	0	5	0	0	0	0	0	7	0	0	4	0	0	0	0	0
Sedum divergens	50	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0
Ivesia gordonii	13	7	7	0	5	0	0	3	2	0	1	0	0	1	0	0	0	0	0
Trifolium productum	16	6	6	0	7	7	0	0	0	0	0	0	0	0	0	0	0	0	0
Linum perenne lewisii	50	32	32	0	12	9	0	10	3	0	31	0	0	13	0	0	0	0	0
Douglasia laevigata	13	2?	2?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gilia aggregata	25	21	21	0	5	5	0	9	4	0	4	0	0	0	0	0	0	0	0
Linanthus harknessii	50	30	29	29	11	10	10	13	8	8	4	0	0	40	26	26	0	0	0
Navarretia divaricata	50	12	12	12	0	0	0	18	12	12	0	0	0	50*	50*	50*	7*	7*	7*
Mertensia bella	25	9*	9*	0	16*	16*	0	0	0	0	0	0	0	0	0	0	0	0	0
Penstemon deustus	30	4?	4?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Castilleja rupicola	25	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Castilleja pruinosa	50	10	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium bifolium	13	6	6	6	4	4	4	4	4	4	4	4	4	10	10	10	0	0	0
Luina stricta	10	5	5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table VI. Numbers of Seeds Sown, Germinated, and Established in Cleared and Uncleared Plots in Three Habitats on Iron Mountain. (See Explanation, Table IV.)

Species	A	Meadow						Scree Slope						Outcrop					
		Cleared			Uncleared			Cleared			Uncleared			Cleared			Uncleared		
		1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Chamaecyparis nootkatensis	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Allium crenulatum	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polygonum douglasii	8	9*	5*	5*	18*	18*	18*	1	0	0	0	0	0	0	0	0	0	0	0
Polygonum minimum	15	5	5	5	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0
Polygonum cascadense	25	2	0	0	0	0	0	1*	1*	1*	8*	8*	8*	0	0	0	2	0	0
Polygonum kelloggii	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lewisia triphylla	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arabis holboelli retrofracta	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sedum divergens	50	0	0	0	0	0	0	0	0	0	5*	5*	0	0	0	0	0	0	0
Ivesia gordonii	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trifolium productum	16	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0
Linum perenne lewisii	50	3	3	0	15	15	0	0	0	0	0	0	0	2	2	0	0	0	0
Douglasia laevigata	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gilia aggregata	25	20*	20*	0	30*	30*	0	1	0	0	0	0	0	0	0	0	0	0	0
Linanthus harknessii	50	6*	6*	6*	7*	7*	7*	1*	1*	1*	12*	12*	12*	0	0	0	0	0	0
Navarretia divaricata	50	11	11	11	0	0	0	0	0	0	15*	15*	15*	0	0	0	0	0	0
Mertensia bella	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Penstemon deustus	30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Castilleja rupicola	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Castilleja pruinosa	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium bifolium	13	14*	8*	8*	8*	8*	8*	0	0	0	0	0	0	0	0	0	0	0	0
Luina stricta	10	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table VII. Numerical Summary of Species Germinating or Establishing in Various Circumstances.

Species	Number of cleared and uncleared plots (n=14) in which germination occurred	Number of cleared and uncleared plots (n=14) in which species established for one year	Number of cleared plots (n=7) in which no evidence of germination was seen	Number of cleared plots (n=7) in which species germinated but died within one year	Number of uncleared plots (n=7) in which no establishment occurred, while establishment occurred in the corresponding cleared plot	Number of uncleared plots (n=7) in which species established better than in the corresponding cleared plot
Chamaecyparis nootkatensis	0	0	7	0	0	0
Allium crenulatum	5	0	4	3	0	0
Polygonum douglasii	7	4	2	2	2	1
Polygonum minimum	9	6	2	1	2	1*
Polygonum cascadense	9	5	1	2	3	1*
Polygonum kelloggii	2	2	5	0	2	0
Lewisia triphylla	2	0	5	2	0	0
Arabis holboellii retrofracta	4	1	5	1	1	0
Sedum divergens	2	1	6	1	0	1*
Ivesia gordonii	7	2	3	2	2	0
Trifolium productum	5	2	5	1	0	1
Linum perenne lewisii	10	7	1	1	3	1
Douglasia laevigata	1?	1?	6	0	1?	0
Gilia aggregata	8	6	3	1	1	2
Linanthus harknessii	11	10	1	0	2	2*
Navarretia divaricata	8	8	2	0	3	1*
Mertensia bella	2	2	6	0	0	1*
Penstemon deustus	1	1	6	0	0	0
Castilleja rupicola	1	0	6	1	0	0
Castilleja pruinosa	1	1	6	0	1	0
Galium bifolium	9	9	2	0	1	1
Luina stricta	4	1	5	1	1	0

*Species occur naturally in the vicinity.

eliminated by competition as the forest vegetation reinvades the plot. Three species (*Ivesia gordonii*, *Trifolium productum*, and *Luina stricta*), all herbaceous perennials, were established on Rebel Rock even though they are not native to the region.

The Iron Mountain plots, near where most of the seed originated, showed remarkably little germination and establishment (Table VI). Two of the chosen habitats are severe, being exposed to alternate freezing and thawing in winter and having soil surface available for germinating seeds for only a short time in the spring. The meadow plots were sufficiently steep that many of the seeds may have been washed completely out of the cleared plot and were never found in the surrounding dense vegetation. It is likely that competition for light and water from previously established perennial species limited the establishment of seedlings in the undisturbed meadow plot in the early stages of germination. If seeds germinated and died soon thereafter, there would be little likelihood of witnessing the phenomenon in the field. The failure to observe germination, especially in the cleared meadow plot on Iron Mountain, indicates that higher rates of germination and establishment should be expected given more ideal conditions. The numbers reported here thus represent minima of species actually able to establish within a given region. These considerations may explain many of the zeros in Tables IV, V, and VI.

The plots on Sardine Butte are especially interesting since they show establishment of six disjunct species in an area where none existed previously. Of these species the four annuals (*Polygonum kelloggii*, *Linanthus harknessii*, *Navarretia divaricata*, and *Galium bifolium*) all set some seed which appeared viable. It is not yet known whether they will succeed in establishing again in later years.

Conclusions

The tentative conclusions based on this information and presented below are equivocal, given the small number of habitats actually tested, the small number of seeds frequently used, and the short duration of the experiment. On the basis of my field experience with the establishment plots, I believe that few, if any, of the established species will remain for any length of time in their tenuously held new habitats. Nevertheless, the present information does point to important conclusions regarding the establishment potentialities of many of the disjunct species.

If species previously found in or around the germination plots are disregarded, the number of established species in uncleared plots is only 40 percent of the number established in cleared sites. However, as indicated in Table VI, some species, especially those which are often found as "understory" vegetation in mesic meadows, were occasionally better able to establish in uncleared than in cleared plots.

If species germinated and then died (or failed to germinate completely) in a cleared habitat, it must be considered that their elimination was due to some combination of physical properties inherent in the habitat or to predation. Correspondingly, if establishment occurred in a cleared plot with none in the adjacent undisturbed plot, competition with existing vegetation must be invoked to explain lack of establishment in the uncleared site. Table VII shows both phenomena to be important in the situations tested, with competition being the controlling factor much less frequently than environmental unsuitability.

Species which germinated in more than half of the cleared plots showed the highest rates of establishment in all plots, and have been eliminated from some uncleared plots. This evidence suggests that competition is the most important factor in determining the distributions of these species, which include *Polygonum douglasii*, *Polygonum minimum*, *Polygonum cascadense*, *Ivesia gordonii*, *Linum perenne lewisii*, *Navarretia divaricata*, and *Galium bifolium*. All but three of these are widespread in the Western Cascades. *Polygonum cascadense* is endemic to the region, *Linum perenne lewisii* is relatively restricted within the study area, and *Ivesia gordonii* is known from only one locality within the Oregon Cascade Ranges. It seems likely that these three species have much wider potential ranges than they presently inhabit. Historical dispersal factors, together with elimination from many sites by competition, may explain their presently restricted distribution in the Western Cascades.

DISCUSSION

Plant Groups of Similar Geographical Affinity

It is possible to assign disjunct species to groups or elements according to the geographical region or biotic province of their major populations. Such elements may indicate the migrational path by which the species reached the Western Cascades and are theoretically similar to the groups of species showing "equiformal progressive areas" discussed by Hultén (1937). Equiformal progressive areas are more closely tied to glacial history in the boreal regions treated by Hultén than in the Western Cascades. The present groupings are notable in their diversity. Only rarely do the total ranges of even two disjunct species approach identity. In addition, diverse ecological patterns are shown by species within a single geographical group. Nevertheless, it is likely that geographical affinity reflects similarity in migrational history, and qualified use of such groups as Hultén proposes is both warranted and helpful.

Southern and Eastern Element

This large group of disjunct species has major centers of distribution both in the Columbia Basin and the High Lava Plains of eastern Washington and Oregon (Freeman and others, 1945), and in the southern Cascade, Siskiyou-Klamath-North Coast Range, and Sierra Nevada regions of southern Oregon and northern California. Ranges of the 15 species considered to belong in this group overlap with those of the following two groups. In general, species whose distributions indicate that they have occupied both southern and eastern regions for considerable time are included here.

There is evidence that eight species have reached the Western Cascades by migration both across the Cascade crest from the east and northward through the Western Cascades from the Siskiyou-southern Cascades region. These include *Pinus ponderosa*, *Arabis platysperma howellii*, *Gayophytum humile*, *Linanthus harknessii*, *Navarretia divaricata*, *Mimulus breweri*, *Castilleja pruinosa*, and *Lonicera conjugialis*. Their distributions are relatively continuous in the Western Cascades south of the study area, and some specimens are known either from the High Cascade peaks or from the passes between them. *Castilleja pruinosa* is not common east of the Cascade crest, but Western Cascade forms have been implicated in the *C. peckiana* complex of that region, and so are included here.

This group contains ephemeral annuals restricted to habitats where abundant snowmelt is available in early spring, annuals of drier situations, an herbaceous perennial of dry habitats, and a large shrub. One species, *Navarretia divaricata*, grows in disturbed sites and is somewhat weedy in behavior. All the species in this group except *Arabis platysperma*, *Castilleja pruinosa*, and *Lonicera conjugialis* are relatively widespread in the drier portions of the Pacific States.

Although *Nothocalais alpestris* extends almost to the Pacific Ocean in the Siskiyou region, only two collections are known from the Western Cascades. These are both in the vicinity of Olallie Mountain and are evidently westward extensions of the large populations found at higher altitudes in the Three Sisters. Its entry is thus entirely from the east, although it is not found in the lower elevation areas of eastern Washington and Oregon.

Another group of six species, while most common east of the Cascade-Sierra axis, shows no evidence of having reached the Western Cascades from the east and has probably migrated northward through the Western Cascades. These species, *Selaginella scopulorum*, *Linum perenne lewisii*, *Monardella odoratissima*, *Penstemon deustus*, *Galium bifolium*, and *Chrysothamnus nauseosus albicaulis*, are fully as diverse with regard to habit, breeding system, moisture relations, and habitats occupied as the first group discussed. All of these species except the first are widespread in western North America. *S. scopulorum* is primarily confined to the Klamath Mountains and the Wallowa Mountains, but has also been reported from several sites in Washington and Montana. To date, Western Cascade populations comprise half of the species populations known to me. Migrational patterns are thus difficult to interpret.

Species of this element are known from seven different vegetation units but are most abundant in dry rocky areas (Gravel Scree and Outcrop Ridge), Xeric Meadow, and Rocky Melt Seep associations.

Southern Element

Twelve species have major populations only to the south of the study area and appear to have reached the area by northward migration along one or more of several possible routes. Five of these, *Cheilanthes siliquosa*, *Allium crenulatum*, *Silene campanulata glandulosa*, *Cardamine* *integrifolia sinuata*, and *Mimulus pulsiferae*, also have stations in the interior valleys west of the Cascades. In addition, three of them occur near the eastern end of the Columbia Gorge. These species probably reached the Western Cascades by migration up the tributaries of the Umpqua and Willamette Rivers. These species are also ecologically diverse. The only widespread species in this group is the fern *Cheilanthes siliquosa*, whose center of distribution nevertheless seems to be serpentine areas in southwestern Oregon.

The other seven species of this element have migrated northward through the mountains and are not found west of the Cascades except in their parental area. *Trifolium productum* and *Crepis occidentalis* are relatively widespread and have major population centers in the northern Sierra Nevada as well as in the Siskiyou region. *Trifolium howellii*, *Arenaria pumicola*, and *Ribes erythrocarpum* have restricted ranges. The first is found in southern Oregon and northernmost California west of the Cascade crest, and the last two have been considered heretofore to be narrowly restricted to the region around Crater Lake. *Ribes binominatum* and *Erigeron foliosus confinis* have remarkably similar ranges in the southern Cascades, Siskiyou Mountains, and the North Coast Range of California.

Mimulus pulsiferae is the only annual in this group. The herbaceous and woody perennials, however, show a wide range of ecological tolerances, pollinators, and breeding systems. Members of the southern element inhabit 12 of the described vegetation units--more than any other element--but the dry rocky areas are the only units of importance. Seven of the units, most of which are occupied by a single southern species, comprise mesic environments.

Eastern Element

The largest group of disjunct species is centered in the intermountain region of the Western United States. All of these species have evidently entered the Western Cascades across the Cascade crest.

Ten species (*Polygonum kelloggii*, *Lewisia triphylla*, *Arabis holboellii retrofracta*, *Horkelia fusca*, *Lathyrus lanszwertii aridus*, *Gayophytum diffusum parviflorum*, *Gilia aggregata*, *Gentiana calycosa* n. subsp., *Pterospora andromedea*, and *Cryptantha affinis*) are presently established at a few points along the crest, supplying evidence of the proposed migration route.

A second group consisting of *Helianthus cusickii*, *Artemisia tridentata*, and *Arnica parryi* is restricted to the study area (and a few similar spots in the Western Cascades and eastern Siskiyous) west of the Cascade crest but shows no further evidence of migration route.

Two of the species of this group, *Helianthus cusickii* and *Artemisia tridentata*, are hypothesized to be of very recent origin in the Western Cascades. Both are known from only one locality, and the present populations are not in equilibrium with the surrounding vegetation but are associated with diverse habitats. It is not yet certain whether they will be able to persist.

Populus tremuloides, *Collomia linearis*, *Artemisia ludoviciana latiloba*, *Microseris nutans*, and *Crepis acuminata typica* have few localities in southern Oregon or northern California west of the Cascade crest, and I believe these populations to be equally recent in origin to populations in the study area. All western Oregon populations are hypothesized to have come west across the Cascade crest. *Collomia linearis* has two present localities in the Willamette Valley. It is possible that it came west through the Columbia Gorge and reached the Western Cascades through the tributary valleys from the west.

Of the Eastern Element, all the annuals and biennials except *Collomia linearis* are found along the Cascade crest. This may indicate that the annuals and biennials, which have fewer morphological adaptations for long-distance dispersal, typically migrate in shorter steps than do the wind-dispersed perennials. This group is also extremely diverse ecologically, including ephemeral annuals and desert shrubs. *Lewisia triphylla* grows around snowbeds and in running snowmelt, and *Crepis acuminata typica* is restricted to dry south-facing cliffs. The annuals grow in generally moister environments than the larger perennials. These species occur in 11 associations, the most important of which are dry rocky areas and Xeric Meadow and Xeric Forest associations.

Northern Element

Another well-represented element in the disjunct flora occurs to the north and has reached the study area by migration south through the Cascade Ranges.

One subgroup of the northern element is known from the coastal mountains of northwestern North America, from the Cascades, and from the northern Rocky Mountains. This group includes *Polystichum andersonii*, *Arenaria capillaris americana*, *Rhododendron albiflorum*, *Menziesia ferruginea*, *Hydrophyllum fendleri albifrons*, and *Lonicera utahensis*.

The ranges of several of these species are especially noteworthy. *Polystichum andersonii* is a rarely collected boreal species that is presently known from only three populations in Oregon. Two of these are in the study area. *Arenaria capillaris americana* reaches the southernmost points in its range within the study area where it overlaps and merges with *A. pumicola*, a member of the southern element. *Lonicera utahensis* has a uniquely disjunct distribution. It is found commonly in northeastern Oregon, Idaho, and northern Washington but is represented in the Cascades only from the study area south to the region of Mt. Shasta. The species has evidently been poorly collected and there is little evidence concerning its entry into the southern half of the Cascade Ranges.

A second group is known from the northern coast mountains and the Cascades. These species are *Chamaecyparis nootkatensis*, *Sedum divergens*, and *Douglasia laevigata*. The first two species occur as far south as the California-Oregon border, but *Douglasia* reaches its southern limit at the latitude of the study area. The distribution of *Chamaecyparis nootkatensis* is noteworthy in that, like *Menziesia ferruginea*, it is found in the High Cascades as far south as Mt. Jefferson, at which latitude it becomes exclusively a Western Cascade species.

Three species of the northern element, *Castilleja rupicola*, *Haplopappus hallii*, and *Luina stricta*, are restricted to the Cascade Ranges. *Haplopappus hallii* is probably a spurious member of this element, since it is a member of a basically southern genus. It was described from the dry eastern end of the Columbia Gorge, but at present most of its known populations occur in the Western Cascades, extending as far south as Hershberger Mountain. Its parental area is unknown.

Mertensia bella and *Orogenia fusiformis* show remarkably similar and striking distribution patterns. Both species were previously known primarily from the Siskiyou region, but had also been recorded from localities in northeastern Idaho and adjacent Montana. These distribution ranges, together with other evidence, indicate that the species are actually boreal in origin and that the disjunct populations followed separate mountainous routes during a southward migration. *Orogenia fusiformis* is slightly more widespread than *Mertensia bella*, but the present work has more than doubled the known localities for both species.

This element is much less diverse ecologically than those previously considered. Annuals are not represented at all, and more than half of the species grow only in the moistest terrestrial habitats in the Western Cascades. The exceptions are noteworthy. *Chamaecyparis nootkatensis* typically grows on barren south-facing ridges where other tree species cannot establish. It has not been found to exhibit sap tensions over 19 atmospheres, however, in spite of the general dryness of its habitat. This is presumably due to its deeply penetrating root system. This species occurs less frequently under the mesic forest canopy where it reproduces only vegetatively. Trees rarely attain considerable size.

Sedum divergens, *Arenaria capillaris americana*, and *Haplopappus hallii* occur on dry, rocky, south-facing slopes. *Haplopappus* has already been noted as a possible spurious member of this element. *Sedum divergens* has an excellent water-storage organ in its almost globose succulent leaves. Members of this genus have been shown to exhibit little moisture stress until late in the season. *Arenaria capillaris americana* is often found along dry ridgetops near late-persisting snowbanks. It blooms early in the season and has usually set seed by the time water becomes limiting in its environment.

Douglasia laevigata and *Castilleja rupicola* are confined to cliffs which are exposed to the prevailing winds (which are fog- and rain-laden throughout most of the year) and partially shaded from direct insolation.

Thus all disjunct species of the northern element are either directly dependent on an abundant and continuing water supply or have reached adaptive compromises with their seasonally dry environments. Northern species grow in 11 vegetation units, having particular abundance in the Outcrop Ridge, Wet Meadow, and Mesic Forest associations.

Alpine Element

Eight species are characteristic members of the Arctic-Alpine Life Zone (Merriam, 1889), which does not occur in the Western Cascades in its typical form. Most of these species (*Polygonum newberryi*, *Spraguea umbellata*, *Arenaria rubella*, *Luetkea pectinata*, *Polemonium pulcherrimum pulcherrimum*, and *Erigeron compositus*) are found on the uppermost slopes of the High Cascade peaks, especially the Three Sisters. They have presumably reached the study area from these high mountains immediately to the east. *Arenaria rubella*, *Polemonium* *pulcherrimum pulcherrimum*, and *Erigeron compositus* have also developed lower elevation forms, but since only the alpine forms occur in the Western Cascades, they are included in this element.

Two species, *Ivesia gordonii* and *Linanthastrum nuttallii*, are not otherwise known from the Cascade Ranges at this latitude, and their modes of entry into the study area are unknown. Major populations of both species occur to the north, east, and south. *Ivesia* is disjunct by more than 300 km, the closest populations occurring in the Strawberry Mountains of east-central Oregon and on Abert Rim in the south-central portion of the state. Northern Cascade populations also supply a possible point from which immigrants could have reached the Western Cascades.

With the exception of *Spraguea umbellata*, all members of the Alpine element are deep-rooted herbaceous perennials (Bliss, 1956) which live either in crevices in the Outcrop Ridge or Vertical Outcrop associations or in fine scree such as that associated with morainal features at higher elevations (Gravel Scree association). *Spraguea* is a short-lived perennial, and is found (like *Luetkea pectinata* and *Polygonum newberryi*) in barren areas of gravel scree or fine rock fragments where snow lies deep in winter and persists late into summer (Snowbed association). The occurrence of these high alpine species at elevations as low as 1200 m is striking.

Valley Element

More than 30 species that are characteristic of the lower valleys west of the Cascades have been found in the study area. All of these are found at lower elevations, but only five reach an elevation such that they can be found with disjunct species of other elements (about 1100 m). These include *Populus trichocarpa*, *Quercus garryana*, *Polygonum spergulariaeforme*, *Convolvulus nyctagineus*, and *Plagiobothrys scouleri*. All of these species are common on the floor of the Willamette, Umpqua, and Rogue River Valleys in Oregon, and several extend into the Puget Sound region. They are also all found at the dry eastern end of the Columbia Gorge and are comparable with species of the Rogue-Columbia element of Detling (1953). Only *Quercus garryana* has been reported from the Deschutes area of eastern Oregon (Ornduff and French, 1958).

These species range from late-blooming annuals to trees, but are frequently found together, both in their major populations and in the Western Cascades. They are known from eight associations, the primary of which are the Lowland Xeric Meadow and Outcrop Ridge associations.

Widespread Element

Seven species occur in all major geographical-physiographical regions of Oregon in addition to being more or less widespread in the Western or northwestern United States. These species are all restricted to dry habitats and are known from localities in the Willamette Valley, Columbia Gorge, and eastern and southern Oregon. They are less disjunct in the Western Cascades than many other species treated in detail here, but nevertheless comprise an interesting element of the flora. Most of these species (*Polygonum douglasii*, *Polygonum minimum*, *Silene douglasii*, *Lotus nevadensis douglasii*, and *Lupinus arbustus neolaxiflorus*) are also known from the High Cascades at this latitude, perhaps indicating an eastern entry into the Western Cascades. *Sedum stenopetalum* probably migrated northward into the area, while *Phacelia linearis* made its way up the tributary valleys of the west slope of the range. Members of this element appear to be basically eastern in origin and show three possible modes of entry into western Oregon: 1) through the Columbia Gorge; 2) across the crest of the Cascades in central Oregon; and 3) across the low passes of the southern Cascades and north from the valley of the Rogue River, either through the Western Cascades or through the interior valleys. These species are all annuals or herbaceous perennials and occupy similar habitats (especially Outcrop Ridge and Xeric Meadow) in the Western Cascades, although it is likely that they have never acted as a single floristic unit.

Endemic Element

Only three species are endemic to the central and central Western Cascades: *Polygonum cascadense*, *Aster gormanii*, and *Erigeron cascadensis*. This is a surprisingly small number of endemics relative to the floristic complexity of the region.

Polygonum cascadense is a small annual derived from the *P. spergulariaeforme* complex which grows in the Xeric Meadow and Gravel Scree associations. It had the highest recorded sap tension (71.5 atmospheres) of any actively growing Western Cascade species. The two composites are deep-rooted herbaceous perennials occurring in crevices (Outcrop Ridge and Vertical Outcrop), Blocky Talus, or Gravel Scree.

Polygonum cascadense and Erigeron cascadensis have strikingly similar distributions, but Aster gormanii is currently known from only three localities, of which two are in the vicinity of Mt. Jefferson in the High Cascade Range. If it were not so closely limited to this region, it would be considered a member of the Alpine Element.

Summary

The geographical elements described are diverse and often overlapping. Some correlations exist between elements and the habitats occupied by member species. The majority of species from the three southern and eastern elements, which correspond in large part with Detling's "xeric species," occur in dry rocky habitats. In addition, many species of the Eastern, and Southern and Eastern Elements, but not of the Southern Element, occur in the Xeric Meadow association. All elements contain some species which grow in the dry rocky areas, but only the Northern Element contains a majority of species which occur in mesic or wet habitats. Alpine species are rather closely restricted to Gravel Scree and Vertical Outcrop associations, and all endemic species sometimes occur in the Gravel Scree association.

All large elements contain species showing a diversity of moisture regimes. Ephemeral annuals, however, occur only in the three southern and eastern elements, while other life forms are more or less scattered through all groups. The Northern Element is unique among those measured in showing no sap tensions greater than 19 atmospheres. This is partially correlated with the moistness of the habitats occupied by northern species, but is also true where northern species inhabit dry environments.

Breeding systems, pollination mechanisms, dispersal adaptations, and ease of establishment in new environments cannot be correlated with the geographical elements. Each element shows nearly the complete range of variation for these phenomena found in the entire group of disjunct and endemic species.

The evidence indicates that none of the elements, with the possible exception of the Valley Element, constitutes a discrete floristic unit. The likelihood that the elements have migrated as associations is extremely small, but the individual patterns of migration followed by member species are generally similar.

Speciation in Western Cascade Disjunct Populations

Theoretical considerations and evidence compiled by numerous workers predict rapid rates of evolutionary divergence in such ecologically diverse, seasonally arid environments as the Western Cascades. Cain (1944) proposes that a compensation of critical or limiting factors is of major importance in the establishment of extra-limital distribution patterns. Mason (1945) prefers to rely on the ability of species to undergo ecotypic variation and readily adapt to new environments. These proposals are closely related, and both call attention to the fact that selective regimes will differ between continuous and disjunct populations. Wilson (1959) and Carlquist (1966a) strikingly demonstrate this phenomenon on oceanic islands, much more isolated situations than any terrestrial mountaintop "island." Kruckeberg (1967) found numerous examples of ecotypic differentiation in dry regions of serpentine soils.

Lewis (1962) and Warburg (1965) show in both plants and animals that drought, especially if extreme (as was the case in the Western Cascades in the summer of 1967), can be a potent selective factor. In the case of *Clarkia* a single exceptionally dry season brought about a major shift in the physiology and morphology of an annual population (Lewis, 1962). Stebbins (1952) demonstrates that aridity also acts as a stimulus for evolution in the opposite direction, i.e. into more mesic habitats. In addition, Stebbins and Major (1965) clearly show that "ecotonal" regions, in which forms characteristic of two or more provinces overlap, are centers of evolutionary divergence and novelty. The number and diversity of disjunct elements show that the Western Cascades comprise such an "ecotonal" region, and that unique forms should be important in the flora.

In spite of the weight of such considerations, little evidence of divergence has been found in the present study. Relative to the diversity, both ecological and floristic, of the Western Cascades, there are few endemic species. All three of these species are here considered to be relatively recently derived, and never to have had a greatly wider distribution than at present (neo-endemics of Stebbins and Major, 1965). Thus divergence to the level of species within the Western Cascades amounts to considerably less than one percent of the total number of species known from the area.

An equally small proportion of subspecific divergence among the disjuncts has been noted. No subspecific taxa have yet been described from the disjuncts, but some taxonomic recognition might be useful for the Western Cascade forms of *Selaginella scopulorum*, *Allium crenulatum*, *Ivesia gordonii*, *Gentiana calycosa*, and *Haplopappus hallii*. *Lonicera utahensis* and *Cheilanthes siliquosa* show questionably significant differences from parental populations, the former morphological and the latter edaphic. Complex, morphologically variable taxa which contain unique Western Cascade forms that should not now be recognized taxonomically are *Arenaria capillaris*-*Arenaria pumicola*, *Monardella odoratissima*, *Castilleja pruinosa* (*peckiana*), *Castilleja rupicola*, and *Crepis occidentalis*.

There are several possible explanations of this lack of observed divergence. The simplest is that the disjunctions are of such recent origin that they do not yet show morphological divergence. Evidence against this hypothesis is found in the ecological stability of almost all of the disjuncts and the typically large number of sites occupied, as well as in the rapidity with which divergence has occasionally been shown to occur. Perhaps more pertinent is the fact that the multiple-allelic nature of physiological race formation need not involve large morphological differences between sibling races (Clausen, Keck, and Hiesey, 1947). In this connection Mason (1946) has noted that classical taxonomic techniques are generally not sufficiently discriminating to isolate small local differences in morphology or physiology. The problem here is not nearly of the magnitude of that shown by the many amphi-tropical disjunctions, a large number of which show identical variation patterns in both northern and southern hemispheres (Raven, 1963). It does, however, seem likely that further studies with herbarium material and use of transplant and cytological techniques will isolate more differentiation of Western Cascade forms than is presently known.

Geological History of the Area and Its Effects on Plant Distributions

Structure

The history of the relationships between the Western and High Cascade Ranges is poorly known but may have had profound effects on plant migration between the two ranges. Wells and Peck (1961) and Peck and others (1964) imply that the sharp physiographic line separating the ranges, a valley which varies from 300 to 1100 m in depth along the eastern border of the study area, has been cut completely by erosion since the middle or late Pliocene. This hypothesis seems inadequate for several reasons. It seems quantitatively unlikely that at least 1200 m of Plio-Pleistocene flows were deposited and then completely eroded by stream action. In addition, the authors offer no explanation for the marked differences in slope steepness on the eastern and western sides of this physiographic boundary nor for the typical fault-associated features of the area, especially the numerous hot springs which more or less follow the physiographic boundary. Peck and his associates have left unanswered the question of why there should be such a pronounced physiographic boundary if there is no underlying structural one.

If the flat surfaces of Hogg Rock and Hayrick Butte on the crest of the Cascades can be presumed to be remnants of Pliocene flow surfaces (which is unlikely), a maximum of 300 m of glacial stripping from the various ice sheets occupying the region during the glacial maxima can be postulated. Present river valleys are incised into the continuously gentle western slope of the High Cascades a maximum of 100 m.

These considerations also indicate that erosion will not account for the present boundary. This is seen to be true whether or not the uppermost flows in the Western Cascades are properly mapped as Plio-Pleistocene.

It is known that the Western Cascades have been uplifted (Williams, 1953), and in addition that small-scale faulting is not uncommon (G. T. Benson, personal communication, 1968). It thus seems to me that a fault or series of intermittent faults trending north-south along the eastern margin of the Western Cascades best explains the existing physiographic boundary. Such faulting would account for the early entrenchment of the headwaters of the major river systems along this line, for the steepness of the eastern edge of the Western Cascades, and for the broken line of hot springs; but would not preclude the formation of bridges between the two ranges such as are presently found at Outerson Mountain and Olallie Mountain.

A continuous bridge between the two ranges until the Pleistocene such as that implied by Wells and Peck (1961) would have allowed for easy migration from the high peaks to refugia in the Western Cascades with the first advance of the glacial ice, but is not consistent with other physiographic evidence. It is most likely that there has been a distinct boundary between the Western and High Cascades since the origin of the latter.

Physiography

The physiography of the Western Cascades affects plant distribution patterns in various ways. Observations have shown that within the area the isolation of the various peaks and the number of disjunct species they support are inversely correlated. This is considered a function of non-forest habitat size per unit area and resulting ease of dispersal from a given peak to and from its neighbors.

The "island" terminology employed by Detling (1953, 1968) and other workers is not strictly accurate. Patches of non-forest habitat are seldom separated by more than 1 km, and recurrent fires have kept the forest and non-forest habitats in shifting equilibrium, perhaps resulting in changing patterns of bridges between the islands. Thus long-distance dispersal as discussed by Baker (1955) and Carlquist (1966a) need not be invoked within the area nor, for that matter, between the area and surrounding regions in former times.

Cruden (1966) shows "mountain-hopping" dispersal to be an attractive hypothesis even for explaining amphi-tropical distributions. An example of how such a mechanism might operate in the Western Cascades is given below. Families of blue grouse, Dendragapus obscurus, are frequently observed in the Western Cascades, and are particularly abundant in forest-meadow ecotones where large numbers of disjunct species are concentrated. These gallinaceous birds are territorial during the breeding season. They feed primarily on fruits and seeds. Yearly dispersal of young birds to neighboring peaks, as well as the mobile behavior involved in establishing and maintaining territories, likely results in the transfer of numerous seeds from the meadows of almost all of the peaks to their neighbors. Though this mechanism may be of some importance, it is an isolated example from many possibilities, and it is not intended that it should be overstressed in its particulars. My major point is that dispersal of many plant species among the peaks of the Western Cascades must be considered easy, natural, and a function of the distance between them.

Glacial history has had a controlling influence on both the physiography of the area and the distributions of several of the disjunct species. Available evidence indicates that there was no ice sheet, but rather a large number of relatively small alpine valley glaciers scattered through the Western Cascades.

The occurrence of eight basically high alpine disjunct species in regions where signs of glacial activity are concentrated suggests a comparison of these peaks with nunataks (Fernald, 1925; Gjaerevoll, 1963). The classic nunatak, as discussed by Gjaerevoll (1963), is a barren peak emerging from an essentially continuous sheet of ice. Although there has been much argument concerning the possibility of plants surviving the rigors of such environments, observations on the Greenland ice sheet show that many nunataks are characterized by south-facing slopes of loose gravelly material that support a surprising diversity of plant types. This description is striking in its resemblance to many of the highly glaciated Class 1 peaks of the Western Cascades. In addition, Gjaerevoll demonstrates, using floristic considerations and the discovery of a pre-Würm (= Wisconsin) soil surface, that many high arctic species have persisted on Norwegian nunataks through times of glacial maxima to the present. Finally, one of the alpine disjuncts, Polemonium pulcherrimum pulcherrimum has been noted by Van Vechten (1960) to occur in the Three Sisters only above all evidences of glacial activity. In the Western Cascades Arenaria rubella, Ivesia gordonii, *Polemonium pulcherrimum*, *Linanthastrum nuttallii*, and *Erigeron compositus* are all restricted to sites above former glaciers.

Substrate texture is a third important factor in the physiography of the Western Cascades. This characteristic, together with three related variables, has been used to divide the mountain peaks into classes. Mountains with dense, non-scoriaceous volcanic rocks (Class 2) erode into piles of slowly weathering blocks of fallrock. Except near the summits, slopes are relatively gentle and forested unless cleared by recent fires. Meadow areas are not abundant, and there are still fewer open rocky areas available for plant establishment. On the other hand, Class 1 peaks, frequently composed of highly scoriaceous volcanic rocks, erode more rapidly to a fine gravelly scree which is in continuous motion downslope. Near the summits outcrop areas are plentiful, and lower on the slopes accumulation of weathered volcanic material leads to the formation of extensive subalpine meadows which vary greatly in moisture availability. On these peaks the rate of weathering of the parent rock approximately equals the rate of its erosion, and large areas remain in youthful condition, unable to follow the normal successional sequence to closed forest.

Age and Its Effect on Diversity

Margalef (1958, 1963) has proposed that the maturity of an ecosystem is directly and causally correlated with its structural and taxonomic diversity, stability, efficiency, and high longevity and low reproductive potential of member organisms. In fact, maturity of a system is impossible to define objectively other than by use of such measures as Margalef suggests. Such vague criteria as stability do not, however, add to the force of his arguments. Much of his hypothesis is supported by his own work with marine zooplankton, and by others working with various aquatic systems. Related to Margalef's proposal is the well-known time theory of increasing diversity reviewed by Pianka (1966). This theory states that the longer an area is free of major disturbance the more diverse it will be. Pianka concludes that the time theory is undoubtedly true for small areas but is inadequate as a global hypothesis. Comparative observations of the relative diversities of the Western and High Cascades demonstrate the necessity of reconsidering these ideas as they apply to the Western Cascades.

Seven peaks of the lower High Cascades, exhibiting the same range of elevation, slope steepness, and parent material were sampled floristically for comparison with the Western Cascades. The climatic regime at this longitude (about 8 km east of the study area) is slightly drier and windier, since cloudbanks typically begin to lift at the eastern border of the Western Cascades, but the major differences between the two regions are the age and texture of the parent material. Flows of dense volcanic rocks are present but local in distribution, while most of the surface is covered with relatively recent ash fall. The peaks in this area are primarily cinder cones, some of which are eroding at approximately the same rate as Class 1 peaks in the Western Cascades.

These peaks have a markedly less diverse flora than do Western Cascade peaks. Sand Mountain and Hoodoo Butte, relatively recent cinder cones, support 26 and 63 species respectively, while Maxwell

Butte and Grizzly Peak, older mountains with a greater proportion of dense volcanics (the latter is an erosional remnant of the flank of Mt. Jefferson), totaled 122 and 138 species respectively. Typical Class 1 peaks within the study area support 289 (Iron Mountain), 286 (Rebel Rock), 228 (Horsepasture Mountain), and 210 (Browder Ridge) species.

It is likely that diversity of substrate texture and substrate modification by plants with time are inseparable variables in this analysis, since both correlate directly with diversity. Roach's (1952) finding that very recent lava flows are floristically more diverse where abundant moisture was available (bogs, lakes, and streambanks) indicates that substrate modification is important, and perhaps obscures any age factor that might be present in the above data.

This problem can be approached from another point of view by considering habitats within the Western Cascades. When the described habitats from fresh outcropping rock to mature mesic forest are placed in a general successional scheme, analysis shows that it is the younger, dry, open areas which support the greater portion (60 percent) of the floristic diversity within the study area. Combined non-forest habitats contain 80 percent of all Western Cascade species, while only 35 percent are ever found in forest associations. This is quite the opposite of the implication of Roach's data and at first glance seems contradictory to both Margalef's ideas and to the time theory of diversity.

It has been demonstrated that the rocky areas and derived dry meadows cannot be considered stable--the substrate is moving downslope at a considerable rate. It is proposed here that these areas are predictably unstable, and that because of the approximate equilibrium between weathering and mass wasting on floristically diverse Class 1 peaks they are continually rejuvenated. This creates a system low in the successional sequence, but sufficiently predictable that many non-weedy species have been able to continue existence and to adjust competitively to the addition of an unusually large number of species to a basically unproductive habitat. It is likely that these perennially young systems have been evolving for at least 10,000 years.

Thus the Western Cascades are seen to comprise a specialized series of terrestrial environments which do not entirely support Margalef's hypothesis. Although considerable diversity in successionally young habitats can be accounted for by replacing Margalef's stability criterion with one of predictability, the relative lack of diversity in the presumably ancient, stable, structurally diverse, efficient, longevous forest associations contradicts both Margalef and the time theory of diversity.

An Evaluation of the Xeric Island Concept and Theories of Migration

The Hypothesis

The essence of the Xeric Island Hypothesis (Detling, 1953) can be stated as follows: During the post-glacial xerothermal maximum, xeric species from the Rogue River Valley and from east-central Oregon became widespread in western Oregon, occupying dry habitats in the Western Cascades (and to some extent in the Coast Range). Following a climatic reversal, they have persisted as relicts in areas of minimal competition with gradually re-establishing mesic forest species.

The hypothesis is dependent on the palynological studies of Hansen (1942, 1947, 1955) and Heusser (1960), who have demonstrated a xerothermal maximum at about 6000 years ago. Pollen of *Pinus ponderosa*, composites, grasses, and chenopods reach maxima just above a distinctive layer of Mt. Mazama ash in many bogs. Radiocarbon dating of charred stumps has placed the eruption of Mt. Mazama at approximately 6500 years B.P. (Flint & Deevey, 1951). Sears (1942) has pointed out the difficulty in adequately defining and dating xerothermal intervals in eastern North America and Europe. The fortuitous timing of the last violent eruptions of Mt. Mazama and the wide distribution of the resulting ash fall in western North America obviate many of the difficulties experienced in other regions.

Problems Raised by the Hypothesis

Detling's synthesis of information, as represented by the Xeric Island Hypothesis, has been the outstanding contribution to knowledge of the vegetational history of the Pacific Northwest. However, incorporated into the hypothesis are inaccuracies both in theoretical considerations and in supporting data largely because of the imprecise definition of "xeric" in the latter.

One source of error in the supporting information includes several misinterpretations of ecological field evidence. Detling suggests (1953) that heat absorption by the exposed dark rocks results in longer growing seasons for plants occupying these habitats. This conclusion is not warranted since, in any modified Mediterranean climate such as that in western Oregon, growing seasons for most species are limited by lack of moisture, not by low temperatures. This is especially true on steep, bare, south-facing slopes at moderate elevation where growing seasons are considerably shorter than elsewhere in the Western Cascades.

In addition, only 14 of the 32 species discussed as xeric by Detling actually occur in the extreme, hot, dry environments he describes in formulating the hypothesis. The rest are more typically found in meadow associations, which have been shown by sap tension measurements frequently to offer less stressful environments than even the surrounding mesic conifer forest. Species of other habitats, such as snowbeds, are also included in Detling's list.

Like many earlier phytogeographers, Detling relies heavily on the geographic origin of species in interpreting not only their migrational paths but also, with considerably less validity, their ecological relationships to other vegetational elements. Persistence or extinction of a disjunct species cannot be predicted from its direction of origin alone. It is rather a result of many aspects of the ecology of the species, including ranges of tolerance to many factors, opportunism, competitive ability, etc.

Definition of Terms

A major result of these considerations is that it is impossible to determine what Detling and other workers have meant when they have referred to "xeric species" and "xeric environments." In the Western Cascades all habitats are to some degree seasonally dry and could at those times be classified as xeric. Application of the sap-tension pressure-bomb in the Western Cascades has supplied a means of quantifying functional moisture stress. This technique is useful in formulating definitions for individual species in given habitats. Ranges of tolerance can be analyzed and specific habitats can be compared. The resulting definitions of plant-environment associations are complex and involve many variables. Generalizations from them are difficult to make without loss of essential information. The term "xeric" is thus too general to be applied meaningfully in such definitions or wherever moistures regimes are being studied on a specific level.

Patterns of Migration

It has often been assumed, as in Detling's work, that advancing species migrate in a continuous front and that disjunct populations perforce indicate former continuity (at least through time) between them. Deevey (1949) points out that the ranges of virtually all species are characterized by disjunctions of some magnitude. Work with the biota of oceanic islands (Carlquist, 1966a; Wilson, 1959; etc.) has emphasized long-distance dispersal, and others (Raven, 1963; Cruden, 1966) have discussed the likelihood of various types of shorter-distance disjunct dispersal in terrestrial environments. Detling's recognition of the Western Cascade peaks as "islands" in fact requires this kind of dispersal to some extent rather than continuous-front migrational advance. The work of numerous biogeographers has made it clear that in every species disjunction of any magnitude, both kinds of migration must be carefully considered.

Relict Terminology

Failure to recognize the possibility of long-distance dispersal as a factor in migration forces the conclusion that all disjuncts are relictual in nature. Thus an examination of the meaning and implications of relictual status is in order. Fryxell (1962) and Holmquist (1962) are in agreement that relict concepts have been much confused in the past. Working independently, they achieved a botanical-zoological consensus in defining a relict as a plant or animal living on as a fragmentary survival from an earlier period. They term the type of relict suggested by the Xeric Island Hypothesis a geographical or ecological relict--a locally relictual portion of an otherwise non-relict entity.

Most biogeographical studies have deep roots in the relict concept, although several workers have attempted to de-emphasize it. Cain (1944) proposes that relictual status of a disjunct population cannot be assumed, but must require reasonable evidence. Deevey (1949) goes to great lengths to provide alternative hypotheses to those of "persistence" of species in any area during a major climatic change. Such an extreme approach stems from a reaction to Fernald's original "nunatak hypothesis" (1925), which, while in large part wrong, has been in my opinion the greatest single stimulus to phyotogeographic inquiry in North America. Cain's modest argument is sound, but Deevey strains credibility by over-reacting to one-sided presentations such as those of Fernald, Braun (1955, etc.), and Detling. Raup (1941) and Marie-Victorin (1938) offer the least biased but early reviews of these concepts.

Ecological Relicts vs. Recent Adventives

J. C. Nelson made the following statement regarding the ignoral by botanists of newly discovered extra-limital species in western Oregon:

> To say that these species are only recent introductions, and do not belong ecologically to this district, is only to beg the question. How can we show that they have not been here as long as the species which are more characteristic? The desert plants growing on gravelly prairies about Salem are as integral a part of the local flora as any typical west-coast forms. (p. 23)

Nelson's argument appears valid, but it is occasionally disregarded, even today. Conversation with various officers and employees of the Willamette National Forest indicates that the predominant opinion concerning Western Cascade disjuncts in that organization sharply contradicts the ideas of Detling. According to this view, the disjuncts were carried into the area by summer-grazing sheep from eastern Oregon during the last 80 years or so and have persisted because of the profound environmental degradation due to overgrazing. The conclusion reached is that the disjunct species are a product of the activities of man, and that they should thus not be considered a unique or especially interesting feature of the region.

The volume of information gathered in this study about the large number of geographically, ecologically, floristically, and behaviorally diverse disjunct species in the Western Cascades stands as testimony against this hypothesis as any sort of general explanation of Western Cascade disjunctions. It is likely, however, that sheep have had an important effect, together with the native fauna, on dispersal of disjunct plants within the area. It is also important to note that previous overgrazing has probably altered the vegetation aspect of the

Western Cascades, especially the non-forest areas. It is unlikely that many species have become extinct or that large numbers of new species have been added to the area by such mechanisms. However, relative abundances, especially of native grasses and species such as *Pteridium aquilinum* and *Rubus parviflorus* which probably replaced them, have no doubt been considerably altered by such disturbance. Sheep grazing in the Western Cascades was discontinued about 25 years ago. Observations over the last 10 years (John Lincoln, personal communication, 1968) indicate that grasses are currently becoming more abundant in several areas.

The presence of many of the disjunct species in the passes of the Cascade crest does indicate recent and perhaps continuing migration of these species across the high mountains to the Western Cascades. I seriously doubt that these species can accurately be considered relicts.

Two species, *Artemisia tridentata* and *Helianthus cusickii*, are known from only a single locality in the Western Cascades. They are not in equilibrium with the surrounding communities, as is evidenced by their lack of habitat specificity. It is likely that these two species, at least, represent introductions within the last half century, perhaps by sheep.

Thirteen large trees of *Populus tremuloides* with numerous root sprouts have been discovered in Quaking Aspen Swamp. Heartwood is rotten in most of these specimens, but corings and diameter measurements indicate that the age of these trees is well over 100 years. This age significantly decreases the probability of human-related dispersal factors for this species of the Eastern Element.

Thus, recent adventives into the area are considerably more important than thought by Detling, but dispersal within the last century cannot account for the diversity of disjunct forms in the area.

Concluding Comments on the Xeric Island Hypothesis

The basic ideas of the Xeric Island Hypothesis are strong enough to stand independent of the inaccurate information and questionable theory originally used to support them. Detling's general observations, which are essential to any understanding of the vegetational history of the Pacific Northwest, are supported by the present, more intensive study. The situation is, however, much more complex than envisioned by Detling. While further investigations have pared Detling's original list of 32 disjunct species to 13, additional discoveries have brought the number to more than 80. These species are found in every major habitat type in the Western Cascades, show great diversity in patterns of migration and evolutionary divergence from close relatives, and comprise a wide range of life histories. The Xeric Island Hypothesis must be modified and expanded to assimilate all the evidence now at hand.

SYNTHETIC HYPOTHESIS

Results of the present study support the following major conclusions:

1) Western Cascade disjuncts are notable in the diversity of their geographical, ecological, physiological, taxonomic, evolutionary, and behavioral patterns. Generalized geographical elements do not represent floristic or vegetational units, and no single migrational mechanism can account for the presence in the Western Cascades of all the members of any of the elements.

2) Origin of the disjunct populations is best explained using a synthesis of the hypotheses and principles of many workers. Northern and high alpine species are true relicts which have survived in the area since the glacial maxima of the Pleistocene. Many of these species were dispersed over distances of many kilometers. Southern, Eastern, Southeastern, Valley, and Widespread Elements have migrated to the area since the most recent glacial retreat. Such species followed several migrational paths from the east, south, and west, and were dispersed from varying distances to the hotter drier localities within the study area and throughout western Oregon. Dispersals of these elements to the area reached their peak during the xerothermal maximum about 6000 years ago, and for some species have continued in lesser numbers to the present, due both to natural causes and to disturbance. Annuals and biennials establish in new environments more readily and

appear to migrate in shorter steps than wind-dispersed perennials.

3) Endemic species probably evolved between the late Pliocene and the xerothermal maximum, within or near the areas presently occupied. One endemic species may be approaching extinction.

4) Continuance of both disjunct and endemic species populations has been permitted by the near equivalence of the destructive geologic processes of weathering and mass wasting. Continued rejuvenation of outcrop areas, and rockfall and fine scree slopes has produced a predictably young environment for which both high alpine and lower elevation dryland species are suited. Surrounding mesic forest communities are incapable of succeeding into the young environments. The continued existence of Mesic and Wet Meadow associations, which also support numerous disjunct species, is more difficult to interpret but is partially due to heavy snow pack, rapid movement of substrate, abundant moisture, and natural disturbance by fire. The equilibrium between the latter communities and the forest seems to be much less stable than that between forest and the drier perennially young environments.

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APPENDIX A

Introduction

Appendix A is a checklist of the species of vascular plants identified from the Western Cascades during the course of this study. Two families, the Gramineae and the Cyperaceae, have been excluded due to the author's limited knowledge of their taxonomies.

Species are listed in the order they are found in Peck (1961), although Peck's nomenclature is not strictly followed. Authorities are not given here because of space considerations, but can easily be found in Hitchcock and others (1959, 1961, 1964); Cronquist (1955); or Peck (1961). The rank of trinomials can be similarly obtained. Unless trinomials are given, typical subtaxa are assumed.

For the purposes of this checklist, mountains are considered to extend all the way to the drainage systems which separate them from one another. Elevations covered here range from 400 m to over 3100 m, but both limits vary from peak to peak. Several peaks not in the area of intensive study are included for comparison. These are Monument Peak, in the Western Cascades northwest of the main area; Huckleberry Mountain, the Fairview-Bohemia massif, and Hershberger Mountain, progressively more southern peaks of the Western Cascades; Grizzly Peak, Maxwell Butte, Little Nash Crater, Hogg Rock, Hoodoo Butte, and Sand Mountain of the lower High Cascades; the Three Sisters region down to an elevation of 1100 m 3,600 on the western slope and 1900 m 6200 on the eastern slope; and the region of the Crater Lake caldera. Several peaks within the area, which were visited only briefly, are excluded. Information from these peaks was combined with that from nearby, physiographically related peaks which were more completely sampled. Excluded peaks (and their included counterparts) are North Peak (Echo Mt.); Lamb Butte (English Mt.); Yankee Mt. (Tipsoo Butte); and the McKenzie Pass Steptoes or Sand Hills (Three Sisters).

An "X" on the checklist indicates an observation made and noted in writing in the field. For those species treated in Appendix B, documentation of occurrences by previously existing herbarium specimens is included, so that the checklist will reflect the total known range of those species throughout the area covered. Referral to the maps in Appendix B will separate the author's collections from previous ones.

Additional information from published work is included for Monument Peak, Fairview Peak, the Three Sisters, and Crater Lake. These reports of occurrences are respectively denoted "A" (Aller, 1956), "B" (Baker, 1951), "I" (Ireland, 1968), and "W" or "E" (Wynd, 1936; Applegate, 1939). None of these mountains is within the study area, but all were visited at least once during the course of the field work.

	Ophioglossum vulgatum	Botrychium silaifolium	Cystopteris fragilis	Dryopteris linnaeana	Dryopteris dilatata	Polystichum lonchitis	Polystichum munitum	Polystichum munitum imbricans	Polystichum andersonii	Athyrium filix-femina	Asplenium trichomanes	Struthiopteris spicant	Cheilanthes siliquosa	Cheilanthes gracillima	Cryptogramma acrostichoides	Adiantum pedatum aleuticum	Pteridium aquilinum pubescens	Polypodium hesperium	Equisetum arvense	Equisetum giganteum braunii	Lycopodium sabinaefolium sitchense	Lycopodium clavatum	Selaginella scopulorum	Selaginella wallacei	Taxus brevifolia	Pinus monticola
Monument Peak						X	X	X		X		X		X	X	X	X			X				X		X
Bachelor Mt.			X							X			X	X	X		X	X						X	X	X
Three Pyramids			X			X	X	X		X			X	X	X		X	X				X	X	X	X	X
Crescent Mt.			X											X	X		X	X							X	X
Echo Peak			X				X						X	X			X						X		X	X
South Peak			X										X	X	X		X						X		X	
Cone Peak			X				X	X					X	X	X		X	X					X	X	X	X
Iron Mt.			X		X	X	X	X		X			X	X	X	X	X	X					X	X	X	X
Browder Ridge			X				X	X		X			X	X	X		X	X					X	X		X
Jumpoff Joe							X			X				X			X								X	X
Squaw Peak							X			X							X								X	
Twin Buttes			X				X	X	X	X			X		X		X	X						X	X	X
andrews → Carpenter Mt.							X	X						X	X		X								X	X
Tidbits Mt.						X	X	X		X		X		X	X		X	X						X	X	X
andrews → Lookout Mt.							X	X							X		X							X	X	X
andrews → Frissell Pt.			X				X	X		X			X	X	X	X	X	X		X			X	X	X	X
Castle Rock			X				X	X					X	X	X	X	X	X		X				X		X
Olallie Ridge { O'Leary Mt.			X			X		X					X		X		X							X		X
Horsepasture Mt.			X		X	X	X	X	X			X	X	X	X	X	X						X	X	X	X
English Mt.			X					X						X	X		X									X
Lowder Mt.			X				X	X			X		X	X	X		X		X		X					X
Tipsoo Butte							X	X		X			X	X			X	X					X	X		X
Olallie Mt.				X	X	X	X	X		X				X	X	X	X								X	X
Rebel Rock			X				X	X					X	X	X	X	X						X		X	X
Indian Ridge	X	X	X		X	X	X					X	X	X	X		X	X						X		X
Sardine Butte					X		X					X		X			X							X		X
Huckleberry Mt.														X	X		X									X
Bohemia Mt.(reg.)			X		X	X	X			X		B	X	X	X	B	X	X					X	X	X	X
Hershberger Mt.			X			X	X	X		X			X	X			X							X	X	X
Grizzly Peak			X			X	X			X		X	X		X		X	X							X	X
Maxwell Butte														X	X		X									X
Little Nash Cr.						X		X							X		X	X							X	X
Hogg Rock														X	X											X
Hoodoo Butte																	X									X
Sand Mt.														X												X
Three Sisters		I	X				X	X					X	I	X		X	X	X		X				X	X
Crater Lake			X			W	X	X		W			W	X	X	E	X		X						W	X

	Pinus lambertiana	Pinus ponderosa	Pinus contorta murrayana	Tsuga heterophylla	Tsuga mertensiana	Picea engelmannii	Pseudotsuga menziesii	Abies amabilis	Abies grandis	Abies lasiocarpa	Abies concolor	Abies magnifica shastensis	Abies procera	Libocedrus decurrens	Thuja plicata	Chamaecyparis nootkatensis	Juniperus communis saxatilis	Juniperus occidentalis	Typha latifolia	Lysichitum americanum	Juncus parryi	Juncus effusus exiguus	Luzula parviflora melanocarpa	Luzula glabrata	Luzula spicata	Xerophyllum tenax	Tofieldia glutinosa	Stenanthium occidentale	Zygadenus venenosus
Monument Peak			X	X	X		X	X					X		X	X	X			X	X	X		X	X	X			X
Bachelor Mt.			X	X	X		X	X	X				X		X		X						X	X	X	X			X
Three Pyramids			X	X	X		X	X	X				X			X	X									X			X
Crescent Mt.			X	X	X	X	X	X	X				X			X	X	X							X	X			
Echo Peak			X		X	X	X	X	X	X			X			X	X					X			X				X
South Peak			X	X	X		X		X	X			X			X	X						X	X	X				X
Cone Peak			X	X	X	X	X	X	X	X			X		X	X	X						X		X	X			X
Iron Mt.		X	X	X	X	X	X	X	X	X			X		X	X	X				X	X	X	X	X	X			X
Browder Ridge				X	X	X	X	X	X	X			X		X	X	X									X			X
Jumpoff Joe				X			X	X	X							X	X		X				X			X			
Squaw Peak				X	X		X	X															X			X			
Twin Buttes				X			X	X	X	X			X			X	X			X			X			X			
Carpenter Mt.					X		X	X	X	X			X				X						X	X	X	X			X
Tidbits Mt.				X	X		X	X	X				X		X	X	X						X	X	X	X			
Lookout Mt.					X		X	X	X	X			X		X	X	X						X	X	X	X			X
Frissell Pt.		X		X	X		X	X	X				X		X	X	X		X		X		X	X	X	X			X
Castle Rock							X							X	X		X			X									
O'Leary Mt.			X		X		X	X	X				X										X	X	X	X			
Horsepasture Mt.			X	X			X	X	X	X			X		X	X	X			X			X	X	X	X	X	X	
English Mt.			X		X	X	X	X	X	X			X	X		X				X			X	X	X	X	X		
Lowder Mt.			X	X	X	X	X	X	X	X			X			X				X			X	X	X	X	X		X
Tipsoo Butte			X	X	X		X	X	X				X	X											X	X	X	X	
Olallie Mt.			X	X	X	X	X	X	X	X			X								X		X	X	X	X			
Rebel Rock	X			X	X		X	X	X				X	X	X		X				X		X	X	X	X		X	X
Indian Ridge				X	X		X			X			X	X	X	X	X		X	X			X	X	X	X			
Sardine Butte				X	X		X	X	X				X				X			X	X	X	X	X	X	X			
Huckleberry Mt.				X	X		X	X					X	X	X		X								X				
Bohemia Mt.(reg.)				X	X		X	X	X		X			X		X						B	X	X	X	X			
Hershberger Mt.			X	X	X		X	X	X	X	X	X		X		X	X								X				
Grizzly Peak		X	X	X	X	X	X	X		X			X			X	X						X			X			
Maxwell Butte			X	X	X		X	X	X	X			X				X				X	X	X	X		X			
Little Nash Cr.			X	X	X		X	X	X	X				X		X	X				X					X			
Hogg Rock			X		X		X	X	X	X							X									X			
Hoodoo Butte			X		X		X	X		X																X			
Sand Mt.		X	X		X		X	X																		X			
Three Sisters		X	X	X	X	X	X	X	X	X	X		X				X				X	X				X	I		
Crater Lake	W	X	X	X	X	X	X	W		X	W	X		W	W		X			E	X	W	X				W		

	Veratrum viride	Veratrum insolitum	Allium crenulatum	Allium amplectens	Brodiaea pulchella	Brodiaea hyacinthina	Lilium washingtonianum	Lilium columbianum	Erythronium grandiflorum pallidum	Calochortus lobbii	Trillium ovatum	Clintonia uniflora	Smilacina racemosa amplexicaulis	Smilacina racemosa glabrata	Smilacina stellata sessilifolia	Disporum hookeri oreganum	Streptopus amplexifolius	Streptopus curvipes	Iris chrysophylla	Habenaria hyperborea	Habenaria dilatata	Habenaria unalaschensis	Goodyera oblongifolia	Listera cordata	Listera caurina	Corallorhiza maculata	Corallorhiza mertensiana
Monument Peak			X				A	X	X	A	X	X			X	X	A	X		X	A	A			X		
Bachelor Mt.	X		X				X	X	X	X	X	X			X	X	X	X	X	X			X		X	X	
Three Pyramids	X						X	X		X	X	X	X		X	X		X		X		X	X		X	X	
Crescent Mt.	X						X		X	X	X	X	X		X	X						X	X		X	X	
Echo Peak	X		X							X	X	X	X		X	X	X	X							X	X	
South Peak	X		X				X		X	X	X	X	X		X								X		X	X	
Cone Peak	X		X	X	X	X	X	X	X	X	X	X	X		X	X						X	X			X	
Iron Mt.	X		X	X			X	X	X	X	X	X	X		X	X	X	X	X			X	X		X	X	X
Browder Ridge	X		X	X			X	X	X	X	X	X	X		X	X						X	X		X	X	
Jumpoff Joe							X	X			X																
Squaw Peak	X							X			X	X	X		X	X											
Twin Buttes							X			X	X	X	X		X	X						X	X		X	X	X
Carpenter Mt.							X		X	X	X	X			X				X								
Tidbits Mt.	X		X					X			X	X	X		X	X		X		X			X		X		X
Lookout Mt.	X						X	X		X	X		X		X				X								
Frissell Pt.	X							X	X	X	X	X	X		X			X	X				X				
Castle Rock					X			X		X	X		X		X	X			X				X	X		X	X
O'Leary Mt.	X							X	X	X					X				X			X				X	
Horsepasture Mt.	X		X				X	X	X	X	X	X	X		X	X	X	X	X	X			X		X	X	X
English Mt.							X		X	X	X		X		X	X		X							X	X	
Lowder Mt.	X						X			X	X	X	X		X	X			X	X	X		X		X	X	
Tipsoo Butte							X	X		X	X	X	X						X	X	X	X					
Olallie Mt.	X						X	X	X	X	X	X			X	X	X			X			X		X	X	X
Rebel Rock	X			X	X	X	X	X	X	X	X	X	X		X	X		X	X			X	X		X	X	X
Indian Ridge	X						X		X	X	X		X		X	X				X							
Sardine Butte				X						X	X	X							X	X			X				
Huckleberry Mt.	X									X	X	X			X								X		X	X	
Bohemia Mt.(reg.)	X	X	X				X		X	X	X	X	X	X	X	X	B			B		X	X		X	X	B
Hershberger Mt.	X			X					X		X	X		X	X	X				X	X					X	
Grizzly Peak	X									X	X	X	X		X	X	X	X					X	X	X	X	X
Maxwell Butte							X				X	X			X	X									X		
Little Nash Cr.																							X				
Hogg Rock							X																				
Hoodoo Butte							X						X												X		
Sand Mt.																											
Three Sisters	I						I	X	I	I	X	X	I		X	X	I	I	X	I	I		X		X	X	
Crater Lake	W				E	E	W		X		E	X		X	W	E	W	W	E	X	X	W			X	E	E

	Eburophyton austinae	Calypso bulbosa	Populus tremuloides	Populus trichocarpa	Salix sitchensis	Salix scouleriana	Corylus cornuta californica	Betula glandulosa hallii	Alnus sinuata	Quercus garryana	Castanopsis chrysophylla	Comandra umbellata	Arceuthobium abietinum	Asarum caudatum?	Rumex cripsus	Rumex acetosella	Polygonum bistortoides	Polygonum phytolaccaefolium	Polygonum newberryi	Polygonum minimum	Polygonum cascadense	Polygonum douglasii	Polygonum spergulariaeforme	Polygonum kelloggii	Eriogonum nudum	Eriogonum compositum	Eriogonum umbellatum
Monument Peak					X				X	A	X	X		A	X	X	A			X		X					X
Bachelor Mt.						X			X			X				X		X		X		X			X	X	X
Three Pyramids					X				X			X		X		X		X		X		X			X	X	X
Crescent Mt.		X			X				X		X	X		X		X				X						X	
Echo Peak		X				X			X			X		X		X			X	X	X	X				X	X
South Peak					X				X					X		X		X	X	X	X	X			X	X	
Cone Peak					X	X	X		X			X		X		X		X	X	X	X	X			X	X	X
Iron Mt.		X			X	X			X		X	X	X	X		X	X	X		X	X	X		X	X	X	X
Browder Ridge					X				X			X		X		X		X	X	X	X	X		X	X	X	X
Jumpoff Joe					X	X			X		X			X						X		X				X	
Squaw Peak									X							X		X		X							
Twin Buttes					X		X		X		X	X		X				X		X					X	X	X
Carpenter Mt.									X			X		X		X		X		X		X					
Tidbits Mt.									X		X	X	X	X		X	X			X							X
Lookout Mt.					X				X		X	X				X				X		X					X
Frissell Pt.					X		X		X			X				X				X		X				X	X
Castle Rock	X					X			X	X	X	X				X						X	X		X	X	
O'Leary Mt.									X					X		X		X		X	X	X			X	X	X
Horsepasture Mt.					X		X		X		X	X		X	X	X		X		X	X	X			X	X	X
English Mt.									X			X		X		X				X						X	
Lowder Mt.			X		X				X			X		X		X	X	X	X	X	X	X		X	X		X
Tipsoo Butte	X				X				X			X				X				X	X				X	X	X
Olallie Mt.				X					X		X	X		X		X		X	X	X		X				X	X
Rebel Rock	X	X		X	X		X		X	X	X	X		X		X	X	X		X	X	X	X	X	X	X	X
Indian Ridge				X	X				X		X	X				X		X		X							
Sardine Butte					X				X		X	X				X				X		X					
Huckleberry Mt.											X					X											X
Bohemia Mt.(reg.)					X	B			X	X	X			B	B	X	X	X	B	X	X	X			X	X	X
Hershberger Mt.					X		X		X		X			X	X	X	X		X	X		X			X	X	X
Grizzly Peak					X	X			X		X	X		X								X					X
Maxwell Butte					X			X			X								X						X		X
Little Nash Cr.				X							X			X											X		X
Hogg Rock								X			X									X							
Hoodoo Butte					X	X		X			X					X				X							X
Sand Mt.											X																
Three Sisters				I	X	I		X	X		X	I	I			X	X	X	X	X		X		X			X
Crater Lake	E		W	W	W	W	W		W		W			E	W	W	X		X	X	X	X	E	X	X		X

	Claytonia lanceolata	Montia sibirica	Montia parviflora	Montia perfoliata	Montia diffusa	Spraguea umbellata	Lewisia triphylla	Spergularia rubra	Arenaria macrophylla	Arenaria serpyllifolia	Arenaria rubella	Arenaria capillaris americana	Arenaria pumicola	Cerastium arvense	Silene cucubalus	Silene campanulata glandulosa	Silene douglasii	Nuphar polysepalum	Ranunculus occidentalis	Ranunculus uncinatus parviflorus	Ranunculus alismaefolius alismellus	Ranunculus flammula filiformis	Ranunculus gormanii	Trautvetteria caroliniensis	Thalictrum occidentale	Anemone deltoidea
Monument Peak		X	X					X	X					X			X							X	X	X
Bachelor Mt.	X		X				X		X			X					X				X				X	X
Three Pyramids		X	X						X	X	X	X		X			X								X	X
Crescent Mt.	X	X							X			X								X	X					
Echo Peak		X							X			X		X	X			X			X			X		X
South Peak	X		X				X		X			X		X												X
Cone Peak	X	X	X				X	X	X			X		X			X				X				X	X
Iron Mt.	X	X	X				X	X	X	X	X	X		X	X		X			X					X	X
Browder Ridge	X	X	X	X			X		X		X	X		X			X			X						X
Jumpoff Joe									X																	X
Squaw Peak		X	X							X																X
Twin Buttes		X	X							X							X			X						
Carpenter Mt.	X	X	X				X		X			X					X									
Tidbits Mt.			X						X							X	X								X	X
Lookout Mt.		X							X					X			X		X							X
Frissell Pt.		X	X						X	X				X			X									X
Castle Rock		X	X	X	X				X					X			X		X							X
O'Leary Mt.		X		X					X	X	X						X		X	X						X
Horsepasture Mt.		X	X				X		X	X						X	X			X					X	X
English Mt.		X				X	X		X			X					X								X	X
Lowder Mt.		X	X				X		X			X					X			X			X		X	X
Tipsoo Butte									X			X		X		X	X			X						
Olallie Mt.		X				X	X		X	X							X								X	X
Rebel Rock		X	X	X			X		X	X	X	X		X		X	X			X					X	X
Indian Ridge	X	X	X									X					X	X				X			X	
Sardine Butte		X							X								X			X	X					X
Huckleberry Mt.		X							X			X				X										X
Bohemia Mt.(reg.)	X	X	X	B				B	X	B	X		X			X								B	X	X
Hershberger Mt.		X				X	X		X	X						X										
Grizzly Peak		X							X	X																X
Maxwell Butte						X		X																		X
Little Nash Cr.						X																				
Hogg Rock						X																				
Hoodoo Butte						X																				X
Sand Mt.																										
Three Sisters		X		I		X	X	I	I		X	X						I			X		X			X
Crater Lake	W	W	E	E		X	X	X	W	X			X			E	W		W				X			W

	Anemone lyallii	Anemone oregana	Caltha biflora	Coptis laciniata	Aquilegia formosa	Delphinium menziesii pyramidale	Delphinium trolliifolium	Delphinium glaucum	Aconitum columbianum howellii	Actaea rubra	Berberis aquifolium	Berberis nervosa	Vancouveria hexandra	Achlys triphylla	Dicentra formosa	Dicentra uniflora	Thlaspi fendleri hesperium	Barbarea vulgaris	Cardamine bellidifolia pachyphylla	Cardamine integrifolia sinuata	Phoenicaulis cheiranthoides	Arabis glabra	Arabis hirsuta glabrata	Arabis holboellii retrofracta	Arabis platysperma howellii	Erysimum asperum
Monument Peak		X	A		X	A			A	X	A	X	X	X										A		X
Bachelor Mt.		X	X		X	X	X				X			X	X	X						X		X		X
Three Pyramids	X				X					X		X		X	X		X	X						X		X
Crescent Mt.	X				X	X				X	X	X		X	X			X						X	X	X
Echo Peak		X	X			X				X		X		X		X							X	X		X
South Peak	X				X	X				X				X	X	X							X	X		X
Cone Peak	X	X	X		X	X				X		X		X	X	X						X		X		X
Iron Mt.	X	X	X		X	X				X		X	X	X	X	X							X	X		X
Browder Ridge	X				X					X	X	X		X	X									X		X
Jumpoff Joe												X		X										X		
Squaw Peak	X				X					X		X		X	X											
Twin Buttes	X				X	X				X		X	X	X	X									X		X
Carpenter Mt.	X				X	X				X				X	X	X										X
Tidbits Mt.		X				X				X		X	X	X	X		X			X				X		X
Lookout Mt.	X	X			X	X						X	X		X											X
Frissell Pt.		X			X	X	X			X	X	X	X	X	X									X		X
Castle Rock		X		X		X				X		X	X	X	X											X
O'Leary Mt.	X				X	X				X		X		X	X									X		X
Horsepasture Mt.	X				X	X				X		X	X	X	X	X		X						X		
English Mt.	X		X		X	X								X	X									X		X
Lowder Mt.	X		X		X	X				X		X	X	X	X	X						X		X		X
Tipsoo Butte					X					X		X	X										X	X		X
Olallie Mt.	X	X		X	X	X			X	X		X		X	X									X		
Rebel Rock	X			X	X	X				X	X	X	X	X	X	X						X		X		X
Indian Ridge	X					X						X		X	X											X
Sardine Butte	X		X		X	X						X		X	X											
Huckleberry Mt.					X	X						X	X	X	X											X
Bohemia Mt.(reg.)	X		X		X	X			B			X	B	B	X	X	X	X		X	X			X	X	X
Hershberger Mt.		X	X		X			X	X	X		X	X	X	X		X							X	X	X
Grizzly Peak										X		X		X	X											
Maxwell Butte		X			X									X	X				X						X	
Little Nash Cr.												X														
Hogg Rock																										
Hoodoo Butte												X		X	X										X	
Sand Mt.																									X	
Three Sisters	X		X		X	X			X	I		X	X	X	X	X		I	X					X	X	X
Crater Lake	W	E	W		X	W		W	X	W		W	W	W	X	W		W	X		X	E		W	X	

Bald

	Drosera rotundifolia	Drosera anglica	Sedum stenopetalum	Sedum spathulifolium	Sedum divergens	Sedum oreganum	Sedum oregonense	Saxifraga cespitosa	Saxifraga mertensiana	Saxifraga bronchialis vespertina	Saxifraga ferruginea	Saxifraga integrifolia	Saxifraga occidentalis rufidula	Boykinia elata	Boykinia major	Tiarella unifoliata	Tellima grandiflora	Lithophragma parviflora	Lithophragma glabra	Lithophragma bulbifera	Tolmiea menziesii	Mitella caulescens	Mitella breweri	Mitella trifida	Mitella ovalis	Heuchera micrantha	Philadelphus lewisii gordonianus
Monument Peak				X	A		X			A	X		X		X	X	X				X		X			X	
Bachelor Mt.					X		X		X	X	X	X	X		X	X	X	X					X				
Three Pyramids				X	X		X			X	X	X	X	X	X	X	X				X		X	X			
Crescent Mt.			X		X		X	X		X		X	X			X	X	X									
Echo Peak			X		X	X				X		X	X	X	X	X	X	X			X		X				
South Peak			X		X		X			X		X	X			X		X	X	X			X				
Cone Peak			X		X		X			X		X	X			X	X	X	X	X			X	X		X	
Iron Mt.			X		X	X	X	X		X	X	X	X		X	X	X	X	X	X	X	X	X	X		X	
Browder Ridge			X	X	X		X			X	X	X	X			X	X				X		X	X		X	
Jumpoff Joe				X						X					X	X										X	
Squaw Peak											X					X	X				X		X				
Twin Buttes				X	X		X			X	X		X		X	X	X				X		X	X		X	
Carpenter Mt.							X				X	X		X							X		X	X		X	
Tidbits Mt.				X	X	X	X			X	X		X	X	X	X							X			X	
Lookout Mt.							X				X						X				X			X			
Frissell Pt.			X			X	X				X		X			X	X				X		X			X	
Castle Rock				X										X		X	X									X	X
O'Leary Mt.			X	X			X				X	X	X				X	X			X		X	X		X	
Horsepasture Mt.			X					X		X	X			X		X	X				X		X	X		X	
English Mt.							X			X	X					X	X				X			X		X	
Lowder Mt.	X	X	X				X					X	X		X	X	X				X		X	X			
Tipsoo Butte			X	X	X	X					X						X						X	X		X	
Olallie Mt.							X				X			X		X	X				X	X	X				
Rebel Rock			X	X			X				X	X	X	X		X	X	X	X	X	X		X	X		X	X
Indian Ridge	X			X	X		X		X	X	X		X	X		X	X				X		X	X		X	
Sardine Butte							X			X			X		X	X	X							X			
Huckleberry Mt.							X									X											
Bohemia Mt.(reg.)			X	X	X		X		X	X	X		X	X	X	X	X	X	X				X	X		X	B
Hershberger Mt.							X				X					X											
Grizzly Peak											X					X					X	X	X		X	X	
Maxwell Butte											X																
Little Nash Cr.																											
Hogg Rock																											
Hoodoo Butte																											
Sand Mt.																											
Three Sisters	X						I				X		X			I						X	I		X	X	
Crater Lake	W	W	X	W			X		E		W	X				W	W		W			W	W	W		X	E

	Whipplea modestus	Ribes lobbii	Ribes binominatum	Ribes cruentum	Ribes lacustre	Ribes sanguineum	Ribes bracteosum	Ribes viscosissimum	Ribes cereum	Ribes erythrocarpum	Physocarpus capitatus	Spiraea densiflora	Spiraea douglasii menziesii	Holodiscus discolor	Aruncus sylvester	Luetkea pectinata	Potentilla gracilis	Potentilla drummondii	Potentilla glandulosa	Comarum palustre	Horkelia fusca parviflora	Ivesia gordonii	Fragaria vesca bracteata	Geum macrophyllum	Rosa gymnocarpa	Sanguisorba officinalis	Rubus lasiococcus
Monument Peak					X		X	X						X					X				X		X		X
Bachelor Mt.			X		X		X	X		X				X	X	X			X				X		X		X
Three Pyramids					X		X	X						X	X				X				X	X	X		X
Crescent Mt.					X			X						X					X				X		X		X
Echo Peak			X		X		X	X	X					X	X	X	X	X	X		X		X		X	X	X
South Peak			X		X			X						X			X		X				X	X	X		X
Cone Peak			X		X		X	X						X			X	X	X			X	X		X	X	X
Iron Mt.			X		X	X	X	X						X			X	X	X			X	X	X	X	X	X
Browder Ridge			X		X		X	X						X			X		X				X	X	X		X
Jumpoff Joe	X	X						X						X					X				X		X		X
Squaw Peak	X		X		X		X	X							X										X		
Twin Buttes		X	X				X							X	X				X				X		X		X
Carpenter Mt.					X		X							X					X				X	X	X		X
Tidbits Mt.					X		X	X						X	X				X				X		X		X
Lookout Mt.	X		X		X			X						X	X				X				X		X		X
Frissell Pt.			X		X		X	X						X	X				X						X		X
Castle Rock	X		X		X									X					X				X		X		
O'Leary Mt.			X		X			X						X					X				X		X		
Horsepasture Mt.			X				X	X						X	X		X		X				X		X		X
English Mt.			X											X					X				X		X		X
Lowder Mt.			X		X			X						X				X	X				X	X	X		X
Tipsoo Butte						X		X						X									X		X		X
Olallie Mt.			X		X		X	X		X				X	X	X		X	X				X		X		X
Rebel Rock	X		X		X		X	X		X	X			X	X		X		X				X	X	X		X
Indian Ridge	X		X		X	X	X	X						X	X				X	X					X		X
Sardine Butte					X		X	X						X											X		X
Huckleberry Mt.	X							X						X											X		X
Bohemia Mt.(reg.)	X		X		X	X	X							X	X		X	X	X				X		X		X
Hershberger Mt.			X					X	X	X			X	X					X						X		X
Grizzly Peak					X	X		X		X				X	X	X									X		X
Maxwell Butte								X	X	X		X	X	X		X		X					X	X	X		X
Little Nash Cr.		X		X				X	X					X									X		X		
Hogg Rock									X																		
Hoodoo Butte									X					X									X		X		
Sand Mt.									X																		
Three Sisters		X		X	X			I	X			X	X	X		X	X	X	X	X	X		X	X	X		X
Crater Lake		W	W		X	E		X	X	X		X	E	X		X	W	X	X		E		X	X	X		X

	Rubus spectabilis	Rubus parviflorus	Rubus ursinus	Rubus procerus	Sorbus sitchensis	Amelanchier alnifolia semiintegrifolia	Prunus emarginata	Cytisus scoparius	Lupinus lepidus lobbii	Lupinus arbustus neolaxiflorus	Lupinus sericeus	Lupinus latifolius	Lupinus andersonii	Trifolium productum	Trifolium howellii	Trifolium longipes	Trifolium repens	Trifolium pratense	Trifolium variegatum	Trifolium oliganthum	Trifolium microcephalum	Medicago hispida	Lotus crassifolius	Lotus micranthus	Lotus pinnatus	Lotus nevadensis douglasii
Monument Peak	X	X	X	X	X	X	X	A				X					X	A								
Bachelor Mt.	X	X	X		X	X	X			X						X							X			X
Three Pyramids	X	X	X		X	X	X			X			X											X		X
Crescent Mt.			X		X	X	X			X	X															
Echo Peak		X	X		X	X				X						X	X			X				X		X
South Peak		X	X		X	X	X			X		X														X
Cone Peak		X	X			X	X		X	X		X		X		X	X							X		X
Iron Mt.	X	X	X		X	X	X			X	X	X		X		X	X	X					X	X		X
Browder Ridge	X	X	X		X	X	X			X		X	X				X							X		X
Jumpoff Joe		X	X			X	X					X														X
Squaw Peak	X	X			X							X														
Twin Buttes	X	X	X		X	X	X	X				X														X
Carpenter Mt.	X	X	X			X	X			X		X														X
Tidbits Mt.	X	X	X		X	X	X					X											X			
Lookout Mt.	X	X	X			X				X		X											X			X
Frissell Pt.	X	X	X			X	X			X		X					X						X			X
Castle Rock		X	X			X											X	X	X					X		X
O'Leary Mt.		X	X		X	X				X		X			X		X									X
Horsepasture Mt.	X	X	X		X	X	X			X		X		X			X									X
English Mt.		X	X		X	X				X																
Lowder Mt.		X	X		X		X			X		X				X										
Tipsoo Butte		X	X			X	X			X		X	X													
Olallie Mt.	X	X	X		X	X	X			X		X				X										
Rebel Rock	X	X	X	X	X	X	X			X	X	X				X	X		X		X	X	X	X		X
Indian Ridge	X	X	X		X	X				X		X					X	X						X		
Sardine Butte		X	X			X						X											X		X	
Huckleberry Mt.		X	X		X	X				X		X											X		X	
Bohemia Mt.(reg.)	X	X	X		X	X	X		B	X		X	X	X	X		X						X			X
Hershberger Mt.		X	X		X	X						X	X		X								X			X
Grizzly Peak	X	X	X		X	X							X													
Maxwell Butte		X	X			X						X	X				X									
Little Nash Cr.		X	X			X	X		X																	X
Hogg Rock						X																				
Hoodoo Butte		X	X		X								X													
Sand Mt.									X																	
Three Sisters		X	X		X	X	I		X	I		I	X			X	X									
Crater Lake		X	W		X	X	X		X			X	X	W		X	W	W					E	E		

	Psoralea physodes	Vicia americana truncata	Vicia americana minor	Lathyrus holochlorus	Lathyrus polyphyllus	Lathyrus lanszwertii aridus	Lathyrus nevadensis lanceolatus philosellus	Linum perenne lewisii	Erodium cicutarium	Oxalis oregana	Oxalis suksdorfii	Rhus diversiloba	Pachystima myrsinites	Acer macrophyllum	Acer circinatum	Acer glabrum douglasii	Rhamnus purshiana	Ceanothus sanguineus	Ceanothus velutinus	Ceanothus integerrimus	Ceanothus prostratus	Hypericum perforatum	Hypericum formosum scouleri	Hypericum anagalloides	Viola palustris	Viola macloskeyi
Monument Peak	X	X			X					X			X	X	X		X		A			X		X		A
Bachelor Mt.		X				X	X						X		X	X	X		X			X				
Three Pyramids		X					X						X		X	X			X							
Crescent Mt.		X				X	X						X		X	X	X		X						X	
Echo Peak		X				X	X	X					X	X	X	X	X		X				X	X	X	X
South Peak		X					X						X		X							X				
Cone Peak		X					X	X					X		X	X	X					X	X		X	X
Iron Mt.		X	X				X	X		X			X		X	X	X					X	X		X	X
Browder Ridge		X					X	X					X		X											
Jumpoff Joe		X											X		X				X							
Squaw Peak													X		X											
Twin Buttes		X					X						X	X	X	X	X		X							
Carpenter Mt.		X					X						X		X											
Tidbits Mt.													X	X	X	X			X							
Lookout Mt.		X		X			X				X			X	X	X	X		X							
Frissell Pt.		X					X						X	X	X	X	X		X			X				
Castle Rock		X					X			X				X	X	X		X								
O'Leary Mt.		X					X		X				X		X		X		X			X				
Horsepasture Mt.		X					X			X	X		X	X	X	X	X		X	X		X		X		
English Mt.							X						X		X	X	X		X				X			
Lowder Mt.		X					X						X		X	X			X					X	X	X
Tipsoo Butte		X											X		X	X	X		X	X		X	X			
Olallie Mt.		X					X						X		X	X	X		X				X			
Rebel Rock		X			X		X	X				X	X	X	X	X	X	X	X	X		X				
Indian Ridge													X	X	X	X			X			X				
Sardine Butte	X	X			X								X		X				X	X		X				
Huckleberry Mt.	X				X								X		X				X			X				
Bohemia Mt.(reg.)		X					X	X	X	X			X	X	X	X						X		X		
Hershberger Mt.		X			X	X	X	X					X			X			X		X			X		
Grizzly Peak						X							X		X	X			X							
Maxwell Butte						X							X		X		X		X				X		X	
Little Nash Cr.						X							X		X		X		X			X				
Hogg Rock													X		X											
Hoodoo Butte															X		X		X			X				
Sand Mt.													X		X				X							
Three Sisters						I							X		X	X	X		X	X		X	X	X	X	X
Crater Lake		W					W	E					X	E		X	X		X	E	X	X	W	X		E

	Viola bellidifolia	Viola adunca	Viola glabella	Viola nuttallii bakeri	Viola sempervirens	Viola orbiculata	Epilobium angustifolium	Epilobium watsonii	Epilobium glaberrimum	fastigiatum	Epilobium glandulosum	Epilobium alpinum clavatum	Epilobium alpinum nutans	Epilobium paniculatum	Epilobium minutum	Clarkia rhomboidea	Clarkia amoena	Gayophytum humile	Gayophytum diffusum parviflorum	Circaea alpina	Oplopanax horridum	Aralia californica	Sanicula graveolens	Sanicula crassicaulis	Orogenia fusiformis	Osmorhiza chilensis	Osmorhiza occidentalis
Monument Peak			X		X	X	X				X	X	X	X	X			X		X	X				A	X	X
Bachelor Mt.			X	X		X	X							X				X							X	X	
Three Pyramids			X			X	X								X			X		X	X					X	
Crescent Mt.			X				X																X			X	
Echo Peak			X	X	X	X	X											X	X		X		X		X	X	
South Peak			X		X	X	X											X					X		X		
Cone Peak		X	X				X		X		X		X		X			X	X		X		X		X	X	
Iron Mt.		X	X	X		X	X		X		X		X	X	X			X	X	X	X		X		X	X	
Browder Ridge			X	X		X	X							X	X			X	X	X	X		X		X	X	
Jumpoff Joe			X			X	X	X							X											X	
Squaw eak						X	X						X							X	X					X	
Twin Buttes			X			X		X	X			X		X				X		X	X					X	
Carpenter Mt.			X	X		X	X				X			X				X					X		X	X	
Tidbits Mt.			X			X	X	X				X						X			X					X	
Lookout Mt.			X				X						X					X			X	X				X	
Frissell Pt.			X			X	X	X					X		X			X	X		X	X	X			X	
Castle Rock			X			X									X	X	X					X		X		X	
O'Leary Mt.			X										X		X			X					X			X	
Horsepasture Mt.			X	X	X		X	X					X		X			X			X	X	X		X	X	
English Mt.			X	X	X		X								X			X			X		X		X	X	
Lowder Mt.		X	X	X		X												X					X		X	X	
Tipsoo Butte	X						X				X		X					X					X			X	
Olallie Mt.			X	X		X	X				X	X	X					X	X	X		X	X		X	X	X
Rebel Rock			X	X	X	X	X	X			X				X	X	X	X	X		X	X	X	X	X	X	
Indian Ridge			X		X		X						X								X	X			X		
Sardine Butte			X				X	X				X						X									
Huckleberry Mt.						X	X																				
Bohemia Mt.(reg.)			X		B		X	X			X	X	X	B	X		B	X	X	X			X		X	X	X
Hershberger Mt.			X			X	X	X					X					X	X				X			X	X
Grizzly Peak			X		X	X	X					X								X	X					X	
Maxwell Butte						X	X	X				X	X						X								
Little Nash Cr.							X																				
Hogg Rock																											
Hoodoo Butte						X	X					X			X												
Sand Mt.							X																				
Three Sisters		I	I	X	X	X	X		I			X	I						X							X	X
Crater Lake		W	W	X		E	X	X	E	X	X	E	X	W	W	W		X	X	W	E					X	

	Daucus carota	Ligusticum grayi	Cicuta douglasii	Angelica arguta	Lomatium hallii	Lomatium martindalei	Lomatium nudicaule	Heracleum lanatum	Cornus stolonifera occidentalis	Cornus nuttallii	Cornus canadensis	Garrya fremontii	Chimaphila umbellata	Chimaphila menziesii	Pyrola secunda	Pyrola asarifolia purpurea	Pyrola picta	Pyrola dentata	Pyrola aphylla = P. picta?	Allotropa virgata	Monotropa uniflora	Hypopitys monotropa	Pleuricospora fimbriolata	Pterospora andromedea	Rhododendron albiflorum	Rhododendron macrophyllum	Menziesia ferruginea
Monument Peak				X		X		X			X			A	X		X	A					A			X	A
Bachelor Mt.		X		X		X		X			X		X	X	X	X	X	X							X	X	
Three Pyramids				X		X		X			X		X	X	X		X									X	
Crescent Mt.				X	X	X		X			X		X	X	X		X	X								X	
Echo Peak	X			X		X		X			X		X	X			X										
South Peak				X		X		X			X		X	X	X		X										
Cone Peak		X		X		X		X	X		X		X	X	X		X										
Iron Mt.		X		X	X	X		X	X		X		X	X	X	X	X	X	X							X	
Browder Ridge		X		X		X		X			X		X	X	X		X									X	
Jumpoff Joe											X		X				X									X	
Squaw Peak								X			X				X											X	
Twin Buttes						X					X		X	X	X		X	X							X	X	
Carpenter Mt.		X		X		X		X					X	X	X											X	
Tidbits Mt.		X		X	X						X	X	X	X	X	X	X	X		X		X				X	X
Lookout Mt.		X		X		X				X																X	
Frissell Pt.		X		X		X				X	X		X		X											X	
Castle Rock						X	X			X		X	X	X			X		X	X				X		X	
O'Leary Mt.		X		X		X							X	X	X												
Horsepasture Mt.				X		X	X	X	X		X	X	X	X	X		X									X	
English Mt.				X				X			X		X	X	X										X	X	
Lowder Mt.		X		X		X		X			X		X	X	X		X										
Tipsoo Butte		X															X				X						
Olallie Mt.		X		X			X	X			X		X	X	X		X									X	
Rebel Rock		X		X	X	X	X	X	X		X	X	X	X	X		X	X	X			X				X	
Indian Ridge			X			X		X		X	X									X			X		X	X	
Sardine Butte						X						X		X			X	X								X	
Huckleberry Mt.						X							X	X												X	
Bohemia Mt.(reg.)		X			B	X		X			X	B	X	B	X	B	B					X				X	
Hershberger Mt.		X						X		X			X		X		X										
Grizzly Peak				X		X					X		X	X	X	X	X	X				X			X	X	
Maxwell Butte						X					X		X		X		X		X					X		X	
Little Nash Cr.											X		X	X			X										
Hogg Rock																											
Hoodoo Butte						X							X		X												
Sand Mt.						X																		X			
Three Sisters		X	X	X	X	X			I	X	X		X	I	I	X	X	I				I		X	X	X	
Crater Lake		X		X		X		X	E	E	E	E	X	W	X	W	X	W	W	X	W	E		X			

	Kalmia polifolia	Phyllodoce empetriformis	Gaultheria shallon	Gaultheria ovatifolia	Gaultheria humifusa	Arbutus menziesii	Arctostaphylos nevadensis	Arctostaphylos patula	Arctostaphylos columbiana	Vaccinium uliginosum	Vaccinium occidentale	Vaccinium scoparium	Vaccinium cespitosum	Vaccinium membranaceum	Vaccinium ovalifolium	Vaccinium parvifolium	Trientalis latifolia	Douglasia laevigata	Dodecatheon jeffreyi	Gentiana calycosa (n. subsp.)	Apocynum androsaemifolium	Convolvulus nyctagineus	Polemonium carneum	Polemonium pulcherrimum	Polemonium pulcherrimum calycinum	Phlox adsurgens	Phlox diffusa longistylis
Monument Peak			X				X		X					X	A	X	X		X				X			X	A
Bachelor Mt.				X			X							X		X	X		X		X		X				X
Three Pyramids				X			X							X			X	X	X	X			X				X
Crescent Mt.				X			X							X			X										X
Echo Peak							X										X	X	X				X				X
South Peak							X							X					X				X				X
Cone Peak														X				X	X				X				X
Iron Mt.							X					X		X			X		X				X	X			X
Browder Ridge							X							X			X	X			X		X				X
Jumpoff Joe							X							X			X										
Squaw Peak														X			X						X				
Twin Buttes							X							X			X						X			X	
Carpenter Mt.							X							X			X					X	X				
Tidbits Mt.			X	X			X							X	X	X	X			X						X	X
Lookout Mt.			X											X			X						X				
Frissell Pt.			X				X							X		X	X										X
Castle Rock			X			X	X		X							X	X				X	X				X	X
O'Leary Mt.							X							X								X	X			X	
Horsepasture Mt.			X				X							X		X				X		X	X			X	X
English Mt.	X						X							X					X				X				X
Lowder Mt.	X				X		X			X		X		X			X		X				X			X	X
Tipsoo Butte							X							X			X						X				
Olallie Mt.				X			X					X		X		X	X						X				
Rebel Rock			X			X	X	X	X					X		X	X				X		X				X
Indian Ridge					X	X	X		X				X	X			X						X				X
Sardine Butte							X		X					X	X				X								X
Huckleberry Mt.			X			X	X		X					X			X										X
Bohemia Mt. (reg.)			X	B			X					X		X	B	X	X			B	B		X				X
Hershberger Mt.							X	X						X			X		X		X				X		X
Grizzly Peak		X		X			X	X				X		X		X	X				X		X				
Maxwell Butte		X		X			X	X				X		X			X				X						X
Little Nash Cr.							X							X													X
Hogg Rock																											
Hoodoo Butte							X			X	X			X													
Sand Mt.								X																			
Three Sisters	X	X	X	X	I		X	X			X	X	X	X	X	X	X		X					X	X	I	X
Crater Lake	W	W		E	W	E	X	X			W	X	X	X			W		X		E			X	X		X

	Microsteris gracilis	Gilia capitata	Gilia aggregata	Linanthastrum nuttallii	Linanthus harknessii	Linanthus bicolor	Navarretia divaricata	Collomia heterophylla	Collomia tinctoria	Collomia linearis	Collomia mazama	Hydrophyllum fendleri albifrons	Hydrophyllum tenuipes	Hydrophyllum occidentale	Nemophila parviflora	Phacelia heterophylla	Phacelia linearis	Romanzoffia suksdorfii	Romanzoffia sitchensis	Cryptantha intermedia	Cryptantha affinis	Plagiobothrys scouleri	Hackelia jessicae	Mertensia bella	Mertensia paniculata	Agastache urticifolia	Prunella vulgaris lanceolata
Monument Peak	X	X											X			X									X		X
Bachelor Mt.	X	X	X				X					X	X	X		X							X	X	X		
Three Pyramids	X	X					X					X	X			X				X					X		X
Crescent Mt.	X		X							X						X							X		X		
Echo Peak	X	X	X		X		X			X			X	X	X	X			X				X	X	X		X
South Peak	X	X	X				X			X		X	X	X		X			X				X	X	X		
Cone Peak	X	X	X		X		X			X		X	X	X	X	X			X				X	X	X		X
Iron Mt.	X	X	X		X		X			X		X	X	X	X	X			X		X		X	X	X		
Browder Ridge	X	X	X				X						X	X		X			X			X	X	X	X		X
Jumpoff Joe	X	X						X								X											
Squaw Peak	X															X								X	X		
Twin Buttes	X		X					X					X	X		X								X	X		
Carpenter Mt.	X												X	X		X								X			
Tidbits Mt.	X		X										X			X											
Lookout Mt	X	X					X						X			X											
Frissell Pt.	X	X					X						X			X											
Castle Rock	X	X						X							X	X	X										
O'Leary Mt.	X	X	X		X		X							X		X							X	X			
Horsepasture Mt.	X	X	X		X		X	X				X	X	X	X	X				X			X	X			
English Mt.	X		X									X	X	X		X								X			
Lowder Mt.	X	X			X		X					X	X	X	X	X							X	X	X		
Tipsoo Butte	X	X	X				X									X											
Olallie Mt.	X	X	X				X					X	X			X								X	X		
Rebel Rock	X	X	X	X	X	X	X	X		X				X	X	X	X			X			X	X	X		X
Indian Ridge												X	X			X		X						X			
Sardine Butte	X	X														X											
Huckleberry Mt.	X															X											
Bohemia Mt.(reg.)	X	X	X	X			X	X	X			X	X	X	B	X		X	B	B			X			X	
Hershberger Mt.	X		X		X		X		X	X	X	X				X							X		X	X	
Grizzly Peak																X											
Maxwell Butte			X													X											
Little Nash Cr.	X																				X						
Hogg Rock																											
Hoodoo Butte																X											
Sand Mt.	X															X											
Three Sisters	X	X	X				X					X	X		X	X							I				X
Crater Lake	W		X	X	X		W		W	X	W	E				X					X	E	X		W		

	Stachys cooleyae	Stachys rigida	Monardella odoratissima	Satureja douglasii	Lycopus uniflorus	Verbascum thapsus	Collinsia grandiflora	Collinsia parviflora	Penstemon cardwellii	Penstemon davidsonii	Penstemon rupicola	Penstemon nemorosus	Penstemon deustus	Penstemon procerus brachyanthus	Penstemon cinicola	Penstemon euglaucus	Penstemon serrulatus	Mimulus moschatus	Mimulus pulsiferae	Mimulus breweri	Mimulus lewisii	Mimulus guttatus	Digitalis purpurea	Veronica americana	Veronica wormskjoldii	Veronica serpyllifolia	Synthyris reniformis
Monument Peak	X	X					A	X	X		X	X		X			X	X		X		X	X	A			
Bachelor Mt.		X						X	X		X	X		X			X			X		X					
Three Pyramids	X							X	X		X	X		X			X	X		X	X	X				X	
Crescent Mt.								X	X		X			X						X						X	
Echo Peak	X	X				X	X	X	X		X	X		X			X			X	X	X					
South Peak								X			X	X		X				X		X		X					
Cone Peak		X	X				X	X	X		X	X	X	X			X	X		X		X					X
Iron Mt.	X			X		X		X	X		X	X	X	X			X	X	○	X		X				X	X
Browder Ridge		X					X	X	X		X	X		X				X		X	X	X				X	
Jumpoff Joe		X					X		X		X	X					X										
Squaw Peak		X						X	X																		
Twin Buttes							X	X	X		X	X					X	X		X		X					
Carpenter Mt.		X						X	X			X		X				X		X		X				X	
Tidbits Mt.								X	X		X	X					X					X					
Lookout Mt.		X						X	X					X						X		X					
Frissell Pt.	X							X	X		X	X		X				X		X							
Castle Rock		X		X				X			X	X	X				X		X			X					
O'Leary Mt.		X					X	X	X		X	X		X				X	X	X		X				X	
Horsepasture Mt.	X	X						X	X	X	X	X		X				X		X		X		X		X	X
English Mt.		X						X	X					X				X		X							
Lowder Mt.	X	X						X	X			X		X				X		X		X		X		X	
Tipsoo Butte											X	X					X	X		X							
Olallie Mt.	X								X			X		X			X	X		X		X					
Rebel Rock		X		X			X	X	X		X	X	X	X				X	X	X		X					X
Indian Ridge					X				X			X		X						X		X					
Sardine Butte	X					X		X	X			X		X													
Huckleberry Mt.									X		X	X															
Bohemia Mt.(reg.)		X	X					X	X		X	X		X				X		X		X	X	B		X	B
Hershberger Mt.	X	X	X					X			X	X	X					X		X							
Grizzly Peak	X								X			X				X											
Maxwell Butte				X					X	X					X	X										X	
Little Nash Cr.				X					X	X				X		X											
Hogg Rock																									X		
Hoodoo Butte									X			X		X						X					X		
Sand Mt.									X	X																	
Three Sisters						X		I	X	X	X	X		X	X	X	X	I		X	I	X		I	X	X	
Crater Lake	E	X	E			X		W		X	X		E		X			X		X	X	X		W	X	W	

	Castilleja arachnoidea	Castilleja suksdorfii	Castilleja miniata	Castilleja hispida	Castilleja parviflora oreopola	Castilleja rupicola	Castilleja pruinosa	Orthocarpus hispidus	Orthocarpus attenuatus	Orthocarpus imbricatus	Pedicularis racemosa	Pedicularis bracteata flavida	Pedicularis groenlandica	Pedicularis contorta	Orobanche fasciculata	Orob~~r~~anche uniflora minor	Plantago major	Plantago lanceolata	Galium triflorum	Galium trifidum pacificum	Galium oreganum	Galium aparine	Galium bifolium	Kelloggia galioides	Sambucus cerulea	Sambucus racemosa pubens arborescens
Monument Peak			X	X						X	X					A	X		X		X					X
Bachelor Mt.			X	X						X	X	X				X			X				X		X	X
Three Pyramids			X	X		X				X	X	X				X			X	X	X		X			X
Crescent Mt.			X	X							X								X		X		X			X
Echo Peak										X	X		X			X	X	X	X	X	X		X			X
South Peak				X		X				X	X								X		X		X			
Cone Peak		X	X	X		X				X	X	X	X			X	X		X		X		X			X
Iron Mt.			X	X						X	X	X			X	X	X	X	X		X	X	X		X	X
Browder Ridge			X	X						X	X	X			X			X	X		X		X		X	X
Jumpoff Joe			X	X							X								X		X				X	X
Squaw Peak											X								X		X					
Twin Buttes				X							X								X		X					X
Carpenter Mt.												X								X	X		X			X
Tidbits Mt.			X	X		X					X	X		X					X		X					X
Lookout Mt.				X																X	X	X			X	X
Frissell Pt.				X							X								X		X		X		X	X
Castle Rock				X													X	X	X		X					
O'Leary Mt.				X						X		X				X		X	X		X		X			X
Horsepasture Mt.			X	X		X				X	X	X				X			X		X		X			X
English Mt.				X						X	X	X	X								X		X			
Lowder Mt.				X							X		X						X		X		X			X
Tipsoo Butte			X	X			X			X									X	X	X				X	
Olallie Mt.	X		X				X				X	X							X		X		X			X
Rebel Rock			X	X			X	X	X	X	X					X			X		X	X	X			X
Indian Ridge			X	X										X					X	X	X				X	X
Sardine Butte				X							X							X								
Huckleberry Mt.				X								X		X		X			X		X					
Bohemia Mt.(reg.)			X	X			X			X	X	X		B	B	X	X	X	X		X	B	X		X	X
Hershberger Mt.			X				X			X	X	X				X			X		X	X			X	X
Grizzly Peak				X	X		X				X								X							X
Maxwell Butte					X						X								X	X	X			X		X
Little Nash Cr.											X								X					X		X
Hogg Rock																										
Hoodoo Butte																										X
Sand Mt.																										
Three Sisters	X	X	X	X	X					I	X	I	X				X	X	X	I	X		I	X		X
Crater Lake	X	X	X				X			W	W		X		W	W		X	X	W	E	X	X	W	W	X

	Linnaea borealis longiflora	Symphoricarpos albus laevigatus	Lonicera involucrata	Lonicera utahensis	Lonicera conjugialis	Valeriana sitchensis	Plectritis congesta	Marah oreganus	Githopsis specularioides	Campanula prenanthoides	Campanula scouleri	Campanula rotundifolia	Chrysothamnus nauseosus albicaulis	Haplopappus bloomeri	Haplopappus hallii	Haplopappus whitneyi	Haplopappus greenei	Solidago canadensis salebrosa	Aster alpigenus	Aster foliaceus frondeus	Aster radulinus	Aster shastensis glossophyllus	Aster ledophyllus	Aster gormanii	Erigeron cascadensis	Erigeron aliceae
Monument Peak	X	X				X					X				A					X			X			X
Bachelor Mt.	X	X				X					X				X								X			X
Three Pyramids		X				X									X											X
Crescent Mt.	X	X				X																				X
Echo Peak	X	X													X			X		X	X		X			
South Peak		X				X									X											X
Cone Peak		X				X					X				X			X		X	X		X			X
Iron Mountain	X	X				X					X		X		X			X		X	X		X	X		X
Browder Ridge						X									X								X			X
Jumpoff Joe	X	X				X					X															
Squaw Peak						X					X															
Twin Buttes	X	X				X					X				X			X								X
Carpenter Mt.		X				X																	X			X
Tidbits Mt.	X	X				X					X	X			X										X	
Lookout Mt.	X	X				X																				
Frissell Pt.	X	X				X					X				X					X						X
Castle Rock	X	X					X	X	X		X															
O'Leary Mt.		X				X			X		X				X										X	X
Horsepasture Mt.	X	X				X					X				X											X
English Mt.		X				X					X															
Lowder Mt.		X		X		X					X				X				X							X
Tipsoo Butte						X					X														X	
Olallie Mt.	X	X				X					X															X
Rebel Rock	X	X			X	X	X		X		X		X		X					X	X		X		X	X
Indian Ridge	X					X																				
Sardine Butte																									X	
Huckleberry Mt.											X														X	
Bohemia Mt.(reg.)	B	X		B	X	X		B		B	X				X						X		X		X	X
Hershberger Mt.	X			X		X				X	X			X	X	X									X	X
Grizzly Peak	X	X				X					X			X			X									X
Maxwell Butte	X	X		X							X			X			X			X			X			
Little Nash Cr.	X																X									
Hogg Rock																										
Hoodoo Butte			X																X			X	X			
Sand Mt.																	X					X				
Three Sisters	X	X	X	X	X	X					X	X		X			X	I	X	X	I	I	X			X
Crater Lake	E	W	X	E	X	X				E	W		X	X				X				X	X		X	X

	Erigeron compositus glabratus	Erigeron foliosus confinis	Erigeron acris debilis	Conyza canadensis	Gnaphalium microcephalum thermale	Anaphalis margaritacea	Antennaria racemosa	Antennaria rosea	Adenocaulon bicolor	Rudbeckia occidentalis	Helianthus cusickii	Madia gracilis	Madia exigua	Eriophyllum lanatum	Achillea millefolium lanulosa	Matricaria matricarioides	Chrysanthemum leucanthemum	Artemisia ludoviciana latiloba	Artemisia tridentata	Petasites frigidus palmatus	Luina stricta	Arnica parryi	Arnica latifolia	Arnica longifolia	Arnica diversifolia	Arnica cordifolia
Monument Peak						X	X	X	X	X			X	X	X		X			X			X		X	
Bachelor Mt.		X				X	X	X		X	X			X	X		X	X			X				X	X
Three Pyramids		X				X	X	X	X	X			X	X	X			X		X			X			
Crescent Mt.						X	X	X	X	X				X	X			X		X	X		X			
Echo Peak								X		X			X		X		X	X			X					
South Peak						X		X	X					X	X			X			X		X			
Cone Peak						X	X	X	X	X				X	X		X	X			X	X	X		X	
Iron Mt.		X			X	X	X	X	X	X		X		X	X		X	X			X		X			
Browder Ridge	X	X				X	X	X	X	X				X	X		X	X			X		X			
Jumpoff Joe					X	X		X	X						X		X						X			
Squaw Peak						X				X													X			
Twin Buttes		X				X	X		X	X				X	X								X			
Carpenter Mt.						X	X	X		X				X	X			X			X		X			
Tidbits Mt.		X				X	X	X	X					X									X			
Lookout Mt						X		X	X					X	X					X			X			
Frissell Pt.		X				X		X	X					X	X								X			X
Castle Rock		X			X	X	X	X	X			X	X		X											
O'Leary Mt.		X				X	X	X				X		X									X			
Horsepasture Mt.		X				X	X	X	X	X				X	X			X		X		X	X			
English Mt.		X				X	X	X	X	X												X	X			
Lowder Mt.		X				X		X		X				X									X			
Tipsoo Butte							X	X							X							X	X			
Olallie Mt.						X	X	X	X	X					X											
Rebel Rock		X		X		X	X	X	X	X		X	X	X	X				X			X	X			
Indian Ridge					X	X	X	X				X			X					X						
Sardine Butte		X					X	X		X							X									
Huckleberry Mt.		X					X	X	X							X							X			
Bohemia Mt.(reg.)		X				X	X	X	B						X			X			X	X	X		X	X
Hershberger Mt.		X			X	X		X	X	X				X									X	X		
Grizzly Peak						X	X		X						X						X		X			
Maxwell Butte			X			X			X						X						X		X			
Little Nash Cr.						X	X	X																		
Hogg Rock					X																					
Hoodoo Butte						X																	X			
Sand Mt.					X																					
Three Sisters			I			X		X	X					X	X		X						I		I	I
Crater Lake	X	E	W		X	X	W	X	X	W		E		W	X		X	E	E	X		X		X		W

	Senecio sylvaticus	Senecio jacobea	Senecio harfordii	Senecio triangularis	Senecio integerrimus exaltatus	Cirsium vulgare	Cirsium centaurea	Hypochaeris radicata	Taraxacum officinale	Microseris nutans	Nothocalais alpestris	Agoseris aurantiaca	Agoseris grandiflora	Agoseris heterophylla	Hieracium albiflorum	Hieracium scouleri	Crepis acuminata	Crepis occidentalis
Monument Peak	X	X		X		X	X	X	A			X			X	X		
Bachelor Mt.					X		X					X	X		X	X		
Three Pyramids				X			X								X	X		
Crescent Peak				X	X		X		X	X								
Echo Peak					X		X		X	X				X	X	X		
South Peak					X		X								X	X		X
Cone Peak				X	X		X		X	X		X	X		X	X		X
Iron Mt.			X	X	X		X		X	X		X	X		X	X		X
Browder Ridge				X	X		X					X	X		X	X		X
Jumpoff Joe				X			X	X					X		X			
Squaw Peak				X											X			
Twin Buttes			X	X			X								X	X		
Carpenter Mt.				X	X		X		X						X	X		
Tidbits Mt.			X	X			X								X	X		
Lookout Mt.							X								X			
Frissell Pt.		X	X	X	X		X	X		X			X		X	X		
Castle Rock			X			X	X							X	X			
O'Leary Mt.				X	X		X			X				X	X	X		
Horsepasture Mt.			X	X	X	X	X			X			X	X	X	X		
English Mt				X	X								X		X	X		
Lowder Mt.				X	X		X		X	X			X	X	X	X		
Tipsoo Butte					X		X			X		X	X		X			
Olallie Mt.				X	X		X				X	X	X		X	X		
Rebel Rock	X	X		X	X		X			X			X	X	X	X	X	
Indian Ridge				X			X		X	X					X	X		
Sardine Butte				X	X										X	X		
Huckleberry Mt.					X		X								X	X		
Bohemia Mt.(reg.)			X	X	X		X	B		X		X	X		X	X	X	X
Hershberger Mt.				X	X		X						X		X	X		
Grizzly Peak				X			X								X	X		
Maxwell Butte				X			X					X	X		X			
Little Nash Cr.				X											X			
Hogg Rock																		
Hoodoo Butte							X					X			X			
Sand Mt.																		
Three Sisters				X	X	I	I	X			X	I		X	X	I		
Crater Lake				X	X			X	W	E	X	X	W		X	X		

APPENDIX B

Introduction

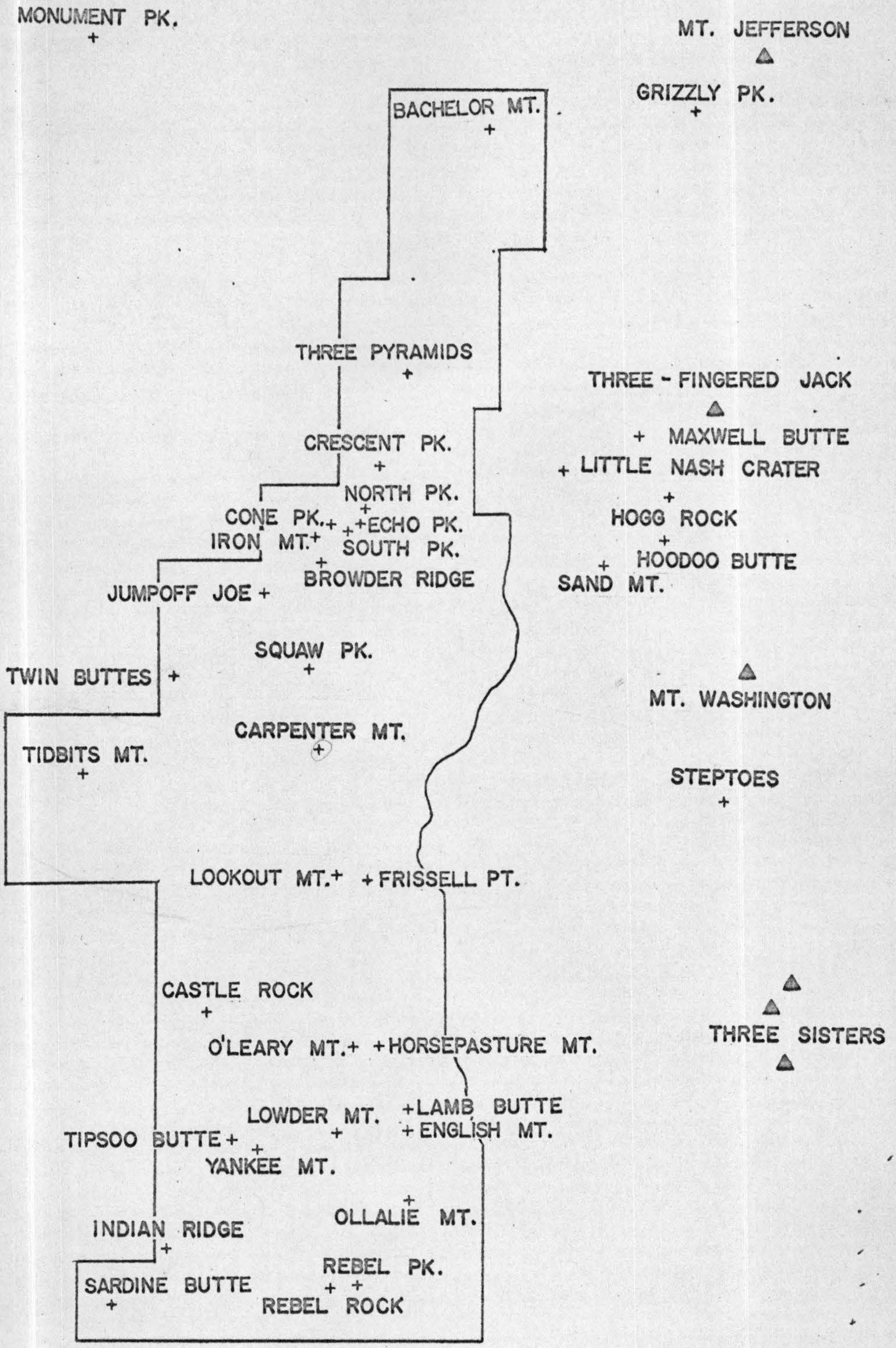
This appendix contains summaries of the taxonomy and ecology of 85 disjunct or endemic Western Cascade species and dot distribution maps of 79 of these species compiled from field, herbarium, and literature searches.

Monographic references have been studied wherever possible. In many cases where no such works are available and where the species seem to comprise well-differentiated taxa, the taxonomic treatment of standard manuals (Hitchcock and others, 1959, 1961, 1964; Cronquist, 1955; Peck, 1961; Munz and Keck, 1959; Jepson, 1925; Abrams, 1940, 1944, 1951; Abrams and Ferris, 1960) is followed. In other instances where taxa seem to be poorly understood, additional taxonomic studies were undertaken on species or larger groups in order to determine and help in the understanding of present distribution patterns.

Families are ordered according to the standard Englerian system to correspond with most manuals and herbaria. The order of genera and species follows Peck (1961), with the exception of the genus Polygonum, where species have been shuffled to achieve a more coherent discussion. References to descriptions of taxa cited in this appendix will not be listed in the bibliography. Synonymies are not complete; only names which are occasionally still used for these taxa occur in the lists of selected synonyms.

Citations of herbarium specimens follow the code of Lanjouw and Stafleu (1964) except for specimens from the Herbarium of the University of Oregon, which are not followed by an herbarium code.

Dot distribution maps contain information from several West Coast herbaria, including those of the University of Oregon (ORE); Oregon State University (OSC); Peck Herbarium, Willamette University (WILLU); Dudley Herbarium, Stanford University (DS); University of California, Berkeley (UC); California Academy of Sciences (CAS); University of Washington, Seattle (UW); Washington State University (WSC); and Crater Lake National Park. Collections by the author from new localities are noted with circles rather than dots. Occasional specimens cited in published literature or previous dot maps are also included. An index map for the peaks of the Cascade Range included in the inset is found immediately following this introduction.



Index Map to Western and High Cascade Range Mountains.

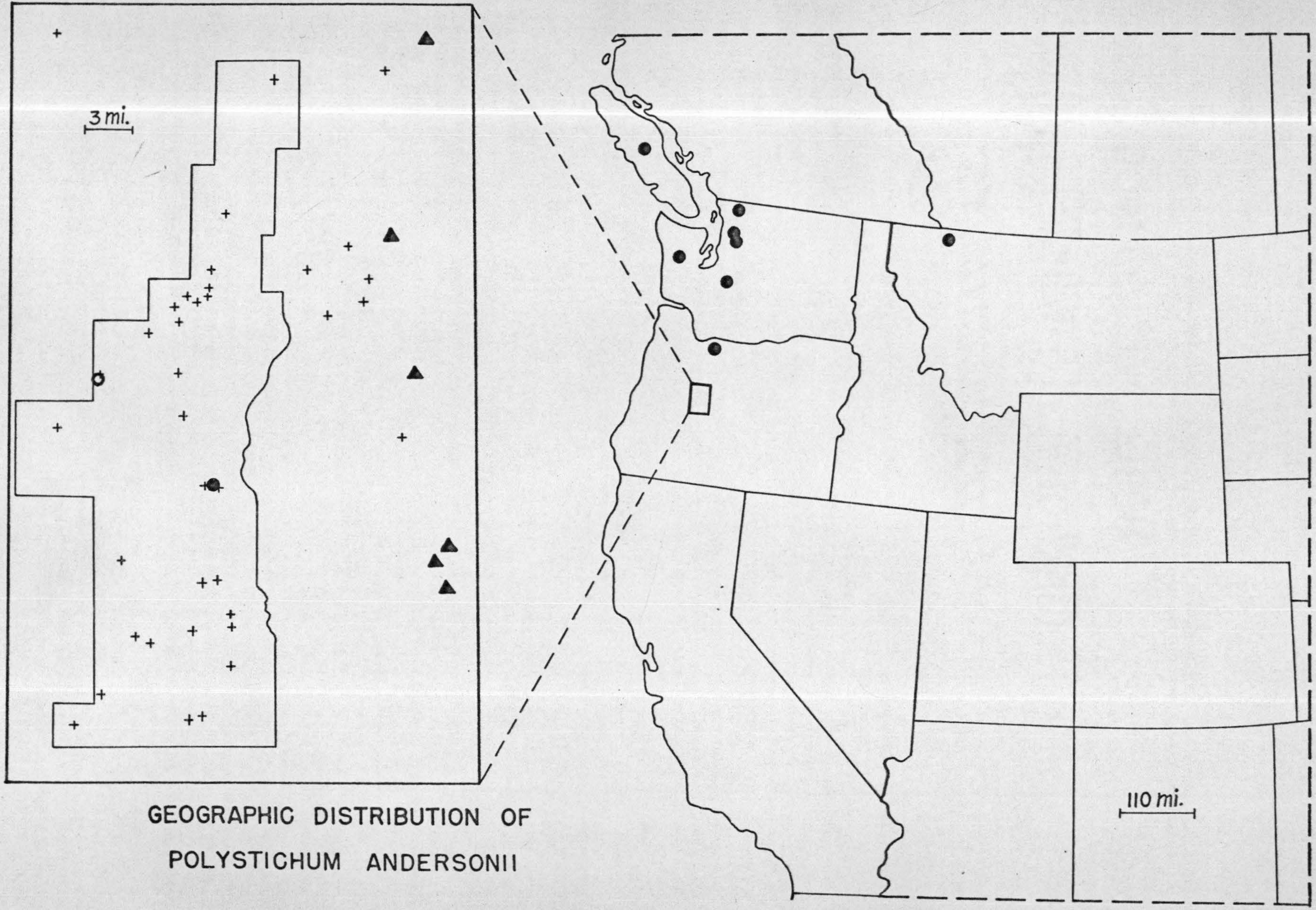
Polystichum andersonii Hopkins, Am. Fern Journ. 3:116, pl. 9. 1913.

Selected synonyms:

Polystichum braunii subsp. *andersonii* (Hopk.) Calder and Taylor, Can. Journ. Bot. 43:1388. 1965.

This rarely collected species is readily distinguished from other ferns of the Pacific Northwest by its centrally peltate sori and large, doubly-pinnate fronds, the teeth of which are long-awned. It is closely related to *P. alaskense* Maxon, a boreal species; and to *P. californicum* (Eat.) Underw. and *P. dudleyi* Maxon, plants of the Coast Ranges of central California. Originally described from Vancouver Island, the center of distribution of *P. andersonii* seems to be in the northern Cascades of Washington (Thompson, 1931; Abrams, 1923). It has also been collected from Glacier National Park, Montana, and from three sites in the Oregon Cascades, two of which lie within the study area.

A species of rather obvious boreal derivation, *P. andersonii* is often found in wet soil under alder thickets. In the Western Cascades, it is also associated with alder (*Alnus sinuata*), but with a number of other boreal species as well, notably *Chamaecyparis nootkatensis* and *Mertensia bella*. The two Western Cascade localities are at the margins of springs which are wet throughout the summer. Other Wet Meadow species present include *Senecio triangularis*, *Ribes bracteosum*, *Oplopanax horridum*, *Mitella breweri*, *Hydrophyllum fendleri albifrons*, *Montia sibirica*, *Valeriana sitchensis*, and *Veratrum viride*.



GEOGRAPHIC DISTRIBUTION OF POLYSTICHUM ANDERSONII

Cheilanthes siliquosa Maxon, Am. Fern Journ. 8:116. 1918.

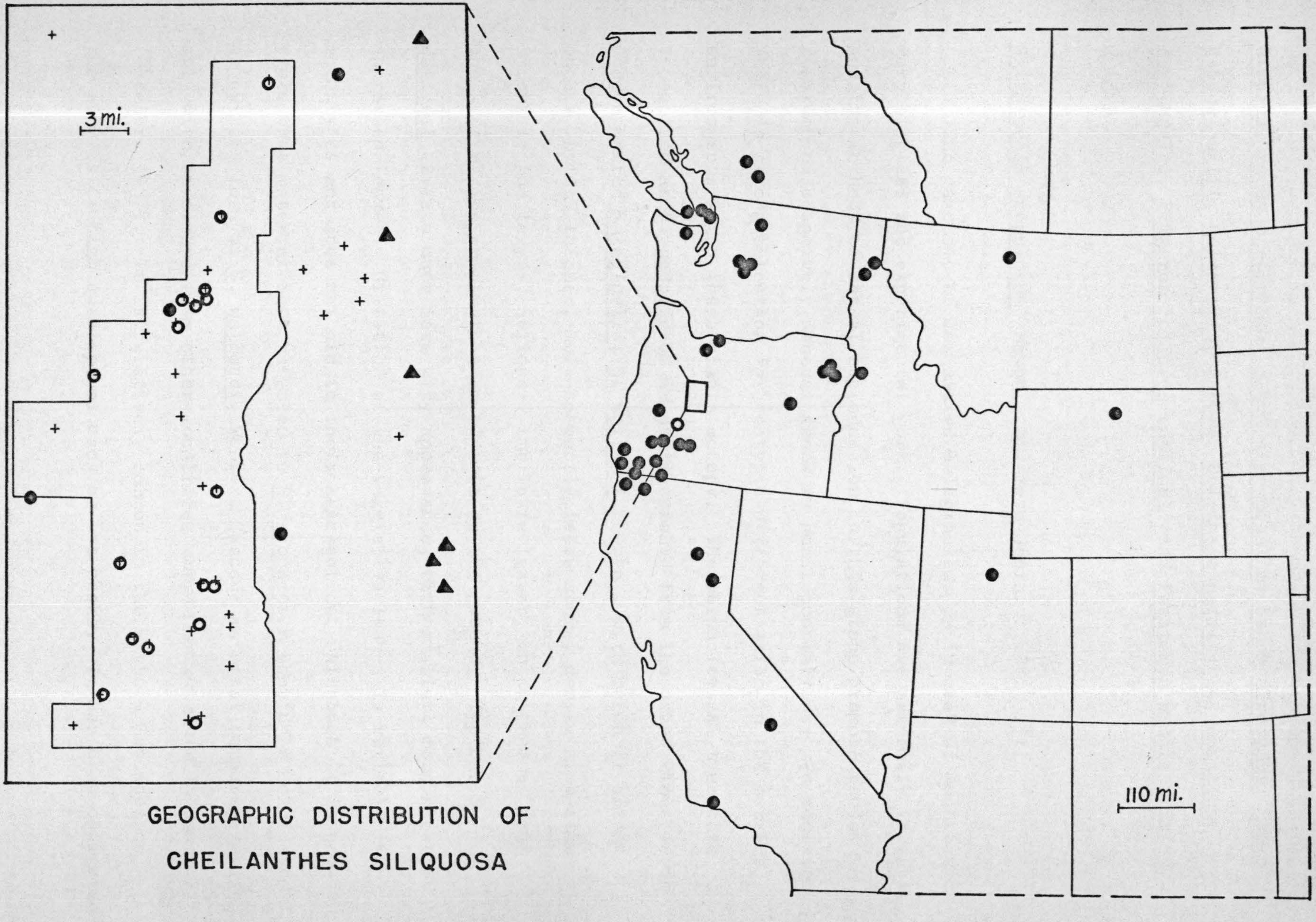
Selected synonyms:

Onychium densum Brack. in Wilkes, U. S. Expl. Exped. 16:120. 1854.

Pellaea densa Hook., Sp. Fil. 2:150, pl. 125. B. 1858.

Cheilanthes siliquosa is immediately recognizable by its small ovate fronds, marginal sori, the inrolled edges of the narrowly lanceolate leathery pinnules, and the lustrous brown stipes. Its center of distribution is in the Klamath Region of southwestern Oregon and northwestern California, where it is typically restricted to serpentine rocks and soils. It also is found in serpentine habitats in the Wenatchee Mountains of central Washington (Kruckeberg, 1964) and in Quebec but occurs in scattered non-serpentine sites throughout much of the Western United States. Evidently this species has responded adaptively to different soil types.

C. siliquosa is common in the Western Cascades, where it grows in light brown rocky loams on steep open slopes. It is typically found under the lower side of a boulder that is creeping down slope. Whether the boulder provides a favorable habitat for the gametophyte or whether the boulder is simply arrested in its downhill slide by the dense root and rhizome system of the fern remains open to question. Other ferns, especially Cheilanthes gracillima and Cryptogramma acrostichoides have been noted under boulders on well stabilized slopes, suggesting that the former hypothesis may be correct. C. siliquosa is also found rooted in crevices of scoriaceous basalt or andesite with such members of the Outcrop Ridge association as Delphinium menziesii pyramidale, Castilleja

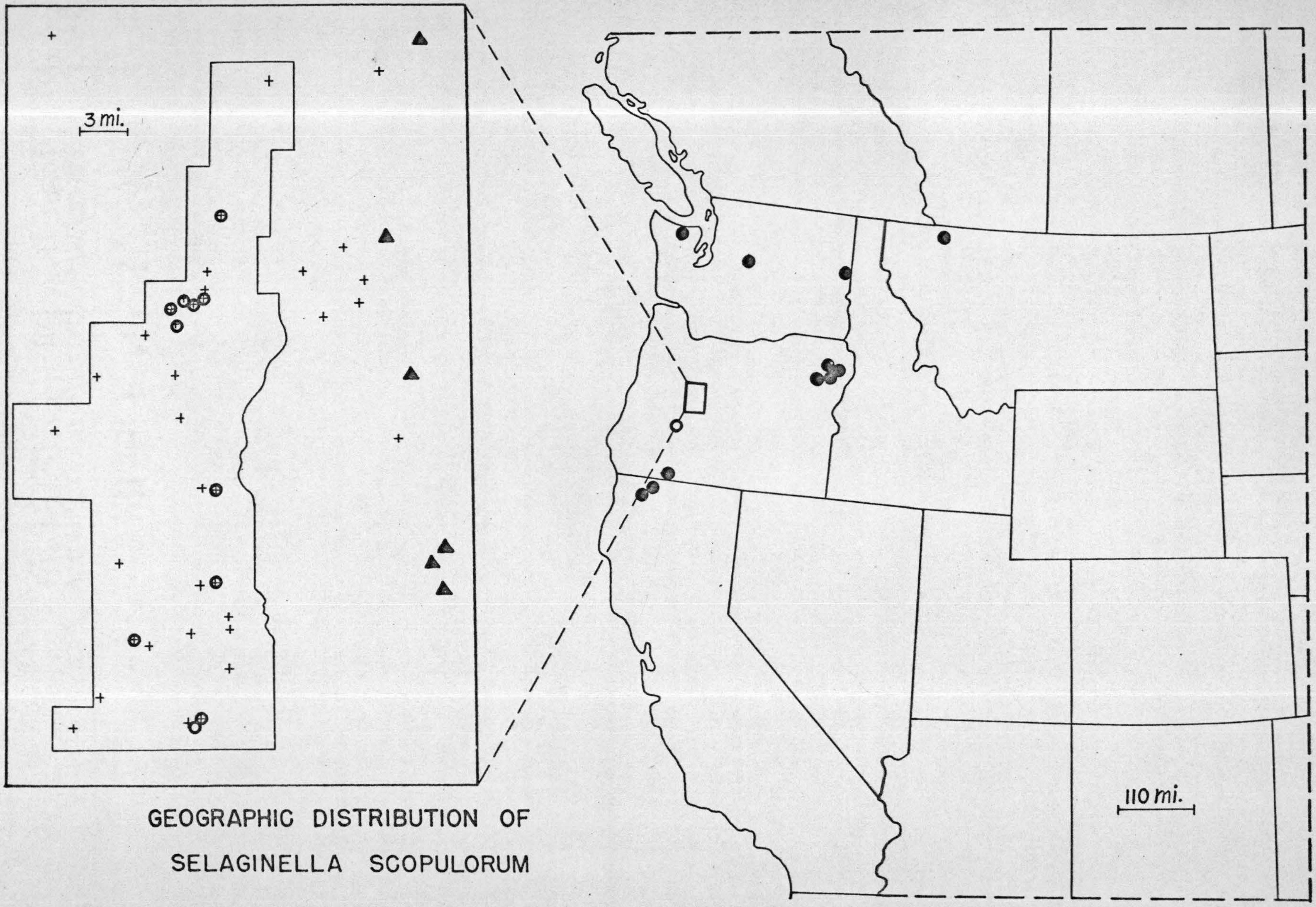


GEOGRAPHIC DISTRIBUTION OF
CHEILANTHES SILIQUOSA

hispida, *Sedum oregonense*, *Sedum stenopetalum*, *Sedum divergens*, *Haplopappus hallii*, *Calochortus lobbii*, *Collinsia parviflora*, *Lomatium martindalei*, *Erigeron foliosus confinus*, and *Penstemon procerus brachyanthus*.

Selaginella scopulorum Maxon, Am. Fern Journ. 11:36. 1921.

The taxonomy of low matted selaginellas is in need of much basic morphological and experimental work. Populations are extremely variable, and the methods of sexual reproduction in this group promote random fixation of adaptively neutral genes in small populations. In addition, there is strong selection for ecotypic differentiation in the extreme environments which these plants occupy. The morphological type here recognized as *S. scopulorum* is distinguished from the other widespread Oregon matted *Selaginella*, *S. wallacei* Hieron., with which it often occurs, by its thicker, more compactly leafy stems; dense, club-like strobili; and larger, obliquely imbricate leaves, which bend up from the side of the prostrate stem closest to the ground. Typical *S. wallacei* gives a much more wiry appearance, with smaller, more closely appressed leaves. Ciliation of the vegetative leaves is variable in both types and does not aid in their segregation. Although it is possible that material here referred to *S. scopulorum* should be considered an extreme form of *S. wallacei*, Western Cascade material compares favorably with specimens from other localities annotated or cited by Maxon (Wheeler, 1937). It is relatively common in the Western Cascades on the summits or high outcrops of many of the peaks. It has been collected



GEOGRAPHIC DISTRIBUTION OF SELAGINELLA SCOPULORUM from scattered localities in much of northwestern North America, especially the Rocky Mountains, but in Oregon, specimens have heretofore been taken only from the Wallowa Mountains and the Siskiyou region.

All of the matted selaginellas are pioneer species with mosses and lichens on nearly bare rock. They are most abundant where outcrops are close to the surrounding ground level or are otherwise disposed to afford some protection from drying winds. Few other plants besides moss species are associated with Selaginella in the Western Cascades.

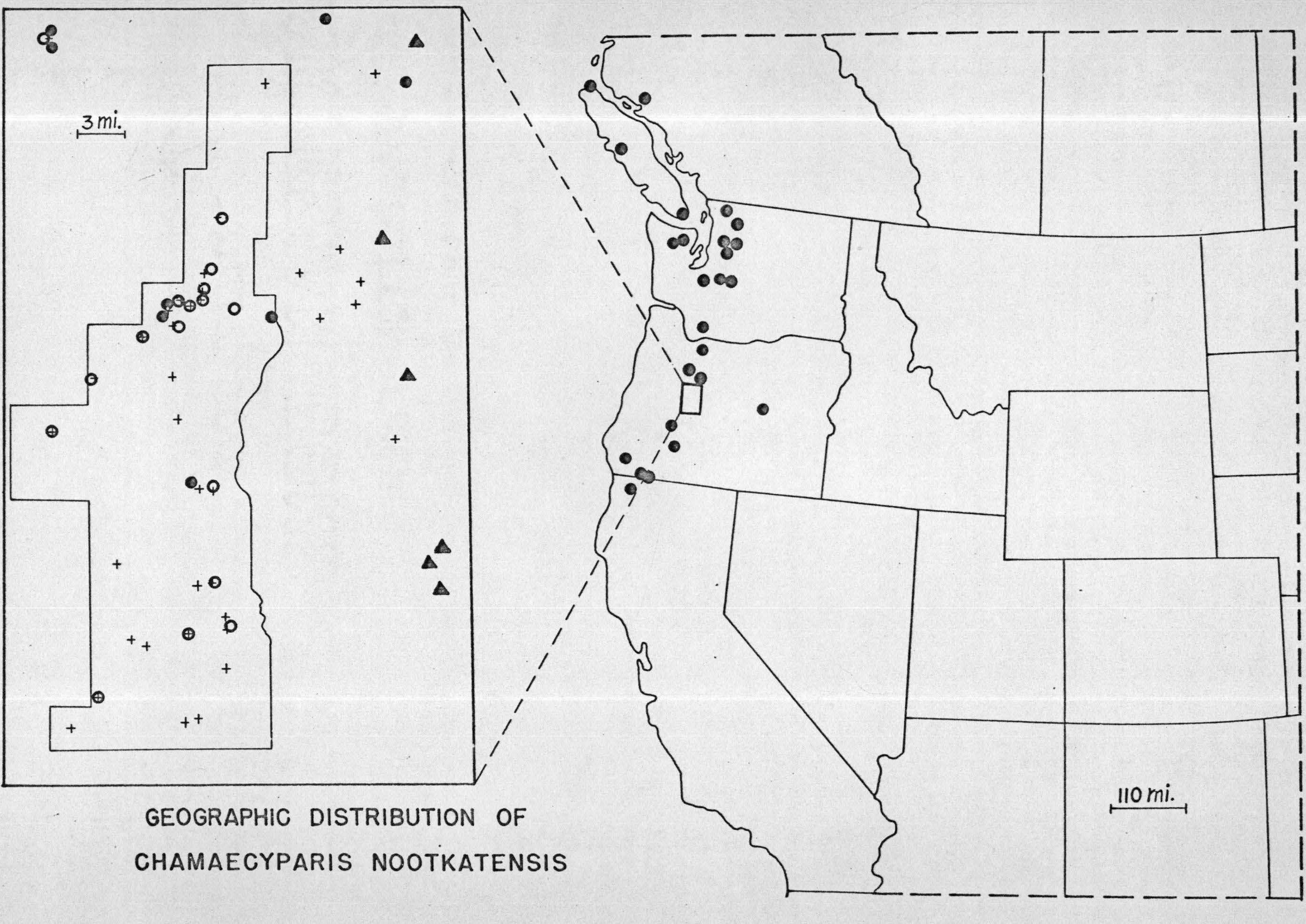
Pinus ponderosa Dougl. in Lawson, Agric. Man. 354. 1836.

In the Pacific Northwest Pinus ponderosa is mostly restricted to a narrow, horseshoe-shaped band around the edge of the intermountain province (Detling, 1968). It is also common in the Siskiyou region of southwestern Oregon, through the Sierra Nevada, and in isolated small stands in the Willamette Valley and Puget Trough. It is the most characteristic tree of the Arid Transition Zone, and typically forms open, park-like forests (Abrams, 1923). Except where it overlaps with P. jeffreyi Murr., ponderosa pine is easily recognized by its reddish platy bark, three-needled fascicles, and sharply pungent cone scales.

Detling (1953) has noted many typical associates of ponderosa pine in "xeric islands" in western Oregon, and finds it difficult to explain the absence of the tree from these areas. There is no reason to assume that the Arid Transition flora would have migrated as a unit, but there are now two localities for native ponderosa pine known from the "xeric islands" in the Western Cascades. One is Iron Mountain, where a single stunted, but old specimen was found growing in fine gravel scree on a southeast-facing slope. The other has been reported by J. F. Franklin (personal communication, 1967) from Frissell Point, where three specimens were found on rocky, south-facing slopes. These occurrences are noteworthy, but no map of the total distribution of *P. ponderosa* is given here.

Chamaecyparis nootkatensis (Lamb.) Spach, Hist. Veg. 11:333. 1842.
Selected synonyms:
Cupressus nootkatensis Lamb., Pinus 2:18. 1824.

Alaska cypress is normally an easily recognizable tree. The small peltate cones; scarcely flattened, slightly rough branchlets; and lack of glands set it off from other members of the Cupressaceae. From a distance it can often be confused with *Thuja plicata* D. Don, which has similar drooping branches and shredding bark. However, in most specimens of *C. nootkatensis* the branch tips curve up again, while those of *Thuja* do not. Alaska cypress is a self-layering species which reproduces vegetatively more often than sexually, occasionally establishing large clones of trunks from a single specimen. All seed collected from this species has failed to germinate even after long periods of stratification. In windswept rocky habitats branches may trail horizontally over the rocks for a distance of 20 m, producing numerous small vertical side branches. In southeastern Alaska the species is found from tidewater to timberline, usually with *Tsuga mertensiana*, and has been known to reach a diameter of 2 m and a height of 40 m, although such stature



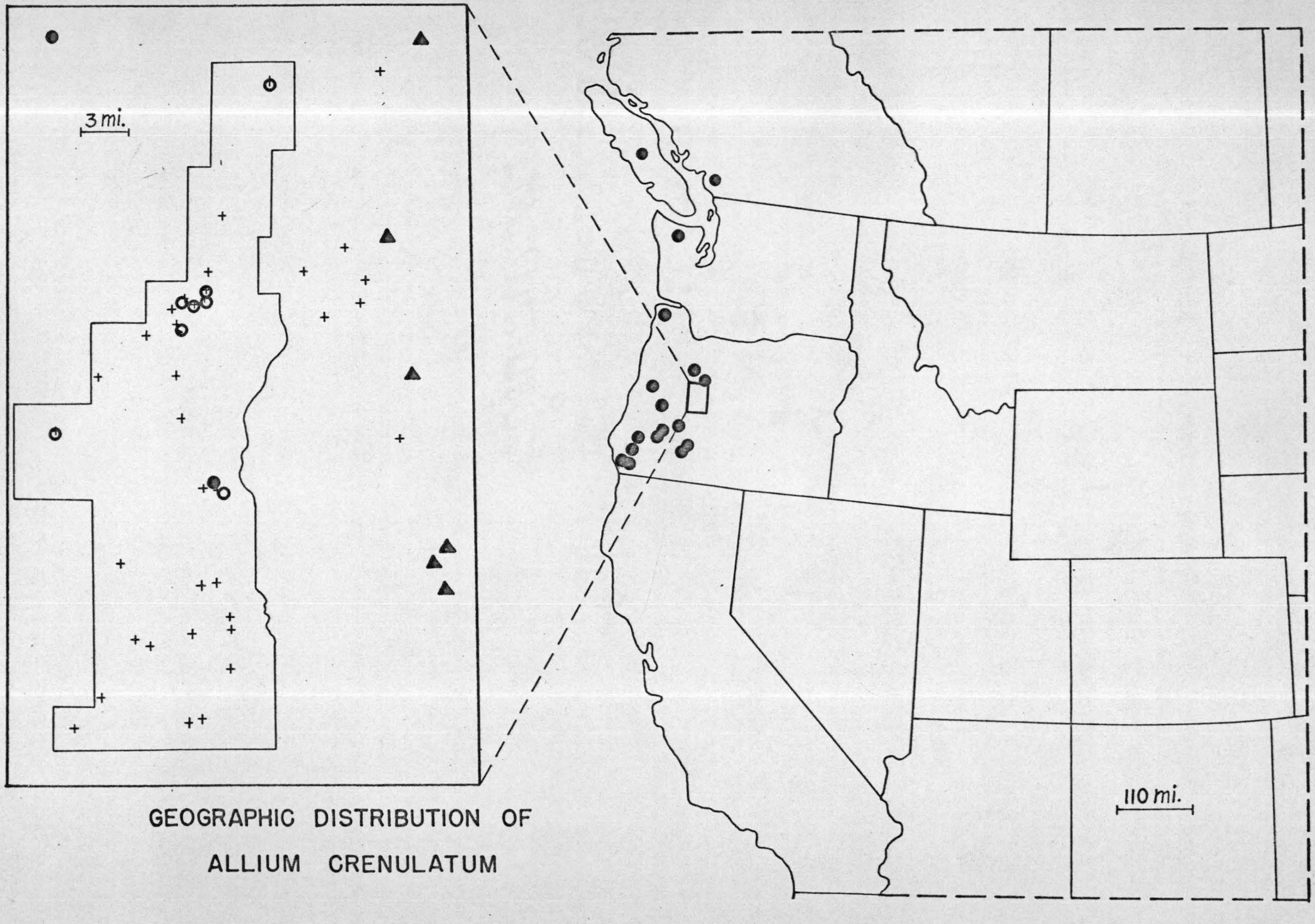
GEOGRAPHIC DISTRIBUTION OF
CHAMAECYPARIS NOOTKATENSIS

is unusual (Heusser, 1960). It ranges from the Kenai Peninsula south along the coast of British Columbia and through the Cascades to the Klamath Mountains of Siskiyou County, California. It is highly disjunct in the southern part of its range, typically occupying exposed, windswept ridges at high altitudes from which other conifers are excluded. Occasional clones are found beneath the Mesic Forest canopy. Populations are scattered but not uncommon in the Western Cascades. Although most trees are rather scrubby, one stand on Twin Buttes contains trees over 1.5 m in diameter and over 30 m in height. The tops were broken out of these trees, which were the largest of any species in the immediate area. A single stand of large trees has been found in eastern Oregon near Fields Peak, Grant County (*Cronquist 7646*: DS).

Allium crenulatum Wieg., Bull. Torr. Bot. Club 26:135, pl. 355. 1899.
Selected synonyms:

Allium cascadense Peck, Proc. Biol. Soc. Wash. 49:109. 1936.
Allium watsonii Howell, Fl. N. W. Am. 1:642. 1902.

Low onions growing on dry barren summits in western Oregon present difficult morphological and taxonomic problems (Ownbey, personal communication, 1968). Typical *A. crenulatum* from the Olympic Mountains and *A. siskiyouense* Ownbey constitute the ends of a north-south cline. Intermediate specimens have been segregated as *A. watsonii* and *A. cascadense*. All of the numerous isolated populations of this complex show some distinctive morphological differences, produced either by local selective factors or by genetic drift. Ownbey, who has examined the author's material from the Western Cascades and has verified their



GEOGRAPHIC DISTRIBUTION OF
ALLIUM CRENULATUM

identification, concludes that the proposed segregates cannot stand as distinct species, or even as varieties, and has broadened the concept of A. crenulatum to accommodate them. A. siskiyouense at present remains a distinct taxon. A. crenulatum is characterized in general by lack of bulbcoat reticulations; two long, flattened leaves which exceed the flowering stem in length and are normally somewhat falcate; and a flattened, somewhat winged upper scape. Closely related species include A. tolmiei, a species restricted to the eastern slopes of the Cascades and eastward.

In the Western Cascades, A. crenulatum is a member of the Fine Gravel Scree association, occupying sites which have abundant moisture during the first part of the growing season but desiccate by midsummer. These are normally open, south-facing slopes which are subject to considerable frost heaving and have little vegetative cover. It is commonly associated with Lotus nevadensis douglasii, Aster gormanii, Trifolium productum, Crepis occidentalis, Ivesia gordonii, Gilia aggregata, Sedum oregonense, and Linanthus harknessii.

Populus tremuloides Michx., Fl. Bor. Am. 2:243. 1803.

Quaking aspen is a characteristic Canadian Zone tree throughout North America. Although taxonomy in Populus is generally difficult due to extensive hybridization, this species is easily recognized by smooth white or yellow bark; oblong-conical capsules; and broadly ovate, finely serrate, small leaves with strongly flattened petioles. It is found along streams and in other moist habitats and is closely related to, but distinct from, P. tremula L. of Eurasia. This species is known from only one population west of the Cascade crest. Thirteen large trees, averaging over 100 years of age, are found in the wet clay loam of Quaking Aspen Swamp, in the French Pete drainage. No map of the total distribution of *P. tremuloides* is given here, but this single locality within the study area is noteworthy. The trees are all of about the same age, although the heartwood of many is rotten, and exact ages cannot be determined. They are not reproducing by seeds, but numerous stunted root sprouts are found around the bases of the trees. The trees are located on somewhat higher ground at the west end of the swamp and are surrounded by such Mesic Meadow species as *Mertensia paniculata*, *Senecio triangularis*, *Rubus parviflorus*, and *Rudbeckia occidentalis*. Within a few meters to the east are Wet Meadow species, including *Veratrum viride*, *Ligusticum grayi*, *Mertensia bella*, *Habenaria dilatata*, *Mitella breweri*, and *Kalmia polifolia*.

Populus trichocarpa T. and G. ex Hook., Icon. Pl. 9: pl. 878. 1852.
Selected synonyms:

> *P. balsamifera* L. var. *californica* S. Wats., Am. Journ. Sci. 115:135. 1878.

P. trichocarpa, or black cottonwood, is the western form of *P. balsamifera* L., a characteristic tree of open environments along streams in northeastern North America. Both species have rough yellow-green or gray bark, but *P. trichocarpa* is differentiated from all other closely related poplars by its densely hairy capsules. Widespread throughout western North America, this species is normally confined to lake margins, stream banks, and other sites with abundant moisture. It is especially abundant along the rivers of western Oregon up to elevations of about 450 m. Specimens are not uncommon along the South Fork of the McKenzie River up to 900 m, and one small population has been located in evidently dry, blocky talus of a small, east-facing cirque on Olallie Mountain ridge at more than 1500 m. This group of relatively large trees (about 20 m) was growing with Sambucus callicarpa, Abies procera, Epilobium angustifolium, Actaea rubra, and Anaphalis margaritacea. Although this constitutes a notable entry of a mesic lowland species into the high Western Cascades, no map of the total range of P. trichocarpa is presented here.

Quercus garryana Dougl. ex Hook., Fl. Bor. Am. 2:159. 1838.

The only white oak of the northern half of Oregon is normally restricted to dry habitats in the valleys west of the Cascade Range from Vancouver Island to California. Q. garryana also is found in the Columbia Gorge and north and south from its eastern end to Yakima, Washington, and Warm Springs, Oregon, in the Columbia Basin grassland and juniper scrub (Ornduff and French, 1958). Isolated individuals or small stands of oaks have been discovered in clearings in the Mesic Conifer Forest in the Western Cascades at elevations of about 700 m; the summit of Castle Rock (1150 m) supports a grove of moderate-sized trees (6-10 m); and a population of stunted individuals was discovered near Musick Mine, Bohemia Mountain, southern Lane County, at an elevation of over 1500 m. Although no map of the distribution of Q. garryana is presented in this work, these disjunct occurrences of a common lowland species well into the mountains are noteworthy.

Polygonum spergulariaeforme Meisn. ex Small, Bull. Torr. Bot. Club 19:366. 1892.

Polygonum douglasii Greene, Bull. Cal. Acad. Sci. 1:125. 1885.

Polygonum minimum Wats., Bot. King Exp. 315. 1871.

Polygonum cascadense Baker, Madrono 10:62. 1949.

The genus *Polygonum* is of special interest in this study. It is the most highly diversified genus occurring in the Western Cascades of Oregon: the nine species present include members of three subgenera which are found in markedly different habitats. Both widespread and narrowly restricted species occur together in the Western Cascades. Comparative examination of their biologies is proving of help in interpreting disjunctions and endemism in the area.

Further comments will center on members of the subgenus *Duravia*: small-flowered annuals which are sometimes spring ephemerals, but more often persist into the driest parts of the summer. Anthers often dehisce before the flowers open, indicating modal autogamy. Most species are represented by typical material, but many intermediates are known. This indicates that allogamy and interspecific hybridization occur at frequent intervals. Breeding barriers are primarily autogamy and phenological and ecological differentiation.

The taxonomic problems in *Duravia* attain considerable proportions when considered over the total range of the species involved. Intergrades in as many as five separate directions from a single "species" may occur, clinally connecting species which are perfectly distinct where they coexist in other regions.

Oddly, there are no taxonomic problems in *Duravia* as it is found in the Western Cascades. The various species are here morphologically and often ecologically quite distinct, and few intermediate forms have been observed. The most striking feature of the group in this region is the ability of such closely related species to coexist in small areas. Occasionally four distinct species may be found within one square meter.

Duravia is divisible into relatively coherent groups having approximately the status of sections. Figure 11 presents the author's conception of the composition and inter-relationships of the groups and the species comprising them. Heavier connecting lines indicate more complete morphological intergradation. These groups will be discussed separately in the following pages.

P. spergulariaeforme, which forms a major plexus of intergradation within *Duravia*, is normally found on low rocky or gravelly hillsides at low elevations in the valleys west of the Cascades with other members of the Lowland Xeric Meadow association. It typically blooms after many of its close relatives have set seed and withered, hence the common names "fall knotweed" and "farewell to summer." Flowers are large for this group, often 7 mm in diameter, and are frequently visited by small flies and beetles. *P. spergulariaeforme* is the only species of *Duravia* known by the author to have animal pollinators. This species and *P. majus* (Meisn.) Piper are the only two species in this section with stamens equalling the perianth tube or exserted and are traditionally differentiated only by the abrupt downward flexion of the pedicels shortly after anthesis, a character shared by *P. majus*, *P. douglasii*,

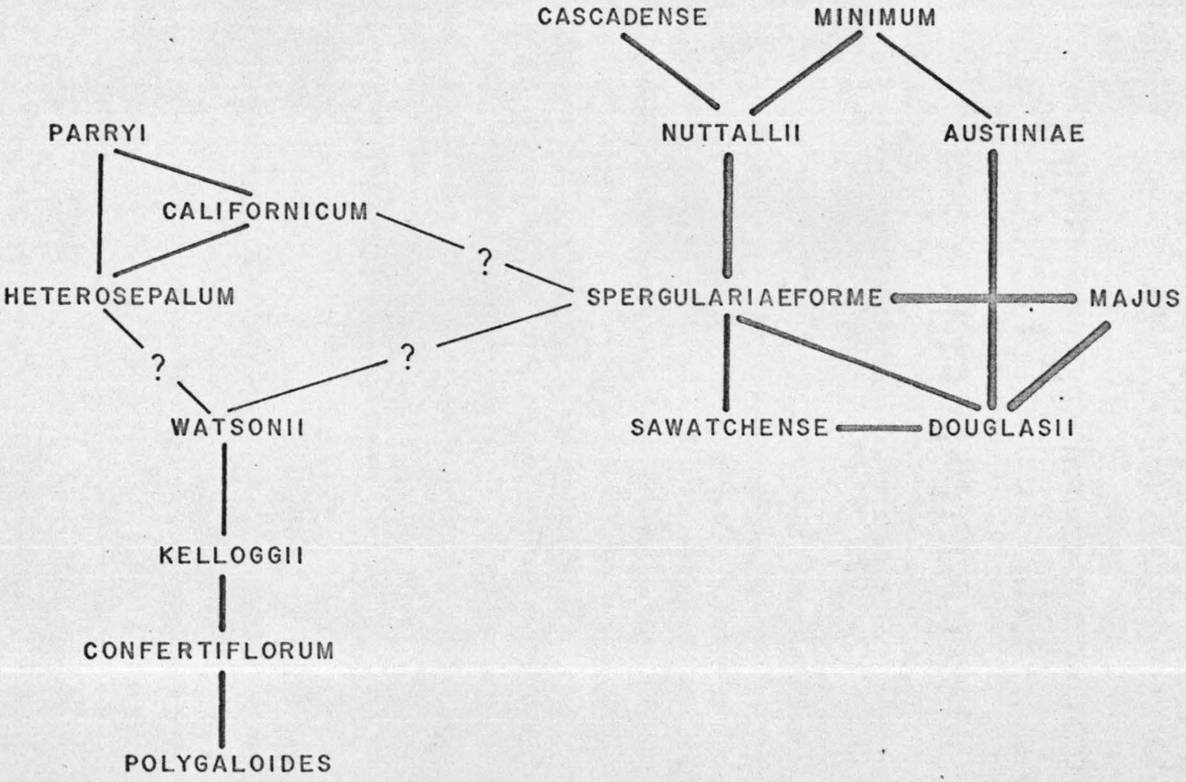


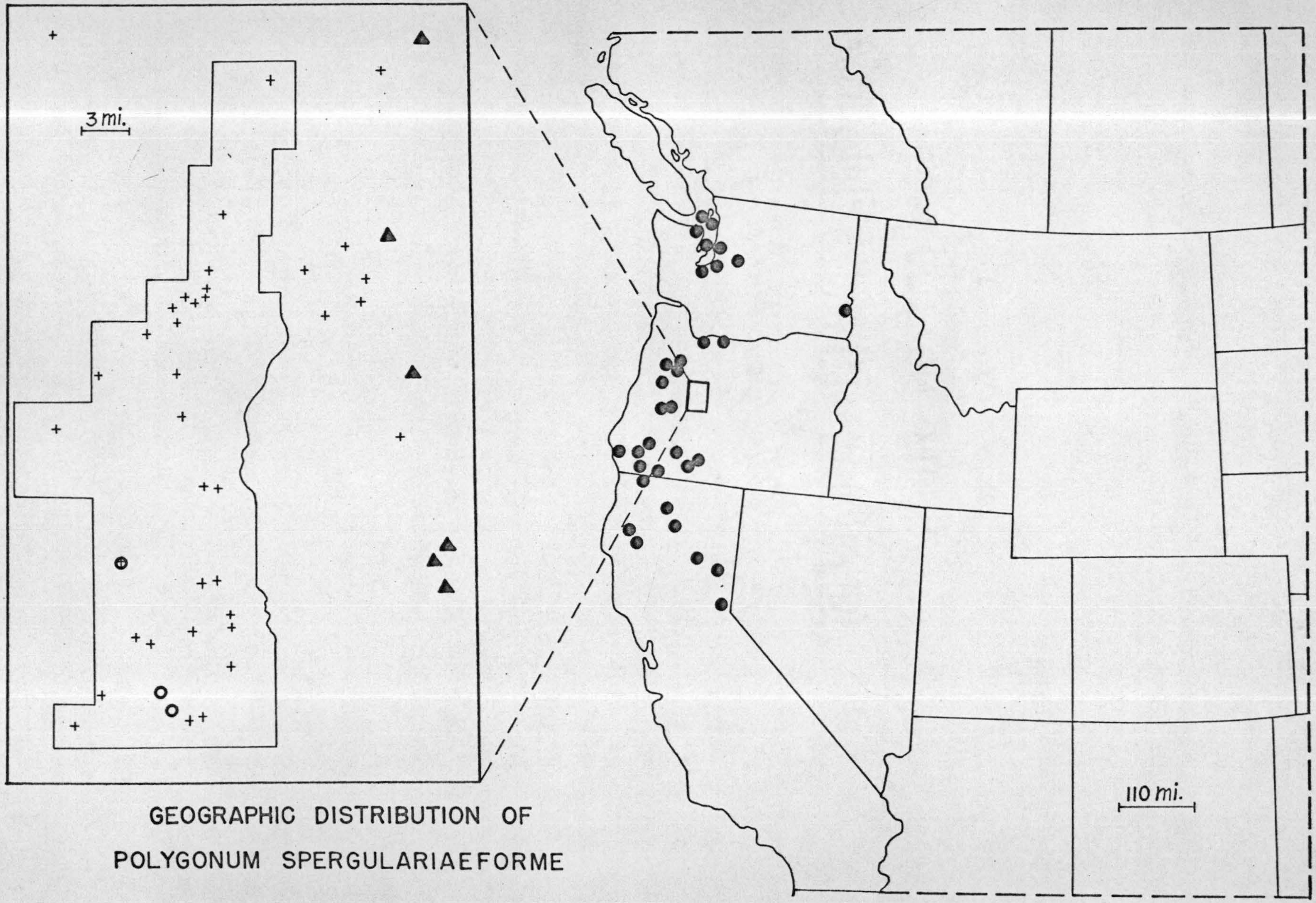
Figure 11. Relationships of Species of Polygonum, Subgenus Duravia (line width indicates degree of relatedness).

and *P. austiniae* Greene. The most recent student of this group has identified specimens with a single reflexed pedicel (and otherwise indistinguishable from *P. spergulariaeforme*) as *P. majus* (Coolidge, 1964). The latter species is normally confined to areas east of the Cascades, but the two co-occur in the Columbia Gorge and the Klamath Mountains of Oregon and California. While concurring with Coolidge that these species should be considered distinct taxa, at least at the subspecific level, I disagree with his manner of segregating them. In this case, phenology and geography must be considered at least as important as the variable morphological trait of pedicel reflexion.

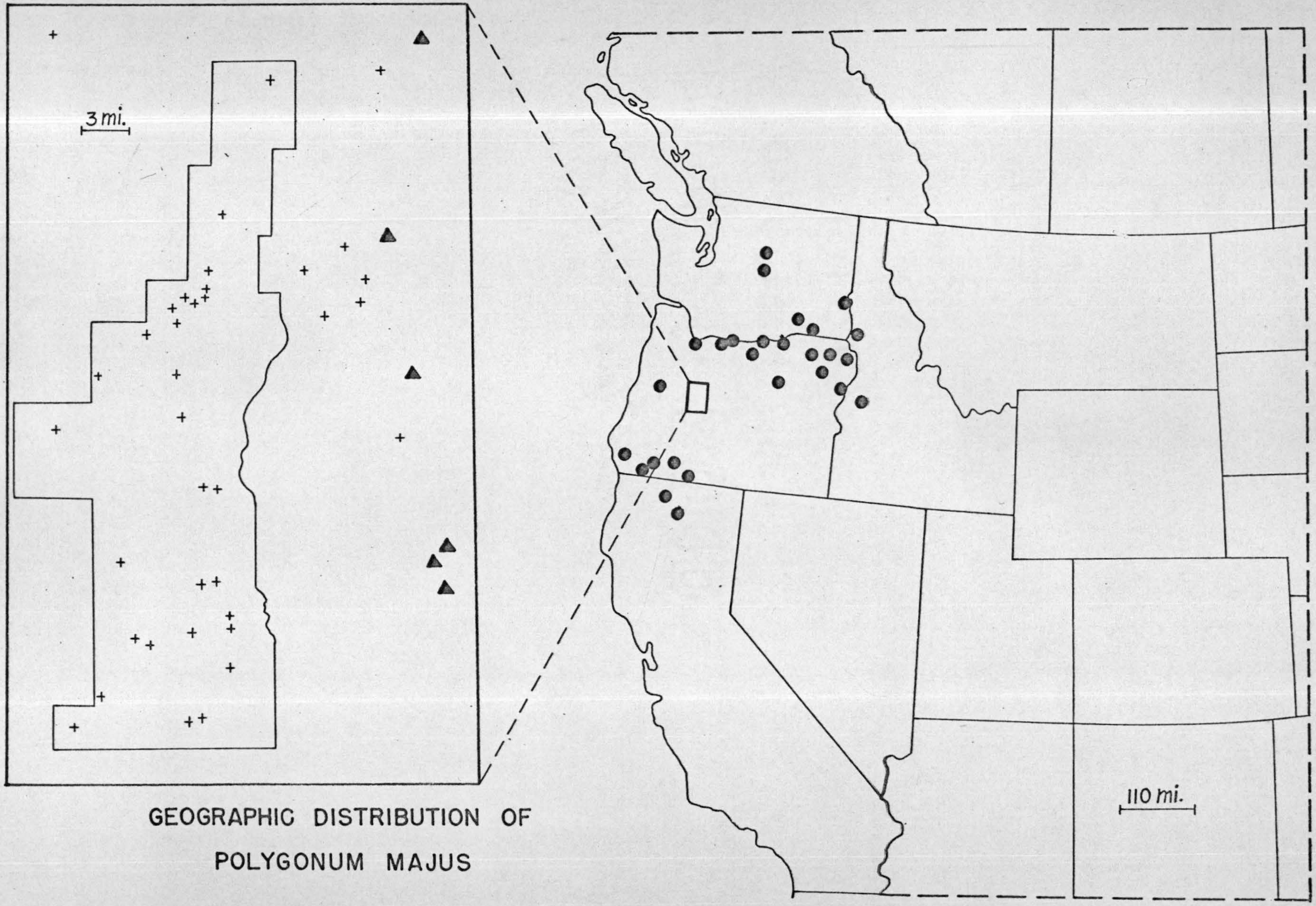
P. spergulariaeforme also merges freely with *P. douglasii*, the most widespread species of *Duravia* and the only member found in the central and eastern United States. The two species are ecologically and phenologically separated where they occur in close proximity in the Western Cascades. One variable series of intermediates between *P. douglasii* and *P. spergulariaeforme*, which ranges through the intermountain regions of the Western United States, has been segregated as *P. sawatchense* Small. Coolidge has proposed a further segregate, *P. triandrous* Cool., for the slightly less widespread three-anthered phase of *P. sawatchense*. The latter species typically has eight anthers, although the present author has discovered a number of specimens having five anthers. Anther number, while important elsewhere, is obviously of dubious taxonomic value in this portion of *Duravia*.

Leaf, flower, and achene size separate *P. douglasii* from *P. majus*. These are variable characters, and the whole range of intermediates is known. Geographical distinctions between these two species are not clear, except that *P. douglasii* is common west of the Cascade crest, while *P. majus* is rare in this region. *P. austinae* has broader leaves than P. douglasii, crowded at the base of the stem, with an almost leafless terminal spike of flowers. It is confined to eastern Oregon in its pure form, but is partially represented in the Western Cascades by material transitional to *P. douglasii* from Bohemia Mountain (*Hickman 0-120*).

In yet another direction, *P. spergulariaeforme* tends toward forms with smaller flowers and leafier stems, the leaves being broader as well as more numerous. These have been segregated as *P. nuttallii* Small, a poorly-collected or rare species that is found through the Cascade region of Washington and Oregon. Although it has not been found in the Western Cascades, its leaf morphology and long internodes indicate that it is a transitional form between *P. spergulariaeforme* and two species which are common there, *P. cascadense* and *P. minimum*. Both are separable from *P. nuttallii* on the basis of leaf form, *P. minimum* having broadly elliptic to almost orbicular leaves, and *P. cascadense* having more narrowly oblanceolate, obtuse, inrolled leaves and more flowers per axil than *P. nuttallii*. *P. minimum* is widespread, occurring in montane habitats throughout the Western United States. It is almost ubiquitous in high elevation moist to dry meadows in the Cascade Mountains. *P. cascadense* is a highly restricted species (Baker, (1949b) presently known only from the region of Crater Lake north to the Echo Mountain ridge in Linn County, and is confined, except for one locality from the southwestern boundary of Crater Lake National Park (*Anderson and Simpson 116*: OSC), to the central Western Cascades of



GEOGRAPHIC DISTRIBUTION OF
POLYGONUM SPERGULARIAEFORME



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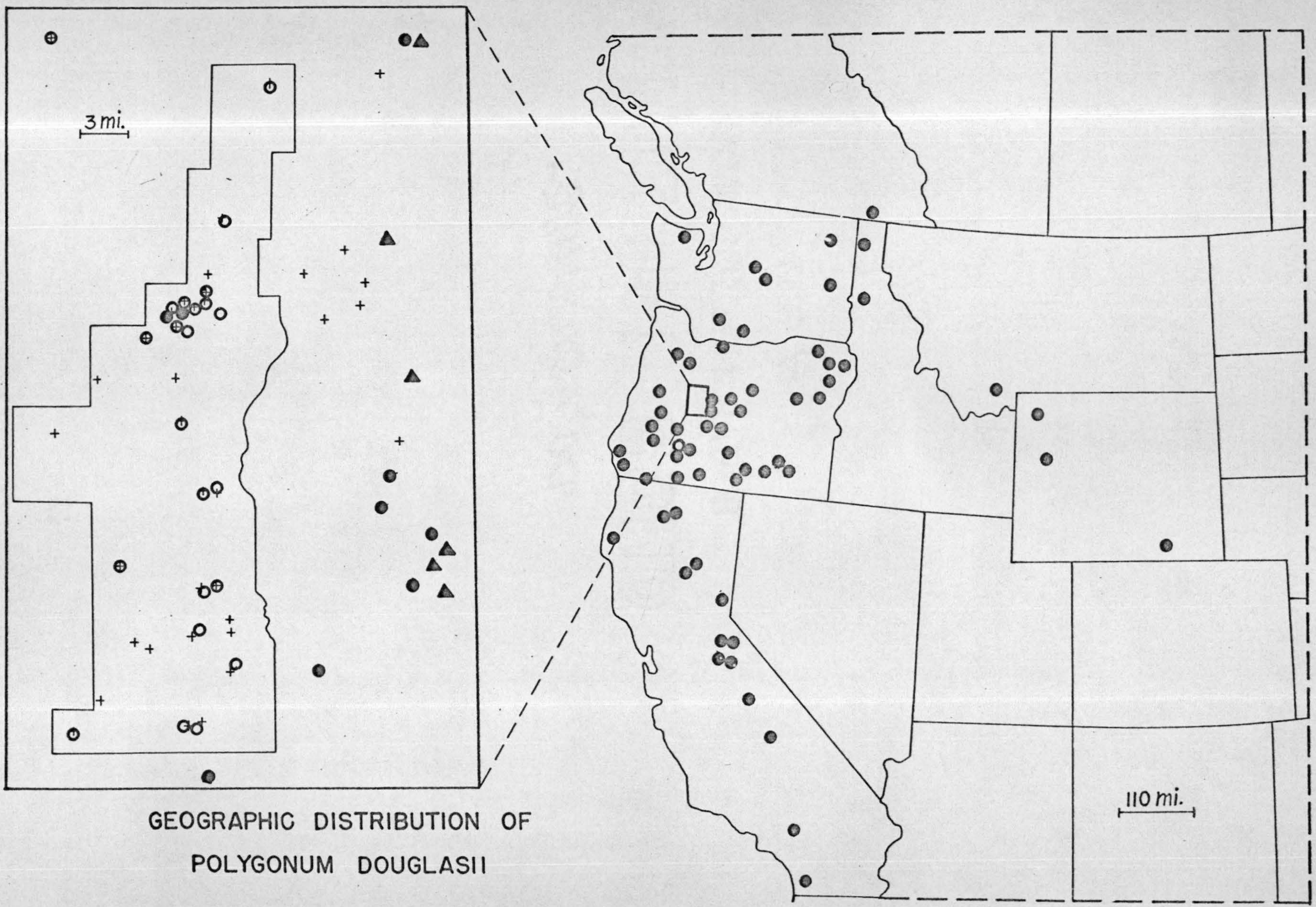

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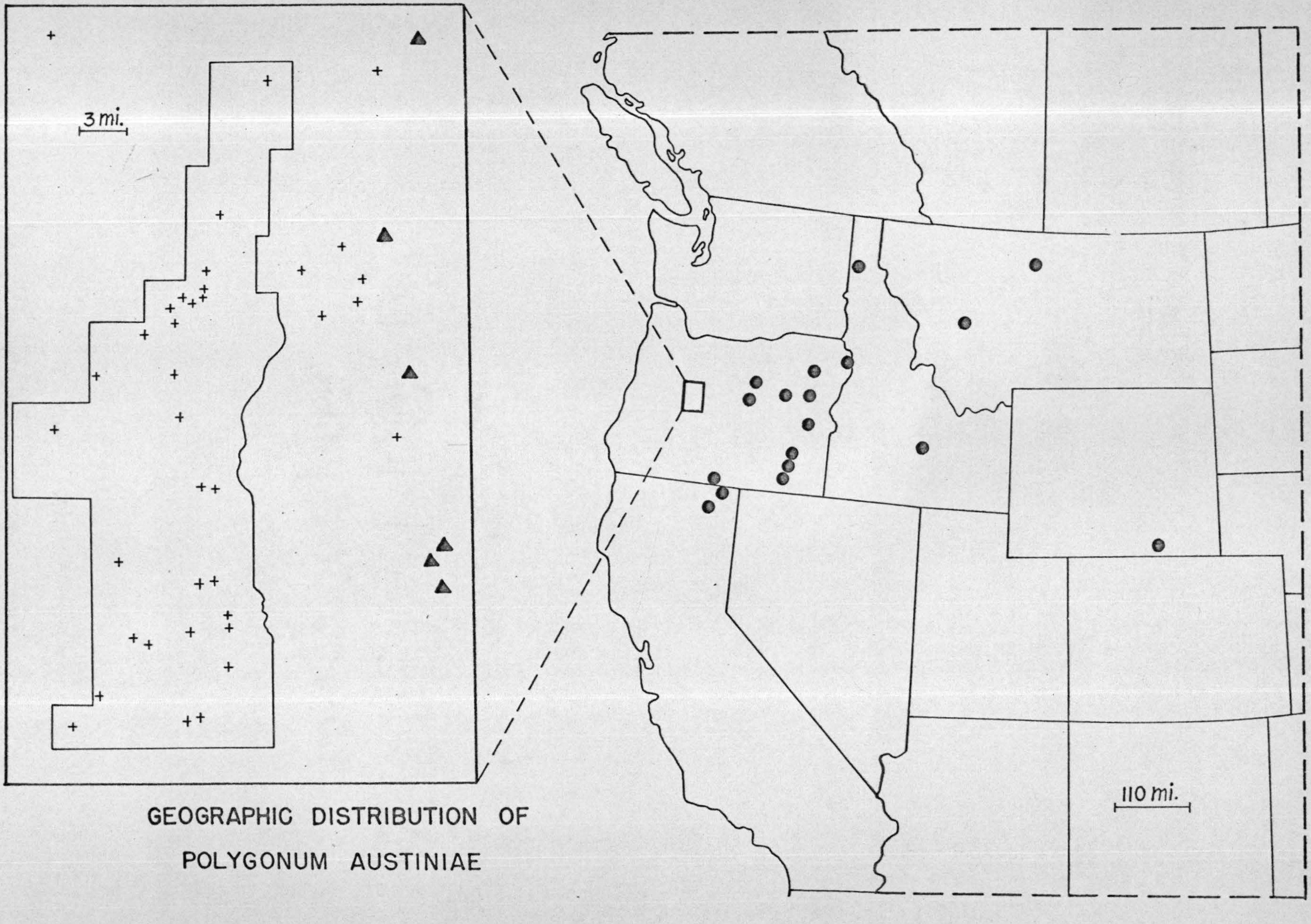

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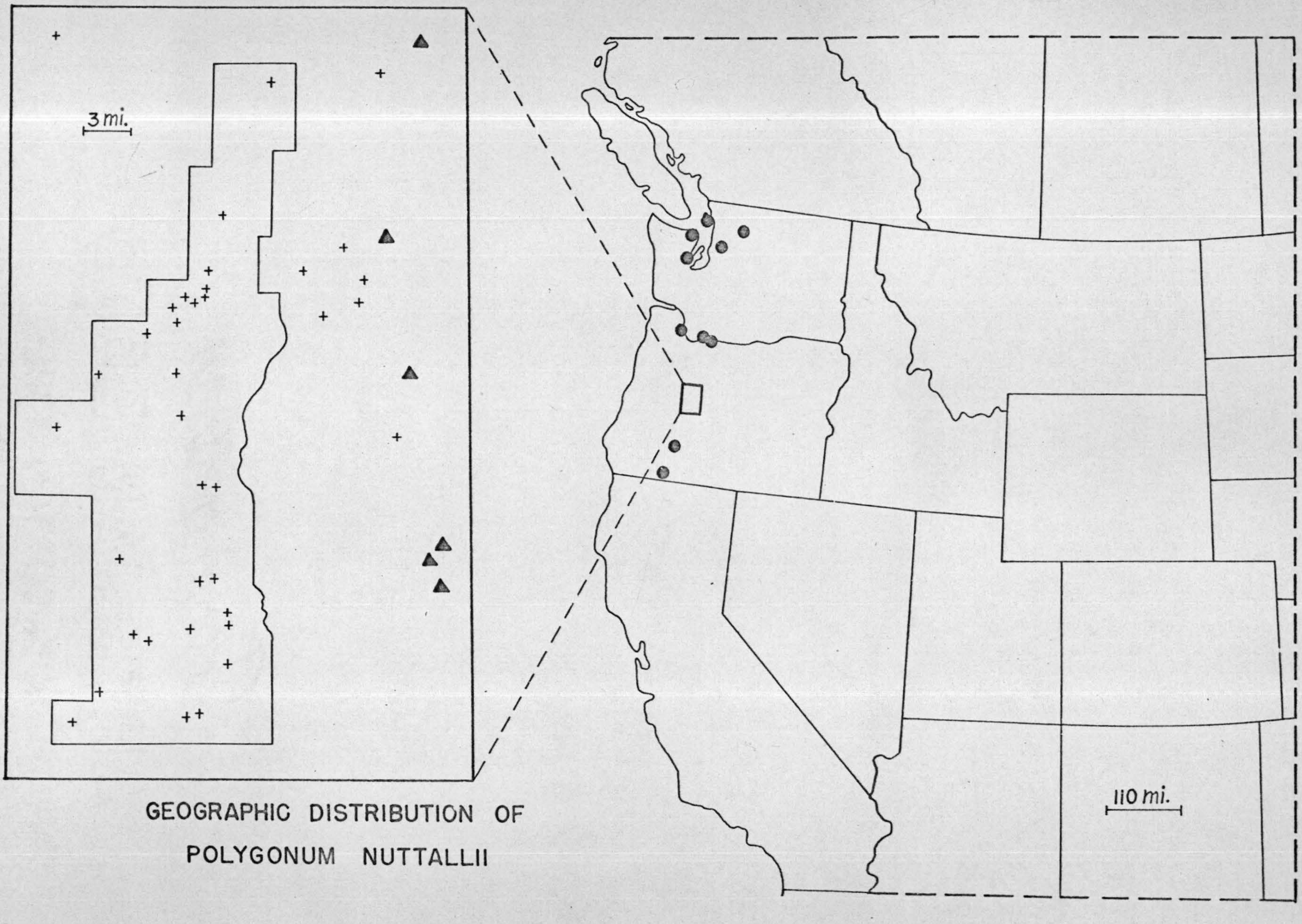
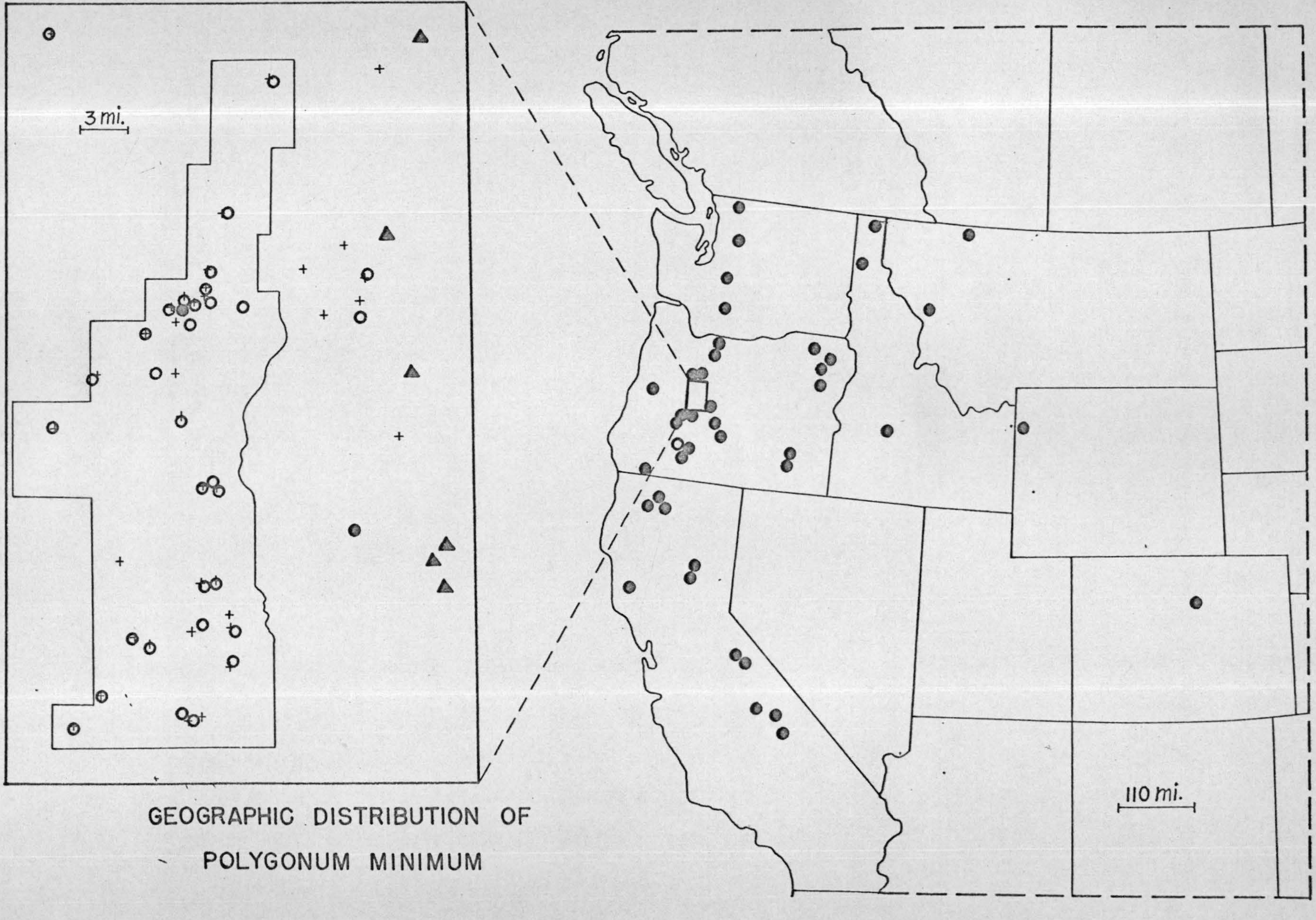
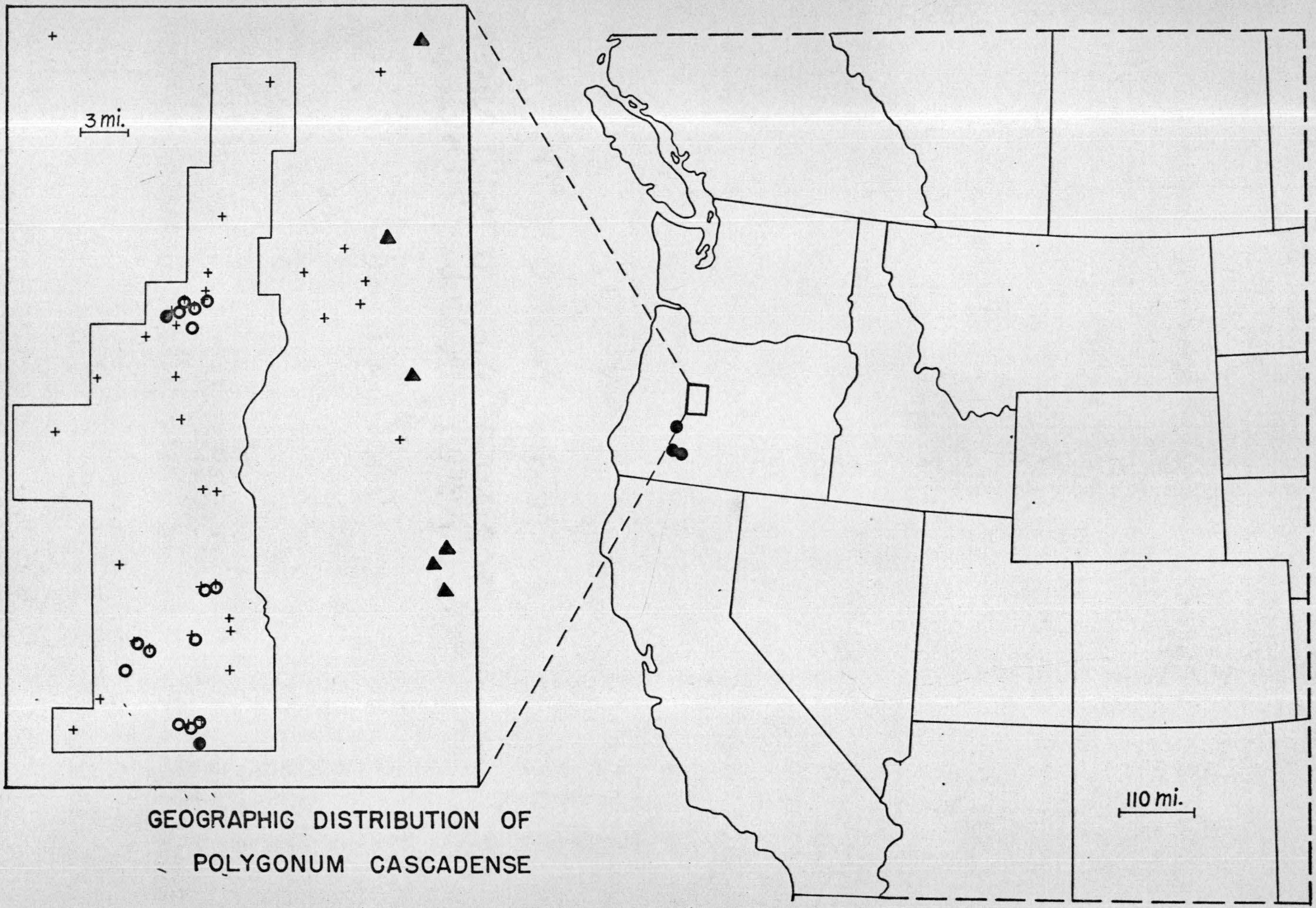
POLYGONUM AUSTINIAE



GEOGRAPHIC DISTRIBUTION OF
POLYGONUM NUTTALLII



GEOGRAPHIC DISTRIBUTION OF POLYGONUM MINIMUM



GEOGRAPHIC DISTRIBUTION OF
POLYGONUM CASCADENSE

Oregon.

In the Western Cascades *P. douglasii*, *P. minimum*, and *P. cascadense* exhibit only subtle ecological differentiation and are frequently found growing together in open rocky spots on southwest-facing meadow slopes between 1400 and 1800 m. Typical coexisting members of the Xeric Meadow association include *Gilia aggregata*, *Collomia linearis*, *Orthocarpus imbricatus*, *Gayophytum diffusum parviflorum*, *Navarretia divaricata*, *Linum perenne lewisii*, *Lupinus arbustus neolaxiflorus*, *Eriogonum nudum*, *Microsteris gracilis*, *Cerastium arvense*, and *Artemisia ludoviciana latiloba*.

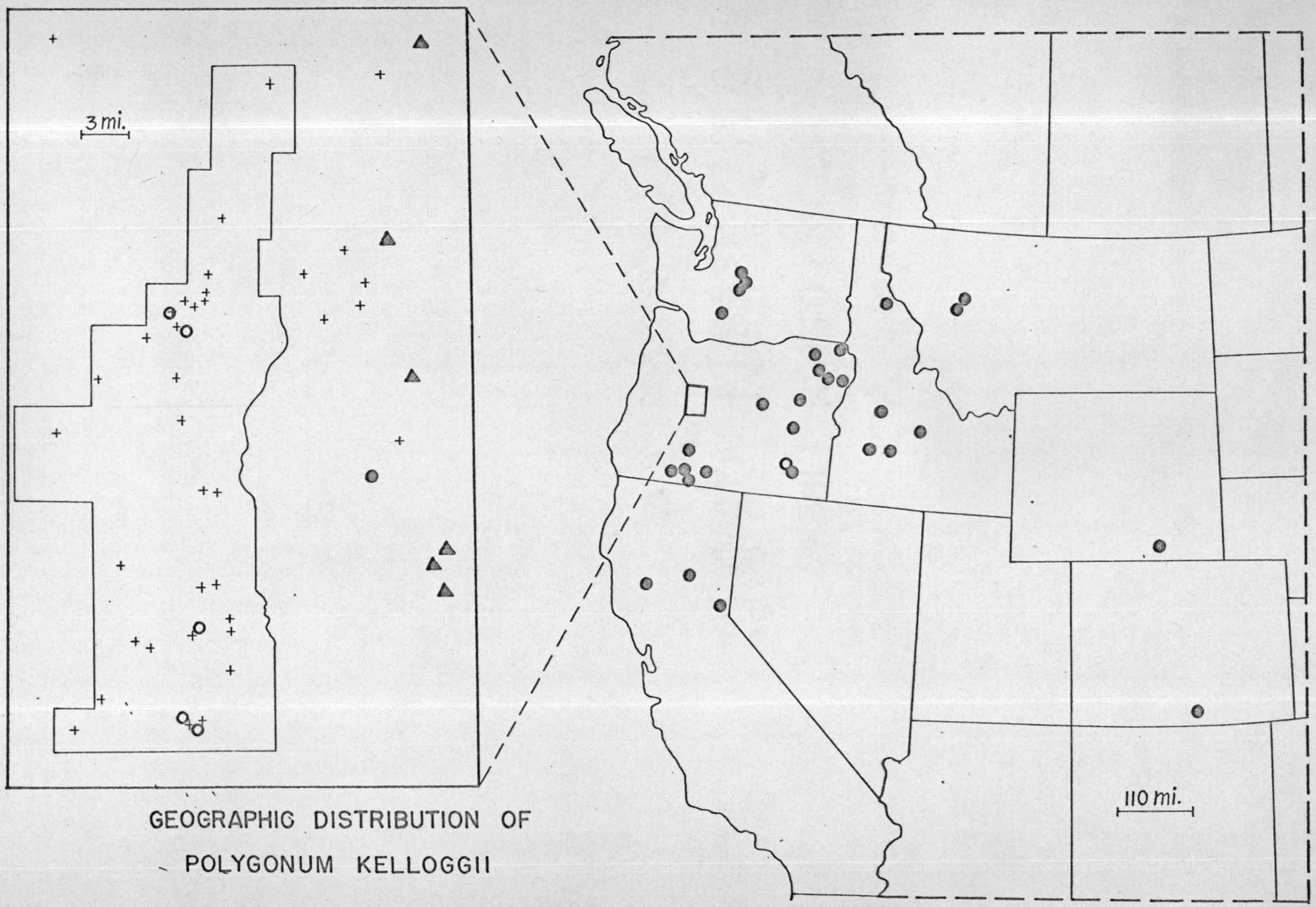
Polygonum kelloggii Greene, Fl. Fran. 134. 1891.

The *Polygonum kelloggii* complex may be an offshoot from the *P. spergulariaeforme* complex, but it obviously forms a relatively distinct and compact grouping within the subgenus *Duravia* and perhaps deserves separate sectional status. *P. heterosepalum* Peck and Ownbey forms a morphological link between *P. watsoni* Small and the group including *P. californicum* Meisn. and *P. parryi* Greene, which lack the distinctive joint at the juncture of stem and leaf which is common to all other species of *Duravia*.

The *P. kelloggii* complex is adapted to vernal pool environments in arid regions. Typically of very small size, individuals mature seed rapidly during the early spring season of abundant moisture and quickly desiccate and disappear as the volume of snowmelt begins to decrease. Several factors, especially localization of vernal pool habitats and autogamy, tend to isolate small populations of these knotweeds even when they occur in the same region. Thus, ecotypic variation and random fixation are likely within the various species. This isolation is not absolute, however, as is evidenced by occasional truly intermediate forms.

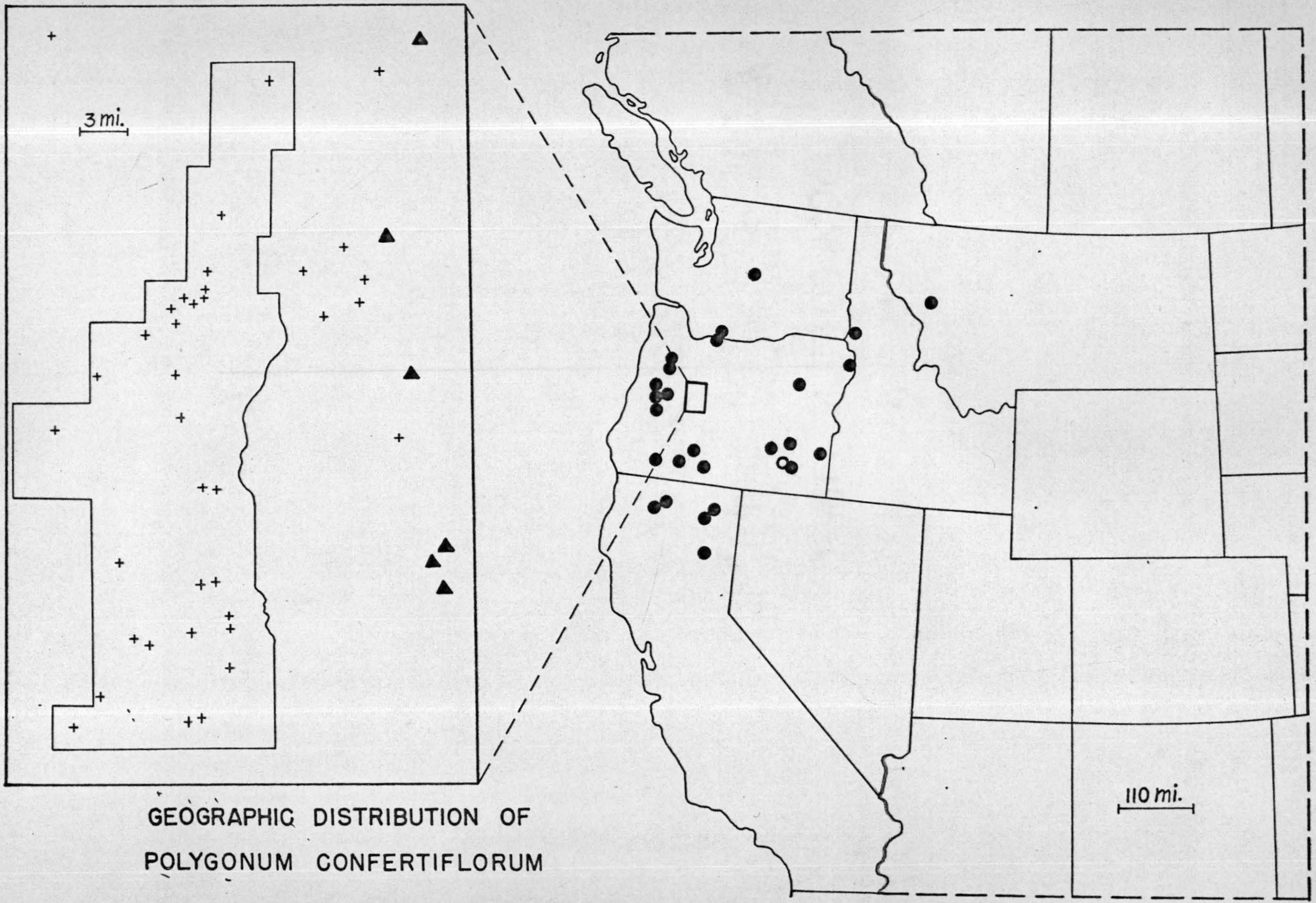
The range of *P. kelloggii* includes much of the Western United States. It has not been reported previously from west of the Cascade crest except for a single specimen from southernmost Oregon and several sheets from Hand Lake, near McKenzie Pass. This species has long been confused with *P. watsonii*, a species with eight anthers and deeply lacerate ochreae, which approaches *P. heterosepalum* and *P. californicum*. Of ten collections formerly labeled *P. watsonii* in the Herbarium of the University of Oregon, one is indeed *watsonii*, seven are *P. kelloggii*, and *P. polygaloides* Meisn. and *P. confertiflorum* Nutt. account for the remaining two. *P. watsonii* is evidently quite distinct, and would not have been so readily confused with other taxa if authors of manuals had more carefully segregated and accurately described morphological types. This confusion is perhaps due to the fact that good material of *P. watsonii* has seldom been collected.

All these species are habitally quite different. Growth habit, leaf and bract shape and color, anther number, and ochrea differences are all useful in segregating them. After studying several thousand sheets of *Polygonum*, the present author has yet to experience grave difficulty in assigning material of this complex to one of the four described species. This statement is not intended to obscure the fact that many of the characteristics are gradational and that the individual



GEOGRAPHIC DISTRIBUTION OF

POLYGONUM KELLOGGII



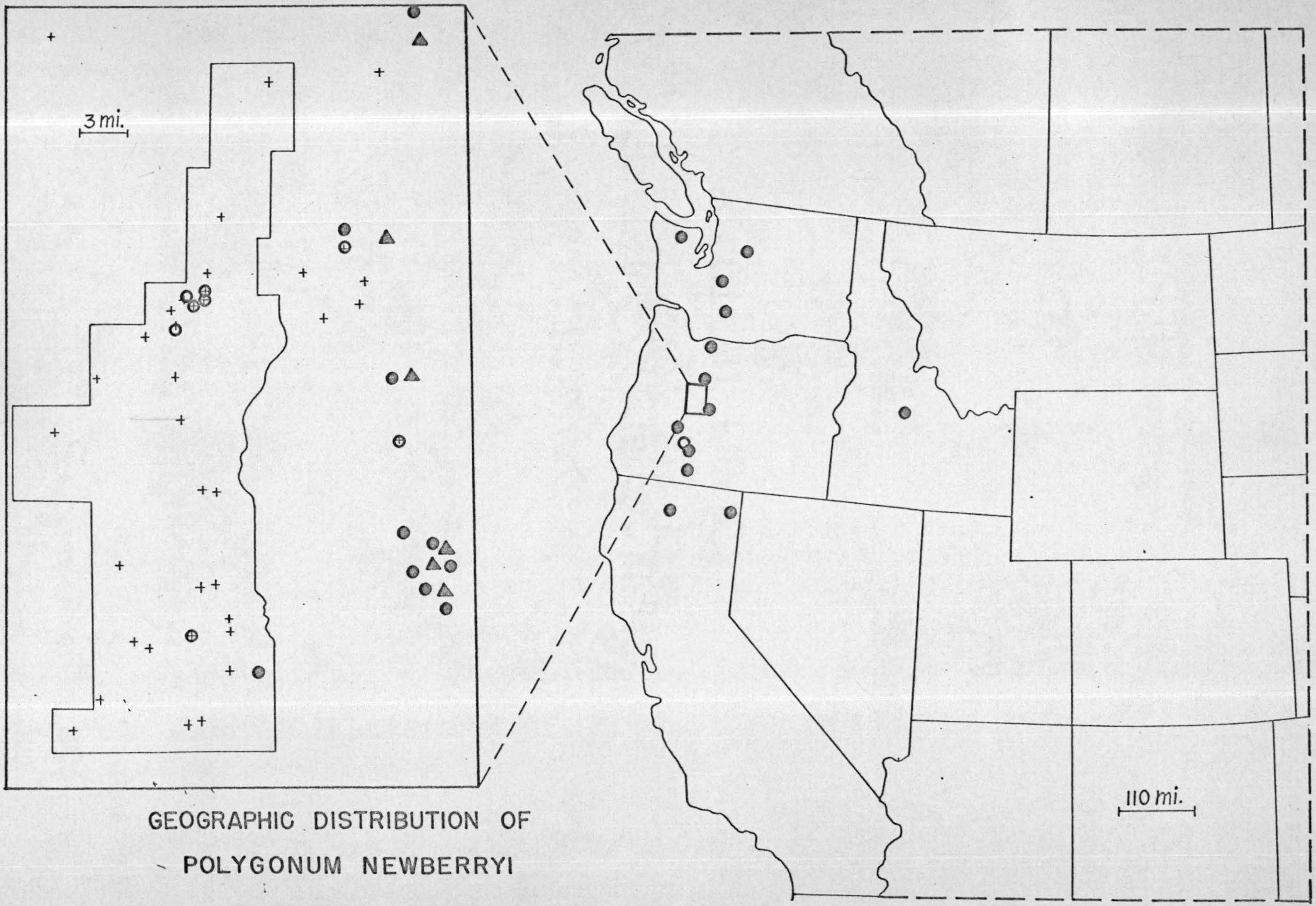
GEOGRAPHIC DISTRIBUTION OF
POLYGONUM CONFERTIFLORUM

taxa are highly variable, but rather to indicate that the existing taxonomy, as described by Wheeler (1938), is entirely workable.

In the Western Cascades, *P. kelloggii* is found on open gravelly banks and slopes, and in well-established rocky trails where snowmelt runs in the early spring. Although *P. cascadense*, *P. minimum*, and *P. douglasii* are frequently found in closely adjacent areas, the flowering time of *P. kelloggii* scarcely overlaps that of the former group, members of which continue to bloom until well into August, and occasionally until October. Other members of the Rocky Melt Seep association include *Lewisia triphylla*, *Mimulus breweri*, *Linanthus harknessii*, *Allium amplectens*, *Gayophytum humile*, and *Romanzoffia sitchensis*.

Polygonum newberryi Small, Bull. Torr. Bot. Club 21:170. 1894.

A broad-leaved species of subgenus *Aconogon*, *P. newberryi* is characterized by its alpine habitat; yellow-green axillary flowers; and petiolate, densely soft-pubescent leaves. Its closest relative is *P. davisiae* Brewer, a plant of similar habitat in southern Oregon and California, which has mainly sessile glabrous leaves. Although *P. newberryi* is a variable taxon, it seems to remain distinct from *P. davisiae* even where the two co-occur in southern Oregon and northern California. With the exception of specimens from the Olympics; the Warner Mountains, Modoc County, California; and central Idaho, this species is limited to the Cascade Range from Washington to California. It has previously been reported only from high elevations around the major peaks, where it is often abundant in areas of pumice or fine scoriaceous gravel. It has also been found to occur in several



GEOGRAPHIC DISTRIBUTION OF POLYGONUM NEWBERRYI ecologically similar spots at somewhat lower elevations in the Western Cascades on or near the gravelly summits of some of the higher peaks, often in snowbed areas or spots that receive runoff. It is often found with *Luetkea pectinata*, *Ribes binominatum*, *Penstemon cardwellii*, *Lotus nevadensis douglasii*, *Crepis occidentalis*, *Eriogonum umbellatum*, *Dicentra uniflora* and other species of varied floristic affinities.

Eriogonum nudum Dougl. ex Benth., Trans. Linn. Soc. 17:413. 1837.

Eriogonum compositum Dougl. ex Benth., Lindl. Bot. Reg. 21: pl. 1774. 1835.

Eriogonum umbellatum Torr., Ann. Lyc. N. Y. 2:241. 1828.

Eriogonum is a large, fascinating, and difficult genus which has undergone great and evidently very recent differentiation in the Western United States. Species are extremely variable and tend to be poorly delimited from one another. The genus as a whole inhabits dry environments, and two of the three perennial species listed here have been called disjunct xeric indicators by Detling (1953). Since they are more continuous in their distribution ranges than many other species encountered and are well known in western Oregon, no maps of their total distributions are given here, but they are briefly described and discussed below.

E. nudum lacks pseudostipes (stem-like extensions of the bases of the perianth) and pubescence around the inflorescence, and has large, umbellately compound, naked flowering stems which arise from a basal rosette of prostrate leaves. The flowers are white, and the leaves are green above and densely woolly beneath. This species is highly variable and is sometimes lumped with the Californian *E. latifolium*, which then contains about eight subspecific taxa which are differentiated with difficulty. Throughout much of its range, *E. nudum* is essentially a coastal species, but the type locality is the Willamette Valley. It is found from southern Washington to southern California and in Oregon is common in the Cascades, as well as in other dry spots west of the Cascade crest. It also occurs in the Sierra Nevada of California.

Both *Eriogonum compositum* and *E. umbellatum* have pseudostipes, reflexed or spreading involucral lobes, and naked flower stems topped by occasionally compound umbels of involucres. *E. compositum* has large (4-10 cm) cordate leaves and creamy white flowers in large heads, while *E. umbellatum* has smaller cuneate leaves and sulphur yellow flowers. Both species are variable, but *E. umbellatum* is especially so, comprising at least 50 proposed taxa which intergrade in many different directions. Hitchcock (in Hitchcock and others, 1964) recognizes only seven poorly differentiated geographical races. Western Cascade material seems to be intermediate between var. *hausknechtii* (Dammer) Jones and var. *umbellatum*. The latter variety tends toward *E. marifolium* T. and G., which differs mainly in its erect, shorter involucral lobes. *E. umbellatum* is found in varied habitats throughout almost all of the Western United States. While it is more common east of the Cascade crest in Oregon, it is abundant in both the High and Western Cascade Ranges. *E. compositum* is more limited in distribution. It occurs widely east of the Cascades through the Pacific Northwest, but is also found in dry areas throughout western Oregon.

Occasionally all three of these species are found coexisting in the Western Cascades on dry, gravelly, south or west-facing slopes. In general, however, E. nudum and E. compositum are found in slightly damper sites with finer, more highly organic soil, and E. umbellatum is restricted to crevices of small outcrops or deflation armor flats.

Lewisia triphylla (Wats.) Rob. in Gray, Syn. Fl. 1^1:269. 1897.

Selected synonyms:

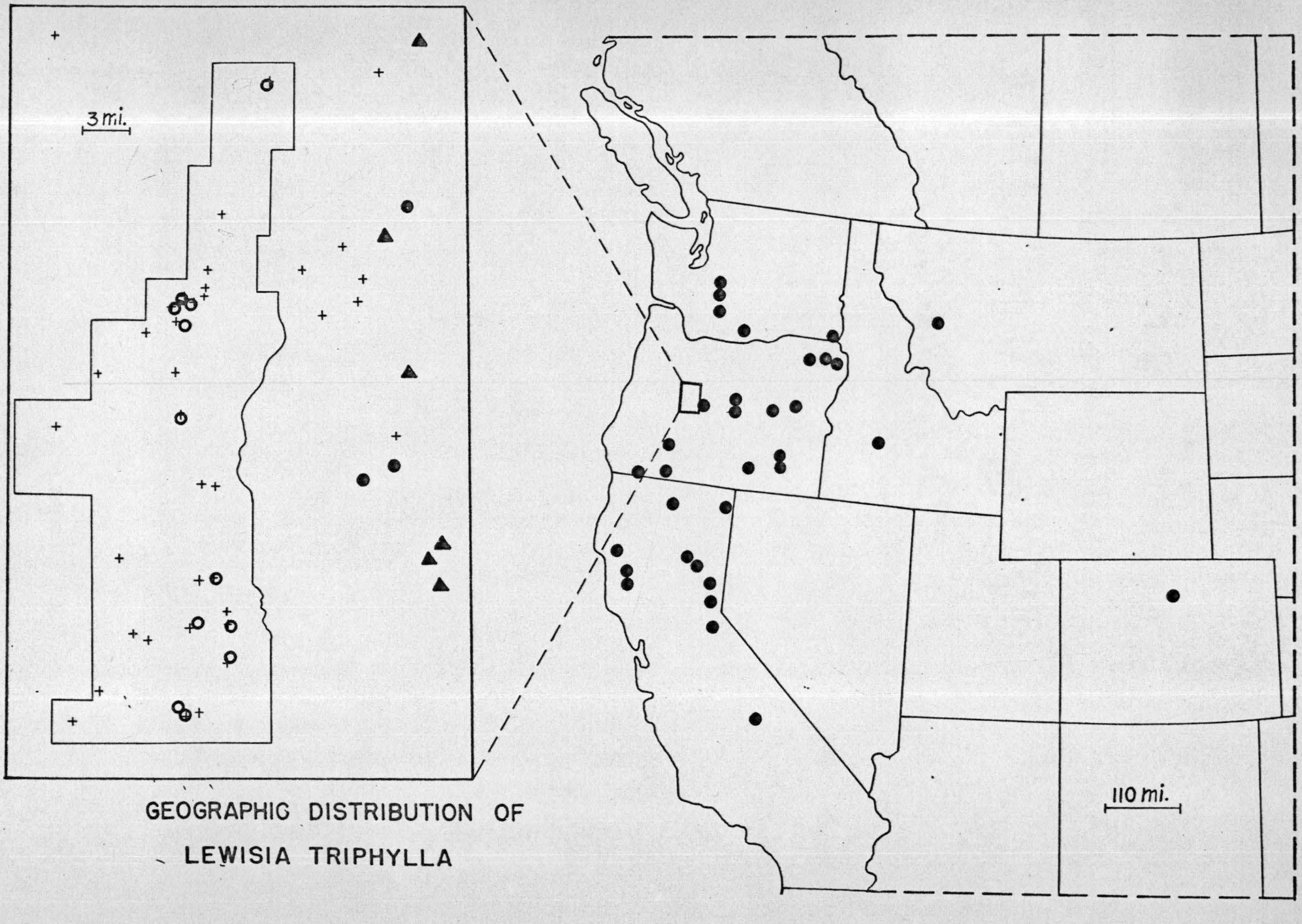
Claytonia triphylla Wats., Proc. Am. Acad. 10:345. 1875.

A diminutive Lewisia that occupies areas near snowbanks or in runoff rivulets, this species is the only member of the genus with a globose corm--a feature characteristic of the genus Claytonia. It differs from Claytonia, however, in regularly lacking basal leaves, and in its circumcissile rather than laterally dehiscent capsule.

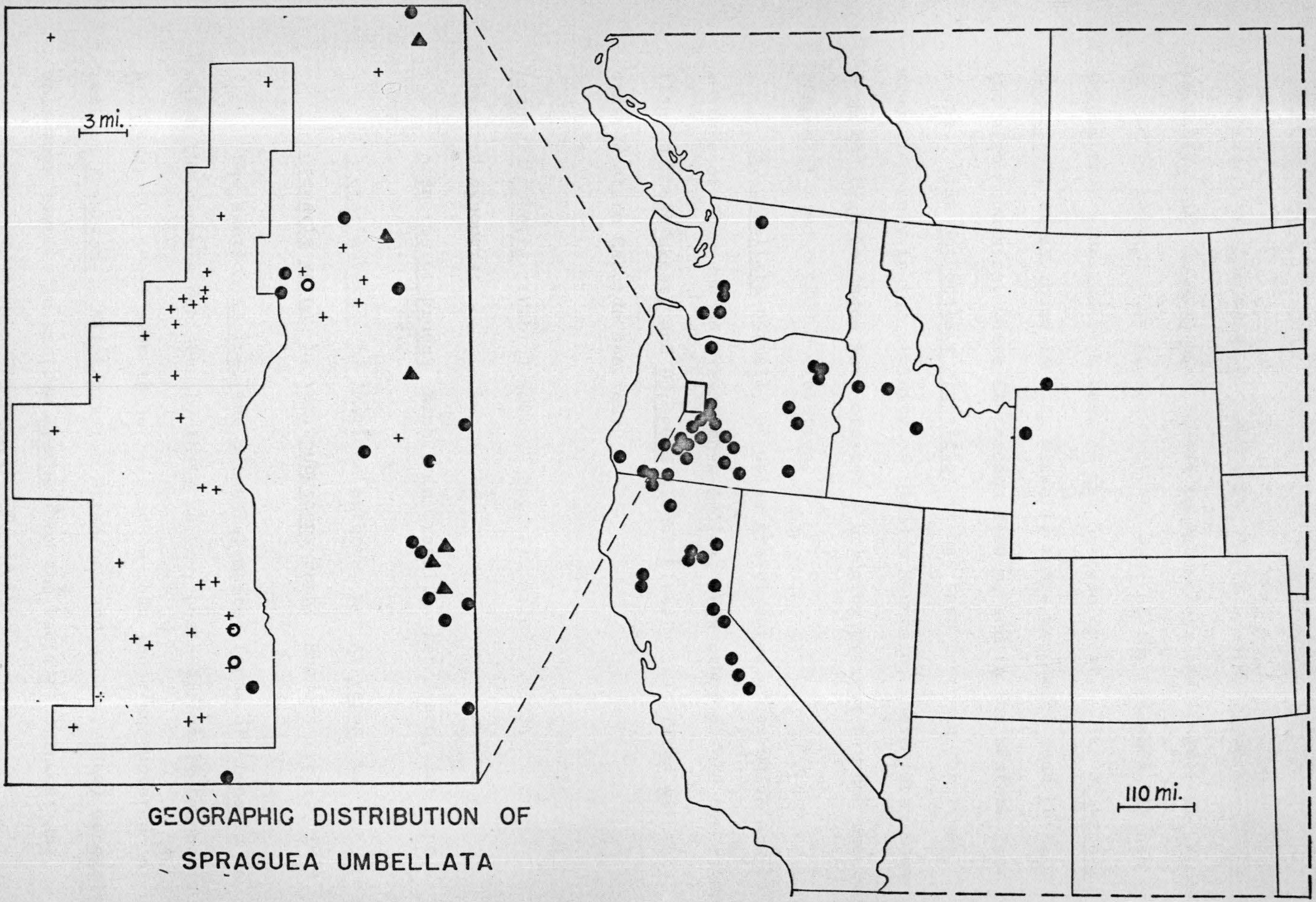
L. triphylla is widespread in arid regions east of the Cascade Range but has only rarely been collected from these mountains, and never previously from the Western Cascades. It is relatively common in high elevation Rocky Melt Seeps, together with Mimulus breweri, Romanzoffia sitchensis, Dodecatheon jeffreyi, Polygonum kelloggii, Allium amplectens, Linanthus harknessii, Gayophytum humile, and Saxifraga occidentalis rufidula.

Spraguea umbellata Torr. in Smith, Contr. Knowl. 6:4. 1853.

This typically high elevation species is immediately recognized by its basal rosettes of red or green fleshy leaves and its often



GEOGRAPHIC DISTRIBUTION OF LEWISIA TRIPHYLLA



GEOGRAPHIC DISTRIBUTION OF SPRAGUEA UMBELLATA prostrate globular heads of membranous white or pink flowers. It is variable, particularly with regard to robustness and longevity. Widespread in subalpine or higher habitats east of the Cascades, it has seldom been reported from west of the Cascade crest. Like Polygonum newberryi, it is found in open gravelly soils or pumice sand both in the high mountains, where it reaches 2600 m, and in the Western Cascades. Like Nothocalais alpestris, it has been found in the lower mountains only in the vicinity of Olallie Mountain, where lava flows from the High Cascades have created a bridging plateau between the two ranges at almost 1500 m elevation.

S. umbellata normally occupies gravel scree areas which are in a state of flux due to freeze-thaw cycles. Few other plants can establish in these areas, and Spraguea is not closely associated with any other Western Cascade species.

Arenaria rubella (Wahl.) Smith, Eng. Fl. 4:267. 1828.

Selected synonyms:

Arenaria propinqua Rich., in Frankl., 1st Journ. Bot. App. 738. 1823.

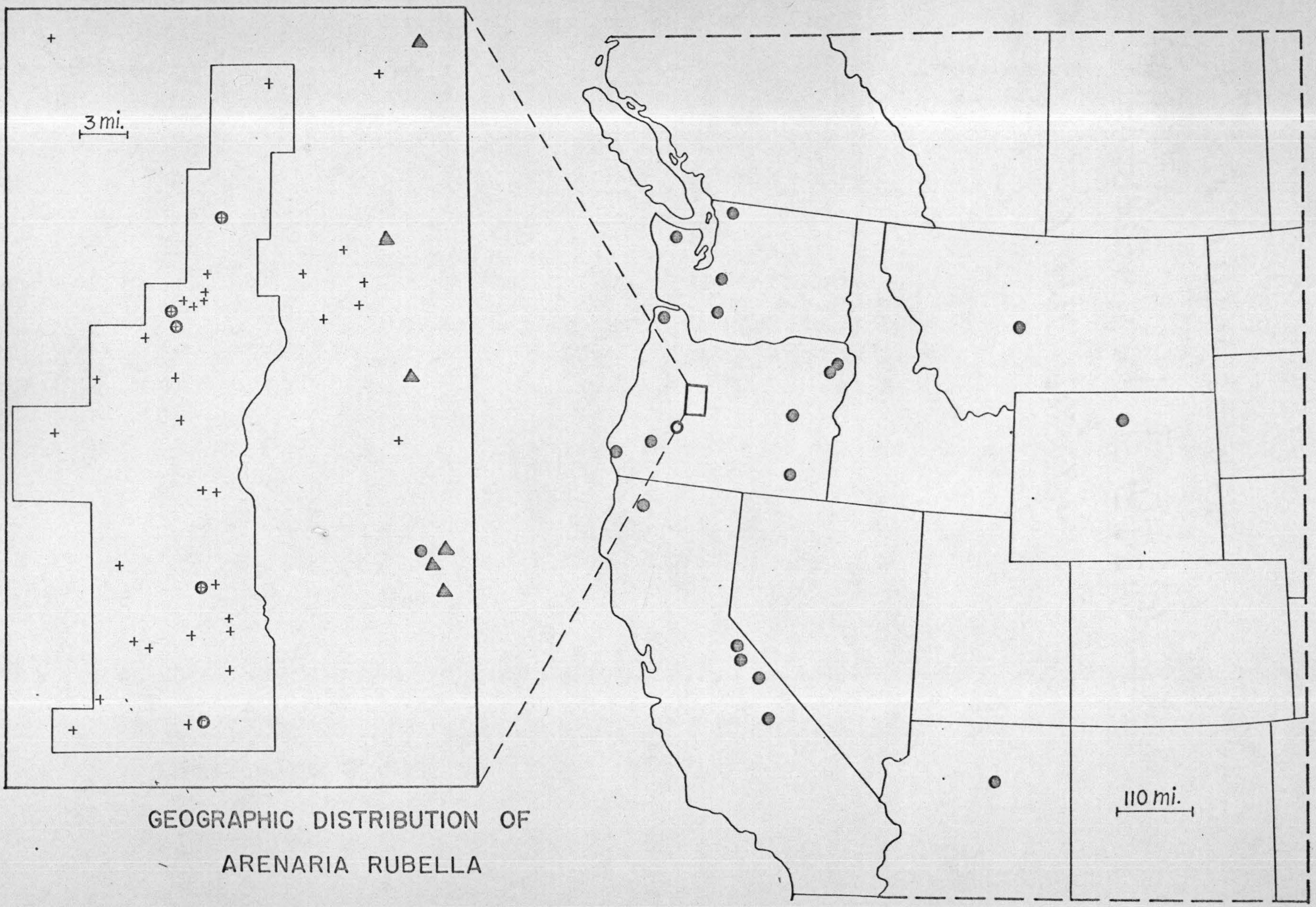
Arenaria verna of American authors, not A. verna L.

Arenaria verna L. var. pubescens Fern. Rhodora 21:21. 1919.

The section Alsine, the perennial matted forms of Arenaria in which the capsule dehisces by three valves, poses difficult taxonomic problems; but these seem to be less acute than those encountered in the section Eremogone. Hitchcock (in Hitchcock and others, 1964) recognizes only four species in section Alsine from the Pacific Northwest and defines these very broadly. *A. rubella* is the only species in this group forming small compact mats with a single well-defined taproot. More robust open forms from lower or more sheltered habitats may approach *A. nuttallii* Pax or *A. obtusiloba* (Rydb.) Fern. in habit. This is especially true of material from Saddle Mountain, Clatsop County, Oregon, and from the Olympic Peninsula.

A. rubella is a cliff-dwelling plant, with its taproot firmly anchored in crevices of vertical volcanic faces, normally exposed to prevailing winds. According to Maguire (1951), this species is circumpolar and circumboreal, occurring in North America from Greenland, the Arctic Archipelago, and Alaska south along the Atlantic Coast, in the Rockies and Cascades to the Gaspé Peninsula, northern Arizona, and northern California. It is extremely polymorphic when considered throughout its range. Compact forms, such as those found in the Western Cascades, are normally restricted to Arctic-Alpine elevations at this latitude, but the species is occasionally found lower than 300 m above sea level. It has not often been collected in the United States, and except for one locality on the Three Sisters, the specimens collected in this study constitute the only Oregon Cascade material known to the author.

Other members of the Vertical Outcrop association, such as *Penstemon rupicola*, *Saxifraga bronchialis vespertina*, *Erigeron cascadensis*, *Douglasia laevigata*, *Castilleja rupicola*, *Polypodium hesperium*, *Polemonium pulcherrimum*, and *Heuchera micrantha*, are associated with *Arenaria rubella* in the Western Cascades.



GEOGRAPHIC DISTRIBUTION OF ARENARIA RUBELLA

Arenaria capillaris Poir. subsp. americana Maguire, Bull. Torr. Bot. Club 74:41. 1947.

Selected synonyms:

Arenaria nardifolia of American authors, not A. nardifolia Ledeb.

Arenaria formosa of American authors, not A. formosa Fisch.

Arenaria capillaris Poir. subsp. formosa (Fisch.) Mag., Madrono 6:24. 1941.

Arenaria pumicola Cov. and Leib., Proc. Biol. Soc. Wash. 11:169. 1897.

> Relationships among members of the American Capillaris-group are complex and obscure. Within it little clear-cut specific differentiation has taken place, or at least most species are so variable within themselves as to transgress all specific lines, removing discontinuity, and to leave only emphatic notes in a basally continuous series . . . . The interpretation of populations, specific and subspecific, depends largely on accurate evaluation of the interplay of sepal, leaf, and inflorescence form. Gland size and disposition, seed, and rootstock offer supporting characterization. Of no little aid is the final summation of intangibles that comes of familiarity with the plants, and that gives populations an "appearance" or "look"--indefinite properties that defy descriptive analysis. (Maguire, 1947, p. 38-40)

This statement by the most recent student of Arenaria briefly summarizes the present state of taxonomy in the genus. Even those characters mentioned by Maguire, however, do not always stand up on close scrutiny. Large-scale geographical considerations may help, but presumably diagnostic characters may occur far outside the natural range of the "species" they characterize.

A. capillaris americana has been observed (Hickman, in preparation) to intergrade with all other species of section Eremogone that are found in Oregon. Occasional specimens show obvious diagnostic characters of three or perhaps more of these species (A. kingii, *A. aculeata*, and *A. congesta*, in addition to the two under discussion here). *A. capillaris americana* is found in pure form from southern British Columbia and Alberta south in the Cascades to the Three Sisters and in the Rocky Mountains south to northern Idaho and western Montana. Intergrades with *A. pumicola*, *A. aculeata*, and *A. kingii* extend the range of certain characteristics diagonostic of *A. capillaris americana* south to Josephine County, Oregon, and White Pine County, Nevada. Since *A. capillaris* has the northernmost range of any American species in this circumboreal section, it is generally considered the most primitive American taxon, from which other, more southerly species have been derived.

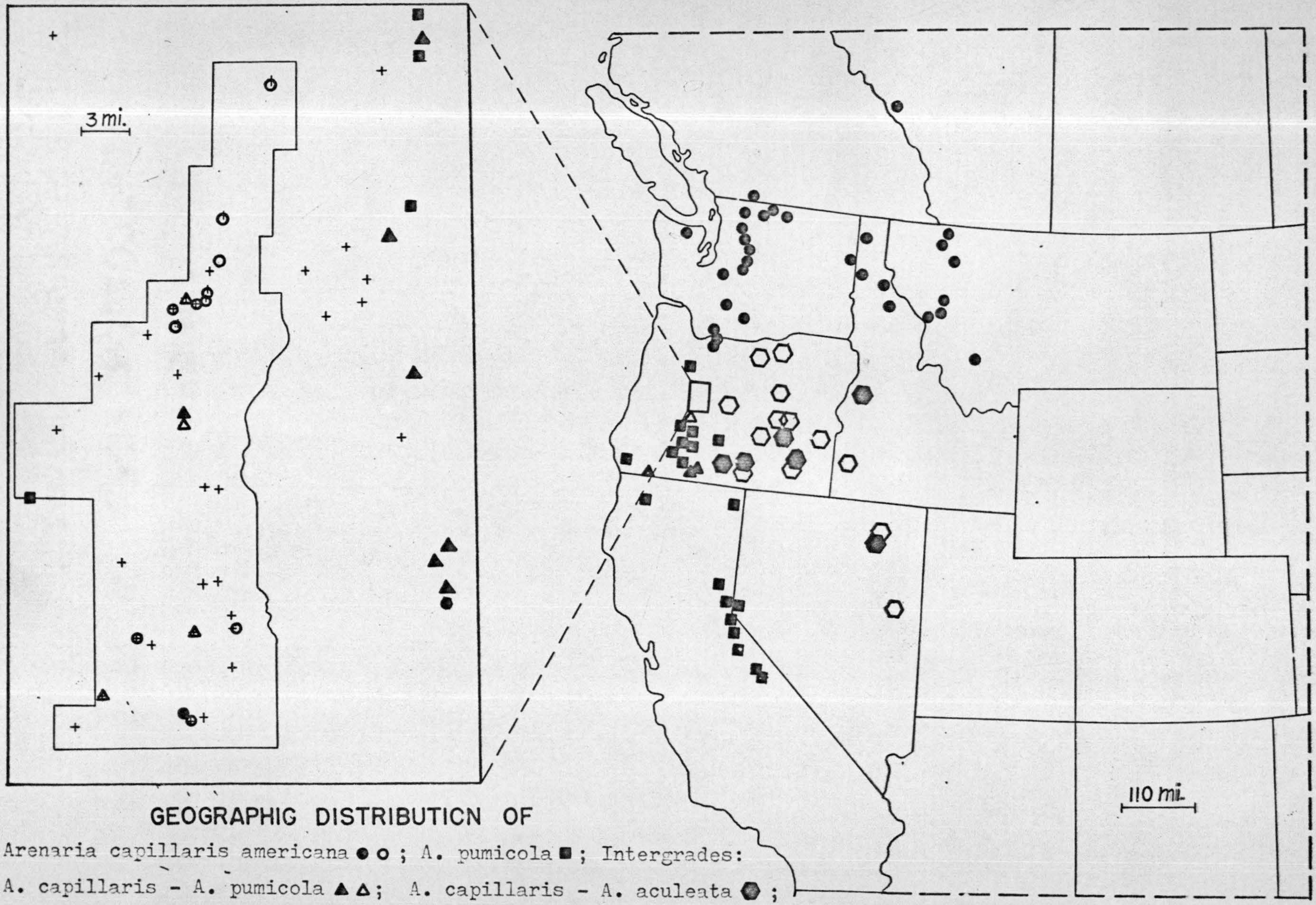
A. pumicola is characterized by straight, rigidly ascending, deciduous basal leaves; relatively wide, fleshy cauline leaves which are abruptly reduced at the inflorescence; and a naked, stout, erect caudex which branches just below the soil surface. Numerous intergrades with *A. capillaris americana* are found, and intermediates between this species and *A. aculeata* and *A. congesta* have been collected on rare occasions. *A. pumicola* is abundant at Crater Lake, the type locality, and is also found south and west to the Siskiyou Mountains of Curry County, and north to the north slope of Mr. Jefferson, Marion County. Intergrades with *A. capillaris americana*, especially alpine forms, carry some diagnostic characters of this species as far north as Mt. Rainier. The variety *californica* Maguire occurs from Sierra to Mono Counties, California, centering around the Lake Tahoe region. It is morphologically intermediate between typical *A. pumicola* and *A. kingii* of the Great Basin. *A. ursina* Robins. of the mountains of southern

California may in turn be derived from *A. pumicola californica*.

Morphological evidence points to a complex pattern of reticulate evolution in this group of species, where breeding barriers are evidently poorly developed. A small number of genes may be responsible for many of the critical diagnostic characters, making the evolutionary and geographical significance of their occurrence in isolated populations at least disputable. Much further work needs to be done on the biology of these species.

It is certainly significant that the study area includes the latitudinal limits of the pure forms of both *A. capillaris americana* and *A. pumicola* and is the only area in which such forms co-occur. A number of intergrades have been collected here.

The narrowly linear leaves and perennial, more or less cespitose habit of all members of the section *Eremogone* are characteristic of plants growing in dry habitats. These species are found either high in the mountains or in dry plain or desert environments. In the Western Cascades, *A. capillaris americana* and *A. pumicola* are often rooted in crevices of volcanic rock in exposed but seldom south-facing situations. Although they have not been found together, they are both commonly associated with *Penstemon procerus brachyanthus*, *Sedum stenopetalum*, *Sedum oregonense*, *Arctostaphylos nevadensis*, *Eriogonum umbellatum*, *Silene douglasii*, *Juniperus communis saxatilis*, and other members of the Outcrop Ridge, Gravel Scree, or Small Boulder Creep Slope associations.



GEOGRAPHIC DISTRIBUTICN OF

Arenaria capillaris americana ● ○ ; A. pumicola ■ ; Intergrades:

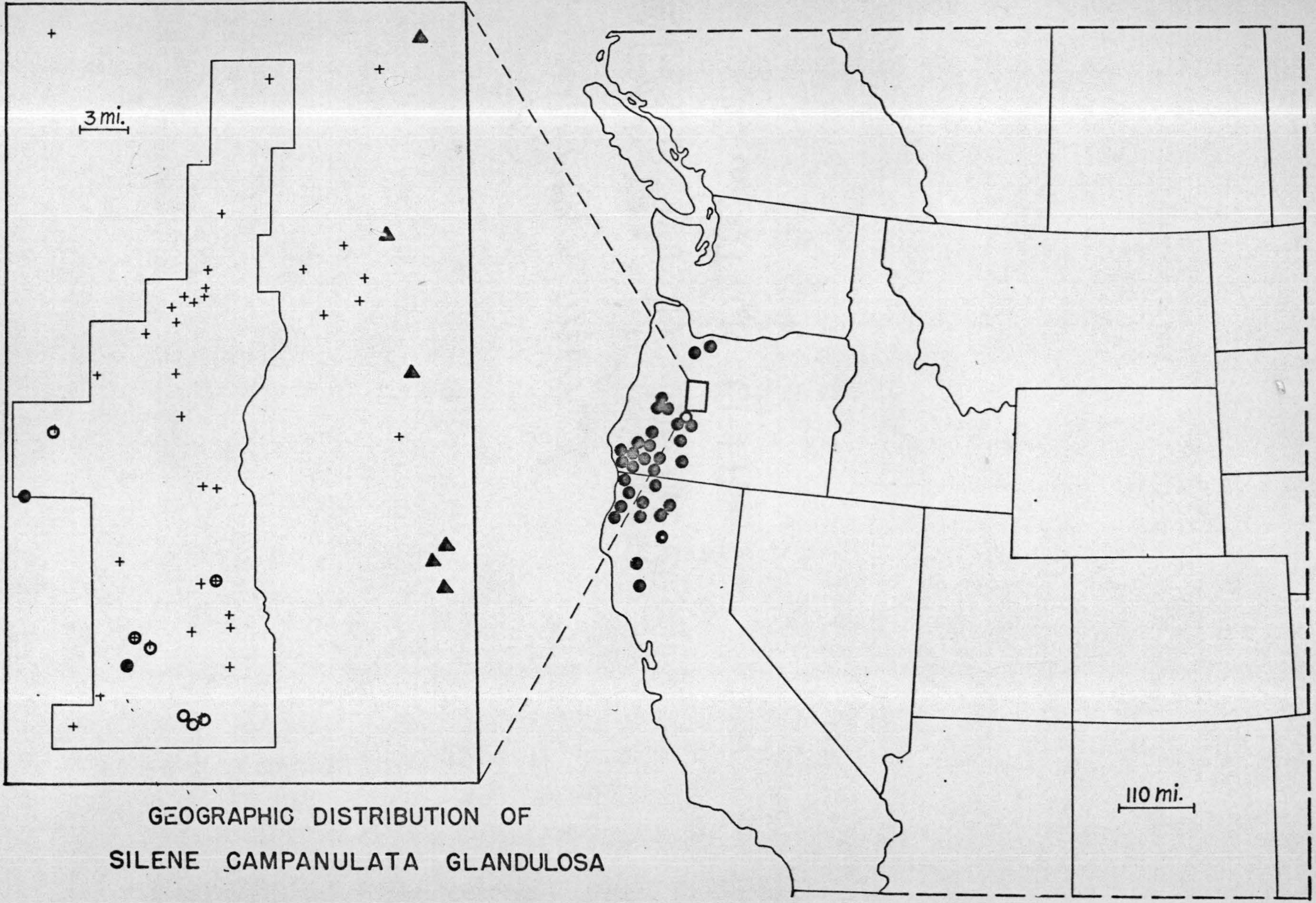
A. capillaris - A. pumicola ▲ △ ; A. capillaris - A. aculeata ⬢ ;

A. capillaris - A. kingii glabrescens ⬡ .

Silene campanulata Wats. subsp. *glandulosa* Hitch. and Mag., Univ. Wash. Publ. Biol. 13:1-71. 1947.

According to Hitchcock and Maguire (1947), *Silene campanulata* is not closely related to any other western American silenes. It is a member of the subgenus *Melandyrum*, which is primarily characterized by unilocular capsules. The calyx is broadly campanulate, and the petals are finely divided into linear lobes, making the flowers quite distinctive. Three subspecies have been described. *S. campanulata* subsp. *greenei* (Wats.) Hitch. and Mag. is known from northern California and southwestern Oregon. It is considerably less glandular than subsp. *glandulosa*. A few intergrades are known between these two subspecies. Subspecies *typica* Hitch. and Mag. is known only from its type locality on Red Mountain, Mendocino County, California. Its leaves are linear, rather than broadly lanceolate, and the stem pubescence is shorter than that of subsp. *glandulosa*.

S. campanulata glandulosa ranges from the Klamath Mountain and north Coast region of California through the Siskiyous and southern Cascades of Oregon. Specimens have been collected from dry rocky sites at the head of the Willamette Valley, from the vicinity of Mt. Hood, and at scattered locations through the southern part of the Western Cascades, where it is commonly rooted in crevices of andesite or basalt on steep south-facing slopes. As a member of the Outcrop Ridge association, it often occurs with *Haplopappus hallii*, *Comandra umbellata*, *Lomatium martindalei*, *Erigeron foliosus confinis*, and *Arenaria capillaris americana*.



GEOGRAPHIC DISTRIBUTION OF
SILENE CAMPANULATA GLANDULOSA

Silene douglasii Hook., Fl. Bor. Am. 1:88. 1830.

Both this species and *Silene campanulata glandulosa* are inordinately well defined for members of their genus and family (Caryophyllaceae). *Silene douglasii*, a member of the subgenus *Melandryum*, has perhaps been derived from stock of *S. parryi* (Wats.) Hitch. and Mag., since where the ranges of the two overlap, sterile hybrids are sometimes formed (Hitchcock, in Hitchcock and others, 1964). Specific distinctions are not clear in this genus as a whole, however, and relationships are notably difficult to determine (Hitchcock and Maguire, 1947).

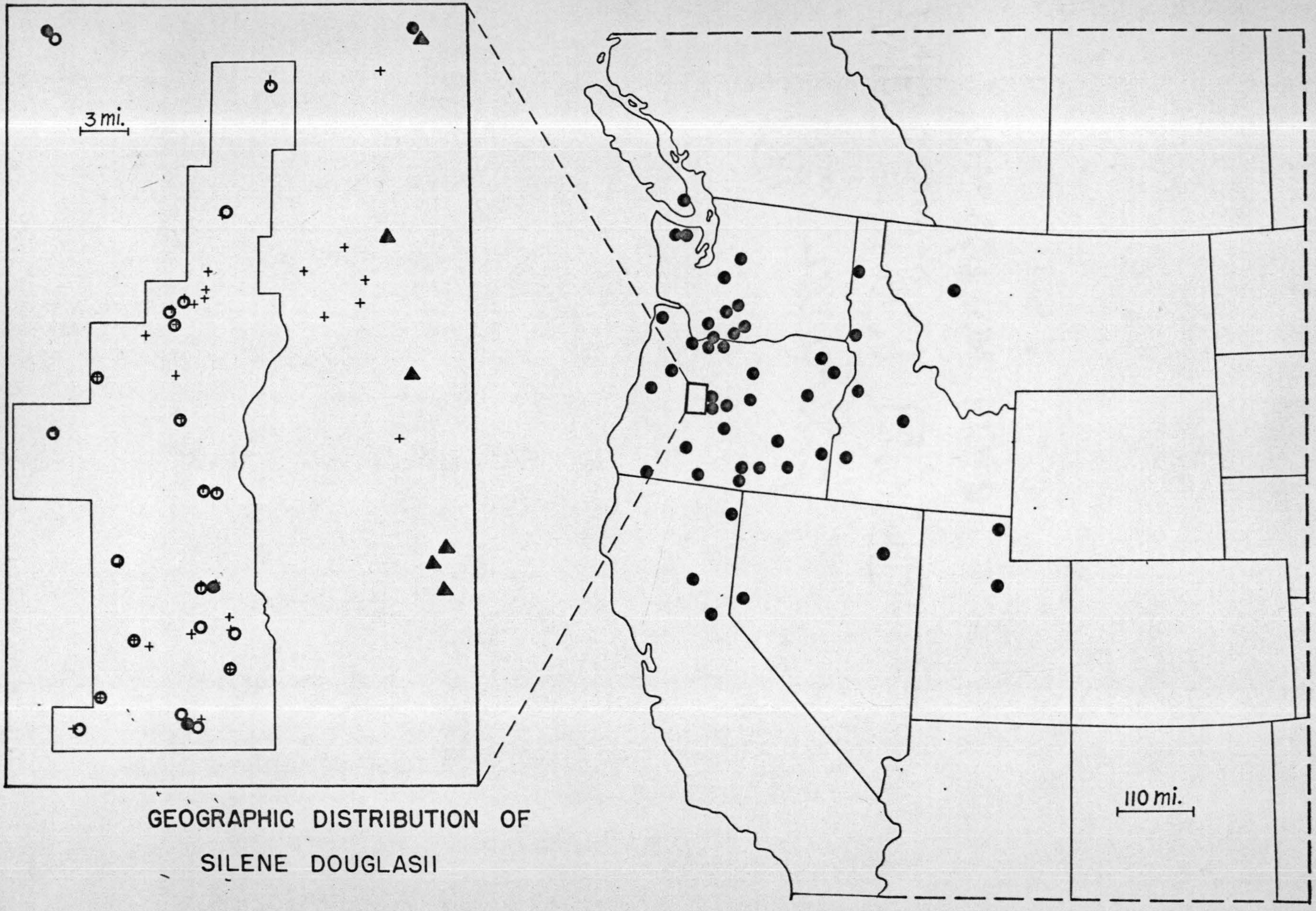
S. douglasii is widespread in Oregon, occurring both east and west of the Cascades, and extending to British Columbia, Montana, Utah, and central California. Throughout its range it is found in dry habitats. In the Western Cascades, where it is abundant, it grows in crevices of rock on well-drained slopes with either a southern or western aspect. It is typically less exposed to desiccating influences than *S. campanulata*. Other members of the Outcrop Ridge association with which *S. douglasii* occurs include *Penstemon procerus brachyanthus*, *Haplopappus hallii*, *Arenaria capillaris americana*, *Sedum stenopetalum*, and *Polygonum douglasii*.

Arabis holboellii Hornem. var. *retrofracta* (Grah.) Rydb., Contr. U. S. Nat. Herb. 3:484. 1896.

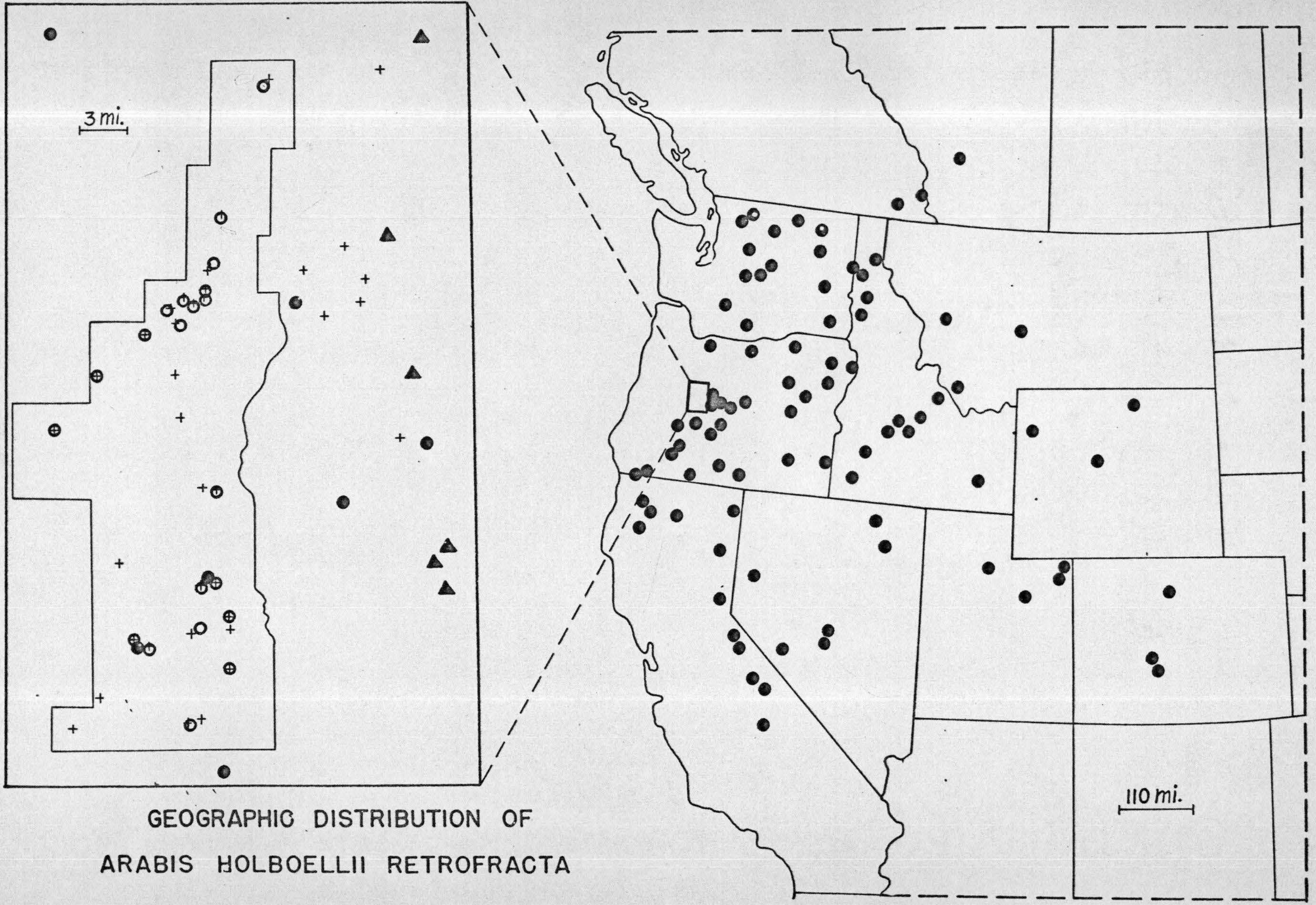
Selected synonyms:

Arabis secunda Howell, Erythea 3:33. 1895.

Arabis holboellii var. *secunda* Jeps., Man. Fl. Pl. Calif. 430. 1925.



GEOGRAPHIC DISTRIBUTION OF
SILENE DOUGLASII



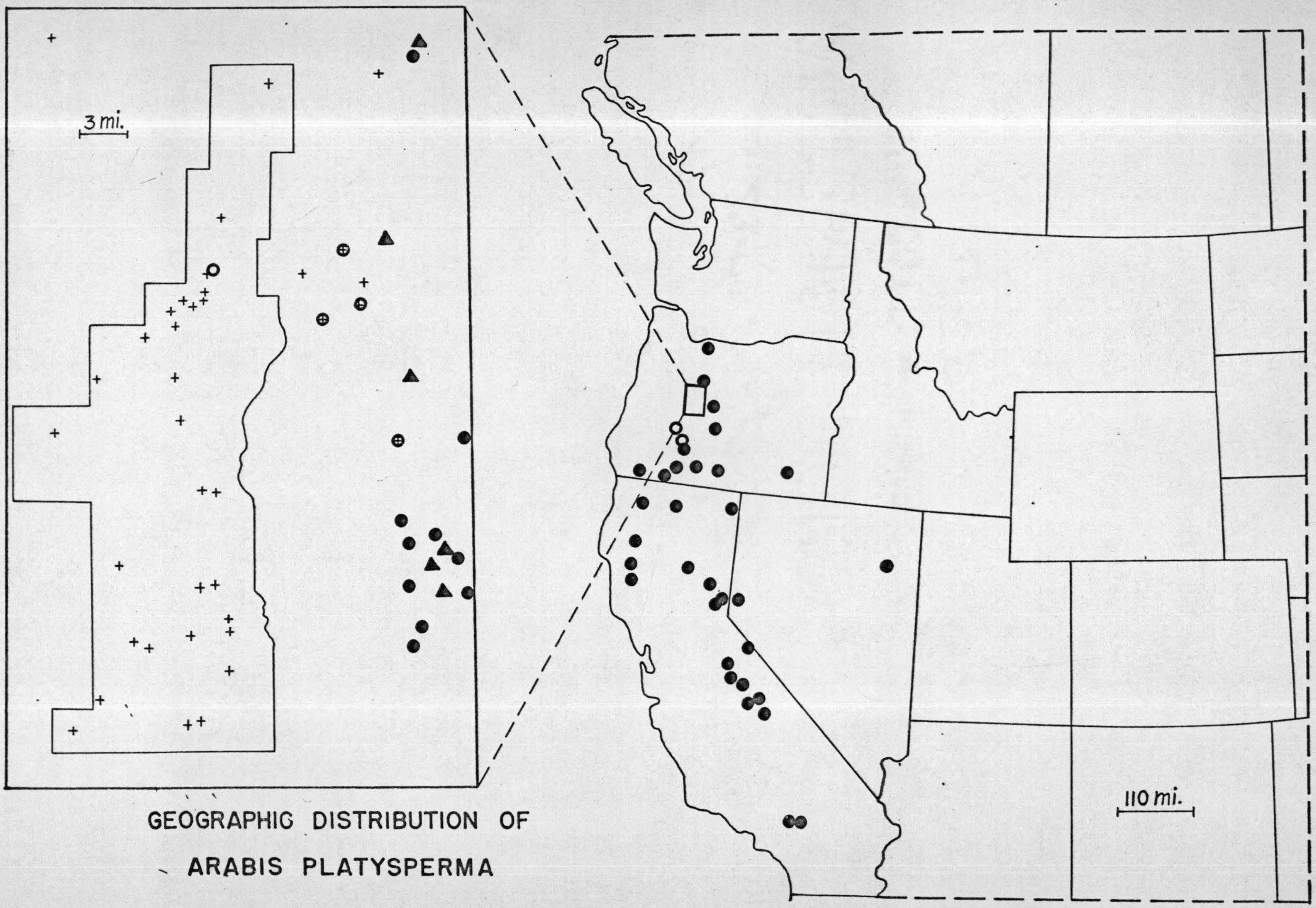
GEOGRAPHIC DISTRIBUTION OF
ARABIS HOLBOELLII RETROFRACTA

Arabis is one of the most difficult genera of the *Cruciferae*, and certainly the most highly diversified genus of this family in western North America. All species are variable, and complete morphological delimitation is sometimes impossible. *A. holboellii* is one of the most variable species of *Arabis*, as a complete synonymy would testify. Relatively conservative workers (Rollins, 1941) have recognized only five subtaxa, all of which occur in the Pacific Northwest. Variety *retrofracta* is recognized by its auriculate, revolute, cauline leaves; sharply reflexed fruiting pedicles; and narrow siliques. It ranges throughout most of the Western United States and has been reported from as far east as Quebec. It typically inhabits sagebrush or ponderosa pine communities.

Only rarely collected from west of the Cascade crest, this species is a dominant member of the Outcrop Ridge and Small Boulder Creep Slope associations of the hot, summer-dry south or west-facing slopes of the Western Cascades. It is commonly rooted in crevices of andesite or in dry gravelly loam with *Delphinium menziesii pyramidale*, *Castilleja hispida*, *Penstemon procerus brachyanthus*, *Calochortus lobbii*, *Haplopappus hallii*, *Silene douglasii*, *Arctostaphylos nevadensis*, and *Juniperus communis saxatilis*.

Arabis platysperma Gray var. *howellii* (Wats.) Jeps., Man. Fl. Pl. Calif. 432. 1925.

A wide-podded (4-6 mm) species, *A. platysperma* is distinguished from its closest relative, *A. suffrutescens* Wats., by its erect rather than reflexed siliques and its more scapose stem. The common Oregon



GEOGRAPHIC DISTRIBUTION OF
ARABIS PLATYSPERMA

phase, var. *howellii*, is glabrous and glaucous. It merges with the stellate-pubescent var. *platysperma* south and east from Mt. Shasta. The species as a whole ranges from Mt. Hood south to eastern Nevada and southern California. The two varieties are mapped together in this work.

A. platysperma is abundant and has often been collected from the Three Sisters, Lane and Deschutes Counties, but heretofore has not been reported from the Western Cascades. Two localities have been discovered there, plus several sites in the lower peaks of the High Cascades of Lane and Linn Counties. In all sites, plants occur in moist rocky soil near the summits, partly shaded by boulders or other vegetation. A perennial, *A. platysperma* sheds its broadly winged seeds before summer moisture stresses become great. It grows in association with *Phyllodoce empetriformis*, *Erigeron acris debilis*, *Luetkea pectinata*, *Polygonum newberryi*, *Castilleja parviflora oreopola*, *Senecio triangularis*, and *Eriogonum pyrolaefolium*.

Cardamine integrifolia Greene var. *sinuata* (Greene) Hitch., Vasc. Pl. Pac. N. W. 2:469. 1964.

Selected synonyms:

Dentaria integrifolia Nutt., in T. and G., Fl. N. Am. 1:88. 1838.

Dentaria californica Nutt., in T. and G., Fl. N. Am. 1:88. 1838.

Cardamine integrifolia Greene, Bull. Calif. Acad. Sci. 2:389. 1887.

Cardamine californica Greene, Fl. Fran. 266. 1891.

Dentaria sinuata Greene, Pitt. 3:123. 1896.

Cardamine californica var. sinuata Schulz, Eng. Bot. Jahrb. 32:387. 1903.

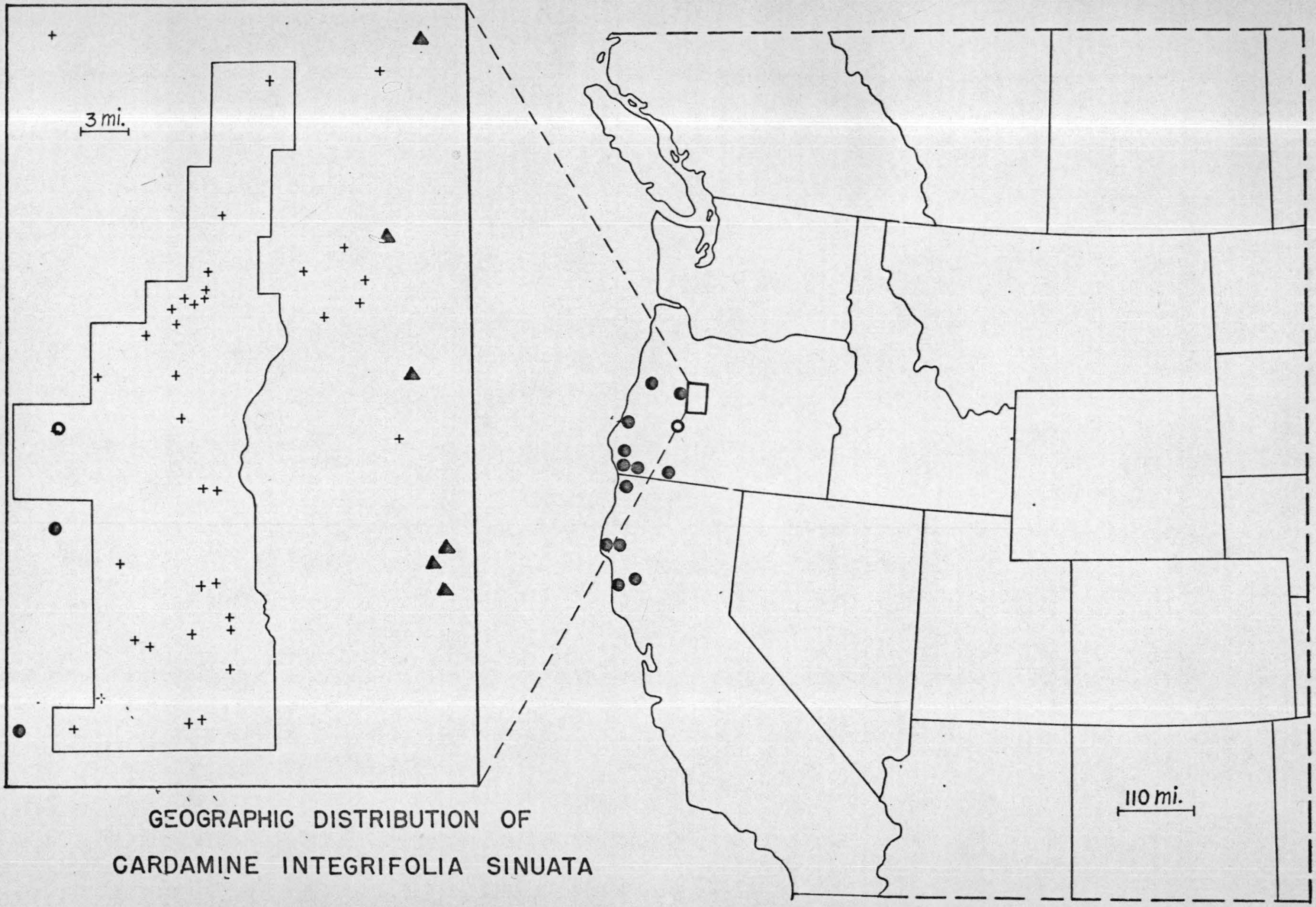
Dentaria integrifolia var. californica Jeps., Man. Fl. Pl. Calif. 426. 1925.

Dentaria californica var. integrifolia Detl., Am. Journ. Bot. 25:576. 1936.

This is a complex species, comprising several varieties in California, but its nomenclature is far more confusing than its taxonomy. Hitchcock (in Hitchcock and others, 1964) notes that Dentaria, a segregate of those species having larger flowers, tuberous rhizomes, and fewer cauline leaves, merges completely with Cardamine s.s. through C. constancei and D. rupicola, both of which could be placed in either genus (Detling, 1936). Following Hitchcock, I recognize only the older genus in this work. There has also been confusion in the literature (Jepson, 1925; Detling, 1936, 1937) as to which of several proposed specific epithets is valid for the present taxon. Again, I concur with Hitchcock.

C. integrifolia differs from C. pulcherrima (Robins.) Greene in its larger subglobose tubers, the leathery texture of the foliage, and more numerous flowers. Var. sinuata is distinguished from other varieties by its simple rhizomal leaves, which have sinuate margins; and by its mostly compound cauline leaves.

This is normally a coastal variety, entering the Cascades of southern Oregon, and occurring sporadically northward through the lower mountains to Tidbits Mountain, Linn County. In the Western Cascades it always occurs in dense blocky talus on north-facing slopes at the base of cliffs with the tubers deep among the boulders. Other members of



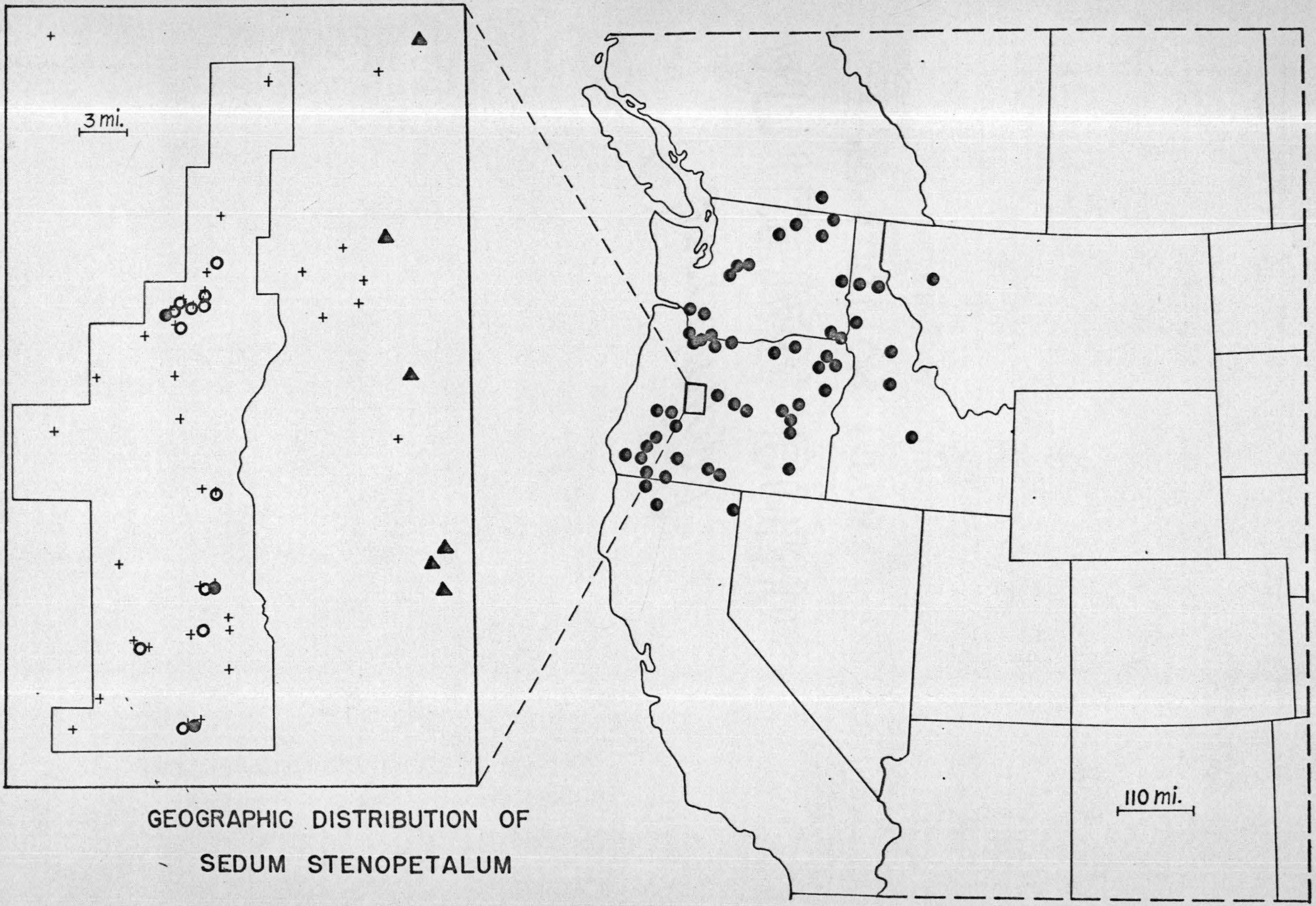
GEOGRAPHIC DISTRIBUTION OF
CARDAMINE INTEGRIFOLIA SINUATA

the Blocky Talus association include *Sambucus racemosa pubens arborescens*, *Acer circinatum*, *Aquilegia formosa*, *Thalictrum occidentale*, *Erigeron cascadensis*, and *Campanula rotundifolia*.

Sedum stenopetalum Pursh, Fl. Am. Sept. 324. 1814.
Selected synonyms:

Sedum douglasii Hook., Fl. Bor. Am. 1:228. 1834.

This species has commonly passed under the name *S. douglasii*. Hitchcock (in Hitchcock and others, 1964) reports the discovery that Pursh's holotype of *S. stenopetalum* actually comprises two distinct species, and that the description most closely approximates not the one which has been since referred to as *S. stenopetalum*, but to *S. douglasii* of Hooker. This discovery necessitates shifting several widely accepted names. *S. stenopetalum*, as presently constituted, is characterized by alternate dorsally-keeled leaves, the bases of which are broadened and membranous. The scarious leaf bases and midribs are persistent, giving the stems a ragged look late in the season. Single yellow flowers are borne by many stems and are visited by bees but appear to set no seed. Reproduction is accomplished by bulblets, which form in the axils of the upper cauline leaves. These bulblets drop off when the stems desiccate in August and overwinter on the soil surface. The many non-flowering stems are biennial, appearing in the spring as fragmented pieces of the previous season's matted stems, and blooming during their second growing season. They are recognizable by being considerably larger than the axillary bulblets.

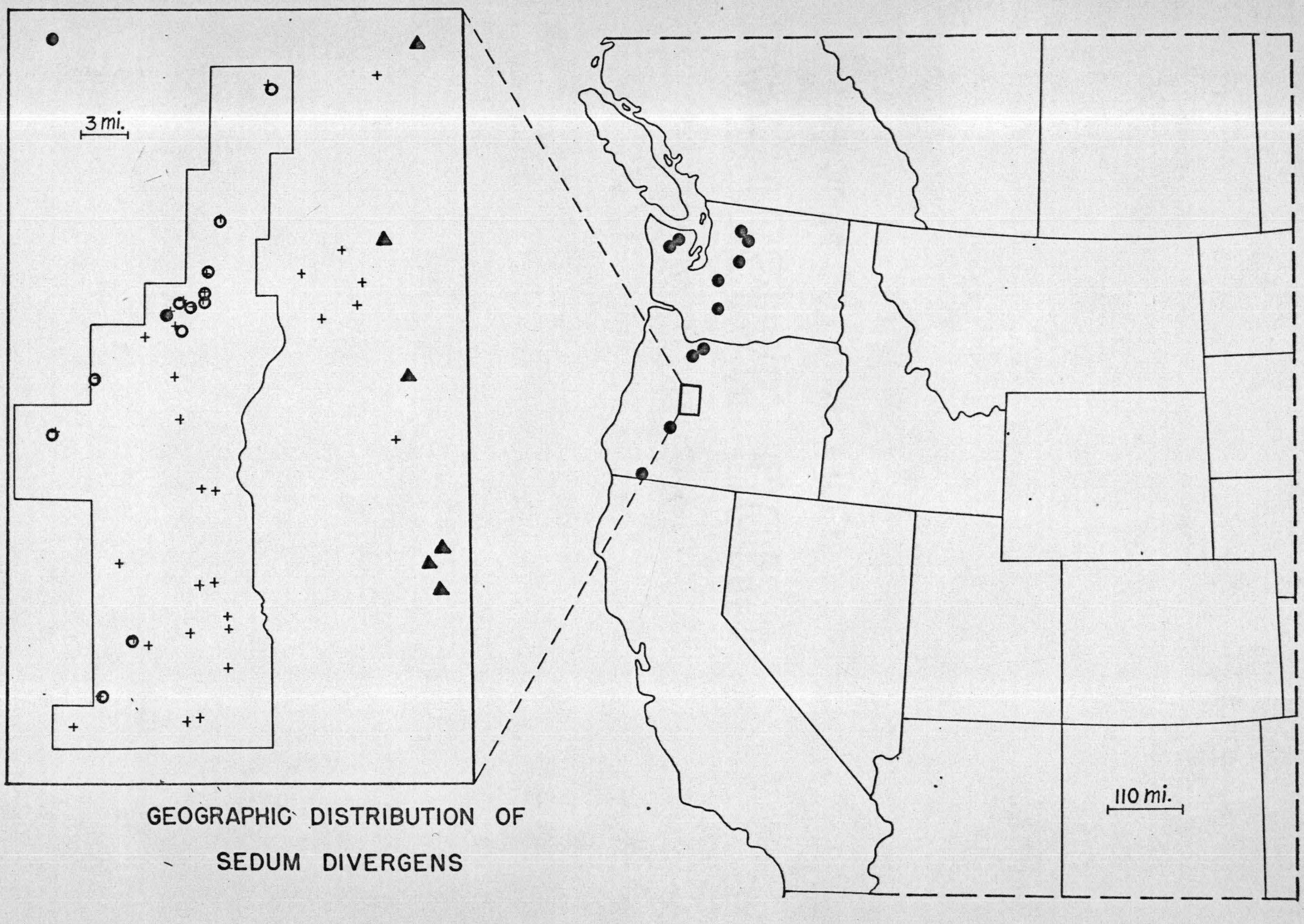


GEOGRAPHIC DISTRIBUTION OF
SEDUM STENOPETALUM

S. stenopetalum is common in dry areas of eastern Oregon and Washington east to Montana and in the Siskiyou region. It has occasionally been reported from "xeric islands" in the Willamette Valley, and from the Western Cascades. It was frequently encountered in the latter area on rocky, dry, south-facing slopes. Other members of the Boulder Creep association include *Penstemon procerus brachyanthus*, *Delphinium menziesii pyramidale*, *Castilleja hispida*, *Cerastium arvense*, *Potentilla glandulosa typica*, *Sedum divergens*, *Eriogonum umbellatum*, *Lomatium martendalei*, and *Arenaria capillaris americana*.

Sedum divergens Wats., Proc. Am. Acad. 17:372. 1882.

A bright reddish stonecrop with subglobose opposite leaves and strongly divergent carpels, *S. divergens* is easily recognized in the field or herbarium. The perennial stems are often matted and root at the nodes. Flowers are bright yellow and are borne profusely. Viable seed is set, but most reproduction is evidently vegetative by rooting of broken pieces of stem. This species is characteristic of the Washington Cascades and the Olympic Mountains and has been reported in the literature from only as far south as Mt. Hood (Hitchcock, in Hitchcock and others, 1964). However, old undated herbarium specimens are available from as far south as the Oregon Caves region, Josephine County (*Mrs. Clarice Nye*). This *Sedum* has been found to be almost ubiquitous on gravelly, open, south-facing slopes in the northern half of the central Western Cascades with a much more sporadic distribution to the south. A member of the Boulder Creep Slope association, it often occurs with *Penstemon procerus brachyanthus*, *Delphinium menziesii pyramidale*,



GEOGRAPHIC DISTRIBUTION OF
SEDUM DIVERGENS

Castilleja hispida, *Cerastium arvense*, *Potentilla glandulosa typica*, *Sedum stenopetalum*, *Eriogonum umbellatum*, *Lomatium martindalei*, and *Arenaria capillaris americana*.

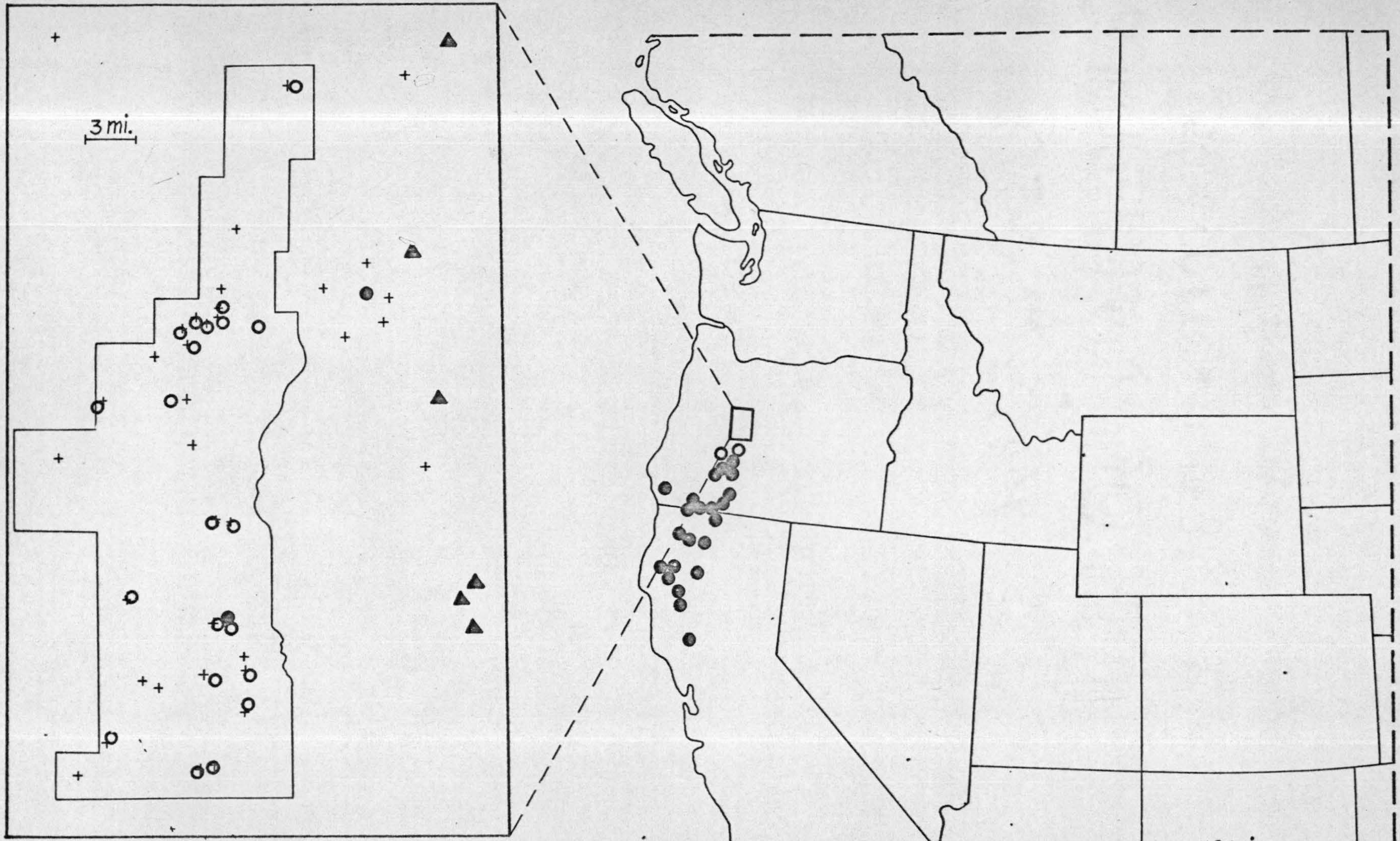
Ribes binominatum Heller, Cat. N. Am. Pl. ed. 2. 5. 1900.

Selected synonyms:

Grossularia binominata Cov. and Britt. N. Am. Fl. 22:218. 1908.

The three species which form the compact section *Watsonianae* should perhaps be considered only subspecifically distinct. *R. binominatum* is the most widespread and abundant of these three species, and it is proposed here that it has spread from its center of distribution in the Siskiyou Mountains of southwestern Oregon and the Coast Ranges and Klamath Mountains of northwestern California north and south through the mountains, differentiating slightly with distance from its ancestral region. The extreme morpho-geographical forms have been described as separate species.

R. tularensis (Cov.) Fedde is presently found in the Sierra Nevada of Tulare County, California. It is differentiated from *R. binominatum* in having slightly shorter filaments, slightly stronger internodal spines, and more glandular hairs on the leaves and ovaries. It has the trailing habit, tripartite nodal spines, silky leaves, and large berries armored with yellow-green spines of *R. binominatum*. The latter species was formerly thought to extend no farther north than Douglas County. *R. watsonianum* Koehne occurs from the eastern slopes of Mt. Hood north through the Cascade Mountains of Washington to Chelan



GEOGRAPHIC DISTRIBUTION OF RIBES BINOMINATUM

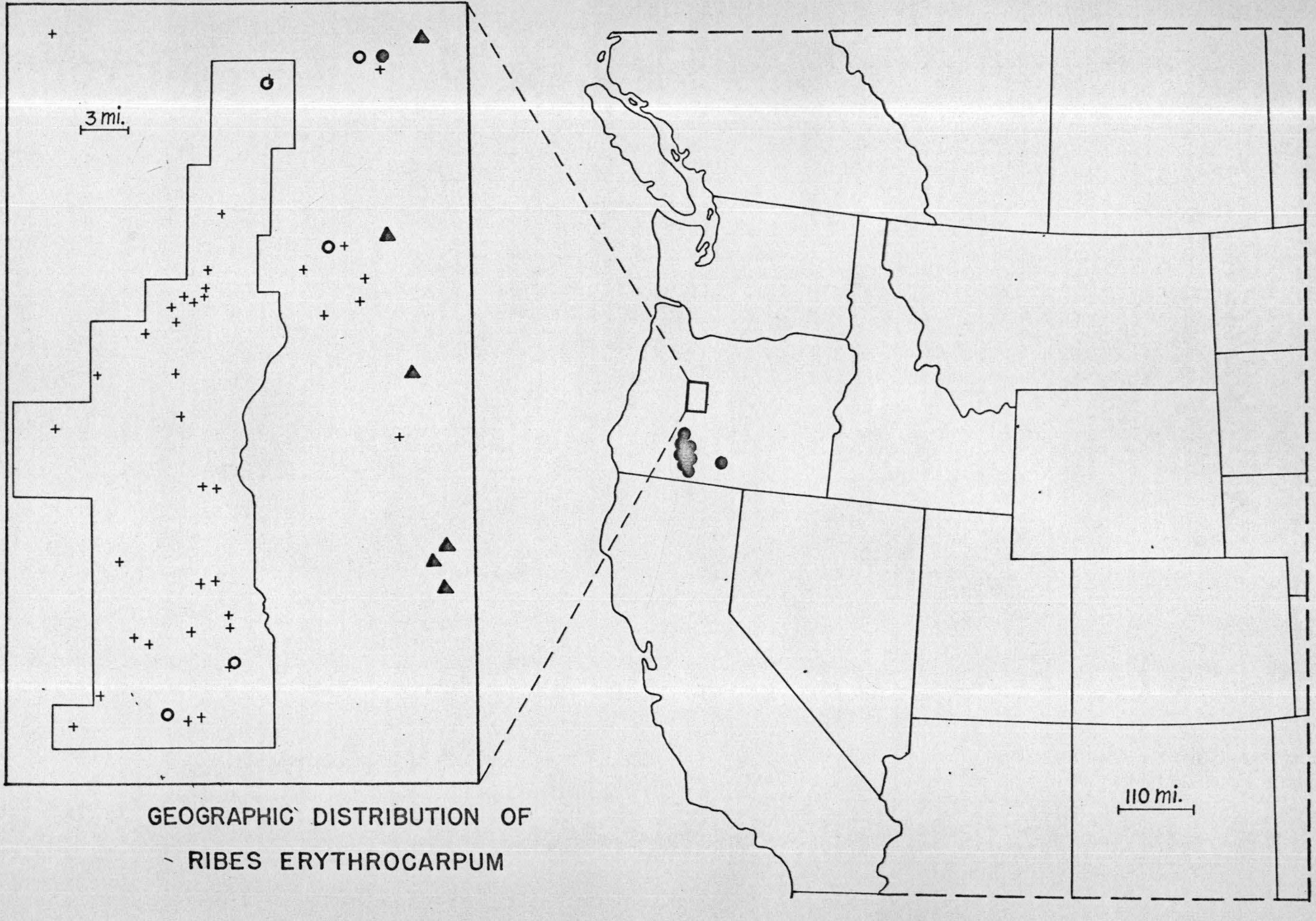
County. It has not been abundantly collected but is differentiated from *R. binominatum* by erect habit, slightly shorter filaments, glandular hairs on the leaves (but not twigs), and berries with somewhat more slender glandular spines.

R. binominatum has been found in this study to be widespread and common in the Western Cascades. Specimens are partially intermediate to both *R. watsonianum* and *R. tularensis* with regard to abundance of glandular hairs on stems, leaves, and ovaries; and the weak, ephemeral, internodal bristles. It is not unlikely that populations of *R. binominatum* and *R. watsonianum* are quite continuous, and that morphological intergradation continues in more northerly populations than those discovered in this study. Further field work is needed to solve this problem.

In the Western Cascades, *R. binominatum* is found trailing over fallen logs or partly shaded by overgrowing Mesic Meadow species such as *Pteridium aquilinum*, *Rudbeckia occidentalis*, *Lupinus arbustus neolaxiflorus*, *Luina stricta*, *Aquilegia formosa*, and *Erigeron aliceae*. It may become so extensively buried in taller vegetation that specimens are difficult to locate late in the season, even in spots where it is known to be common. This species is occasionally an alternate host to the white pine blister rust.

Ribes erythrocarpum Cov. and Leib., Proc. Biol. Soc. Wash. 10:132. 1896.

This distinctive spineless currant, with trailing glaucous stems and erect branches, salmon-colored flowers, and bright red

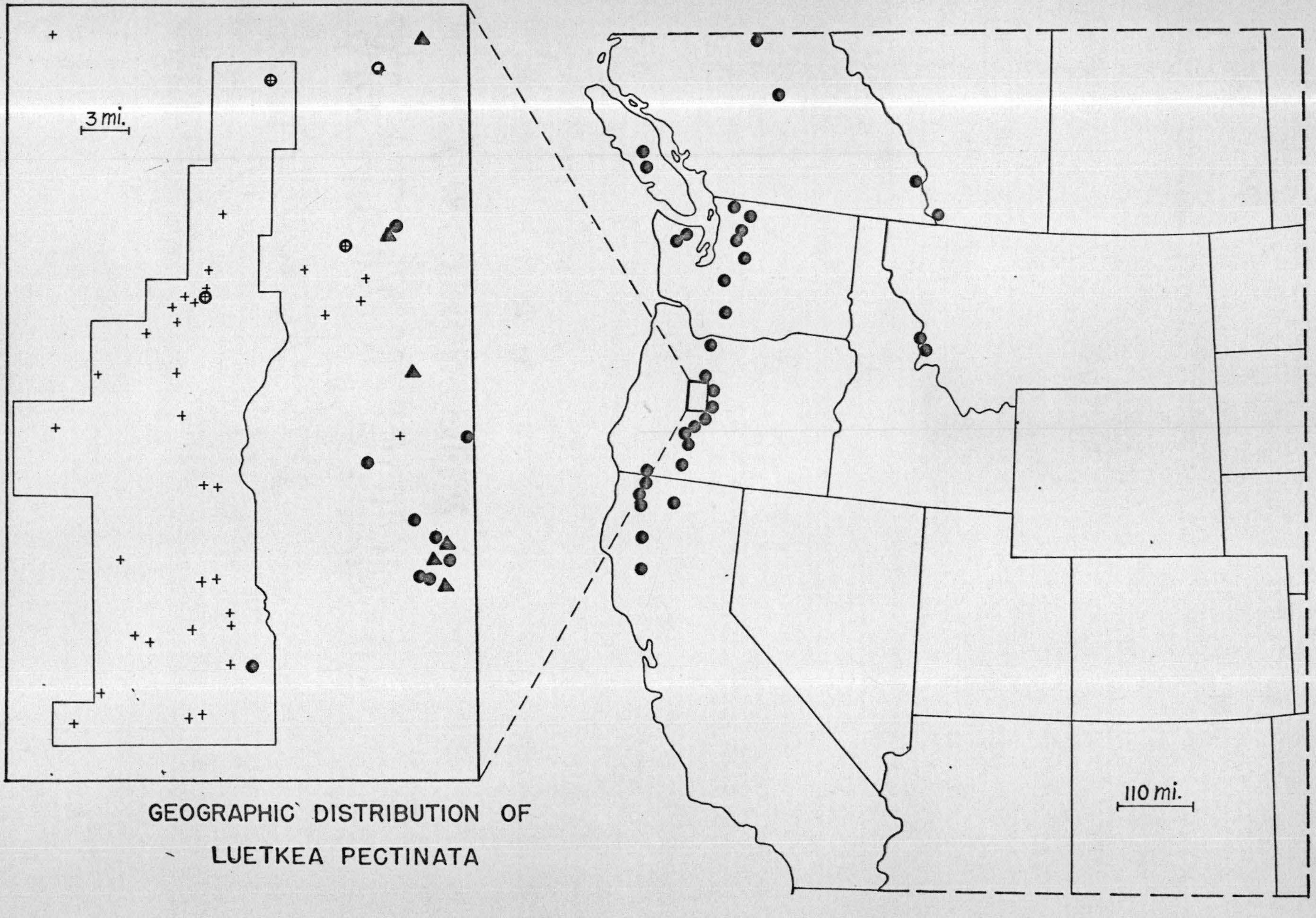


GEOGRAPHIC DISTRIBUTION OF RIBES ERYTHROCARPUM glandular-pubescent berries was formerly thought to be closely restricted to the Crater Lake region of the southern Cascades. A single locality was known from Gearhart Butte, Lake County. It is now known from six sites in the central Cascades, five of which are new with this study. The sixth site is represented by a specimen previously identified as *R. cereum* from near Mt. Jefferson. Large populations of this species were found only on Bachelor Mountain and Olallie Mountain. Other localities represent isolated occurrences of non-flowering material.

The large populations grow in light moist soil under *Abies procera* or *Abies amabilis*. Pockets of snow remain in both sites until July. Associated species include *Xerophyllum tenax*, *Ribes viscosissimum*, *Smilacina sessilifolia*, *Vaccinium membranaceum*, *Tsuga mertensiana*, *Abies amabilis*, *Valeriana sitchensis*, *Actea rubra*, *Achlys triphylla*, *Ribes lacustre*, *Asarum caudatum*, and *Taxus brevifolia*.

Luetkea pectinata (Pursh) Kuntze, Rev. Gen. 1:217. 1891.

A monotypic genus of northwestern North America, *Luetkea* is closely related to *Spiraea* and *Petrophytum* from which it differs in its bi- or triternate leaves and its rhizomatous habit. Primarily a species of the Cascade Range, *L. pectinata* is also found on Vancouver Island, in the Olympics, through the Canadian Rockies, and in the Bitterroot Range of Idaho and Montana. In the Cascades it is almost completely restricted to the highest peaks, where it is common around snowbeds, and in and around rivulets of snowmelt. Uncommon in the Western Cascades, *Luetkea* has been collected twice at the edges of summit snowbanks. It is also



GEOGRAPHIC DISTRIBUTION OF LUETKEA PECTINATA reported here for the first time from some of the lower peaks of the High Cascades. Other Snowbed species with which L. pectinata occurs include Orogenia fusiformis, Trillium ovatum, Erythronium grandiflorum pallidum, Castilleja parviflora oreopola, Arabis platysperma howellii, and Senecio triangularis.

Ivesia gordonii (Hook.) Torr. and Gray in Newberry, Pac. R. R. Rep. 63:72. 1857.

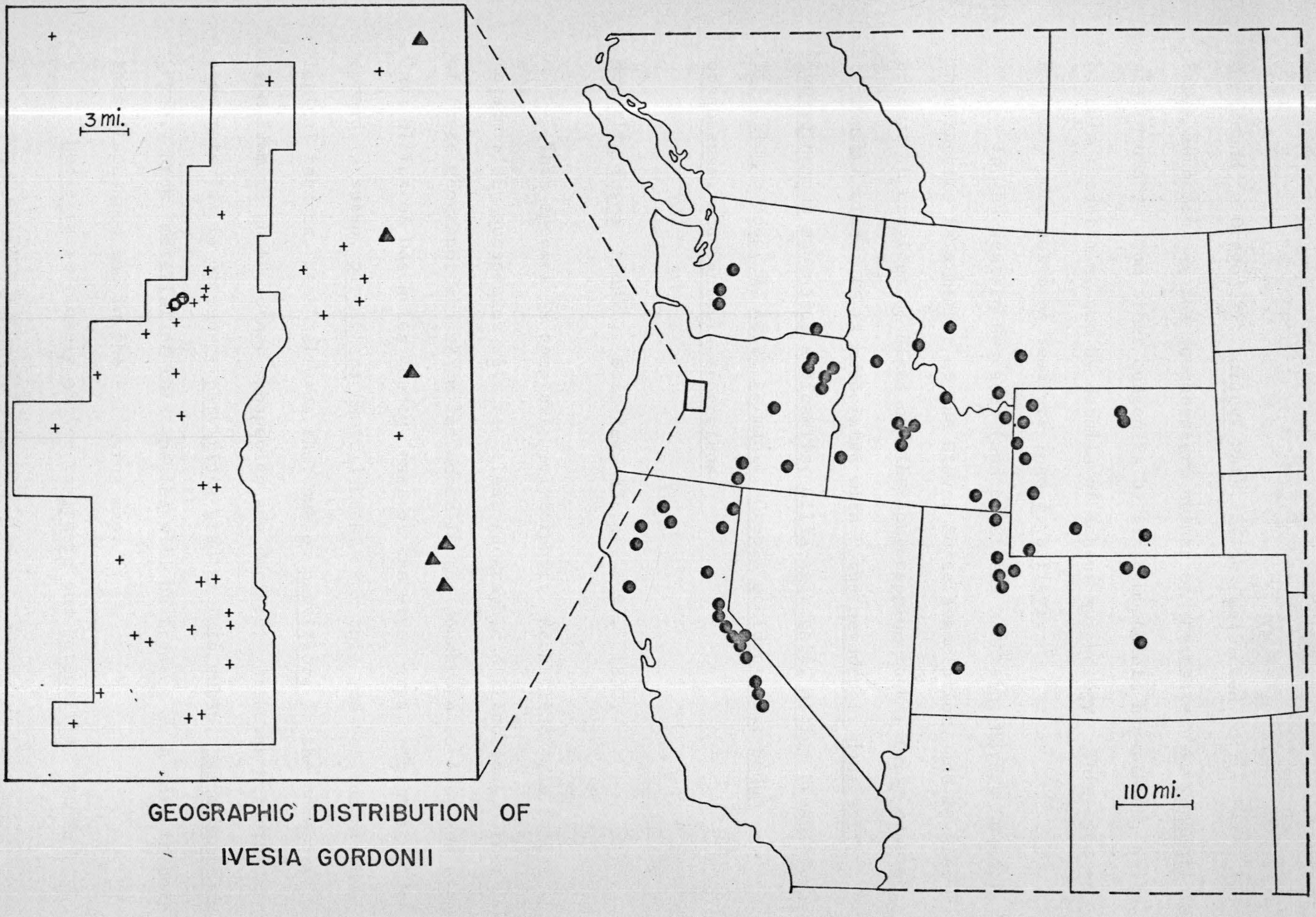
Selected synonyms:

Horkelia gordonii Hook., Journ. Bot. and Kew Misc. 5:341, pl. 12. 1853.

Ivesia alpicola Rydb. ex Howell, Fl. N. W. Am. 182. 1898.

This remarkable species, while widespread in western North America, has never previously been collected in the western half of Oregon. It occurs in abundance on the ridge connecting Iron Mountain and Cone Peak in Linn County, from which the nearest localities for the species are Mt. Adams, 230 air km to the north, and Drake's Peak, 300 air km to the southeast. Throughout its range I. gordonii is found at very high elevations, seldom below 2400 m and typically from 3000 to 4200 m. The disjunct Western Cascade populations occur between 1300 and 1700 m. The Washington Cascade populations are fully as disjunct as those in the Western Cascades, but they are found only above 3000 m.

Ivesia is separated from the closely related genera Horkelia and Potentilla by its stamen number (5 in I. gordonii), shallow hypanthium, few achenes, undilated filaments, low receptacle, yellow petals (often), and lack of distinctive odor (Keck, 1938). Although Ivesia as constituted by Keck contains 22 western American species, only two of these



GEOGRAPHIC DISTRIBUTION OF

IVESIA GORDONII

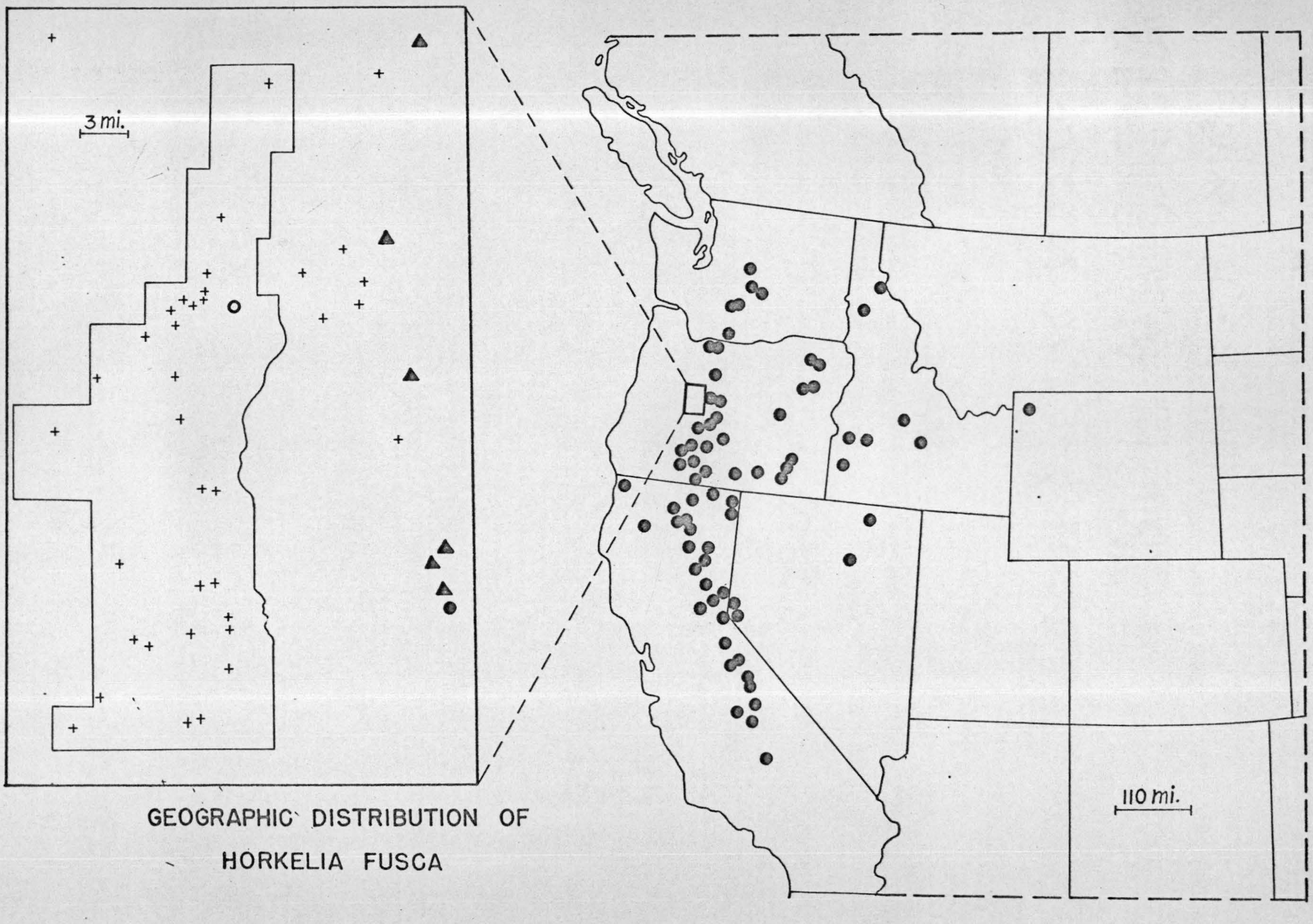
are found in Oregon, *I. baileyi* Wats. being restricted to the Basin and Range mountains in the southeastern corner of the state. *I. gordonii* is distinguished from other congeners by its campanulate hypanthium, white-hirsute receptacle, and by details of achene morphology. This species has many more pairs of leaflets than *I. baileyi*.

In the Western Cascades (and on Steens Mountain, Harney County) this species is a member of the Gravel Scree association, and is also present in crevices of dikes or other outcropping rocks, fully exposed to sun and wind. It is associated with *Lotus nevadensis douglasii*, *Chrysothamnus nauseosus albicaulis*, *Gilia aggregata*, *Allium crenulatum*, *Trifolium productum*, *Aster gormanii*, *Crepis occidentalis*, *Sedum oregonense*, and *Sanicula graveolens*.

Horkelia fusca Lindl., Bot. Reg. 23: pl. 1997. 1837.

This species is complexly polymorphic. Keck (1938) was forced to admit six subspecies with few clear geographic distinctions. Four of these geographical subspecies occur in the ponderosa forests and high lava plains of Deschutes County east of the study area. The most widespread is subsp. *parviflora* (Nutt.) Keck. For this and various morphological reasons, Keck believes that subsp. *parviflora* is the ancestral type from which the other subspecies are derived. Although Western Cascade material is of subsp. *parviflora* grading into subsp. *pseudocapitata* (Rydb.) Keck, material of this species will be treated as a unit in both this discussion and in the following map.

Horkelia is closely allied to *Ivesia* and *Potentilla*. It is



GEOGRAPHIC DISTRIBUTION OF
HORKELIA FUSCA

distinguished from both by having 10 stamens and a deep hypanthium. *H. fusca* is set apart from other horkelias by its 15-25 carpels, erect pedicels, 5-10 pairs of leaflets, entire stipules, and glabrous filaments and inner hypanthium. One collection of the species has been taken from west of the Cascade crest, high on the flank of Mt. Hood (*Gorman*, in 1891). In the Western Cascades, there is a large population of robust individuals at Lost Prairie, growing in an open gravelly flat at an elevation of 1000 m. A frost pocket, the area is surrounded by a *Picea engelmannii*-*Pinus monticola* dominated forest. Associated species in the meadow are *Solidago canadensis salebrosa*, *Potentilla drummondii*, *Erigeron aliceae*, *Viola bakeri*, *Anemone oregana*, *Sambucus racemosa pubens arborescens*, *Polygonum douglasii*, and *Prunella vulgaris lanceolata*.

Lupinus arbustus Dougl. ex Lindl. subsp. *neolaxiflorus* Dunn, Leafl. West. Bot. 7:254. 1955.

Selected synonyms:

Lupinus laxiflorus Dougl. ex Lindl., Bot. Reg. 14: pl. 1140. 1828.

Lupinus silvicola Heller, Muhl. 6:81. 1910.

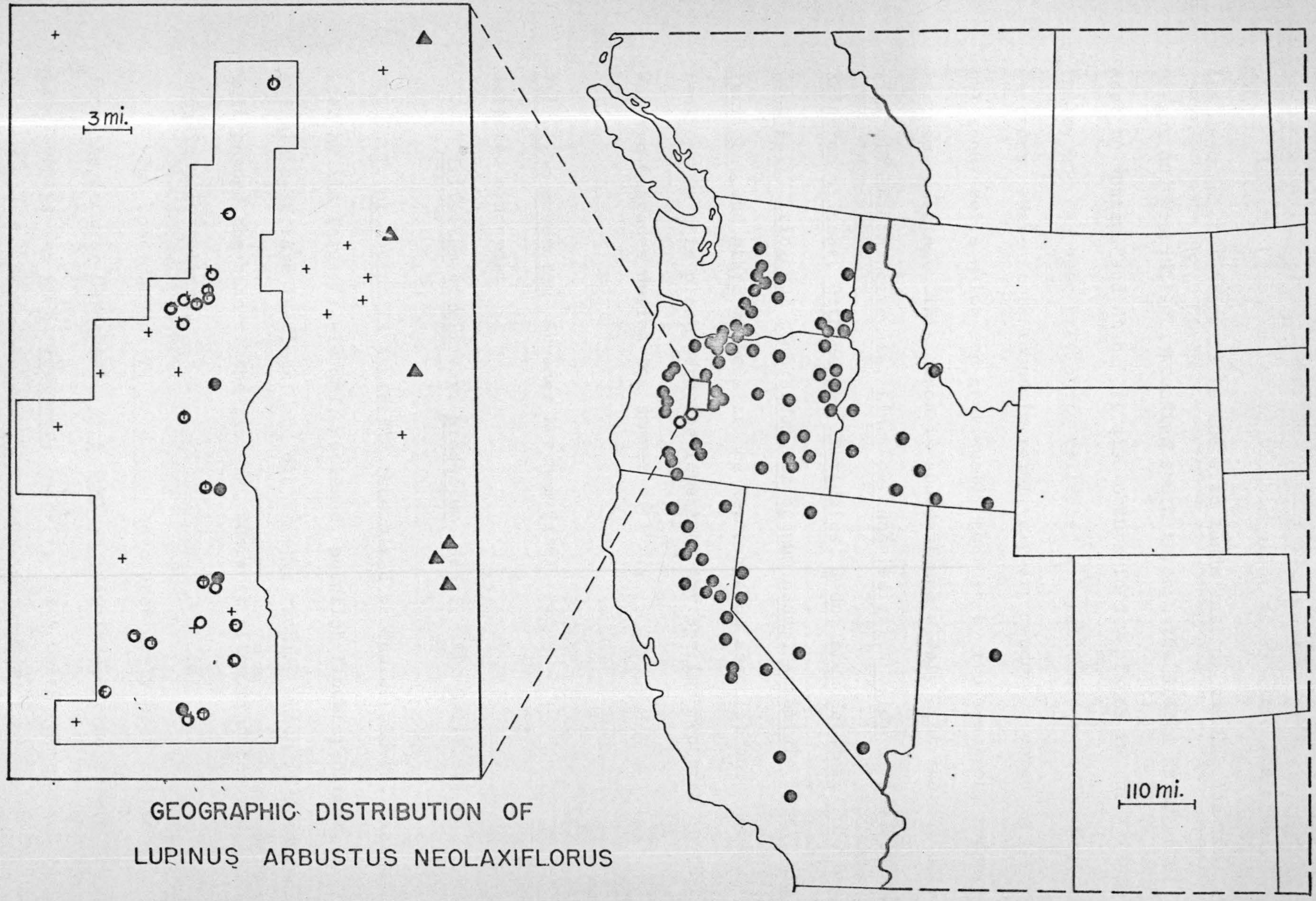
Lupinus laxiflorus var. *silvicola* C. P. Smith ex Jeps., Man. Fl. Pl. Calif. 527. 1925.

Lupinus arbustus subsp. *silvicola* Dunn, Leafl. West. Bot. 7:255. 1955.

Lupinus arbustus subsp. *arbustus* var. *montanus* (Howell) Dunn, Leafl. West. Bot. 7:254. 1955.

This taxon has a long and confusing nomenclatural history, due in part to a presumed later mislabelling of the holotype and in part to the difficult nature of taxonomy in the genus *Lupinus*. These problems are reviewed by Phillips (1955), Dunn (1955, 1957), and Hitchcock (in Hitchcock and others, 1961). While Hitchcock concedes that Dunn's arguments for reducing the complex taxon *L. laxiflorus* to a subtaxon of *L. arbustus* are probably correct, he continues to use the traditional nomenclature. Dunn's arguments are convincing to the present author, and for the most part, his nomenclature is followed here.

Dunn (1957) admits that intermediates are known among almost all combinations of the six subtaxa he proposes for the *L. arbustus* group. In addition he cites hybridization between members of this species and *L. caudatus*, *L. sulphureus*, *L. burkei*, and *L. rubricaulis*, as well as close morphological affinities with *L. lepidus* and *L. argenteus*. Although all these taxa are highly variable, *L. arbustus* subsp. *neolaxiflorus* is, in the main, a distinctive perennial lupine with an abaxially pubescent banner petal, a slightly spurred calyx, and a small patch of hairs near the upper tip of the wing petals. Material from the Western Cascades is morphologically subsp. *neolaxiflorus* according to Dunn's key (1957), but occurs in what he considers the range of subsp. *silvicola* Dunn and subsp. *arbustus* var. *montanus* Dunn. I see no morphological or geographical justification for segregating these three subtaxa, and the taxonomy, but not the nomenclature, of Hitchcock (in Hitchcock and others, 1961) is followed in this regard. The following map treats *L. arbustus* subsp. *arbustus*, subsp. *silvicola*, and subsp. *neolaxiflorus* as a single taxon under the last name. Subsp. *calcaratus* (Kell.) Dunn and subsp. *pseudoparviflorus* (Rydb.) Dunn are here recognized as separate taxa, not included on the map.



GEOGRAPHIC DISTRIBUTION OF
LUPINUS ARBUSTUS NEOLAXIFLORUS

Detling (1953) referred to this plant as a "xeric indicator." Its major distribution is in the arid lands east of the Cascades in Oregon and Washington, extending south through the Sierra Nevada and east to Montana and Utah. It also occurs in dry places in the Willamette Valley and has been previously collected several times from the Western Cascades. Here it is found in relatively dry meadows, rooted in light but rocky soils which are continually churned by frost action, rodents, and mass wasting. This taxon is abundant and widely distributed, occurring with *Gilia aggregata*, *Linum perenne lewisii*, *Collomia linearis*, *Erigeron aliceae*, *Orthocarpus imbricatus*, *Sedum stenopetalum*, *Polygonum douglasii*, *Eriogonum compositum*, *Eriogonum nudum*, *Artemisia ludoviciana latiloba*, and other members of the Xeric Meadow association. Moisture tensions in this plant were the lowest of any species measured in the Western Cascades during the summer of 1967.

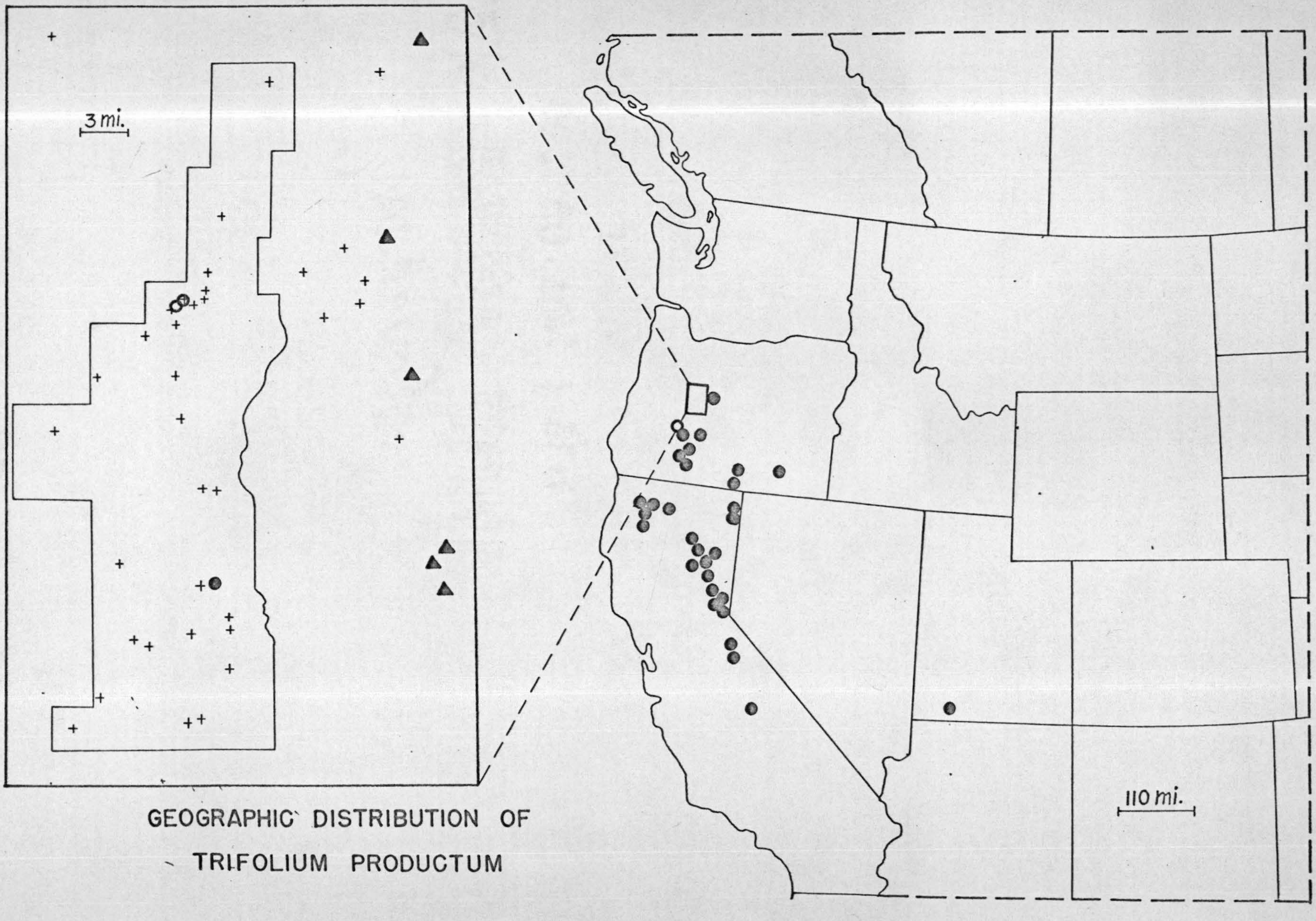
Trifolium productum Greene, Erythea 2:181. 1894.

Selected synonyms:

Trifolium kingii var. *productum* Jeps., Fl. Calif. 2:304. 1936.

T. productum is an easily recognized perennial clover, characterized by its large (11-18 mm), reflexed, purplish flowers; narrow, spinulose-serrate leaflets; and distinctive rachis, which is produced well beyond the head of the flowers, where it often branches and is occasionally foliose.

Two specimens of *T. productum* have previously been collected from the central Cascades: *J. B. Leiberg*, in 1934, Horsepasture Mt., Lane County; and *A. R. Sweetser*, in 1927, "Jack Creek, Metolius Region,



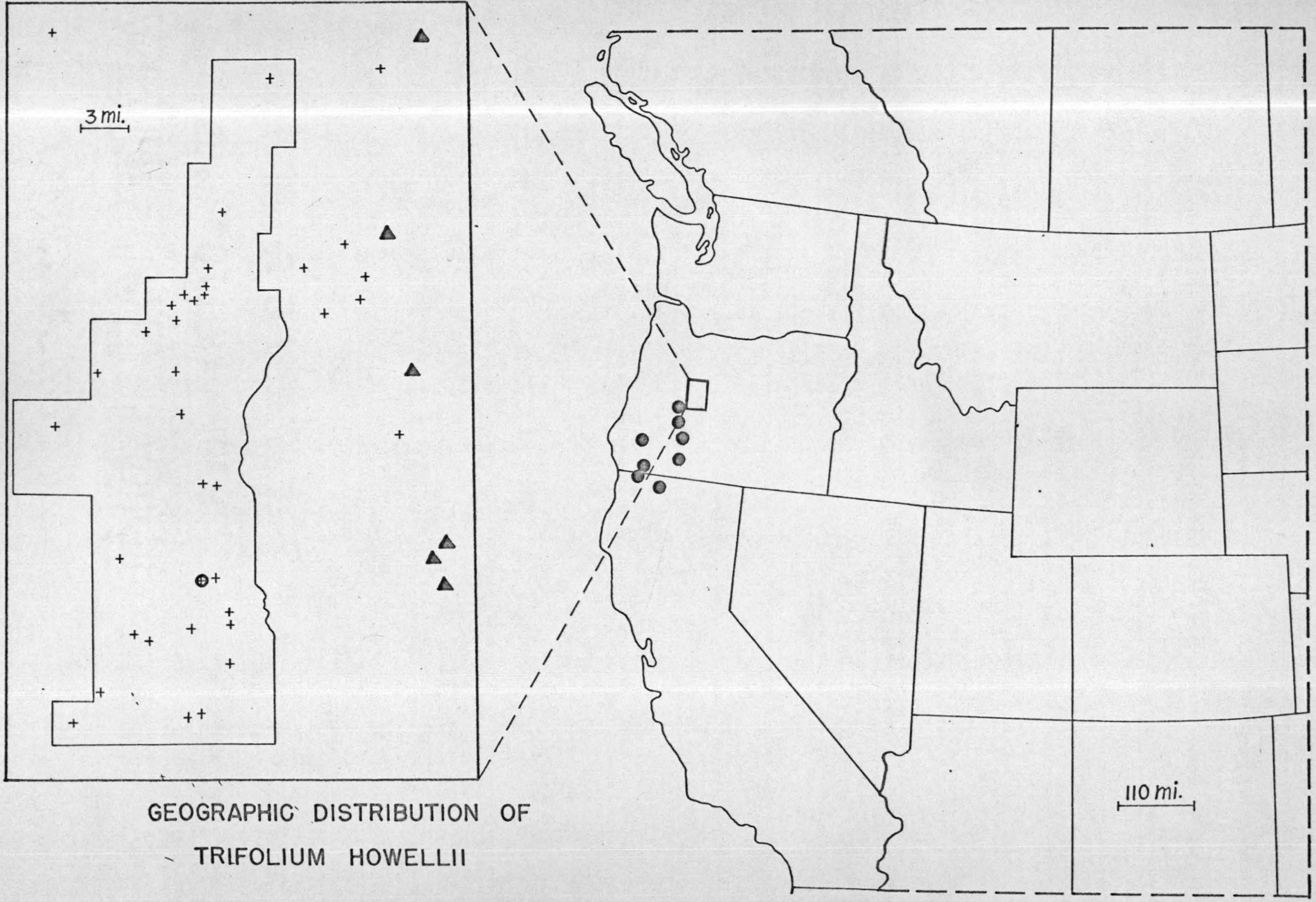
GEOGRAPHIC DISTRIBUTION OF
TRIFOLIUM PRODUCTUM

Crook County." It is the last specimen on which Martin (1943) bases the northwestern limit of his range description, but Jack Creek is in the southwestern part of Jefferson County, not Crook County as stated on Sweetser's label. In addition to the population on Horsepasture Mt., three other large populations have been collected in the Western Cascades by the author: Bohemia Mountain, Iron Mountain, and Cone Peak. In all of the Western Cascade localities, this clover is found rooted in crevices of dark volcanic outcrops or in the scoria gravel derived from them. A plant of hot, dry, south-facing slopes, *T. productum* is typically associated with *Crepis occidentalis*, *Aster gormanii*, *Ivesia gordonii*, *Gilia aggregata*, *Allium crenulatum*, *Lotus nevadensis douglasii*, and *Castilleja rupicola*.

Trifolium howellii Wats., Proc. Am. Acad. 23:262. 1888.

A distinctively robust clover of damp, often marshy places, *T. howellii* can be separated easily from other clovers by lack of an involucre, glabrous calyx, globose heads, large flowers (11-15 mm), trifoliate leaves, and large leaflets (2.5-5 cm in breadth). Its relationships to other members of this large genus are not clear.

The range of *T. howellii* is rather restricted. It occurs west of the Cascade crest from Lane County south to the Siskiyou Mountains of northern California. It reaches its northernmost limit in the central Western Cascades, near the summit of O'Leary Mountain, where it is occasionally encountered in moist shady spots on the north and west-facing slopes under *Abies amabilis* and *Pseudotsuga menziesii*. The



GEOGRAPHIC DISTRIBUTION OF TRIFOLIUM HOWELLII author has also collected this species on Bohemia Mountain, Lane County, where it is relatively abundant in open springy areas along with *Caltha bifolia*, *Mimulus moschatus*, *Veratrum viride*, and *Boykinia major*.

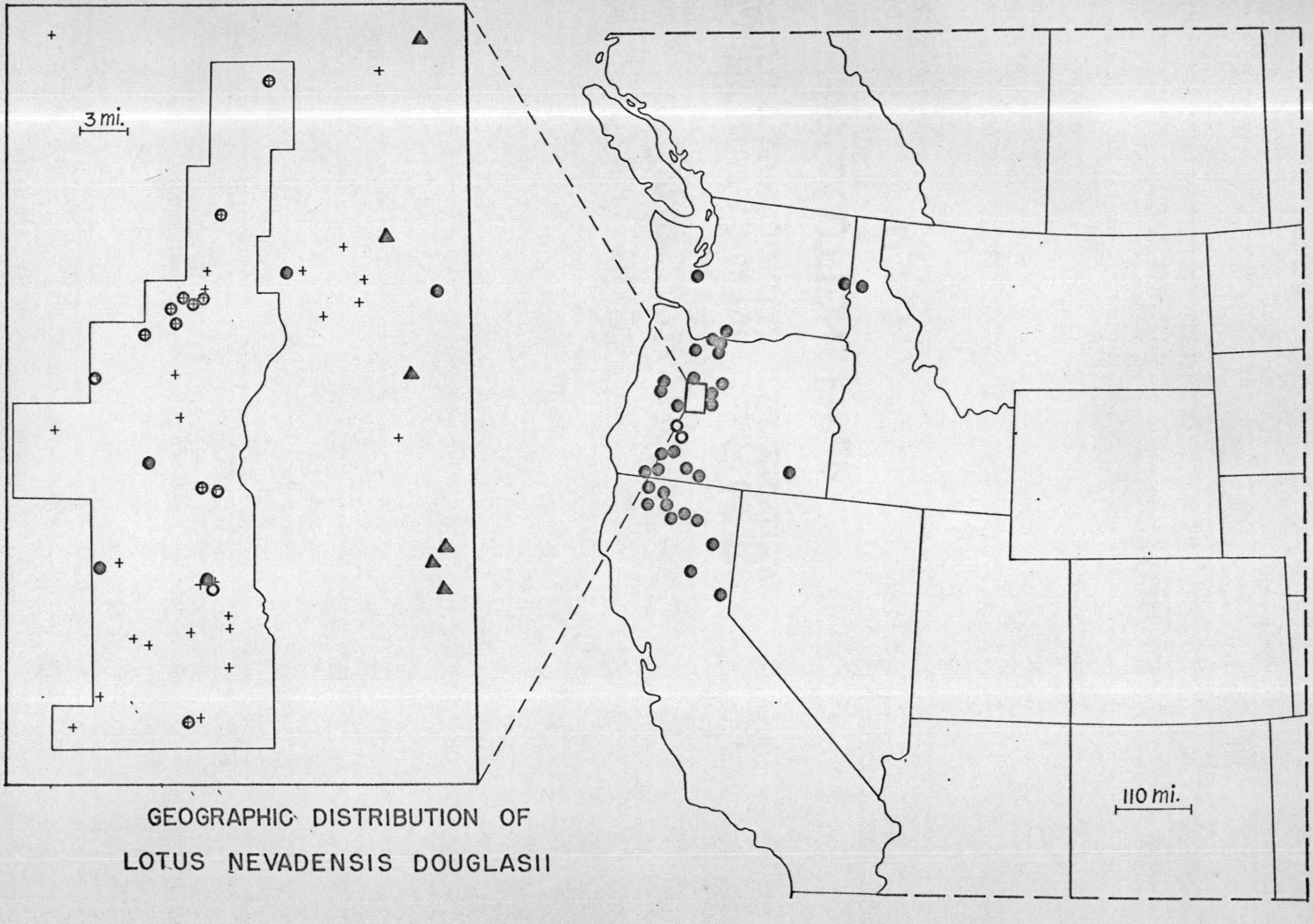
Lotus nevadensis (Wats.) Green var. *douglasii* (Greene) Ottley,
Britt. 5:81. 1944.

Selected synonyms:

Lotus douglasii Greene, Pitt. 2:149. 1890.
Hosackia decumbens Benth., Bot. Reg. 15: under pl. 1257. 1829.

The most recent monographer of Western American loti recognizes three varieties of *L. nevadensis* (Ottley, 1923, 1944). The variety *congestus* has shorter branches and internodes, and is found along the northern California coast. Variety *nevadensis*, which is smaller in all respects, is found throughout southern California and adjacent Nevada. Variety *douglasii*, the most northern subspecific taxon, grades into both other varieties in northern California. It is found primarily through the Sierra-Cascade chain, with some localities in the Willamette Valley, near Puget Sound, and in eastern Oregon and Washington.

It normally grows in dry rocky places, but its prostrate habit and indehiscent beaked legumes make it well adapted to life as a weed. In Oregon it is typically found in soil disturbed by human activity. It is especially abundant along trails and has been called "mule clover" by observant outdoorsmen. Occasionally it occurs along trails in shady woods, where it becomes erect and larger in all respects but does not flower. It is not consistently associated with any other species, although it is commonly a member of the Gravel Scree association with



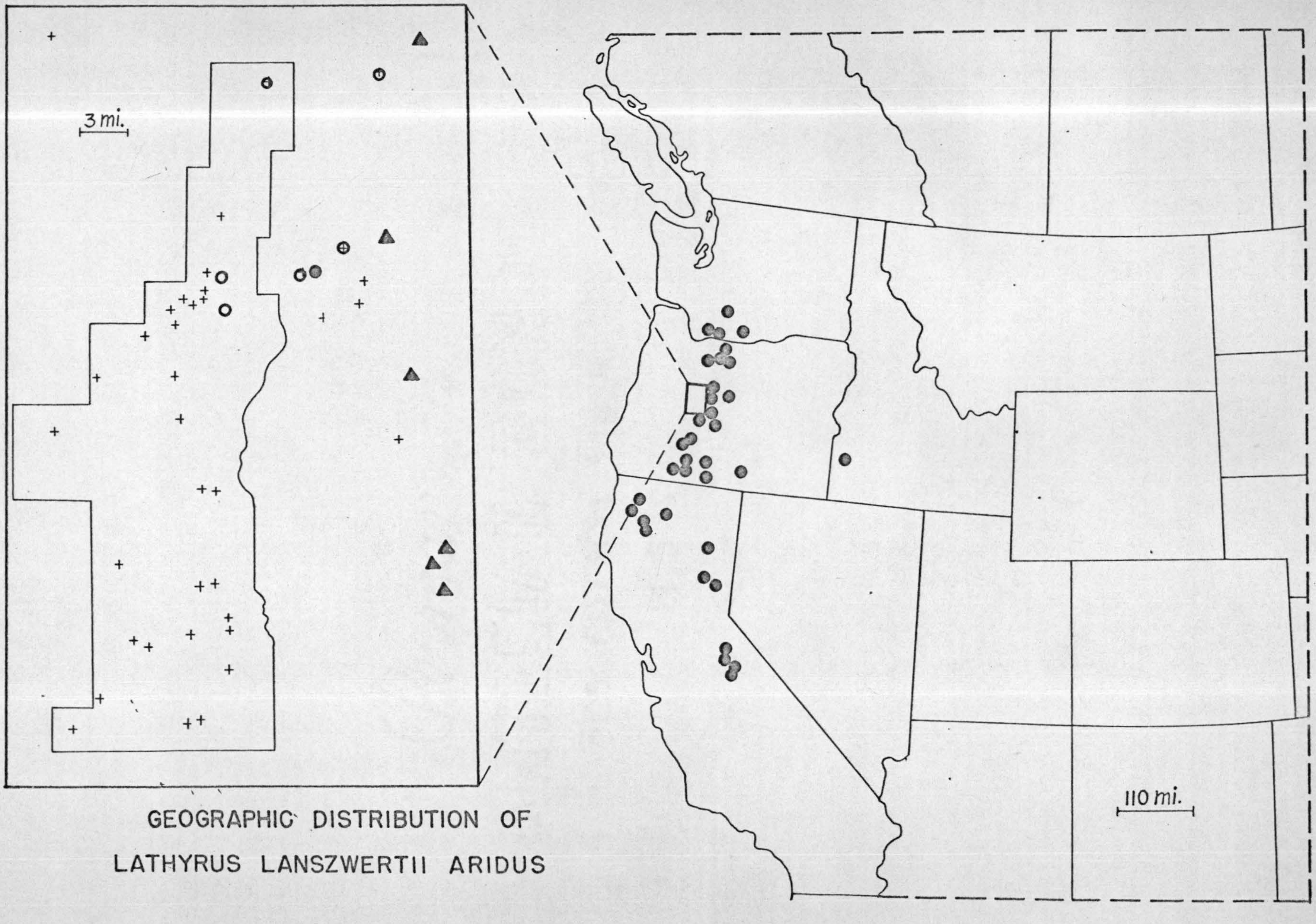
GEOGRAPHIC DISTRIBUTION OF
LOTUS NEVADENSIS DOUGLASII

Chrysothamnus nauseosus, *Gilia aggregata*, *Crepis occidentalis*, *Ivesia gordonii*, and *Eriogonum compositum*.

Lathyrus lanszwertii Kell. var. *aridus* (Piper) Jeps., Fl. Calif. 2:389. 1936.

Lathyrus is one of the more difficult genera of the Leguminosae, exhibiting a great deal of what Hitchcock (1952) terms "fortuitous variation." Leaf shape, flower color, pubescence, and other potentially diagnostic characters vary widely, to the taxonomist's distress. *L. lanszwertii aridus* is, however, an easily recognized taxon, characterized by six narrowly linear leaflets appressed in pairs, a non-functional or completely absent tendril, and small white flowers, often with lavender or ochroleucous highlights. The variety *lanszwertii* has more leaflets; a functional tendril; and larger, more highly colored flowers. It is widespread in eastern Oregon and extends to Washington and Idaho, Utah, and central California. Variety *aridus* is more limited in distribution but is more abundant where it does occur. It is found in a narrow belt on the east side of the Cascades from Mt. Adams to Mt. Shasta, approximately occupying the ponderosa pine belt. In California it occurs in the Klamath Mountains and the northern Sierra Nevada. A single locality has been recorded from Owyhee County, Idaho, where this variety is typically replaced by variety *lanszwertii*.

New localities in the Western Cascades include dry gravel scree slopes at high elevations and dry partly-shaded forest floors on the lower eastern slope of the range. One other collection from the junction of the Santiam highways, Linn County (*Peck 25911*: OSC) has been



GEOGRAPHIC DISTRIBUTION OF
LATHYRUS LANSZWERTII ARIDUS

discovered from west of the Cascade crest in northern Oregon.

Linum perenne L. subsp. *lewisii* (Pursh) Hultén, Fl. Alas. 7:1122. 1947.

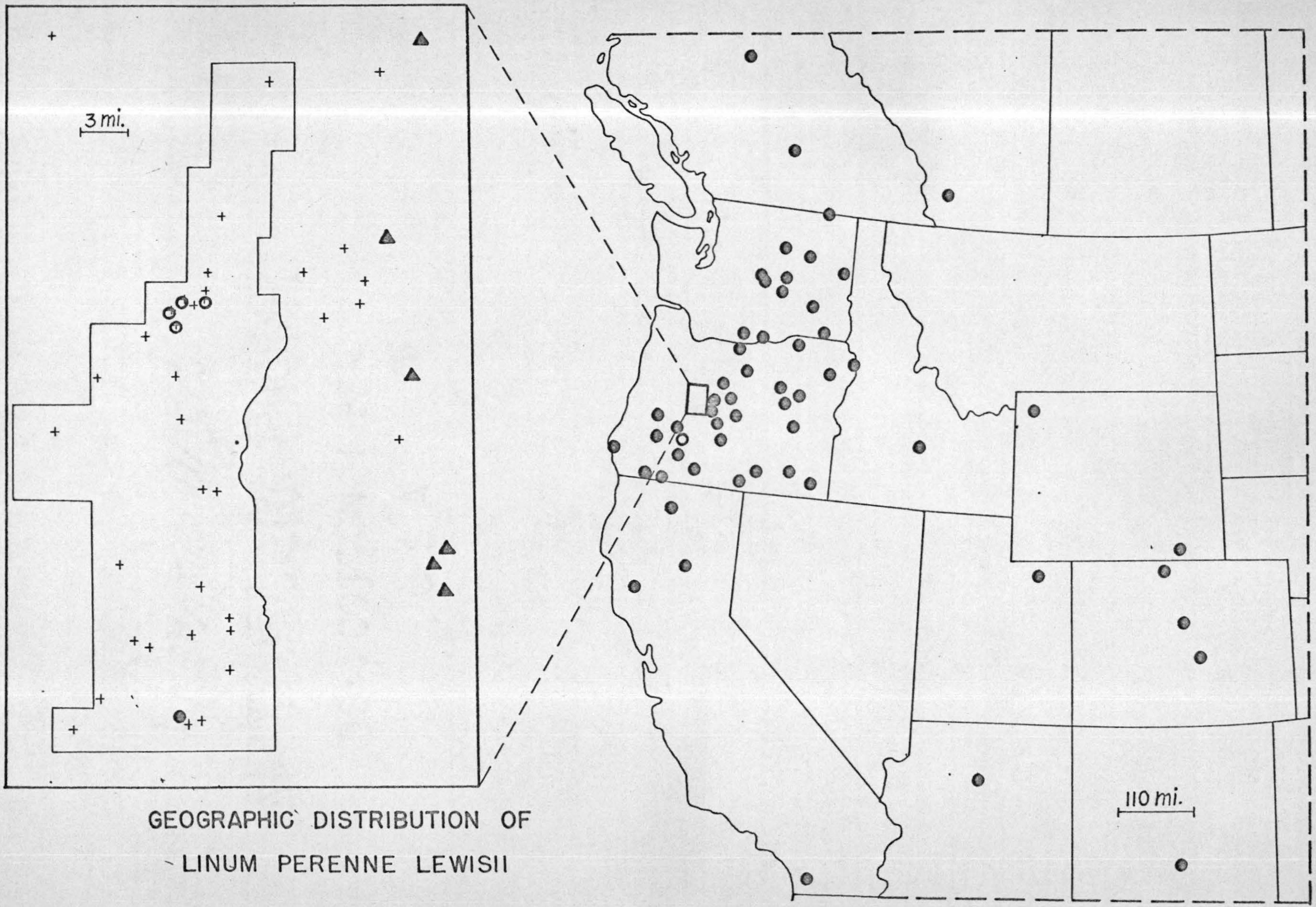
Selected synonyms:

Linum lewisii Pursh, Fl. Am. Sept. 210. 1814.

Linum perenne var. *lewisii* Eat. and Wright, N. Am. Bot. 302. 1840.

Although *L. lewisii* of western North America has traditionally been considered specifically distinct from *L. perenne* of Europe and Asia, there is only one significant difference between them: Eurasian material is heterostylous, while American populations are homostylous. Thus, it seems most accurate to consider the morpho-geographical forms as taxonomic subspecies.

L. perenne is the only perennial American flax with blue flowers. A widespread, variable, montane species, it ranges from Alaska south to Cerro Potosi in the Sierra Madre Oriental of Mexico (Beaman and Andresen, 1966), where it occurs above 3500 m. Prior to this study, the species had been collected twice from the central Cascades west of the crest (*Gilkey*, in 1936: OSC; *L. E. Detling 7021*). It is also common in the dry southwest-facing meadow slopes of Iron Mountain, Echo Mountain, and Browder Ridge, where it is associated with *Artemisia ludoviciana latiloba*, *Gayophytum diffusum parviflorum*, *Gilia aggregata*, *Eriogonum compositum*, *Eriogonum nudum*, *Polygonum douglasii*, *Orthocarpus imbricatus*, *Lupinus arbustus neolaxiflorus*, *Cerastium arvense*, and other members of the Xeric Meadow association.



GEOGRAPHIC DISTRIBUTION OF
LINUM PERENNE LEWISII

Gayophytum diffusum T. and G. subsp. parviflorum Lewis and Szweyk.,
Britt. 16:386. 1964.

Selected synonyms:

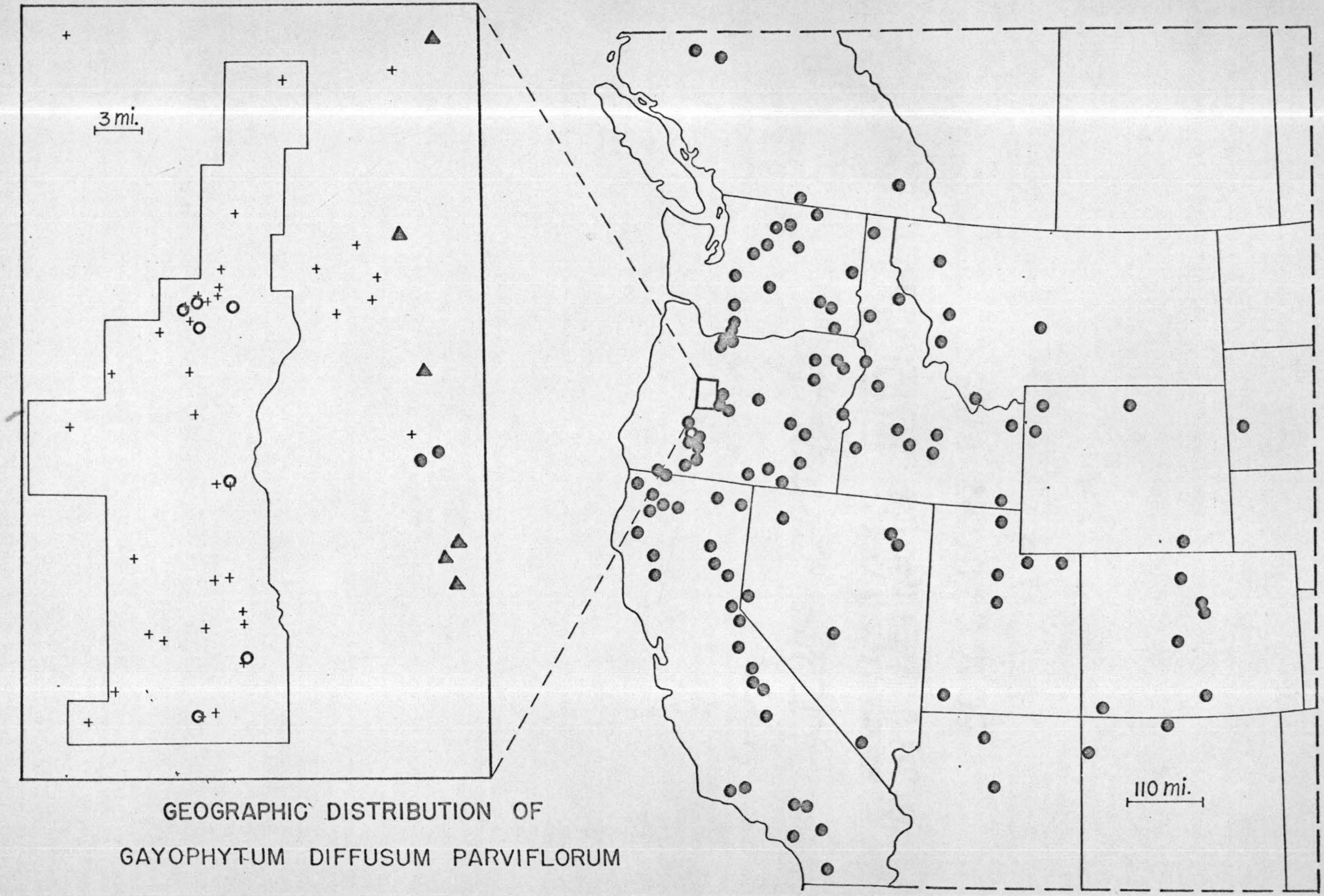
Gayophytum lasiospermum Greene, Pitt. 2:164. 1891.

Gayophytum ramosissimum T. and G. var. strictipes Hook.,
Lond. Journ. Bot. 6:224. 1847.

Gayophytum intermedium Rydb., Bull. Torr. Bot. Club 31:569.
1904.

Gayophytum nuttallii T. and G. var. abramsii Munz, Am. Journ.
Bot. 19:774. 1932.

The Gayophytum nuttallii complex as discussed by Hitchcock (in Hitchcock and others, 1961) has long been puzzling to taxonomists. The large number of synonyms for the present taxon is an indication of the variety of opinions concerning its identity and status (Munz, 1932). A significant breakthrough in the understanding of the genus came with the application by Lewis and Szweykowski (1964) of cyto-evolutionary techniques. These workers verified the existence of both diploid and tetraploid taxa within the group and thereby discovered that many of the traditional key characters for these species are of no taxonomic value. Four of the diploid species (G. decipiens, G. ramosissimum, G. oligospermum, and G. eriospermum) are quite closely related, the two former being widespread through the western United States and the latter pair being restricted to different portions of California. They have retained the ability to interbreed freely, as evidenced by the existence of G. heterozygum, a postulated diploid hybrid between G. oligospermum and G. eriospermum. This proposed hybrid is found through the Cascade-Sierra chain and along the California coast. The variable and widespread tetraploid, G. diffusum, seems to have been derived by



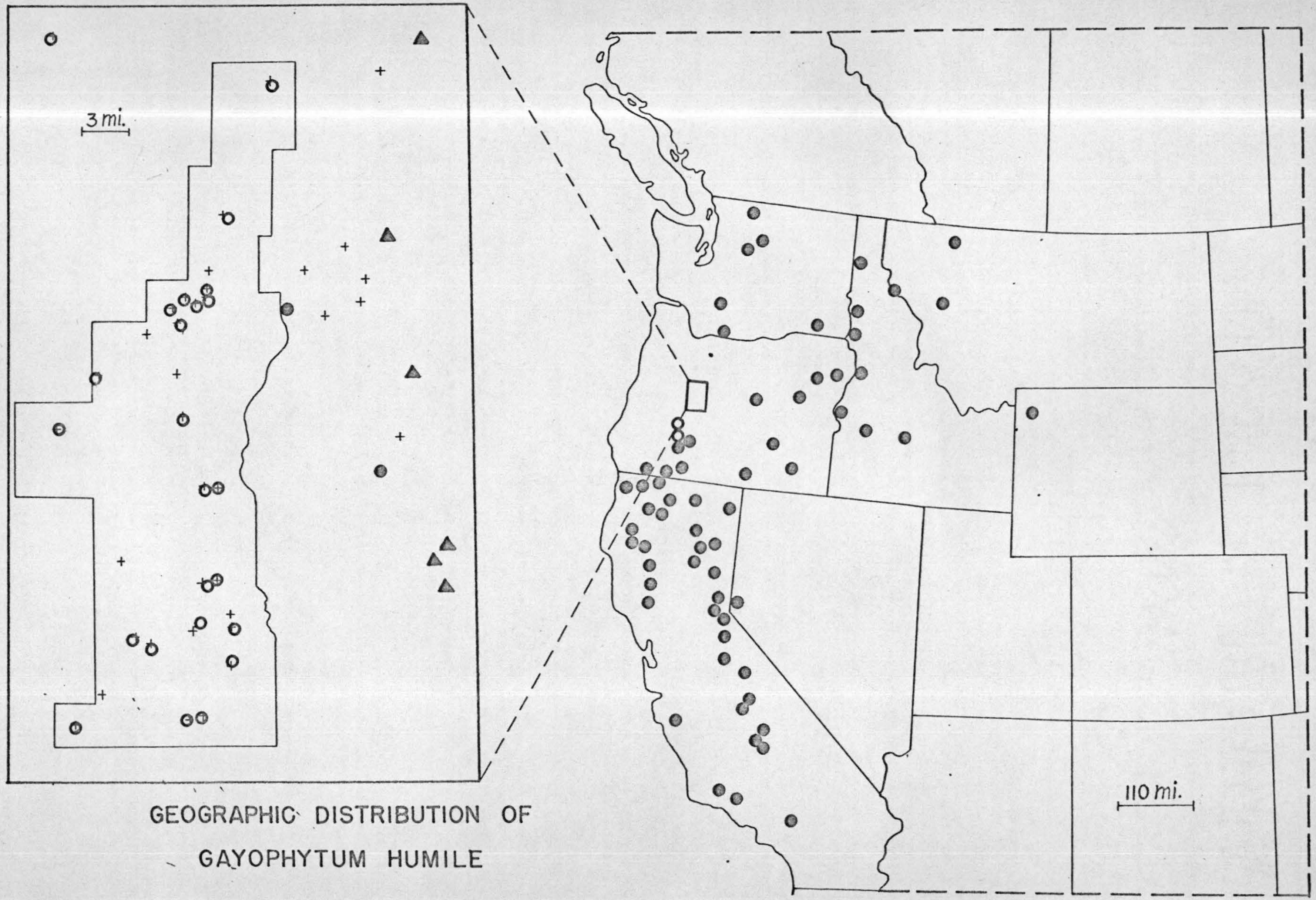
GEOGRAPHIC DISTRIBUTION OF GAYOPHYTUM DIFFUSUM PARVIFLORUM contributions of genes from all of these species. The small-flowered subspecies *parviflorum* is the most widespread taxon in the genus and is so variable that it is easily confused with any of the parental diploids if chromosome counts are not made. An indication of its morphological variability is that in their careful key to the 10 taxa of the genus, Lewis and Szweykowski arrive at *G. diffusum parviflorum* through six different dichotomies. Western Cascade material is all readily identifiable as *G. diffusum parviflorum* of the "*lasiospermum*" type.

It is my opinion that because the geographical range of *G. diffusum diffusum* is completely contained within that of *G. diffusum parviflorum*, the two entities should be considered as varieties and not subspecies, but no new combinations are proposed here. The two taxa are commonly found growing together, but subsp. *diffusum*, with large flowers, is modally outcrossing, while subsp. *parviflorum* is almost completely self-fertilizing. Intermediates between these two forms are common in some localities, indicating that some outcrossing must normally occur in populations of *G. diffusum parviflorum*.

All members of the genus except *G. humile* occur in dry habitats. In the Western Cascades, *G. diffusum parviflorum* occurs in the loose soil of dry meadows, flowering late in July or August. It is easily missed in the spring. Common Xeric Meadow associates include *Polygonum douglasii*, *Polygonum minimum*, *Galium bifolium*, *Cirsium centaurea*, *Orthocarpus imbricatus*, *Collomia linearis*, and *Microsteris gracilis*.

Gayophytum humile Juss., Ann. Sci. Nat. I. 25:18, t.4. 1832.

Gayophytum humile occurs in widely-separated areas in North and



GEOGRAPHIC DISTRIBUTION OF
GAYOPHYTUM HUMILE

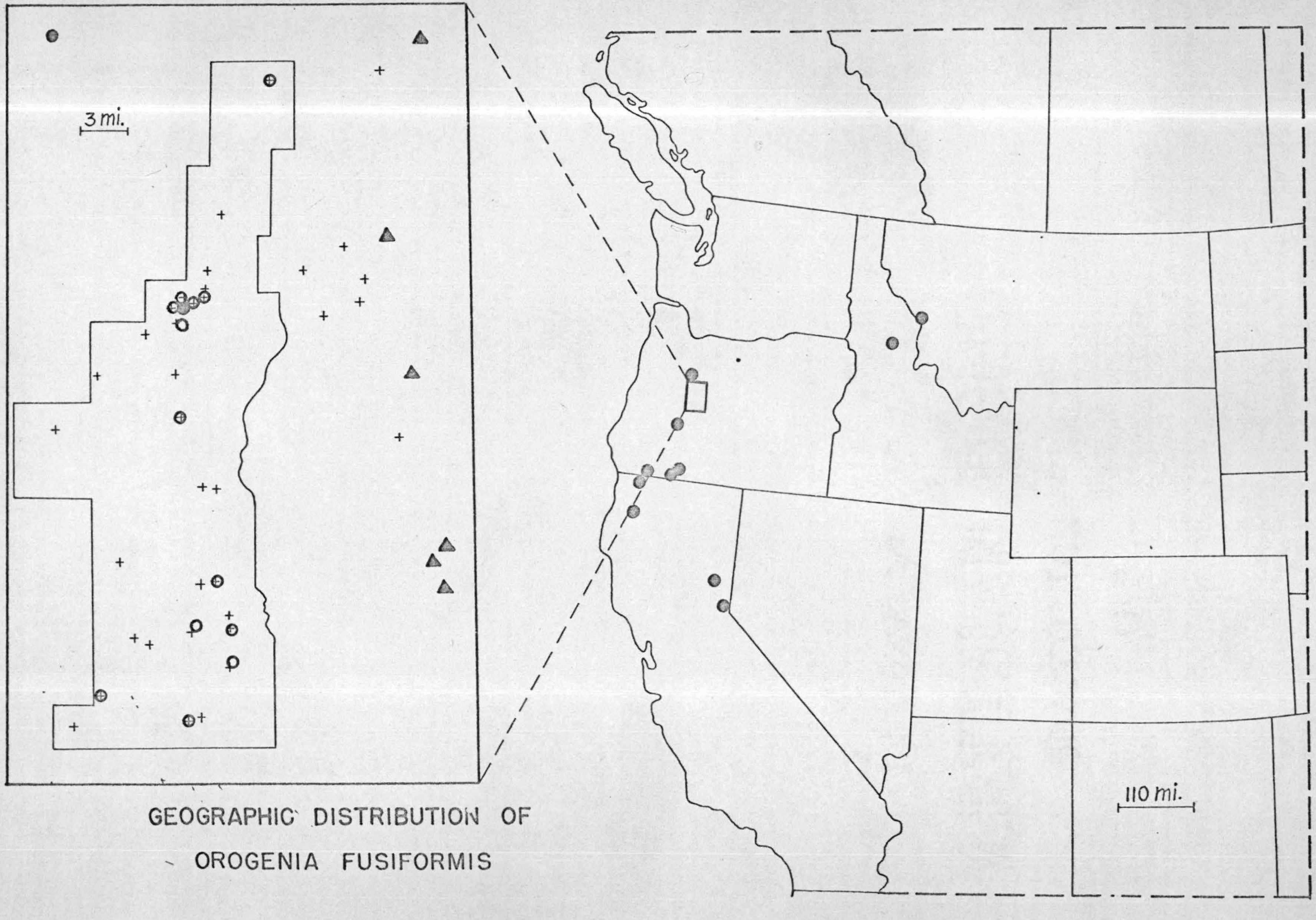
South America. Numerous other distantly-related species exhibit similar amphi-tropical distributions (Raven, 1963). A number of populations of this species exist in the Andes of Chile and Argentina at the approximate latitude of Santiago. They are morphologically identical to North American material (Lewis and Szweykowski, 1964).

Because of its dense branching pattern, low habit, and numerous seeds aligned obliquely in the capsule, *G. humile* is the most distinctive member of this confusing genus. It is, however, very closely related to other members of the group and seems to have produced the tetraploid *G. racemosum* by amphidiploidy with *G. decipiens* (Lewis and and Szweykowski, 1964). In North America this species occurs in the Klamath Mountain-Sierra arc of California and southern Oregon and again in the Columbia Intermontane Province of Washington, northeastern Oregon, and adjacent Idaho. A few specimens have also been reported from the Rocky Mountains of Idaho, Montana, and Wyoming. The species has evidently never before been collected from west of the Cascade crest north of Jackson County.

In the Western Cascades *G. humile* occurs in the spring in running snowmelt or in the dampest and shadiest portions of Mesic Meadow slopes. It is ephemeral, disappearing when water becomes limiting. Other common species in the Rocky Melt Seep association are *Mimulus breweri*, *Lewisia triphylla*, *Polygonum kelloggii*, *Allium crenulatum*, and *Romanzoffia sitchensis*.

Orogenia fusiformis Wats., Bot. King Exp. 120. 1871.

Orogenia is a small and poorly collected genus of western North



GEOGRAPHIC DISTRIBUTION OF OROGENIA FUSIFORMIS

America. Evidently closely related to Lomatium, the genus is characterized by subterete glabrous fruits with corky lateral wings and obsolete stylopodium and carpophore. The two component species, O. fusiformis and O. linearifolia Wats., differ in overall size and shape of the root, O. fusiformis having a spindle-shaped taproot and larger, more fully developed leaves, while O. linearifolia is characterized by a globose root and smaller leaves. The latter species occurs in the Rocky Mountains from southeastern Washington and Ravalli County, Montana, south to Utah and western Colorado. O. fusiformis has a disjunct distribution similar to that of Mertensia bella. It occurs in north-central Idaho and in the Western Cascades from Marion County south to northern California, where it enters the Siskiyou Mountains. Populations are also known from the northern Sierra Nevada in the Lake Tahoe region. The present study has approximately doubled the number of collecting sites known for this species.

Both species of Orogenia are snowbed plants, blooming with the earliest vernal assemblages and growing almost without fail at the edge of slowly melting snowbanks. Some specimens have been observed pushing flowering stalks up through compacted snow. Such early blooming times are undoubtedly factors contributing to the paucity of collections. O. fusiformis is commonly found with Dicentra uniflora, Trillium ovatum, Erythronium grandiflorum pallidum, Senecio triangularis, Hydrophyllum occidentale, and other Snowbed association species.

Pterospora andromedea Nutt., Gen. Pl. 1:269. 1818.

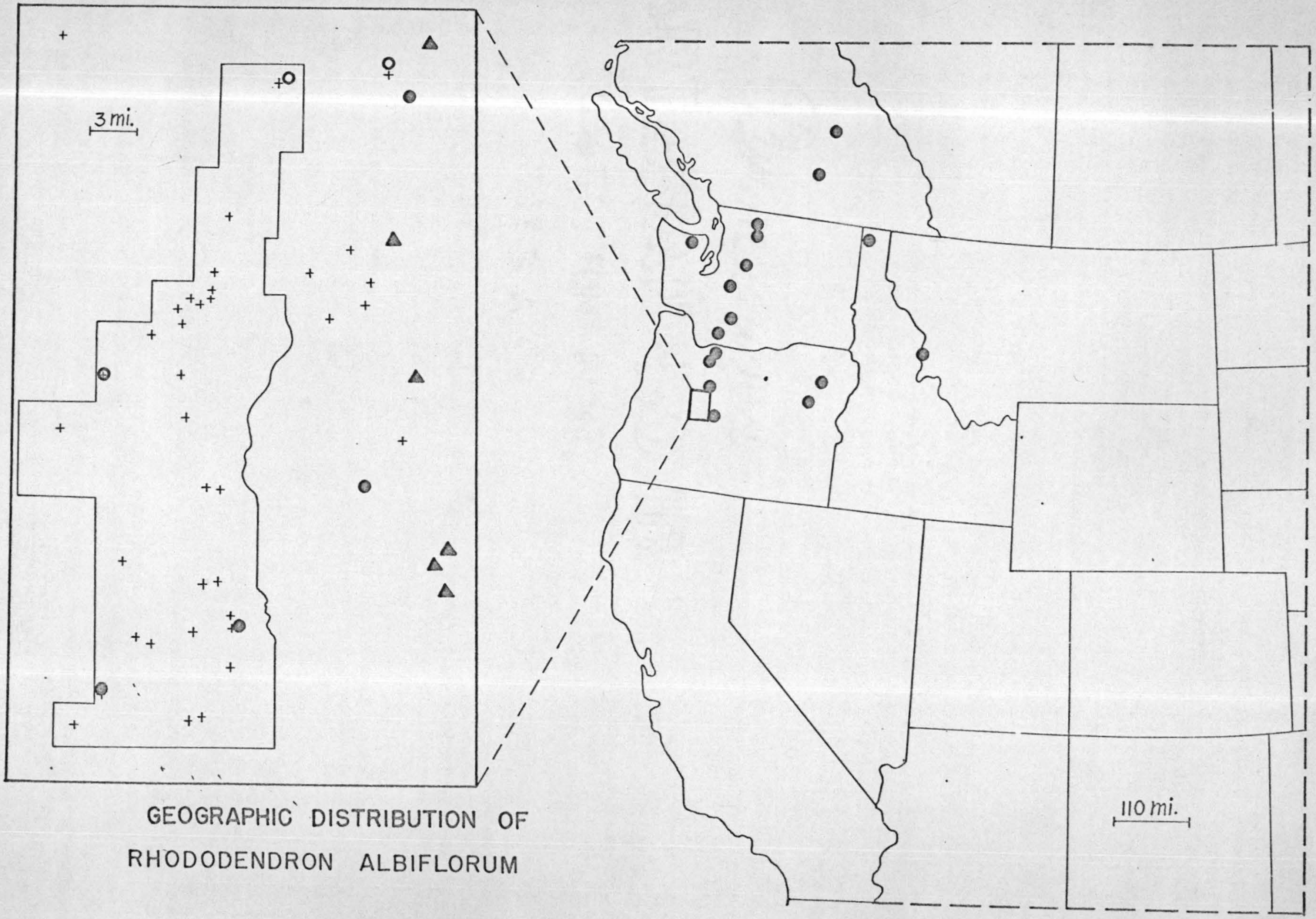
Pterospora is a monotypic genus of saprophytic heaths. Although the type was collected near Niagara Falls, it is typically western, occurring normally in dry open forests, usually under *Pinus ponderosa* in the Pacific Northwest (Copeland, 1941). The stem is viscid and woody, growing to a height of nearly two meters. It does not, therefore, make a manageable herbarium subject and has been poorly collected. No map of the distribution of *Pterospora* is presented in this work.

The occurrence of the genus *Pterospora* west of the Cascade crest has been documented previously by at least one worker (Hopson, 1946). During the course of the present study, this species was found growing under a Mesic Conifer Forest canopy dominated by *Pseudotsuga menziesii* on Castle Rock and Tidbits Mountain.

Rhododendron albiflorum Hook., Fl. Bor. Am. 2:43. 1834.

This interesting species reaches its southernmost limit of known range within the study area. It is distinct from all other rhododendrons, having 10 stamens, deciduous leaves, and relatively small (2 cm) white corollas. *R. albiflorum* ranges from the Selkirk Mountains of British Columbia south in the Rocky Mountains to Baker County, and to Indian Ridge in the central Western Cascades. It grows in damp sites, either along streams or lakes or on shaded north-facing slopes where snowmelt runs late in the season. It is typically a high montane species, occurring as low as 1200 to 1500 m only in the Western Cascades, where it has now been collected from four localities.

A member of the most mesic subdivision of the Mesic Conifer Forest, *R. albiflorum* is commonly associated with *Menziesia ferruginea*,



GEOGRAPHIC DISTRIBUTION OF
RHODODENDRON ALBIFLORUM

Vaccinium membranaceum, *Senecio triangularis*, *Ligusticum grayi*, and *Valeriana sitchensis*.

Menziesia ferruginea Smith, Pl. Ic. Ined. pl. 56. 1791.

Selected synonyms:

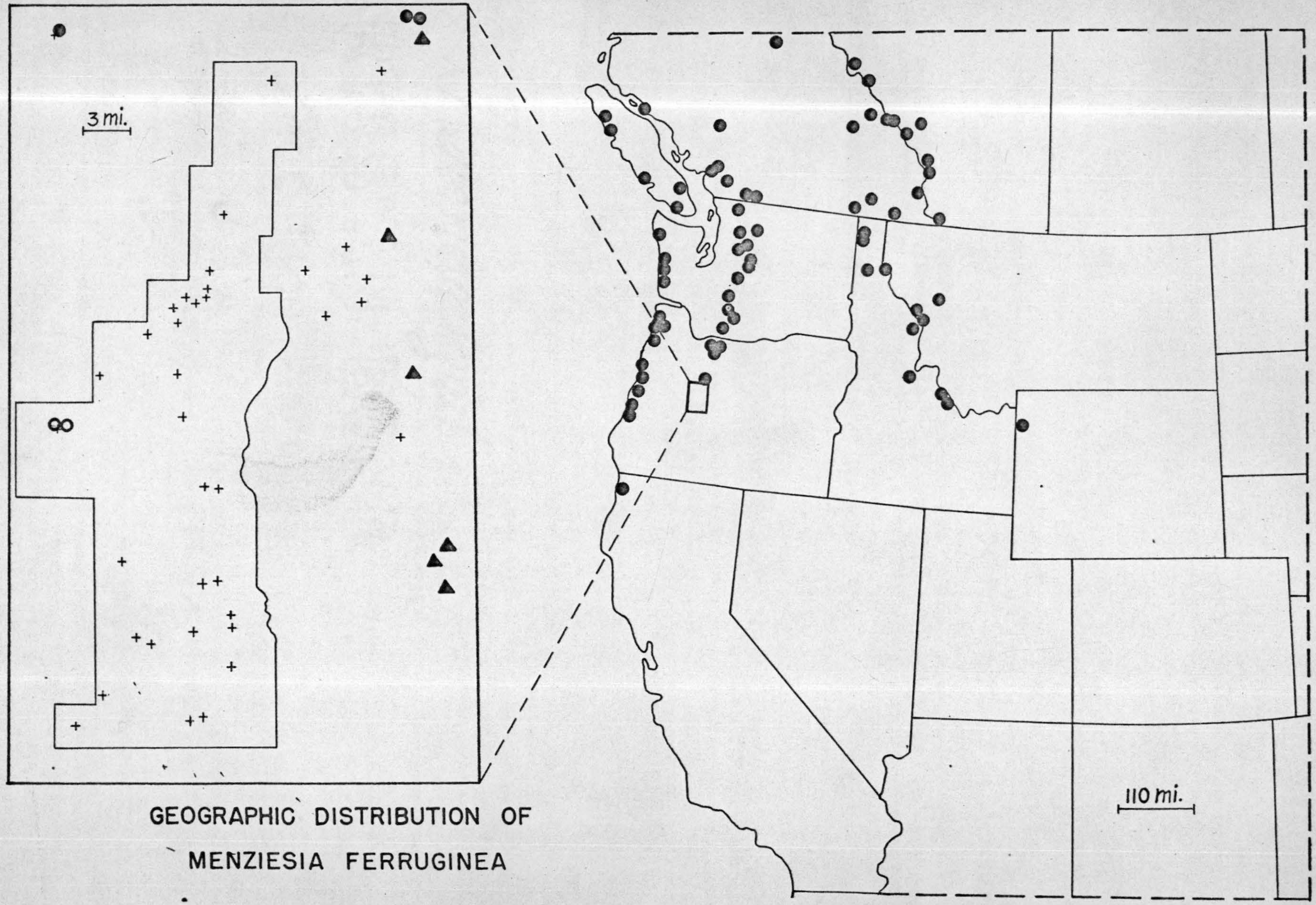
Menziesia glabella Gray, Syn. Fl. 2^1:39. 1878.

Menziesia ferruginea var. *glabella* Peck, Man. High. Pl. Oreg. 542. 1941.

Menziesia ferruginea subsp. *glabella* Calder and Taylor, Can. Journ. Bot. 43:1398. 1965.

Recent work has shown that the two extreme forms of western North American *Menziesia* must be considered conspecific, and further that there are no justifiable grounds for drawing coherent subspecific lines (Hickman and Johnson, 1968). *M. ferruginea* is most closely related to the Appalachian *M. globularis* Salis., although there are also several species of this genus native to Japan. *M. ferruginea* occurs from the Kenai Peninsula south along the coast to Humboldt County, California, and through the Cascades and Rocky Mountains to Tidbits Mountain and northwestern Wyoming, respectively.

M. ferruginea is always found in moist habitats similar to those occupied by *Rhododendron albiflorum*, with which it is often associated in the Western Cascades. Other members of the Mesic Conifer Forest frequently found in the vicinity include *Vaccinium membranaceum*, *Senecio triangularis*, *Ligusticum grayi*, and *Valeriana sitchensis*. *M. ferruginea* is evidently quite localized and highly disjunct in the central Western Cascades. Populations occurring here constitute the southernmost known occurrences of the montane form.



GEOGRAPHIC DISTRIBUTION OF MENZIESIA FERRUGINEA

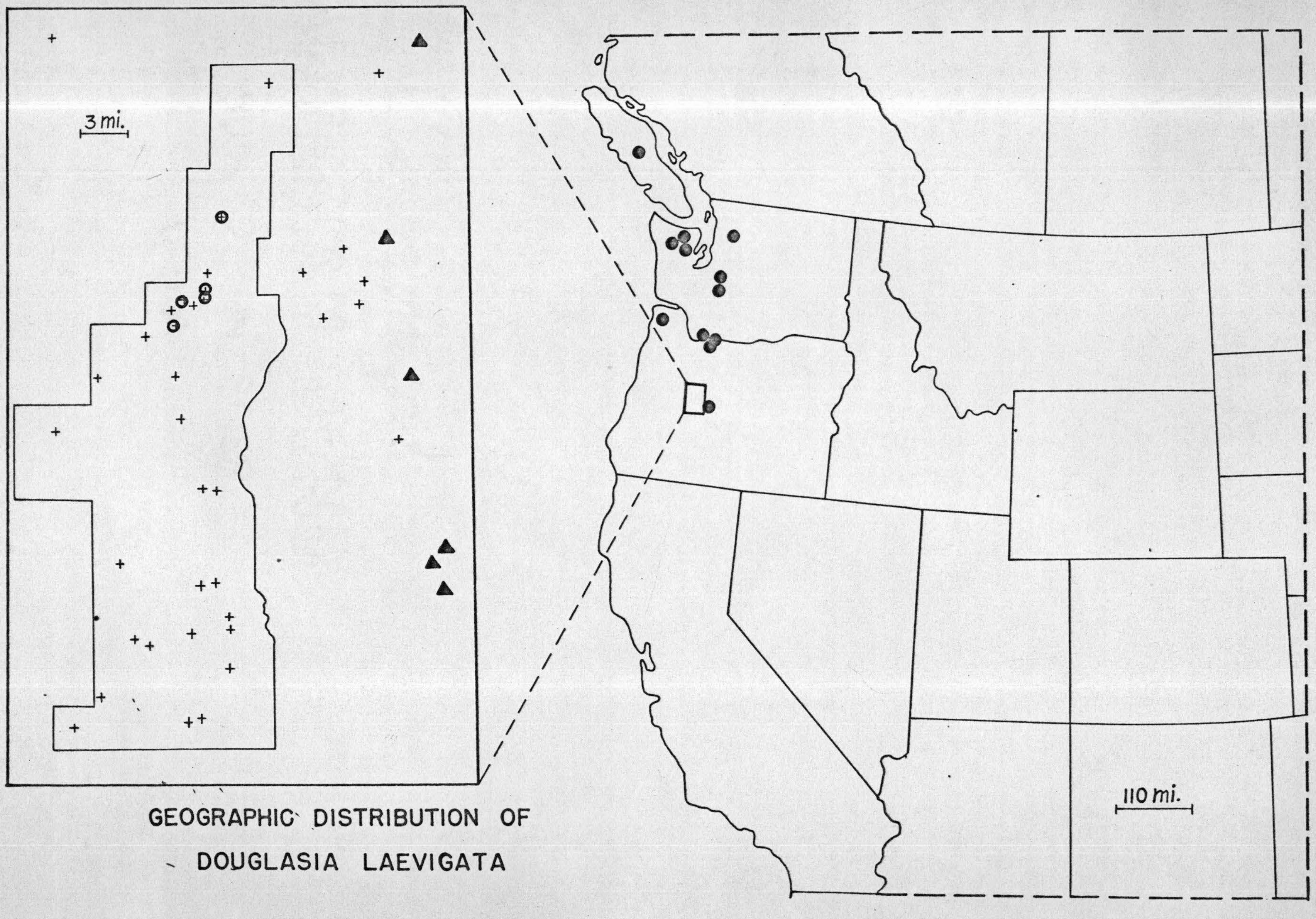
Douglasia laevigata Gray, Proc. Am. Acad. 16:105. 1880.

Selected synonyms:

Douglasia laevigata var. ciliolata Const., Am. Mid. Nat. 19:254. 1938.

Douglasia laevigata subsp. ciliolata Cald. and Tayl., Can. Journ. Bot. 43:1398. 1965.

Constance (1938) notes that generic distinctions in this portion of the Primulaceae (Androsaceae-Primulinae) are weak. Douglasia's closest relatives are probably Androsace and Primula, all three of which have obvious arctic affinities. There are six species of Douglasia. Two are arctic American, three are from the higher western Cordillera, and the remaining, which is sometimes segregated into the genus Gregoria, is from the Alps-Pyrenees chain. Constance believes that Douglasia is probably a pre-glacial genus whose distribution can now be considered relictual. D. nivalis, a form with stellate pubescence and an umbellate inflorescence, occurs from the northern Rocky Mountains to the Wenatchee Mountains of Washington and is probably the closest relative of D. laevigata. Constance divides the present species into two varieties, the typical form occurring in the Columbia Gorge at elevations as low as 30 m. The more widespread variety ciliolata, differentiated by the number and size of the simple cilia on the leaf margins and the more compact umbellate inflorescence, is found in the mountains of Vancouver Island to the Olympic Peninsula, where it is abundant, and also on Saddle Mountain, Clatsop County. In the Cascades its previously known range was from Snohomish County, Washington, south to Mt. Hood. The Western Cascade populations are intermediate between the two named varieties, and their separation is questioned by the present author.



GEOGRAPHIC DISTRIBUTION OF DOUGLASIA LAEVIGATA

Accordingly, they are treated as a single taxon here.

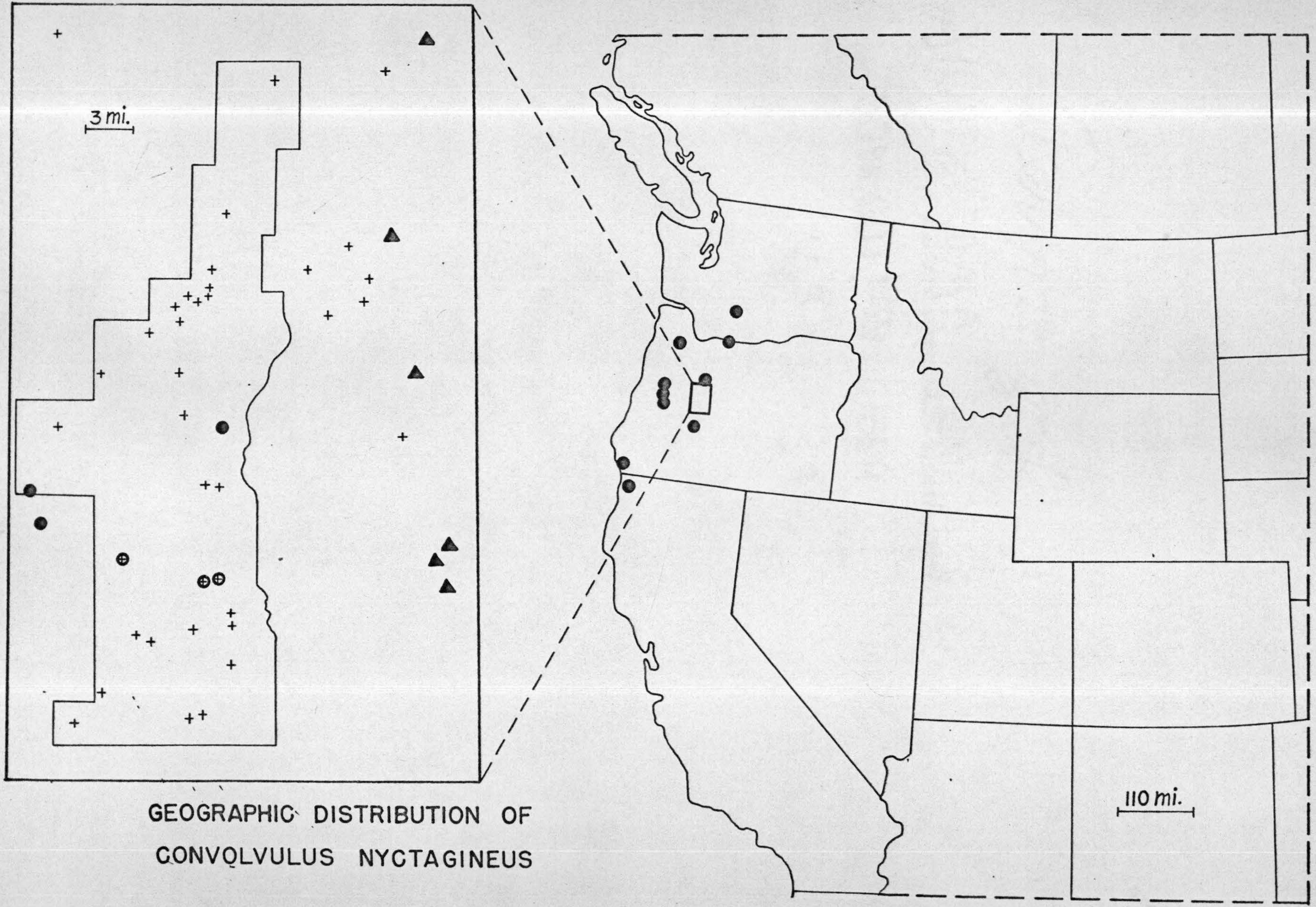
In the Western Cascades, as on Saddle Mountain, *Douglasia* grows on vertical faces of basalt or andesite, rooted in crevices. An interesting aspect of its local habitat is that it grows only on faces that are well exposed to the prevailing winds. It seems likely that moisture in the forms of mist and fog, common in all the areas where the species occurs, is a critical factor in its distribution. Other species of the Vertical Outcrop association include *Saxifraga bronchialis vespertina*, *Penstemon rupicola*, *Castilleja rupicola*, and *Heuchera micrantha*.

Convolvulus nyctagineus Greene, Pitt. 3:327. 1898.

Selected synonyms:

Convolvulus atriplicifolius House, Muhl. 4:54. 1908. (not *C. atriplicifolius* Poir.)

A typically Oregonian species, *C. nyctagineus* is distinguished from other native morning glories by its broad floral bracts, which conceal the calyx; its deltoid-hastate leaves; and its trailing to erect (but not twining) habit. Although it has been collected from the coast mountains of Curry County and Del Norte County, California, it is primarily found in dry places in the Willamette Valley and in the Western Cascades. It has also been collected occasionally from the eastern end of the Columbia Gorge and north to the vicinity of Mt. Adams on the eastern slope of the Cascades. Three new localities are reported here, two of which (O'Leary and Horsepasture Mountains) include the highest elevations yet reported for the species (1650 m).



GEOGRAPHIC DISTRIBUTION OF
CONVOLVULUS NYCTAGINEUS

In the Willamette Valley, C. nyctagineus is a plant of gravelly roadsides and dry fields and pastures. In the Western Cascades it is restricted to dry south-facing slopes of open gravelly loam. Here it occurs with Erigeron foliosus confinis, Phacelia linearis, Polygonum spergulariaeforme, Githopsis specularioides, Plectritis congesta, Gayophytum diffusum parviflorum, Microsteris gracilis, and other members of the Lowland Xeric Meadow association.

Polemonium pulcherrimum Hook., Curtis' Bot. Mag. 57: pl. 2979. 1830.
Selected synonyms:

Polemonium viscosum Nutt. var. pilosum Greenm., Bot. Gaz. 25:263. 1898.

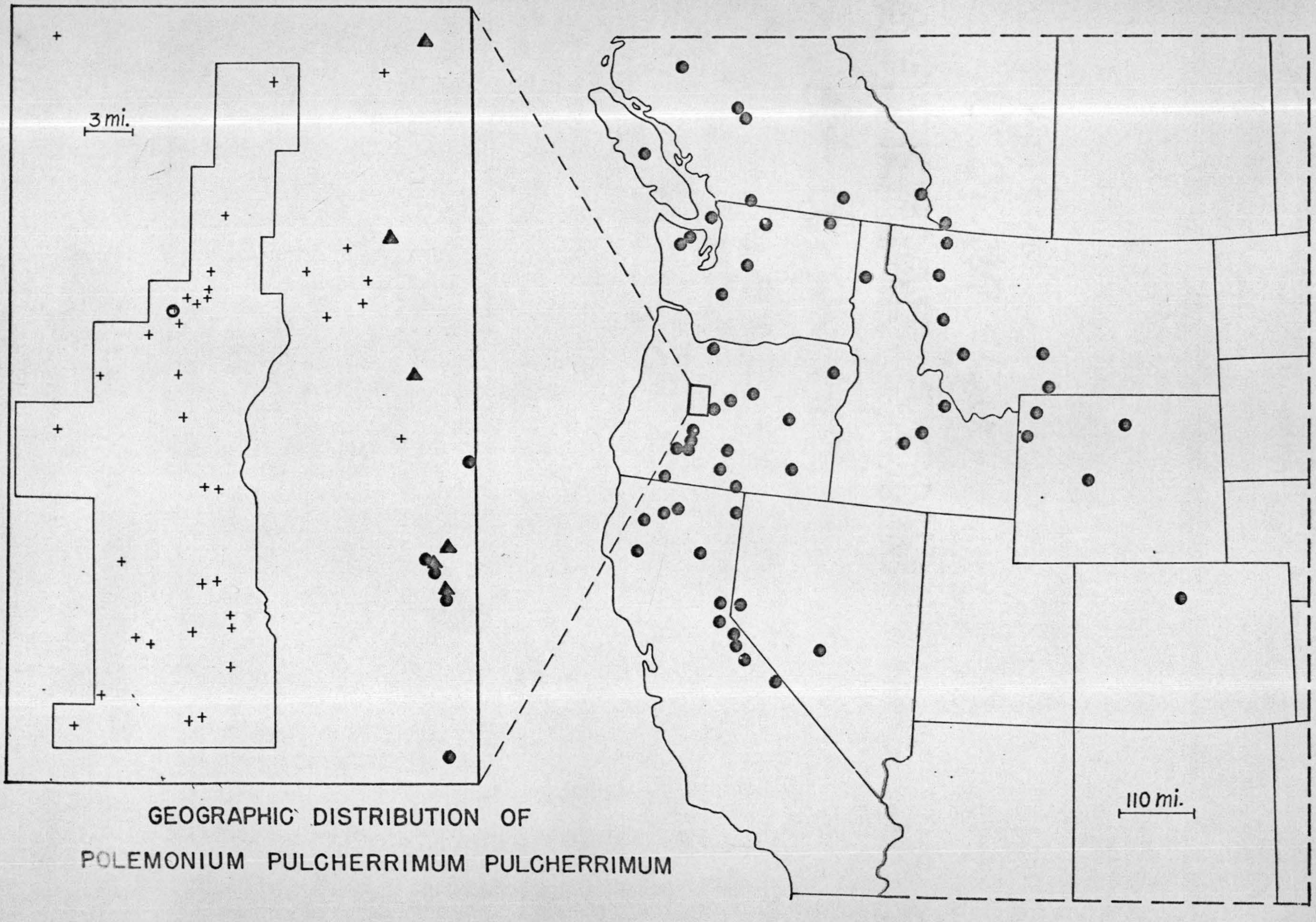
Polemonium pilosum Jones, Univ. Wash. Publ. Biol. 5:125. 1936.

Polemonium shastense Eastw., Bull. Torr. Bot. Club 32:205. 1905.

Wherry (1967) recognized "six major taxa" of temperate tufted polemoniums. Of these, four (perhaps five) should be treated as members of a single polytypic species. Besides typical P. pulcherrimum, they include P. parvifolium Nutt., P. delicatum Rydb., P. californicum Eastw., and possibly P. nevadense, all of which intergrade completely and together range through the mountainous regions of western North America. Although the most recent monograph of the genus retains these taxa at the subspecific level (Davidson, 1950), Cronquist (in Hitchcock and others, 1959) lumps all of these close relatives under the name P. pulcherrimum, recognizing three "varieties," two of which occur along the Cascade-Sierra axis. Variety calycinum (Eastw.) Brand is the more robust larger-flowered ecotype which is found at lower elevations, especially on the high peaks, while var. *pulcherrimum* comprises the reduced alpine and subalpine forms. All intermediate stages are known between these two varieties, but in some localities (such as the Three Sisters region) they are ecologically and morphologically quite distinct.

Davidson (1950) proposes that both the *P. viscosum* complex (in which he includes *P. elegans* Greene) and the *P. pulcherrimum* group are descended from the northern *P. boreale*. He does not, however, note the connection between these two major clusters of species through *P. elegans* and the alpine forms of *P. pulcherrimum*, which approach one another so closely that most of the high alpine Oregon material of the former has been identified as the latter. Specimens from the central Cascades of Oregon are clearly intermediate between the more robust forms of *P. pulcherrimum* from Crater Lake National Park and southward and *P. elegans* from Mt. Rainier and northward. Although this close relationship needs to be emphasized, the two species do seem to be separable, mainly by subtle differences in growth habit. Due to the uniformity of *P. elegans* as it occurs in the Washington Cascades, it seems likely to the present author that on morphological grounds all Oregon material to date belongs in the more variable taxon *P. pulcherrimum*. It is, however, perhaps instructive to note the similarities between the ranges of *P. elegans* (if the Western Cascade forms could be assigned to this species) and other boreal species such as *Castilleja rupicola*. Both species grow in quite similar habitats and localities in the Washington Cascades (especially on Mt. Rainier) and reappear together in the Western Cascades of Oregon.

A single population of *P. pulcherrimum* is known from the Western



GEOGRAPHIC DISTRIBUTION OF

POLEMONIUM PULCHERRIMUM PULCHERRIMUM

Cascades. This species is well-established in vertical crevices on the southwest-facing basalt cliffs of Iron Mountain. Morphologically identical forms are the highest flowering plants occurring on Middle Sister, Lane County, at elevations of over 3000 m. Lower elevation forms normally identified as *P. californicum*, but equivalent to *P. pulcherrimum* var. *calycinum*, have also been collected from the lower slopes of the High Cascade peaks throughout Oregon but have never been found in the Western Cascades.

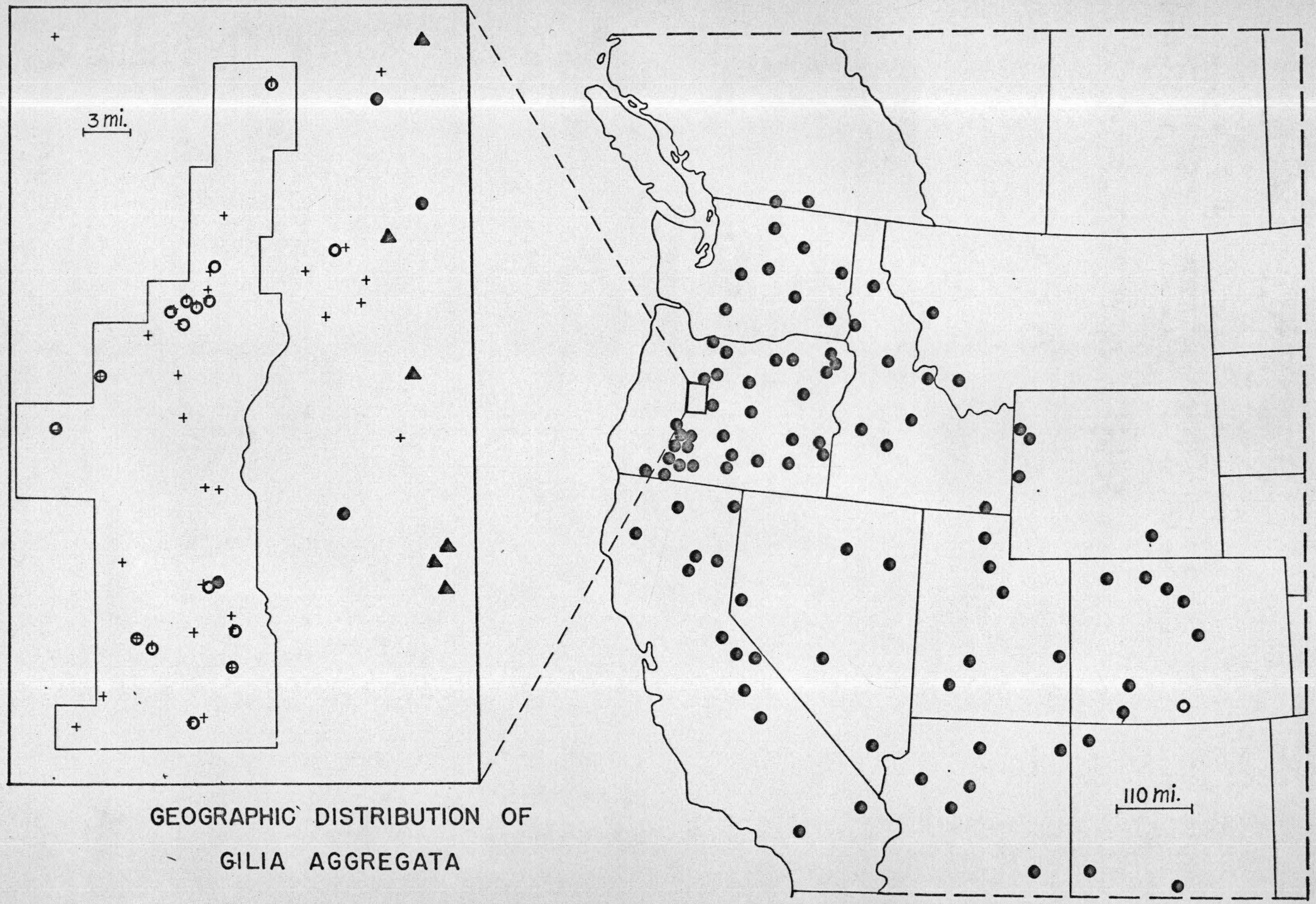
On Iron Mountain *P. pulcherrimum* is a member of the Vertical Outcrop association, and occurs with *Saxifraga bronchialis vespertina*, *Penstemon rupicola*, *Selaginella wallacei*, *Saxifraga cespitosa*, *Heuchera micrantha*, and *Polypodium hesperium*.

Gilia aggregata (Pursh) Spreng., Syst. 1:626. 1825.

Selected synonyms:

Ipomopsis aggregata (Pursh) Grant, El Aliso 3:360. 1956.

Although Grant (1956) presents arguments for the separation of *Ipomopsis* from *Gilia* for the sake of internal consistency within the Polemoniaceae, his arguments have not been generally accepted by other taxonomists (Cronquist, in Hitchcock and others, 1959). Cronquist's treatment is followed here. *Gilia aggregata* is the showiest of the gilias, immediately recognizable by its large (2-4 cm), scarlet, long-tubular corollas. It is, however, a variable taxon, divided at times into as many as seven barely delimited species (Grant, 1956; Wherry, 1946, 1961a). In the Pacific Northwest, *G. aggregata* is quite uniform, dry regions of the southwestern United States being the center of



GEOGRAPHIC DISTRIBUTION OF
GILIA AGGREGATA

variability for the species. All ecotypes studied have been shown to be self-incompatible (Grant, 1956) and are visited by hummingbirds (in the Western Cascades *Selasphorus rufus*) throughout the flowering season.

G. aggregata is widespread throughout the montane and intermontane regions of western North America, but has heretofore been considered to be strictly limited to areas east of the Cascade crest in the Pacific Northwest (Cronquist, in Hitchcock and others, 1959). It has been found in the course of the present study that this species occurs in dry south or west-facing meadows or on open gravelly slopes in the Western Cascades where it is frequently a dominant. Other members of the Xeric Meadow association with which it is often found are *Collomia linearis*, *Gayophytum diffusum parviflorum*, *Orthocarpus imbricatus*, *Polygonum minimum*, *Polygonum cascadense*, *Polygonum douglasii*, *Lupinus arbustus neolaxiflorus*, and *Linum perenne lewisii*.

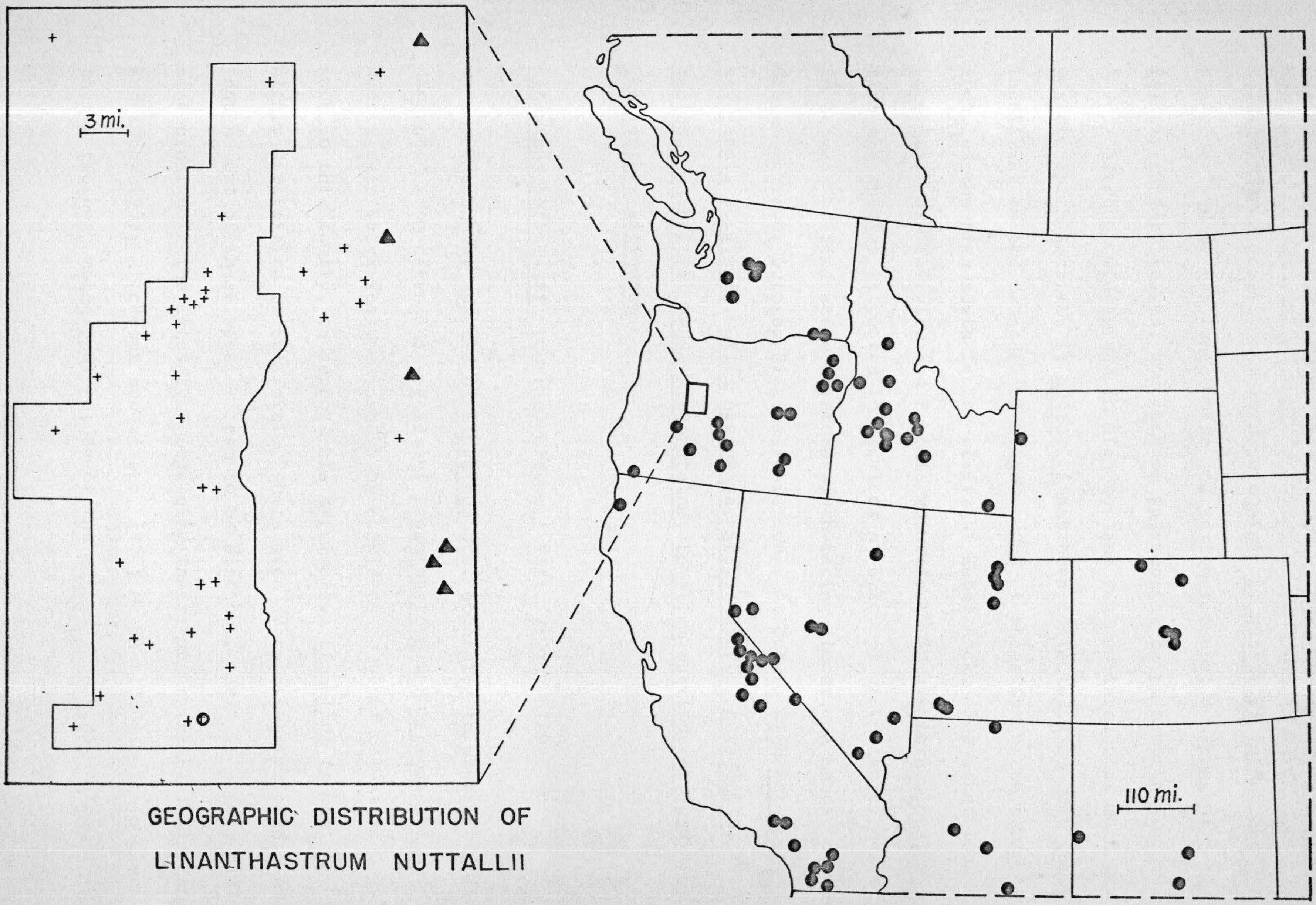
Linanthastrum nuttallii (Gray) Ewan, Journ. Wash. Acad. Sci. 32:139. 1942.

Selected synonyms:

Gilia nuttallii Gray, Proc. Am. Acad. 8:267. 1870.

Linanthus nuttallii Greene ex Milliken, U. Cal. Publ. Bot. 2:54. 1904.

This recently constituted monotypic gilioid genus is morphologically intermediate between the older genera *Leptodactylon* and *Linanthus* in habit, ecology, and leaf and calyx morphology. *Linanthastrum* may, in fact, be the modern representative of the stock from which *Linanthus*, an annual genus, has evolved (Ewan, 1942; Wherry, 1961b). A

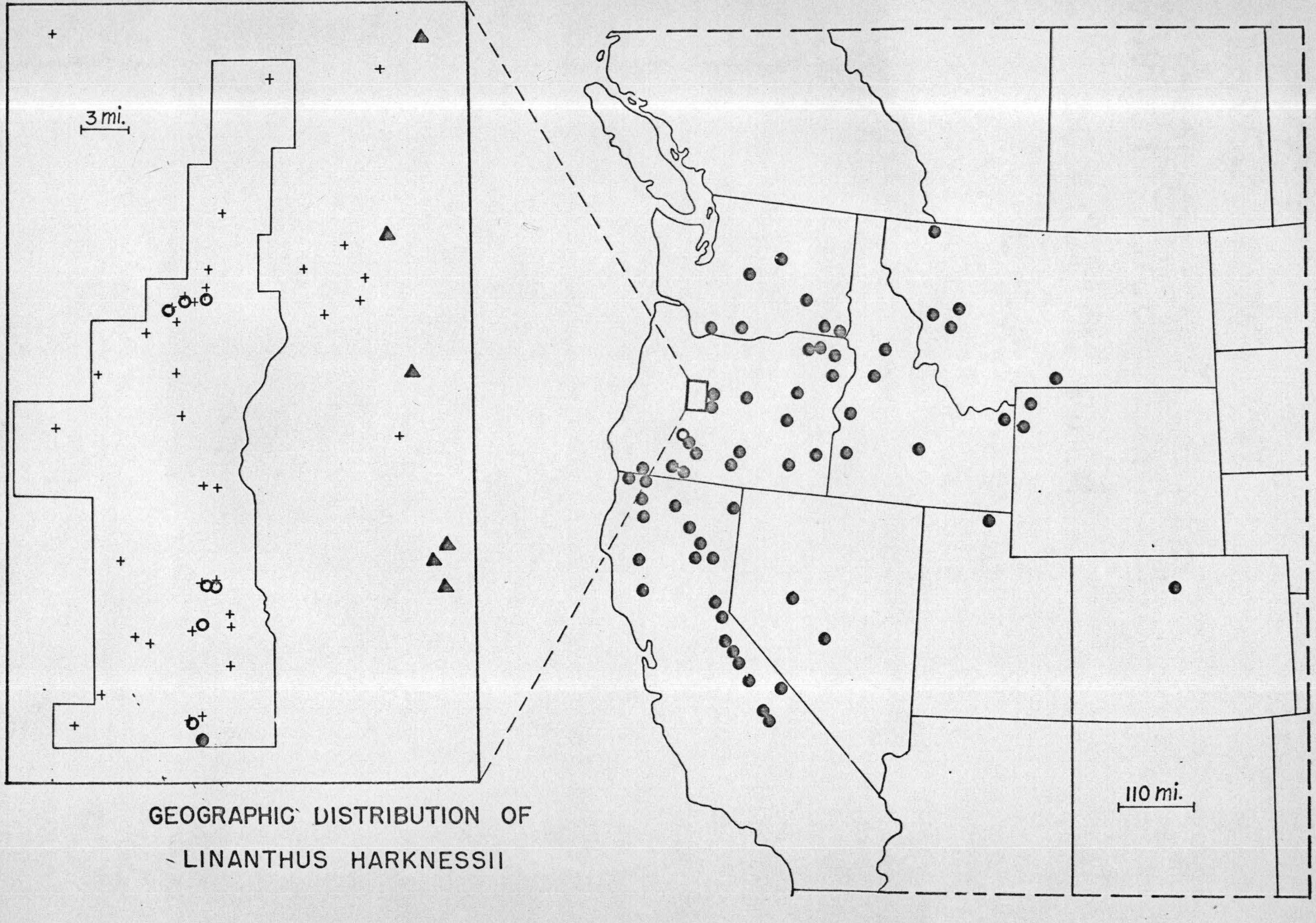


GEOGRAPHIC DISTRIBUTION OF LINANTHASTRUM NUTTALLII suffrutescent, sometimes matted perennial, *L. nuttallii* is further characterized by its large white and yellow flowers, non-pungent falsely-whorled leaves, and lack of intercostal calyx membranes.

Although widespread in high montane regions throughout much of western North America, *L. nuttallii* has been collected from only three localities in the Cascades of Oregon. One of these is in the study area, on the high south-facing cliffs of Rebel Rock. The other two localities are Fairview and Bohemia Mountains. At all three localities the species is rooted in crevices of outcrops of volcanic rock or in pockets of fine scree on steep south-facing slopes. A member of the Gravel Scree or Outcrop Ridge associations, it occurs with *Lotus nevadensis douglasii*, *Gilia aggregata*, *Arctostaphylos nevadensis*, *Haplopappus hallii*, *Sedum stenopetalum*, *Lomatium martindalei*, and *Cheilanthes siliquosa*.

Linanthus harknessii (Curran) Greene, Pitt. 2:255. 1892.

The annual species of *Linanthus* are, according to Wherry (1961b), descended from perennial species of *Linanthastrum* and *Leptodactylon*. Wherry uses calyx features, which he considers to be of utmost importance in this family, to support his arguments. *Linanthus* is most highly diversified in California, where over 30 species are found. Although most of these species seem to be distinct, there is a good deal of confusion in the literature regarding their ranges (Peck, 1961; Munz and Keck, 1959; Hitchcock and others, 1959; Mason, 1938). It is clear that a thorough monographic study of the genus is needed.



GEOGRAPHIC DISTRIBUTION OF LINANTHUS HARKNESSII

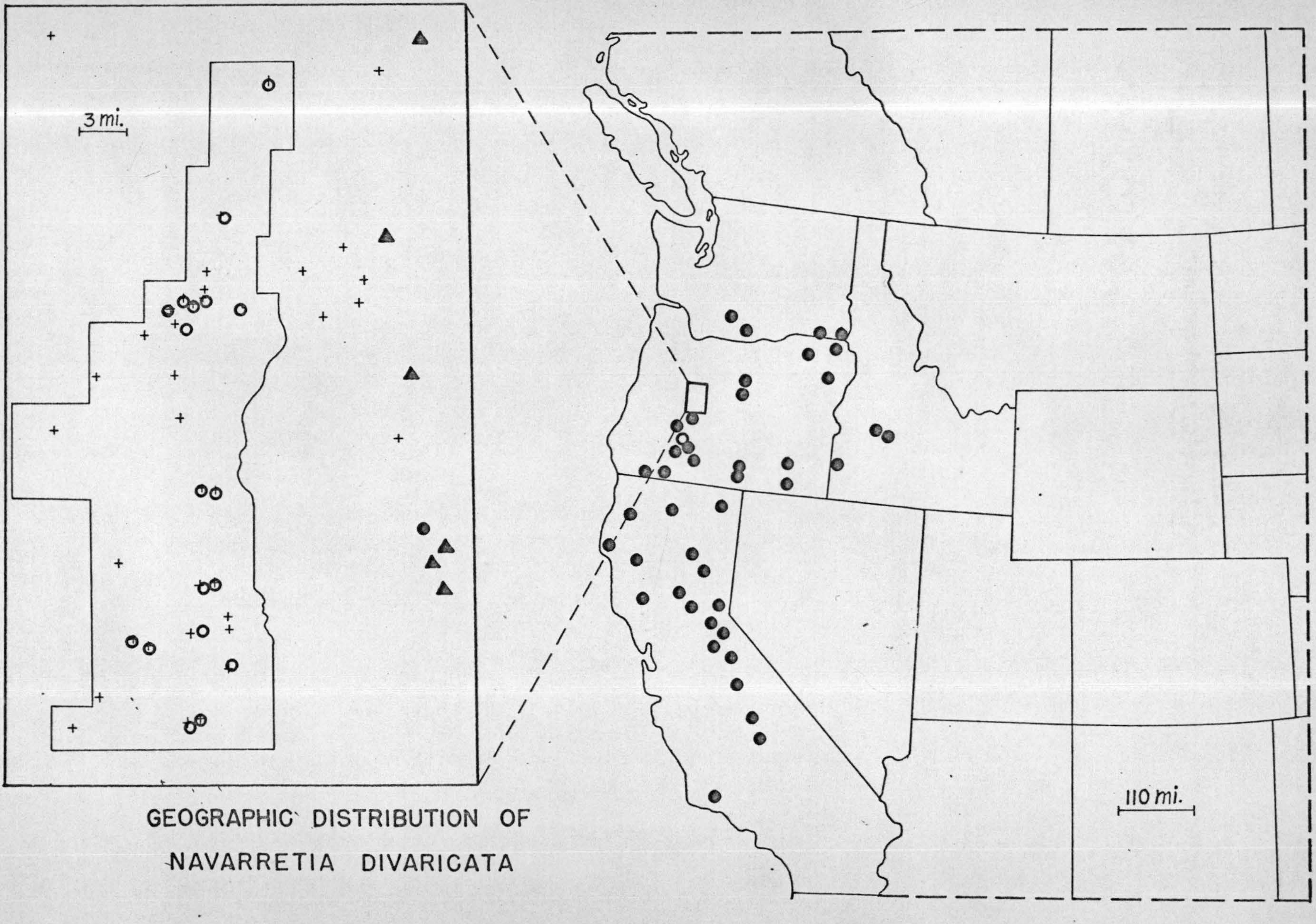
L. harknessii as here treated is differentiated from its closest relative, *L. septentrionalis* Mason, by its habit of growth, smaller glabrous corolla and single seed per locule. Both species are found extensively throughout eastern Oregon, often growing in the same stand. *L. septentrionalis* becomes more common farther east and is the dominant species in the Rocky Mountains. *L. harknessii* occasionally extends westward across the Cascade crest into the Western Cascades. An annual, it grows in moist, open, gravelly sites on ridgetops or in trails. It rapidly desiccates as snowmelt diminishes. Other members of the Rocky Melt Seep or Gravel Scree associations with which it frequently occurs include *Allium amplectens*, *Lewisia triphylla*, *Mimulus breweri*, *Polygonum kelloggii*, *Polygonum cascadense*, *Navarretia divaricata*, *Gayophytum humile*, and *Saxifraga integrifolia*.

Navarretia divaricata (Torr.) Greene, Pitt. 1:136. 1887.

Selected synonyms:

Gilia divaricata Torr. ex Gray, Proc. Am. Acad. 8:270. 1870.

Crampton (1954) recognizes two evolutionary lines within the gilioid genus *Navarretia*. Section *Fragiles*, adapted to vernal pool environments, has uninervate corollas, entire or shallowly lobed stigmas, indehiscent capsules, and shallow stamen insertion. This section finds its highest development in the southwestern United States. Section *Eunavarretia*, which includes *N. divaricata* and 20 other species, comprises those forms with variable ecologies, trinervate corollas, deeply cleft stigmas, and low stamen insertion. *N. divaricata* is distinguished from other species of its section by its red or brown pigmented stems,

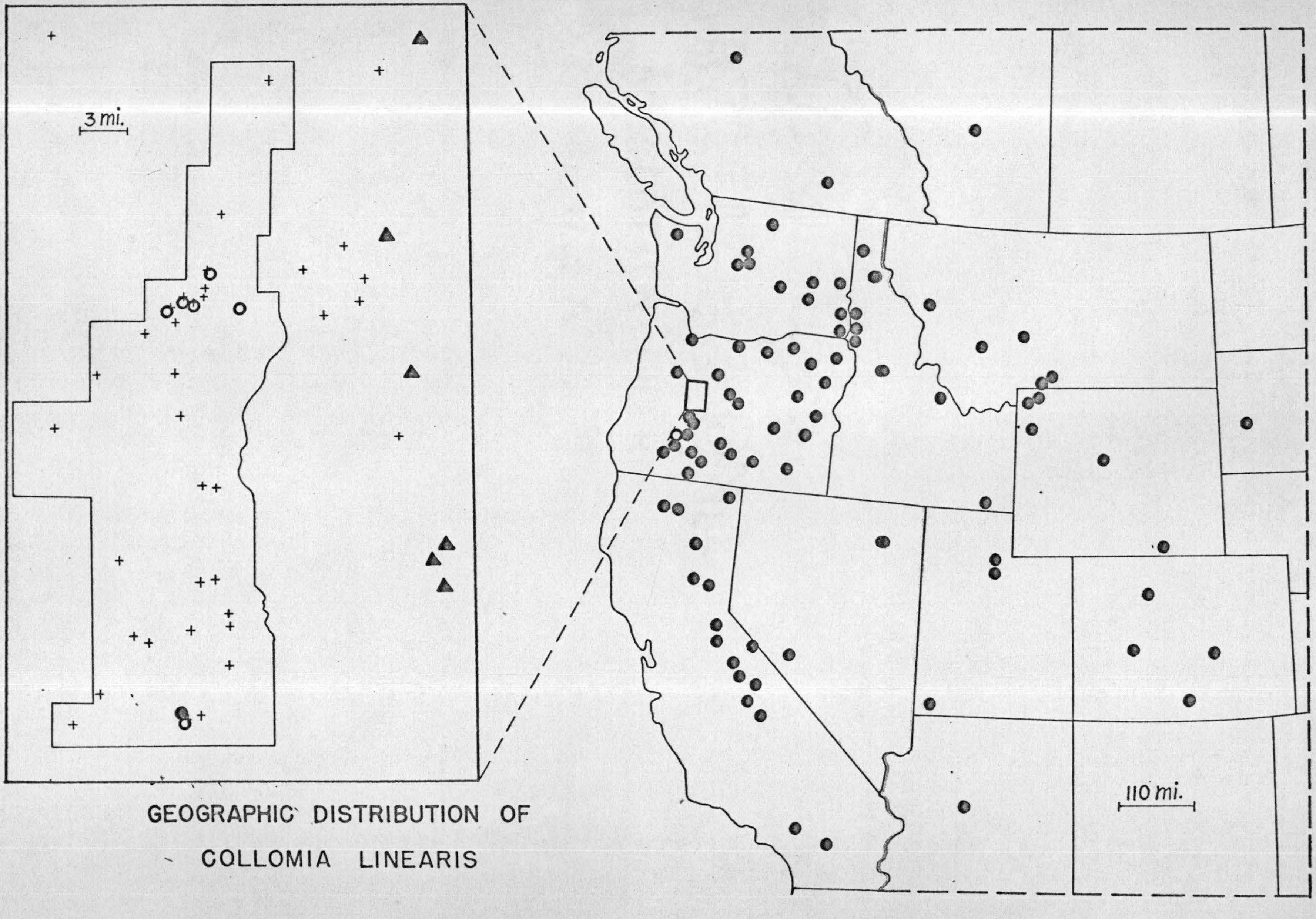


GEOGRAPHIC DISTRIBUTION OF NAVARRETIA DIVARICATA which branch divaricately from just below the terminal head of flowers. It is most closely related to *N. peninsularis* Greene of southern and Baja California, *N. prolifera* Greene of the Sierra Nevada foothills, and *N. breweri* (Gray) Greene, a yellow-flowered form of the intermontane regions from Washington to Arizona.

Throughout its range, from southern Washington east to central Idaho and south to southern California, *N. divaricata* occurs in dry open spots, typically rooted in fine mineral soil or gravel. It has not been previously reported from the Cascade Range north of the 44th parallel. It commonly grows in trails in the Western Cascades, and its slightly mucilaginous seeds may indicate animal dispersal. *N. divaricata* is a member of the Xeric Meadow association and commonly grows with *Gayophytum diffusum parviflorum*, *Gayophytum humile*, *Orthocarpus imbricatus*, *Polygonum douglasii*, *Eriogonum nudum*, *Polygonum cascadense*, *Cerastium arvense*, and *Artemisia ludoviciana latiloba*.

Collomia linearis Nutt., Gen. Pl. 1:126. 1818.

This easily recognizable *Collomia* is the most widespread member of the genus, occurring throughout the dry open lands of the Western United States and Canada. It has also been reported from Wisconsin, Ontario, and Quebec. *C. linearis* has evidently been introduced into some areas (Hitchcock, in Hitchcock and others, 1959). It is possible that recent introduction has established it in the Western Cascades, where the species is relatively common in some of the more heavily grazed, dry, south or west-facing slopes between 1350 and 1650 m

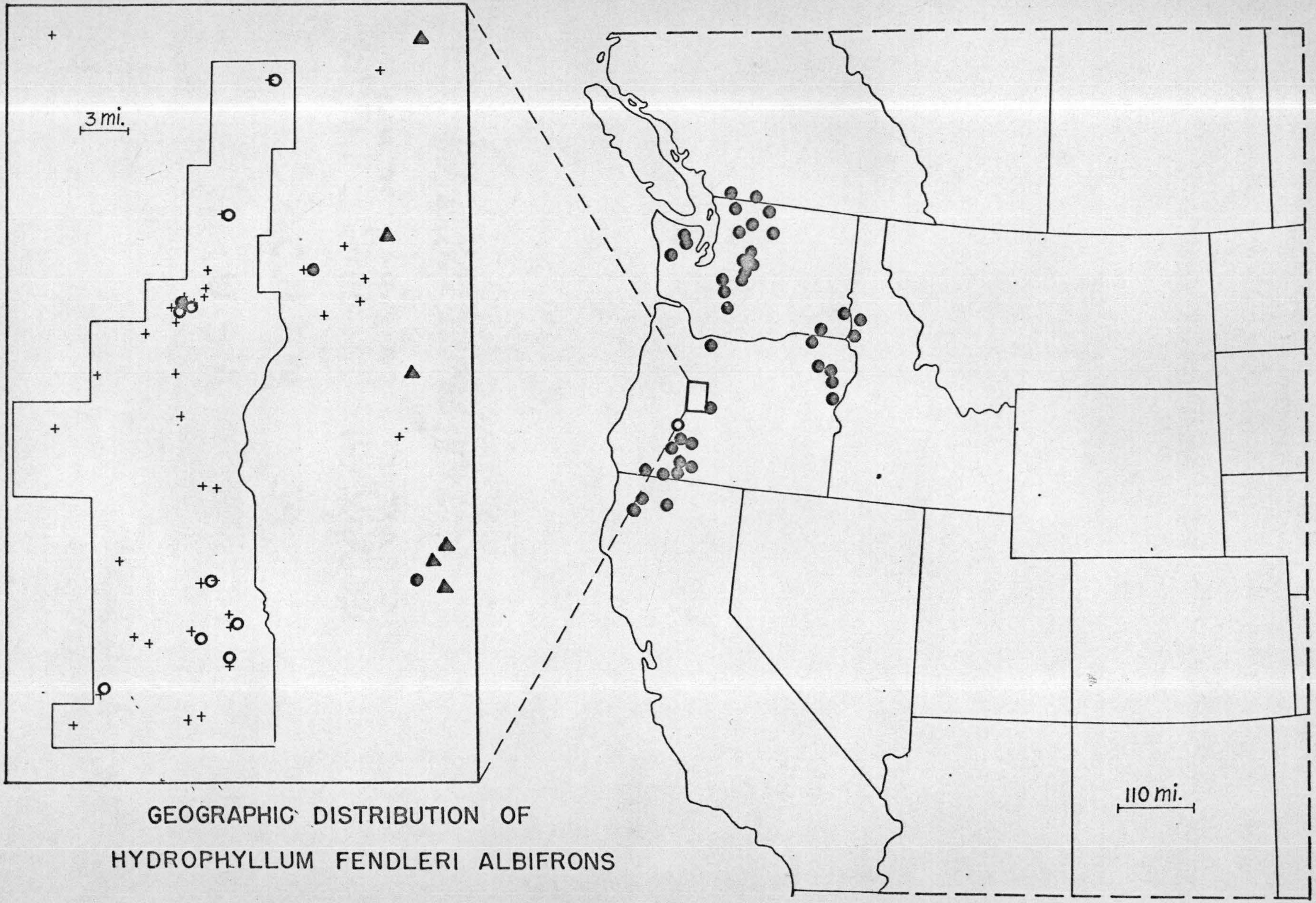


GEOGRAPHIC DISTRIBUTION OF COLLOMIA LINEARIS elevation. *C. linearis* has previously been reported from only three localities in Oregon north of the 44th parallel and west of the Cascade crest. Two of these collections are from dry areas in the Willamette Valley, the third from the Western Cascades.

Other members of the Xeric Meadow association found with *C. linearis* are *Gilia aggregata*, *Gayophytum diffusum parviflorum*, *Luina stricta*, *Orthocarpus imbricatus*, *Polygonum douglasii*, *Microsteris gracilis*, and *Collinsia parviflora*.

Hydrophyllum fendleri (Gray) Heller var. *albifrons* (Heller) Macbride, Cont. Gray Herb. n. s. 49:23. 1917.

The genus *Hydrophyllum* is composed of two distinct assemblages of species; one occurs in the eastern United States and the other west of the Rocky Mountains. The two groups are partially linked through *H. tenuipes* and *H. virginianum*, which are geographically distinct but morphologically very similar (Constance, 1942). *H. fendleri* is intermediate in leaf and inflorescence morphology between *H. tenuipes* and *H. occidentale*. Its range can be divided into three distinct parts. Variety *fendleri* occurs from the Medicine Bow Mountains of Wyoming south through Colorado and Utah to central New Mexico. Variety *albifrons* is found from the Cascade Mountains of British Columbia south through the Cascades and Klamath Mountains. In the Snake River region of Oregon, Washington, and Idaho, a disjunct set of populations containing members of both varieties occurs (Constance, 1942). There is some disagreement in the literature concerning the existence of intermediate forms. If it is eventually shown that the two taxa represent biologically discrete



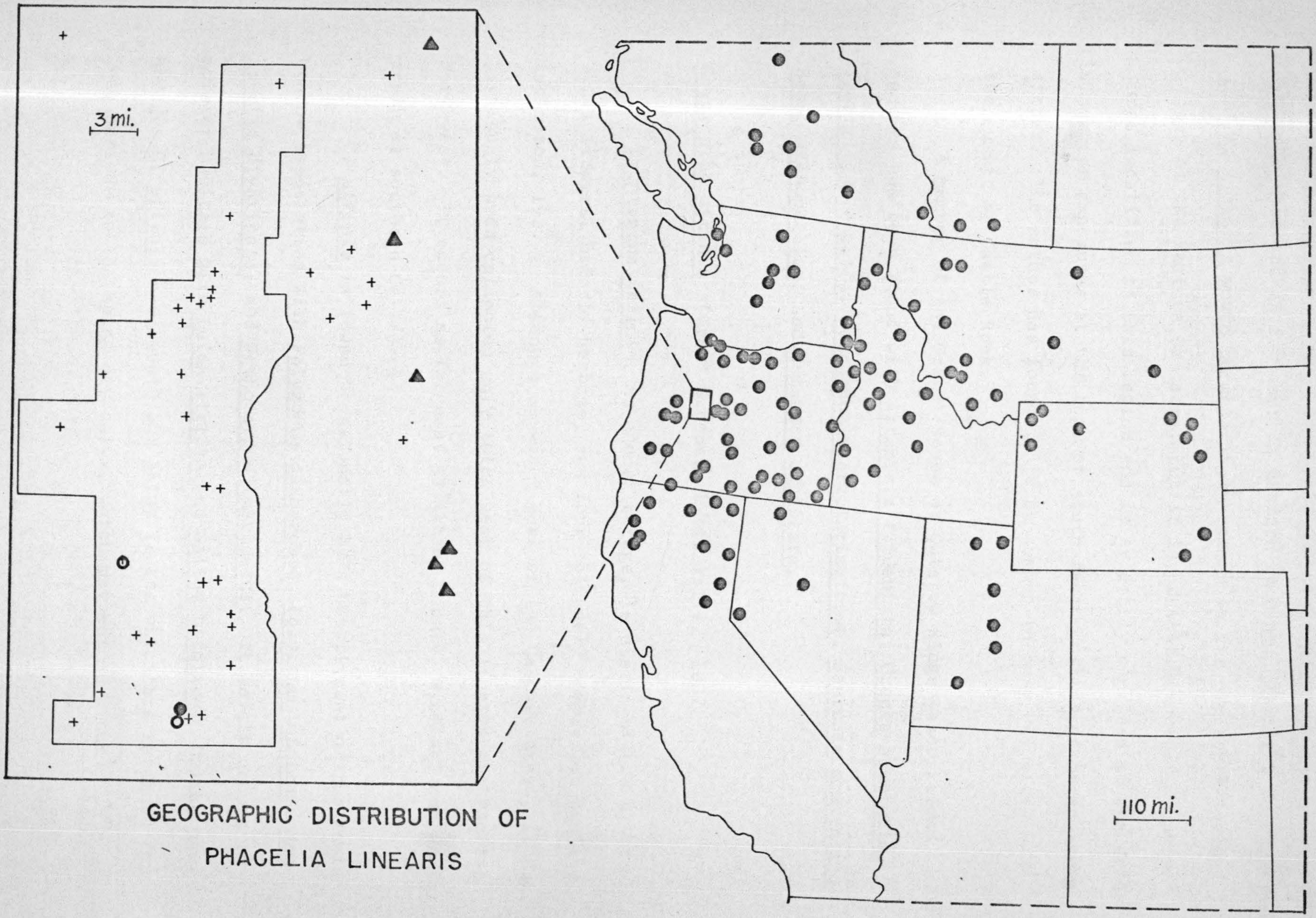
GEOGRAPHIC DISTRIBUTION OF HYDROPHYLLUM FENDLERI ALBIFRONS species, this most unusual distribution pattern will prove easier to explain.

In the Western Cascades *Hydrophyllum fendleri albifrons* is typically a plant of moist shady meadows or streamsides, growing only in areas of rich soil that does not dry completely during the summer. It is commonly associated with *Mertensia bella*, *Mitella breweri*, *Ligusticum grayi*, *Veratrum viride*, *Valeriana sitchensis*, *Hydrophyllum tenuipes*, *Senecio triangularis*, *Rubus spectabilis*, and other Wet Meadow species. It also occurs commonly beneath dense thickets of *Alnus sinuata* or *Acer circinatum*.

Phacelia linearis (Pursh) Holz., Contr. U. S. Nat. Herb. 3:242. 1895.

Although *P. linearis* has generally been considered a close relative of the *P. franklinii* complex (Howell, 1945), more recent experimental work has indicated that it has probably constituted a monotypic evolutionary line within this complex genus for some time (Gillett, 1962). Although species of *Phacelia* do not seem to have developed genetic isolating barriers to any considerable extent, *P. linearis* does not set seed when crossed with any other species yet tried. Plants are self-compatible, but protandry results in modal outcrossing for this species (Gillett, 1962).

P. linearis is a widespread and common species. Although several localities are known from the Willamette Valley and the area immediately around Puget Sound, it is primarily confined to dry open areas east of the Cascades, extending from central British Columbia to



GEOGRAPHIC DISTRIBUTION OF
PHACELIA LINEARIS

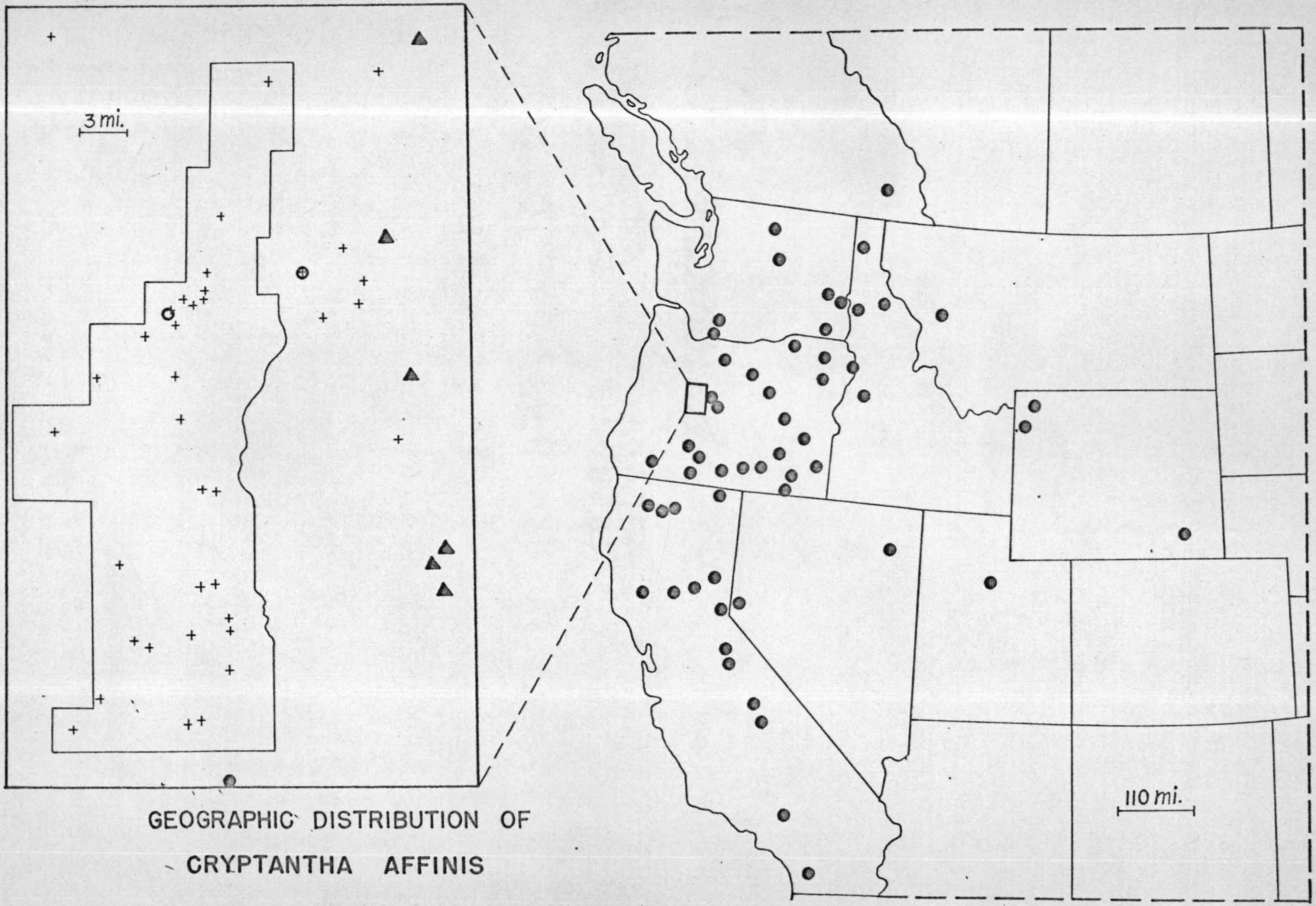
southern Utah and as far east as eastern Wyoming. It might be expected that *P. linearis* would be relatively common in the dry south-facing slopes of the Western Cascades, but it is presently known from only three localities in this region and is evidently confined to the driest windswept exposures at the tops of south-facing cliffs or steep rocky slopes. The author has found it to be common in only one site--near the summit of Castle Rock.

A member of the Gravel Scree or Outcrop Ridge associations, this species has been found with *Artemisia tridentata*, *Crepis acuminata*, *Plectritis congesta*, *Polygonum spergulariaeforme*, *Sanicula graveolens*, *Sedum stenopetalum*, and *Comandra umbellata*.

Cryptantha affinis (Gray) Greene, Pitt. 1:119. 1887.

Cryptantha affinis, an annual borage, is distinguished by its small flowers, bristly herbage, and four obliquely compressed nutlets (Johnston, 1925). Although abundant east of the Cascade crest, it had previously been collected only twice west of this line in the Pacific Northwest. It occurs as far east as Albany County, Wyoming, and as far south as southern California.

C. affinis is found occasionally as a constituent of the Xeric Meadow association with *Polygonum cascadense*, *Polygonum minimum*, *Navarretia divaricata*, and *Orthocarpus imbricatus*. It rarely occurs in moister habitats with *Luina stricta* and *Galium bifolium*. Unlike many borages *C. affinis* has smooth and shiny fruits which are retained for long periods in the spiny dry calyx, which may act as a bur.



GEOGRAPHIC DISTRIBUTION OF CRYPTANTHA AFFINIS

Plagiobothrys scouleri (H. and A.) Johnst., Contr. Gray Herb. n. s. 68:75. 1923.

Selected synonyms:

Allocarya scouleri Greene, Pitt. 1:18. 1887.

Allocarya media Piper, Contr. U. S. Nat. Herb. 22:107. 1920.

Plagiobothrys medius Johnst., Contr. Arn. Arb. 3:58. 1932.

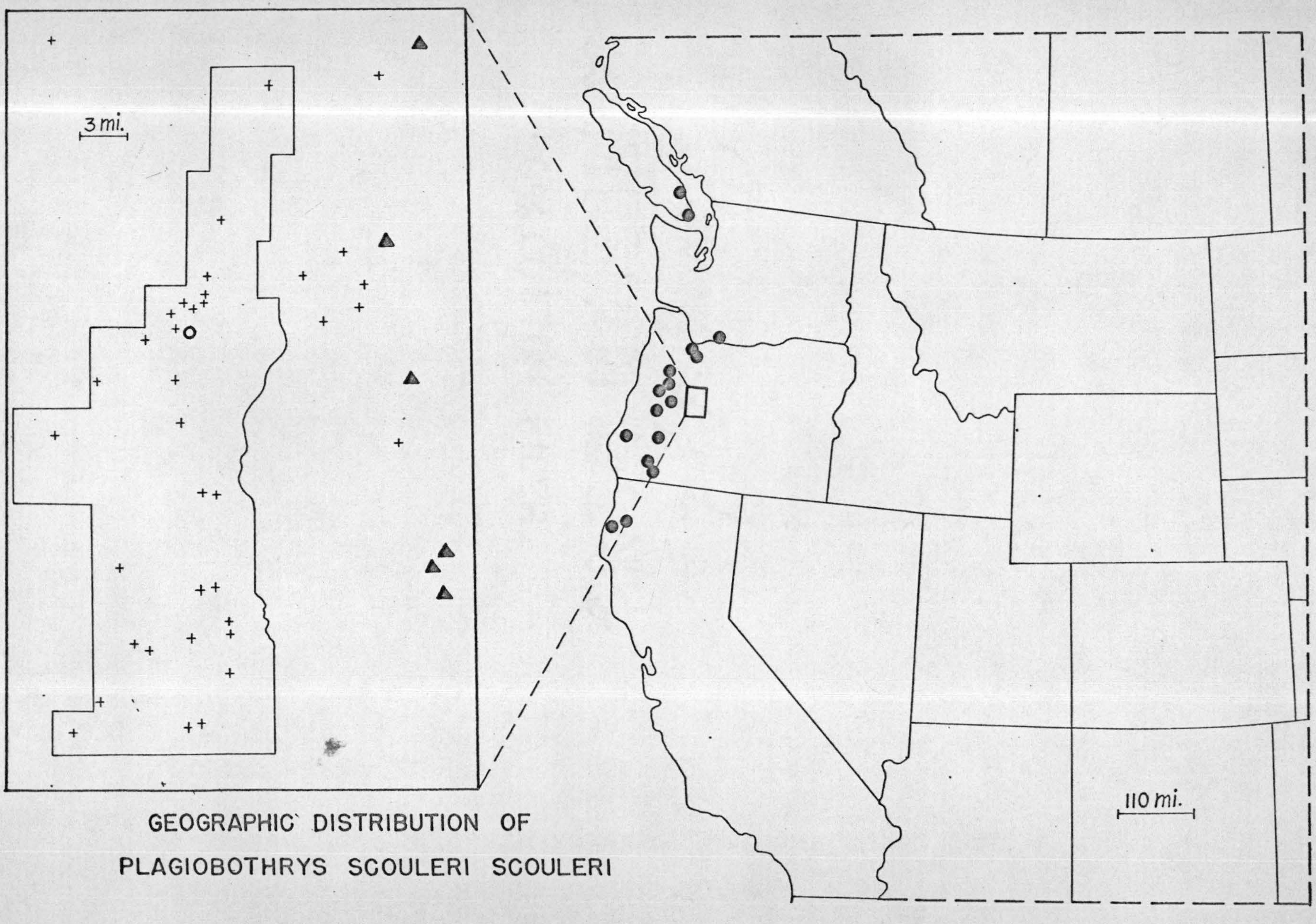
Allocarya granulata Piper, Contr. U. S. Nat. Herb. 22:109. 1920.

Plagiobothrys granulatus Johnst., Contr. Arn. Arb. 3:57. 1932.

Allocarya fragilis Brand, Fedde Rep. Sp. Nov. 18:312. 1922.

This species, widespread as a whole, is polytypic and has a confusing nomenclatural history (Piper, 1920; Cronquist, in Hitchcock and others, 1959). There are two modes of variation. The first and most common, var. penicellatus (Greene) Cronq., consists of vernal pool forms which are prostrate in habit and show great diversity of nutlet sculpturing. These forms are widespread throughout western North America east of the Cascades (Ornduff and French, 1958). Variety scouleri is more constant in morphology and is limited to areas west of the Cadcade crest except for one locality on the eastern end of the Columbia Gorge. It ranges from Humboldt County, California, to Vancouver Island and is the form of interest here. It is erect in habit, larger-flowered than var. penicellatus, and is not found in vernal pool habitats but in dry rocky areas, especially in the Willamette Valley and occasionally along the Pacific Coast. Only variety scouleri is included in the following map.

One population of P. scouleri is known from the Cascade Mountains of Oregon. It occurs in dry meadow and scree areas on the south-facing



GEOGRAPHIC DISTRIBUTION OF
PLAGIOBOTHRYS SCOULERI SCOULERI

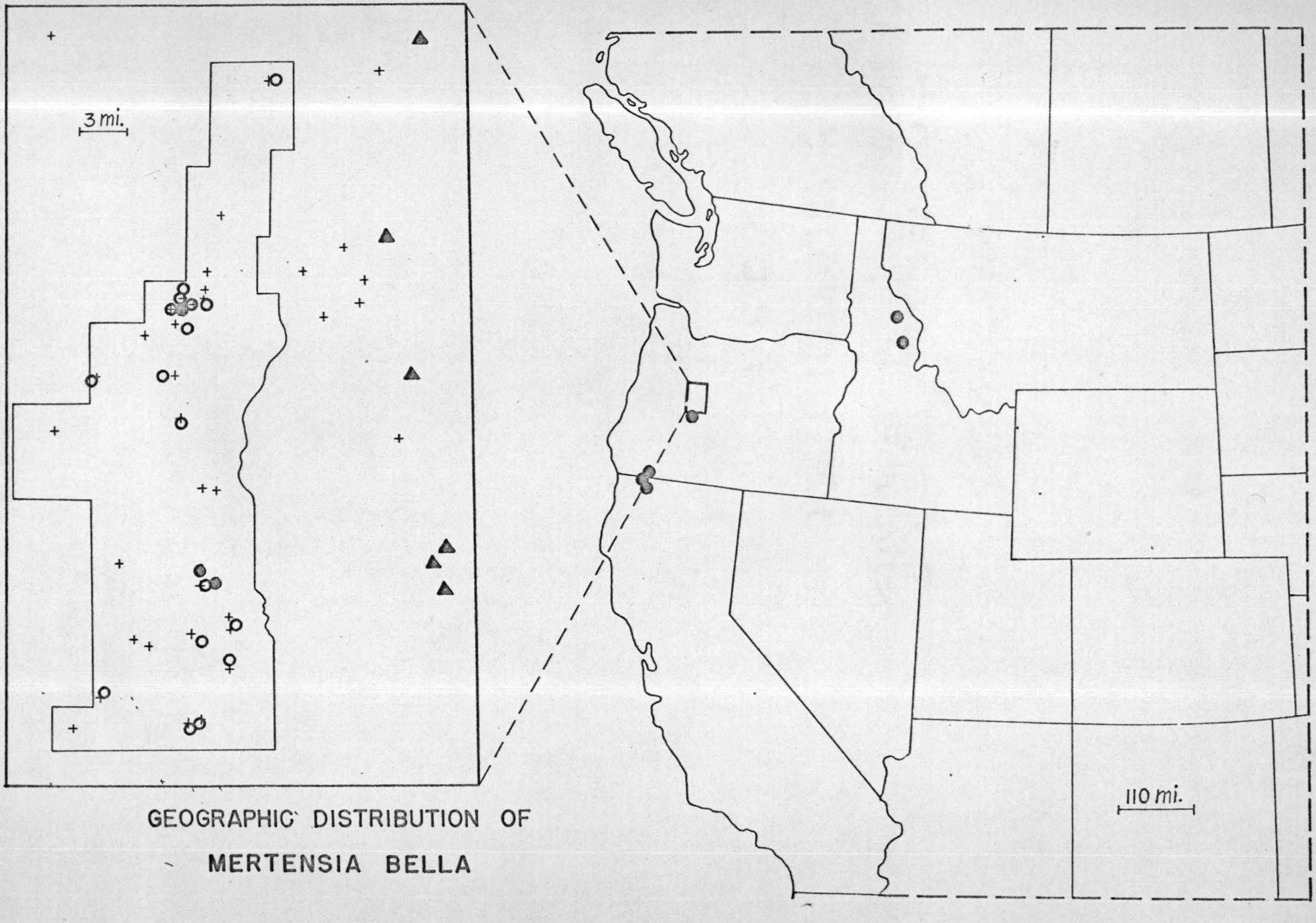
slope of Browder Ridge, where it is associated with such members of the Xeric Meadow and Gravel Scree associations as *Sanicula graveolens*, *Eriogonum umbellatum*, *Sedum oregonense*, and *Juniperus communis saxatilis*.

Mertensia bella Piper, Proc. Biol. Soc. Wash. 31:76. 1918.

This beautiful and distinctive member of an extraordinarily difficult genus comprises the monotypic section *Neuranthia* (Williams, 1937). It is distinguished by its cormlike globose root and campanulate corolla, which flares from the base without any constriction marking the division between tube and limb that is characteristic of all other members of the genus *Mertensia*. It seems to have no close relatives (Piper, 1918).

The distribution of *M. bella* is remarkably disjunct. It has been collected from several localities near the Oregon-California border in Josephine and Siskiyou Counties; from the Western Cascades (type locality: Horsepasture Mountain); and from one locality each in Idaho and Clearwater Counties, Idaho. It has been poorly collected and was thought until the present to be rare throughout its range. However, 15 additional collecting localities for the species have been found in the Western Cascades. It appears that this species, while local in its occurrence, is a common and well-established member of the Cascade flora.

Mertensia sites can often be located by attention to other species which are more easily noticed and occur faithfully with this borage. They include members of the Wet Meadow association, particularly *Veratrum viride*, *Senecio triangularis*, *Valeriana sitchensis*, *Ribes bracteosum*,

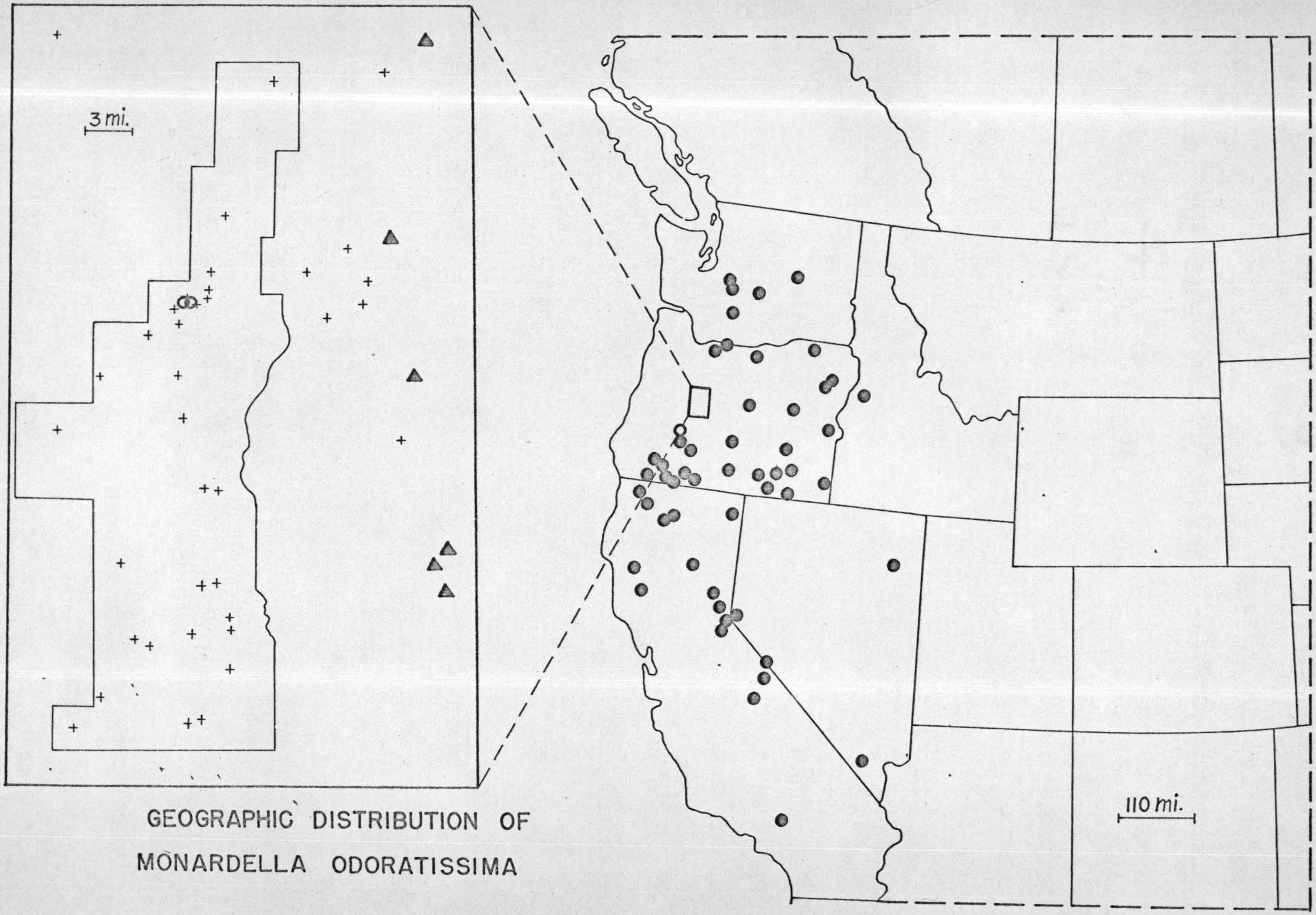


GEOGRAPHIC DISTRIBUTION OF
MERTENSIA BELLA

Rubus spectabilis, *Hydrophyllum fendleri albifrons*, and *Mitella breweri*.

Monardella odoratissima Benth., Lab. Gen. and Sp. 332. 1834.

The genus *Monardella* continues to be problematic. The member taxa compose a highly complex network of variable and interfertile populations. Little has been done in the way of cytogenetic or breeding analysis. It seems highly unlikely to the present author that the numerous morphologically defined entities, which show poor geographical differentiation, can represent biologically discrete species or subspecies. Epling's 1925 monograph is the most recent thorough study of the genus. He considers *M. odoratissima* one of the points of central tendency around which sections of the genus are established. This species, though relatively distinctive for the genus, seems nevertheless to intergrade completely with the *M. villosa* complex. *M. odoratissima* subsp. *odoratissima* is normally found along the western edge of the Rocky Mountains from northeastern Washington and northern Idaho south to central and northeastern Oregon and central Idaho. Epling also included isolated specimens from Nevada, New Mexico, and the Columbia Gorge in this subspecies, which Western Cascade material most closely approximates. Intervening between the Rocky Mountain and Cascade populations of *M. odoratissima odoratissima* in the dry regions of the Columbia Plateau and the High Lava Plains of Deschutes County, Oregon, is the much more densely pubescent subspecies *discolor*. Subspecies *glauca*, also closely related to subspecies *odoratissima*, occurs in the Siskiyou region and the Wallowa Mountains. It is extremely difficult to imagine any of these forms as discrete evolutionary units.



GEOGRAPHIC DISTRIBUTION OF
MONARDELLA ODORATISSIMA

Perhaps all three "subspecies" have contributed to the Western Cascade gene pool. Leaf pubescence characteristics are in large part diagnostic of the described subspecific taxa. Western Cascade specimens have glabrous leaves for the most part, with southern specimens showing a distinct tendency toward hirsuteness along the veins, especially on the undersurface of the leaves. This tendency may represent an influx of "*discolor*-like" genes into *glauca*-*odoratissima* populations. The latter taxa are distinguished by Epling on the basis of bract shape and pubescence. Subspecies *odoratissima* typically has round pubescent bracts, and subspecies *glauca* has elliptical puberulent to glabrous bracts. These populations thus seem to represent a combination of genes such as are presently typical of the Columbia Gorge and Columbia Plateau, the Siskiyou Mountains, the Great Basin, and the Wallowa Mountains.

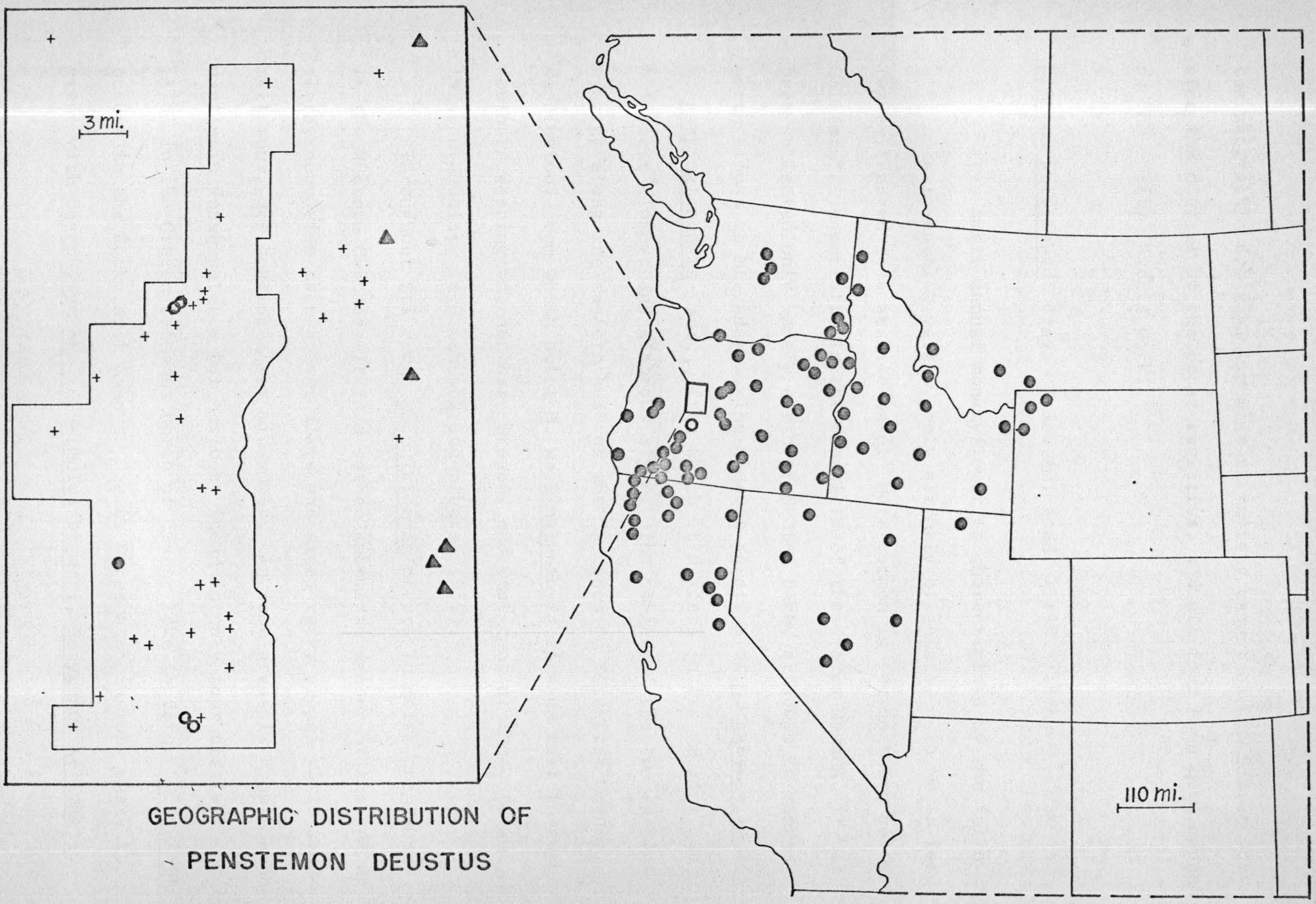
The genus *Monardella* is characteristic of dry rocky habitats throughout its range. In the Western Cascades it grows in crevices in volcanic rock on south-facing slopes or along barren ridgetops. Typical Xeric Meadow associates are *Castilleja pruinosa*, *Penstemon procerus brachyanthus*, *Sedum stenopetalum*, *Comandra umbellata*, *Lomatium martindalei*, *Gilia aggregata*, and *Sanicula graveolens*.

Penstemon deustus Dougl. ex Lindl., Bot. Reg. 16: pl. 1318. 1830.

Penstemon deustus is the only common member of its immediate group, which includes three narrowly endemic species of subsections *Deusti* and *Arenarii* of Section *Graciles*. *P. tracyi*, a montane endemic of Trinity County, California, is the other member of the subsection

Deusti and is the single closest relative of *P. deustus* (Keck, 1940). *P. deustus* is easily distinguished by its sharply toothed leaves and small, purple-veined, creamy-white corollas. It is common in arid country from central Washington and western Montana and Wyoming south to central California and Nevada. Douglas' type locality, "scorched rocky plains in the interior of northwest America . . .," is the basis for the common name "scorched penstemon." In the Western Cascades it grows in andesitic crevices on south-facing outcrops that become very hot and dry in midsummer when these plants bloom. A member of the Outcrop Ridge association, it occurs with *Chrysothamnus nauseosus albicaulis*, *Eriophyllum lanatum*, *Gilia aggregata*, *Arenaria capillaris americana*, *Lotus nevadensis douglasii*, *Silene douglasii*, and *Haplopappus hallii*.

P. deustus has been divided into four intergrading varieties which are treated together here. All Western Cascade material is of the widespread variety *deustus*, which occurs commonly east of the Cascades and in two sites in the Willamette Valley. Variety *variabilis* (Suks.) Cronq., which has frequently whorled narrower leaves which are not as sharply toothed as those of var. *deustus*, is found in and east of the Columbia Gorge in Washington and Oregon. Variety *heterander* (T. and G.) Cronq., with a completely or mostly glabrous corolla, occurs in south-central Oregon and adjacent California and Nevada. Variety *sudans* [subsp. *sudans* (Jones) Penn. and Keck] is limited to volcanic rocks and soils in southwestern Oregon and south to Lassen County, California. It is characterized by prominent glandulosity of corollas and herbage. Although Cascade material is clearly representative of variety *deustus*,



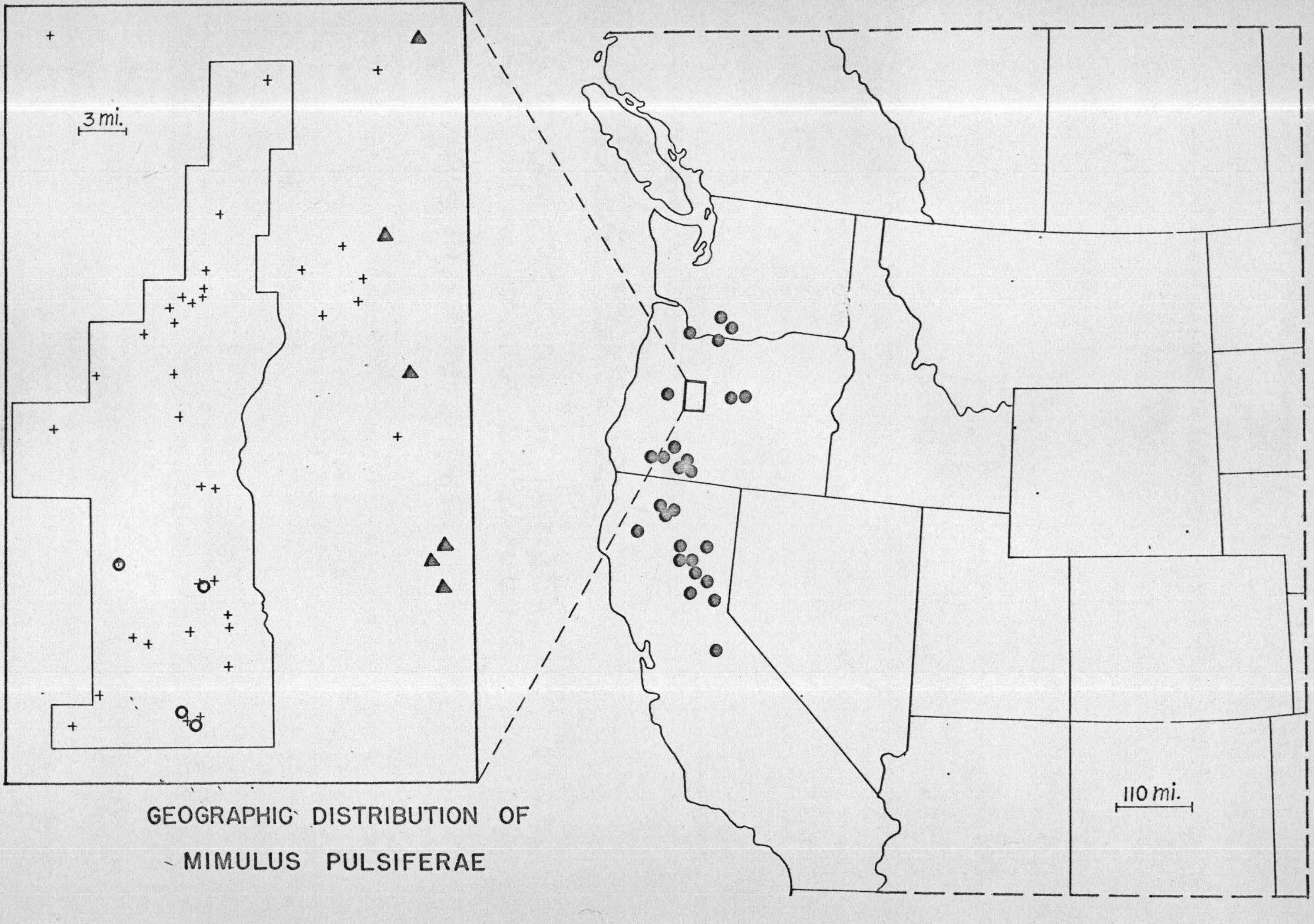
GEOGRAPHIC DISTRIBUTION OF
PENSTEMON DEUSTUS

the geographic distribution of this variety cannot be considered outside the context of the other varieties, and all four have been mapped as one entity in this work.

Mimulus pulsiferae Gray, Proc. Am. Acad. 11:98. 1876.

This small annual monkeyflower is characterized by the following attributes: corolla yellow, only slightly bilabiate, 8-16 mm in length; leaves tapered to a sessile base. More common in the northern half of California, especially in the foothills of the Sierra Nevada, it has been collected only rarely north of Crater Lake, although it ranges north almost to Mt. Adams. The closest relative of M. pulsiferae is M. washingtonensis Gand., from which it differs in its smaller less bilabiate flowers and glabrous style. The ranges of the two species overlap along the eastern base of the Cascades in Klickitat County, Washington, from which point M. washingtonensis spreads east through southern Washington, northern Oregon, and west-central Idaho (Grant, 1924; Cronquist, in Hitchcock and others, 1959).

Throughout its range M. pulsiferae occurs in moist open areas. In the Western Cascades it is a rather ephemeral member of the spring flora, occupying open gravel flats and steep rocky slopes while snowmelt runs, desiccating after midsummer. In some areas it occurs abundantly in dense patches but has been found in only four distinct localities in the Oregon Cascades north of Crater Lake to date. M. pulsiferae occurs in the Rocky Melt Seep or Gravel Scree associations where it grows with Gayophytum humile, Mimulus breweri, Polygonum kelloggii,



GEOGRAPHIC DISTRIBUTION OF MIMULUS PULSIFERAE

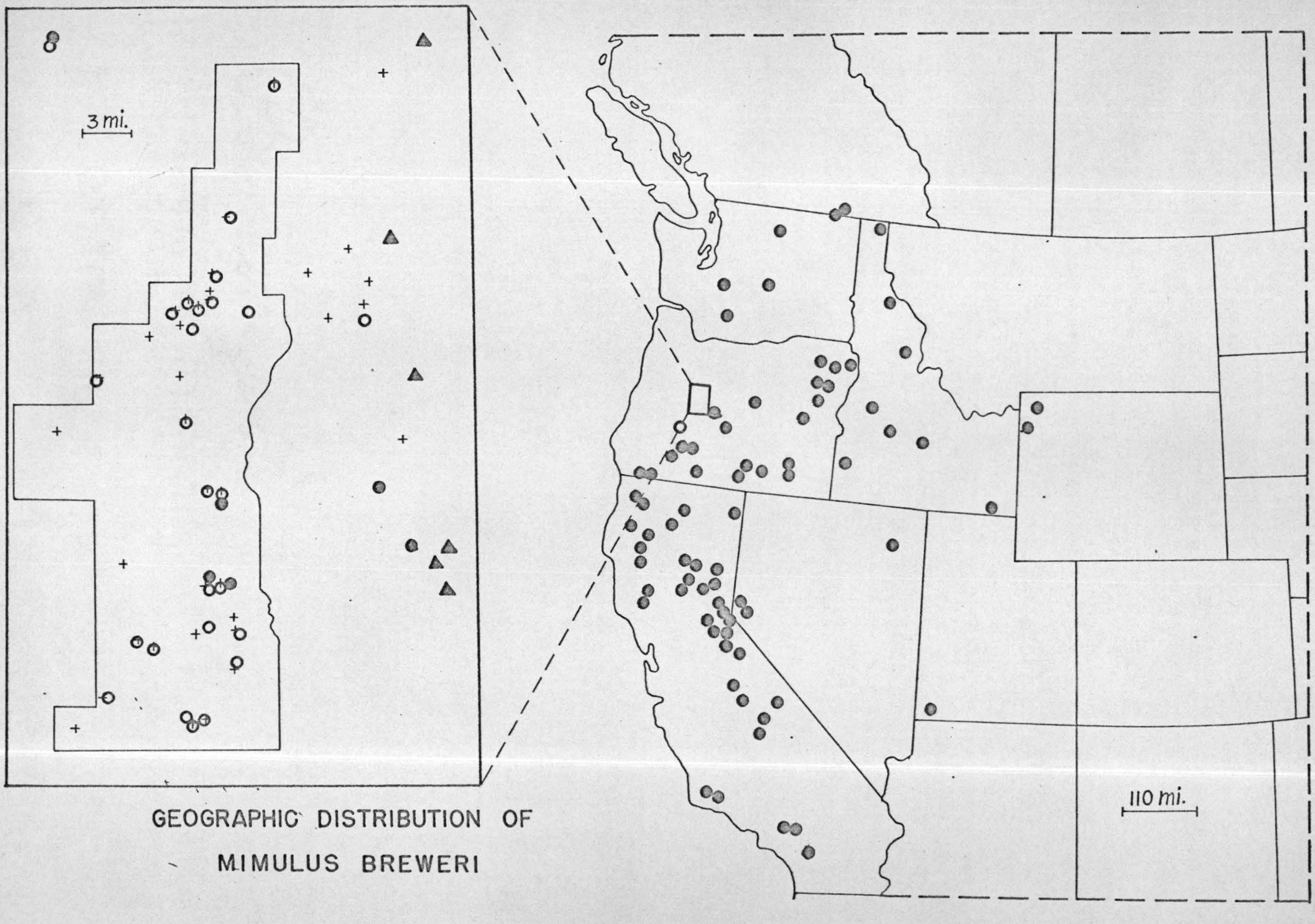
Linanthus harknessii, *Eriogonum nudum*, *Artemisia tridentata*, *Navarretia divaricata*, and *Polygonum cascadense*.

Mimulus breweri (Greene) Coville, Contr. U. S. Nat. Herb. 4:171. 1893.

M. breweri is a glandular anthocyaniferous annual with very small purple and red flowers. It is evidently closely allied both to the larger yellow-flowered *M. suksdorfii* Gray and to *M. rubellus* Gray, a species of the Rocky Mountain region which may have either red or yellow corollas. Under dry or otherwise adverse conditions *M. breweri* may attain a height of less than 2 cm with one pair of leaves beyond the cotyledons and a single flower. Many rapidly-maturing minute seeds are produced in each capsule. These plants are markedly ephemeral under most conditions but will attain a height of 15 cm and produce hundreds of thousands of seeds if sufficient moisture remains available for continued growth. Other members of the Rocky Melt Seep association with which *M. breweri* is frequently found include *Lewisia triphylla*, *Linanthus harknessii*, *Polygonum kelloggii*, *Gayophytum humile*, *Galium bifolium*, *Allium amplectens*, *Polygonum minimum*, and *Collinsia parviflora*.

Castilleja pruinosa Fern., Erythea 6:50. 1898.

There is no satisfactory treatment of *Castilleja* in the literature. It is one of the most difficult genera in the Pacific Northwest. Although *Castilleja* is a relatively well-defined genus, the possibilities for hybridization among the numerous species seems limitless. The morphological evidence points to reticulate evolution in at least



GEOGRAPHIC DISTRIBUTION OF
MIMULUS BREWERI

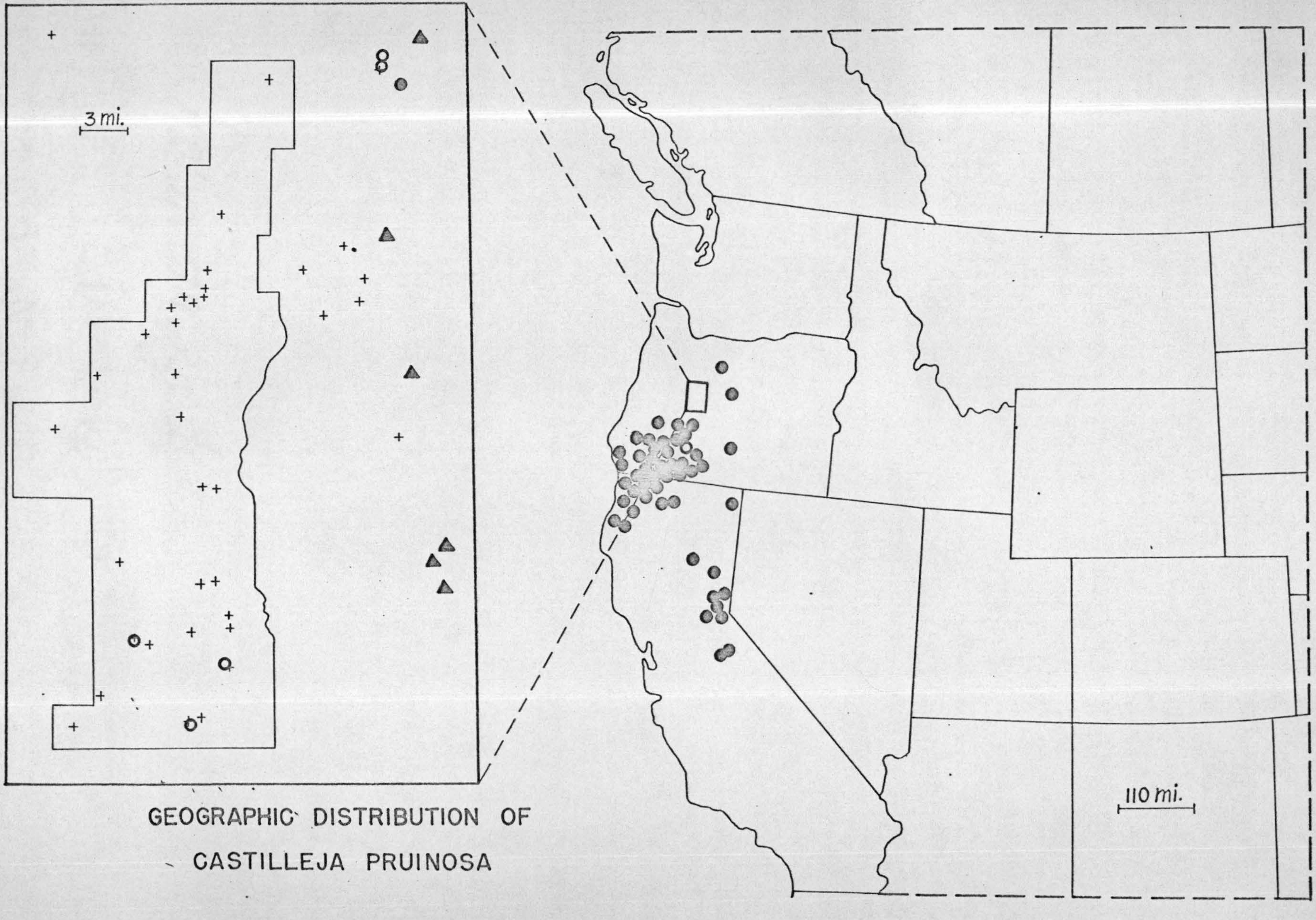
portions of the genus. Our commonest species is C. miniata Dougl., which evidently intergrades to some extent with most other species of Castilleja occurring within its range. Two students of the genus, Noel Holmgren and Rimo Bacigalupi, have examined my material and have helped greatly with its interpretation.

According to Ownbey (in Hitchcock and others, 1959), C. pruinosa is the only member of the Section Pruinosae (characterized by branched hairs on the leaves and stem) occurring in the Pacific Northwest. It is evidently closely related to the shorter galead more tomentose C. mollis Penn. of the coastal dunes of San Luis Obispo County, California, although on the California coast the two species are separated by nearly 640 km.

Typical C. pruinosa has numerous branched hairs, giving the lower stems and leaves a singular whitish cast even from a distance. The leaves are long and narrowly linear and the inflorescence relatively long and open. Some specimens from the Western Cascades (e.g. Hickman 8-20, 124-9, 272-1) are perfectly good C. pruinosa, but other material with some branched hairs is quite problematical. Bacigalupi hypothesizes that these specimens contain genes of C. pinetorum Fern. and C. affinis H. and A. Holmgren cites the congested inflorescence and broad leaves of these specimens as support for his opinion that they represent intergrades with C. miniata and are actually closer to that species than to C. pruinosa. Recent work by Heckard (1968), which centers on the role of polyploidy in the evolution of this genus, has implicated C. pruinosa in the complex centered around C. peckiana Penn. The latter species approaches C. miniata on one hand and C. hispida

Benth. subsp. *acuta* Penn. on the other. Ownbey (in Hitchcock and others, 1959) found a discontinuity in this clinal progression and reduced *C. peckiana* to synonymy with *C. minnata*. Heckard has proposed a more complex relationship, however, in which *C. chromosa* and *C. pruinosa* also contribute genic material to the complex. Two specimens were collected (*Bacigalupi and Heckard 7900*, *7905*: UC) from south-central Wasco County which, though otherwise like typical *C. peckiana*, have a number of branched trichomes. Heckard also notes that these records help substantiate the presence of *C. pruinosa* (at least in its chief diagnostic characteristic) north of the Siskiyou-southern Cascades region. A single record had previously been reported from Hunt's Cove near Mt. Jefferson (*Leach 4601*), which was doubted as to locality by Ownbey (in Hitchcock and others, 1959). Other specimens from Grizzly Peak (*Hickman 438-1*, *438-2*), only one kilometer from the Hunt's Cove locality, also help confirm accurate labelling of the Leach collection. These plants show some characteristics of *C. miniata* and *C. hispida*. Thus presently available evidence indicates to this writer that all of the Western Cascade specimens should be considered part of the *C. peckiana* complex, comprising a polymorphic group of intergrades among *C. miniata*, *C. hispida*, and *C. pruinosa*.

In the Western Cascades these castillejas are found rooted in crevices of andesite or basalt on precipitous, dry, south-facing cliffs and slopes. Plants are never encountered in large populations, and the collecting localities are few. As members of the Outcrop Ridge association, they usually occur with *Erigeron foliosus confinis*, *Silene campanulata glandulosa*, *Cheilanthes siliquosa*, *Arabis platysperma*



GEOGRAPHIC DISTRIBUTION OF CASTILLEJA PRUINOSA *howellii*, *Eriogonum umbellatum*, *Allium amplectens*, and *Juniperus communis saxatilis*.

Castilleja rupicola Piper, Erythea 6:45. 1898.

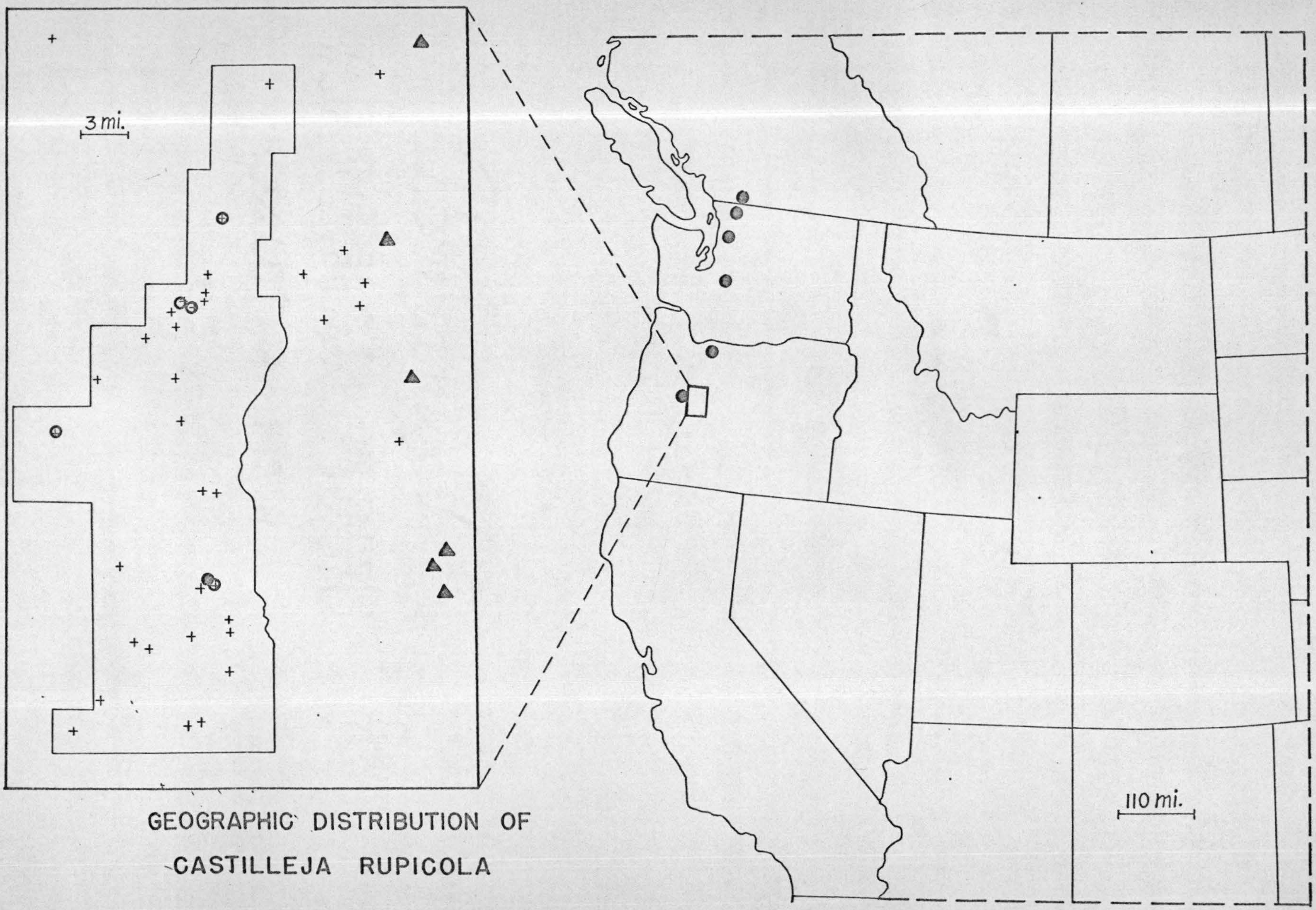
Selected synonyms:

Castilleja andrewsii Henderson, Madrono 3:31. 1935.

Several members of the Section *Parviflorae* occur in the Cascades. They include *C. hispida*, *C. rupicola*, *C. parviflora oreopola*, *C. suksdorfii*, *C. glandulifera*, and *C. applegatei*. All of these but the last occur at the latitude of the Three Sisters, and numerous intergrades are known, not only within this group, but with more distantly related species as well. *C. hispida* is common in rocky dry sites throughout the Cascades as far south as Douglas County. The other species are more restricted in both range and habitat. *C. rupicola* occurs rooted in crevices of north or west-facing outcrops in the northern Cascades from southern British Columbia to Mt. Rainier, and again in the Western Cascades of Oregon. In the fresh state its leaves are markedly purplish; this color is often retained on drying. This characteristic is shared with only one other taxon, *C. parviflora* var. *oreopola* (Greenm.) Ownbey, a close relative. This variety of *C. parviflora* is found only in the High Cascades at this latitude, being common on the Three Sisters and occasionally collected from lower more westerly peaks in the High Cascades (*Detling 3325*, *5393*; *Hickman 439-5*, *499-2*). It also occurs in the high Olympics, and is distinguished from *C. rupicola* by fewer leaf lobes and purplish rather than scarlet bracts and corollas. The habitat it occupies is also quite different; it is typically found in damp scoria gravel or pumice flats near snowbeds.

Ownbey (in Hitchcock and others, 1959) notes two other species as being close relatives of *C. rupicola*. *C. suksdorfii* occurs in high, wet, mountain meadows from Mt. Adams to Crater Lake in the Cascade Range. Like *C. parviflora oreopola*, it has fewer leaf lobes than *C. rupicola*, is much more robust, and seldom branches from the base, as is characteristic of both *C. parviflora oreopola* and *C. rupicola*. Two specimens of *C. suksdorfii* are known from near Fish Lake, Linn County (*E. P. Sheldon 12570*, *12555*), and one from a perennially wet meadow seep at the top of Tombstone Meadow on Cone Peak in the interior of the Western Cascades (*Hickman 190-7*). *C. rupicola* also occurs on this peak at higher elevations. *C. covilleana* is strikingly similar to *C. rupicola* except for its shorter and less exserted galea. It occurs at high altitudes in the mountains of central Idaho and southwestern Montana.

Most collections of *C. rupicola* from the Western Cascades are essentially identical to *Piper 2071* or *Gorman 2891* from Mt. Rainier and Mt. Baker, respectively. A few specimens tend morphologically toward *C. hispida* as shown by a widening of the undivided base of the leaves (*Hickman 493-2*, Tidbits Mountain). The type specimen of Henderson's *C. andrewsii* (*Andrews 233*) from Horsepasture Mountain consists of two stems, one of which is *C. rupicola* so completely introgressed with *C. hispida* as to be almost identifiable as that species. Leaves of this stem are wide, the lobes are broad and rounded, as in *C. hispida*. This portion of the type is entirely lacking in purple leaf pigments. The other smaller stem is more typical of *C. rupicola* but still shows several *hispida* characters. Locality information is too vague to permit



GEOGRAPHIC DISTRIBUTION OF
CASTILLEJA RUPICOLA

accurate recollection of this aberrant population. Further material from Horsepasture Mountain (Hickman 305-5) is nearly identical to material of C. rupicola from Mt. Rainier, the type locality.

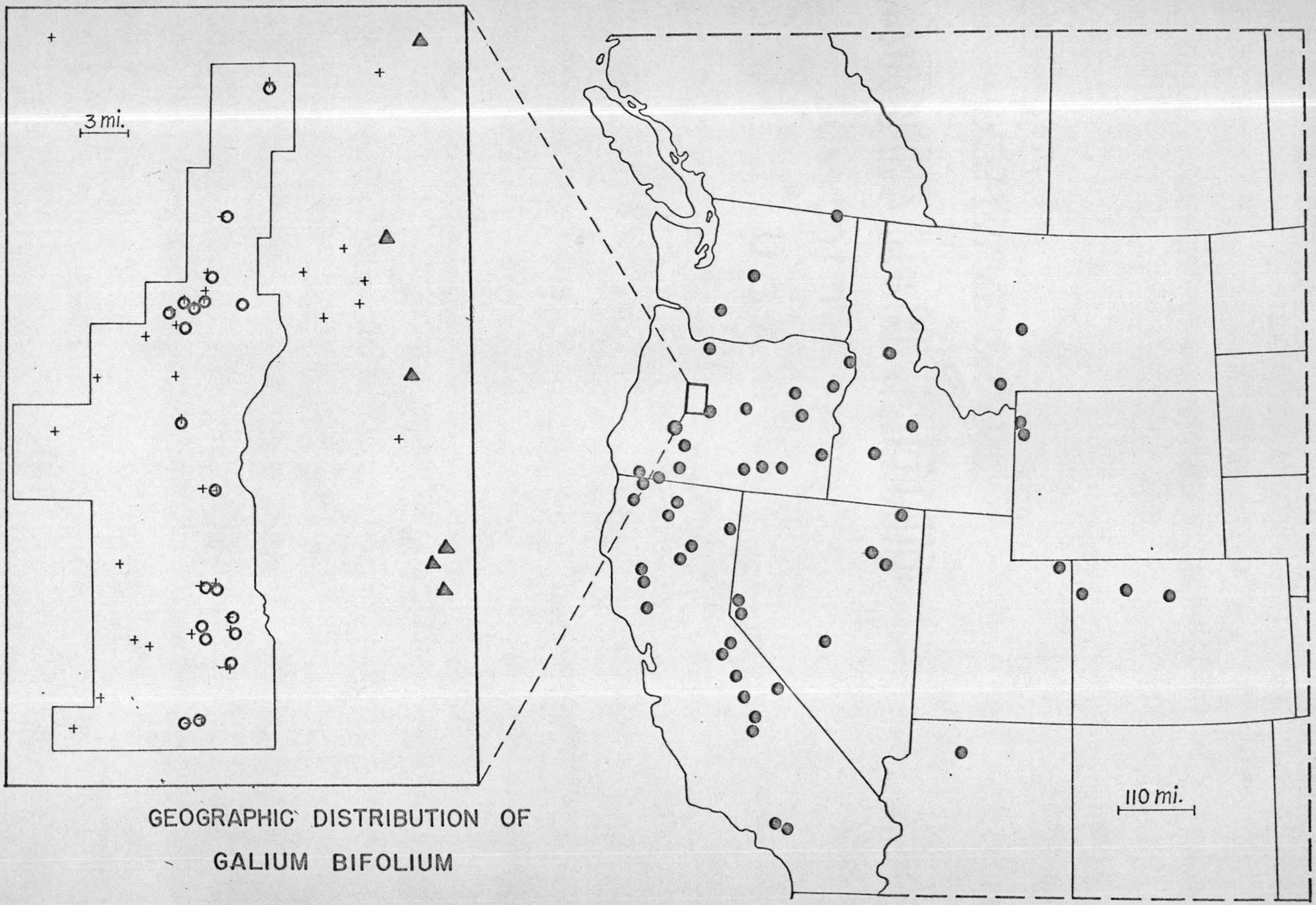
Another population from Tidbits Mountain (Hickman 556-1) has a matted webby pilosity about the inflorescence that is characteristic of C. arachnoidea Greenm., which is common 50 km to the east on the Three Sisters. A single collection of C. arachnoidea has been taken from Olallie Meadows at the western edge of the High Cascade Range. This species, of the Section Pilosae, is strikingly different from C. rupicola in its floral morphology, but some crossing between these taxa may nevertheless have occurred.

The conclusion that must be drawn from presently available information is that C. rupicola, a species of basically northern ancestry, is beginning to lose its identity in the southernmost parts of its range in the Western Cascades of Oregon, where it freely interbreeds with C. hispida and occasionally with more distantly related species. Nevertheless, most material from this area compares favorably with typical C. rupicola.

Vertical Outcrop associates include Saxifraga bronchialis vespertina, Penstemon rupicola, Selaginella scopulorum, Selaginella wallacei, Gentiana calycosa n. subsp., Saxifraga occidentalis rufidula, Valeriana sitchensis, Campanula rotundifolia, and Douglasia laevigata.

Galium bifolium Wats., Bot. King Exp. 134. 1871.

This species is one of the most distinctive of all the bedstraws.



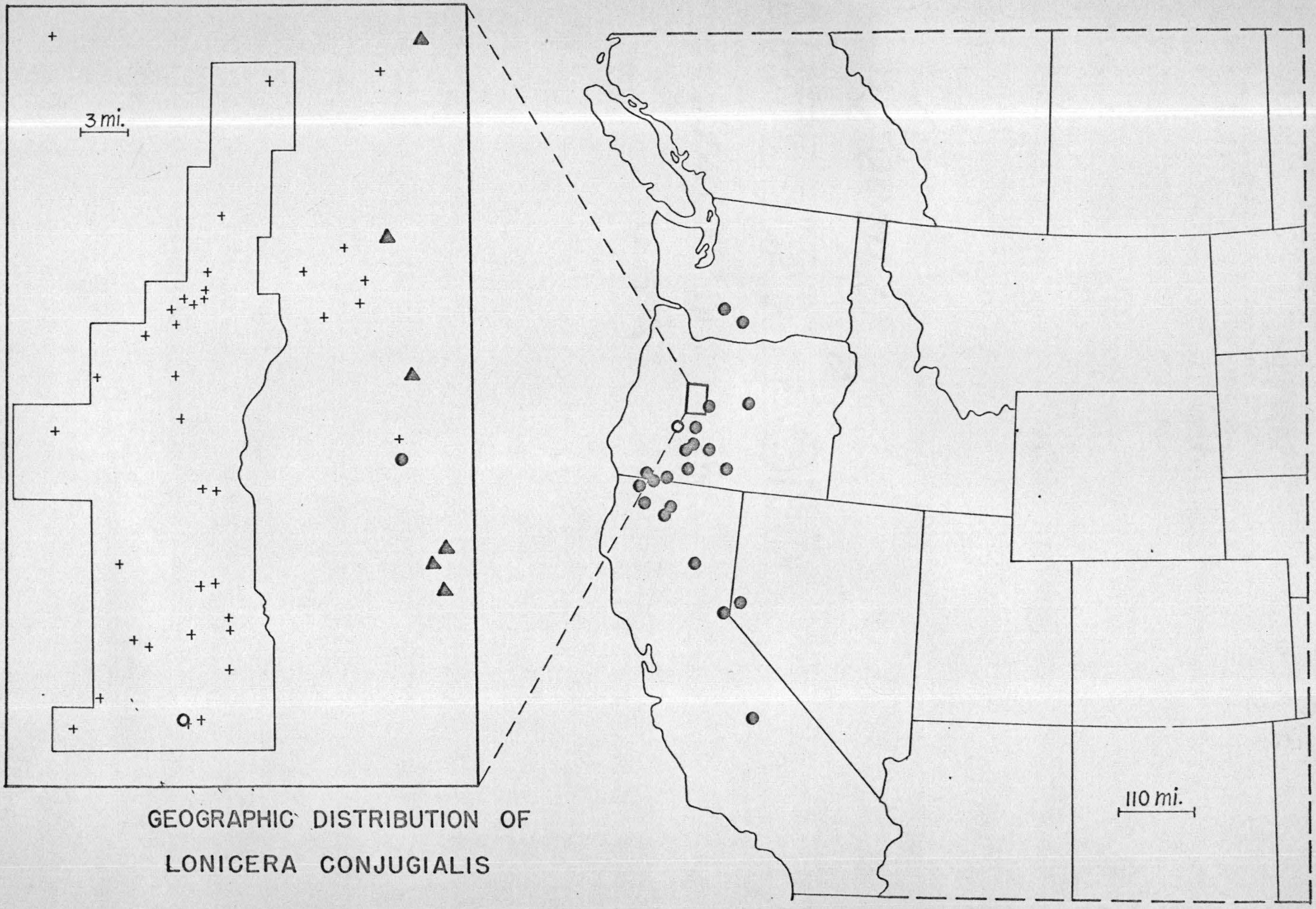
GEOGRAPHIC DISTRIBUTION OF GALIUM BIFOLIUM

It is an annual, having only one or two pairs of leaves at each node (if two, the pairs are of unequal size), glabrous stems, and strongly divaricate pedicels with solitary nodding fruits. Its affinities to other species of *Galium* are not clear.

G. bifolium occurs throughout the mountainous regions of the Western United States but has only rarely been collected from the High Cascades or further west. In the course of this study, however, it was found to be relatively abundant on all of the Western Cascade peaks that have been mapped (Peck and others, 1964) as Plio-Pleistocene High Cascade volcanic rocks. It is generally a spring ephemeral but may persist for some time shaded by taller species in mesic middle or high altitude meadows where the moist soil is loose and continually mixed by mass wasting and the action of rodents. Other members of the Mesic Meadow association are *Rubus parviflorus*, *Pteridium aquilinum*, *Rudbeckia occidentalis*, *Aquilegia formosa*, *Erigeron aliceae*, *Gayophytum humile*, *Polygonum minimum*, *Luina stricta*, and *Ribes binominatum*.

Lonicera conjugialis Kell., Proc. Cal. Acad. Sci. 2:67. 1863.

In his detailed synopsis of the genus *Lonicera*, Rehder (1903) recognized 157 species, most of which are restricted to subtropical regions of the world. The taxonomy and nomenclature of this group are difficult, but the western North American species do not present grave problems. *L. conjugialis* is the only species from this region having dark reddish flowers. The largely united ovaries are also distinctive. This species ranges from Mt. Adams south through the High Cascades and



GEOGRAPHIC DISTRIBUTION OF
LONICERA CONJUGIALIS

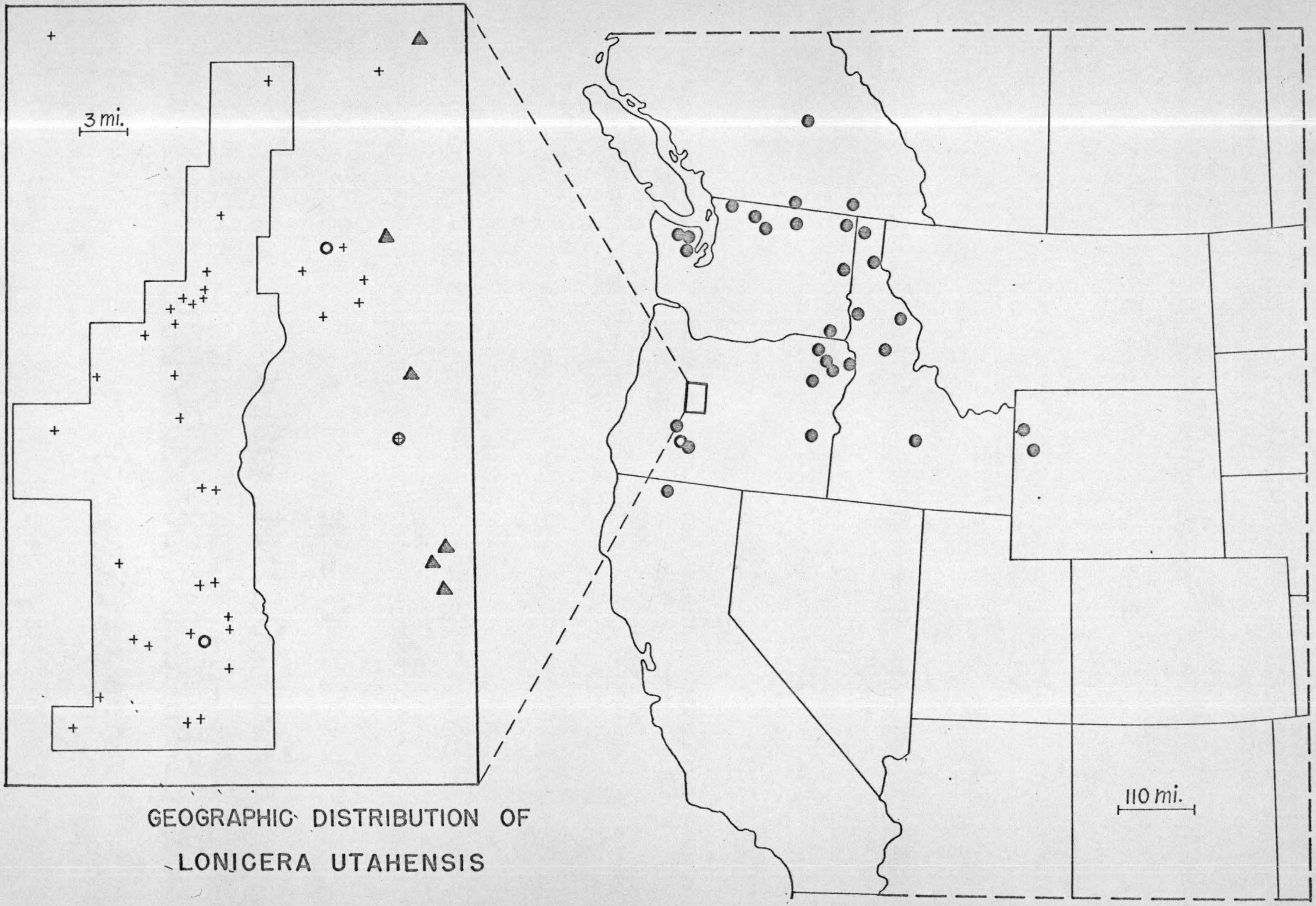
Great Basin to the Siskiyou Mountains of Oregon and California and southward through the Sierra Nevada to central California. It had not previously been collected from west of the Cascade crest except in the Siskiyou region.

In the Western Cascades *L. conjugialis* occurs uncommonly on south or west-facing slopes above 1500 m in open grass-*Carex* meadows or in partial shade along forest-meadow ecotones. It has been found rooted among rocks or in dry meadow soils. Associated species include *Bromus carinatus*, *Eriogonum umbellatum*, *Veratrum insolitum*, *Luina stricta*, *Abies amabilis*, *Sambucus callicarpa*, and *Calochortus lobbii*.

Lonicera utahensis Wats., Bot. King Exp. 133. 1871.

This species shows a strangely disjunct distribution. Most collections have been taken from moist mountain slopes in the Olympics north and east through Washington, British Columbia, and Idaho, and south in the Rocky Mountains reportedly to Utah. Most Oregon material has been collected in the Wallowa Mountains. Another disjunct series of populations extends from the central Cascades of Oregon south in the mountains to northern California. Only three localities in this area were previously known; this study adds four more Cascade populations.

L. utahensis is distinguished by its yellow axillary flowers and small bractlets, which do not enclose the ovaries. It has been found only in the saturated soil of bogs and on north-facing seepage slopes where snow remains until midsummer or later. Typically a high elevation species, *L. utahensis* occurs as low as 1300 m in the Western Cascades.



GEOGRAPHIC DISTRIBUTION OF LONICERA UTAHENSIS

On north-facing cinder slopes it is associated with *Anemone occidentalis*, *Pinus contorta murrayana*, *Polygonum newberryi*, *Vaccinium membranaceum*, and *Penstemon euglaucous*. In boggy areas associated species include *Boykinia major*, *Kalmia polifolia*, *Aster alpigenus*, *Hypericum anagalloides*, *Mertensia bella*, *Habenaria dilatata*, *Drosera longifolia*, *Valeriana sitchensis*, and *Viola palustris*

Chrysothamnus nauseosus (Pall.) Britt. var. *albicaulis* (Nutt.) Rydb. Mem. N. Y. Bot. Gard. 1:385. 1900.

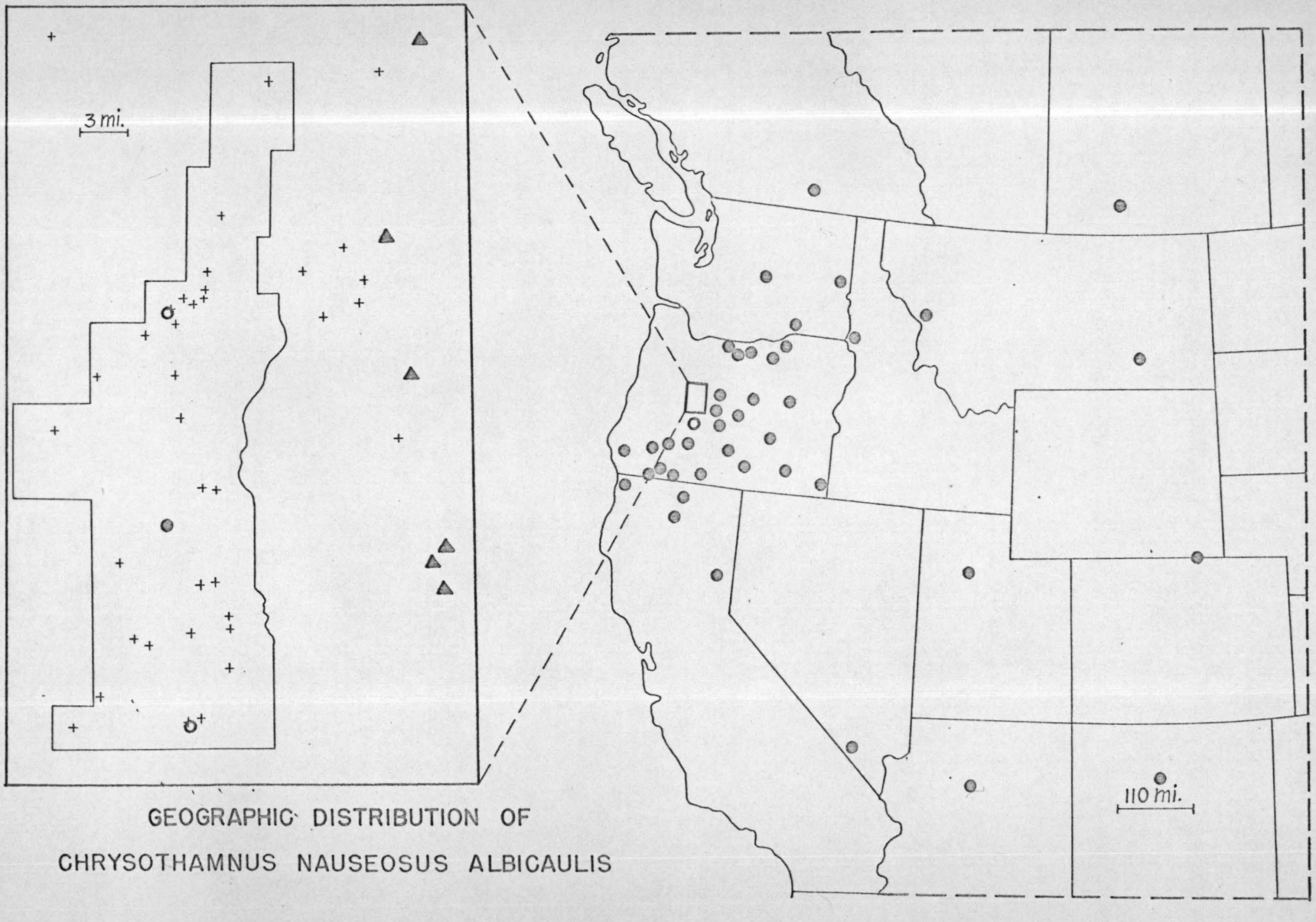
Selected synonyms:

Chrysothamnus speciosus Nutt., Trans. Am. Phil. Soc. II 7:323. 1840.

Chrysothamnus nauseosus var. *speciosus* Hall, U. Cal. Publ. Bot. 7:169. 1919.

This species is composed of a complex of poorly defined varieties of which the present one is the most widespread and common. It is distinguished from other taxa of *Chrysothamnus* by the shape and pubescence of the involucral bracts, by the presence of a felt-like tomentum on the twigs, and by pubescent achenes. It occurs throughout the Western United States and southern Canada in sub-desert or high cold desert regions. Hall and Clements, in their 1923 monograph, recognize 20 subspecies of *Chrysothamnus nauseosus* with 83 listed synonyms. The relationships between these subtaxa are highly complex, and it is unlikely that they all represent natural evolutionary groups.

Throughout much of its range, *C. nauseosus albicaulis* occurs with sagebrush, *Artemisia tridentata*. Stems have been shown to die back under great and prolonged moisture stress by McKell (1956) and in the present



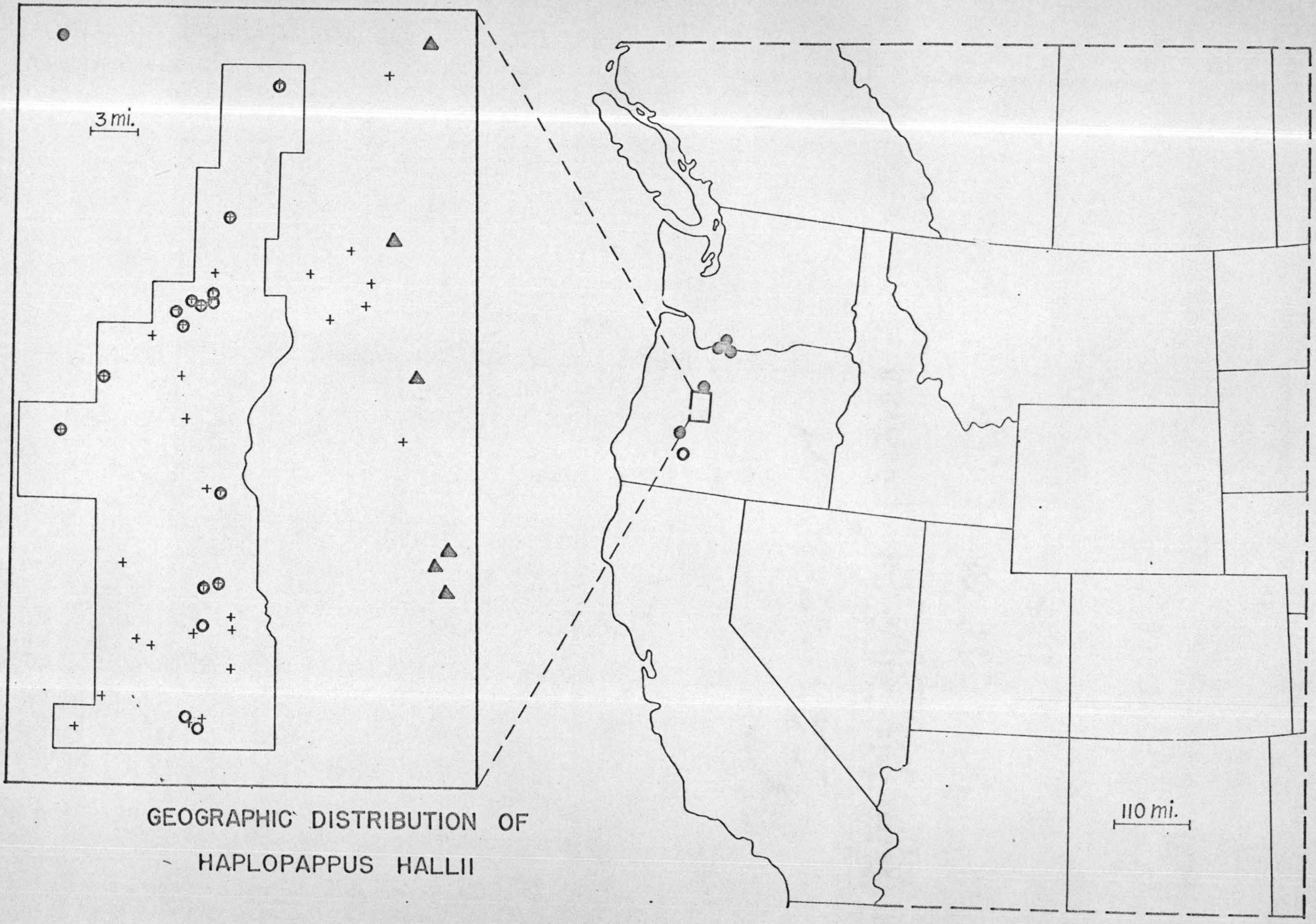
GEOGRAPHIC DISTRIBUTION OF
CHRYSOTHAMNUS NAUSEOSUS ALBICAULIS

work, but resprouting from the crown has occurred with application of water in every instance. Deeply penetrating root systems insure that such drought stress will be infrequent. A large population has been collected by the author on gravelly terraces of the South Umpqua River near Canyonville, although this species is typically part of the Juniper-Sage association of the Great Basin. In the Western Cascades, *Chrysothamnus* is restricted to a few sites on exposed south-facing cliffs, where it roots in crevices of andesite or in pockets of fine gravelly talus. One specimen has been found growing in a gravel highway embankment just below precipitous rocky slopes. Although areas in which this species grows are harsh enough that it has no close associates, *Eriogonum compositum*, *Eriogonum umbellatum*, *Lotus nevadensis douglasii*, *Penstemon deustus*, and other Gravel Scree species frequently grow in the general vicinity.

Haplopappus hallii Gray, Proc. Am. Acad. 8:389. 1872.

Hall's 1928 monograph of the genus *Haplopappus* has been called "one of the landmarks of American taxonomy" (Cronquist, 1955, p. 211). Hall calls attention to the fact that *Haplopappus* is an ancient and complexly diversified genus with several presumably derivative genera of the Astereae such as *Chrysothamnus*, *Grindelia*, and *Chrysopsis*, and several closely related groups with which hybridization may have occurred in the past. The latter include such presently problematical genera as *Solidago* and *Aster*.

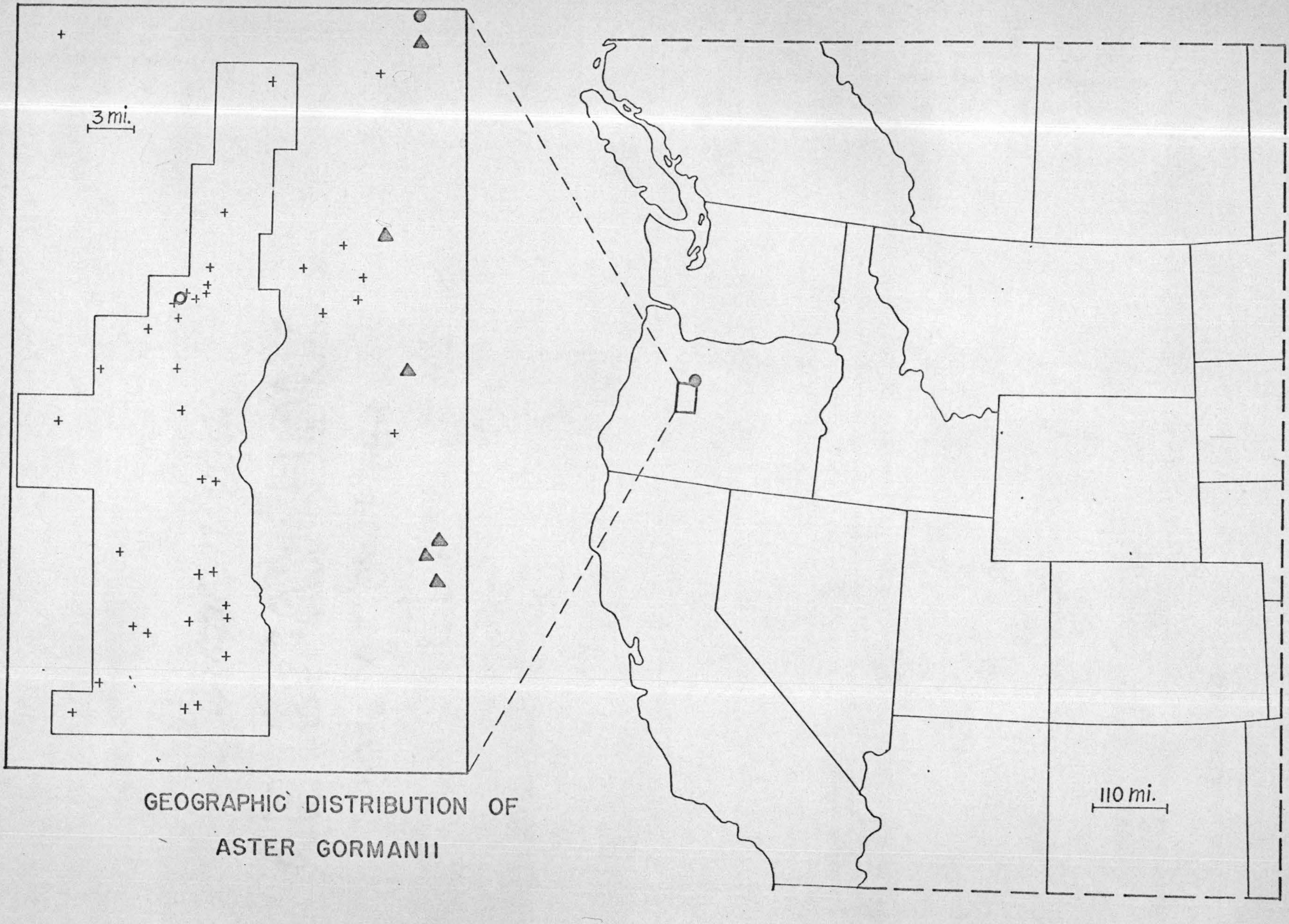
Hall recognized 16 sections of *Haplopappus*. One of the small sections is *Hesperodoria*, which contains *H. halli* and an eradiate species



GEOGRAPHIC DISTRIBUTION OF HAPLOPAPPUS HALLII of the southern Colorado Plateau, *H. scopulorum* (Jones) Blake. The two species are differentiated from other species of *Haplopappus* by their perennial habit, narrowly campanulate or turbinate inflorescences, and fine white pappus. The last character allies this section with certain species of *Solidago*. Both species are quite distinctive and confined to rather narrow ranges. Hall was aware of only one locality outside of the eastern end of the Columbia Gorge for *H. Halli* (*Applegate 2755*: US; near Breitenbush Hot Springs), but the present work has shown the species to be quite common in the Western Cascades as far south as Hershberger Mountain, southern Douglas County. It occurs in crevices of volcanic outcrops or on gentle deflation armor slopes in exposed south-facing habitats. Flowers appear late in August, making this one of the last Western Cascade species to bloom. It often occurs with such members of the Outcrop Ridge association as *Sedum divergens*, *Castilleja hispida*, *Erigeron foliosus confinis*, *Cheilanthes siliquosa*, *Silene douglasii*, *Eriogonum umbellatum*, and *Juniperus communis saxatilis*.

Aster gormanii (Piper) Blake, Rhodora 30:228. 1928.

This highly restricted and distinctive member of a most complex genus is characterized by a small number (8-13) of white ray flowers, typically solitary heads, and sessile entire leaves reduced but little to the inflorescence. It differs from the closely allied *A. paucicapitatus* Rob., which occurs in the Olympic Mountains and on the south end of Vancouver Island, in its smaller size and wider involucral bracts. *A. gormanii* has previously been reported from only two localities: the



GEOGRAPHIC DISTRIBUTION OF
ASTER GORMANII

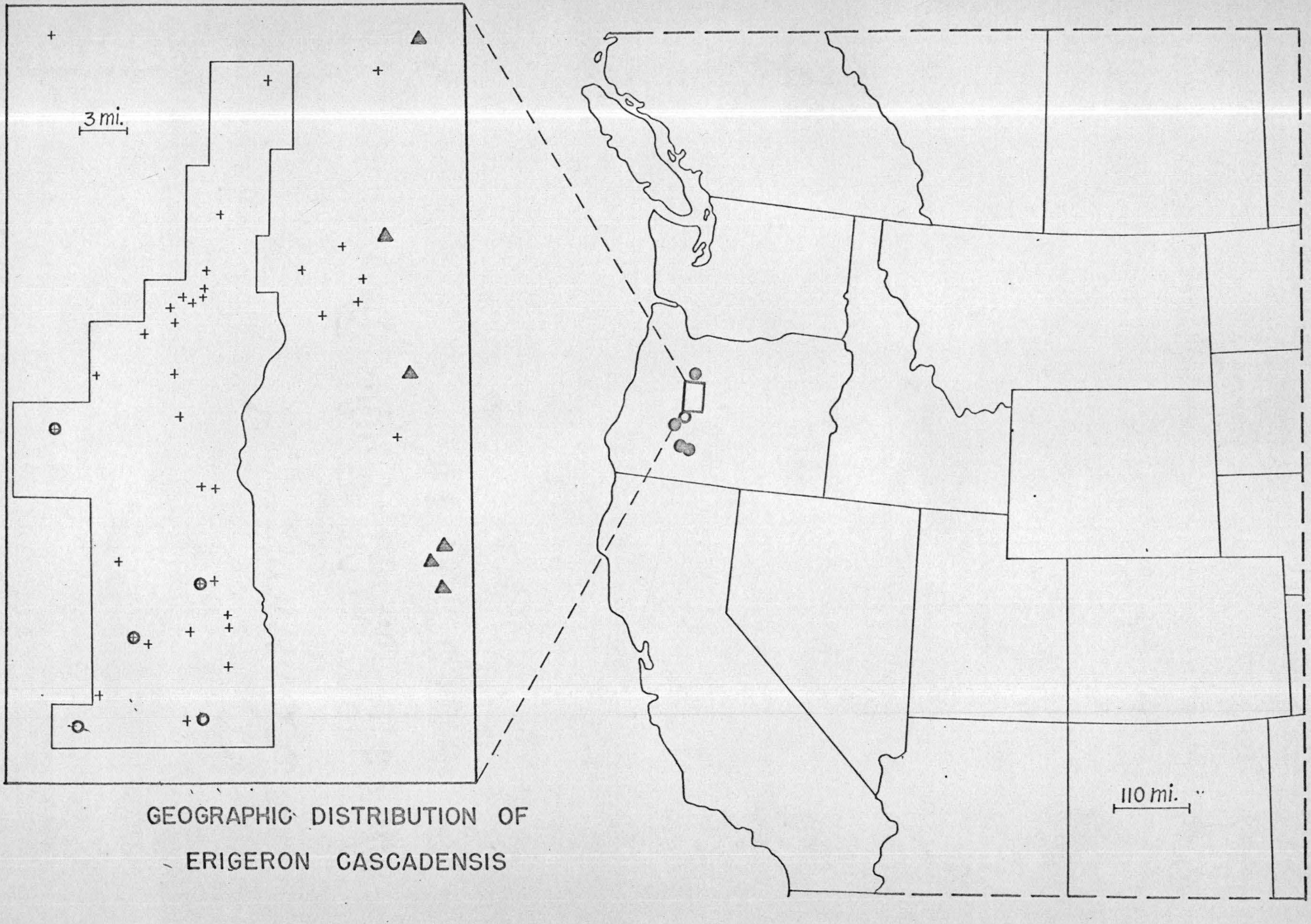
type locality on the northern slope of Mt. Jefferson, Marion County, and from cliff faces around Harvey Lake about six km to the north. A third well-established population was discovered in a gravel scree on the northeast side of Iron Mountain, almost 50 km southwest of the type locality.

The Western Cascade population occurs with *Ivesia gordonii*, *Trifolium productum*, *Gilia aggregata*, *Lotus nevadensis douglasii*, *Crepis occidentalis*, *Sanicula graveolens*, and *Linum perenne lewisii*.

Erigeron cascadensis Heller, Muhl. 1:6. 1900.
Selected synonyms:

Erigeron spatulifolius Howell, Fl. N. W. Am. 1:317. 1900.
Erigeron pachyrhizus Greene, Leafl. 2:216. 1912.

Erigeron cascadensis is one of many species of the Section *Euerigeron* that evidently has been derived from *E. peregrinus* stock (Cronquist, 1947). Its closest relatives are *E. cervinus*, endemic to the Klamath Mountain region, and *E. leibergii*, a species of the eastern slope of the Cascades of Okanogan, Chelan, and Kittitas Counties, Washington. It is morphologically intermediate between these two species. *E. cascadensis*, although quite distinctive, has been poorly collected and evidently is very locally distributed in addition to having a limited range. It has been collected from fewer than half a dozen sites between Fairview Peak in the Calapooya Range and Crater Lake, and at Pansy Camp on the Marion-Clackamas County Line. One specimen (*Lloyd*, in 1893) is reportedly from the "45th parallel, Cascade Mountains," but since early



GEOGRAPHIC DISTRIBUTION OF
ERIGERON CASCADENSIS

collectors evidently used this designation to include most of the central Cascades of Oregon, the exact locality is open to question.

This species grows in rock rubble and in crevices of weathering volcanic outcrops at the summits of several Western Cascade peaks. It occurs both on moist north-facing slopes and on hot, exposed, south-facing cliff faces. Its phenology is greatly affected by exposure aspect, but its lack of habitat specificity, except for substrate texture, makes its geographical restriction puzzling. Commonly found with *Erigeron cascadensis* in Fine Gravel Scree or Vertical Outcrop associations are *Penstemon rupicola*, *Erigeron foliosus confinis*, *Selaginella wallacei*, *Silene douglasii*, *Silene campanulata glandulosa*, *Arenaria capillaris americana*, and *Linanthastrum nuttallii*.

Erigeron compositus Pursh, Fl. Amer. Sept. 2:535. 1814.

Selected synonyms:

Erigeron compositus Pursh var. *discoideus* Gray, Am. Journ. Sci. II 33:237. 1862.

Erigeron compositus Pursh var. *glabratus* Macoun, Cat. Can. Pl. 2:231. 1884.

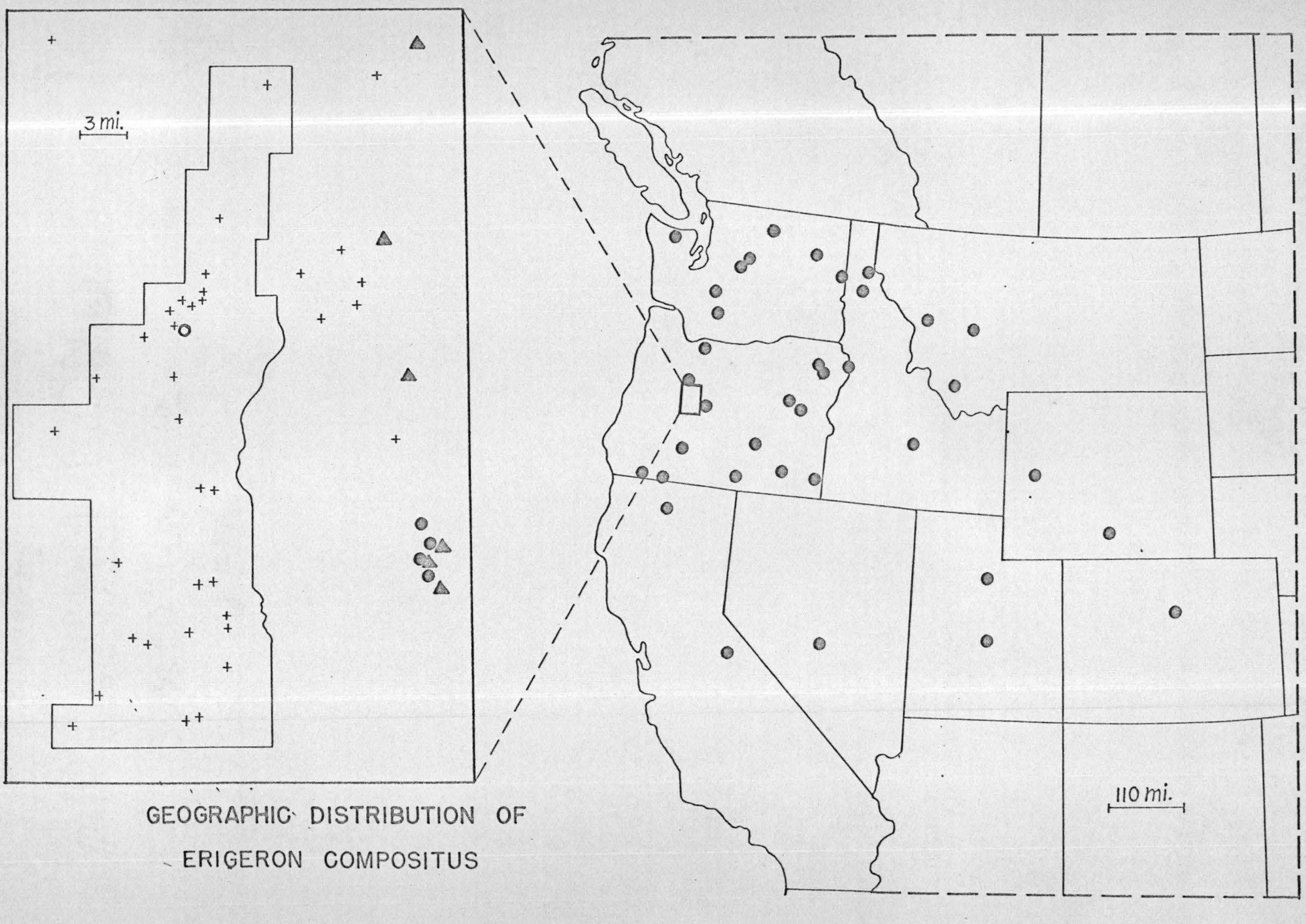
Erigeron compositus Pursh var. *submontanus* Peck, Torreya 28:56. 1928.

This highly variable species has been the center of much taxonomic and nomenclatural confusion (see Macbride and Payson, 1917; Payson, 1926; Cronquist, 1947, 1955). Slight variants have often been recognized as distinct species, and the taxon as a whole shows a history of the progressive lumping of subspecific taxa after an initial spurt of specific descriptions. The three varieties listed above have been to the present maintained as merely morphological groupings (Payson, 1926). They evidently constitute at best a series of ecotypes adapted to progressively higher elevations. Variety *glabratus* is the most common and shows the greatest elevational range. This intermediate form is found from 1000 m to 3500 m. Since all three of these varieties have been collected in the central Cascades of Oregon, and none has a discrete geographic range, they must here be lumped and discussed as a unit. Experimental work is needed in this group.

Other closely related species include such members of the series *Multifidi* as *E. flabellifolius* Rydb., *E. vagus* Payson, and *E. pinnatisectus* (Gray) A. Nels. *E. compositus* is distinguished from these taxa by having a much heavier less branched caudex and more deeply and finely divided leaves.

Erigeron compositus is widely distributed throughout western North America as far south as central California and Colorado and is primarily restricted to high elevations. Previous specimens from the Cascades have all come from the Arctic-Alpine zones of the highest peaks, with the single exception of the type collection of *E. compositus* var. *submontanus* (*Peck 14804*: WILLU), a robust form with finely divided leaves from near Detroit, Marion County, at an elevation of about 400 m (Peck, 1928). This is now considered to be the only collection of variety *compositus* from Oregon, others being confined to the eastern Columbia Basin of Washington.

A sizable population of *E. compositus* occurs in crevices and on coarse gravel scree on the south slope of Browder Ridge. These specimens are typical subalpine to alpine forms and are found here at an unusually

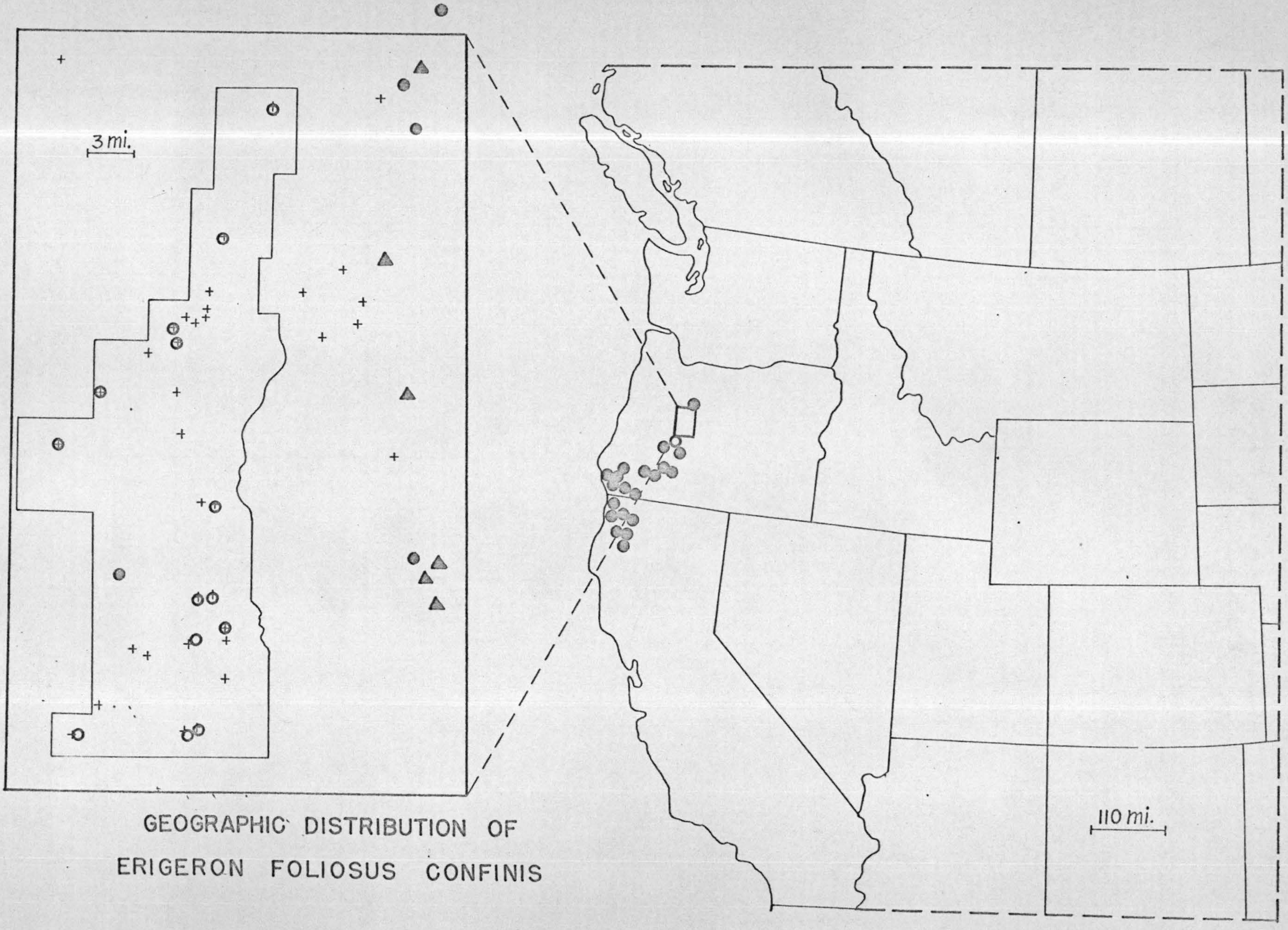


GEOGRAPHIC DISTRIBUTION OF ERIGERON COMPOSITUS low elevation (1700m). They are associated with *Eriogonum compositum*, *Eriogonum umbellatum*, *Allium amplectens*, and *Delphinium menziesii pyramidale*.

Erigeron foliosus Nutt. var. *confinis* Jeps., Man. Fl. Pl. Calif. 1056. 1925.

This taxon is readily recognized by its narrowly linear, entirely cauline leaves and strigose to scabrous pubescence. A more robust and less pubescent form, *E. foliosus* var. *hartwegii* Jeps., is also found throughout the range of var. *confinis* but has not been collected in the Western Cascades. These two varieties are common in northwestern California and the southwestern corner of Oregon, east to Crater Lake, and north in the Cascades to Mt. Jefferson. Several other varieties are found in the southern half of California and Baja California. Another closely related species, into which *E. foliosus confinis* passes in the southern part of its range, is *E. breweri*, which occurs from Mt. Shasta through the Sierra Nevada to the San Bernardino Mountains (Munz and Keck, 1959).

In the Cascades most collections of this species have come from the high peaks, with the exception of Castle Rock, where a specimen was collected early in the present century (*A. R. Sweetser*, in 1903). *E. foliosus confinis* seems, however, to be more common in the Western Cascades and is commonly firmly rooted in crevices of dark volcanic rock on dry, exposed, south-facing slopes from 1000 to 1600 m. A member of the Outcrop Ridge association, it grows commonly with *Sedum stenopetalum*, *Eriophyllum lanatum*, *Arctostaphylos nevadensis*, *Silene campanulata*



GEOGRAPHIC DISTRIBUTION OF ERIGERON FOLIOSUS CONFINIS *glandulosa*, *Haplopappus hallii*, and *Penstemon procerus brachyanthus*.

Helianthus cusickii Gray, Proc. Am. Acad. 21:413. 1886.

H. *cusickii* is distinguished from other Pacific Northwest sunflowers by its loose, narrow, acuminate involucral bracts; its narrowly lanceolate leaves; and its thickened taproot, the crown of which bears numerous simple stems. A species of the dry regions of the Columbia Basin and the Basin and Range Province, *H*. *cusickii* is known from only one locality west of the Cascade crest, where it may have been introduced within the last century. The upper south-facing slopes of Bachelor Mountain support an extensive population of plants which are morphologically variable and which occur in diverse habitats on open south or west-facing slopes near the summit. Stems from a single crown were noted to bear leaves in either strictly opposite or completely alternate arrangement. Some specimens were encountered in wet meadow loams partially shaded by other vegetation while others were rooted in dry, rocky, mineral soils on exposed ridges. Individuals were not consistently associated with any other plant species.

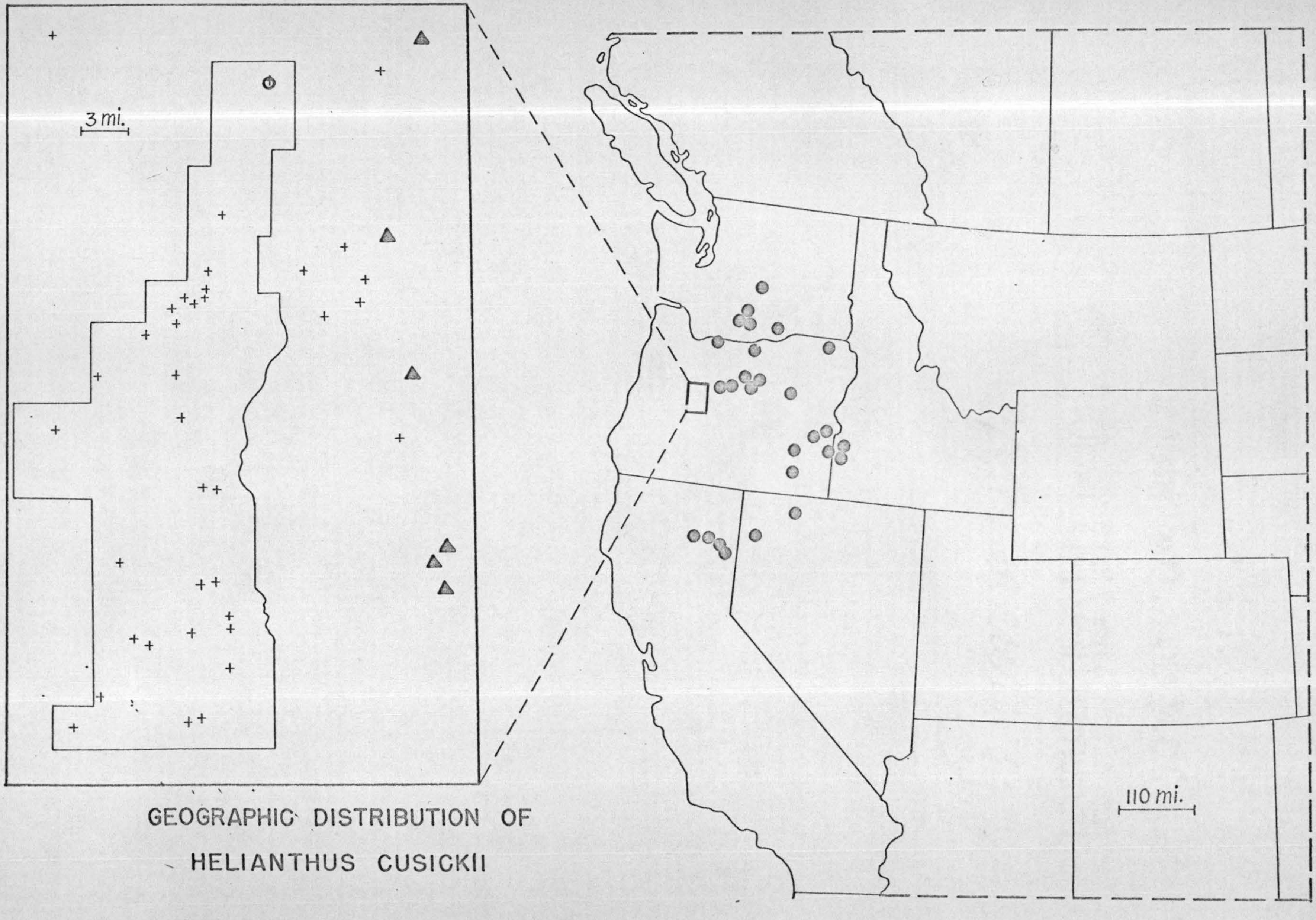
Artemisia ludoviciana Nutt. var. *latiloba* Nutt., Trans. Am. Phil. Soc. II 7:400. 1841.

Selected synonyms:

Artemisia candicans Rydb., Bull. Torr. Bot. Club 24:296. 1897.

Artemisia ludoviciana Nutt. subsp. *candicans* (Rydb.) Keck, Proc. Cal. Acad. Sci. IV 25:447. 1946.

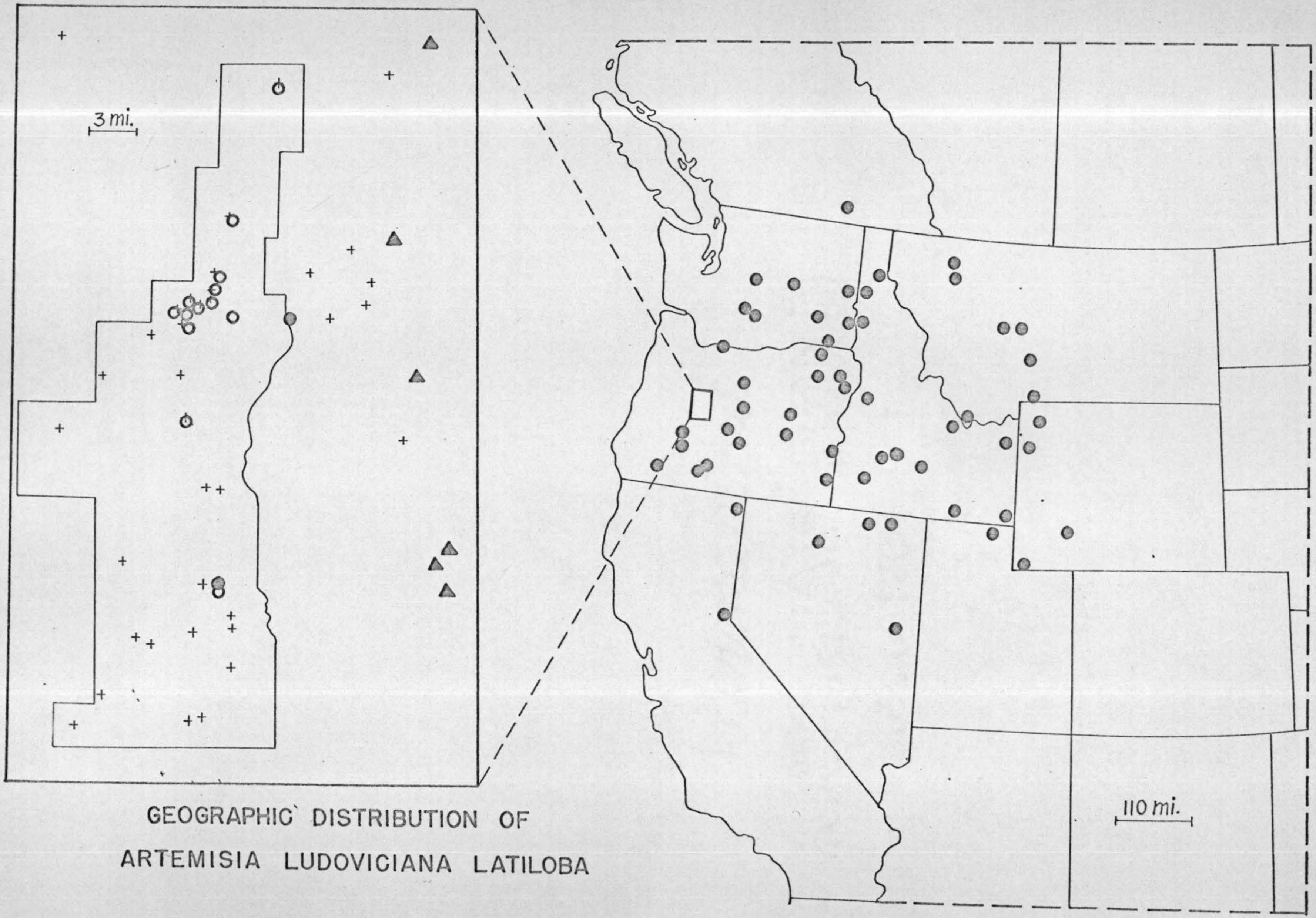
As a tetraploid member of the *Artemisis vulgaris* complex (Keck,



GEOGRAPHIC DISTRIBUTION OF HELIANTHUS CUSICKII

1946), this species is closely related to all other members of the group of herbaceous perennial wormwoods. Members of the complex, which are differentiated mainly on the basis of leaf morphology, are sufficiently confusing that they have received a variety of treatments in the taxonomic literature. In 1916 Rydberg recognized 54 distinct species from North America. Seven years later Hall and Clements (1923) proposed only the European *A. vulgaris* L. as a distinct species and considered the American material to constitute 15 morphological and geographical subspecies. With the addition of cytological evidence, Keck (1946) found Hall and Clements' morphological work to be basically sound, but following a more moderate species concept than either of the previous monographers, he recognized 9 species with 11 subspecies, 7 of the latter included under *A. ludoviciana*. Using a more geographically rigorous definition of subspecies, Cronquist (1955) admits only a northern and a southern subspecies, keeping Keck's seven subtaxa of *A. ludoviciana* as varieties. Both authors admit that since no type of *A. ludoviciana* var. *latiloba* Nutt. has been located, it may well prove to be *nomen nudum*, but since I agree with Cronquist that the varietal level is the proper one for this taxon, and not here wishing to propose a new combination using Rydberg's later epithet *candicans*, I will accept Nuttall's name as correct.

The geographical range of the complex as a whole includes the temperate and boreal portions of the northern hemisphere with the Western United States as its present center of diversity. Here, superimposed on a small number of ancient and stable diploid species, relatively recent evolution has produced a vast polyploid network of morphological and ecological types, mostly poorly isolated from one another. *A. ludoviciana* is the most widespread and polymorphic species of the complex. The variety *latiloba* is found throughout the Columbia Plateau region of Washington and Oregon, in the northern portions of the Basin and Range province, and through the Rocky Mountains from northern Montana and Idaho to southwestern Wyoming. It has not previously been reported in the literature from west of the Cascade crest. On the lower western slope of the Cascades and in the Willamette Valley it is replaced by *A. douglasiana* Bess., a hexaploid (n=27) whose origin seems to have been by amphidiploidy from *A. ludoviciana* (n=18) and *A. suksdorfii* Piper, a diploid (n=9) of the immediate coast (Clausen, Keck, and Hiesey, 1940). *A. douglasiana* is morphologically, ecologically, and geographically intermediate between its proposed parent species. Two varieties of *A. ludoviciana* (var. *ludoviciana* and var. *latiloba*) are known to occur presently with *A. suksdorfii* in the Columbia Gorge, supplying a possible point of origin for the hybrid. Occurrence of *A. ludoviciana* in the Western Cascades, although presently in disjunct populations well removed from the closest populations of *A. suksdorfii*, may offer an alternative explanation for a hybrid origin of *A. douglasiana*. Here *A. ludoviciana latiloba* occurs in moderately dry meadows from 1300 to 1700 m, where it may constitute the dominant vegetation over small areas. It is also sometimes weedy, occurring at lower elevations along dry gravelly roadsides. Common associates include such Xeric Meadow species as *Gilia aggregata*, *Collomia linearis*, *Gayophytum diffusum parviflorum*, *Orthocarpus imbricatus*, *Lupinus arbustus neolaxiflorus*, and *Linum perenne lewisii*.



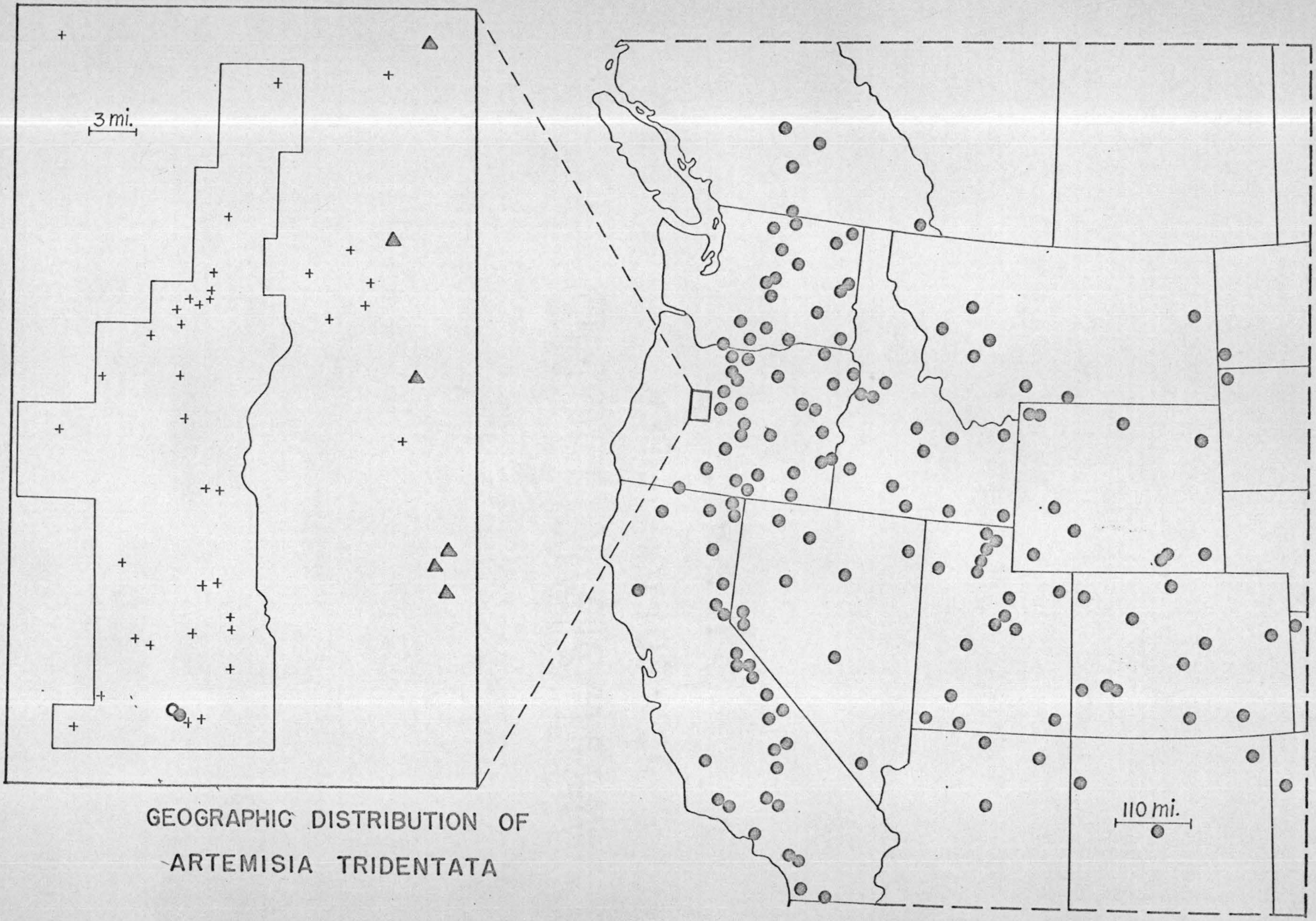
GEOGRAPHIC DISTRIBUTION OF ARTEMISIA LUDOVICIANA LATILOBA

Artemisia tridentata Nutt., Trans. Am. Phil. Soc. II 7:398. 1841.

Recent work in the *Section Tridentatae* (Ward, 1953; Holbo and Mozingo, 1965) has indicated that the taxonomic relationships in this group are exceedingly complex. Cytotaxonomic and chromatographic studies have resulted in alternative taxonomic schemes, but conclusions based on these types of evidence are often at odds with each other as well as with conclusions based on morphology. A conservative taxonomic treatment is therefore used here.

Artemisia tridentata subsp. *tridentata* is the common sagebrush through most of the Western United States. Diploid and tetraploid races occur throughout the total range of the subspecies, and while the two may be ecotypically differentiated within a given region, the pattern of differentiation may be quite different or even reversed in other regions. Ward (1953) notes that it is impossible to predict accurately the relative chromosome number of a given individual. The total range of morphological and ecological variation in this subspecies is greater than in any other member of the complex.

A. tridentata is alkali-intolerant, but grows in extremely diverse habitats in the arid portions of the West. A single locality for this species is known in the Western Cascades--on ridgetops and on west-facing rocky meadow slopes in the Rebel Rock Geological Area. The plants are robust, and many flower annually. The population is well-established and individual plants occupy a variety of micro-habitats and are associated with numerous species. This indicates to the author that *Artemisia* may have been introduced to this spot within the last 70 years.



GEOGRAPHIC DISTRIBUTION OF ARTEMISIA TRIDENTATA

Luina stricta (Greene) Rob., Proc. Am. Acad. 49:514. 1913.

Selected synonyms:

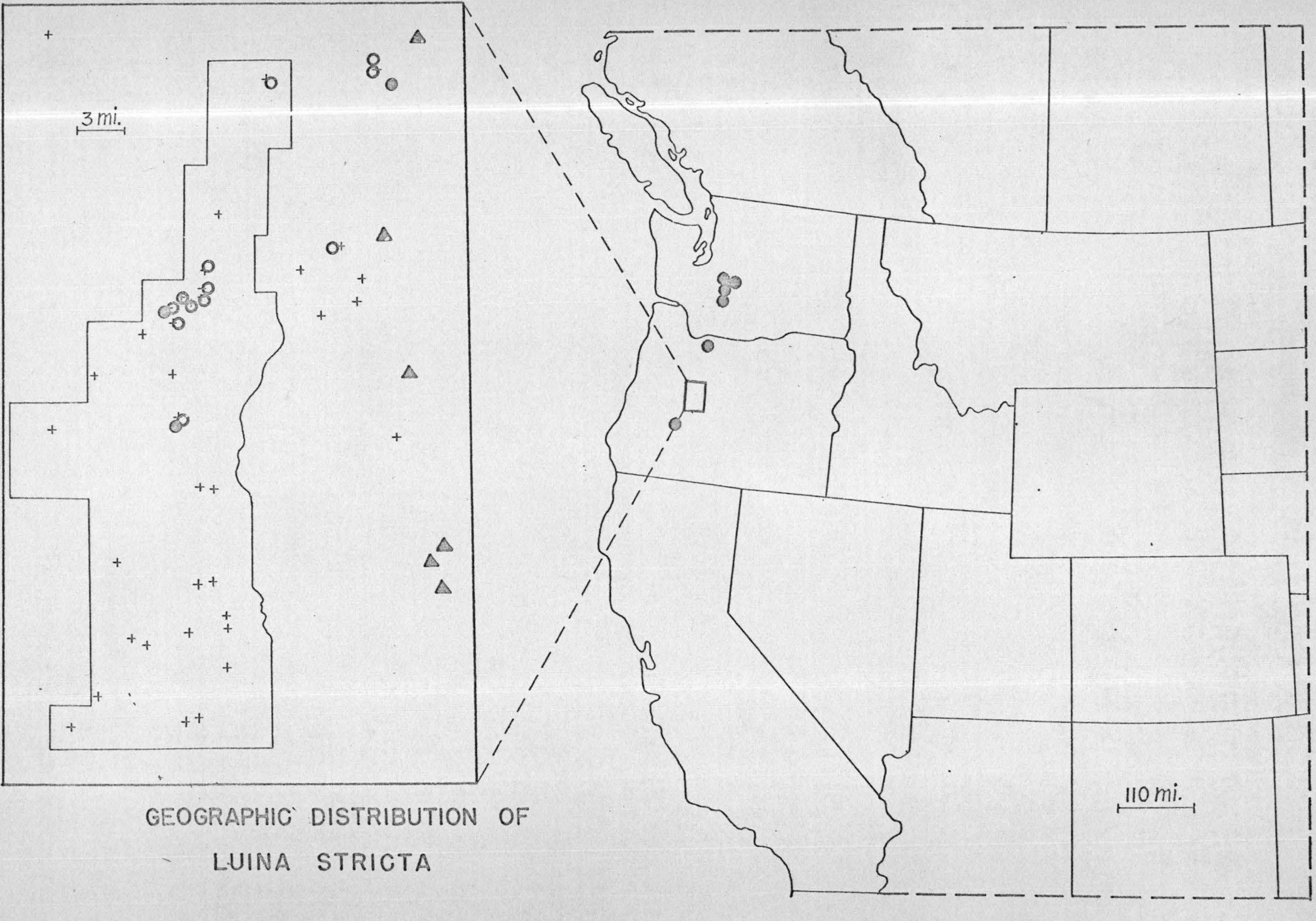
Rainiera stricta Greene, Pitt. 3:291. 1898.

L. *stricta* is easily distinguished from other members of the Tribe Senecioneae by its moderately large eradiate heads borne in a narrowly racemose inflorescence and its large, narrowly oblanceolate leaves. It was originally thought to be endemic to Mt. Rainier (hence Greene's generic name) but has since been found to be common in the Cascades as far south as Bohemia Mountain, Lane County. In some localities it forms a sub-dominant in the moist soils of Mesic Meadow associations, occurring with *Orthocarpus imbricatus*, *Ribes binominatum*, *Erigeron aliceae*, *Polygonum douglasii*, *Lupinus arbustus neolaxiflorus*, *Lupinus latifolius*, *Microsteris gracilis*, *Artemisia ludoviciana latiloba*, *Linum perenne lewisii* *Mertensia paniculata*, and *Polygonum phytolaccaefolium*.

A single collection (*D*. *C*. *Ingram*, in 1920: OSC) is labeled "6th Umatilla Collection, Umatilla National Forest." Due to the lack of specific locality, and since Ingram collected largely in the Cascades rather than in the Umatilla region, the author believes that this collection is probably mislabeled. If not, this constitutes an important first collection of the species from eastern Oregon. The locality has not been included in the following map of *Luina stricta*.

Arnica parryi Gray, Am. Nat. 8:213. 1874.

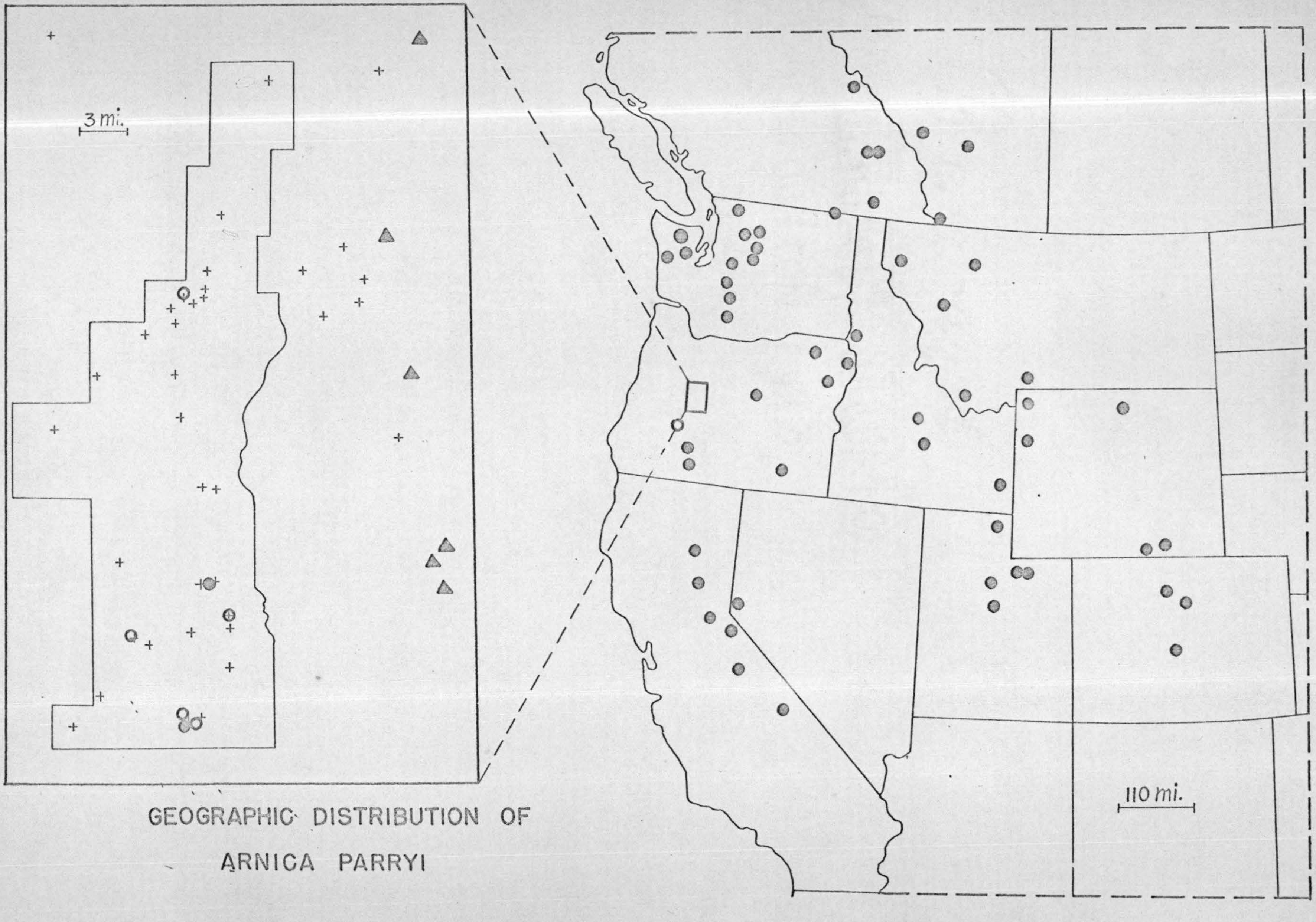
A. *parryi* is eradiate throughout most of its range. In the Sierra Nevada of California there occurs a radiate form, var. *sonnei*



GEOGRAPHIC DISTRIBUTION OF LUINA STRICTA

(Greene) Maguire. Except for this variation the present species is well marked by its open cymose inflorescence, nodding young heads, and narrow long-petioled leaves. Its relationships, however, are not clear. Maguire (1943) places *Arnica parryi* in the subgenus *Chamissonis*, arguing from the fine, abundantly rooting rhizomes; the tawny pappus color; and the width of the leaves. However, there are a number of characteristics which tend to ally *A. parryi* more closely to subgenus *Austromontana*, such as the typically eradiate heads, three pairs of cauline leaves, turbinate-campanulate involucres, and long-petioled lower leaves. This taxon in intermediate between these proposed subgenera. Evidently, *Arnica* varies in too complex a fashion to lend itself well to such nebulous subgeneric categories as Maguire proposes. Perhaps *A. parryi*, *A. grayi* Heller, *A. parviflora* Gray, and *A. discoidea* Benth. (if they are considered distinct) represent a series of intermediates derived both from *A. mollis* Hook. of subgenus *Chamissonis* and from various members of the subgenus *Austromontana*, including radiate *A. cordifolia* Hook. and eradiate *A. spathulata* Greene. *A. parryi* does overlap geographically with such eradiate forms as *A. spathulata*, *A. parviflora*, and *A. discoidea* (*sensu* Maguire) in the southern Cascades, Klamath, and California Coast Ranges, and with *A. grayi* in the Columbia Gorge. These species are still confused in the literature (Cronquist, 1955). Neither Maguire nor Cronquist admit the existence of *A. parryi* in the central or northern Cascades of Oregon, but as far as the author can determine, the present material is identical to typical *A. parryi*. A more precise statement of relationships in this group must await further work.

In the Western Cascades, *A. parryi* is found in meadow-forest



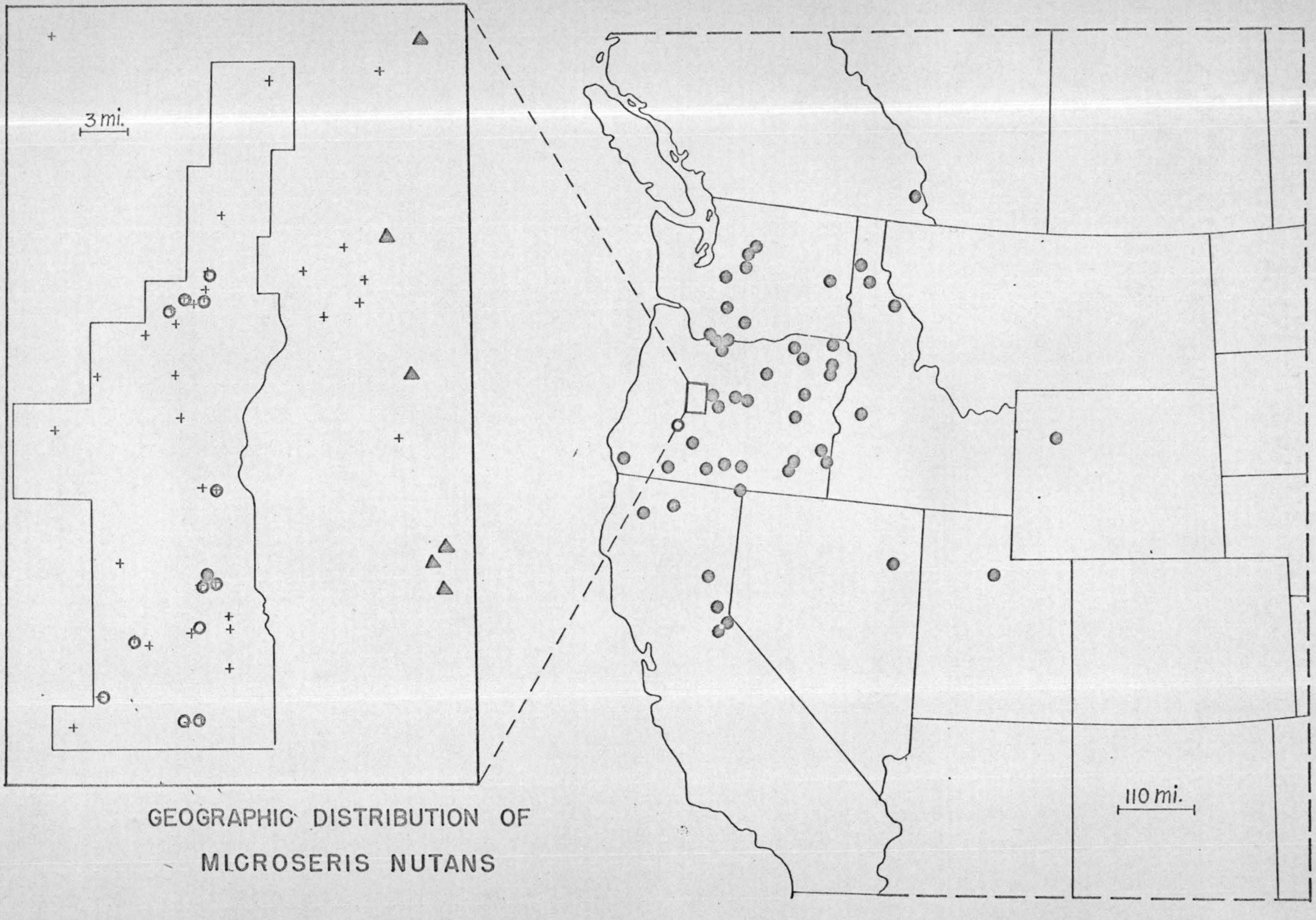
GEOGRAPHIC DISTRIBUTION OF
ARNICA PARRYI

ecotones, rooted in relatively dry gravelly loam in areas of partial shade. It is often associated with *Lonicera conjugialis*, *Xerophyllum tenax*, *Carex* spp., *Vaccinium membranaceum*, *Sambucus racemosa pubens arborescens*, and *Aster ledophyllus*. Seeds set during the course of the present study appear shriveled and non-viable but germinate freely after an extended stratification period.

Microseris nutans (Geyer) Schulz-Bip., Pollichia 22-24:309. 1866.
Selected synonyms:
Scorzonella nutans Geyer, Lond. Journ. Bot. 6:253. 1847.
Ptilocalais nutans Greene, Bull. Cal. Acad. Sci. 2:54. 1886.

M. nutans is a distinctive species which may someday be placed in a smaller genus. The re-establishment of the genus *Nothocalais* from *Microseris* (Chambers, 1955, 1957) perhaps presages such an event. Its pappus is unique, consisting of bidentate basal paleaceous scales surmounted by a long, white, plumose awn. It is also unusual for this group in having entire leaves and a stem that branches several times near the base. Like several closely related species, it has a fusiform perennial taproot.

Contrary to recent statements (Cronquist, 1955), the species seems to be fairly common west of the Cascade crest in Oregon, although it has heretofore been rarely collected. The species is abundant in eastern Oregon and extends to Montana, Colorado, and central California. In the Western Cascades it occurs in open rocky meadows that are moist in the spring but dry after midsummer. It occurs with such members of the Xeric Meadow or Small Boulder Creep Slope associations as *Gilia aggregata*,



GEOGRAPHIC DISTRIBUTION OF
MICROSERIS NUTANS

Lotus nevadensis douglasii, *Chrysothamnus nauseosus*, *Comandra umbellata*, *Arctostaphylos nevadensis*, *Juniperus communis saxatilis*, *Cheilanthes siliquosa*, and *Bromus carinatus*.

Nothocalais alpestris (Gray) Chambers, Contr. Dud. Herb. 5:66. 1957.

Selected synonyms:

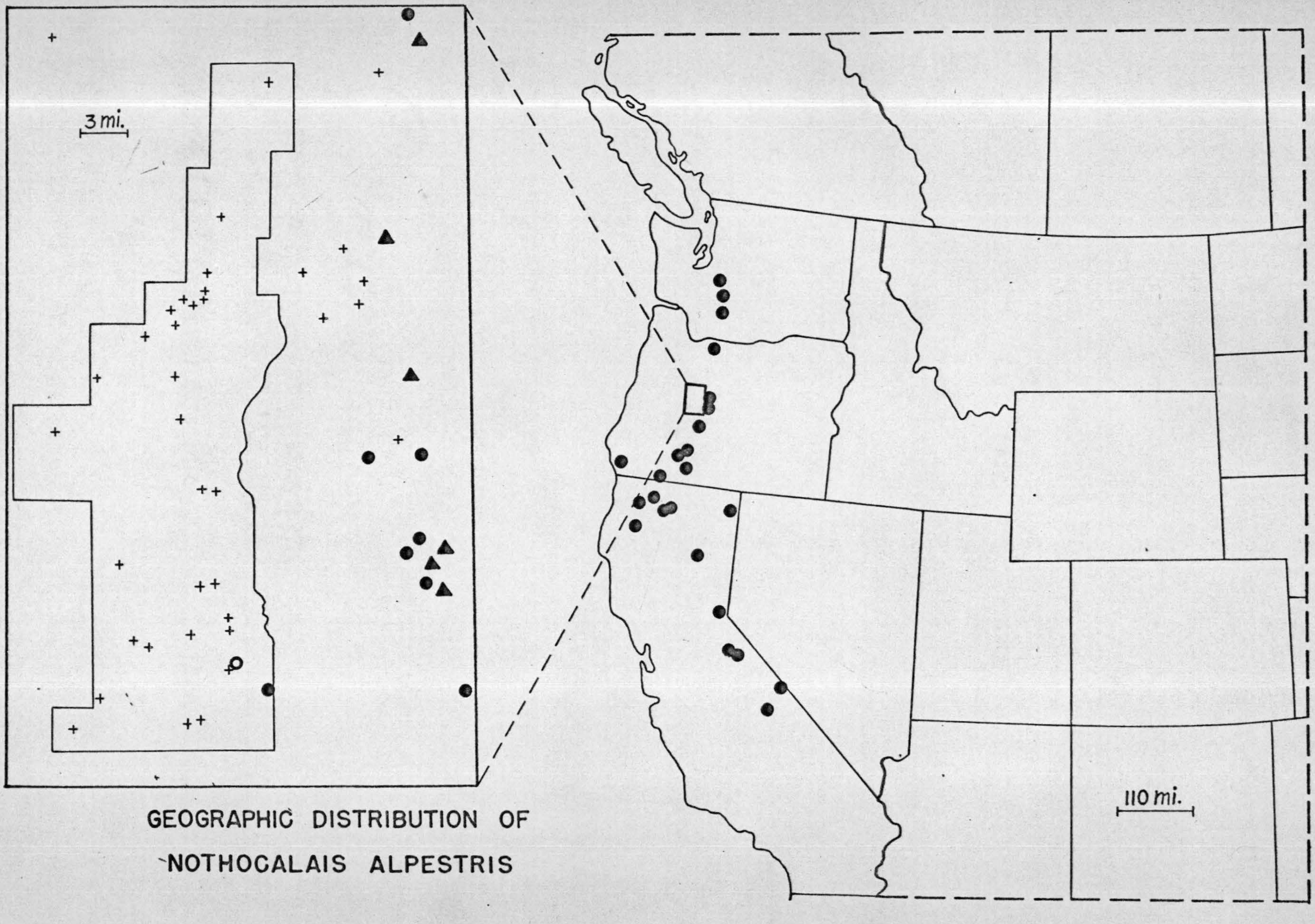
Troximon alpestre Gray, Proc. Am. Acad. 19:70. 1883.

Agoseris alpestris Greene, Pitt. 2:177. 1891.

Microseris alpestris Q. Jones, Vasc. Plants Pac. N. W. 5:267. 1955.

This small genus of northwestern American composites is closely allied to *Agoseris* but lacks the distinctive beak to the achene. Pappus bristles are essentially capillary or sometimes flattened, with paleaceous bases. *N. alpestris* is the only species of the genus occurring as far west as the Cascade Range, others being sagebrush scrub or prairie species. It is typically found at very high elevations, although it occasionally descends to 1500 m in the high mountains. Two stations have been discovered in the Western Cascades, where flows from the high peaks have resulted in a continuous high plateau between High and Western Cascades.

A variable plant in the high mountains, *N. alpestris* is uniformly robust as it occurs in the Mesic Meadows of the Western Cascades with *Sambucus racemosa pubens arborescens*, *Ribes erythrocarpum*, *Valeriana sitchensis*, *Aster ledophyllus*, *Galium bifolium*, *Abies amabilis*, and *Lupinus latifolius*.

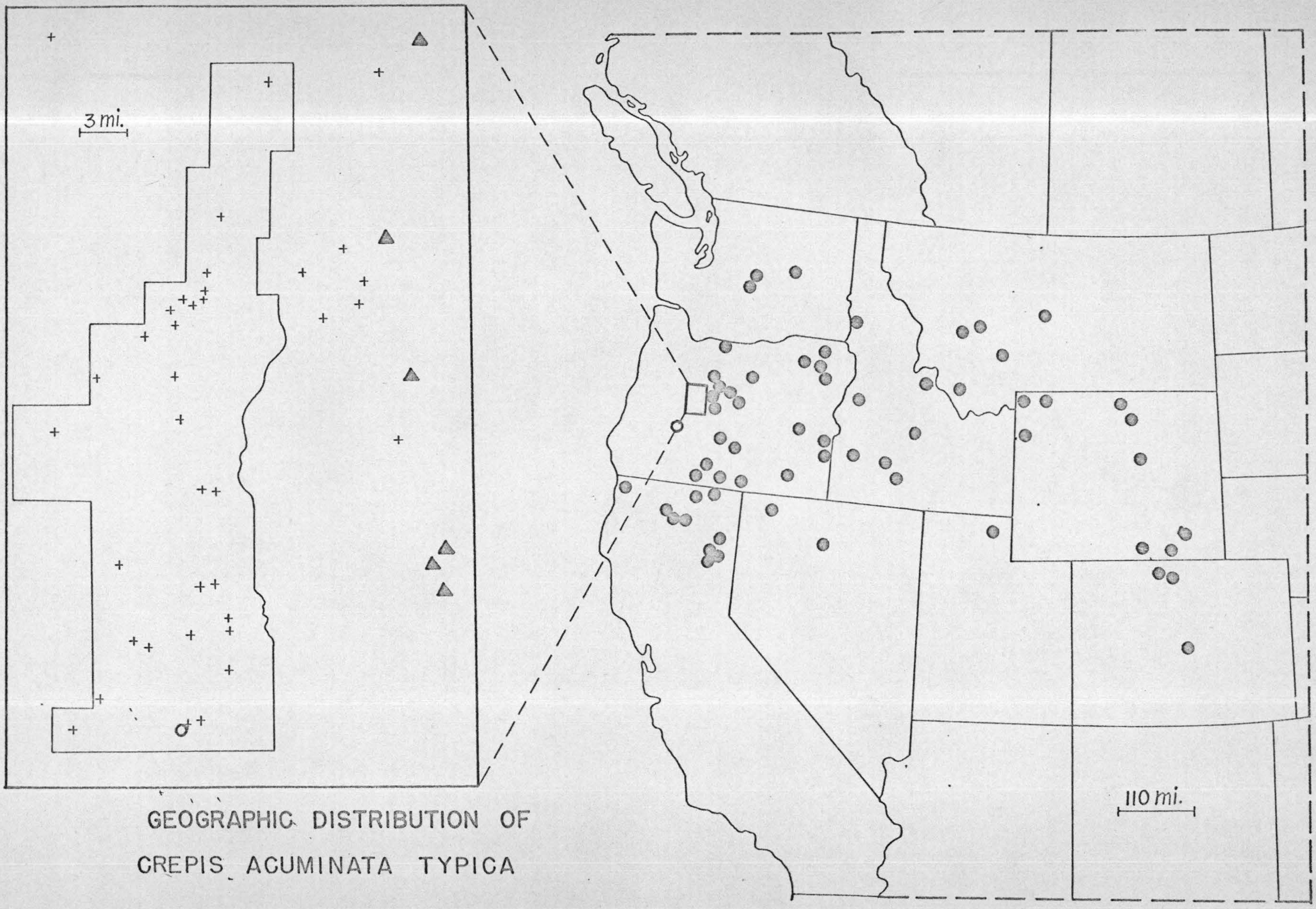


GEOGRAPHIC DISTRIBUTION OF NOTHOCALAIS ALPESTRIS

Crepis acuminata Nutt. subsp. *typica* Babc. and Steb., Carn. Inst. Wash. Pub. 504:170. 1938.

E. B. Babcock's monumental work on the genus *Crepis* (1947) is one of the classic studies in modern taxonomy. The complexity of this group is well known, and will not be discussed in detail here. Many species of *Crepis* include both a fertile outcrossing diploid and a series of polyploid apomictic forms which have been derived from them. *C. acuminata* is one of these. The typical subspecies includes all of the diploids and 16 apomictic races. As opposed to all other western species of *Crepis*, here the diploids constitute the most widespread and generally successful forms. They are extremely variable but can be differentiated from asexual forms by the smaller size of the individual bracts and the amount and regularity of pollen produced. Usually apomicts produce no pollen at all. The range of fertile diploids includes the northern half of the Western United States, but the species has never before been collected west of the Cascade crest in Oregon or Washington. *C. pleurocarpa* Gray, a closely related species, is common in the Klamath Mountains and the southern Cascades of Oregon. Only the diploid form of *C. acuminata* is plotted on the following map.

Throughout its range *C. acuminata* grows in dry open habitats in foothills or mountains. In the Western Cascades rare populations of fertile diploids are found in exposed, dry, south-facing environments at the tops of precipitous rocky slopes associated with *Castilleja pruinosa*, *Phacelia linearis*, *Eriogonum umbellatum*, *Arabis platysperma howellii*, *Selaginella wallacei*, *Lotus nevadensis douglasii*, and *Arctostaphylos nevadensis*, members of the Outcrop Ridge association.



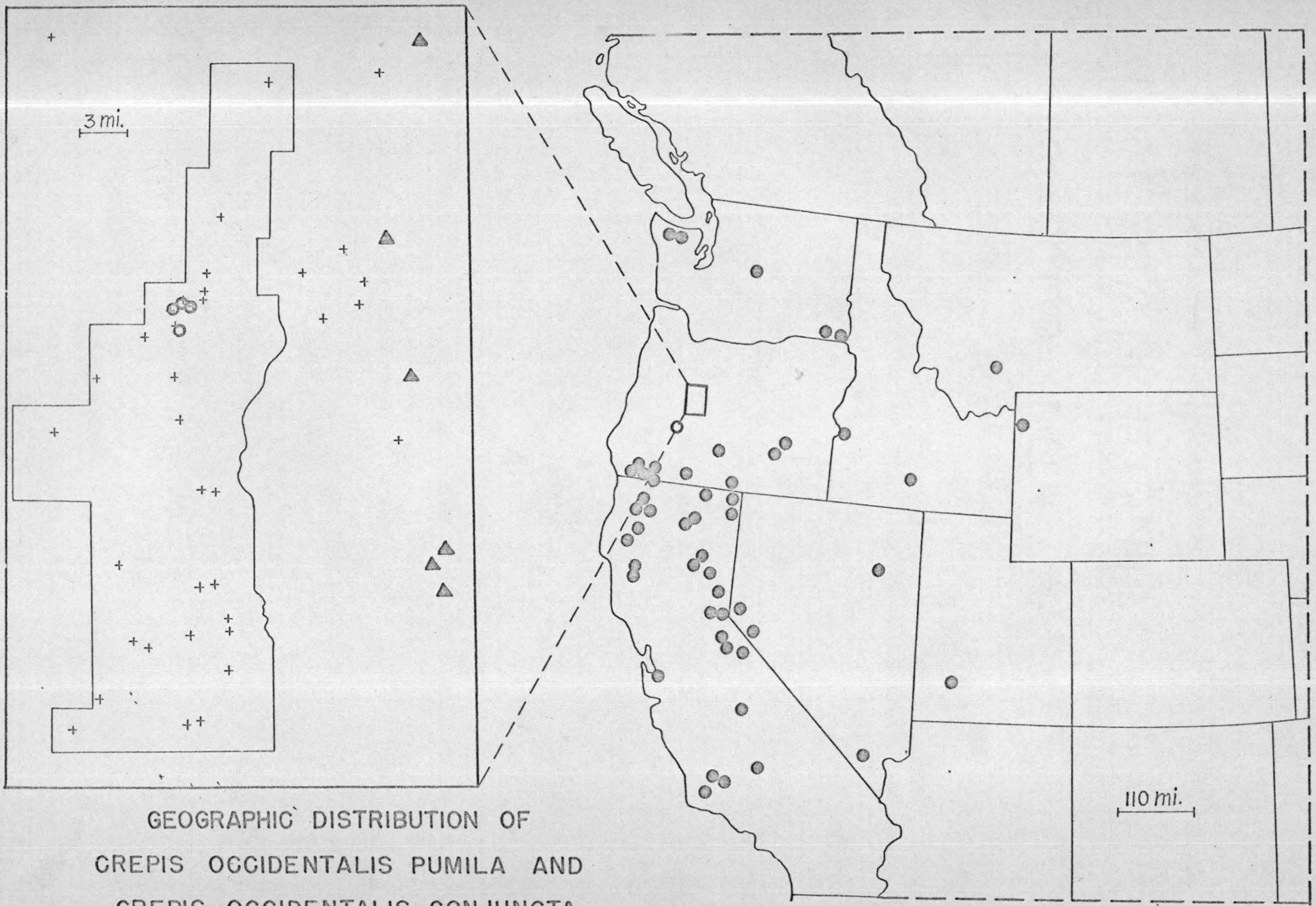
GEOGRAPHIC DISTRIBUTION OF
CREPIS ACUMINATA TYPICA

Crepis occidentalis Nutt. subsp. *pumila* (Rydb.) Babc. and Steb. (related to apomict *rydbergii*) x subsp. *conjuncta* Babc. and Steb. (related to apomict *jepsonii*)? Carn. Inst. Wash. Publ. 504:128, 130-131, 134, 136-137. 1938.

The involved name listed above is the best determination possible with the finely discriminating keys of Babcock and Stebbins (1938). The name is necessary to communicate the fact that the Western Cascade populations are composed of individuals intermediate between the two subspecies *pumila* and *conjuncta*. Babcock and Stebbins realized that such intermediates occur, and erected the apomictic taxon *rydbergii* for the form of *pumila* most like subsp. *conjuncta* and apomict *jepsonii* for the converse. The Western Cascade individuals are far outside the described ranges of both of these apomicts; furthermore, they are morphologically intermediate between them and cannot be considered to belong in either described taxon. Perhaps more is known of the complex morphology and evolution of *Crepis* than can be satisfactorily expressed in taxonomic terms. All of the subspecies of *C. occidentalis* intergrade with one another and with other species as well. The various apomictic forms have been considered nodes on the clines connecting the larger taxa. That the subspecies themselves are probably not evolutionarily discrete entities is suggested by their complexly disrupted ranges. For example subsp. *pumila* is a rather widespread taxon, occurring in a ring around the central valley of California, in the Siskiyou Mountains, in the Basin and Range of Oregon, Nevada, and Utah and at scattered localities in Idaho and Montana. A series of populations disjunct by over 480 km from the other *pumila* populations occurs in the Olympic Mountains. All of the three other subspecies are found in the intervening area. Subspecies *conjuncta* is even more striking in this respect. Most individuals occur in the northern Sierra Nevada and in the Siskiyou Mountains of northern California and southern Oregon. However, one locality is known from the Wenatchee Mountains of central Washington, several from the southeastern corner of that state, and one from the Teton Range in Wyoming. Again, other subspecies now fill the intervening areas.

Thus, with regard to the Western Cascade specimens, I feel that it is impossible to discriminate between the two subspecies in considering the parent taxon. Obviously both subspecies have contributed to the gene pool of the Western Cascade plants and apparently in about equal proportions. Since the two are known to merge completely in the Siskiyou Mountains, it is here proposed that this is the parental area for Cascade forms, and that a combined stock of the two subspecies has spread northward through the Western Cascades. The material from Bohemia Mountain is most similar to subsp. *pumila*; that from Iron, Cone, and South Peaks, farther to the north, more closely approximates subsp. *conjuncta*. The differences between these specimens are, however, much less than is admitted for a single apomictic form.

Like *C. acuminata*, *C. occidentalis* grows in dry sites normally on poorly developed soil throughout its range. In the Western Cascades specimens are found on steep slopes of fine scoria gravel, or more rarely, rooted among denser volcanic rocks on high exposed areas of deflation armor. Several of the following species of the Fine Gravel Scree association may be found in the immediate vicinity: *Ivesia gordonii*, *Trifolium productum*, *Lotus nevadensis douglasii*, *Gilia aggregata*, *Eriogonum umbellatum*, *Allium crenulatum*, *Arabis platysperma howellii*, and *Gilia capitata*.



GEOGRAPHIC DISTRIBUTION OF
CREPIS OCCIDENTALIS PUMILA AND
CREPIS OCCIDENTALIS CONJUNCTA

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