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STUDIES OF POPULATION VARIABILITY LEADING TO A NEW CLASSIFICATION OF POTENTILLA SECT. MULTIJUGAE (ROSACEAE)

University of Colorado at Boulder PH.D. 1980

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STUDIES OF POPULATION VARIABILITY LEADING TO A NEW CLASSIFICATION OF *POTENTILLA* SECT. MULTIJUGAE (ROSACEAE)

by

Barry Cummins Johnston

B.S., University of Colorado, 1966

A thesis submitted to the Faculty of the Graduate
School of the University of Colorado in partial
fulfillment of the requirements for the degree of
Doctor of Philosophy
Department of Environmental, Population,
and Organismic Biology
1980

This Thesis for the Doctor of Philosophy Degree by

Barry Cummins Johnston

has been approved for the

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Johnston, Barry Cummins (Ph.D., Biology)

Studies of Population Variability Leading to a New Classification of *Potentilla* sect. Multijugae (Rosaceae)

Thesis directed by Professor David J. Rogers

This study had two goals: to produce a classification of a section of the difficult genus *Potentilla*; and to show how population variation affects this taxonomic classification. This genus is lacking a monograph which expresses natural relationships, or one which allows accurate identification, especially for North America.

A new classification was made of *Potentilla* sect. Multijugae, a section of eleven species inhabiting western North America. In order to define this section, a new classification was also made of two related sections, Concinnae and Subjugae.

Field studies on the species of these sections in the Rocky Mountains and Great Basin from New Mexico to Idaho and Montana yielded many population samples. Analysis of these population samples greatly improved the interpretation of approximately 7000 herbarium specimens representing these sections. Statistical analysis of variance and correlation of the population samples, character analysis (program CHARANAL), and single-linkage clustering (program GRAPH) provided objective methods of selection, structuring, and use of characters for classification.

Potentilla sect. Multijugae consists of eleven species and four subspecific taxa, most of which had been previously described: *P. breweri, P. breweri* var. *bruceae, P. breweri* var. *viridis, P. candicans, P. diversifolia, P. diversifolia* ssp. *ranunculus, P. diversifolia* var. *perdissecta, P. drummondii, P. hickmanii, P. millefolia, P. multijuga,* *P. multisecta, P. ovina, P. ovina* var. *decurrens,* and *P. plattensis. P. uliginosa,* related to *P. multijuga* and inhabiting Sonoma Co., California, is to be proposed.

Potentilla sect. Concinnae consists of two species and two varieties: *P. oblanceolata, P. concinna,* and *P. concinna* var. *bicrenata. P. concinna* var. *curvata* from Nye Co., Nevada, is to be proposed.

Potentilla sect. Subjugae has seven species and four varieties: *P. ambigens, P. crinita, P. crinita* var. *lemmonii, P. effusa, P. effusa* var. *rupincola, P. hippiana, P. hippiana* var. *argyrea, P. macounii, P. pulcherrima, P. subjuga,* and *P. subjuga* var. *minutifolia.*

Relationships among these sections and their species were clarified as a result of the statistical, information-theoretical, and clustering methods used.

This abstract is approved as to form and content. I recommend its publication.

Signed David J Rogers
Faculty member in charge of thesis

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I must first extend my sincere thanks to the members of my committee, who showed an invaluable blend of guidance, instruction, and patience. Dr. David J. Rogers was a continual source of insight into the otherwise obscure methods and attitudes of traditional taxonomists; this work's seeming arbitrariness is made more of a science thereby. I have learned much of *Potentilla* from Dr. William A. Weber, who guided me through the early phases of this project, and shared his sensitive appreciation of the interplay of plants and environment, both in the field and in the herbarium. Dr. Robert A. Bye contributed his unique appreciation for manifold alternative methods of approach, combined with an unbiased critical attitude to the works of others, certainly rare in systematics. Dr. John W. Marr kept me aware of the need for reversing the taxonomic matrix to look at the association among species. Dr. Michael C. Grant brought me closer to careful statistics, and made my approach more biological. Dr. Horace F. Quick gave his views from a not-so-different world.

The University of Colorado Museum and its Director, Dr. Peter Robinson, gave an assistantship during which the earlier portions of this study were begun. The U. S. Forest Service, Rocky Mountain Region, especially Wally Gallaher and Robert Buttery, employed me at other work during much of this study, both providing the means for maintenance of my addiction to field botany, and also giving me a long list of populations to return to on my own time. The University of Colorado

Computing Center, through its allocation to the University of Colorado Museum and (mostly) to the Department of E. P. O. Biology, gave computer time for most of the calculations.

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CHAPTER I

INTRODUCTION

Potentilla is, in the strict sense, a genus of annual or perennial herbs of the Northern Hemisphere, in the family Rosaceae. It is distributed from the subtropical to the arctic zones, but is best represented on mountain ranges, especially the subalpine and alpine, and in the arctic. The genus is notoriously complex, and is known to be taxonomically difficult.

> Various monographic treatments of the genus have not succeeded in bringing even an approximately natural order into the North American species, as is evident after even a brief study of the situation. Causes for this result may be suggested: lack of intimate field knowledge of the species; lack of appreciation for the importance of geographic distribution in speciation; lack of sufficient material; failure to consider the role of hybridization in nature, which shuffles the morphological characters, and the possibility of apomixis as a factor; dependence on unit characters for specific criteria, particularly the unreliable one of pubescence; and oversight of certain dependable characters in the genus (Keck 1940, p. 128).

J. C. G. Lehmann, the leading 19th-century taxonomist of *Potentilla*, produced a system (1856) which is still usable today, but which has no key to species. Lehmann's species and varieties are very carefully circumscribed, but no direct use is made by him of the characters used to circumscribe them.

P. A. Rydberg, the last reviser of the species of this genus for North America (1898,1908), "depended upon unit morphological characters for species and sections alike. Forms obviously to be included in the same subunit of the species he has often separated by 30 or 40 'species' of very different affinity"(Keck 1940, p. 128). As a result, Rydberg's species are often exceedingly difficult to identify, and usually have strangely disjunct distributions. Some of the characters he used are good ones, but his use of only one at a time resulted in a classification of species (1908) that is justifiably ignored by all modern workers.

Th. Wolf, the last world-wide monographer of the genus (1908), used several characters simultaneously, but his choice of characters was in some places natural, in some places artificial. He divides *Potentilla* into "subsections" based on pubescent versus glabrous achenes, and the form of the style; the largest "subsection," however, is divided solely on the presence or absence of tomentum, which artificially separates closely related species.

Thus, both leading revisers of the genus have had their greatest difficulty in their use of characters for classification, Rydberg because he used "unit" characters one at a time, and Wolf because he lacked an objective method for choosing characters.

As Keck pointed out (quotation above), a factor which might bear on taxonomic classification of *Potentilla* is the possibility of apomixis. Gustafsson (1946-7) summarized the occurrence of apomixis in the genus: there are a large number of local biotypes in the old and new worlds, many of which have received names. The European forms have received the most attention, in which apospory with parthenogenesis and pseudogamy (Rutishauser 1948, terminology in Nygren 1967) is most common, but some forms have also been found to produce seed by diplospory with parthenogenesis and pseudogamy; the apomixis is often facultative. There are a very few forms that are diploid and apomictic ($x = 7$

throughout the genus); most complexes that have been studied have the diploids obligately sexual and the polyploids with increasing degrees of apomixis. Gustafsson (1946-7) identified 27 apomictic species-complexes in *Potentilla*, many with high polyploidy, in which is found intricately complex polymorphism. There is evidence that the apomictic biotypes are at least as heterozygous as the sexual ones, perhaps more so; species-crosses are common wherever two or more species come into contact. By the combined processes of hybridization and dispersal, "many apomictic micro-species are continually being split up into populations having wide ecological range" (Gustafsson 1946-7).

In several of the genera that Rydberg and others (e.g., Dansereau 1955) have segregated from *Potentilla*, generative apospory is unknown. All investigations of breeding structure in *Pentaphylloides, Comarum, Drymocallis,* and *Argentina* have shown them to be sexual, outcrossing, and self-incompatible; *Pentaphylloides* and *Drymocallis* are largely diploid (Löve 1954; Clausen, Keck, and Hiesey 1940; Clausen and Hiesey 1958), whereas *Comarum* and *Argentina* are predominantly tetraploid with rare, sporadic populations at higher ploidy levels. The closely related genus *Fragaria* (probably closer to *Potentilla* s.s. than *Pentaphylloides, Drymocallis,* or *Argentina* are) is entirely sexual, outcrossing, and self-incompatible, with different widespread species at diploid, tetraploid, hexaploid, and octoploid levels (Staudt 1968). In *Fragaria*, there is a clear correlation between ploidy and degree of dioecy, the octoploids being completely dioecious; there is some evidence that the higher polyploidy in this genus has been produced by pre-meiotic reduplication of the chromosomes, which accords with the studies showing genetic segregation of several loci in the manner of autoploids (Staudt 1968, Asker 1971). In this regard, it is significant that all the intergeneric hybrids successful between *Fragaria* and *Potentilla* have been with species of *Pentaphylloides* and *Drymocallis*: the crosses attempted between *Fragaria* and *Potentilla* s.s. have all failed (Ellis 1962, Asker 1969). The breeding system of *Potentilla* s.s. is strikingly different from that of related genera.

The chromosome numbers in *Potentilla* are mostly euploid, that is, at integral multiples of the basic number, $x = 7$. There is a small aneuploid series in sect. Potentilla, and long series with very high chromosome numbers in sect. Graciles and sect. Multijugae; in these groups there have been no diploids or tetraploids reported. The chromosome numbers reported in Multijugae to date have been: $2n = 72$-73, 99, 100, and 102 in *P. breweri*; $2n = 64$-108 and 105 in *P. drummondii*; $2n = 82$-84, 91, 101, and 42 in *P. diversifolia* (Shimotomai 1930, Clausen et al. 1940, Gustafsson 1946-7). From the high aneuploid numbers, one can infer some degree of apomixis, but as far as known, this mode of reproduction has not been shown for any member of this section.

If the populations of this genus reproduce largely apomictically, one might expect local populations to be largely homogeneous for morphological characters, with many local populations sharply different from one another. This would produce the "large number of biotypes" described by Gustafsson, and partially explain why Rydberg's "unit character" method resulted in the recognition of so very many species. This hypothesis would complicate a classification by presenting a large number of small units.

On the other hand, if morphological characters vary greatly within populations, the "local clone" population effect hypothesized above would not predominate, and classification would be hampered by populations whose individuals are indistinguishable for most characters. Morphological characters were used throughout this study, because one of the purposes of the study was to examine the relationships between population variation and taxonomic classification, which necessarily uses morphological characters. This approach facilitated the use of statistical methods, and of the large body of data available in the form of herbarium specimens.

Potentilla sect. Multijugae is restricted to western North America, with disjunct populations in central Mexico and Greenland. A set of population samples was subjected to statistical analysis of variance and of correlation, and a set of herbarium specimens subjected to character analysis, to determine which characters might be useful in constructing a classification.

The characters shown to be most useful were then used to construct a new classification of sect. Multijugae, aided by a single-linkage clustering technique which allowed many characters to be considered simultaneously.

A similar approach—character analysis followed by classification aided by clustering—was followed to produce a new classification of *Potentilla* sect. Concinnae and sect. Subjugae.

CHAPTER II

HISTORY OF CLASSIFICATION OF *POTENTILLA* SECT. MULTIJUGAE

The first species of this section described was *Potentilla candicans* Humboldt and Bonpland, described in Schlechtendahl's (1815) conspectus of *Potentilla* in Willdenow's herbarium, from a collection made by Humboldt and Bonpland near Tianguillo in central Mexico. It is still one of the most distinct species of the section, and widely disjunct geographically from the others. *P. candicans* was described again as new and figured in Nestler's (1816) Monographia de Potentilla, the first monograph of the genus. Nestler also mentions a *P. candicans* β *nana*, based on another collection of Humboldt and Bonpland from central Mexico, but does not describe it; this was done by the collectors with Kunth in 1818. *P. candicans* β *nana* was raised to specific rank by Trattininck in 1824, as *P. humboldtiana*.

Johann Georg Christian Lehmann began his forty years of work on *Potentilla* with his Monographia Generis Potentillarum (1820), a work considerably improved and expanded from Nestler's 18th-century-like treatment; at the date of this work, the only species of this section was still *P. candicans*. A bare ten years later, explorations of North America by Douglas, Drummond, Richardson, James, and others made possible the descriptions of many new species. In one of the most important descriptive accounts of the genus in North America, Lehmann (1830) described two new species of this section, *P. drummondii* and *P. diversifolia*; also described as new in this work are *P. hippiana* (the paper was dedicated to Carl Frederick Hipp), *P. effusa, P. pulcherrima, P. rubricaulis,* and *P. flabelliformis.* New descriptions were given of *P. concinna* and the still-obscure *P. dissecta.*

Two years later, Lehmann contributed the account of *Potentilla* in William Jackson Hooker's Flora Boreali-Americana (1832), in which he mentioned specimens of the species that had been published in 1830. Hooker added a beautiful plate of *P. drummondii* and a long discussion of variation in *P. diversifolia.*

John Torrey and Asa Gray published in 1840 their Flora of North America, which contained many manuscripts of new species by Thomas Nuttall, in addition to their own observations. Nuttall's species and other taxa were based on his own collections in western North America, particularly northwestern United States. Torrey and Gray recognized *P. drummondii* and *P. diversifolia* (*P. candicans* was out of the range of their flora). In addition, Nuttall contributed *P. plattensis* from his collection on the Sweetwater River in what is now Wyoming. No varieties of these three were recognized, but they cited two synonyms of *P. diversifolia*: *P. glaucophylla* Lehmann, which had been described in 1836, perhaps from a Nuttall collection; and *P. campestris* Nuttall, an unpublished manuscript name.

As an addition to the 1849 seed catalog of the Hamburg Botanic Garden, Lehmann published twenty new species of *Potentilla*, based on specimens in his own herbarium. Among then was *P. multijuga* Lehmann, cited as growing "in California," collected by an unknown person; no other species was described there from western North America. For most of the following years, Lehmann worked on the literature survey for his upcoming revision of the genus; part of this literature survey was published in W. G. Walpers' Annales for 1851, which included *P. plattensis, P. multijuga,* and *P. candicans* in "Tribus" Multifidae. *P. drummondii* was included in "Tribus" Tanacetifoliae, and *P. diversifolia* in "Tribus" Subpalmatae. All of these "Tribes" (not acceptable as a rank between Genus and Species under terms of the present International Code of Botanical Nomenclature) were named after one of the species included within each one, which constitutes an indirect way of typifying them; none of these "Tribes" had as type any of the species in sect. Multijugae.

Lehmann finally published his Revisio Potentillarum Iconibus Illustrata as a supplement to volume 23 of the Verhandlungen der Leopoldinisch Akademie in 1856. This culminating work by the premier authority on *Potentilla* of the nineteenth century was widely used throughout the world for over 50 years, and formed the basis for the classifications of Per Axel Rydberg and Theodor Wolf. It is notable that they both (40-50 years after Lehmann) began their work by recognizing the considerable contribution that Lehmann made to the classification of *Potentilla* (Rydberg 1896, p. 244; Wolf 1908, p. v). This work by Lehmann retains the system that he had published in 1851; he recognized *P. candicans* var. *nana,* and *P. glaucophylla* was reduced to a variety of *P. diversifolia*. *P. candicans* var. *crocea* was described as new, and *P. multijuga* was figured.

In 1871, Sereno Watson wrote the botanical report for Clarence King's U. S. Exploration of the Fortieth Parallel, in which he described two new varieties of *P. diversifolia,* var. *multisecta* and var. *pinnatisecta*. Both were based on Watson's own collections made in the mountains of Utah and Nevada. Watson revised the North American (except Mexico) species of the genus in 1873. He recognized *P.*

plattensis and synonymized his *P. diversifolia* var. *pinnatisecta* under it. *Potentilla diversifolia* itself was synonymized under *P. dissecta* Pursh, a still confusing species, and var. *glaucophylla* and var. *multisecta* were transferred to *P. dissecta*. A new variety of this species, var. *decurrens*, was described from one of Watson's collections made in the Uinta Mountains. Watson described *P. breweri*, based on a collection made by Brewer in the Sierra Nevada, and surmised *P. multijuga* to be an *Horkelia*, since he had seen no specimens of it.

In 1876 Watson, in the Botanical Report to the Geological Survey of California, described var. *expansa* to his own *P. breweri*, and cited *P. plattensis* and his *P. dissecta* as also occurring in California. In 1880, Johannes Lange described and figured *P. ranunculus* from Greenland, first published in Flora Danica and recopied in his Conspectus Florae Groenlandicae that same year.

In the Proceedings of the American Academy for 1885, Sereno Watson described plants collected by J. G. Lemmon and his wife in northern Arizona, among them two species of *Ivesia*, *I. pinnatifida* and *I. lemmonii*; the first belongs to *Potentilla* sect. Multijugae and the second to sect. Subjugae. Edward L. Greene transferred them both to *Potentilla* in 1887, the former species renamed as *P. arizonica*, since *P. pinnatifida* was preoccupied. Greene later (1891) wrote a flora of the San Francisco area, in which he cited *P. plattensis*, *P. dissecta*, and *P. multijuga* from California, the last species confused with *Horkelia* spp., as in Watson's 1876 treatment. In 1893 Greene described *P. plattensis* var. *leucophylla*, based on a collection of C. F. Sonne from the northern Sierra Nevada.

In 1895 James M. Macoun described *Potentilla ovina*, based on John Macoun's collections from the Canadian Rocky Mountains.

In 1896-1897 Per Axel Rydberg began his publication in *Potentilla* with the journal series Notes on Potentilla, in which he sketched what was planned to be a revision of the genus in North America. In Part IV of these notes, he included *P. dissecta* (in the sense of Watson) in his Aureae, under which he accepted var. *glaucophylla* and var. *rubricaulis*, based on *P. rubricaulis* Lehmann. He raised Watson's varieties *decurrens* and *multisecta* to specific rank. In Part V he first described the Multijugae, obviously using the same etymological pattern as Lehmann's names for his "Tribes", and like Lehmann's, based on one of its constituent species. Rydberg included *P. plattensis, P. pinnatisecta* (raised to species from Watson's variety by Aven Nelson), *P. richardii* Lehmann, *P. multijuga,* and *P. drummondii.* He described and figured a new species, *P. millefolia*, based on a collection of J. G. Lemmon from northern California, which was the Californian *P. plattensis* cited earlier by Watson and Greene. *P. breweri* and *P. breweri* var. *expansa* were included in Rydberg's Hippianae in Part VI.

In 1898 Rydberg published A Monograph of North American Potentilleae as volume two of the Memoirs from the Department of Botany of Columbia University, including not only *Potentilla* but also *Horkelia* (including *Ivesia*), *Fragaria, Duchesnea, Sibbaldia,* and *Chamaerhodos.* From the Lehmannian concept of *Potentilla* he separated as genera *Stellariopsis, Comarella, Argentina, Comarum, Sibbaldiopsis, Dasiphora* (now called *Pentaphylloides*) and *Drymocallis.*

Rydberg's system in 1898 was similar to that of 1896-1897. In his Aureae he recognized *P. dissecta* and its var. *glaucophylla, P. decurrens,* *P. ranunculus,* and *P. multisecta*; in the Multijugae, *P. millefolia, P. arizonica, P. pinnatisecta, P. plattensis, P. richardii, P. drummondii,* and *P. multijuga*; in Leucophyllae (renamed from Hippianae) *P. breweri* and its var. *expansa*. In the Multijugae he described *P. cascadensis* as new, based on a collection by Wilhelm N. Suksdorf made in Washington. He reported the rediscovery of *P. multijuga*, and that it is a true *Potentilla*.

In 1900 Aven Nelson described *P. plattensis* var. *pedicellata, P. monidensis,* and *P. wyomingensis*, all based on his collections from Wyoming. Alice Eastwood described a plant in 1902 that she had collected near Monterey, California, as *P. hickmanii*, named after its discoverer.

During the early part of the 1900's, Theodor Wolf was working on a monograph of *Potentilla* on a world-wide scale, for which he made extensive use of the herbaria in Germany, Russia, and eastern Europe, including Lehmann's. His work was apparently unknown to Rydberg until Wolf's monograph was published in early 1908, as volume 16 of Bibliotheca Botanica, even though he had made extensive use of Rydberg's own monograph and other publications. Wolf's monograph is a very complete work, with long descriptions and keys in Latin and discussion in German. He divided the genus first into "sections," then "subsections," then "series," then "greges" or groups. In his Grex Multijugae, he included *P. multijuga, P. arizonica, P. drummondii* and its var. *cascadensis; P. plattensis* and its three varieties *pedicellata, pinnatisecta,* and *wyomingensis, P. millefolia, P. monidensis, P. candicans, P. dissecta; P. diversifolia* and its two varieties *glaucophylla* and *decurrens*. In the closely related Grex Ranunculoides he places *P. ranunculus*; *P. breweri* falls into his Grex Graciles-Pinnatae.

Later in 1908, Rydberg published his treatment for North American Flora, volume 22. The system of division of the genus into sections was the same as in 1898, but he described two new species in Aureae (*P. perdissecta* and *P. vreelandii*) and raised *P. glaucophylla* back to species rank; in Multijugae he described three new species (*P. klamathensis, P. versicolor,* and *P. nelsoniana*) and accepted every other species ever before published. In Leucophyllae he described a new species, *P. bruceae*.

Willis L. Jepson wrote A Manual of the Flowering Plants of California in 1925, in which he described *P. breweri* var. *viridis* ("*viridia*"), and reduced *millefolia* and *klamathensis* to varieties of *P. plattensis*. In 1936, in his Flora of California, Jepson returned to recognizing *P. millefolia* as a species, and added two new varieties, *densa* and *algida*, to the already-made var. *klamathensis*. Also in 1936, M. E. Peck described *P. anomalifolia* based on one of his collections from southern Oregon.

David D. Keck, in Clausen, Keck, and Hiesey's often-cited Experimental Studies on the Nature of Species (1940) recognized that *P. breweri* and *P. drummondii* are closely related, and reduced *bruceae* to a subspecies of *P. drummondii*.

C. Leo Hitchcock wrote the treatment of *Potentilla* for Vascular Plants of the Pacific Northwest in 1961, in which he recognized Rydberg's *perdissecta* as a variety of *P. diversifolia* in addition to Watson's var. *multisecta*; he synonymized *anomalifolia* and *cascadensis* under *P. drummondii*; under *P. ovina* he included *wyomingensis, monidensis, klamathensis, versicolor,* and *nelsoniana*.

CHAPTER III

LITERATURE SURVEY: POPULATIONS AND TAXONOMY

The choice of which characters to use in a classification is of paramount importance, since they are the basis upon which the classification is made (Davis and Heywood 1963, Camp and Gilly 1943). The characters and their states that are chosen in large measure predict the classification that will result, as shown by Bisby and Nicholls (1977), working with a group of genera of Leguminosae. They demonstrated that different character formulations lead to "quite different" classification schemes.

It is often stated that use of characters that are highly correlated with one another is one of the basic ideas of classification (Stafleu 1969, Raven 1977). That taxa are based on those correlations, is one of the precepts of Adanson (Davis and Heywood 1963, Sneath and Sokal 1973). This idea was tested by Bisby (1973), who found that choice of a set of characters that were highly intercorrelated improved the classification of species of *Crotalaria* (Leguminosae), when improvement was measured by congruence of the resulting classification with one that had been made by traditional taxonomic methods. Bisby and Nicholls (1977) showed that choosing a set of well-correlated characters produced a classification with more clear-cut structure. The characters chosen by such a procedure are often those that had been most useful in the classifications of traditional taxonomists (Bisby 1970).

Variation of characters within populations

Another component of a classification is variation of the characters among the units to be classified. If a study focuses, for example on a genus, then it might use the variation among the species of that genus as this component; often, however, it is advisable to use units that are *two* levels below the unit describing the study, so that study of a genus would deal with the variation among subspecific taxa. The lowest category of unit usually used in classification is the population (Davis and Heywood 1963, Stebbins 1960).

In its modern, restricted sense, *population* means "the community of potentially interbreeding individuals at a given locality...[that] share in a single gene pool...by definition a panmictic (randomly interbreeding) unit" (Mayr 1970, p. 82). This definition is obviously applicable only to individuals that are in the habit of crossing with one another in a local area; asexual reproduction, such as gametophytic apomixis, as is common in many plant groups (Fryxell 1957, Grant 1971, etc.), renders the definition nearly unworkable. Plants in which there is a large proportion of inbreeding may also cause the definition to become unworkable, although in this case there are often small clusters of individuals at a locality that can be detected morphologically or biochemically (Allard and Kannenberg 1968; Allard, Jain, and Workman 1968).

The presence of the word "potentially" in Mayr's definition of population cited above would seem at first glance to make the definition applicable to a wider range of organisms, but in fact the definition is only made more obscure thereby, since it is not clear which barriers to reproduction may be included within a population, and which are excluded.

Particularly this point is important in plants, where there are many examples of the plants of a species in a local area, divided into populations by edaphic, topographic, or ethological barriers (Levin 1978). The phrase "potentially interbreeding" was originally included in the famous definition of *species* given by Mayr in 1963; however, Mayr himself apparently dropped the phrase from the definition of species after about 1969 (Mayr 1970, p. 12; Sneath and Sokal 1973, p. 364).

These difficulties with the definition of population have been approached in several ways. The most common way of attempting a solution is to restrict the discussion of populations to sexual, outcrossing forms (e.g., Mettler and Gregg 1969, pp. 26,30); this approach does not really solve the problem. A more satisfying, albeit less biological, method, is to define population operationally: "any group of individuals considered together at any one time because of features they have in common" (Davis and Heywood 1963, p. 353). This is a more practical definition, especially since breeding relationships of individuals are difficult to measure and assess in the field; the operational definition of population also suggests the use of morphological characters, as Davis and Heywood point out (1963, p. 355), and allows more direct sampling techniques, rather than progeny, biochemical, or breeding studies. This practical definition will be used in this study, except that it will be restricted to those plants which appear to form a coherent local unit. In other words, an estimate will be made of a population as if it were a breeding unit, without performing the genetic studies necessary to establish population size. This definition also makes it possible to use herbarium specimens as a kind of population sample.

The morphological, operational definition of population seems to be more appropriate when the relationships of the population made up of individuals, to the species made up of populations, is considered. The simplest case is that of a species with only one population, which is exceptional; most species have many populations. The species is the taxonomic unit of greatest concern and controversy, the central, fundamental level of systematic focus and also of the nomenclatural hierarchy. The species concept cannot be precisely defined in such a way that fits every case; however, most generalized definitions include a phrase like "cluster of populations" (Mayr 1970, p. 12; Davis and Heywood 1963, p. 90; etc.).

Characters used in classification usually vary both within and among populations. Table 1 is a survey of a few selected values for the coefficient of variation (the standard deviation divided by its mean, expressed as a percentage) in some higher plant populations. Most of these in Table 1 have been measured on natural populations; a few (8 and 10) are from garden samples. There are wide differences among the populations shown in the amount of variation each has within it; there are approximately equally wide differences among characters within the same population, or among populations for the same character.

Variation of characters among populations

In studies of variation among plant populations, Allard (1970) surveyed the history of methods of sampling populations to date, and reported that there seem to be two kinds of pattern in character variation among populations: 1) clinal, in which a morphological character increases (or decreases) continuously with some ecological or

TABLE 1. Coefficients of variation, CV, in per cent, for selected populations of higher plants cited in the literature.

Reference	Character and species	CV	Mean
a	1. Leaf length in *Asclepias tuberosa*		
	a. Population 6	20.7	71.9
	b. Population 25	8.8	99.0
	c. Population 27	32.1	81.3
	d. Population 50	10.1	68.2
b	2. Leaves and flowers in *Clarkia unguiculata*		
	a. Petiole length	61.5	10.5
	b. Petal width	27.0	10.6
	c. Style length	18.2	20.3
c	3. Leaves and plants in *Collinsia heterophylla*		
	a. Plant height	10.4	4.2
	b. Leaf length	4.9	38.8
	c. Number of branches	6.1	5.2
d	4. Number of flowers at second verticil in *Stachys* spp.		
	a. Population P8	45.2	7.7
	b. Population P14	20.6	13.0
	c. Population S15	4.3	6.1
e	5. Flowers in *Clematis fremontii*		
	a. Sepal length, glade 1	8.7	33.6
	b. Sepal length, glade 19	20.7	33.9
	c. Sepal width, glade 6	9.6	10.1
	d. Sepal width, glade 19	20.2	9.7
f	6. Leaves and flowers in *Potentilla erecta* in Assoc. Nardetum		
	a. Length of central leaflet	17.1	20.2
	b. Number of teeth on leaflet	19.5	9.5
	c. Length of [bractlet]	25.8	22.8
	d. Number of flowers	52.8	7.4
	e. [Stem length]	19.2	25.0
	f. Width of [calyx-lobe]	15.3	12.1
g	7. Plant diameter of *Potentilla erecta* in Assoc. Molinetum		
	a. Site L in 1964	29.1	29.5
	b. Site B in 1964	23.3	21.5
	c. Site B in 1965	13.5	
h	8. Flowers in cultivated *Fragaria*		
	a. Number of sepals, 2*x* plants	3.5-21.4	10.1-11.8
	b. Number of stamens, 2*x*	9.6	18.0
	c. Number of stamens, 6*x*	6.5	19.3
	d. Number of stamens, 8*x*	7.7	26.7
i	9. Plant height in *Festuca microstachys*		
	a. Within families	19.0	
	b. Among families	66.0	

TABLE 1. (Continued).

Reference	Character and species	CV	Mean
j	10. Leaves and flowers in 6x *Argentina anserina* in uniform garden, population 17		
	a. Number of leaflets	20.4	
	b. Length of leaf	27.2	
	c. Number of teeth	19.5	
	d. Depth of teeth	16.0	
k	11. Leaves and flowers of *Drymocallis glandulosa*		
	a. Leaf length, ssp. *glandulosa* .	18.2	21.3
	b. Leaf length, ssp. *reflexa* . .	20.4	22.4
	c. Leaf length, ssp. *hansenii* . .	30.4	10.1
	d. Leaf length, ssp. *nevadensis* .	38.1	6.3

a. Woodson (1947)
b. Vasek (1968)
c. Weil and Allard (1964)
d. Wilcock (1974)
e. Erickson (1945)
f. Staszkiewicz (1974)
g. Watson (1969)
h. Haskell and Williams (1954)
i. Kannenberg and Allard (1967)
j. Rousi (1965)
k. Clausen and Hiesey (1958)

geographical variable, such as altitude, moisture, mean temperature, or soil depth; and 2) patchwork or mosaic, in which sharp differences can be detected among local populations, without any apparent functional relationship to any ecological or geographical variable. Clinal variation (type 1) has been found in many species of a wide variety of breeding modes, in fact, Allard states that similar clines have been found "in all species for which adequate measurement data are available" (1960, p. 99). In contrast, most of the instances of patchwork or mosaic variation (type 2) that he cites are in grasses with predominantly self-pollinated breeding (e.g., Marshall and Allard 1970, Allard and Kannenberg 1968); recent examples can be found among outcrossing plants, for example in the perennial prairie herb *Liatris cylindracea* (Schaal 1975, Schaal and Levin 1976). Kannenberg and Allard (1967) found that some morphological characters are more variable locally in outcrossing species, and some are more variable in inbred species. Intra- and inter-population variation is apparently not a function of breeding structure or mode taken by itself, as once thought (Stebbins 1957), but other factors must be taken into account.

Many studies on plant populations have focused on the role of hybridization in evolution, which studies have provided an opportunity to examine variation within and among populations. Notable in this discussion is the work of Anderson (1949,1953), who advocated studying populations directly in their natural state, "so that the effects of the evolutionary forces at work could be measured in natural populations" (1953, p. 280). His vehicle for demonstrating the effects of evolution in populations was the investigation of introgressive hybridization, in which two related biotypes hybridizing in a zone of contact show directional variation in a number of characters from one biotype towards the other. Anderson (1948,1949) showed that introgression would proceed most effectively where a range of habitats intermediate between the two "parental" habitats occurred in the zone of overlap, and that this introgression proceeded from hybrid individuals back-crossing to one of the parental biotypes. Introgression may be a method by which hybrids are stabilized (Stebbins 1959); in recent years, as the number of documented cases of hybridization has increased, its role in speciation has become more important (Stebbins 1970).

Anderson (1941,1943) advocated the use of "mass collections" to adequately measure the variation within and among local populations; these are large collections of whole plants of parts of plants from one locality. Woodson (1947,1953) used this technique with some modifications in his amazing study of leaf variation in *Asclepias tuberosa*. He measured leaf apex and basal angles, leaf width and leaf length on many herbarium specimens and population samples of this species throughout its range in eastern, central, and southwestern U. S. A., in which he found clinal variation in the two leaf angles, and evidence of introgression at many localities.

Some studies have shown difficulties in defining subspecific entities. Kruckeberg (1951) found that species growing on serpentine soils in California formed local populations on outcrops that were highly differentiated from one another, yet he could find no units between the populations and species. Bradshaw (1959) showed that the perennial grass *Agrostis tenuis* formed well-defined local populations with regard to the plants' physiological tolerance to various contaminants in the soil; yet these populations were not morphologically differentiated.

Bradshaw concluded that subspecific classification is not warranted; yet he overlooked a later paper by Kruckeberg (1957), in which he demonstrates that the annual crucifer *Streptanthus glandulosus* forms well-marked geographical races based on morphological characters. Hybrids between geographical races, which Kruckeberg identifies as subspecies, show markedly reduced pollen fertility. Hickman and Johnson (1969), in a geographical analysis of morphological variation in the shrub *Menziesia ferruginea* in the Pacific Northwest, revealed that "no single character or set of characters studied can be used to separate individuals into geographically or ecologically coherent categories. Thus, the erection of subspecific taxa is unwarranted."

All of the population studies surveyed have shown a large degree of morphological variation among individuals within a population. When the variation among populations is considered, it may be seen that some of the variation may be clinal; a cline may have a geographical axis closely approximating the axis for other characters, as in *Asclepias tuberosa*, or the variation may be in a more complex multivariate pattern, as in *Menziesia ferruginea*. The examples of clinal variation are mostly from outcrossing, sexual, perennial species. Variation among populations may also be in a patchwork or mosaic pattern, usually accompanied by smaller populations, with a large number of these "micro-populations" in a local area; this pattern is often seen among predominantly self-pollinating species such as *Festuca microstachys*, or species where there are fairly strong local forces restricting dispersal or pollination, as *Liatris cylindracea*. A more complex situation may be seen in apomicts, where local populations may not be formed; all characters vary continuously in complex, multifactorial fashion, with no apparent relationship to locality or geographical region.

From the studies surveyed, no trend seems evident in whether, based on morphological data, subspecific clusters of populations can be recognized; in some studies such clusters can be shown, in others they can be shown after some difficulty, and in still others no such cluster can be shown. From some of the examples in Table 1, it can be seen that the most common situation is that in which two populations have different means (they may even be statistically significantly different), but the variation within each population is such that the distributions overlap. Certain individuals from the populations may be indistinguishable for the character.

If all units were population samples in the style of mass collections as Anderson suggests, we would know more of the variation in characters within and among populations; but the data set would be very large within any modestly wide-ranging species, as shown by the studies of Woodson (1947) or Erickson (1943). However, even in this ideal case, if units are to be chosen for classification into clusters above the population level, specimens chosen to represent the population may not adequately represent the population mean for a character; it may be one of the individuals in the overlapping portion of the distribution for that character, which would lead to the population's not being as sharply distinguished as the means were. To accept a composite description as definition for a unit is to commit a kind of typological error, as discussed by Davis and Heywood (1963, p. 127).

From this situation follows the notion that at least several characters must be used together to make a classification, and that these characters should be well-correlated with one another. If one character only is used, it may not be effective in distinguishing two populations; addition of a second character, also partially distinguishing between the two populations and correlated with the first one, increases the probability that the two populations can be separated.

Sneath and Sokal (1973) discuss selection of characters, and although they cite Adanson's principle of correlation, their discussion shows that they advocate the use of many characters without weighting, giving equal weight to each character. This attitude has been criticized by a number of plant taxonomists (e.g., Stafleu 1969, Raven 1977). Davis and Heywood (1963) agree with Sneath and Sokal in the case of a general-purpose classification, but go on to show how character weighting is appropriate for a special-purpose classification or to construct a phyletic classification. However, Bisby (1970) points out that the decision to include a character is in effect a weighting of it.

Several workers have used an information-theoretical approach for analyzing characters as to their usefulness in classification. The method, as described and discussed by Estabrook (1967), Hawksworth, Estabrook, and Rogers (1968), and Legendre and Rogers (1972), has probably been most extensively used by Bisby and his co-workers (1970, 1973,1977). He has shown in these studies that improvement can be effected in a classification by use of characters that are highly intercorrelated. In his terminology, "correlation" has a broader definition than statistical correlation. Nevertheless, it is apparent that variables that are significantly correlated in the statistical sense will have a large proportion of their information in common, and hence be correlated in the sense of Bisby's applications.

Subspecific clusters of populations

There are several levels of variation between population and species. Clausen and Hiesey (1958), in their classic study of ecological races in *Drymocallis glandulosa*, detected four such levels of variation: 1) between individuals of a population; 2) between isolated local populations in one climatic or edaphic region; 3) between populations growing in different climatic or edaphic regions; and 4) the taxonomic subspecies, morphologically easily recognizable over a broad region and ecologically distinct. As they state and abundantly show, the overlapping interaction among these entities and the four levels they occupy provides a very complex structure. The variation at level (3), if it defines clusters of populations based on different climatic or edaphic regions, may be said to describe *ecotypes*; if they are morphologically distinguishable they may be described as subspecies. Clausen, Keck, and Hiesey (1940) found ecotypes within *Drymocallis glandulosa*, the *Potentilla gracilis* complex (including *P. diversifolia*), and the *P. drummondii--P. breweri* complex (in sect. Multijugae), but they were morphologically distinguishable only in *D. glandulosa*, whereas the ecotypes were in general not morphologically distinguishable (and therefore, not meriting subspecies rank) in the other two complexes. These latter two complexes are largely apomictic and high-polyploid.

The structure of formal nomenclature, as distinct from the levels of variation described above, includes the following ranks below the species level:

species
subspecies
variety
subvariety
forma

subforma,

for which see Lanjouw et al. (1966) or Davis and Heywood (1963). The subspecies is usually though of as "a regional, distinct facies of a species" (Davis and Heywood 1963, after Du Rietz), which concept is obviously dependent upon the prior delimitation of the species; that is, for a subspecies to be recognized, the particular species within which it occurs must be defined and delimited. Many plant taxonomists use the level of "subspecies" as the only level below that of species; a few use "variety" in addition to subspecies, and a few use the terms alternatively. Often the variety is taken as a "local variant" (Davis and Heywood 1963), with a geographical extent much less than that of the subspecies.

Occasionally a plant taxonomist will use the category "forma" (e.g., Wolf 1908), usually in the sense of "a sporadic variant distinguished by a single or a few linked characters, without a distinct distribution" (Davis and Heywood 1963, p. 101). Camp and Gilly advocate the use of subspecies and forma as the only categories below that of species, with the definitions much as cited above; they seem to indicate that there may be cases where naming of taxa is not justified at either level.

It is not clear how these levels of the formal taxonomic hierarchy mesh with the "levels of variation" based on incrasingly larger clusters of populations described by Clausen and Hiesey. The variety may possibly correspond with levels 2 or 3, however it is significant that Keck in 1940 only recognized the subspecies of *Drymocallis glandulosa* and did not attempt to formally recognize varieties. The forma is even less certain as a classification mechanism for populations, since it fails to account for the rather considerable variation expected within and among populations; only a forma showing intrapopulation uniformity with regard to some (morphological) feature of interest is consistent with the taxonomic system.

In some cases, for example in the classification of cultivars within a cultigen, formal nomenclatural recognition of clusters of populations may not be justifiable or possible. In such cases, informal terms without official status may be more realistic, for example, the "divisions" and "groups" of cultivars in *Manihot esculenta* (Rogers and Fleming 1973).

Numerical methods of analyzing taxonomic structure

Multi-character methods are most useful in taxonomic studies, because at best, a small set of characters must be chosen which will effectively classify the organisms in the study, and traditional taxonomy lacks an objective method of selecting these characters. At worst, which is probably the case in this study, the classification may have to be based on a number of characters considered simultaneously. It is difficult for a taxonomist (or anyone else) to consider a number of characters simultaneously over a large set of objects without the aid of an automated method.

The two leading automated methods of analyzing taxonomic structure based on data from many characters are ordination and clustering. Many different applications of each of these are given in Sneath and Sokal (1973). As they emphasize, most studies have focused on the species level or higher, and relatively few at the population level (pp. 367-368).

At the species level and higher, there have been several studies contrasting methods of classification. Prance, Rogers, and White (1969) compared two different principal-components analyses (methods of ordination) and two different clustering methods, compared and contrasted with a pre-existing taxonomic system, which had been made using traditional taxonomic procedures. They found that the single-linkage clustering technique based on graph theory of Wirth, Estabrook, and Rogers (1966) gave the most useful results and allowed these results to be displayed in a way that more information about taxonomic structure could be visualized. Their study was designed to re-evaluate and complement the traditional taxonomic system, and to focus on problem areas, rather than to supplant the traditional taxonomy.

Bisby (1973) and Bisby and Polhill (1973) compared the traditional classification of the genus *Crotalaria* with three numerical procedures: single-linkage clustering, principal-coordinates analysis, and median clustering (a method by which clusters are connected by their medians). They found, as before, that the single-linkage method with subgraph representation, was the best of the three methods. The method they chose illustrated the patterns of similarities of the groups formed, and indicated marginal and isolated species, and thus showed where improvements might be made in the existing classification.

At the population level, Sneath and Sokal (1973) point out that few studies have used clustering techniques; most have used ordination. However, there is no reason to believe that the reservations expressed in the studies by Prance et al. (1969) or Bisby (1973) against the use of ordination for classification would not also apply at the population level. Rogers and Fleming (1973) used single-linkage clustering with subgraph representation to classify population samples within a cultigen, and produced a useful classification of cultivars.

At levels between the population and species, based on the comparative studies that have been made, single-linkage clustering with subgraph representation seems to be the best method for extracting information helpful in making a taxonomic classification. As Prance et al. (1969) state, this method makes it possible to follow the progress of the classification process and detail the procedure by which each item contributes to the clustering.

CHAPTER IV

MATERIALS AND METHODS

Whole plants were sampled from each of 21 populations found in Colorado, Nevada, Utah, and Wyoming; the sites chosen were those that had been determined to contain plants of critical interest. The locations of these critical populations were determined by subjective examination of herbarium specimens. From these population samples, ten were chosen (Table 2) that were representative of the taxa in sect. Multijugae and of a sufficient size to allow later statistical analysis. The populations were sampled in such a way that their boundaries would be conspicuously identifiable; most populations occupied a little less than a hectare, and were defined by homogeneity of habitat characteristics such as slope, exposure, soil type, soil drainage and sorting, and dominant vegetation. However, the area of each population always contained a mosaic of microhabitats. In addition, the plants making up each population were clearly distinguishable morphologically from other populations of *Potentilla* in the area. If the population was large enough, every plant was sampled within a strip along a transect through the population; sometimes two or three such transects were necessary. The whole plants sampled were collected in the manner of herbarium specimens, as "mass collections" (Anderson 1941), but left unmounted through the later analysis; they will later be distributed to the herbaria from which loans were received (see list below) as voucher specimens.

TABLE 2. Collection localities, species determinations (based on conclusions in the taxonomic revision, chapter VI), and sample sizes, for populations used in statistical analysis.

Population number	Sample size	Locality (species)
1	12	NEVADA. Elko Co., cirque above and SSW of Island Lake, Ruby Range, NW¼ S36 T32N R58E, ca. 10600 ft; wet meadow (*P. breweri* var. *bruceae*)
2	5	WYOMING. Albany Co., crossing of small creek and county road, 2.5 mi southeast of Centennial, SE¼ S12 T15N R78W, 7820 ft; heavily-grazed boggy meadow (*P. plattensis*)
3	3	WYOMING. Albany Co., rocky alpine ridge NW of Glacier Lake, Snowy Range, SW¼ S3 T16N R79W, ca. 11500 ft (*P. nelsoniana* topotype [the same locality at which the Type was collected])
4	7	COLORADO. Park Co., beside highway 285 0.3 mi NE of Jefferson, SE¼ S5 T8S R75W, 9500 ft; gravelly slope above meadow-bog (*P. plattensis*)
5	13	WYOMING. Carbon Co., flat windswept limestone ridge ca. 25 mi south of Rawlins, ca. S30 T17N R87W, 8000 ft; mat-plant community (*P. ovina* var. *ovina*)
6	15	UTAH. Juab Co., road to headwaters of Basin Creek, Deep Creek Range, 8 mi WSW of Callao, ca. S10 T11S R18W, 7800 ft; under cliffs in *Pinus monophylla*-*Cercocarpus ledifolius* woodland (*P. multisecta*)
7	10	NEVADA. Elko Co., cirque above and SSW of Island Lake, Ruby Range, NW¼ S36 T32N R58E, ca. 10600 ft; wet meadow (*P. breweri* var. *breweri*)
8	13	WYOMING. Park Co., south end of Clay Butte, SW¼ S1 T57N R106W, 9800 ft; rocky grassy meadow on limestone soil (*P. ovina* var. *ovina*)
9	6	COLORADO. Moffat Co., limestone cap on Zenobia Peak, NW¼ S33 T8N R102W, 9000 ft; in soil pockets on flat summit (*P. ovina*)
10	11	UTAH. Duchesne Co., headwaters of south fork Log Hollow, SW¼ NW¼ S31 T2N R7W, 11100 ft; in grassy tundra (*P. ovina* var. *decurrens*)

For each plant in these ten populations, twenty characters were scored (Table 3). For each plant, at least two leaves (usually three) and an equal number of stems were paired, producing thereby two (or three) sets of measurements. Most of the characters are explained in the table; but character 11 (LT) was measured by taking the ratio $\frac{a}{b}$ of two measurements, both taken at right angles to the midrib of one of the leaflets of the second pair: a = distance from the tip of the longest tooth to the bottom of the deepest serration; and b = distance from the tip of the longest tooth to the midrib. Characters 14 and 15 (SL and SW) were both measured on a stipule at the approximate middle of the stem. Characters 8 and 9 (S and C) show the pubescence on the surface of the lower leaf.

For each of the ten populations, analysis of variance was calculated for each of the twenty characters, and the portion of the variance due to among-plant interactions was tested for statistical significance using the F-test (Sokal 1965, Sokal and Rohlf 1969). Analysis of variance was also made for the whole sample. Before these analyses were done, the characters that were ratios (characters 3,11,12,19) were transformed by taking the $\log_{10}$ of each value, as recommended in Sokal and Rohlf (1969).

For each of the ten populations, Pearson product-moment correlation coefficients were calculated for each pair of characters (Sokal and Rohlf 1969), and the statistical significance of each of the correlation coefficients was tested; correlation coefficients were also calculated and tested for the total sample of all plants measured. The analysis of variance and correlation coefficients were calculated using computer programs written by the author (Appendix).

TABLE 3. Characters used for statistical analysis of populations, with symbols used in later diagrams.

Character number	Symbol	Character (units)
1	RA	Root-stem angle (degrees)
2	LF	Length of longest basal leaf rachis (cm)
3	PR	Percent of rachis occupied with leaflets
4	NL	Number of leaflets
5	NT	Number of leaf-segments (teeth) on terminal leaflet
6	NT2	Number of leaf-segments (teeth) of leaflet of second pair
7	LL	Length of terminal leaflet (mm)
8	LL2	Length of leaflet of second pair (mm)
9	S	Density of straight hair, subjective: 1 None 2 Slight or scattered-patchy 3 Sparse but uniform 4 Dense but not covering surface 5 Dense and covering surface
10	C	Density of curly hair (same states as 9)
11	LT	Relative length of teeth (see text)
12	RT	Width/length ratio of terminal tooth
13	LS	Length of stem (cm)
14	SL	Stipule length (mm)
15	SW	Stipule width (mm)
16	PA	Pedicel angle (degrees)
17	NF	Number of flowers
18	LC	Length of calyx, including lobes (mm)
19	RC	Width/length ratio of a calyx lobe
20	SY	Style length (mm x 10)

Approximately 7000 herbarium specimens were borrowed on loan from 25 herbaria: ALTA, ARIZ, ASC, BRY, CAN, CAS, COLO, DAO, GH, ID, MNA, MONTU, ND-G, NY, ORE, PH, POM, RM, UC, UNM, US, UTC, WIN, WS, and WTU (standard abbreviations from Index Herbariorum, Holmgren and Keuken 1974). These herbarium specimens were found on inspection to mostly be of sect. Multijugae, with a lesser number of sect. Concinnae and sect. Subjugae. The specimens were sorted first by section (key in Chapter VI), then each section was sorted into rough species complexes. From each section , specimens were chosen from each morphologically distinguishable unit, so that approximately 200 specimens were chosen to represent the variation evident in each section, and these sections were subjected to character analysis separately by section, using computer program CHARANAL (Fleming and Appan 1971, Estabrook 1967, Legendre and Rogers 1972).

Program CHARANAL uses the theory of information, in which the total amount of information ("entropy") in a character has been derived as

$$H_J = - \sum_{i=1}^{n} p_i \log_2 p_i,$$

where p_i = the probability of the ith state of character J, and H_J = the information in character J (Legendre and Rogers 1972). The conditional entropy shared between two characters is

$$H_{I/J} = - \sum_{g=1}^{n_1} \sum_{h=1}^{n_2} p(J_h/I_g) \log_2 p(J_h/I_g),$$

where n_1 and n_2 are the number of states in characters I and J, respectively, and $p(J_h/I_g)$ = conditional probability of state h of character J, given state g of character I. The program CHARANAL displays, for each unequal pair of characters, the total information contained in each character, all the conditional probabilities for all states of both characters, and the conditional entropy shared between the two characters, among other quantities. Bisby (1970) has used two other quantities, both designed by Henry Fleming and displayed by CHARANAL, namely SUMRAT_I and SAMRAT_I (the last called "information contribution of character I" by Bisby). These two quantities are defined as:

$$\mathrm{SUMRAT}_I = \sum_{g=1}^{n_1} \frac{H_I - H_{I/J_g}}{H_{J_g}}$$

$$\mathrm{SAMRAT}_I = \sum_{g=1}^{n_1} \frac{H_I - H_{I/J_g}}{H_I} .$$

In other words, SUMRAT_I is the sum of fractions of other characters J also in I; SAMRAT_I is the sum of fractions of character I also contained in other characters J. It can be seen from these definitions, that both SUMRAT and SAMRAT are a measure of how much information in character I is shared by other characters (Fig. 1). The characters were refined according to the results of this program.

The herbarium specimens were sorted again into sets that were morphologically homogeneous ("morphotypes") based on the refined set of characters from CHARANAL and results of the statistical analysis of characters within populations. From each of these sets, a few specimens were chosen to represent the variation within each set (192 specimens for sect. Multijugae, 174 specimens for sects. Concinnae and Subjugae). These specimens were primarily chosen to provide a good morphological sample of all the specimens, and secondarily to give a good geographical sample within sets.

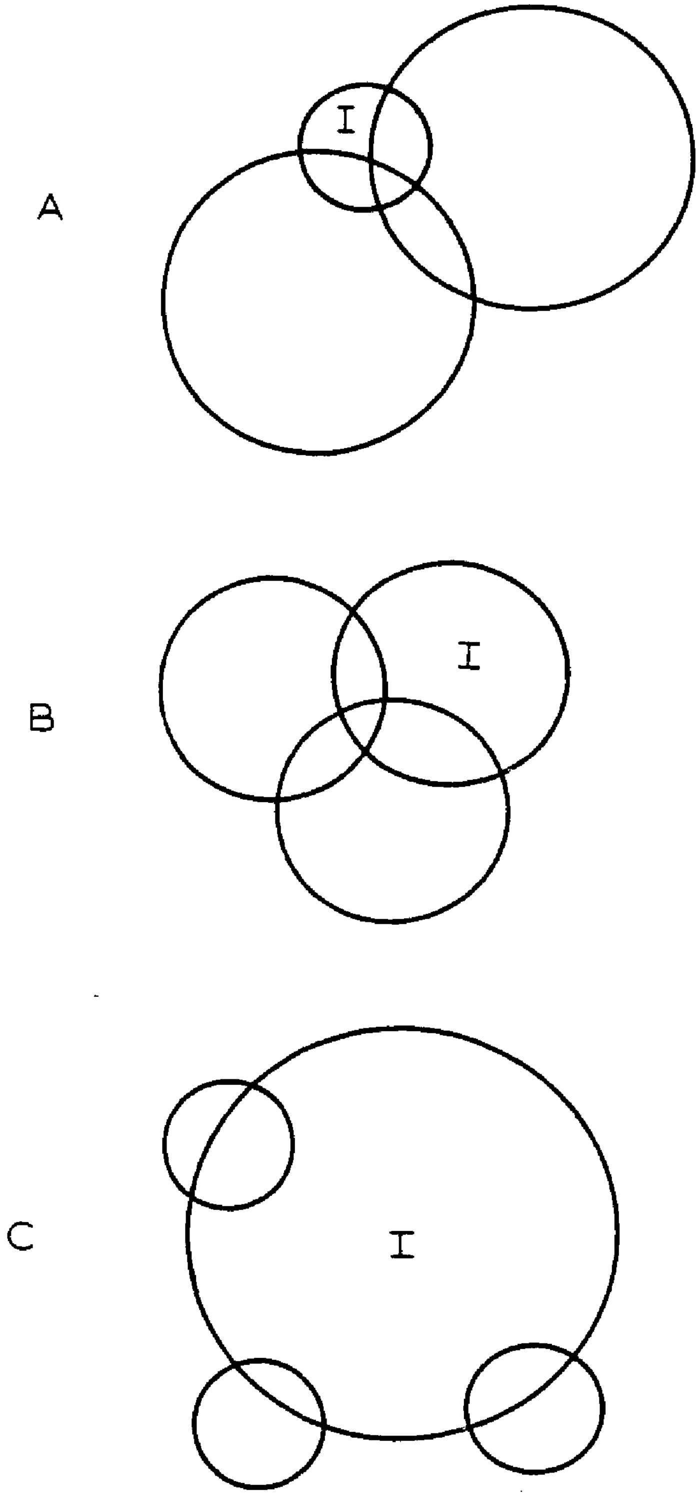


FIG. 1. Showing three possible relationships between SUMRAT and SAMRAT, for character I. A. SUMRAT low, SAMRAT high; B. both medium to low; C. SUMRAT high, SAMRAT low.

Suspected disjunct outliers of a species' distribution were necessarily always included. Specimens representing an extreme expression in a character were usually included; however, suspected hybrids between species known to be sympatric there were excluded. At least one type or authentic specimen was included for each name, if they were available.

These herbarium specimens were then coded for input into the single-linkage clustering program GRAPH (Fleming and Appan 1972, Wirth, Estabrook, and Rogers 1966, Legendre and Rogers 1972). This program is based on a portion of the mathematical theory of graphs, as outlined in Estabrook (1966); this method has been used in many other studies of classification, in biology and other disciplines. Different characters were used for the different studies, one set for sect. Multijugae (Table 11), another for sects. Concinnae and Subjugae (Table 15). For each study, a complete set of subgraphs was drawn in the manner of Prance, Rogers, and White (1969); one level of the drawing was chosen as being best representative of the relationships of species-clusters, and based on that level the diagram was tentatively divided into species-clusters. These species-clusters were then drawn individually, showing all the connections and levels at which those connections were made, with the aim of deciding whether definition of specific or subspecific taxa was warranted.

Based on the subgraphs, the herbarium specimens were again sorted, and geographical ranges of the clusters and subclusters carefully mapped. Specimens which bridged gaps among several clusters were set aside until the next step.

A table was made of the character expressions of each "core-cluster," that is, the tightly-clustered center of each cluster or subcluster; from such tables, the characters which had contributed to the cluster's separation from other clusters were determined. This information was used, with the geographical information mapped in the previous step, to make decisions about which cluster should include specimens that were bridging gaps between clusters or subclusters, or specimens which clustered very loosely. This was done to produce, as nearly as possible, morphologically distinguishable taxa with well-defined ranges. The subgraphs were slightly adjusted and redrawn to allow for these decisions.

For each cluster or subcluster, a table was made of the character expressions for all the specimens in the cluster, to indicate the total variation in each character within each cluster for the sample. These tables were used to make keys and descriptions for a taxonomic revision of the sections studied, including discussion of critical specimens and lists of specimens used in the clustering. In the lists, the specimen number used in the subgraphs is shown in [brackets].

CHAPTER V

RESULTS AND DISCUSSION: SECT. MULTIJUGAE

When analysis of variance was computed for each of 20 characters within each of the 10 populations, the F-test for significance of variance due to among-plant interactions had the results shown in Table 4. The means for each of the characters are given in Table 5. To facilitate comparison of variances between populations, the coefficient of variation was calculated for each character (except the ratios) in each population (Table 6). These results will be discussed for each character.

Character 1 (stem angle) varied significantly among populations, but in most populations among-plant variance was not significant, meaning that much of the variance was within plants. The means showed that the population of *P. plattensis* from Park Co., Colorado, was nearly prostrate and the population of *P. ovina* from Moffat Co. was ascending, with other populations scattered between these extremes. The coefficients of variation for this character were large to very large.

Character 2 (leaf rachis length) varied significantly among populations (as did every character this study used). The populations of *P. plattensis, P. ovina* var. *decurrens*, and one population of *P. ovina* var. *ovina* did not vary significantly among plants; these populations tended to have larger coefficients of variation, showing that in them much of the variation was within plants. In the remaining populations, most of the variation was (significantly) among plants. The means ranged

TABLE 4. Results of analysis of variance for 20 characters measured on 10 populations of *Potentilla* sect. Multijugae.

Character	Population											
and symbol	1	2	3	4	5	6	7	8	9	10	T	TP
1 (RA)	–	–	***	–	*	–	–	–	–	–	***	***
2 (LF)	***	–	*	–	***	***	*	***	–	–	***	***
3 (PR)	–	–	**	–	–	–	–	–	–	–	***	***
4 (NL)	***	**	–	–	***	***	–	**	–	–	***	***
5 (NT)	–	–	–	–	–	***	–	–	–	**	***	***
6 (NT2)	–	–	–	–	–	–	–	***	–	***	***	***
7 (LL)	***	–	–	–	***	*	–	–	–	–	***	***
8 (LL2)	–	–	**	–	**	–	–	**	–	–	***	***
9 (S)	–	–	–	–	***	–	–	–	–	***	***	***
10 (C)	–	–	–	–	–	–	–	***	**	***	***	***
11 (LT)	–	–	–	–	–	–	–	–	–	–	***	–
12 (RT)	–	–	**	–	–	–	–	–	–	–	***	***
13 (LS)	***	–	***	–	**	**	**	**	*	–	***	***
14 (SL)	***	–	–	–	***	–	*	–	–	–	***	***
15 (SW)	***	–	–	–	***	–	–	***	–	–	***	–
16 (PA)	–	–	–	–	–	–	–	–	–	–	***	–
17 (NF)	***	–	–	–	–	–	–	–	–	–	***	***
18 (LC)	–	–	–	–	***	–	–	–	*	–	***	–
19 (RC)	–	–	–	–	–	**	–	–	–	–	***	***
20 (SY)	–	–	–	–	***	***	***	***	–	–	***	***

T = significance among populations for the whole sample
TP = significance among plants for the whole sample
* = significant at 1% or better
** = significant at 0.5% or better
*** = significant at 0.1% or better
– = not significant

TABLE 5. Means of 20 characters from 10 populations of *Potentilla* sect. Multijugae. Values shown for characters 3, 11, 12, and 19 have been reconverted from the $\log_{10}$-transformed values used in the analysis, and hence are true means.

Character and symbol	Population 1	2	3	4	5	6	7	8	9	10	T
1 (RA)	18.94	37.00	21.29	8.53	29.82	42.05	34.04	38.68	56.57	26.83	31.44
2 (LF)	49.53	34.40	30.43	68.90	23.77	71.29	63.27	57.24	37.79	45.17	50.35
3 (PR)	34.51	57.28	69.18	61.52	32.73	2.65	51.40	51.64	37.93	58.08	29.79
4 (NL)	9.56	16.87	11.14	18.32	6.21	5.26	14.23	13.89	7.50	12.48	10.79
5 (NT)	6.86	6.47	6.00	9.58	7.18	7.34	5.89	8.16	9.07	4.61	7.15
6 (NT2)	4.06	6.07	2.57	6.95	4.46	4.97	3.27	4.92	5.50	3.04	4.58
7 (LL)	16.31	10.53	16.14	18.32	11.72	26.13	11.85	14.76	15.36	15.13	16.04
8 (LL2)	13.64	10.53	14.57	15.53	8.62	20.24	11.62	12.08	9.50	12.52	13.08
9 (S)	1.00	2.87	2.00	2.16	2.44	2.34	1.00	2.19	2.43	1.74	1.97
10 (C)	2.33	1.00	1.00	1.00	1.15	1.00	3.54	1.14	1.64	1.70	1.59
11 (LT)	64.27	87.50	65.46	87.72	82.60	88.51	76.03	89.74	82.99	76.91	80.17
12 (RT)	33.50	32.66	37.60	50.00	43.15	29.58	46.77	30.90	39.63	38.55	36.80
13 (LS)	26.75	12.13	7.57	18.32	4.95	14.40	27.23	22.19	9.14	12.26	16.63
14 (SL)	14.92	12.00	6.43	10.90	5.46	7.92	11.96	12.08	9.07	8.13	10.06
15 (SW)	5.14	5.87	2.29	3.74	2.13	2.32	4.04	2.60	2.07	2.78	3.25
16 (PA)	31.47	22.93	25.71	29.05	15.90	39.05	28.58	23.32	16.57	27.52	26.71
17 (NF)	6.17	7.93	3.00	16.37	1.95	3.63	6.08	3.97	1.79	3.87	5.14
18 (LC)	8.44	7.20	5.43	6.84	4.72	6.47	9.39	7.68	5.43	5.30	6.84
19 (RC)	41.88	44.98	47.86	54.95	53.70	47.10	50.70	44.57	47.10	49.20	47.86
20 (SY)	29.33	18.53	18.43	19.80	21.10	25.79	23.08	25.43	24.93	18.22	23.43

T = means for combined sample

TABLE 6. Coefficients of variation, %, for 16 characters in the 10 populations of *Potentilla* sect. Multijugae.

Character and symbol[a]	Population									
	1	2	3	4	5	6	7	8	9	10
1 (RA)	77.2	81.0	92.7	155.2	82.1	54.3	44.9	55.5	39.9	82.6
2 (LF)	12.7	21.7	37.9	37.4	30.6	16.9	29.7	38.4	23.2	32.8
4 (NL)	23.5	20.9	15.0	39.1	20.6	12.2	19.2	15.7	17.9	19.3
5 (NT)	23.4	21.8	16.7	17.9	14.9	19.8	21.1	15.4	6.8	36.9
6 (NT2)	31.7	15.8	2.1	22.7	40.4	27.4	23.8	20.5	26.4	43.7
7 (LL)	34.1	14.7	31.9	31.6	22.2	24.8	18.3	22.8	54.6	17.5
8 (LL2)	24.7	13.4	32.2	27.9	25.8	23.7	16.3	19.2	17.4	16.1
9 (S)	0.0	12.3	0.0	6.5	20.6	20.5	0.0	18.1	21.1	52.6
10 (C)	22.9	0.0	0.0	0.0	83.3	0.0	16.4	30.5	30.3	72.1
13 (LS)	32.3	36.4	26.3	37.0	27.0	26.9	23.2	32.1	12.8	19.7
14 (SL)	22.5	20.2	17.6	19.1	22.2	25.1	13.9	15.5	92.4	15.0
15 (SW)	41.3	133.3	21.3	2.4	37.6	40.3	29.5	24.8	12.9	28.6
16 (PA)	29.8	31.2	36.9	25.8	97.7	50.5	30.7	35.7	96.4	56.8
17 (NF)	66.2	48.2	27.2	38.3	42.4	47.7	98.2	48.7	39.2	36.8
18 (LC)	11.1	9.3	14.5	8.8	18.2	14.2	77.6	10.7	9.5	13.3
20 (SY)	11.4	2.8	4.3	6.6	7.5	6.9	7.3	11.7	5.6	7.4

Characters 3, 11, 12, and 19 have been omitted, because they are ratios of measured values uniformly, with the *P. ovina* population from near Rawlins having the smallest leaves, and the population of *P. multisecta* the largest. Coefficents of variation were medium-sized to small for this character.

Character 3 (per cent of rachis occupied) was designed as a measure of the "pinnateness" of the leaf, with a value of 0 signifying a completely digitate leaf. This character varies significantly among populations, but only one population (*P. nelsoniana*) had significant among-plant variation; much of the variation in other populations was within plants. However, one population (*P. multisecta*) was almost digitate, with the rest showing a range of 29-57% of rachis occupied.

Character 4 (number of leaflets) varied significantly among plants within five of the populations, with no apparent taxonomic importance. Coefficients of variation were fairly small in general, but the largest value of CV was medium-sized in the population of *P. plattensis* from Park Co., Colorado. The number of leaflets varied with the "pinnateness" (character 3), as discussed below under correlation, with the subdigitate *P. multisecta* having the smallest number of leaflets and the apparently-pinnate *P. plattensis* the largest.

Character 5 (number of teeth in the terminal leaflet) was scored somewhat differently than in the studies to follow; the character is most difficult to score in *P. breweri* and its relatives (and several other species not in this section) which have terminal leaflets dissected pinnately into lobes, each of which is toothed (Fig. 16[5]). In these, it is difficult to tell just where the terminal leaflet ends and where the lower pairs begin. Therefore, the values scored for this character represent the number of teeth in the terminal lobe, whether this is the lobe of a terminal leaflet or whether it is a leaflet in itself. The result is that the mean values may not be strictly comparable between populations. This character varied significantly among plants in two populations only, those of *P. multisecta* and *P. ovina* var. *decurrens*; otherwise, in the other populations much of the variation was within plants.

Character 6 (number of teeth in a leaflet of a lower pair) was measured with more certainty; here, again, in most populations much of the variation was within plants, but in two populations, *P. ovina* from Park Co., Wyoming, and *P. ovina* var. *decurrens*, the variation was significantly among plants. The fewest number of teeth was shown on the plants of the *P. nelsoniana* population, which had by far the lowest coefficient of variation for this character. In order to decide which of the means were significantly different from one another, a Student-Newman-Keuls test (or SNK; Sokal 1965, Sokal and Rohlf 1969) was performed on the means of character 6, with results shown in Table 7. The two populations of *P. breweri* (both from the same alpine cirque in the Ruby Range of Nevada) and the two populations of *P. ovina* var. *decurrens* (including *P. nelsoniana*) were in a non-significant group with the smallest number of teeth, with the two populations of *P. breweri* having more teeth but not significantly so. The two populations of *P. plattensis* were in another non-significance group with the greatest number of teeth. The populations of *P. ovina* and *P. multisecta* fall in between, with one non-significance group including just these populations. Considering the medium-sized to small values of CV, this character seems to separate the populations fairly well into three groups. Frequency distributions for three of the populations are shown in Fig. 2.

TABLE 7. Results of SNK test for homogeneity of means of the 10 populations of *Potentilla* sect. Multijugae, for character 6 (number of teeth in the second-pair leaflet).

	Population									
	3	10	7	1	5	8	6	9	2	4
Variance	0.2857	1.7708	0.6046	1.6540	3.2551	1.0210	1.8642	2.1154	0.9238	2.4971
Sample size	7	23	26	36	39	37	38	14	15	19
Mean	2.571	3.043	3.269	4.056	4.462	4.919	4.974	5.500	6.067	6.947
	—	—	—	—					—	—
				—	—	—	—			
					—	—	—	—		
						—	—	—	—	

A line drawn under a set of population means indicates that the range included was found to be not significantly different at 1%

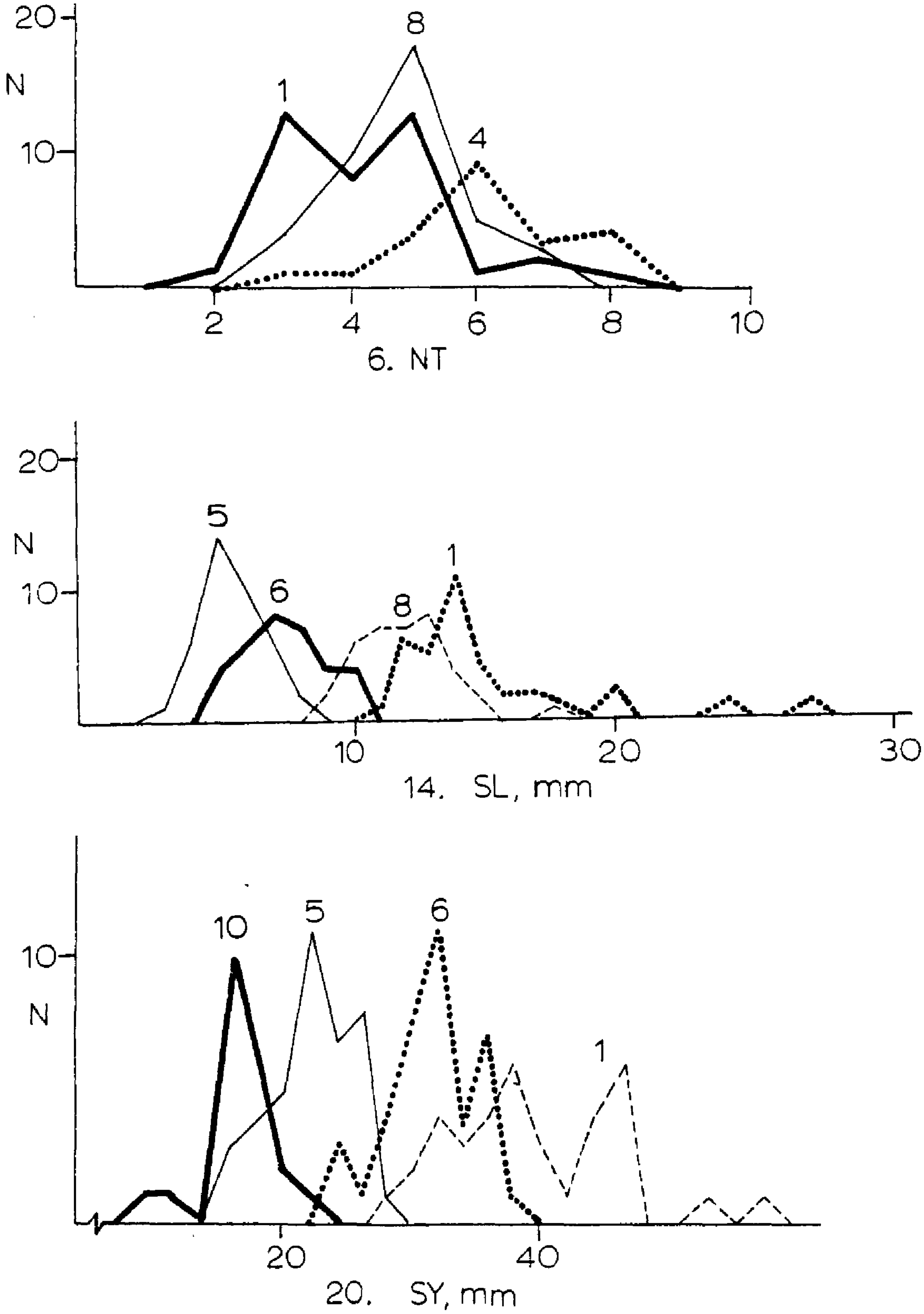


FIG. 2. Frequency distributions of three characters, for several populations from different non-significance groups (Tables 7,8,9) for those characters. Top, number of teeth; middle, stipule length; bottom, style length.

Character 7 (length of terminal leaflet) suffered from the same difficulties as character 5; for the reasons given under that character, suffice it to say that *P. multisecta* had the longest terminal leaflets by far, and there was no apparent pattern to the variation, much of which was, as before, within plants.

Character 8 (length of a leaflet of a lower pair) was consistently measured, as in character 6; nonetheless, except that *P. multisecta* had longer leaflets, there was no apparent pattern to the variation.

Character 9 was scored as a subjective estimate of the density and coverage of straight hair on the lower leaflet surfaces. The populations of *P. breweri* and the population of *P. nelsoniana* were completely homogeneous for this character, with *P. breweri* having no straight hair and *P. nelsoniana* having sparse straight hair only. The variation was medium-sized to large in four populations: in *P. multisecta* and the Moffat Co. population of *P. ovina*, which had fairly hairy leaflets, much of the variation was within plants; in *P. ovina* from near Rawlins and *P. decurrens*, which had hairy and sparsely-hairy leaflets respectively, the variation was significantly among plants. The variation in straight hair in *P. plattensis* was small and largely within plants.

Character 10 was scored similarly to character 9, but for curly (crinkly) hair. The populations of *P. plattensis, P. nelsoniana,* and *P. multisecta* were completely homogeneous for this character, with no curly hair in any of them. The greatest amount of curly hair was found in the two populations of *P. breweri*, with less in var. *bruceae*. There was some curly hair in populations of *P. ovina* except that of *P. nelsoniana*; in these, the variation was largely among plants. Only in the population from near Rawlins was the variation largely within plants, and there was found the greatest variation in this character.

Character 11 was a measure of the relative length of teeth (see discussion above for an explanation of how this was measured). Although this character was significantly variable among populations, for no population was it significantly variable among plants; the means were smallest for *P. breweri* var. *bruceae* and *P. nelsoniana*, but ranged more or less continuously from there, with no apparent taxonomic meaning.

The general interpretation of character 12 (width/length ratio of the terminal tooth) was that there was no apparent meaning in the pattern of variation.

Character 13 (length of stem) varied significantly among plants within most of the populations; only in the two populations of *P. plattensis* and the one of *P. ovina* var. *decurrens* was the variation largely within plants. The variation in this character was the greatest in the *P. plattensis* populations, which shows a pattern similar to that of previously discussed characters. The stems were smallest in the *P. nelsoniana* and Rawlins populations, which are both plants of sites characterized by prostrate, matted growth forms, alpine tundra and windswept limestone benches, respectively. The stems are the longest in the two populations of *P. breweri*.

Character 14 (length of midstem stipule) showed significant among-plant variation only in the two populations of *P. breweri* and the Rawlins population of *P. ovina*; the *P. ovina* population from Moffat Co. had a very large coefficient of variation, much of it within plants. The means showed a wide range; in order to test the significance of differences in these means, a SNK test was performed on this character, with results shown in Table 8; frequency distributions for four of the populations are shown in Fig. 2. Population 1, *P. breweri* var. *bruceae*, had a significantly larger stipule than any other population, although the other *P. breweri* population was the next largest. The other populations were roughly divided into three groups: one, *P. nelsoniana* and the Rawlins population, with the smallest stipules; two, *P. multisecta*, the Moffat Co. population, and *P. decurrens*, with medium-sized stipules; and three, *P. plattensis, P. breweri*, and the Park Co., Wyoming, population of *P. ovina*, with medium-large stipules. This character appears to have some value in distinguishing populations, especially into rough groups or in the case of large stipules.

Character 15 (width of the same stipule as in character 14) showed a similar pattern of variation as the previous character, although on a smaller scale; this situation will be discussed in the section on correlation. The coefficients of variation were very different from one population to another, with the Park Co., Colorado, population of *P. plattensis* being almost invariant, and the Albany Co. population of the same species highly variable, both largely within plants.

Character 16 (pedicel angle) was not significantly variable among plants within any population; the means ranged uniformly, with no apparent trends. This character was fairly difficult to score, mainly because of the difficulty of choosing flowers in the same phenological stage for all plants. Another problem was how to measure angle for a curved pedicel.

Character 17 (number of flowers) showed large to very large coefficients of variation, yet in only one population, *P. breweri* var. *bruceae*, was this variation among plants. The Park Co. population of

TABLE 8. Results of SNK test for homogeneity of means of the 10 populations of *Potentilla* sect. Multijugae, for character 14 (stipule length).

	Population									
	5	3	6	10	9	4	7	2	8	1
Variance	1.4656	1.2857	3.9666	1.4822	70.225	4.3216	2.7585	5.8571	3.5210	11.279
Sample size	39	7	38	23	14	19	26	15	37	36
Mean	5.462	6.429	7.921	8.130	9.071	10.895	11.962	12.000	12.081	14.917
	———	———				———	———	———	———	
		———	———	———	———					
					———	———	———	———		

A line drawn under a set of population means indicates that the range included was found to be not significantly different at 1%

P. plattensis had the greatest number of flowers, differering sharply from all the others.

Character 18 (length of the calyx, including lobes) was one of the most reliable, uniform characters within populations, as shown by the small coefficients of variation; the populations of *P. breweri* had the largest flowers, with those of *P. plattensis* medium-large, *P. multisecta* medium-sized, and those of *P. ovina* the smallest. The population of *P. breweri*, however, is outstanding in its large coefficient of variation, and the largest mean calyx length; this variation is largely within plants.

Character 19 (width/length ratio of a calyx lobe) varies principally within plants, with no clear trend in mean values. The *P. multisecta* population was the only one in which variation was significant among plants.

Character 20 (style length) is one of great interest in the taxonomy of *Potentilla*, used by some monographers in section delimitation. It is interesting that in these 10 populations, this was the most uniform character within populations, as shown by the uniformly low values for coefficient of variation. However, the significance of the analysis of variance showed no pattern related to taxonomy. A SNK test was performed as before on this character, with the results shown in Table 9; frequency distributions of four populations are shown in Fig. 2. The population of *P. breweri* var. *bruceae* is significantly different from all other populations (as shown before for stipule length). The others are divided into two rough groups: one, *P. plattensis, P. ovina* var. *decurrens*, and the Rawlins population; two, *P. multisecta, P. breweri*, and the Moffat Co. and Park Co. populations of *P. ovina*. Another

TABLE 9. Results of SNK test for homogeneity of means of the 10 populations of *Potentilla* sect. Multijugae, for character 20 (length of style).

	Population									
	10	3	2	4	5	7	9	8	6	1
Variance	1.8142	0.5306	0.2667	1.7310	2.5155	2.8738	1.9176	8.8078	3.1437	11.257
Sample size	23	7	15	19	39	26	14	37	38	36
Mean	18.217	18.429	18.533	19.789	21.103	23.077	24.929	25.432	25.789	29.333

A line drawn under a set of population means indicates that the range included was found to be not significantly different at 1%

non-significance group links the populations of *P. plattensis, P. nelsoniana, P. breweri*, and the Rawlins and Moffat Co. populations.

In general, these characters vary significantly among populations; much of this variation is within plants, especially in *P. plattensis*. Only two characters, length of calyx and style length, showed significant variation among populations and small variation within populations. Five characters, per cent of rachis occupied, densities of straight and curly hair, relative length of teeth, and width/length ratios of terminal teeth and calyx lobes, were not suitable for full statistical analysis, since they either were ratios or represented non-linear subjective decisions; of these, the width/length ratios were the most doubtful statistically, and had been used only subjectively in previous taxonomic treatments. The remaining leaf characters tended to have medium-sized coefficients of variation, but the stem characters had more widely different CVs from population to population.

Correlation of characters within populations

Fig. 3 shows the correlation coefficients calculated between each pair of characters used in the study, for all measurements made on all populations (the total sample). This figure serves as a guide to the other figures, since only in this one do the names of the characters appear in full. In these figures, characters of the leaves (lower left) and those of the stems and flowers (upper left) are shown separately, since in these plants, basal leaves and stems are not paired. One set of stem-character measurements and one set of leaf-character measurements have been grouped together for ease of input to the computer, so pairing a leaf-character with a stem-character in the same

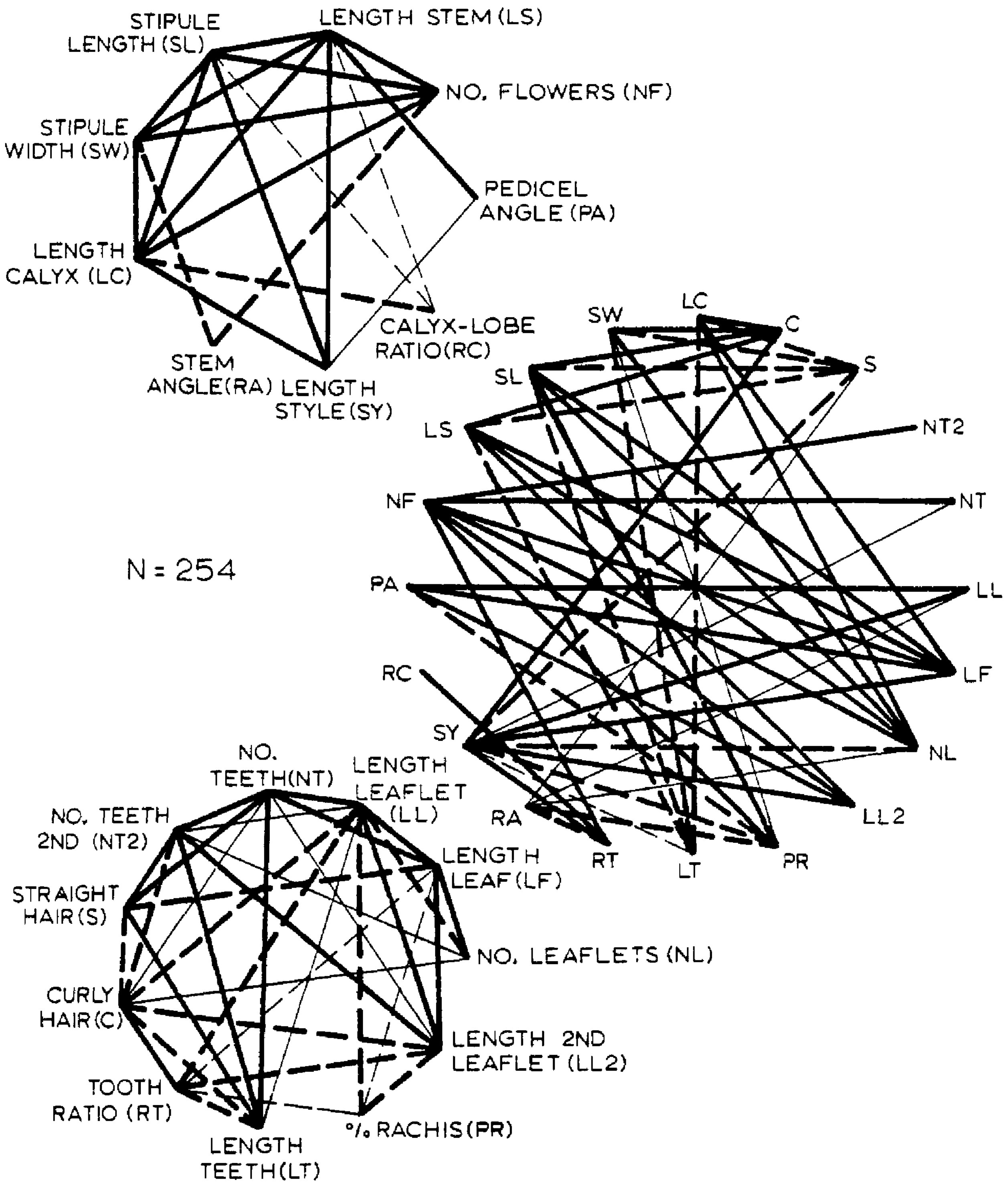


FIG. 3. Graphical representation of three significant groups of correlation coefficients, for total population sample. Upper left, for stem characters; lower left, for leaf characters; right, between stem and leaf characters. Shown are: positive correlations significant at 1% or better (thick solid lines); positive at 5% or better (thin solid lines); the corresponding negative correlations are shown as dashed lines. The code symbols shown in parenthesis are those in Tables 4-6 and the following figures.

item may not be justified, and may result in aberrant results. Nonetheless, these correlation coefficients between stem-characters and leaf-characters are shown to the right in each diagram, but will be relied on less heavily. The populations will be discussed in turn.

Population 1 (Fig. 4) (*Potentilla breweri* var. *bruceae* from Elko Co., Nevada) shows a similar pattern in correlation of stem-characters as the total sample; calyx length, stipule width, stipule length, stem length, and number of flowers are all positively intercorrelated. A notable addition is this population's high positive correlation between stem angle and length of style. In its leaves, number of teeth, length of leaflet and length of leaf are positively intercorrelated as in the total sample, and the number of teeth and the length of the second leaflet are correlated, as well as leaflet length and per cent rachis occupied. Additionally, number of leaflets and per cent rachis are correlated, which is expected, since in general the more leaflets there are, the more rachis is taken up with them. However, the longer leaflets have less curly hair (which is the only hair this population has), which indicates the possibility of the leaflets losing part of their pubescence in age. Number of teeth and length of the terminal leaflet are much more correlated with stem characters in this population, and number of flowers more correlated with leaf characters.

Population 2 (Fig. 5) (*Potentilla plattensis* from Albany Co., Wyoming) is not well-correlated among its characters. Stem length, number of flowers, and stipule width are positively intercorrelated; the interesting addition is that the longer stems have shorter calyces, whereas they are longer in the total sample and in most other populations. The leaves have number of teeth, length of the terminal leaflet, and

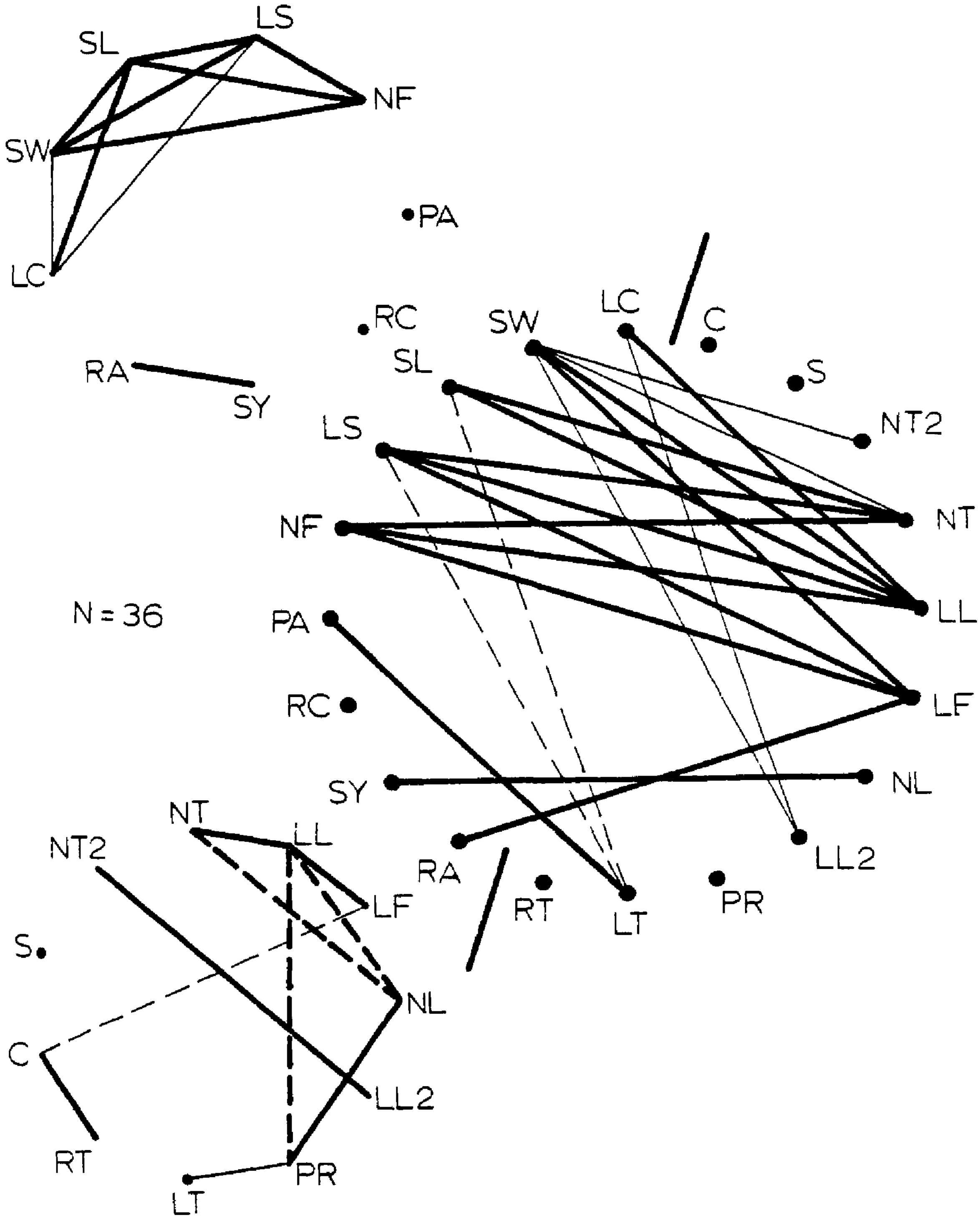


FIG. 4. Graphical representation of three significant groups of correlation coefficients, for population 1. Explanation of symbols in Fig. 3.

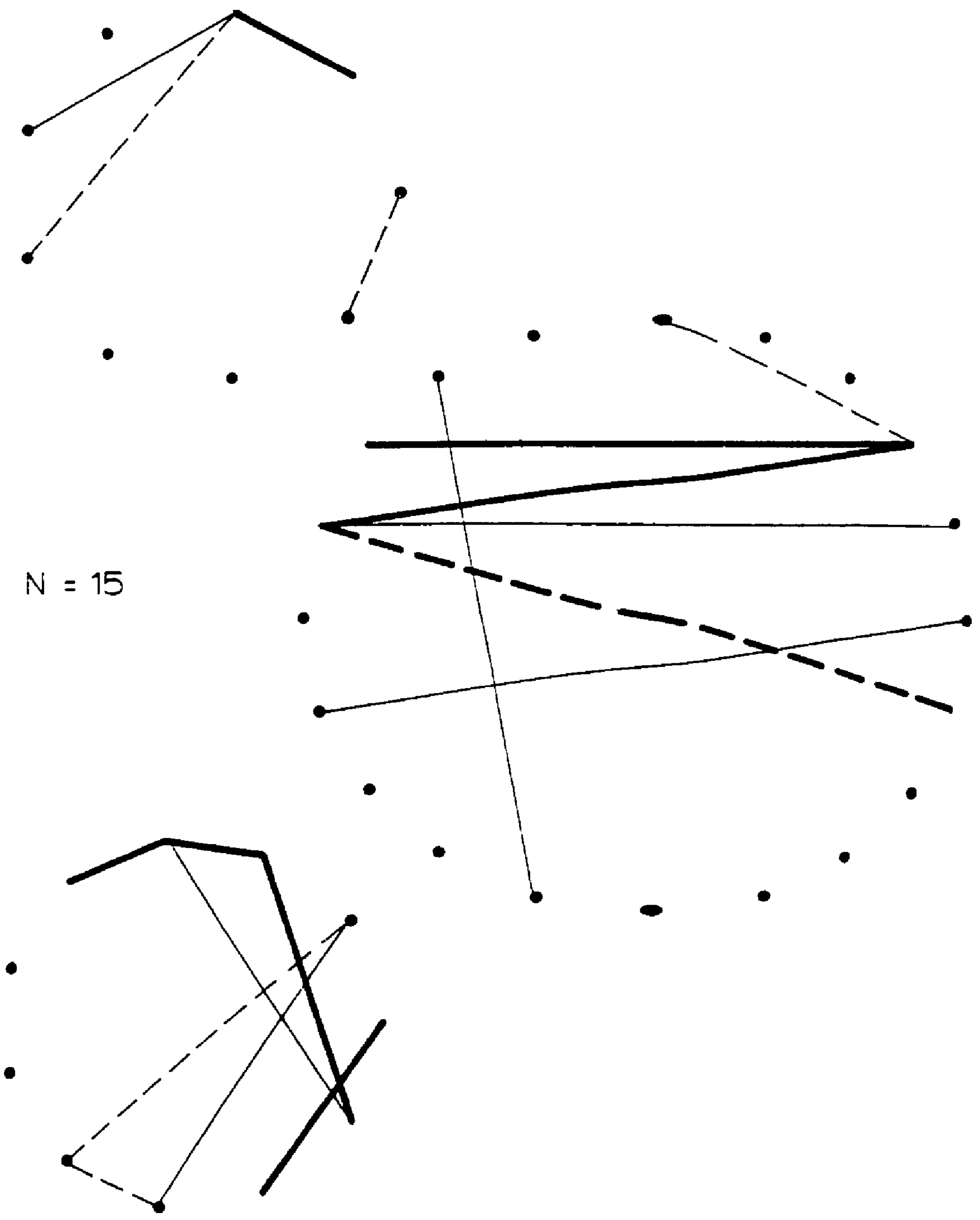


FIG. 5. Graphical representation of three significant groups of correlation coefficients, for population 2. Explanation of symbols in Fig. 3.

length of the second leaflet all positively correlated; however, the longer leaves have longer teeth, a departure from the total sample and from most populations. In this population, as in the previous one, leaves with more leaflets have a longer rachis. Among stem-leaf correlations, the most striking is a negative one between leaf length and the number of flowers. A larger calyx apparently means a shorter stem, and fewer teeth in the second leaflet.

Population 3 (Fig. 6) (topotype of *P. nelsoniana* from Albany Co., Wyoming) has a very different pattern of correlations. Here the longer stems are more erect, and those with more flowers have shorter styles. Those with longer second leaflets have longer terminal leaflets and longer rachis, but less of the rachis is occupied and the teeth are narrower. Those that have more of the rachis occupied have broader teeth; and those that have longer leaves have more leaflets. None of the stem-leaf correlations seem outstandingly different from the total sample.

Population 4 (Fig. 7) (*Potentilla plattensis* from Park Co., Colorado) is more like the total sample in its stem correlations than it is like the other *P. plattensis* (no. 2). Number of flowers, length of stem, stipule length and width are all positively intercorrelated, as in the total sample. In the leaves, per cent of rachis, length of the leaflets, number of leaflets, length of the leaf, and number of teeth in the terminal leaflet are all positively intercorrelated. Here, those with longer teeth occupy more of the rachis. There is almost total absence of stem-leaf correlations: only NC--NL and RC--LL are positively correlated.

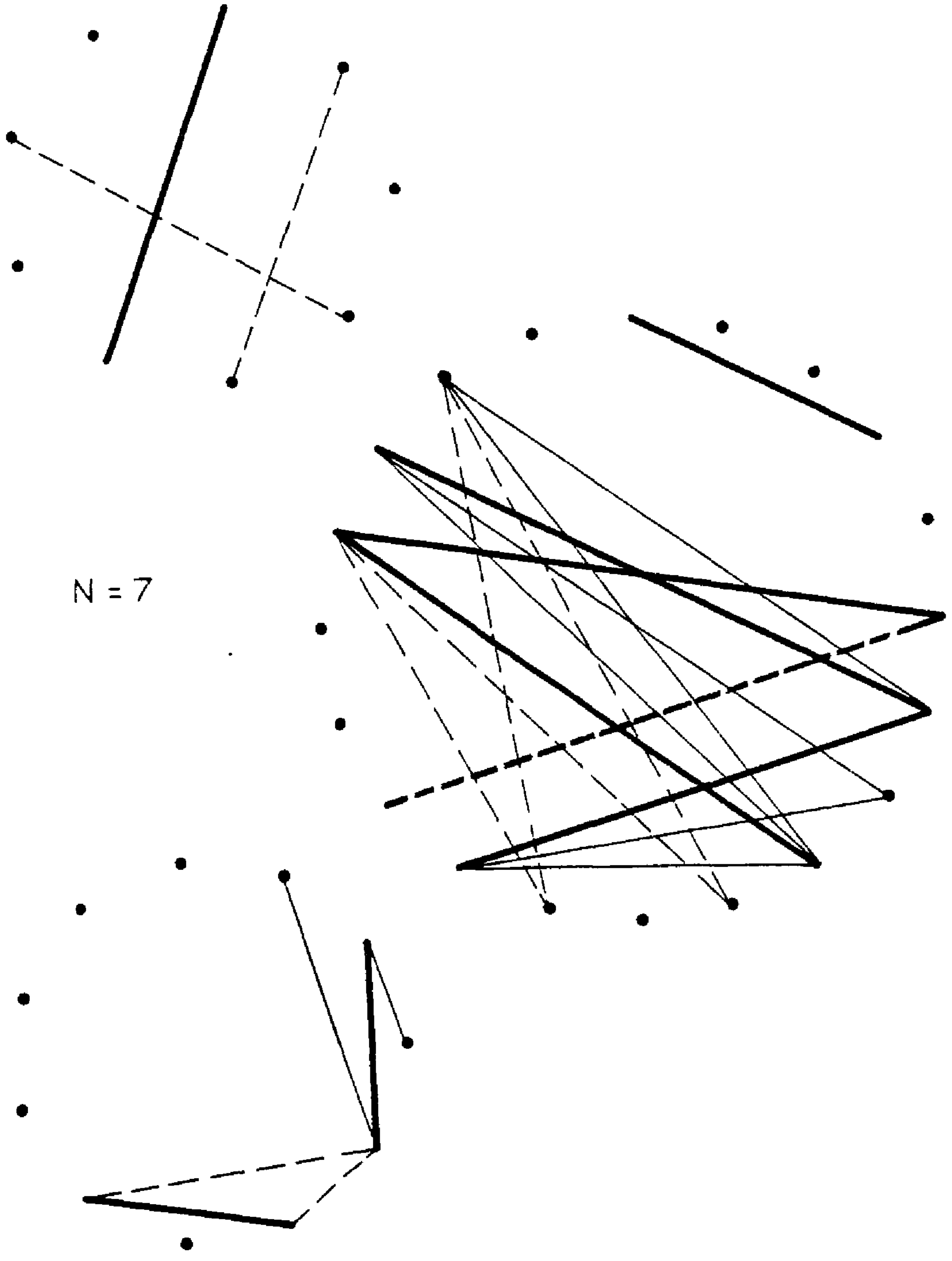


FIG. 6. Graphical representation of three significant groups of correlation coefficients, for population 3. Explanation of symbols in Fig. 3.

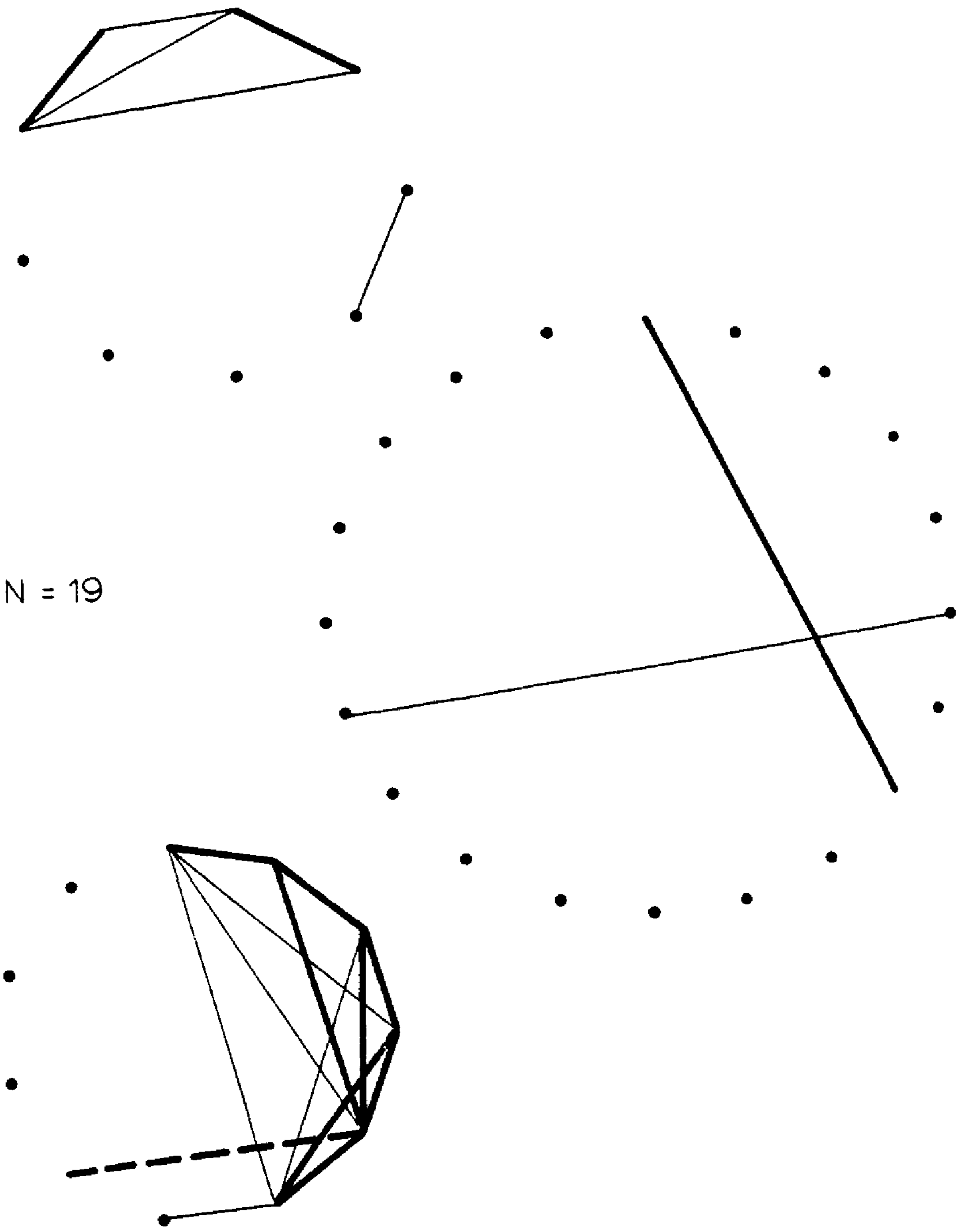


FIG. 7. Graphical representation of three significant groups of correlation coefficients, for population 4. Explanation of symbols in Fig. 3.

Population 5 (Fig. 8) (*P. ovina* from near Rawlins, Wyoming) has the usual positive intercorrelation among number of flowers, length of stem, stipule length and width that characterize most populations and the total sample; in this case, pedicel angle has been added to the group, and the longer calyces have wider lobes, rather than narrower in the total sample. The leaf-correlations come in two separate groups: one, strong positive intercorrelation among the number of teeth in both leaflets and the length of both leaflets; and two, positive intercorrelation among leaf length, number of leaflets, and per cent rachis, with negative correlation between number of leaflets and length of teeth. There are no novelties in the stem-leaf correlations.

Population 6 (Fig. 9) (*Potentilla multisecta* from the Deep Creek Range) starts with the usual positive intercorrelation among number of flowers, length of stem, stipule length and width, and adds to it a negative correlation with the calyx-lobe ratio. In other words, those with longer stems have more flowers, bigger stipules, broader calyx-lobes, and are more decumbent in habit. Also those with longer calyces have a more recurved pedicel, which probably reflects the fact that in this species, the pedicels recurve as the flower matures its fruit. The leaf correlations begin with a typical pattern of positive intercorrelations among number of teeth in both leaflets, length of leaflets, and length of leaf; however, in this population these are negatively correlated with density of hair (this species has no curly hair). Those with more teeth have narrower teeth, which might be expected, and longer teeth. The tooth ratio, which was negatively correlated to measured characters of the leaflets and number of teeth, is positively correlated with the cluster of stem characters such as stem length, stipule length and

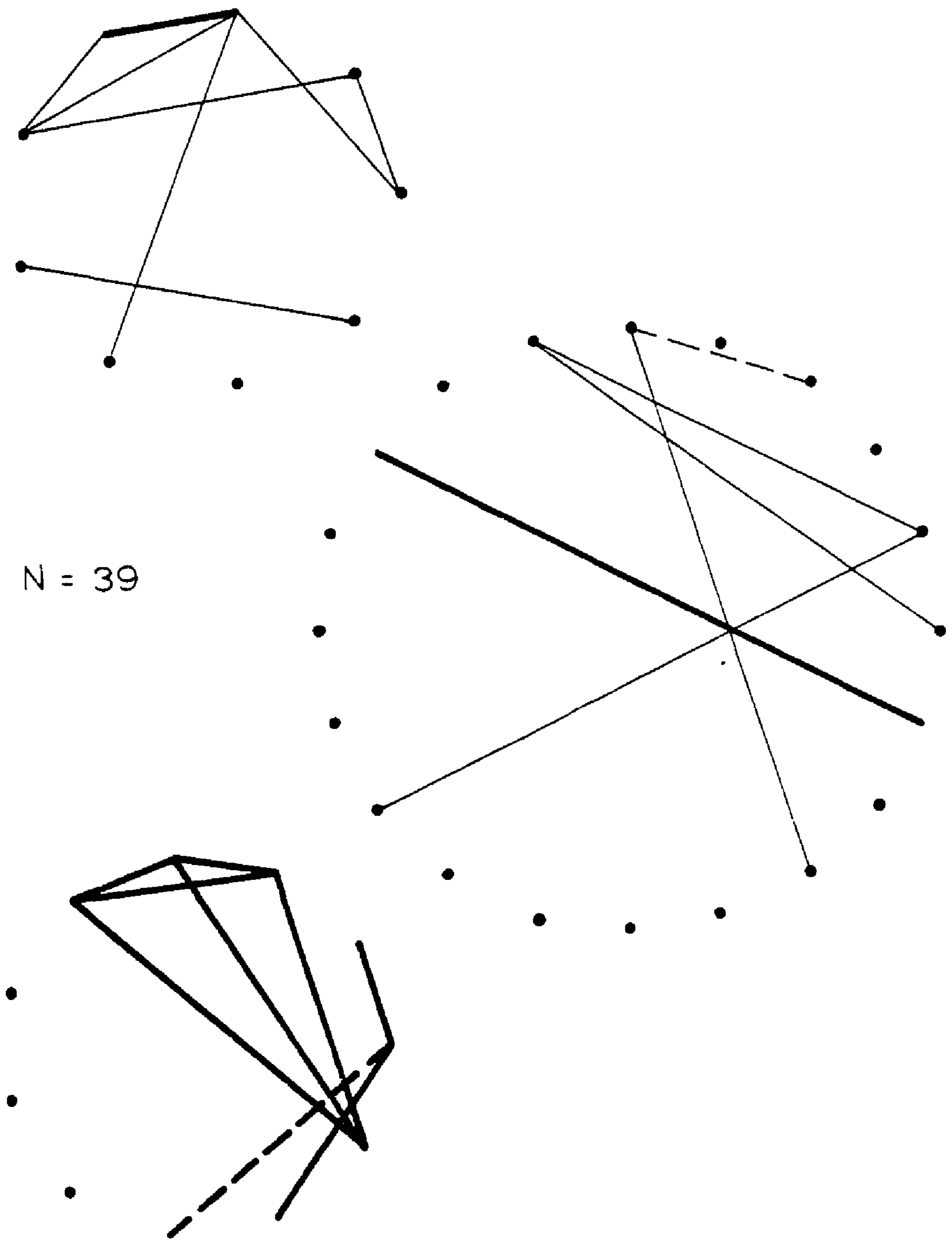


FIG. 8. Graphical representation of three significant groups of correlation coefficients, for population 5. Explanation of symbols in Fig. 3.

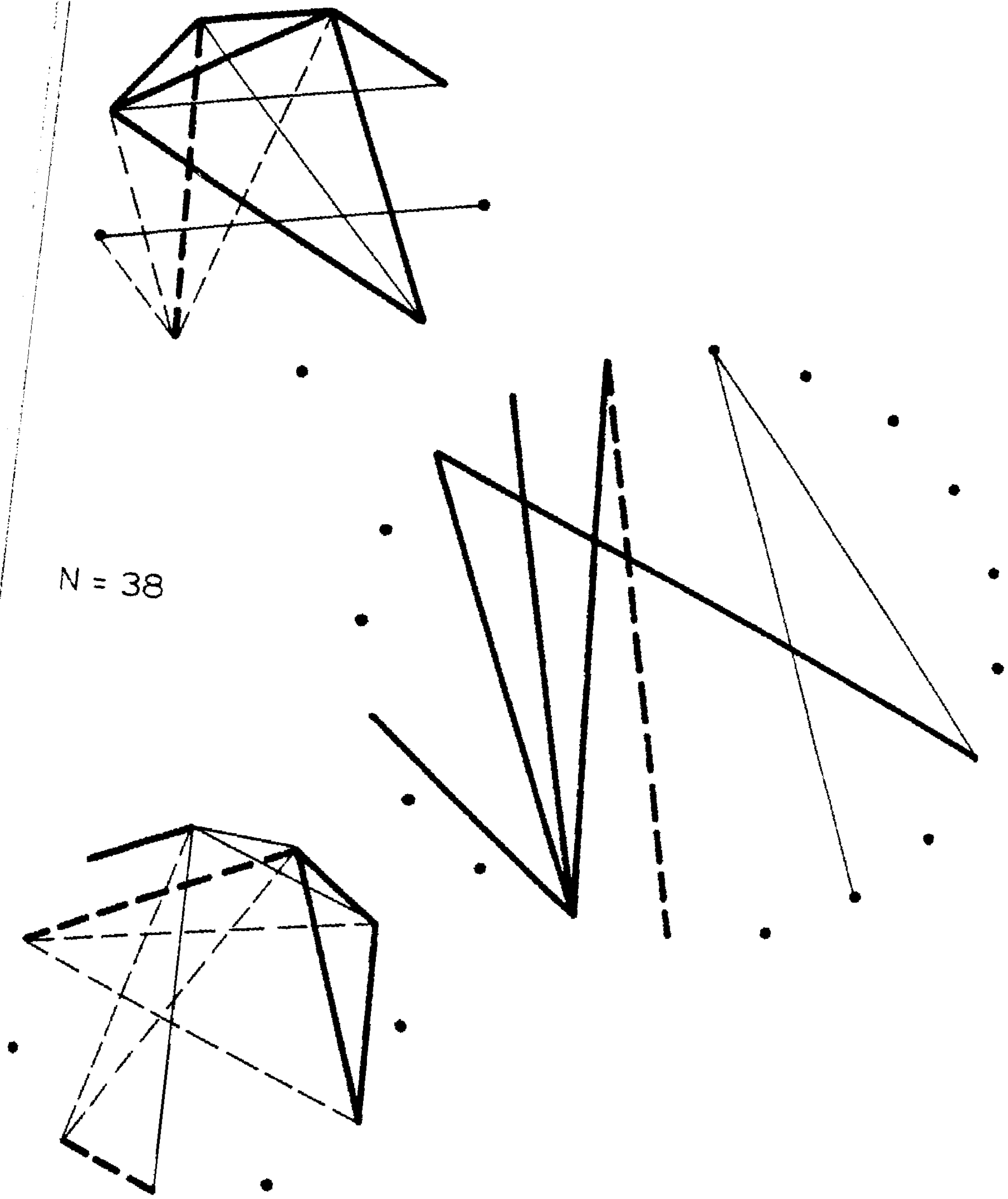


FIG. 9. Graphical representation of three significant groups of correlation coefficients, for population 6. Explanation of symbols in Fig. 3.

and width; these are in turn negatively correlated with the length of the teeth, thus confirming what we saw in the leaf-correlation diagram.

Population 7 (Fig. 10) (*Potentilla breweri* from the Ruby Range) has a few of the positive correlations among measured characters of the stem; those with longer stipules have shorter styles, in contradiction with the total sample. Those with a great proportion of the rachis occupied have a larger number of leaflets and shorter secondary leaflets, as in the total sample, but longer terminal leaflets. This may reflect the unique nature of the terminal leaflet in this species; perhaps it tends to become more dissected, and hence longer, since the dissection is taking place acropetally (Zhitkov 1973). The leaf-stem correlations show few surprises.

Population 8 (Fig. 11) (*Potentilla ovina* from Clay Butte, Wyoming) shows a variation on the familiar pattern of leaf correlations; here, as in the previous *P. ovina* population, the larger flowers have broader calyx-lobes. In the leaves, there are a few familiar correlations, for example per cent rachis is positively correlated with number of leaflets and negatively correlated with length of leaf. But here, those with more teeth have more leaflets and greater amount of tomentum, and the teeth are shorter, which contradicts the total sample and previously discussed populations. The ones with denser tomentum have shorter calyces and shorter styles as well.

Population 9 (Fig. 12) (*Potentilla ovina* from Moffat Co., Colorado) has few correlations in stem characters. The only unusual feature is that, those with longer calyces have more recurved pedicels, as in the previously discussed population of *P. multisecta*. The leaves also have

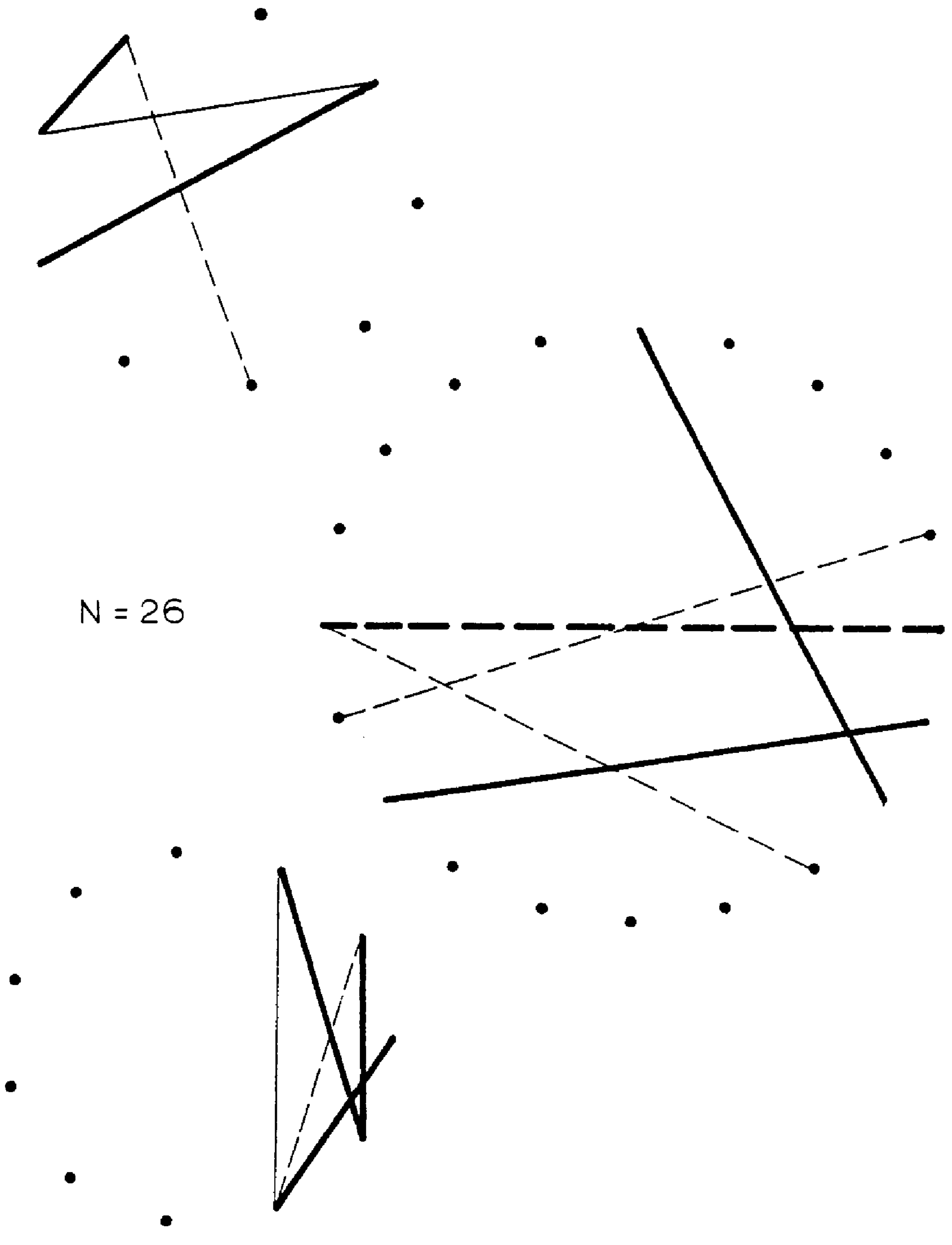


FIG. 10. Graphical representation of three significant groups of correlation coefficients, for population 7. Explanation of symbols in Fig. 3.

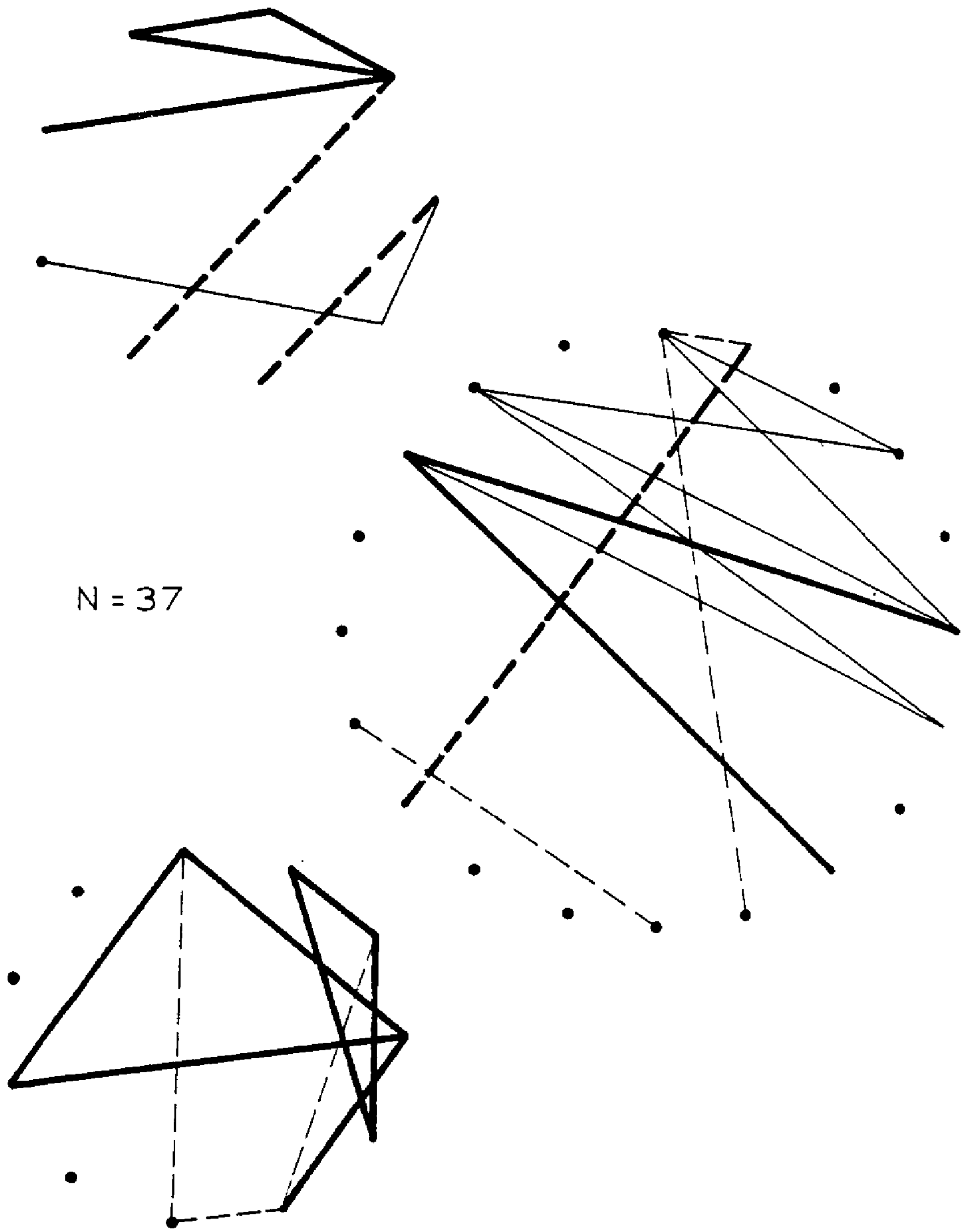


FIG. 11. Graphical representation of three significant groups of correlation coefficients, for population 8. Explanation of symbols in Fig. 3.

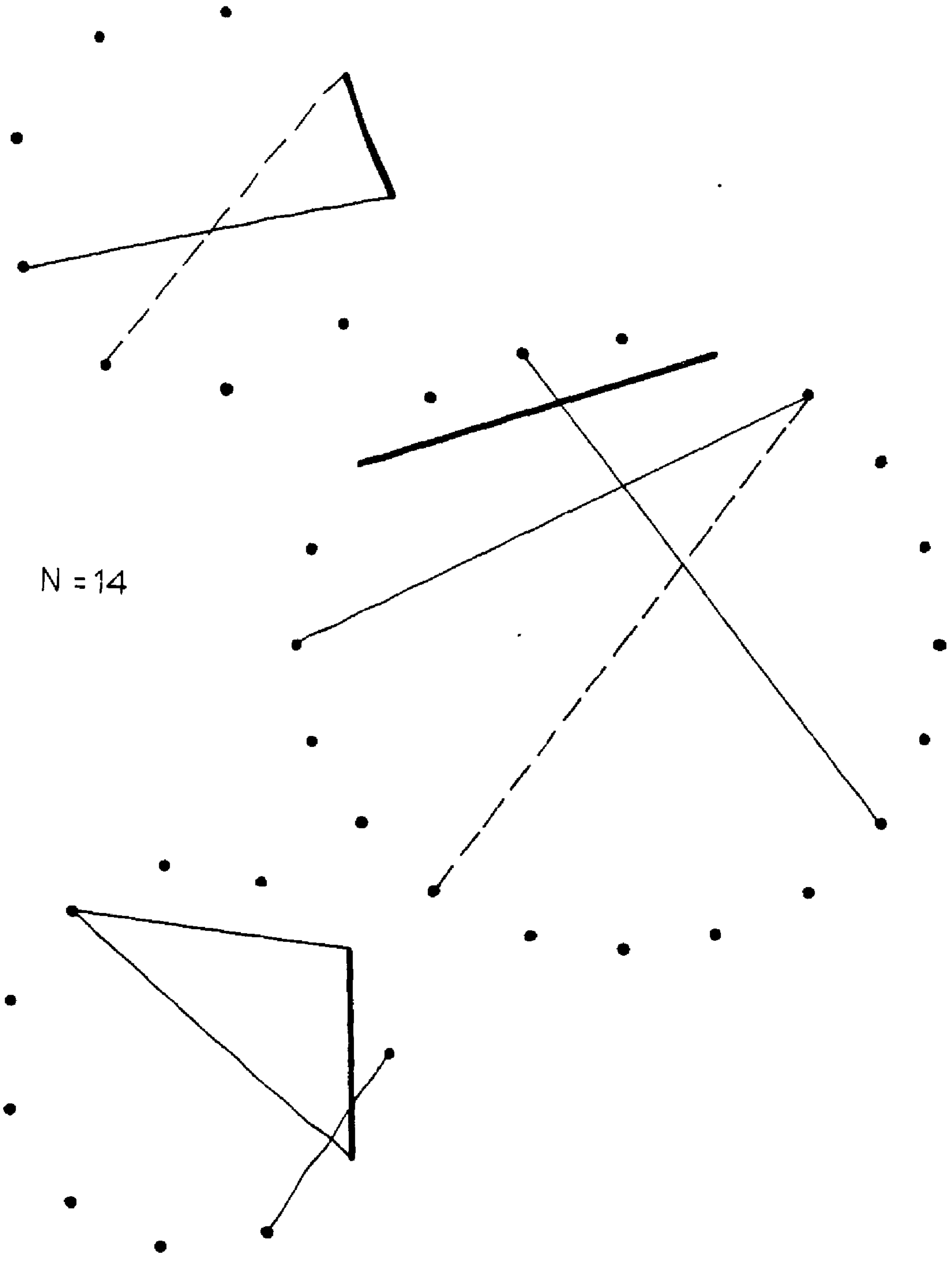


FIG. 12. Graphical representation of three significant groups of correlation coefficients, for population 9. Explanation of symbols in Fig. 3.

few correlations, which includes the familiar one between per cent rachis and number of leaflets.

Population 10 (Fig. 13) (*Potentilla ovina* var. *decurrens* from Log Hollow, Utah) also has few correlations; those with more decumbent stems have longer styles, which is unusual. The density of curly hair (tomentum) is here correlated with number of leaflets and number of teeth, which was observed in a previously discussed population of *P. ovina* (no. 8); here in addition, density of curly hair is also positively correlated with number of teeth in the second leaflet, and negatively with length of the terminal leaflet. Notable among the stem-leaf correlations is that between density of curly hair and several of the size characters of the stem, such as stipule size and length of the calyx.

Looking at the two populations of *P. breweri* (populations 1 and 7, from different habitats at the same site), it can be seen that very few correlations have been found significant in both of them. The only exceptions are: stipule length and width (positive), stipule width and number of flowers (positive), number of leaflets and per cent rachis (positive). Length of the terminal leaflet and per cent rachis are strongly negatively correlated in population 1, but weakly positively so in population 7; in general, population 1 is much more intercorrelated (usually positively) and has more of the positive intercorrelations among size characters, but more negative correlations among leaf characters than average. These populations are the only ones in this study with predominantly curly hair, but only in population 1 was this character correlated with anything, possibly due to loss of part of the pubescence in age. Both populations have significantly longer stems

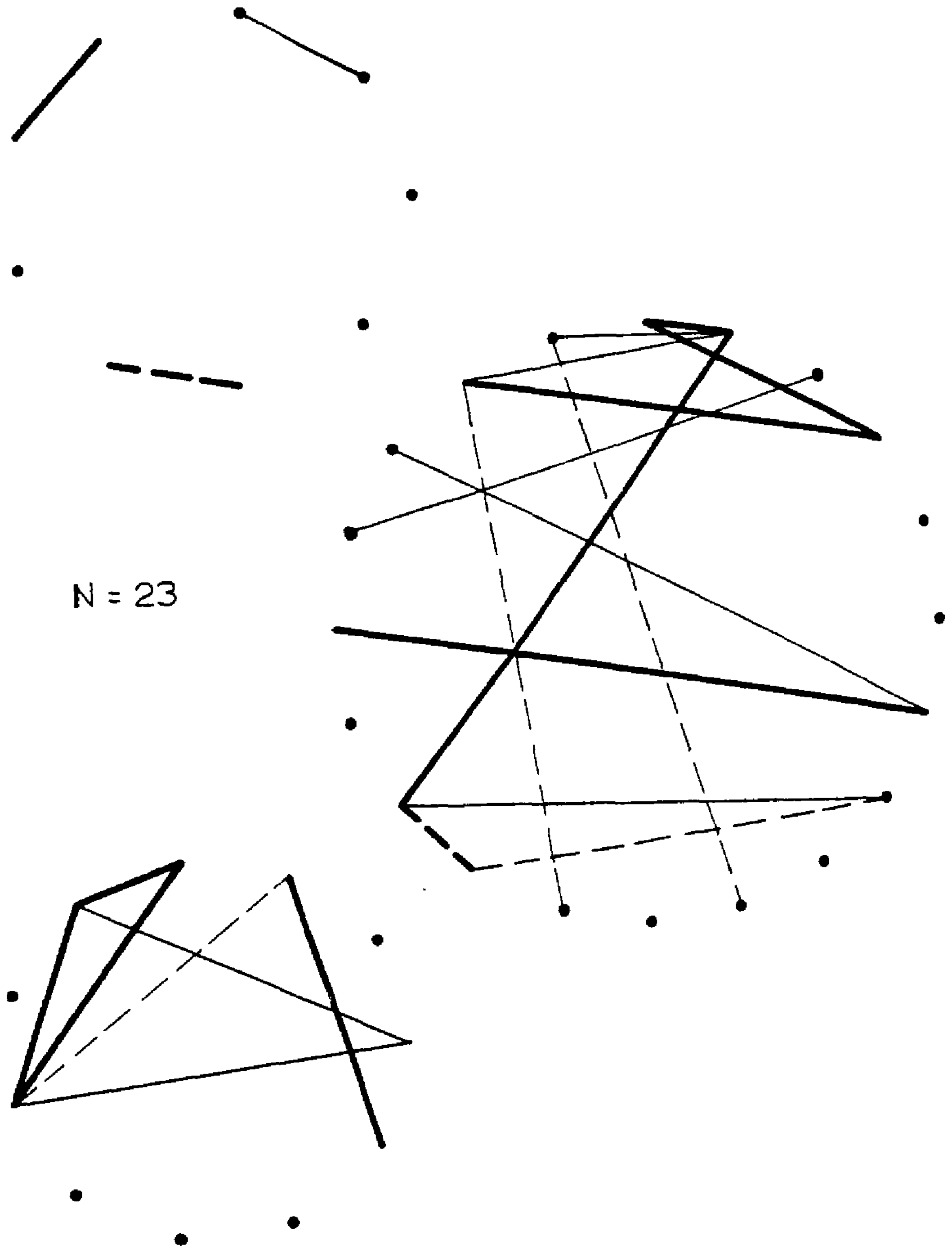


FIG. 13. Graphical representation of three significant groups of correlation coefficients, for population 10. Explanation of symbols in Fig. 3.

than other populations, which character has a large proportion of its variation among plants within these two populations; however, only in population 1 is this character correlated with other stem characters, notwithstanding that it is positively correlated there with several size characters of the leaf, and negatively with length of teeth. Population 1 had significantly longer stipules than in any other population, and significantly longer styles (Tables 8 and 9). Population 7 is not sharply different from population 1 in the means of its characters, but it is quite different in its correlations among them.

The two populations of *Potentilla plattensis* (populations 2 and 4) represent the two different growth habits of this species, as mentioned by Rydberg (1898) and Wolf (1908). The two populations share a number of correlations, especially in size characters of the leaves. Population 2 is not as highly correlated as population 4; both populations have positive correlations between number of teeth and length of the leaflets; among number of flowers, stem length, and stipule width; and between per cent rachis and number of leaflets. Both populations have negative correlations between width of the teeth and size characters such as leaflet length. In population 2, the more recurved pedicels bear flowers with narrower calyx-lobes, but in population 4 they are broader. Population 2 has many more correlations between stems and leaves than the few in population 4. It is interesting that, even though these two populations have the greatest density of straight hair in the study, no correlations were found in either population involving the density of straight hair. These two populations are more alike in mean values of their characters, and in patterns of correlation, than the two populations of *P. breweri* are; the means are not significantly different for number of teeth in the second leaflet (Table 7), stipule length (Table 8), and style length (Table 9); number of teeth was probably the best of these characters in separating these two populations from the others. Population 4 had more prostrate stems with more flowers than population 2. However, as noted above in the discussion of analysis of variance, both of these populations were outstanding in the study in that all characters had most of their variation within plants rather than among plants, the sole exception being number of leaflets in population 2.

The two populations of *Potentilla ovina* var. *decurrens* (populations 3 and 10, including *P. nelsoniana*) shared few correlations, perhaps due to the small population size in population 3. These two populations are sharply different in stem characters; neither population is well-correlated, but perhaps population 10 has more of the typical correlations. In leaf characters, the two populations share a positive correlation between length of the terminal leaflet and length of the second leaflet; here, in contrast to the picture in stem characters, population 10 is the one that departs the most from the norm. Most of the correlations of population 10 are concerned with an intercorrelation among number of teeth in the leaflets and density of curly hair, negatively correlated (as before) with length of leaflet and positively with number of leaflets. In distinction with this, is the observation that in population 3 most of the correlations are familiar ones, centered around the length of the second leaflet, positively correlated with leaf length and number of leaflets, and negatively with width of teeth and per cent rachis. Population 3, *P. nelsoniana*, has no curly hair; otherwise the two populations are not distinctly different in their mean values for any character. Both populations fall into the same non-significance group in their means for number of teeth, stipule length, and style length (Tables 7,8,9). Possibly the best of these three characters is number of teeth, in which these two populations are grouped with those of *P. breweri*, from which *P. ovina* var. *decurrens* can readily be separated on other characters, such as pubescence, dissection of terminal leaflet, or stem length.

There are three populations of *Potentilla ovina* var. *ovina* (populations 5,8,9). Of these, population 9 is quite different from the other two in pattern of correlation; all three share a positive correlation of number of leaflets and per cent rachis, which is shared by most other populations. Population 9 is perhaps closer in this regard to population 8, with which it shares positive correlations of leaf length and number of teeth and length of the second leaflet, and negative correlation between stem angle and number of flowers. Population 9 shares with population 5 positive correlations between number of flowers and pedicel angle, and between per cent rachis and number of leaflets. Population 9, as mentioned before, has the positive correlation between pedicel angle and length of calyx that is more characteristic of *P. multisecta*; population 9 is somewhat difficult to place taxonomically, and the relationships to populations 5 and 8 underscore this difficulty. Population 5 and 8, on the other hand, are very similar in their patterns of stem correlations, but population 8 has negative correlations between style length and pedicel angle, and between stem angle and number of flowers. Population 5 is not significantly different from population 9 in the mean values for style length, but does have a significantly smaller style than population 8 (Table 9); the three populations are not significantly different in number of teeth, but are best separated from one another by stipule length, which does not include any two of these populations in a non-significance group (Tables 7 and 8). Populations 5 and 8 both have positive intercorrelations among the leaf size characters; but population 5 emphasizes in addition a positive intercorrelation among the characters involved with number of teeth, and population 8 emphasizes density of curly hair. Population 8 is outstanding among these three in the larger means for many of the size characters of stem and leaf, such as leaf length, per cent rachis, number of leaflets, length of second leaflet, length and width of stipule, and length of calyx. Population 8 also has more straight hair, whereas population 9 has more curly. The three populations of this species are notable in this study as being the only group in which most characters are variable significantly among plants within each population; this is true generally for populations 5 and 8, but population 9 stands out once again in being relatively highly variable within plants.

The remaining population, *P. multisecta* (no. 6), has already been discussed, but in addition it can be noted that it is one of the highest correlated populations in the study. Much of this correlation is of a familiar sort that is repeated in the total sample, the exception being the positive correlation between pedicel angle and length of calyx, discussed above.

Information-theoretical character analysis

Table 10 shows the value of SAMRAT (Bisby's "information contribution") for the 22 characters (Table 11 and Fig. 14) used in the classification

TABLE 10. Values of SAMRAT ("information contribution" of Bisby 1970) for each of the 22 characters of *Potentilla* sect. Multijugae studied, in descending order of SAMRAT.

Character number	SAMRAT	Group (see text)
11	3.728	I
4	3.623	
12	3.307	
6	3.269	
13	2.741	
7	2.619	
8	2.575	II
2	2.562	
16	2.560	
14	2.560	
15	2.552	
21	2.339	
3	2.290	
9	2.210	
5	2.186	
10	2.173	III
18	2.079	
19	2.039	
17	2.037	
22	1.871	
1	1.844	
20	1.652	

TABLE 11. Characters used in classification of *Potentilla* sect. Multijugae.

Character number and description	States
1. Stem-ground angle	1 0° or less
	2 5-20°
	3 25-45°
	4 45-60°
	5 65° or greater
2. Length of leaf rachis	1-M x 1 cm[a]
3. Per cent rachis <u>not</u> occupied	1-A x 10%[a]
4. Petiole pubescence	1 strigose/-[b]
	2 strigose/tomentose
	3 sericeous/-
	4 sericeous/tomentose, or hair intermediate between the two types
	5 -/tomentose sparsely
	6 -/tomentose densely covering
	7 puberulent
	8 glabrous
5. Number of leaflets	1 3
	2 5-6
	3 7-8
	4 9-10
	5 11-12
	6 13-14
	7 15-16
	8 17-18
	9 19 or more
6. Terminal leaflet division	See Fig. 14
7. Mid-rachis leaflet division	See Fig. 14
8. Mid-rachis leaflet length	1-a x 5 mm[a]
9. Total number of teeth in mid-rachis leaflet	1 2-3
	2 5-6
	3 7-8
	4 9-10
	5 11-12
	6 13-14
	7 15-16
10. Depth of teeth (see Fig. 14)	1-A x 10%[a]
11. Lower leaf pubescence	As in character 4 above
12. Lower leaf tomentum density	1 none!
	2 scattered-patchy
	3 uniform but light
	4 dense but not covering
	5 densely covering

TABLE 11. (Continued).

Character number and description	States
13. Lower leaf straight hair density	As in character 12 above
14. Stem length	1-B x 5 cm[a]
15. Midstem stipule length	1-M x 1 mm[a]
16. Midstem stipule width	1-C x 1 mm[a]
17. Fruiting pedicel type	1 ascending 2 erect 3 recurved
18. Number of flowers per stem	1 1-2 2 3-5 3 6-10 4 11-15 5 16-20 6 more than 20
19. Calyx height, including lobes	1-C x 1 mm[a]
20. Style length	1 1.5-1.8 mm 2 1.8-2.1 3 2.1-2.4 4 2.4-2.7 5 2.7-3.0 6 3.0-3.3 7 3.3-3.6 8 3.6-3.9 9 3.9-4.2 A 4.2-4.5
21. Leaflets verticillate	1 none 2 some (lower) nodes 3 all nodes
22. Stipule divided	1 no 2 yes

a. shown are the range of states, and the interval between them. State numbers allowed in CHARANAL or GRAPH are 1-9, then A--; so that A = 10, B = 11, C = 12, and so on.

b. in characters 4 and 11, the slash separates the upper layer from the lower layer; a dash (-) indicates absence of pubescence in that layer.

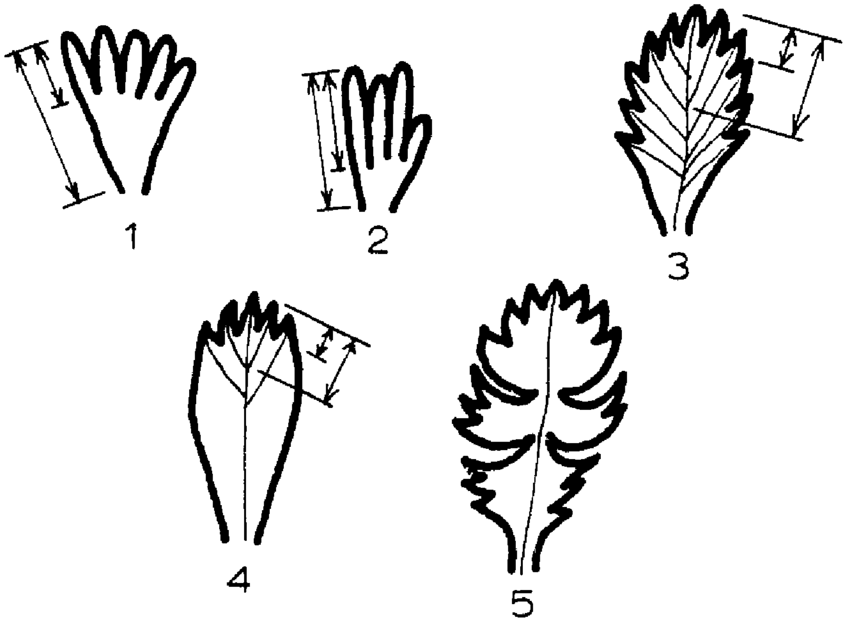


FIG. 14. The five states of characters 6 and 7, leaflet division. Depth of teeth (character 10) is measured by dividing the shorter measurement shown by the longer one. Character 10 is not coded for leaflet division type 5, since in many cases this type is only found on the terminal leaflet.

of sect. Multijugae. Fig. 15 shows some values of the information contributed between pairs of characters, selected for their high values. The quantities shown in Fig. 15 are the terms in the summation for SAMRAT (discussed in the last chapter), or

$$\frac{H_I - H_{I/J_g}}{H_I} .$$

Only the highest values for this quantity have been shown in Fig. 14.

From the figure and Table 10, one can see that the characters are divided into three rough groups, based on the amount of information held in common. Group I (characters 4,6,7,11,12,13) consists of the pubescence and leaflet-dissection characters, with large amounts of information held in common. This is partially expected, since *P. breweri* and *P. millefolia*, with distinctive leaf-dissection types, both have dense pubescence, *P. breweri* tomentose and *millefolia* strigose.

A second group, group II (characters 2,3,5,8,9,14,15,16,21) comprises the stem and stipule sizes, number of leaflets and per cent rachis occupied (the information shared between the last two confirming the results of the analysis of correlation), and toothing and relative crowding of leaflets. Characters 9 and 21 (leaflets verticillate and number of teeth) are transitional between Groups I and II.

Group III (characters 1,10,17,18,19,20) consists of characters with lesser information shared with others. Of these, characters 18 and 19 (number of flowers and calyx length) are more closely shared with Group II; character 22 (stipule divided) is partially transitional between the two groups; and character 17 (pedicel type) is weakly linked with Group I. Other characters in this group have almost no information shared with any others.

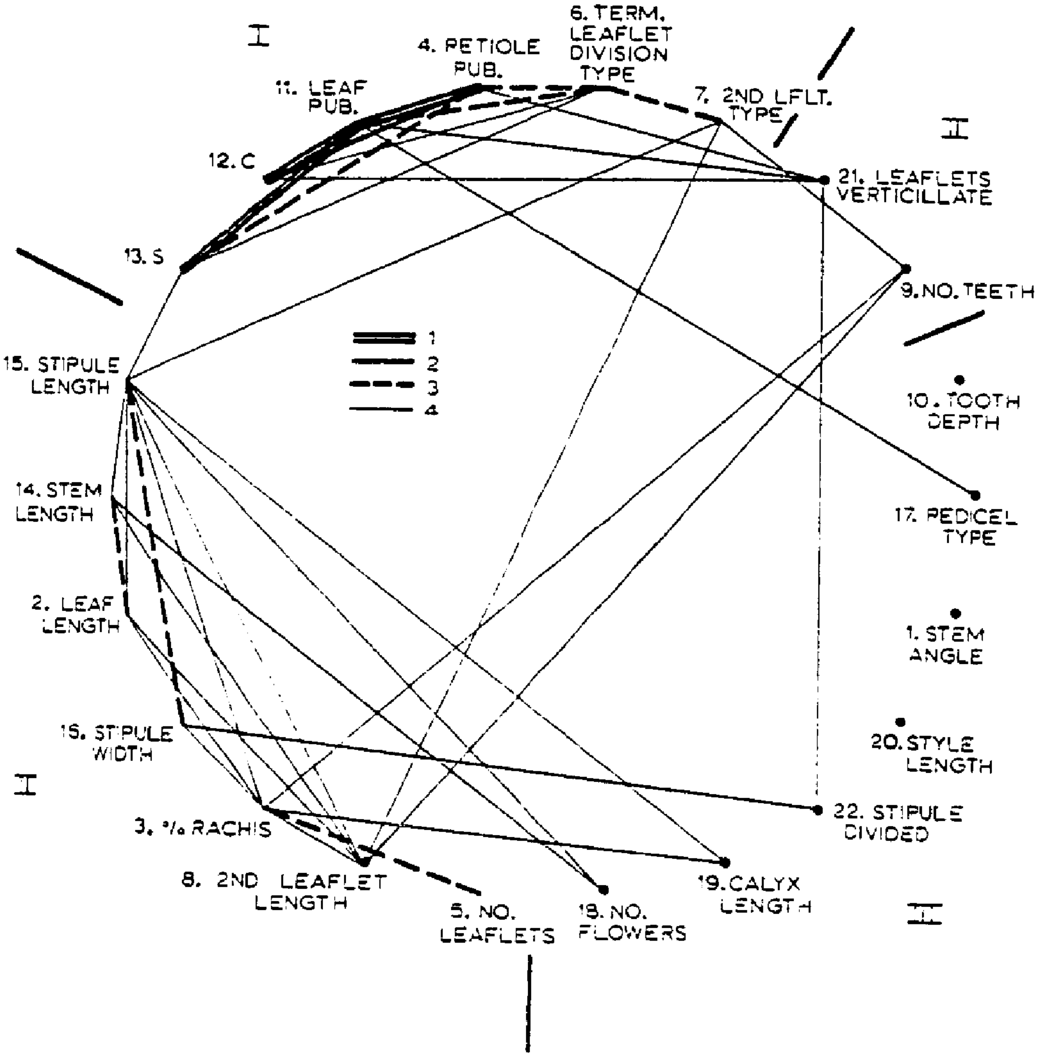


FIG. 15. Graphical representation of results from CHARANAL showing relative proportion of information in 22 characters that is shared with other characters. 1 = proportion shared is greater than 0.5; 2 = 0.4-0.5; 3 = 0.3-0.4; and 4 = 0.2-0.3. Proportions less than 0.2 are not shown. Explanation of Roman numerals in text.

All of these characters will be retained for use in the clustering procedure to follow, but the interpretation of the clustering results for classification will be tempered by these results from character analysis. Character 1, stem angle (corresponds to character 1[RA] in the statistical analysis) is probably not of much value in this study, since it varies greatly within plants, and does not share much information with others. On the other hand, character 20, style length (SY) shares less information than any other character, yet was shown to be significantly useful in distinguishing certain populations (Table 9). It also varied little within populations. Character 22, stipule divided, has only two states, hence it is surprising that it shares any information at all (amount of information in a character often varies directly with the number of states); it was included mostly as a test of its possible usefulness, and was not used at all in the classification. Character 17, pedicel type, was designed as a substitute for (PA) used in the statistical analysis; PA was erratic in its variation within populations, with no apparent systematic meaning, and it was thought by reducing the number of states to three, its efficiency might be improved. Character 17 was included mostly to attempt to differentiate the species that have recurved pedicels in fruit, which are mainly species with dense-strigose pubescence, explaining its information shared with leaf pubescence type (character 11).

Characters 18 and 19, calyx length (LC) and number of flowers (NF), share some information with the stipule and stem size characters (Group II), as confirmed by the correlation studies. LC was one of the least variant characters within populations. Character 10, tooth depth (± LT) was modified somewhat from the method used in statistical analysis in hopes of improving its usefulness; it still did not share much information with other characters.

The other characters not discussed in the paragraphs above were included mostly because of their high degree of correlation with others, supported by their high amount of information shared with other characters.

Fig. 16 shows frequency distributions in four characters, from data output by CHARANAL.

Clustering of items

Characters used for this section are shown in Table 11 and Fig. 14. The output of program GRAPH was used to draw a complete set of sub-graphs (linkage diagrams, in Bisby's terminology). These diagrams were drawn using the following conventions:

1. Thin lines were drawn to show connections between items that were made in a previous group of levels.
2. Thick lines were drawn to show connections between items that were made in this group of levels; solid lines to show connections that made new clusters form, and dashed lines for new internal connections.
3. When a "tight cluster" began to form, it was included in a circle. A group of more than three items qualified as a "tight cluster" when there were at least three connections from each item to other members of the "tight cluster." Once a circle was drawn, only those items were shown within it that made connections to the outside; other items were omitted. Internal connections were

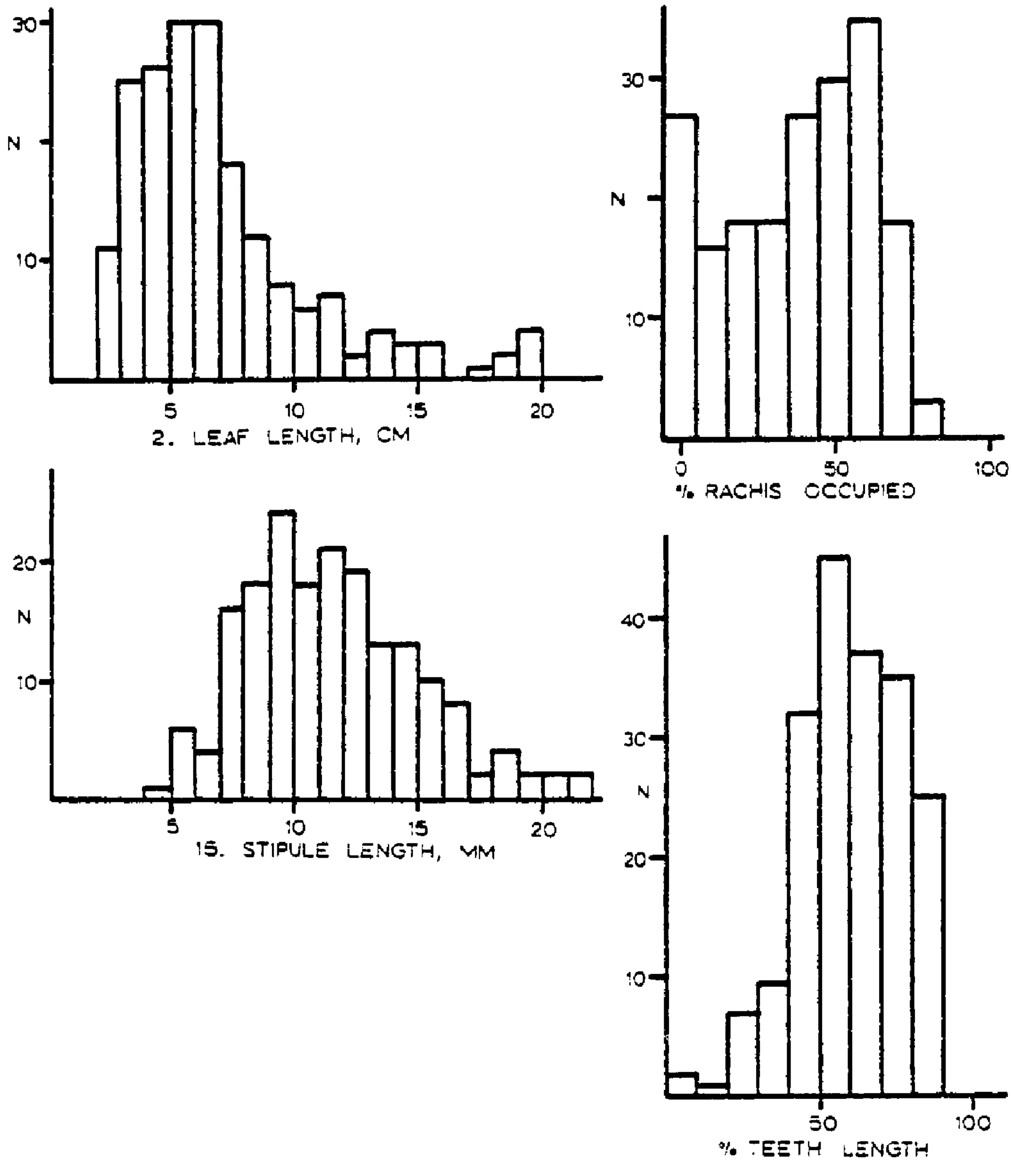


FIG. 16. Frequency distributions for four characters used in character analysis, data from 192 specimens of *Potentilla* sect. Multijugae.

shown within circles only when the items they connect were both already on the diagram. The same convention was used to decide whether to include additional items in a "tight cluster."

4. Diagrams were re-drawn, and in general the placement of items on a diagram was made solely for convenience in showing connections. As far as possible, the distances between items were made proportional to their dissimilarity; but this is clearly an impossible task even for the most simple of subgraphs.

In this case, there were many levels (155) at which new cluster connections were made, making complete drawing of every level excessively repetitive. Therefore, the levels were grouped into ten "groups" of levels, shown in Table 12. The boundaries between groups were decided for convenience, as the subgraphs were being drawn; when a diagram began to get complex, and a number of clusters began to form, the drawing of that group was stopped and the next group began. In this way, the ten groups in this study are analogous to super-levels, and will be referred to as "levels" in the discussion to follow.

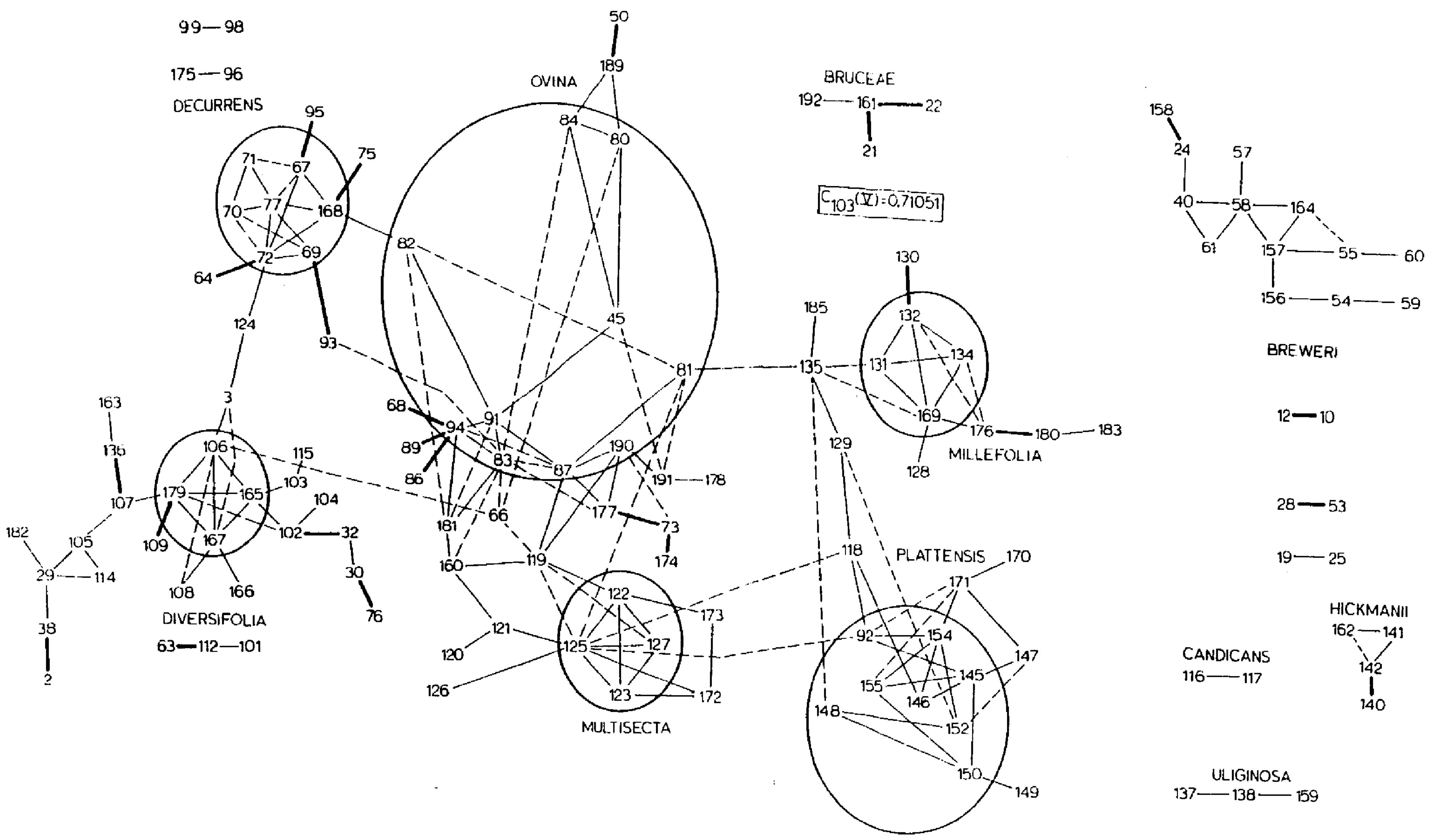
The sub-graphing procedure was continued up through Group VI, at which point several major clusters began to be obscured by interconnections and submergence in other clusters. The diagram of Group V (level 103) was chosen as most illustrative of the gross clusters that had formed; this group subgraph is shown in Fig. 17. The eleven clusters named in Fig. 17 were then drawn on separate diagrams, and all of the connections between the items of a cluster were shown. In addition, connections with other clusters were shown.

These subgraphs for each cluster were then compared with each other and with the specimens, with three goals:

TABLE 12. Showing the symbols used in the subgraph diagrams, the levels at which the items cluster, the group numbers (Roman numerals), and the corresponding value of the similarity function (C).

LEVEL No.	GROUP	C-VALUE	SYMBOL
50	I	0.772	≣≣≣≣≣
67	II	0.746	══════
80	III	0.731	≡≡ ≡≡ ≡≡
84	IV	0.729	━━━━━━
103	V	0.711	━━ ━━ ━━
110	VI	0.701	••••••••••••••
116	VII	0.695	=======
128	VIII	0.681	= = = = =
143	IX	0.650	──────
155	X	0.600*	- - - - -

*. Not all connections at these levels were included; the few that were included were necessary to show primary connections of an item to a cluster.


OVINA
DECURRENS
DIVERSIFOLIA
MULTISECTA
PLATTENSIS
MILLEFOLIA
BRUCEAE
BREWERI
HICKMANII
CANDICANS
ULIGINOSA
$C_{103}(\mathrm{V}) = 0.71051$
99 — 98
175 — 96
63 — 112 — 101
192 — 161 — 22
21
12 — 10
28 — 53
19 — 25
162 — 141
142
140
116 — 117
137 — 138 — 159
50
189
84
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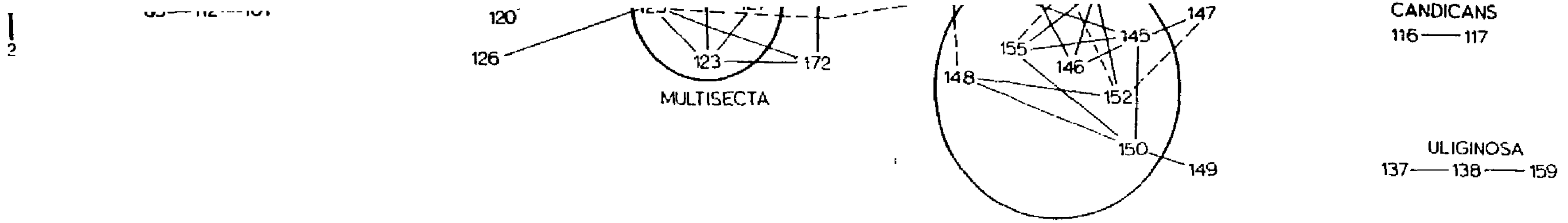


FIG. 17. Subgraph of *Potentilla* sect. Multijugae, at the 103rd level (Group V of Table 12). At this level there are 50 items still not joined to the clusters shown, and these are: 1,4,5,6,7,8,9,11,13,14,15,16,17,18,20,23,26,27,31,33,35, 36,37,39,41,42,43,44,46,47,48,49,51,52,56,62,65,74,79,97,100, 110,111,113,143,144,159,186,187,188. New cluster connections made at the level (dark solid lines); connections made at previous levels (light solid lines); internal connections made at this level (dashed lines).

1. To make a decision about the cluster membership of each item, particularly if it was a late-level outlier or intermediate between clusters;

2. To re-draw the clusters to reflect readjustments based on the decisions in (1); and

3. To recognize taxa that not only had some degree of morphological homogeneity as shown by the subgraphs, but also had geographical and ecological integrity, as shown by the specimen labal data.

To make the decisions of class (1) above, there are two aids that were found useful. One is the observation that the fact of a connection between two items was more important than the level at which the connection was made; this so because an item may connect at an early level to a cluster on the basis of characters other than the "best" characters for defining that cluster. Also, since geographical and ecological data are not included in GRAPH, adjustments sometimes have to be made. This will be illustrated in more detail below.

A second useful aid is a "character table." To make this, one selects two clusters that one wishes to compare, and determines the core of each cluster. The core is usually the items that first cluster together tightly, and includes all items other than those about which one wishes to make type (1) decisions. The states possessed by all items in a "core-cluster" are then tabulated for all characters, and compared with those for another core as, for example. in Table 13. From this character table it is not difficult to see that there are many differences between the two species (in this case), but in most characters the ranges overlap. The only really differential characters are no. 7, lower leaflet type, and no. 19, calyx length. The two species are also disjunct geographically.

The subgraphs for each of the eleven clusters are shown in Figs. 18-25; in Table 12 are shown the symbols used in these figures. In all figures, the numbers of type or authentic specimens used are enclosed in boxes; a list of the names corresponding with these specimens is shown in Table 14. The subgraphs will be discussed in the order of their difficulty, starting with the easiest to interpret.

Fig. 18 shows three species. In (a), two endemic California coastal-marsh species are shown, *Potentilla hickmanii* and *P. multijuga*. The four specimens of *P. hickmanii* (including the holotype [162]) cluster together fairly early, afterwards attaching to no. 118, a critical specimen of *P. millefolia* (connections A and C on Fig. 20). Later, *P. hickmanii* joins with the two specimens of *P. multijuga*, which in turn later join with *P. multisecta*. The two species shown on this subgraph are distinctively different from each other and from all others, and are disjunct geographically.

Fig. 18(b) shows *Potentilla candicans*, a species disjunct from the rest of the section in central Mexico. Its two specimens join to each other at the first level, and remain together and unjoined to other clusters until the last level, when they join to part of the *P. breweri* complex. *P. candicans* is probably the most distinctive species in this section.

Fig. 19 shows *Potentilla plattensis*, a distinctive species of wet bottoms around the Rocky Mountains and surrounding ranges, particularly the southern Rocky Mountains. The core-cluster is quite densely connected, mostly at the first or second levels, and includes the type of

TABLE 13. Character table contrasting the characters of the core-clusters of *Potentilla plattensis* and *P. millefolia*. Item numbers used in each core-cluster are shown below the table.

Character	States *millefolia*	 *plattensis*
1. Stem angle, degrees	0-45	0-45
2. Length of leaf rachis, cm	8-13	4-11
3. Per cent rachis occupied	60-80	40-70
4. Petiole pubescence	Strigose	Strigose
5. Number of leaflets	19-25	11-21
6. Terminal leaflet type	3 or 5	3
7. Secondary leaflet type	2	3
8. Secondary leaflet length, cm	0-20	10-15
9. Number of teeth	5-6	5-8
10. Tooth depth, %	70-90	70-90
11. Leaf pubescence type	Strigose	Strigose
12. Tomentum density	None	None
13. Straight hair density	Scatter-uniform	Scatter-uniform
14. Stem length, cm	10-25	10-25
15. Stipule length, mm	9-13	7-15
16. Stipule width, mm	4	2-6
17. Pedicel type	Recurved	Recurved
18. Number of flowers	3-10	3-15
19. Calyx length, mm	9-11	7-8
20. Style length, mm	2.1-3.3	1.5-2.7
21. Leaflets verticillate	Some or all	Some or all
22. Stipule divided	Yes	Yes or no

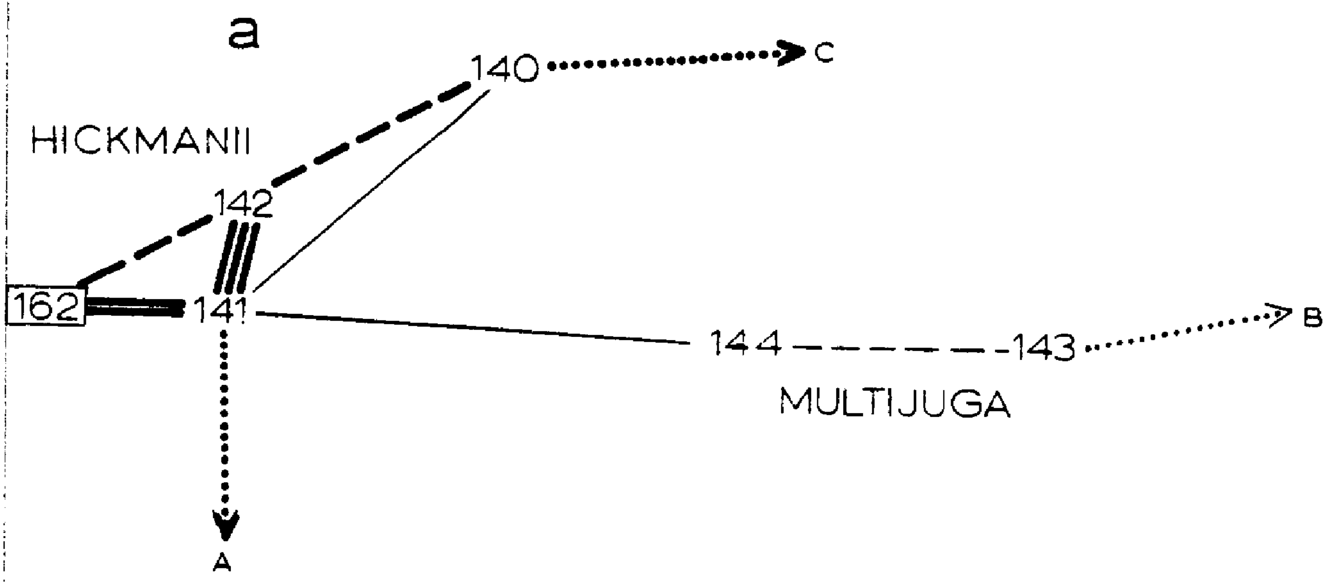
P. millefolia core-cluster: items 130,131,132,133,134,169,176

P. plattensis core-cluster: items 145,146,147,148,150,151,152, 153,154,155,170,171,184

TABLE 14. Type and authentic specimens used for subgraphs, Figs. 18-25.

Number in subgraph	Name
46	*Potentilla drummondii* Lehmann (not type or authentic specimen, but matches exactly the type plate and description)
143	*Potentilla multijuga* Lehmann (not type or authentic specimen, but matches exactly the type plate and description)
156	*Potentilla breweri* S. Watson
157	*Potentilla breweri* var. *expansa* S. Watson
158	*Potentilla cascadensis* Rydberg
159	*Potentilla anomalifolia* Peck
160	*Potentilla monidensis* A. Nelson
161	*Potentilla bruceae* Rydberg
162	*Potentilla hickmanii* Eastwood
163	*Potentilla sierrae-blancae* Wooton and Rydberg
164	*Potentilla plattensis* var. *leucophylla* Greene
165	*Potentilla diversifolia* Lehmann (authentic)
166	*Potentilla campestris* Nuttall
167	*Potentilla diversifolia* Lehmann (authentic)
168	*Potentilla diversifolia* Lehmann (authentic)
169	*Potentilla millefolia* Rydberg
170	*Potentilla plattensis* Nuttall
171	*Potentilla plattensis* var. *pedicellata* A. Nelson
172	*Potentilla dissecta* var. *linearis* M. E. Jones
173	*Potentilla diversifolia* var. *multisecta* S. Watson
174	*Potentilla dissecta* var. *decurrens* S. Watson
175	*Potentilla nelsoniana* Rydberg
176	*Potentilla klamathensis* Rydberg
177	*Potentilla perdissecta* Rydberg
178	*Potentilla ovina* J. M. Macoun
179	*Potentilla vreelandii* Rydberg
180	*Potentilla versicolor* Rydberg (Topotype)
181	*Potentilla wyomingensis* A. Nelson
182	*Potentilla intermittens* Rydberg
183	*Potentilla versicolor* Rydberg
184	*Potentilla arizonica* Greene
185	*Potentilla millefolia* var. *densa* Jepson
186	*Potentilla breweri* var. *viridis* Jepson
187	*Potentilla millefolia* var. *algida* Jepson
188	S. Watson 331 (US); see chapter VII
189	*Potentilla diversifolia* var. *pinnatisecta* S. Watson: S. Watson 332 (US)

Specimens are Types unless otherwise indicated



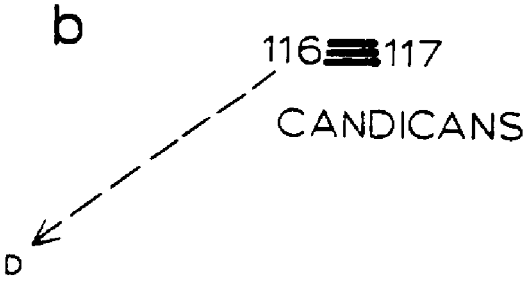


FIG. 18. Subgraphs of: a. *Potentilla hickmanii* and *P. multijuga*; and b. *P. candicans*. Symbols as in Table 12. Type or authentic specimens shown in boxes.

Potentilla arizonica [184]. The types of *P. plattensis* [170] and its var. *pedicellata* [171] are partial outliers, but become very tightly interwoven with the core-cluster at later levels. Of particular interest is the first-level connection of no. 92 through G to no. 118 on the *P. millefolia* subgraph, which will be discussed below. No. 120 is actually closer to *P. multisecta* because of its dense pubescence and subdigitate leaves; but label details about the bog habitat, and its pinnate shallowly-toothed leaflets (critical characters for *P. plattensis*) allow it to be placed here. The three specimens of *P. uliginosa* (including the type [139]) cluster tightly at the first level and remain untouched until much later, when they join loosely to *P. plattensis*; the two are very distinct morphologically and disjunct geographically.

Fig. 20 shows *Potentilla millefolia*, which has a fairly tight core-cluster including the types of *P. millefolia* [169] and *P. klamathensis* [176]. No. 135 is somewhat transitional to *P. plattensis* and *P. ovina*, but is plainly *P. millefolia* in the important characters (calyx size and secondary leaflet division type; see Table 13) as well as 129; they both fit the range of *P. millefolia* in habitat and geography. The type of *P. millefolia* var. *densa* [185] attaches more loosely; it is plainly merely a reduced form from an extreme site. No. 118 is transitional to *P. plattensis* as mentioned above, and is also connected to other species. The specimen is from central Nevada in wet bottomlands, acceptable into both *P. millefolia* and *P. plattensis*; however, it has the large calyx and digitately-dissected secondary leaflets of *P. millefolia*, allowing it to be placed here. Certainly, more collections from Nevada are desirable. Nos. 180 and 183, Type and topotype of *P. versicolor*, are intermediate between *P. millefolia* and *P. breweri*. Since they are intermediate in most

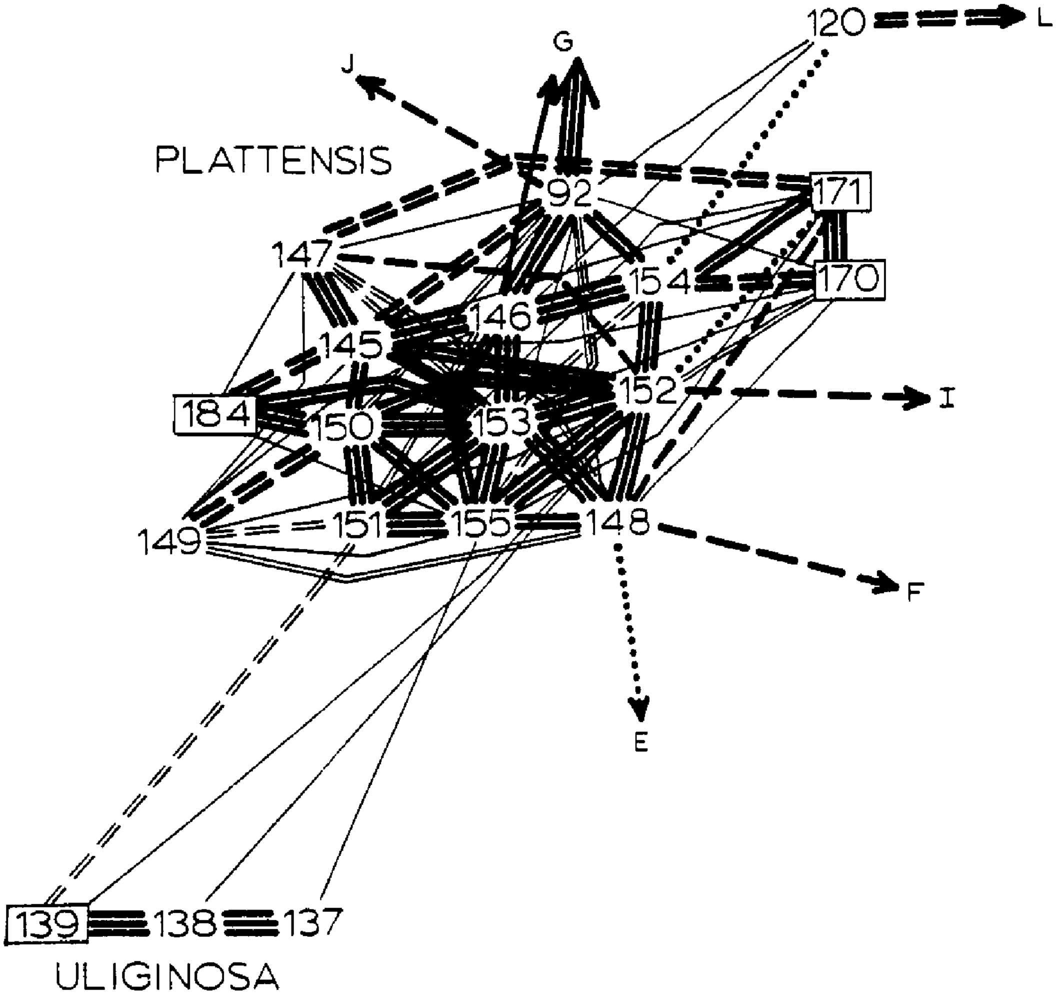


FIG. 19. Subgraph of the *Potentilla plattensis* portion of the subgraph in Fig. 17. Symbols as in Table 12. Numbers in boxes indicate type or authentic specimens.

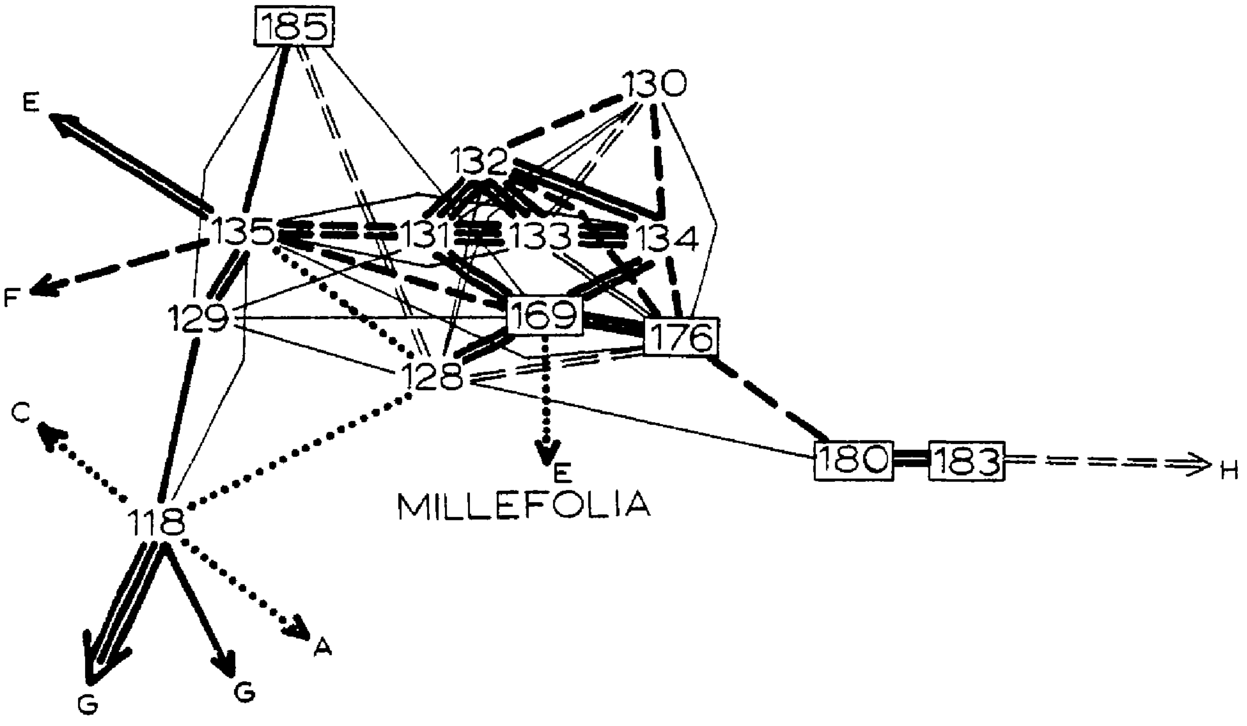


FIG. 20. Subgraph of the *Potentilla millefolia* portion of the subgraph in Fig. 17. Symbols as in Table 12. Numbers in boxes indicate type or authentic specimens.

characters, occur in the region of sympatry of these two species, and have apparently not been collected since the type, I can hypothesize that *P. versicolor* is a hybrid between *P. breweri* and *P. millefolia*.

Potentilla multisecta is shown in Fig. 21. This is a fairly tight cluster in itself, around the types of *P. diversifolia* var. *multisecta* [173] and *P. dissecta* var. *linearis* [172]. However, *P. multisecta* is closely related to several other species, notably *P. ovina* var. *ovina*, one of the authentic specimens of *P. diversifolia*, and *P. plattensis*. It is distinct in habit from the last two, and in range from *P. plattensis*; also, it is morphologically distinctive with its grayish-hairy leaves that are deeply incised, and its pedicels recurved in fruit.

The next four subgraphs (Figs. 22-25) fit together in a series, and they have been drawn so that the diagram flows from one to the next; parts of adjacent species have been shown on each. Fig. 22 shows the *Potentilla ovina* var. *ovina* subgraph, the core-cluster of which is somewhat diverse, but clearly is not separable into subunits; it contains the types of *P. diversifolia* var. *pinnatisecta* [189] *P. monidensis* [160], and *P. wyomingensis* [181]. The type of *P. ovina* [178] stands off somewhat from the core-cluster, but nos. 87 and 91, both cited in the type description of *P. ovina*, are comfortably within the core-cluster, and no. 178 joins with it later. This cluster joins to *P. ovina* var. *decurrens* through the specimen of var. *decurrens* [174], probably because of the small size of the specimen involved.

Potentilla ovina var. *decurrens* is shown in Fig. 23, which is transitional to var. *ovina* on the right side of the diagram, and to *P. diversifolia* on the left. It is composed of a relatively tight cluster (including one of the authentic specimens of *P. diversifolia* [168]) on

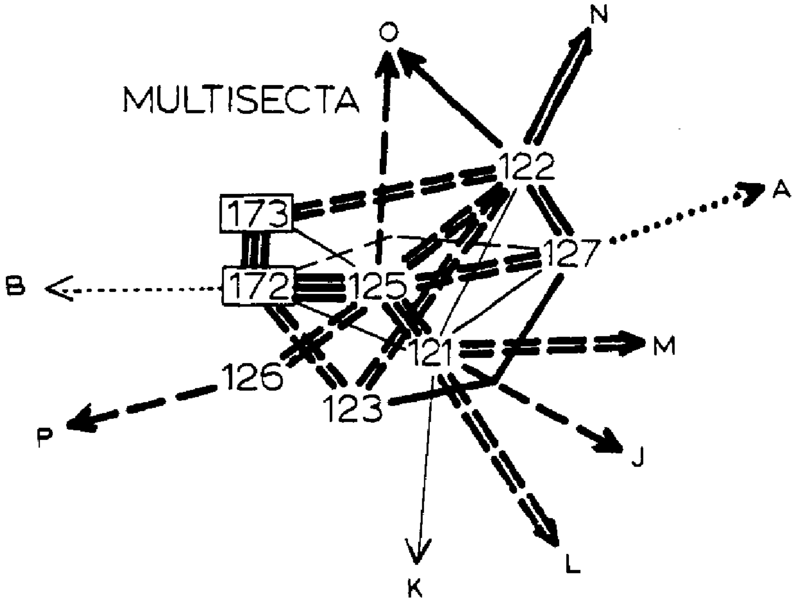


FIG. 21. Subgraph of the *Potentilla multisecta* portion of the subgraph shown in Fig. 17. Symbols as in Table 12. Numbers in boxes indicate type or authentic specimens.

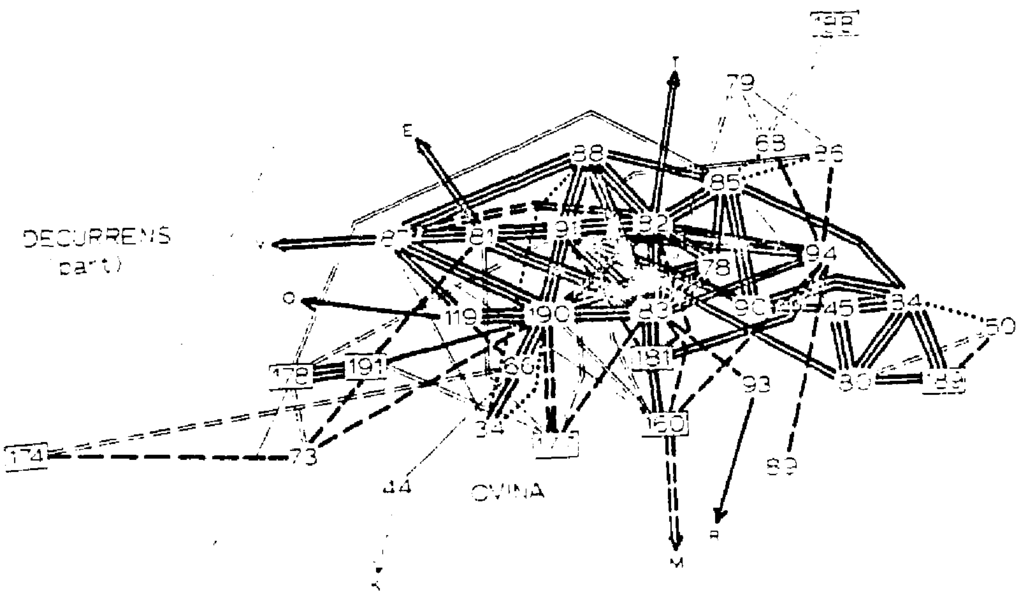


FIG. 22. Subgraph of the *Potentilla ovina* var. *ovina* portion of the subgraph in Fig. 17, showing connections with var. *decurrens* (see Fig. 23). Symbols as in Table 12. Numbers in boxes indicate type or authentic specimens.

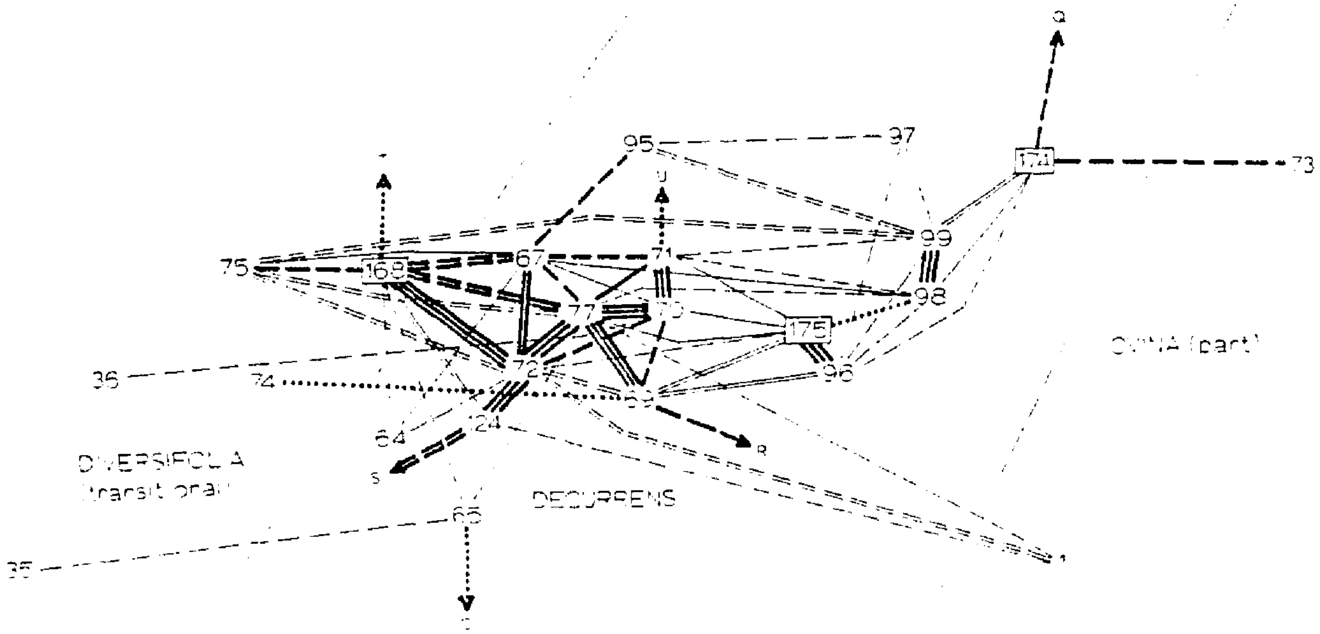


FIG. 23. Subgraph of the *Potentilla ovina* var. *decurrens* portion of the subgraph in Fig. 17, showing connections with var. *ovina* (see Fig. 22) and with *P. diversifolia* (see Fig. 24). Symbols as in Table 12. Numbers in boxes indicate type or authentic specimens.

the left, and a looser cluster (including the types of var. *decurrens* [174] and of *P. nelsoniana* [175]) on the right. Most of the cluster on the left is included because of its more pinnate leaves with more leaflets which are apically few-toothed; these characters are shown to be differential between the core-clusters, and the resulting arrangement allows var. *decurrens* to be largely isolated in the southern Rocky Mountains in the montane to lower subalpine, versus the predominantly alpine *P. diversifolia*, or the alpine and submontane *P. ovina* var. *ovina*. The tighter left-hand cluster contains plants that are taller with larger leaves than the right one, but that is apparently due to their occupation of lower elevations in the same range; there is no reason to recognize the distinction taxonomically.

Potentilla diversifolia is shown in Fig. 24; as one can see, the specific epithet is apt. The typical cluster at the top consists of relatively small plants with digitate leaves from scattered stations all over the range of *P. diversifolia*, and includes two authentic specimens of it [165,167], the type of *P. campestris* [166], and the type of *P. vreelandii* [179]. Another cluster is in the center of the diagram, and consists of taller plants with subdigitate leaves, also scattered over the range of *diversifolia*, including the type of *P. intermittens* [182]. A more diffuse cluster on the left side consists of tall, erect-ascending plants with leaves on long petioles, mostly in the southern half of the range, including some authentic *P. intermittens*. Two specimens in the middle, nos. 30 and 32, are subdigitate with more deeply-lobed leaflets, in the manner of *P. perdissecta*. However, all of these small clusters are intricately connected at lower levels, and no group of items seems to have any geographical range of its own. I conclude that varietal recognition

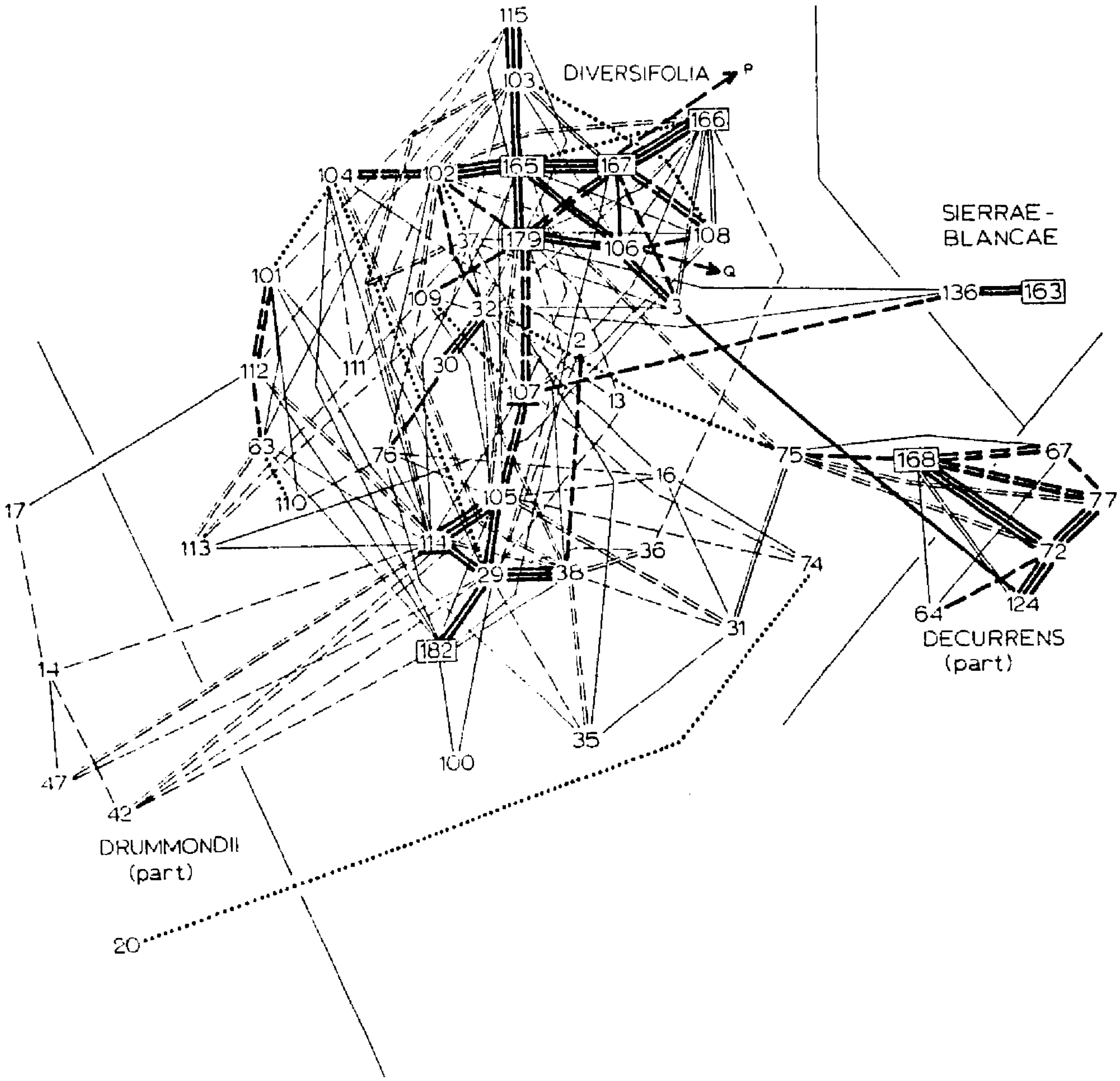


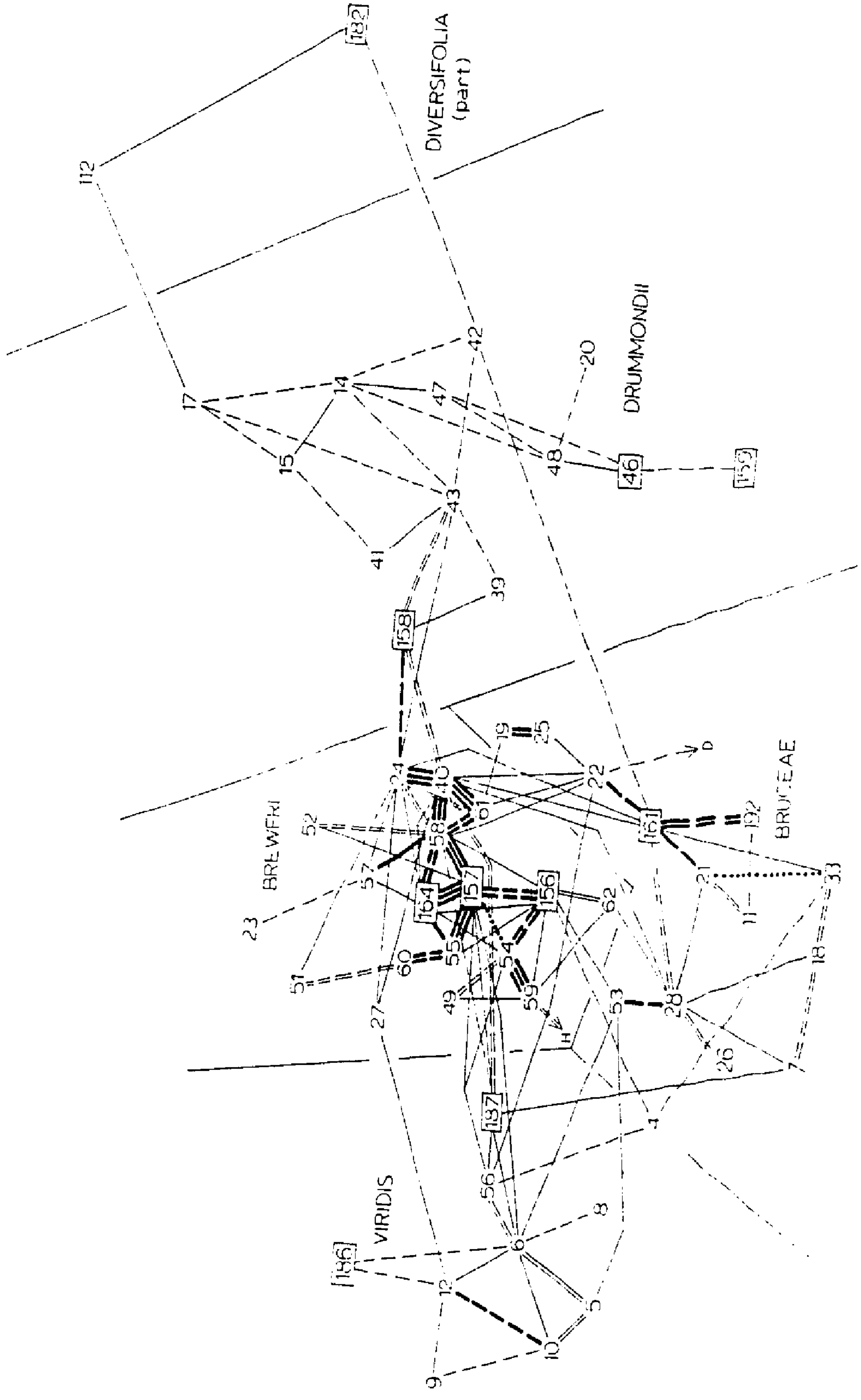
FIG. 24. Subgraph of the *Potentilla diversifolia* portion of the subgraph in Fig. 17, showing connections with *P. ovina* var. *decurrens* (see Fig. 23) and with *P. drummondii* (see Fig. 25). Symbols as in Table 12. Numbers in boxes indicate type or authentic specimens. The two specimens labeled *sierrae-blancae* belong to a different section, *Potentilla* sect. Aureae. The two underlined items are specimens of *P. diversifolia* ssp. *ranunculus*.

is not warranted in this admittedly diverse species. However, there are two distributions disjunct from *P. diversifolia*: ssp. *ranunculus* [107,114], disjunct in Greenland and Labrador but indistinguishable morphologically from *P. diversifolia*; and *Potentilla sierrae-blancae* Wooton and Rydberg from the White Mountains of New Mexico, which belongs to a different section of *Potentilla*, sect. Aureae, because of its distinctive style form (claviform) and thick leaves that are digitate with five leaflets.

Fig. 25 shows *Potentilla drummondii* and *P. breweri*. *P. drummondii* is very loosely connected within and also to *P. diversifolia* and *P. breweri*; it is generally distinguished from *P. diversifolia* by its taller stems with longer, more pinnate leaves, and much longer stipule, and from *P. breweri* by the same characters plus the absence of tomentum. No type specimen was available, but no. 46 matches the type description and plate very well; no. 159 is the type of *P. anomalifolia*, which is probably a local genetic variant with highly dissected leaves, all of the leaflets of type 5 (Fig. 14). No. 158 is the type of *P. cascadensis*, a form with smaller leaves, which is why it connects with *P. breweri*.

Potentilla breweri (Fig. 25) consists of three clusters, the core cluster including types of *P. breweri* [156], its var. *expansa* [157], and *P. plattensis* var. *leucophylla* [164]. Another cluster, at bottom, is more diffuse and includes the type of *P. bruceae* [161]; a third cluster is even more diffuse and includes both var. *viridis* [186] and var. *algida* [187]. There are a number of transitions among all three of these, which indicate that *bruceae* is better as a variety of *P. breweri* than it is a variety of *P. drummondii*. Var. *viridis* is a phase of *P. breweri* with small, subglabrous, green leaves.

FIG. 25. Subgraphs of *Potentilla breweri* and *P. drummondii*, a portion of the subgraph in Fig. 17, showing connections with *P. diversifolia* (see Fig. 24). Symbols as in Table 12. Numbers in boxes indicate type or authentic specimens.


DIVERSIFOLIA
(part)
DRUMMONDII
BREWERI
BRUCEAE
VIRIDIS
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48
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CHAPTER VI

KEYS TO THE CLASSIFICATION OF *POTENTILLA*

Potentilla is in the family Rosaceae, subfamily Rosoideae, tribe Potentillinae, subtribe Potentilleae. In the sense of its latest monographer (Wolf 1908), the genus *Potentilla* contains the species of this subtribe that have 10-to-indefinite stamens attached near the base of the carpophore, which does not become conspicuously fleshy in fruit. This is the broad concept of the genus which in the past has been most often used in Europe and in America.

Rydberg (1898,1908), the leading American systematist of the genus, distinguished several other genera that had been included in *Potentilla* by Wolf and his predecessors, including Lehmann. These segregate genera are: *Argentina (A. anserina); Comarum (C. palustre); Drymocallis (D. glandulosa, D. fissa,* etc.*); Pentaphylloides (P. fruticosa, P. floribunda,* etc.*);* and *Sibbaldiopsis (S. tridentata).* Rydberg actually used the name *Dasiphora* for what is now called *Pentaphylloides.* In recent years, as the genera advocated by Rydberg have been better studied, several taxonomists have confirmed their value as genera (Dansereau 1955, Weber 1976); others have returned to the (European and pre-Rydberg American) tradition of *Potentilla* in the broad sense, apparently for reasons of tradition alone. The genera advocated by Rydberg are very distinct on the basis of several floral and vegetative characters (see key below); information about modes of reproduction confirms their distinctness from *Potentilla*.

Pentaphylloides and *Sibbaldiopsis* are shrubs or subshrubs with hairy achenes and styles attached basally to the ovary; for a discussion see Löve (1954). *Drymocallis* are large plants with large, pinnate leaves and basal styles. *Argentina* has lateral styles and interruptedly-pinnate, bicolored leaves, often a stoloniferous habit, and a chemistry that is unique in the family Rosaceae (Bate-Smith 1962). *Comarum* has large, red flowers, lateral styles, inhabits bogs, and has a receptacle becoming somewhat spongy in fruit.

Pentaphylloides is monoecious or functionally semi-dioecious. *Pentaphylloides*, *Sibbaldiopsis*, and *Drymocallis* are predominantly diploid ($2n = 14 = 2x$, where $x = 7$) with rare tetraploid or hexaploid populations (Clausen et al. 1940). *Argentina* is predominantly tetraploid with rare hexaploid populations (Rousi 1965). *Comarum* has been reported to have tetraploid and hexaploid plants.

Fragaria is closely related to *Potentilla s.s.*, differing from it only in the formation of a fleshy carpophore, yet in *Fragaria* no apospory or parthenogenesis have been reported; these phenomena are widespread and common in *Potentilla s.s.* (Rutishauser 1948). Excluding vegetative reproduction, *Drymocallis*, *Pentaphylloides*, and *Argentina* are (as far as known) completely sexual (Fryxell 1957), similar to *Fragaria*. Several successful crosses have been made between *Fragaria* as female parent, and *Pentaphylloides, Comarum,* and *Drymocallis* as male parents. But no crosses have yet been successful between *Fragaria* and *Potentilla s.s.* (Asker 1969). As Rydberg accurately pointed out, if *Comarum, Sibbaldia, Horkelia,* and *Ivesia* are included in *Potentilla,* then

> ...the only logical course to be taken would have been to include also *Duchesnea* and *Fragaria*... Only two courses can logically be taken. Either the whole [sub]tribe, *Fragaria* also included, must constitute a single genus, or else both *Potentilla*

> and *Ivesia* [must] be divided into several genera (1898, pp. 15-16).

Rydberg (1896,1897,1898) divides *Potentilla* into 21 "groups." These are equivalent to "sections" as presently used, since they are the only taxonomic level used between the genus and its species, and Rydberg used the paragraph symbol (§) to refer to them, as was common for sections in his day. They were all given a short description, and were named in a manner analogous to Lehmann's (1856) "Tribes." Rydberg's species, however, are much too finely split, and have been extensively synonymized by every taxonomist since him.

A key to the genera of this subtribe is presented first; it has been slightly modified from Rydberg (1908), by converting his polychotomous key into a dichotomous one; a few subsidiary characters have been added to some of the couplets. Following that is a key to the North American sections of *Potentilla* written by the author.

Key to the genera of Rosaceae-Rosoideae-Potentillinae-Potentilleae

1. Style terminal or nearly so; ovules pendulous and anatropous . . . . (2)
1. Style lateral to basal; ovules ascending to erect, amphitropous or orthotropous . . . . (9)
2. Anthers oblong, opening by longitudinal slits; pistils two to many . . . . (3)
2. Anthers obcordate, opening by subterminal pores; pistil one . . . . *Stellariopsis*
3. Stamens separated from the receptacle by an open space; no indication of an annular thickening at the base of the filaments . . . . (4)
3. Stamens inserted very near the base of the receptacle on a more or less evident annular thickening . . . . *Potentilla*
4. Hypanthium saucer-shaped to deeply campanulate; petals oblanceolate to obcordate or cuneate; pistils usually more than two . . . (5)
4. Hypanthium wheel-shaped; petals narrowly linear; pistils two . . . . *Comarella*

5. Filaments dilated, petaloid . . . . (6)

5. Filaments filiform . . . . (8)

6. Stamens 10, sepals not reflexed in anthesis . . . . . . *Horkelia*

6. Stamens 20 . . . . (7)

7. Pistils numerous; hypanthium campanulate; sepals reflexed in anthesis . . . . *Horkeliella*

7. Pistils 3–6; hypanthium turbinate; sepals not reflexed in anthesis . . . . *Ivesia*

8. Pistils inserted in the bottom of the hypanthium; bractlets present . . . . *Ivesia*

8. Pistils inserted on a stalked receptacle; bractlets lacking . . . . *Purpusia*

9. Style lateral; ovules ascending and amphitropous . . . . . . (10)

9. Style nearly basal; ovules ascending or nearly erect, orthotropous . . . . (16)

10. Achenes glabrous; herbs . . . . (11)

10. Achenes hairy; shrubs or undershrubs . . . . (15)

11. Achenes numerous; stamens about 20 . . . . (12)

11. Achenes 10–15; stamens 5; leaves trifoliolate . . . . . *Sibbaldia*

12. Leaves odd-pinnate . . . . (13)

12. Leaves trifoliolate; receptacle much enlarged and usually red in fruit . . . . (14)

13. Receptacle not enlarged in fruit; petals yellow, obtuse or retuse; leaves interruptedly pinnate . . . . *Argentina*

13. Receptacle somewhat enlarged in fruit, becoming spongy; petals red, acute or acuminate; leaves regularly pinnate . . . . *Comarum*

14. Receptacle not pulpy; petals yellow . . . . *Duchesnea*

14. Receptacle pulpy; petals white or pinkish . . . . *Fragaria*

15. Style filiform; leaves trifoliolate; petals white . . *Sibbaldiopsis*

15. Style club-shaped; leaves pinnate; petals mostly yellow . . . . *Pentaphylloides*

16. Stamens and pistils numerous; bractlets present; leaves pinnate . . . . *Drymocallis*

16. Stamens 5; bractlets wanting; leaves twice- or thrice-ternate . . . . *Chamaerhodos*

Key to the North American sections of *Potentilla*

1. Flowers solitary in the axils of stem leaves, with long pedicels; stems often either modified into stolons or rooting at the nodes. Moist woods, eastern Canada to New Mexico, south to Georgia, Texas, and northwestern Mexico . . . . sect. Potentilla

1. Flowers principally in terminal cymes, rarely also solitary in the axils of lower leaves; stems sometimes decumbent, but never stoloniferous or rooting at the nodes. Generally distributed . . . (2)

2. Stems branched below the middle, with well-developed leaves subtending most branches, at flowering time with the principal well-developed and largest leaves at about midstem on short petioles, often at that time with the basal rosette long past; style 1.0 mm long or shorter, conspicuously incrassate at base, coniform; plant annual or short-lived perennial with weedy tendencies . . . . (3)

2. Stems branched below the middle or not, usually with well-developed leaves only basal and sharply or gradually reduced in size and number of parts upward, if stem leafy then stem-leaves definitely smaller than basal, at flowering with mature basal leaves, often on long petioles; style 0.8-4.5 mm long, incrassate or not; plant perennial, often with woody rootstock . . . . (6)

3. Bracteoles of the calyx usually 3-lobed; leaves pilose with straight hair, never tomentose nor glandular; plants biennial to short-lived perennial. Guatemala . . . . sect. Heterosepalae

3. Bracteoles nearly always entire; leaves either tomentose below or conspicuously glandular; plant annual to short-lived perennial . . . . (4)

4. Plant biennial or short-lived perennial; leaves conspicuously white-tomentose beneath, small, digitate, dissected into narrow lobes. Adventive from Europe: east and west coasts, and scattered through interior . . . . sect. Argenteae

4. Plant annual; leaves strigose and conspicuously glandular, often sticky, never tomentose, digitate or pinnate; wet meadows and streamside strand. Most of North America at low elevations . . . . (5)

5. Leaves conspicuously pinnate with 7-21 leaflets, the leaflets deeply dissected digitately to near the base into obtuse-crenate segments; stems white, decumbent, hollow, silky-strigose and usually glandular. Southeastern Washington, eastern Oregon, and northeastern California . . . . sect. Arenicolae

5. Leaves digitate to subpinnate, with 3-5 leaflets, rarely with 7, the leaflets shallowly to coarsely toothed, never deeply divided; stems usually green, often erect (except in depressed forms), villous and often glandular. Western North America; Europe and Asia . . . . sect. Supinae

6. Style 1.0 mm long or shorter, often conical, often thickened at the base and tapered to the stigma, relatively thick just below the stigma . . . . (7)

6. Style 1.2 mm long or longer (often much longer), usually thin just below the stigma . . . . (10)

7. Tall, strictly-erect plants, with harsh-spreading, readily visible, bristly-hirsute pubescence; pedicels stiffly straight; leaves strictly digitate, light yellow-green. Introduced in northeastern United States, southeastern Canada, and midwestern and Great Plains states and provinces, scattered westward . . . . . . sect. Rectae

7. Plants usually ascending to decumbent, short to medium-sized; pedicels usually more or less arcuate-ascending or rarely recurved; leaves digitate or pinnate, either with some tomentum beneath (sometimes densely so) or not, but in any case not with harsh, bristly-hirsute pubescence. Generally distributed . . . . . (8)

8. Style claviform (thickened prominently just below the stigma); leaves sericeous or glabrous, usually green or yellowish-green, never tomentose. Arctic-alpine of eastern North America, disjunct in southeastern New Mexico . . . . sect. Aureae

8. Style uniformly-thickened or filiform, never thickened prominently just below the stigma; leaves tomentose at least beneath. Generally distributed; sometimes arctic, but if alpine then principally in western North America . . . . (9)

9. Leaves almost always digitate, often ternate, rarely subdigitate, with flat margins; style often uniformly-thickened; pubescence usually snow-white and formed of long entangled hair; stems short, decumbent-ascending. Arctic and alpine North America, never subalpine; Europe and Asia . . . . sect. Niveae

9. Leaves pinnate to (less commonly) subdigitate, with revolute margins; plants sometimes arctic or alpine but then either clearly pinnate and/or with erect-ascending stems or with off-color pubescence; pubescence snow-white only in one uncommon subarctic species of Alaska and Yukon with highly-dissected leaflets, otherwise greenish, yellowish, or formed of shorter matted hair; stems often tall, especially at lower elevations and latitudes, often ascending to erect . . . . sect. Multifidae

10. Leaves small, with petioles often less than 5 cm long, 5-7-digitate or -subdigitate, tawny or yellowish tomentose (rarely snow-white, very rarely without tomentum) at least beneath, always strigose above and on petioles and calyx, commonly also glandular, the strigae stiff and sometimes pustulate-based; styles 1.6-2.4 mm long, claviform; stems usually prostrate or decumbent, 3-7-flowered; calyx lobes and bractlets blunt-acute or obtuse, the calyx usually broader than long. Dry hills, western Great Plains and Great Basin to the alpine in southern Rocky Mountains. . . . . . . sect. Concinnae

10. Leaves small to large, digitate to pinnate, tomentose or not, if strigose usually not also tomentose, seldom glandular but then without tomentum; styles 1.8-4.0 mm long, if thickened then at the base; stems prostrate-erect, 3-50-flowered; calyx lobes often acuminate (at least in fruit), bractlets sometimes of different texture from calyx lobes. Generally distributed . . . . (11)

11. Leaves, and often stems and flowers, densely viscid-glandular, often also sericeous, strigose, or hispid, never tomentose; leaves digitate or trifoliolate, or if pinnate then plants of southeastern California and adjacent states. Southwestern United States and northwestern Mexico, or alpine of Pacific northwest and central Mexico . . . . (12)

11. Leaves tomentose, sericeous, strigose, or rarely hispid, never prominently (or densely) glandular; leaves digitate or pinnate, sometimes trifoliolate. Generally distributed . . . . (14)

12. Leaves trifoliolate, but the terminal leaflet dissected pinnately into crenate lobes, the leaf thus appearing pinnate with 5-7 leaflets; leaves glandular-puberulent, dark green, turning darker in drying. Alpine of Pacific northwest and central Mexico . . . . sect. Brevifoliae

12. Leaves pinnate to digitate, sometimes trifoliolate but then with three evident leaflets; leaves stalked-glandular, often viscid, often hispid or villous in addition. Lower elevations, southwestern United States and northwestern Mexico . . . . (13)

13. Leaves plainly pinnate with 5-15 leaflets, the leaflets sometimes flabellate; stems 5-30 cm long, prostrate to ascending; petals sometimes acute. Cliffs of desert mountains, southeastern California, southwestern Arizona, and adjacent Baja California and Sonora . . . . sect. Saxosae

13. Leaves digitate with five leaflets or less commonly trifoliolate, the leaflets rarely flabellate; stems 5-50 cm long, ascending to more commonly spreading; petals emarginate. Dry slopes, southwestern United States and northwestern Mexico . . . sect. Subviscosae

14. Leaves pinnate to digitate, tomentose, strigose, sericeous, or glabrous; if digitate or subdigitate then either glabrous to sericeous (not tomentose) in alpine plants of the Rocky Mountains and Great Basin ranges and northern Cascades, or else slightly subdigitate and conspicuously tomentose beneath in plants of the eastern Great Plains, Rocky Mountains, and Great Basin; styles long-filiform, if thickened then slightly so at very base only . . (15)

14. Leaves strictly digitate or ternate, usually tomentose but if subglabrous then ternate, if otherwise not tomentose then either with hairy receptacle or else leaves densely sericeous-villous or else subalpine in central and northern Mexico . . . . (16)

15. Leaves pinnate to digitate, glabrous, strigose, sericeous, or tomentose, but if digitate or subdigitate then not tomentose or very slightly so; stems usually short and ascending, sometimes tall but then leaves glabrous to subglabrous; if tomentose prominently then leaflets verticillate, the terminal one lobed . . . . . . sect. Multijugae

15. Leaves pinnate to digitate, tomentose or less commonly strigose or hispid; if subdigitate then conspicuously tomentose and plants tall; if strigose or hispid then either glandular in addition in plants of Arizona and surrounding states, or else leaflets conspicuously confluent; if plants tall then tomentose or conspicuously hispid . . . . sect. Subjugae

16. Receptacle hairy; leaves digitate, each leaflet dissected nearly to the base into long narrow segments; plants with woody caudex and low stems with few flowers. Central and northern subarctic mountains of Alaska, Yukon, and Mackenzie; Siberia . . . . sect. Biflorae

16. Receptacle not hairy; leaves digitate or ternate, usually merely toothed; plant perennial, stems often tall and many-flowered. Low elevations and lower latitudes, western North America and Mexico . . . . (17)

17. Leaves ternate, leaflets flabelliform and the terminal one petiolulate, glabrous to puberulent. Mountains of central Sierra Nevada to southern British Columbia . . . . . sect. Flabellifoliae

17. Leaves digitately 5-7(-9)-foliolate, rarely flabelliform, leaflets usually sessile, often tomentose or otherwise pubescent . . . (18)

18. Petals red . . . . sect. Haematochroi

18. Petals yellow . . . . (19)

19. Leaves thick and leathery, caudex thick; styles filiform above, thickened at base only. Central Mexico to Guatemala . . . . sect. Subcoriaceae

19. Leaves thinner, nearly almost always tomentose; styles thickened uniformly up to about half its length, then tapered abruptly. becoming filiform just below stigma; plants tall with ascending-erect stems. West of the Sierra Nevada in California, west of the Rocky Mountains in northwestern United States and southwestern Canada; if densely tomentose then strictly digitate and west of the Sierra Nevada and Cascades . . . . sect. Graciles

CHAPTER VII

TAXONOMY OF *POTENTILLA* SECT. MULTIJUGAE

POTENTILLA SECT. MULTIJUGAE Rydberg, Bull. Torrey Bot. Club 23:432 (1896); Mem. Dept. Bot. Columbia Univ. 2:30-31 (1898); Wolf, Bibl. Bot. 16(71):51,488-489 (1908). Type species: *Potentilla multijuga* Lehmann.

Potentilla sect. Aureae Rydberg, Bull. Torrey Bot. Club 23:394 (1896), *non* "Tribus" Aureae Lehmann, Revis. Potent. 6 (1856). No type designated.

Potentilla sect. Candicantes Rydberg, Mem. Dept. Bot. Columbia Univ. 2:32 (1898); North Amer. Flora 22(4):339 (1908). Type species: *Potentilla candicans* Humboldt and Bonpland.

Key to species

1. Petioles, and often also lower leaf surfaces, with curly or twisted hair, never strigose, often more or less tomentose, less often pilose with twisted hair or glabrescent; if glabrescent then sometimes the leaves subdigitate, otherwise plainly pinnate with 9-21(-25) leaflets; at least some leaflets verticillate on the rachis, usually all leaflets verticillate; stipules large, 7-22(-33) mm long and 2-9 mm wide; terminal leaflet often deeply lobed into 3-7 toothed segments . . . . (2)

1. Petioles strigose, not tomentose, sometimes glabrous, not with twisted or curly hair, or if rarely with tomentum sparsely beneath sericae then terminal leaflet pinnately toothed (not with 3-7 toothed segments) and stipules 5-9 mm long; terminal leaflet pinnately toothed or few-toothed at apex, rarely deeply lobed into 3-7 toothed segments . . . . (7)

2. Petioles tomentose under straight hair; stipules 5-9 mm long and 2-3 mm wide; teeth 2-6 in mid-rachis leaflet, cutting 60-90% to midrib; calyx 4-8 mm high . . . . (6)

2. Petioles without straight hair, either glabrous or tomentose, or pilose with twisted hair; stipules 7-22(-33) mm long and 2-9 mm wide; teeth 3-16 in mid-rachis leaflet, cutting 40-70% to midrib; calyx 6-12 mm high . . . . (3)

3. All leaf surfaces covered with pilose pubescence of twisted hair giving a glossy grayish-yellow cast to the plant; leaflets 19-more, all pinnately divided 90% to midrib, with 9-10 teeth; calyx large, 10-14 mm high (including lobes). Central Mexico 1. *P. candicans*

3. Leaf surfaces with curly hair or glabrous, never pilose; leaflets 5-19, the terminal one usually divided into 3-5 toothed lobes, making delimitation of terminal leaflet difficult; lower leaflets with 3-8 teeth cutting 40-70% to midrib, or if with more teeth then plants tall, green, and glabrous. North of Mexico . . . . (4)

4. Leaf rachis (including petiole) 2-7 cm long, bearing 9-21 leaflets; leaf surfaces sparsely to densely tomentose, rarely glabrous, usually grayish-green to gray in color; lower leaflets 5-17 mm long, with 3-8 teeth, often appearing digitately divided; stems decumbent to ascending, 10-35 cm long, with stipules 2-7 mm wide. Mostly south of central Oregon, more sparsely northward and eastward . . . . (5)

4. Leaf rachis 8-18 cm long, bearing 5-16 leaflets; leaf surfaces glabrous or sparsely tomentose, always green; lower leaflets 15-50 mm long, with 5-16 teeth pinnately divided or apically few-toothed; stems ascending to erect, 15-50 cm long, with stipules 7-9 mm wide. Mostly in the Cascade and Coast ranges of the Pacific northwest, across southern British Columbia to the northern Rocky Mountains; more sparsely north to Alaska and in northern Idaho, northeastern Oregon, northwestern Montana, and southern California . . . . 3. *P. drummondii*

5. Leaves subpinnate with 9-14 leaflets occupying 20-40% of rachis; leaflets 10-17 mm long with 5-8 teeth dividing 40-60% to midrib. Most common in Sierra Nevada, more sparsely in Coast and Cascade ranges to Washington, eastern Oregon, and northeastern Nevada . . . . 2a. *P. breweri* var. *bruceae*

5. Leaves pinnate with 13-21 leaflets occupying 40-60% of rachis; leaflets 5-15 mm long with 3-8 teeth dividing 50-70% to midrib. Most common in Sierra Nevada and Cascade range; also in southeastern Oregon, central and northeastern Nevada . . . . (6)

6. Calyx 6-8 mm high; leaf rachis usually much smaller than stems, 2-4 cm long, 40-50% occupied; leaves green to grayish-green, tomentose sparsely to uniformly-light below. Sierra Nevada . . . . 2b. *P. breweri* var. *viridis*

6. Calyx 8-9 mm high; leaf rachis usually proportionally larger, 3-7 cm long, 50-60% occupied; leaves grayish-green to gray, tomentose uniformly light to densely covering below. Sierra Nevada and Cascade range, southeastern Oregon, central and northeastern Nevada . . . . 2c. *P. breweri* var. *breweri*

7. Leaves digitate to subdigitate, with 5-12 leaflets occupying 0-40% of rachis, divided into long narrow lobes; leaflet surfaces usually densely strigose, giving grayish color to plant; lower leaflets pinnately or digitately divided; stipules 8-9 mm long, 2-3 mm wide; pedicels recurved in fruit. Montane of east-central Nevada and west-central Utah . . . . 4. *P. multisecta*

7. Leaves plainly pinnate, with 9-21(-25) leaflets occupying 20-80% of rachis, toothed 30-90% to midrib; leaflet surfaces usually glabrous to obscurely scattered-strigose and green, or if densely pubescent and grayish then with 11-19 pinnate leaflets and pedicels erect in fruit; lower leaflets usually pinnately divided or apically few-toothed, but if digitately divided then leaflets 11-21(-25) and/or flowers large; stipules 7-20 mm long, 2-6 mm wide; pedicels recurved or not in fruit. Western North America, in Nevada or west-central Utah only in the alpine or in damp valleys . . . (8)

8. Pedicels recurved in fruit; leaves apparently pinnate with 11-21(-25) leaflets occupying 40-80% of rachis; calyx 6-11 mm long (including lobes); lower leaflets often digitately divided. Bogs, marshes, and wet meadows of western North America . . . . (9)

8. Pedicels erect or ascending in fruit; leaves digitate or moderately pinnate with 5-19 leaflets occupying 0-70% of rachis; calyx 4-9 mm long; lower leaflets usually pinnately toothed or apically few-toothed, but if digitately lobed then abundantly-hairy alpine plants. Rocky slopes of montane, subalpine, and subarctic western North America, or on rocky submontane benches of the foothills of the northern Great Basin; if rarely in damp meadows then with 3-12 leaflets that are apically- few-toothed . . . . (13)

9. First-pair leaflets pinnately toothed, or very rarely apically few-toothed; flowers usually smaller, with calyx 5-8 mm long, or if 9 mm then styles 3.0-3.6 mm long in rare plants of Sonoma Co., California; leaflets 11-21, occupying 40-70% of rachis; styles usually 1.5-2.7 mm, if longer then rare plants of Sonoma Co. or Los Angeles Co., California . . . . (10)

9. First-pair leaflets (and usually all but the terminal one) digitately divided; flowers large, with calyx 8-11 mm long; leaflets 19-23, occupying 60-80% of rachis, or if 11-12 and 20-50% then rare plants of Monterey Co. or San Mateo Co., California; styles 2.1-3.3 mm long . . . . (12)

10. Leaf rachis 4-11 mm long; mid-rachis leaflets 10-15 mm long; stems 10-25 cm long, decumbent to ascending, with stipules 2-6 mm wide; calyx 5-8 mm long; styles 1.5-2.7 mm long; leaflets all or mostly verticillate on rachis. Low, wet meadows of the western and northern Great Plains, around the end of the southern Rocky Mountains into north-central Arizona and central Utah . . . . . 5. *P. plattensis*

10. Leaf rachis 15-22(-35) cm long; midrachis leaflets 15-20 cm long; stems 20-55 cm long, ascending to erect, with stipules 4-7 mm wide; calyx 6-9 mm high; styles (2.6-)3.0-3.6 mm long; leaflets either all verticillate or none. Rare plants of coastal marshes of Sonoma Co. or Los Angeles Co., California . . . . (11)

11. Leaflets 17-21(-23), all verticillate on rachis; terminal leaflet pinnately toothed; lower leaflets 20-25 mm long, with 7-10 teeth cutting 70-90% to midrib; flowers 6-10, with calyx 9 mm long; styles 3.0-3.6 mm long; stipules entire or divided. Sonoma Co. . . . . 6. *P. uliginosa*

11\. Leaflets 11-14, none verticillate; terminal leaflet deeply parted into 5-7 toothed lobes; lower leaflets 15-20 mm long, with 3-6 teeth cutting 30-40% to midrib; flowers 3-5, with calyx 6-8 mm long; styles 2.4-3.3 mm long; stipules divided. Los Angeles Co. . . . . 7. *P. multijuga*

12\. Leaflets 11-12, occupying 20-50% of rachis; lower leaflets flabelliform, with 3 teeth cutting 50-60% to midrib, glabrous to obscurely scattered-strigose; stems 10-15 cm long with stipules 8-11 mm long and 3-4 mm wide; calyx 8-9 mm high. Monterey Co. and San Mateo Co., California . . . . 8. *P. hickmanii*

12\. Leaflets 19-23, occupying 60-80% of rachis; lower leaflets deeply digitate, with 5-6 teeth cutting 70-90% to midrib, scattered-strigose to densely strigose; stems 10-25 cm long, with stipules 9-13 mm long and 4 mm wide; calyx 8-11 mm long. Northwestern California and south-central Oregon, disjunct in central Nevada . . . . 9. *P. millefolia*

13\. Leaves digitate to subdigitate, with 5-8 leaflets occupying 0-10% of rachis; lower leaflets pinnately divided or apically few-toothed, with 3-10 teeth cutting 40-70% to midrib; midstem stipules 8-18 mm long and 3-6 mm wide; leaflets glabrous to uniformly obscurely-sericeous, usually green; petioles glabrous; stems usually ascending to erect and 15-30 cm long. Subalpine, alpine, and subarctic western North America . . . . (14)

13\. Leaves moderately to conspicuously pinnate, with 9-19 leaflets occupying 20-70% of rachis; lower leaflets apically few-toothed or digitate, with 3-8 teeth cutting 50-90% to midrib; midstem stipules 5-20 mm long and 2-4 mm wide; leaflets glabrous to densely strigose (sometimes with a lower layer of tomentum), green to gray; petioles strigose, rarely glabrous; stems decumbent to ascending or erect and 5-25 cm long . . . . (16)

14\. Plants of Greenland and the coast of Labrador . . . . 10a. *P. diversifolia* ssp. *ranunculus*

14\. Plants of the Rocky Mountains and westward . . . . (15)

15\. Leaflets cut 70-90% to midrib into narrowly oblong segments; plants 15-20 cm tall. Northern and central Rocky Mountains, rarely in the Wallowa Mountains or Uinta Mountains . . . . 10b. *P. diversifolia* var. *perdissecta*

15\. Leaflets cut 40-70% to midrib, usually merely toothed; plants 15-30 cm tall. Wider range . . . . 10c. *P. diversifolia* var. *diversifolia*

16\. Leaflets glabrous to sparsely strigose, usually green, 10-20 mm long; leaf-rachis 3-12 cm long, half or more the length of the stem, often erect or ascending; stipules 7-20 mm long and 2-4 mm wide, divided or not; flowers 3-15, with calyx 6-8 mm high and styles 1.8-2.4 mm long. Mountains of Colorado, southern Wyoming, Utah south of the crest of the Uintas, and eastern Nevada; more scattered on the mountains northward to the northern Rocky Mountains . . . . 11a. *P. ovina* var. *decurrens*

16. Leaflets uniformly to densely strigose, grayish-green to gray, often with a lower layer of sparse tomentum, 5-10 mm long; leaf-rachis 2-6 cm long, usually less than half the length of the stem except in matted forms, usually decumbent to ascending; stipules 4-9 mm long and 1-3 mm wide, divided; flowers 1-10, with calyx 4-8 mm long and styles 1.5-2.7 mm long. Rocky slopes and benches of the high mountains of the central and northern Rocky Mountains, and foothills around the Wyoming Basin; alpine in the Uinta and Wasatch Mountains . . . . 11b. *P. ovina* var. *ovina*

1. *POTENTILLA CANDICANS* Humboldt and Bonpland ex Schlechtendahl, Ges. Nat.-Freunde Berlin Mag. 7(4):285 (1815); ex Nestler, Monogr. Potent. 34 *t*.3 *f*.2 (1816). *Potentilla candicans* α *elatior* Humboldt, Bonpland, and Kunth, Nov. Gen. Spec. Plant. 4:216 (1818). MEXICO. "In excelsis umbrosis prope vicum mexicanum Tianguillo, regione frigida inter Mexico et Toluca, altitud. 1505 hexapod." (Nestler), *Humboldt and Bonpland* 4371 in September (P photo GH!).

Potentilla candicans H. B. var. *nana* Humboldt and Bonpland ex Nestler, Monogr. Potent. 34 *t*.4 *f*.2 (1816), *nom. nud*.; Humboldt, Bonpland, and Kunth, Nov. Gen. Spec. Plant. 4:216 (1818). *Potentilla humboldtiana* Trattininck, Ros. Monogr. 4:41 (1824). MEXICO. "Juxta vicum S. Augustin de las Cuevas et in devexis montis El Guarda, in via ad portum Acapulco, alt. 1200-1400 hex[apod]., regione subfrigida" (H. B. K.), *Humboldt and Bonpland* in April. Specimen not seen.

Potentilla candicans H. B. var. *crocea* Lehmann, Revis. Potent. 32 (1856). MEXICO. "Cruz blanca regionis frigida," Valley of Toluca, *Schiede* 585 *ante* 1840 (Authentic specimen or type, with "fl. croceis" in authentic hand, ex herb. Meisner, NY!)

Plants low, with thick rootstock, with erect leaves and ascending stems; basal leaves 5-7 cm long, pinnately divided into 19-23 leaflets; terminal leaflet pinnately parted into 9-10 narrow segments cutting about 90% to midrib; lower leaflets also pinnately parted, densely pilose with twisted hair, giving a yellowish-silvery color to the plant; stem 15-20 cm long, with midstem stipules 9-11 mm long and 4 mm wide, with 3-5 flowers on straight pedicels; calyx large for size of plant, 10-12 mm long; styles long-filiform, 2.4-2.7 mm long.

Mountain slopes and meadows, high mountains of central Mexico, states of Vera Cruz, Puebla, Tlaxcala, Hidalgo, Morelos, and Mexico, 7200-11000 ft. Map, Fig. 26.

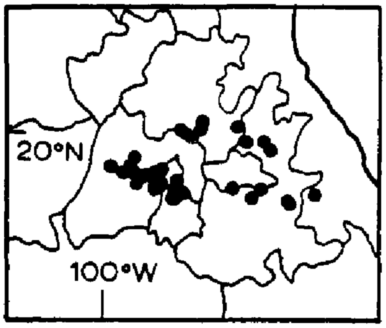


FIG. 26. Central Mexico: Edos. Mexico, Hidalgo, Tlaxcala, Puebla, D. F., and adjoining regions. Distribution of *Potentilla candicans*.

REPRESENTATIVE SPECIMENS. MEXICO. Edo. Mexico, Sierra de las Cruces, *Pringle* 4176 on 16 August 1892 (CAS! [117]); Mpio. Chalco, Rio Frio, Estacion Forestal Zoquiapan, alt. ca. 3500 m, *Garcia M., Rodriguez, and Garcia* 1289 on 16 August 1974 (CAS! [116]).

2. *POTENTILLA BREWERI* S. Watson, Proc. Amer. Acad. Arts Sci. 8:555-556, 564 (1873). CALIFORNIA. [Inyo-Fresno Cos.], summit of Mono Pass, 10765 ft, *Brewer* 1720 in 1863 (Type GH!, 2 isotypes UC! [156]).

2a. *POTENTILLA BREWERI* S. Watson var. *BRUCEAE* (Rydberg) B. C. Johnston, *comb. nov.* *Potentilla bruceae* Rydberg, North Amer. Flora 22(4): 342 (1908). *Potentilla drummondii* Lehmann ssp. *bruceae* (Rydberg) Keck, Canegie Inst. Wash. Publ. 520:180 (1940). OREGON. [Lake Co.], Warner Mountains, *Bruce* 2301 in July 1898 (Type NY! photo and fragment CAS! fragment UC!, isotype CAS! [161]).

Stems decumbent to ascending, 10-20(-25) cm long; basal leaves with rachis 3-11 cm long, with 7-14 verticillate leaflets occupying 10-60% of rachis, petiole glabrous to densely tomentose; terminal leaflet divided into 3-7 toothed lobes; lower leaflets digitate, pinnate, or apically few-toothed, 10-20 mm long, with 5-16 teeth cutting 40-70% to midrib, sparsely to uniformly tomentose, but usually not densely so, and appearing grayish-green; stem with midstem stipules (7-)10-16 mm long and 4-6 mm wide, with 3-15 flowers on erect or ascending pedicels; calyx 6-9 mm high (including lobes), styles 1.8-3.0 mm long.

Mountains meadows and moist slopes at 6100-13000 ft, most abundant in the Sierra Nevada and mountains of northern California, but also in scattered stations through the Cascade Mountains and in the northern Rocky Mountains. Map, Fig. 27.

This is not a sharply-defined variety, as shown by the subgraph (Fig. 25), and has a number of different intermediates to *P. breweri* var. *breweri* and to var. *viridis*. The specimen labeled from Colorado, cited below has tendencies towards *P. drummondii* as well, in its taller stature and larger leaves on longer petioles, but retains the characteristic leaf-dissection and pubescence of var. *bruceae*; it is doubtless a case of a misplaced label. The type of *P. bruceae* is slightly taller than usual, otherwise within normal range for this taxon.

REPRESENTATIVE SPECIMENS. CALIFORNIA. Fresno Co., Upper French Canyon Basin, WNW of Moon Lake, ca. 11000 ft, *Quibell* 5423a on 8 August 1955 (RSA! [011]); Madera Co., glacial amphitheater, Mt. Lyell, 10000 ft, *Jepson* 3336 on 16 July 1909 (UC! [053]); Modoc Co., Warner Mts., Dismal Swamp, Twenty-Mile Creek, S31 T48N R16E, 7300 ft, *Wheeler* 3734B on 1 August 1935 (UC! [026]); Mono Co., Sweetwater Mts., grassy flat near Deep Creek, 10200 ft, *Alexander and Kellogg* 3986 on 2 August 1944 (US! [018]); Tulare Co., Rock Creek, 11300 ft, *Howell* 25542 on 20 July 1949 (CAS! [022]); Tulare Co., between Reflection Lake and Harrison Pass, *Howell* 16045 on 8 August 1940 (CAS! [021]); Tuolumne Co., Yosemite National Park, Gaylor Lakes, *Mason* 747 on 9 August 1923 (UC! [033]). "COLORADO. Teller Co., Divide, *Applegate* 8753 on 17 June 1933 (CAS! [024])" (mislabeled; see text). NEVADA. Elko Co., moist soil, head of Lamoille Canyon, 9500 ft, *Holmgren* 1352AS on 14 July 1941 (UC! [007]); Elko Co., cirque above Island Lake, S36 T32N R58E, ca. 10600 ft, *Johnston* 2271 & 2271A on 27 August 1979 (COLO!). OREGON. Lake Co., slopes of Crane Mtn. near Lakeview, 5000-8000 ft, *Thompson* 13225 on 11 July 1936 (UC! [028]).

2b. *POTENTILLA BREWERI* S. Watson var. *VIRIDIS* Jepson, Man. Flower. Pl. California 488 (1925). CALIFORNIA. Tulare Co., Golden Trout Creek (= Volcano Creek), Mt. Whitney, 8500 ft, *Jepson* 4950 on 3 July 1912 (Type UC! [186]) ("*viridia*").

Potentilla millefolia Rydberg var. *algida* Jepson, Flora Calif. 2:186 (1936). CALIFORNIA. Trinity Co., Salmon Mts., North Fork Swift Creek, glacial meadow, 6500 ft, *Hall* 8698 in July 1909 (Type UC! [187]).

Potentilla millefolia Rydberg var. *glacialis* Jepson, *nom. herbariorum provis. pro P. millefolia* var. *algida* Jepson.

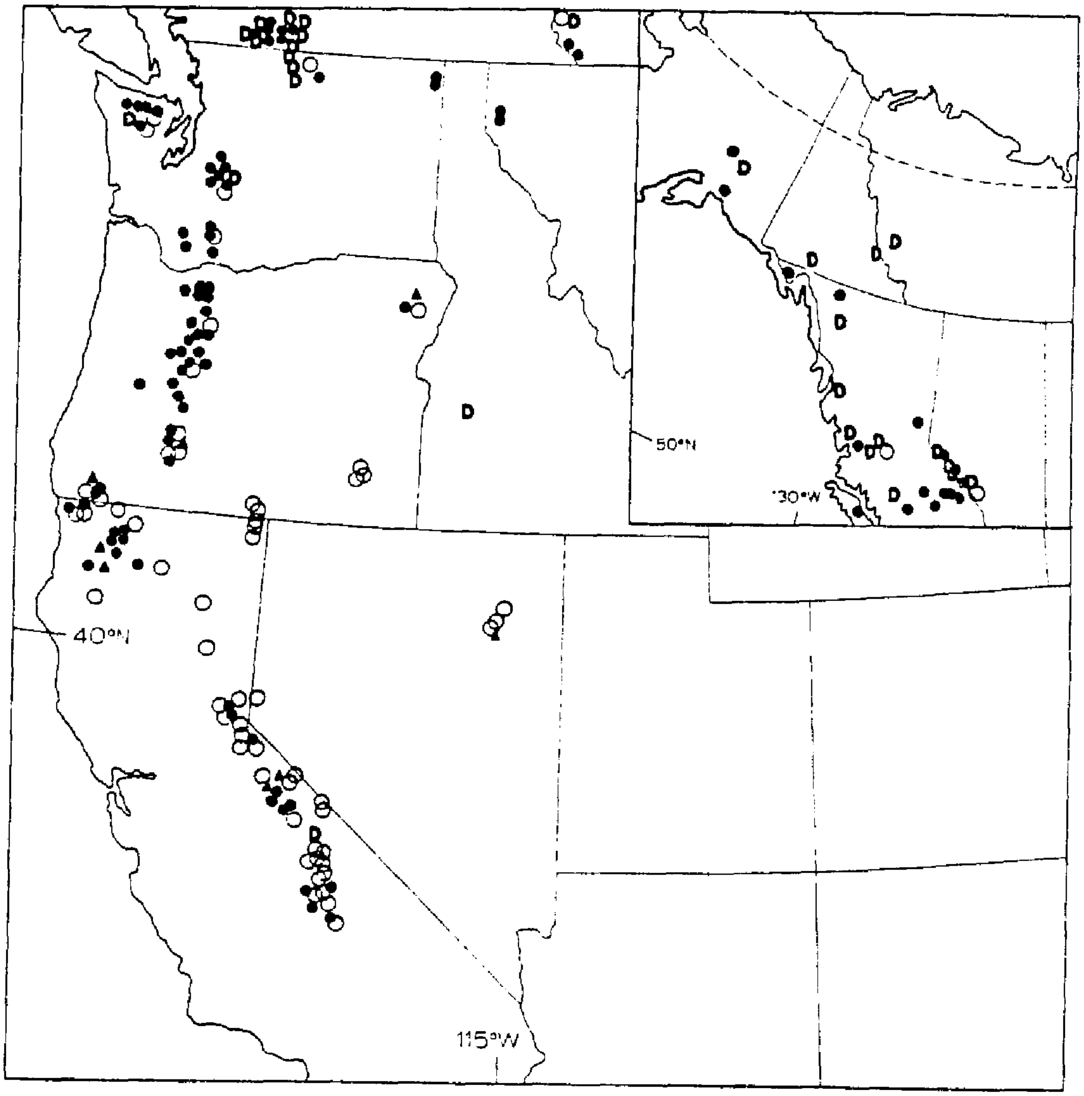


FIG. 27. Western United States; inset: western Canada and Alaska. Distribution of *Potentilla drummondii* (closed circles), its dissected phase "*anomalifolia*" (triangles); and of *P. breweri* var. *bruceae* (open circles). D = subdigitate and digitate transitions from *P. drummondii* to *P. diversifolia*.

Stems decumbent to ascending, 10-30 cm long; basal leaves usually much shorter than stems, with rachis 2-4(-7) cm long, with (9-)11-18 verticillate leaflets occupying 40-60(-70)% of rachis, petiole glabrous to tomentose; terminal leaflet usually divided into 3-7 toothed lobes; lower leaflets digitate or apically few-toothed, with 3-6 teeth cutting 50-70(-80)% to midrib, glabrous or sparsely tomentose, usually appearing green or grayish-green; stem with midstem stipules 9-15(-19) mm long and (2-)4-7 mm wide, with 3-15 flowers on erect (or rarely recurved) pedicels; calyx 6-9 mm high (including lobes), styles 1.5-2.4(-3.0) mm long.

Mountain meadows and damp forest floors, Sierra Nevada and in the Steens Mountains of southeastern Oregon, 9000-11500 ft. Map, Fig. 28.

This variety has the characteristic decumbent stems and small, apparently-pinnate leaves of *P. breweri* var. *breweri*, but has much less pubescence; often the leaves are proportionally smaller than in var. *breweri*. The type of var. *viridis* has a longer, narrower stipule, and some pedicels recurved; the type of var. *algida* has longer leaves, with more of the rachis occupied, deeper-cut leaflets, and a longer style. Otherwise both are within the range of characters for this taxon.

REPRESENTATIVE SPECIMENS. CALIFORNIA. Fresno Co., trail west of Taboose Pass, 11100 ft, *Raven* 9741 on 16 July 1956 (CAS! [012]); Inyo Co., seep above Kearsarge Pass trail, west of Independence, 10500 ft, *Alexander and Kellogg* 3269 on 7 August 1942 (US! [008]); Inyo Co., Big Pine Lakes, west of Sixth Lake, ca. 11200 ft, *Howell* 23866 on 7 August 1947 (CAS! [009]); Nevada Co., meadow northwest of Castle Peak, *Howell* 18558 on 18 July 1943 (CAS! [004]). OREGON. Harney Co., Steens Mts., vicinity of head of Kiger Creek, *Peters s.n.* in August 1962 (CAN! [005], UC! [010]).

2c. *POTENTILLA BREWERI* S. Watson var. *BREWERI*

Potentilla breweri S. Watson var. *expansa* S. Watson, Bot. Calif. 1:179 (1876). CALIFORNIA. Sierra Co., *Lemmon* 64 in 1874 (Type GH!, 2 isotypes NY!).

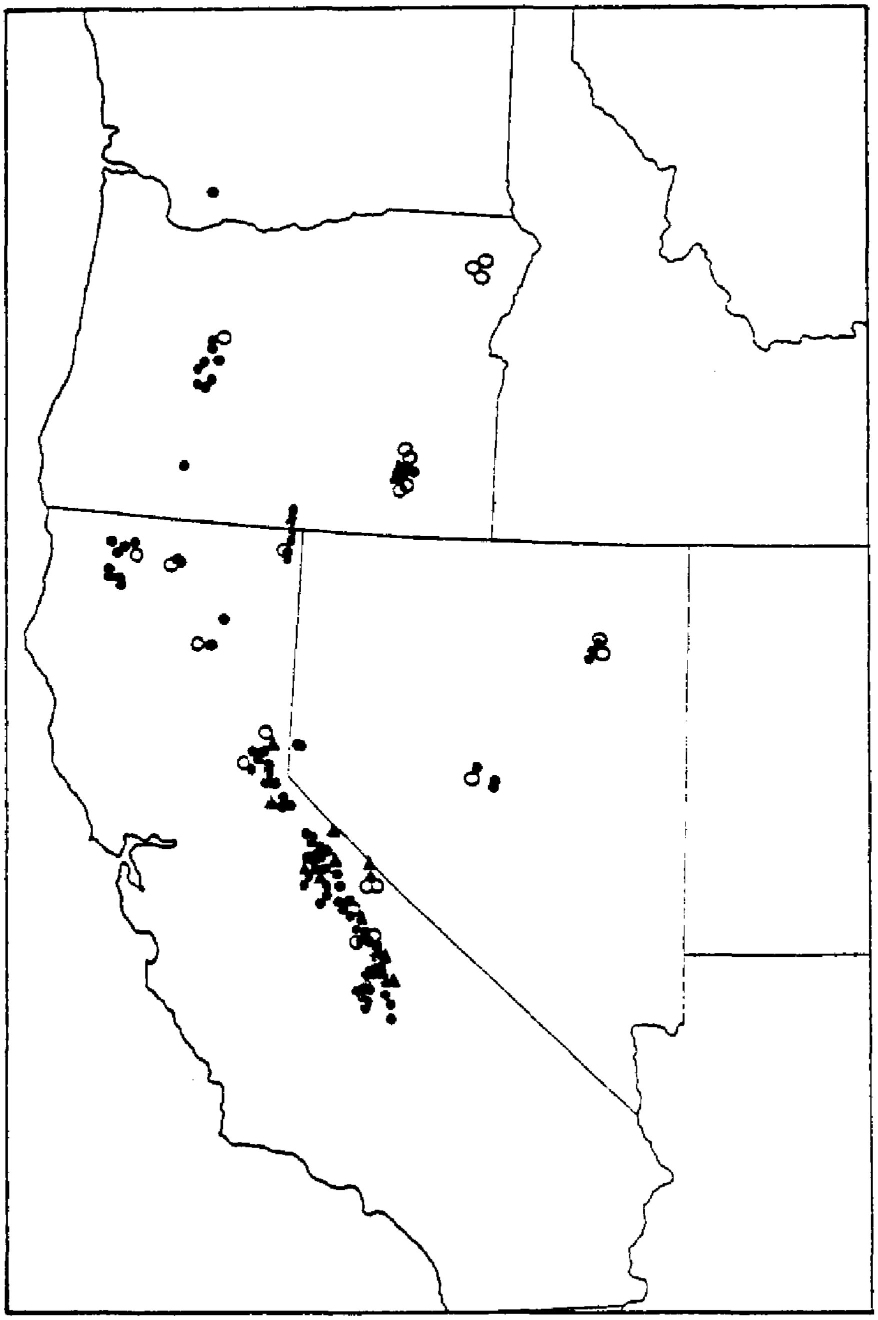


FIG. 28. California, Nevada, Oregon, and parts of adjoining states. Distribution of *Potentilla breweri* var. *breweri* (closed circles), and its lighter-color phase (open circles); and of *P. breweri* var. *viridis* (triangles).

Potentilla plattensis Nuttall var. *leucophylla* Greene, Erythea 1:5 (1893). CALIFORNIA. Nevada Co., Independence Lake, meadows, *Sonne* 1 on 26 June 1893 (1892?) (NY! UC! [164]).

Stems decumbent to erect, 10–40 cm long; basal leaves usually about half as long as stems, with rachis 2-11(-14) cm long, with 9-21(-23) verticillate leaflets occupying (20-)50-70% of rachis, petiole uniformly to densely tomentose; terminal leaflet divided into 3-7 toothed lobes; lower leaflets digitate, apically few-toothed, or lobed, with 3-10 teeth cutting 50-80% to midrib, uniformly to (usually) densely tomentose, usually appearing silvery-gray; stem with midstem stipules (8-)10-17 mm long and 2-8 mm wide, with 3-20 flowers on erect or ascending pedicels; calyx 6-10 mm high (including lobes), styles (1.8-)2.4-3.3 mm long.

Wet mountain meadows, Sierra Nevada and Warner Mountains of California, and in the Cascades to northern Washington; also in central and northeastern Nevada and in eastern Oregon, 4500-12000 ft. Map, Fig. 28.

The typical phase of this variety has silvery-gray leaves and petioles, but another phase has grayish-green leaves, while being like *breweri* in every other character. These two phases may form separate populations at the same site, with the grayish-green phase often occurring on drier habitat, as noted in the collections of *Cronquist* 8698 and *Johnston* 2272. The type of var. *leucophylla* at UC has "1892" in an unknown hand, whereas the NY specimen has "1893" in the collector's hand.

REPRESENTATIVE SPECIMENS (SILVERY-GRAY LEAVES). CALIFORNIA. Mono Co., near Carnegie Alpine Station, Slate Creek, 10000 ft, *Abrams* 13588 on 29 June 1934 (CAS! [055]); Shasta Co., Big Meadow, Thousand Lake Basin, 6400 ft, *Peirson* 10170 on 13 July 1932 (RSA! [049]); Sierra Co., *Lemmon* 85 in 1875 (UC! [052] NY! [058]); Siskiyou Co., Shackelford Canyon, near Marble Mtn., meadow, *Jepson* 2815 on 4 July 1907 (UC! [051]); Tulare Co., Hockelts Meadow, *Culberson* 4458 on 18 July 1904 (CAS! [057]); Tuolumne Co., Dana Fork of Tuolumne River, Yosemite National Park, creek bottoms, *Mason* 723 on 7 August 1923 (CAS! [023]). NEVADA. Elko Co., moist soil on slopes south of basin above Island Lake, Ruby Range, 10600 ft, *Maguire and*

Holmgren 22586 on 16 August 1943 (WTU! [059]); same loc., *Johnston* 2272 on 27 August 1979 (COLO!); Nye Co., basin meadow, head of Pine Creek, Toquima Range, 11000 ft, *Maguire and Holmgren* 25808A on 16 July 1945 (UTC! [062]). OREGON. Lane Co., moist ground along McKenzie Pass, 7 mi west of summit, *Peck* 9805 on 7 August 1920 (WTU! [060]); Harney Co., mountain meadow above Blitzen Gorge, Steens Mts., 7500 ft, *Thompson* 12101 on 15 July 1935 (PH! [054]); Lake Co., alpine slopes of Crane Mtn., near Lakeview, 8000 ft, *Thompson* 13225 on 11 July 1936 (WTU! [061]); wet meadows, Cougar Peak, 1900 m, *Coville and Leiberg* 2800 on 3 August 1896 (ORE! [025]).

(GRAYISH-GREEN LEAVES). CALIFORNIA. Modoc Co., Warner Mts., meadow, Highgrade, north end of range, 7800 ft, *Alexander and Kellogg* 4872 on 30 June 1946 (US! [019]). OREGON. Deschutes Co., Todd Lake, 21 mi southwest of Bend, S18 T18S R8E, 6150 ft, wet meadow, *Crosby* 1017 on 2 September 1976 (ORE! [040]); Harney Co., dry meadows, head of McCoy Creek, Steens Mts., S2 T33S R33E, ca. 9000 ft, *Cronquist* 8699 on 14 July 1959 (CAS! [056]); Harney Co., breaks at head of Big Fish Creek Canyon, Steens Mts., *Maguire and Holmgren* 26793 on 1 August 1946 (NY! [006]). NEVADA. Elko Co., East Humboldt Mts., 10000 ft, *Jones s.n.* on 13 August 1897 (POM! [027]).

3\. *POTENTILLA DRUMMONDII* Lehmann, Stirp. Lehm. Prim. Descript. Pugillus 2:9 (1830); ex Hooker, Fl. Bor.-Amer. 1:189-190 t.65 (1832). CANADA. "Alpine woods in the Rocky Mountains, north of the Smoking River, in latitude 56°, scarce. *Drummond*." (Hooker) Type not seen, see discussion below.

Potentilla cascadensis Rydberg, Mem. Dept. Bot. Columbia Univ. 2:109 (1898). *Potentilla drummondii* Lehmann var. *cascadensis* (Rydberg) Wolf, Bibl. Bot. 16(71):492-493 (1908). WASHINGTON. Skamania Co., Chiquash Mts., "Seenberg," at about 5000 ft alt., *Suksdorf* 2165 on 14 September 1896 (Holotype NY! labeled "Type" by Rydberg, isotypes WTU! UC!); Skamania Co., meadows, Chiquash Mts., *Suksdorf* 2165 on 18 August 1892 (NY! CAS! GH! UC! [158] US!).

Potentilla breweri S. Watson var. *chiquashensis* Rydberg, *nom. herbariorum provis. pro P. cascadensis* Rydberg.

Potentilla anomalifolia Peck, Proc. Biol. Soc. Washington 49:110 (1936). OREGON. Klamath Co., "in a damp meadow 3 mi north of" Klamath Agency, *Peck* 16819 on 10 July 1933 (1932?) (WS! [159] UC!)

Stems ascending to erect, (15-)25-50 cm tall; basal leaves with rachis (6-)10-18 cm long, with 2-12(-16) leaflets occupying (0-)10-50% of rachis, petiole glabrous to sparsely tomentose; terminal leaflet pinnate or divided into 3-7 toothed lobes; lower leaflets pinnate or apically few-toothed (rarely lobed), with 5-16 teeth cutting 30-60(-80)% to midrib, glabrous to uniformly (but lightly) tomentose, usually green, stem with midstem stipules 11-22(-33) mm long and 5-9 mm wide, often divided; stem with 3-20 flowers on erect pedicels; calyx 7-12 mm high (including lobes); styles 1.8-3.0 mm long.

Moist mountain meadows, primarily in the Cascade Mountains, Olympic Peninsula, and northern Rocky Mountains, but also more scattered through the Sierra Nevada, to central Alaska, and in the Wallowa mountains of northeastern Oregon, 6000-11500 ft. Map, Fig. 27.

The typical form of *P. drummondii* is a large plant with large pinnate leaves and large stipules; however, there is considerable variation within this species. Subdigitate or digitate plants occur from the Olympic Peninsula through northwestern Washington and southwestern British Columbia northward to southwest Mackenzie; they can be difficult to distinguish from *P. diversifolia* in the northern part of this range, but in general *P. drummondii* occupies moister habitats and has larger stipules and leaflets. The leaves of *P. drummondii* often are more flabellate with verticillate leaflets, and often are darker green than those of *P. diversifolia* because of varying amounts of anthocyanin; *P. drummondii* is never glaucous or sericeous.

Although the type of *P. drummondii* has not been seen, it is possible to match Hooker's beautiful plate and Lehmann's description with certain specimens; the one I have chosen as matching the typical form is *McCalla* 5225 [046], cited below.

P. cascadensis is somewhat transitional to *P. breweri* in its pubescence, while retaining the characteristic leaf dissection and plant stature of *P. drummondii*; the type specimens of *P. cascadensis* differ from the rest of this taxon only in their smaller leaflets. The form represented as *P. anomalifolia* has lower leaflets divided into 5-7 toothed lobes (like the terminal leaflet), and the ultimate segments are highly dissected 80% or more to the midrib; the lower leaflets have some straight hair in addition to tomentum sparsely. This form appears sporadically through the range of *P. drummondii*; it may be a sporadic genetic variant, or less likely a hybrid.

REPRESENTATIVE SPECIMENS (PINNATE LEAVES). CALIFORNIA. Fresno Co., Piute Creek, 10300 ft, *Peirson* 2629 on 8 August 1921 (RSA! [017]); Trinity Co., North Fork Trinity River, grassy meadow bordering Whites Creek Lake, S28 T36N R12W, 6250 ft, *Carter* 483 on 28 June 1972 (CAS! [039]); Tuolumne Co., Yosemite National Park, moist flat below Lukens Lake, *Hall* 12841 on 21 July 1930 (CAS! [041]); Tuolumne Co., Yosemite National Park, Dana Fork of Tuolumne River, 0.5 mi from mouth of Moraine Creek, *Mason* 736 on 8 August 1923 (UC! [043]). WASHINGTON. King Co., Snoqualmie Pass, *Broadbent s.n.* on 23 June 1935 (CAS! [048]); Pend Oreille Co., along trail north of Shedroof Mtn., S24 T40N R45E, 6400 ft, *Layser* 1072 on 27 July 1969 (WS! [047]); Pierce Co., Berkeley Park, east side of Mt. Rainier, well-watered meadow, *McCalla* 5225 on 20 August 1938 (ALTA! [046]). CANADA. ALBERTA. Banff National Park, vic. Mt. Temple Ski Lodge, 6200-8500 ft, *Porsild and Breitung* 12592 on 4-14 July 1945 (CAN! [042]). BRITISH COLUMBIA. Grassy slopes, mountains north of Griffin Lake, *Macoun* 7310 on 8 August 1889 (CAN! [020]).

(DIGITATE-SUBDIGITATE LEAVES). WASHINGTON. Okanogan Co., alpine meadow, Mt. Tiffany, 6500 ft, *Fiker* 1108 on 17 July 1932 (US! [015]). CANADA. BRITISH COLUMBIA. Ilgachuz Mts., Festuca Pass, wet meadow, 52°45'N 125°15'W, *Taylor, Beil, Marchant, and Oliver* 5819 on 15-25 August 1972 (DAO! [014]).

4. *POTENTILLA MULTISECTA* (S. Watson) Rydberg, Bull. Torrey Bot. Club 23: 397 (1896). *Potentilla diversifolia* Lehmann var. *multisecta* S. Watson, Bot. King's Explor. 86-87 (1871). *Potentilla dissecta* Pursh var. *multisecta* (S. Watson) S. Watson, Proc. Amer. Acad. Arts Sci. 8:557,565 (1873). NEVADA. [Elko Co.], East Humboldt Mountains, 9000 ("10000") ft, *Watson* 330 in July 1868 (Holotype GH!, isotypes NY! US! [173]).

Potentilla dissecta Pursh var. *linearis* M. E. Jones, *nom. herbariorum provis.* NEVADA. Glencoe, *Jones s.n.* on 29 June 1891 (POM! [172]).

Stems decumbent to ascending, 10-15 cm long; basal leaves with rachis (4-)5-8(-9) cm long, digitate to subdigitate with 5-8(-12) leaflets occupying 0-20(-40)% of rachis, petiole strigose; terminal leaflet pinnately dissected into long narrow segments; lower leaflets digitately (rarely pinnately) dissected into long narrow segments, with 3-8 teeth cutting 70-90% to midrib, moderately strigose to densely covered with strigae, often grayish in color; stem with midstem stipules 8-10 mm long and 2-4 mm wide, with 3-10 flowers on recurved (rarely erect) pedicels in fruit; calyx 6-7 mm high (including lobes), styles 2.1-3.0 mm long.

Dry rocky slopes, often in limy granite or limestone gravel, lower slopes to summit ridges, usually montane, Basin Ranges of east-central Nevada and western Utah, 6800-10600 ft. Map, Fig. 29.

In its typical form, which grows on open exposures, the plants are low with short leaf-raches, but these is also a large, lax shade form in moister rock crevices and ledges.

In its digitate leaves and appearance, plants of this species simulate those of *P. concinna* var. *curvata*, but that variety has apically few-toothed leaflets, more caespitose habit, and glandular pubescence in addition to strigose.

REPRESENTATIVE SPECIMENS. NEVADA. Elko Co., sandy loam, north exposure, 18 mi southwest of Wendover, S32 T30N R68E, 6800 ft, *Cooper, Holmgren, and Lund* 88 on 13 May 1939 (UTC! [127]); Elko Co., gravelly soil, top of Spruce Mtn., *Holmgren* on 25 June 1941 (UTC! [125]); Elko Co., granite outcrop, 1 mi south of Harrison Pass, Ruby Mts., ca. 7800 ft, *Tucker* 2399 on 30 May 1952 (CAS! [121]); White Pine Co., White Pine Mts., draw on east side of Currant Mtn., S11 T12N R58E, 10000 ft, *Holmgren, Reveal, and LaFrance* 2191 on 17 July 1965 (NY! [122]); White Pine Co., Egan Range, Ward Ridge, S30 T15N R63E, 10600 ft, *Holmgren and Reveal* 2798 on 3 July 1966 (UTC! [126]). UTAH. Juab Co., road to Basin Creek, Deep Creek Range, S10 T11S R18W, 7600-7800 ft, *Johnston* 2088 on 17 June 1979 (COLO!); Tooele Co., Deep Creek Mts., ca. 7 mi SSE of Ibapah, S19 T10S R18W, 7000 ft, *Welsh, Foster, and Henriod* 16862 on 7 June 1978 (COLO! [123]).

5. *POTENTILLA PLATTENSIS* Nuttall ex Torrey and Gray, Flora North Amer. 1:439 (1840). [WYOMING]. "Plains of the Platte," Upper Platte---Sweetwater, *Nuttall s.n.* no date (Holotype PH! [170], isotypes NY!, GH!, BM photo NY! WS!).

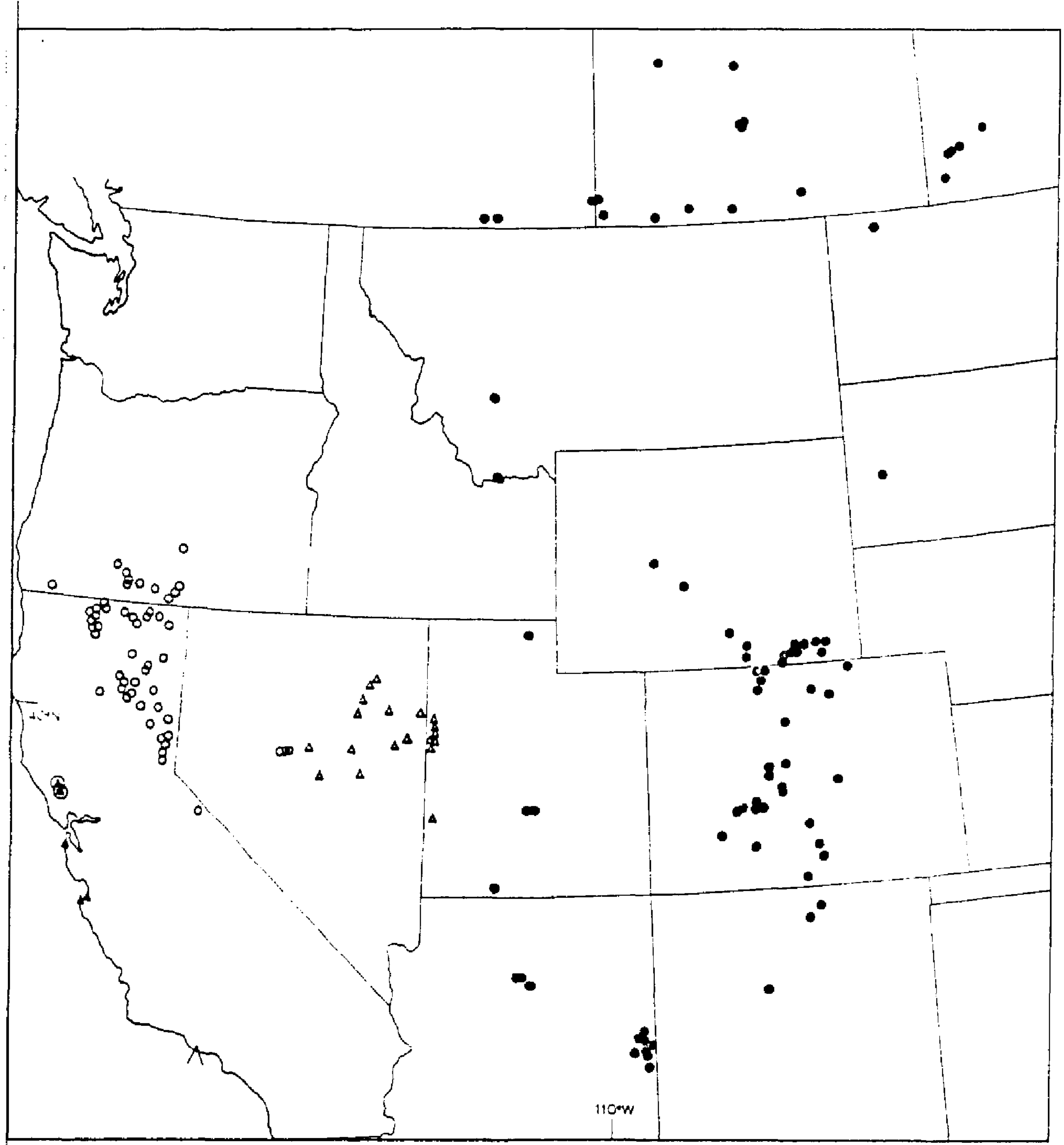


FIG. 29. Western United States and southwestern Canada. Distribution of: *Potentilla hickmanii* (closed triangles); *P. millefolia* (open circles); *P. multijuga* (large open triangle); *P. multisecta* (small open triangles); *P. plattensis* (closed circles); and *P. uliginosa* (closed triangles within circles).

Ivesia pinnatifida S. Watson, Proc. Amer. Acad. Arts Sci. 20:364 (1885), *non Potentilla pinnatifida* Linnaeus (1753). *Potentilla arizonica* Greene, Pittonia 1:104 (1887), based on *Ivesia pinnatifida* S. Watson. ARIZONA. [Coconino Co.], meadows near Flagstaff, *Lemmon and Lemmon* 3200 on 23 August 1884 (September?) (Holotype GH!, 5 isotypes UC! [184]).

Potentilla plattensis Nuttall var. *pedicellata* A. Nelson, Bull. Torrey Bot. Club 28:223 (1901). WYOMING. Albany Co., in the grass on the open borders of a stream, Centennial, *A. Nelson* 7730 on 27 July 1900 (Holotype RM!, isotypes NY! POM! [171]).

Potentilla plattensis Nuttall fma. *stenoloba* Th. Wolf, Bibl. Bot. 16(71):494 (1908). Based on figure in Rydberg, Mem. Dept. Bot. Columbia Univ. 2 *t.*46 *f.*11 (1898), no specimens cited.

Potentilla plattensis Nuttall fma. *platyloba* Th. Wolf, Bibl. Bot. 16(71):494 (1908). "Dies...typische Nuttallsche Form sein."

Stems decumbent to rarely ascending, creeping, 5-25 cm long; basal leaves with rachis 3-11 cm long, pinnate with 11-23 verticillate or subverticillate leaflets occupying 40-70% of rachis, petiole strigose or glabrous; terminal leaflets and lower leaflets pinnately dissected with comparatively narrow segments, with 5-8 teeth cutting 70-90% to midrib, glabrous to uniformly strigose, usually green to slightly grayish-green in color; stem with midstem stipules (7-)9-15 mm long and (2-)4-6 mm wide, with 3-15 flowers on recurved pedicels in fruit; calyx (5-)6-8 mm long, styles 1.5-3.0 mm long.

Wet meadows and streamsides, bogs and sloughs, lowlands from central Alberta and southwestern Manitoba southward along the western edge of the Great Plains to central New Mexico; from east-central and north-central Arizona northward into central Utah; and in wet bottoms of the intermontane valleys of the southern Rocky Mountains, 1200 ft (Manitoba) to 9600 ft (Colorado valleys). Map, Fig. 29.

This species is remarkable uniform, considering its large range. As Rydberg (1898) pointed out, there are two forms, a less-dissected prostrate form, and a laxer, looser, more-dissected form. In several localities, both forms were seen at the same site (*Johnston* 2234-2235 and 2286), the laxer, more-dissected form weaving through tall grasses and sedges of a bog, and the prostrate form on adjacent rocky slopes.

REPRESENTATIVE SPECIMENS. ARIZONA. Greenlee Co., hwy. 666 1 mi north of Blue Jct., meadow, *Pinkava, Keil, and Lehto* 13937 on 7 September 1968 (ARIZ! [147]); Greenlee Co., 1.9 mi east of Buffalohead Jct., *Pinkava, Lehto, and Reeves* P12409 on 14 August 1974 (ARIZ! [146]). COLORADO. Costilla Co., headwaters of Sangre de Cristo Creek, 2700 m, *Rydberg and Vreeland* 6046 on 10 June 1900 (RM! [150]); Jackson Co., North Park on edge of Wyoming, Big Creek Park, *Osterhout* 1742 on 25 July 1898 (RM! [155]); Park Co., 0.3 mi northeast of Jefferson, wet meadow, S5 T8S R75W, 9500 ft, *Johnston* 2234-2235 on 22 August 1979 (COLO!). MONTANA. Beaverhead Co., Monida, *Jones* 8250 on 14 July 1908 (POM! [092]). NEW MEXICO. Taos Co., Red River, meadow, 8600 ft, *Castetter* 1761 on 2 July 1932 (RM! [149]). NORTH DAKOTA. Williams Co., McGregor, edge of coulee, *Stevens* 871 on 29 June 1946 (GH! [154]). UTAH. Cache Co., moist area along trail to Mt. Naomi, 8800 ft, *Snell* 1038 on 6 August 1938 (UTC! [120]); Kane Co., marsh on upper Kanab Creek, *Folks s.n.* on 8 August 1961 (UTC! [151]); Sevier Co., Fish Lake, gravel, 9000 ft, *Jones* 5790f on 9 August 1894 (POM! [148]). WYOMING. Albany Co., ca. 2.5 mi southeast of Centennial, S12 T15N R78W, 7820 ft, *Johnston* 2286 on 30 August 1979 (COLO!). CANADA. MANITOBA. Oak River near Lothair, *Macoun and Herriot* 69812 on 21 June 1906 (2 sheets GH! [153]). SASKATCHEWAN. Lake Centre Dist., saline flat on benchland, slopes of Arm River, *Boivin and Dore* 7535 on 2 July 1951 (MAN! [152]).

6. *POTENTILLA ULIGINOSA* B. C. Johnston, in ed.

TYPE. CALIFORNIA. Sonoma Co., Cunningham Marsh, *Milo S. Baker* 11831 on 26 June 1947 (Holotype UC!, isotypes CAS! [139] RSA!).

OTHER SPECIMENS SEEN. CALIFORNIA. Sonoma Co., Analy Township, *Congdon* 277 on 16 May 1880 (GH! [137]); Sonoma Co., Cunningham Marsh, *Baker* 11550 on 17 August 1946 (RSA! CAS! [138]); same locality, *Howell* 22861 on 17 August 1946 (US! CAS!); same locality, *Baker* 10831 on 26 June 1947 (UC!); same locality, *Howell* 23297 on 26 June 1947 (CAS! NY!).

PLANTA perennis elata caulibus erectis 25-55 cm longis, e caudice crasso verticali non ramoso plerumque unicipiti fuscis stipularum petiolorumque emortuarum dense vestito, in aspecto plerumque stramentosa. CAULES petiolaque graciles, incavi, ferruginei, glabrati vel obscure sparseque strigosi. FOLIA RADICALIA erecti, rhachide 21-25(-29) cm longa, folioliis 17-21(-25) verticillatis pinnatis, 40-60% rhachidis occupantis. FOLIOLUM TERMINALE pinnatim profunde in segmenta longa angusto-lanceolata divisum. FOLIOLA DEMISSIORA similiter pinnatim divisa; foliola demississima palmatim divisescentes; omnes foliolorum segmentis 7-10 angusto-lanceolatis 70-90% ad costam incisi, sparse ad uniformiter utrinque strigosi sed obscure, in aspecto virides glabrescentesque. Caules, STIPULIS medicaulinis 11-16 mm longis

4-5 mm latis plerumque divisis, floribus 6-10 in pedicellis recurvatis tempore fructificantis. CALYX 9 mm altus (lobis inclusis), moderate vel dense strigosus, lobis lanceolatis brevi-acuminatis, bracteolis ovatis lobis 0.7-1.0-plo longioribus. STAMINA 20, antheris 0.7-0.9 mm longis in filamentis 1.5-2.8 mm longis. PISTILLA ca. 20; STYLIS 2.7-3.6 mm longis, filiformibus, e basi leviter angustatis, stigmatibus conspicuis papillosis rubiginosis capitatis. ACHAENIA 2.0-2.6 mm longa, viridula, laevia.

Habitat solum in paludo uliginosa maritima prope Cunningham in California. Speciei distributio in tabulo 29 depicta.

Tall plants with erect stems 25-55 cm tall, from a thick vertical unbranched rootstock, the usually solitary root-crown covered with the dark red-brown remains of previous seasons' stipules, which often remain attached to their petioles, giving the plant a thatched look; stems and petioles thin, hollow, reddish-brown, glabrous to sparsely and obscurely strigose; basal leaves erect, on rachis 21-25(-29) cm long, with 17-21(-25) verticillate leaflets pinnately disposed, occupying 40-60% of the rachis; terminal leaflet pinnately deeply divided into long narrowly-oblanceolate segments; lower leaflets also pinnately divided, lowest leaflets becoming palmately divided, all with 7-10 narrowly-oblanceolate segments cutting 70-90% to midrib, sparsely to uniformly strigose on both surfaces but always obscurely so, appearing green and glabrescent to the naked eye; stems with midstem stipules 11-16 mm long and 4-5 mm wide, usually divided; stems with 6-10 flowers per stem on recurved pedicels in fruit; calyx 9 mm high (including lobes), moderately to densely strigose, with lanceolate short-acuminate lobes and ovate bractlets 0.7 as long as the lobes or longer; stamens 20, anthers 0.7-0.9 mm long on narrow filaments 1.5-2.8 mm long; pistils ca. 20, with styles 2.7-3.6 mm long, filiform and very slightly tapered from the base, with a conspicuous papillose red-brown capitate stigma; achenes 2.0-2.6 mm long, light-green and smooth.

This distinctive species has heretofore been included with *P. hickmanii* Eastwood, to which it has little resemblance, differing in habit, size of stems and leaves, number and pattern and degree of dissection of leaves, and length of styles. *P. uliginosa* is closest morphologically to *P. plattensis*, from which it is geographically disjunct and distinctive in habit, size of stem and leaves, and larger flowers. *P. uliginosa* must be compared with the apparently extinct *P. multijuga*, with which it shares habitat, habit, growth-form, and stature; *P. uliginosa* differs in its larger number of leaflets which have more teeth and are much more deeply incised.

7. *POTENTILLA MULTIJUGA* Lehmann, Delect. Sem. Hort. Hamburg 6 (1849); Lehmann, Revis. Potent. 29 t.7 (1856). "Habitat in California." Type or authentic specimen not seen; see discussion below.

Tall plants, erect to ascending, with stems 20-35 cm long; basal leaves with rachis 15-21 cm long, reddish-brown in color, petiole obscurely strigose; terminal leaflet divided into 3-7 toothed lobes; lower leaflets often confluent with the rachis, pinnately toothed, apically few-toothed, or becoming palmately toothed, with 2-6 teeth cutting 30-40% to midrib, sparsely and obscurely strigose, appearing green and glabrescent to the naked eye; stems with midstem stipules 7-14 mm long and 4-7 mm wide, with 3-5 flowers on recurved pedicels in fruit; calyx 6-8 mm high (including lobes); styles 2.4-3.3 mm long.

Coastal swamp near Bellona, Los Angeles Co., California. Apparently extinct. Map, Fig. 29.

This species, the type species of *Potentilla* sect. Multijugae, was amply described and figured by Lehmann, but he did not cite a locality (other than "California") nor a collector. Sereno Watson (1876) and after him Edward L. Greene (1891) thought it to be an *Horkelia*, even though the flowers in Lehmann's plate were obviously those of a *Potentilla*. In 1890-1893 this species was collected near Los Angeles by Dr. H. E. Hasse, whose specimens are a very good match for Lehmann's description and plate; Hasse's specimens are the only ones known of this species.

There is apparently no type specimen. Wolf (1908, pp. 490-491) had no other specimens besides Hasse's, even though he used Lehmann's personal herbarium extensively. The specimen should be searched for in other European herbaria, especially those of Britain.

REPRESENTATIVE SPECIMENS. CALIFORNIA. Los Angeles Co., *Hasse* 4950 in June 1890 (NY! [143]); Los Angeles Co., near Los Angeles, low brackish meadow, *Hasse s.n.* in April 1892 (ND-G! [144]).

8. *POTENTILLA HICKMANII* Eastwood, Bull. Torrey Bot. Club 29:77-78 (1902). CALIFORNIA. Monterey Co., "in a forest of *Pinus radiata* Don, near the reservoir which supplies Pacific Grove, along the road to Cypress Point," near Monterey, ca. 36.5° lat., *Eastwood s.n.* on 4 April 1900 (Holotype CAS! [162], isotypes NY! GH!).

Low plants, with decumbent to ascending stems 10-15 cm long; basal leaves with rachis 5-8 cm long, with 11-12(-14) non-verticillate leaflets occupying 40-70% of rachis; terminal leaflet divided into 3-5 toothed lobes; lower leaflets often flabelliform, digitately toothed or divided, with 2-3(-5) teeth cutting 50-60% to midrib, glabrous or sparsely and obscurely strigose, appearing green and glabrescent to the naked eye; stems with midstem stipules 10-11 mm long and 3-5 mm wide, with 3-5 flowers on erect or more often recurved pedicels in fruit; calyx 9 mm long (including lobes); styles (2.1-)2.7-3.6 mm long.

Marshy places and wet coastal meadows, Monterey Co., and San Mateo Co., California. Map, Fig. 29.

This distinctive species is like no other, and differs from other species in this section in its flabelliform leaflets with crenate teeth, low growth, and the habitat, among other characters.

REPRESENTATIVE SPECIMENS. CALIFORNIA. Monterey Co., Pacific Grove, Monterey, *Eastwood* 2467 on 9 March 1913 (GH! [141]); Monterey Co., Monterey Peninsula, Indian Village Picnic Grounds, Del Monte Forest, *Norman* 2098 on 23 May 1968 (CAS! [140]); San Mateo Co., Moss Beach, near Halfmoon Bay, *K. Brandegee s.n.* on 20 June 1905 (UC! [142]).

9. *POTENTILLA MILLEFOLIA* Rydberg, Bull. Torrey Bot. Club 23:433-434 *t.*277 *f.*1-5 (1896). *Potentilla plattensis* Nuttall var. *millefolia* (Rydberg) Jepson, Man. Flower. Pl. California 488 (1925). CALIFORNIA. Sierra Co., *Lemmon* 86 in 1875 (Holotype US! [169], isotypes 5 sheets NY! PH! UC!).

Potentilla klamathensis Rydberg, North Amer. Flora 22(4):343 (1908). *Potentilla plattensis* Nuttall var. *klamathensis* (Rydberg) Jepson, Man. Flower. Pl. California 488 (1925). *Potentilla millefolia* Rydberg var. *klamathensis* (Rydberg) Jepson, Flora California 2:186 (1936). OREGON. [Klamath Co.], near Fort Klamath, meadows, low grassy ground, *Leiberg* 660 on 7 August 1894 (Holotype US! [176] photo NY!, isotypes NY! ORE!, possible isotype WS!).

Potentilla versicolor Rydberg, North Amer. Flora 22(4):344 (1908). OREGON. [Lake Co.], Gearhart ("Grayheart") Butte, 2200 m, *Coville and Leiberg* 307 on 9 August 1896 (Holotype US! [183] photo and fragment NY!). Topotype. OREGON. [Lake Co.], wet meadows, "Gayhart" Buttes, alt. 2200 m, *Leiberg and Coville* 2918 on 8 August 1896 (ORE! [180]).

Potentilla millefolia Rydberg var. *densa* Jepson, Flora California 2: 186 (1936). CALIFORNIA. Lassen Co., "montane meadows," Norval Flat, near Westwood Junction, deep volcanic soil, flat slope, 5732 ft ("6000-7000 ft"), *Robinson* 7 no date (Holotype UC! [185]).

Low plants, stems prostrate-decumbent to spreading to sometimes ascending, 5-25 cm long; basal leaves with rachis (2-)5-13 cm long, with 15-23(-25) verticillate leaflets occupying (50-)60-80% of rachis, petiole strigose or occasionally glabrous; terminal leaflet pinnately dissected or more commonly dissected into 3-7 toothed lobes; all other leaflets digitately dissected, with 2-6 teeth cutting 60-90% to midrib, sparsely to uniformly strigose to hispid, the pubescence usually visible to the neked eye as a grayish tinge to the yellow-green color of the foliage; stems with midstem stipules 8-13 mm long and 3-4(-6) mm wide, with 3-10 flowers on recurved pedicels in fruit; calyx (6-)8-11 mm high (including lobes); styles 1.8-3.3 mm long.

Wet meadows of mountain or intermountain valleys, east-central and northeastern California, southwestern Oregon, and central Nevada, 2500-6500 ft. Map, Fig. 29.

This species is usually distinguishable from *P. plattensis* by its digitately divided lower leaflets and comparatively larger flowers. These characters allow the Nevada specimens to be included here; they are otherwise intermediate between the two species.

Var. *densa* is clearly simply a reduced-caespitose form, such as is commonly found in the same site as the loosely-branching form in the closely related species *P. plattensis*. *P. klamathensis* has a more ascending stem, but is otherwise indistinguishable from *P. millefolia*. *P. versicolor* combines the habit and leaflet dissection of *P. millefolia* with the pubescence of *P. breweri*, and thus probably represents a hybrid population, especially since it has not been collected since the type.

REPRESENTATIVE SPECIMENS. CALIFORNIA. Lassen Co., Harvey Valley, *Howell* 12456 on 6 July 1934 (CAS! [134]); Mono Co., 4 mi north of Bridgeport, ca. 6500 ft, *Hitchcock* 6301 on 30 April 1940 (CAS! [135]); Plumas Co., Prattville, 4500 ft, *Jones s.n.* on 3 July 1897 (POM! [133]); Shasta Co., along hwy. 89, 6.5 mi north of Manzanita Lake checking station, ca. 4800 ft, *Gillett* 212 on 21 August 1952 (UC! [132); Siskiyou Co., Bray, *Smith* 226 on 18 May 1913 (GH! [129]). NEVADA. Lander Co., moist pasture at Reese River, ca. 10 mi west of Austin, ca. 5400 ft, *Hitchcock and Martin* 5586 on 31 July 1939 (GH! [118]); Lander Co., gas station east of Carroll Summit, 6700 ft, *Williams, Mills, McPherson, and Austin* 73D7f on 2 June 1973 (NY! [128]). OREGON. Lake Co., near Hot Springs 3 mi north of Lakeview, *Peck* 15358 on 30 June 1927 (UC! [130]); Lake Co., wet ground, Hot Springs, Lakeview, *Peck* 24999 on 30 May 1948 (UC! [131]).

10. *POTENTILLA DIVERSIFOLIA* Lehmann, Stirp. Lehm. Prim. Descript. Pugillus 2:9-10 (1830); ex Hooker, Flora Bor.-Amer. 1:190 (1832). "Alpine prairies, as well as on the higher summits of the Rocky Mountains, between lat. 52° and 56°. *Drummond*." (Hooker). Authentic specimens, labeled "Frankl. Exp.", ex herb. Hooker (PH! [167] PH! [165,168] NY!).

10a. *POTENTILLA DIVERSIFOLIA* Lehmann ssp. *RANUNCULUS* (Lange) Porsild, Bull. Natl. Mus. Canada 146:112 (1957). *Potentilla ranunculus* Lange, Flora Danica 17(50):7 *t.*2964 (1880); Lange, Meddel. Groenl. 3:7 (1887). GREENLAND. "West coast, near Kekertak, 70°," *Berggren s.n.* on 30 July 1870 (Isotype K photo CAN!).

This subspecies does not differ morphologically from *P. diversifolia* var. *diversifolia*, which see for description. However, it is 2000 mi disjunct from the rest of the species. This could possibly be merged into *P. diversifolia* var. *diversifolia*; the disjunction is poorly understood. However, I will tentatively follow A. E. Porsild, who had more field knowledge of the situation than I.

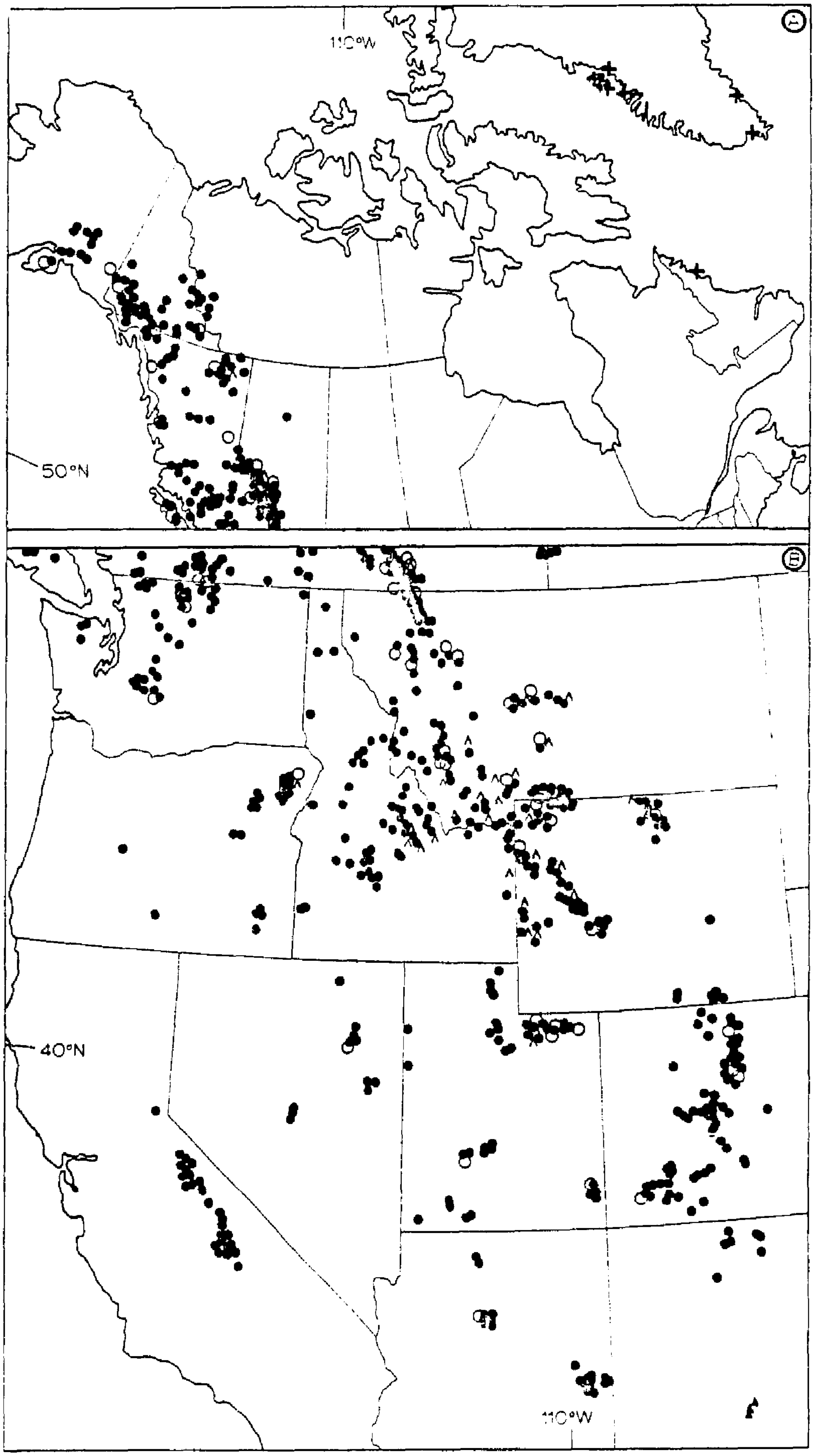
Herbaceous meadows and grassy slopes, sometimes on calcareous soil, both coasts of Greenland, west coast north to Disko Island, and on the coast of northeastern Labrador, 16-1500 ft. Map, Fig. 30.

REPRESENTATIVE SPECIMENS. GREENLAND. Disko Island, east coast, Mudderbugtsdalen, 69°40'N, *Porsild* 388 on 5 August 1937 (UC! [114]); Qingua, 61°14'N 45°31'W, 450 m, *Hansen, Hansen, and Petersen* 76 on 15 July 1962 (COLO! DAO! [107]).

10b. *POTENTILLA DIVERSIFOLIA* Lehmann var. *PERDISSECTA* (Rydberg) C. L. Hitchcock, Vasc. Plants. Pacific Northwest 3:137 (1961). *Potentilla perdissecta* Rydberg, North Amer. Flora 22(4):327 (1908). MONTANA. Madison Range, Spanish Peaks, 7000-8000 ft, *Flodman* 572 on 14 July 1896 (Holotype NY! photo POM!, isotype US! [177]).

This is a poorly defined variety, since some plants of the authentic specimens of *P. diversifolia* seem to fit the variety. The discussion in Hooker's Flora (1832, p. 190) about the range of specimens before him from Franklin's Expedition, also seems to cover plants with more dissected leaflets. Nonetheless, these plants seem to occur principally from west-central Wyoming and northeastern Idaho northward through the range of var. *diversifolia*. The plants also tend to grade into larger forms of *P. ovina* var. *decurrens*, since var. *perdissecta* tends to be more often subdigitate-subpinnate than var. *diversifolia*. Map, Fig. 30.

FIG. 30. A. Canada and Alaska; B. Western United States. Distribution of *Potentilla diversifolia* var. *diversifolia* (closed circles) and its subdigitate forms (open circles); ssp. *ranunculus* (+); and var. *perdissecta* (open triangles).


Ⓐ
110°W
50°N
Ⓑ
40°N
110°W

REPRESENTATIVE SPECIMENS. MONTANA. Bridger Mts., near the Pass, 8000 ft, *Flodman* 575 on 28 July 1896 (NY! [031]); Bridger Mts., *Jones and "E.J.S."* 86 on 1-4 June 1901 (CAS! [075]); Lincoln Co., ridge south of Leigh Lake, Cabinet Mts. Wild Area, 6500 ft, *Woodland and Thomas* 808 on 5 August 1966 (CAS! [035]); Meagher Co., limestone on top of Kings Hill, Little Belt Mts., 7900 ft, *Hitchcock and Muhlick* 12355 (CAS! [074]). CANADA. BRITISH COLUMBIA. Itcha Mts., 26 mi northeast of Anahim Lake, ca. 52°43'N 124°54'W, ca. 6300 ft, *Calder, Parmelee, and Taylor* 20266 on 16-19 August 1956 (WTU! [016]).

10c. *POTENTILLA DIVERSIFOLIA* Lehmann var. *DIVERSIFOLIA*

Potentilla glaucophylla Lehmann, Delect. Sem. Hort. Hamb. 7 (1836). *Potentilla diversifolia* Lehmann var. *glaucophylla* (Lehmann) Lehmann, Stirp. Pugillus 9:44 (1851) or var. *glaucophylla* (Lehmann) Walpers, Ann. 2:483 (1851). *Potentilla dissecta* Pursh var. *glaucophylla* (Lehmann) S. Watson, Proc. Amer. Acad. Arts Sci. 8:556 (1873). "Plains of the first chain of the Rocky Mountains, called the Black Hills," *Nuttall s.n.* no date (BM photo NY! US!, specimens NY! GH!).

Potentilla campestris Nuttall ex Torrey and Gray, Flora North Amer. 1:439 (1840), *nom. nud.*, synonym of *P. diversifolia* Lehmann. Apparently based on the same specimens as cited above under *P. glaucophylla*.

Potentilla concinnaeformis Rydberg, Mem. Dept. Bot. Columbia Univ. 2:54 *t.*15 *f.*6-10 (1898). ARIZONA. [Coconino Co.,], Mt. Agassiz, 10000 ft, *Lemmon* 3294 in August 1884 (GH!).

Potentilla paucidentata A. Nelson, *nom. herbariorum non publ.* WYOMING. Uinta Co., *Nelson and Nelson* 6491 on 16 August 1899 (RM! US!).

Potentilla paucidentata A. Nelson *var. orbicularis* A. Nelson, *nom. herbariorum non publ.* WYOMING. Druid Peak, *Nelson and Nelson* 5784 on 12 July 1899 (RM!).

Potentilla intermittens Rydberg, North Amer. Flora 22(4):318 (1908). COLORADO. Larimer Co., Cameron Pass, 10000 ft, *Baker s.n.* ("25") on 13 July 1896 (Holotype NY! photo and fragment UC!, 2 isotypes ND-G! [182]).

Potentilla vreelandii Rydberg, North Amer. Flora 22(4):325-326 (1908). MONTANA. [Flathead Co., Glacier National Park], Sperry Glacier, 2350 m, *Vreeland* 1092 on 6 August 1901 (Holotype NY!, isotypes US! [179] CAN!).

Medium-sized to large plants, stems ascending to erect, 15-50 cm tall; basal leaves with rachis (2-)5-10(-17) cm long, digitate to subdigitate with 5-8 leaflets, petiole glabrous to strigose; leaflets all pinnately toothed or apically few-toothed, with 5-12(-17) teeth cutting

10-70(-90)% to midrib, glabrous or sparsely to uniformly strigose, appearing green to grayish-green; midstem stipules 8-22 mm long and 3-6(-12) mm wide; stem with 1-25 flowers on erect or ascending pedicels; calyx 5-10 mm high (including lobes); styles 1.8-3.6 mm long.

Widely distributed, highly variable, characteristic Rocky Mountain species; rocky slopes, dry meadows, exposed mountain ridges, alpine meadows. South-central Alaska and west-central Mackenzie southeastward along the Rocky Mountains to northern New Mexico, and southward in the Coast Ranges to central Washington; in the southern Sierra Nevada, central Idaho, eastern Oregon, northern Utah, and scattered on the mountains of Nevada, Utah, and Arizona. Almost always alpine, but also subalpine. Map, Fig. 30.

The three specimens on the sheet at PH, ex herb. Hooker, labeled "Frankl. Exp." present a range of leaf dissection, from strictly digitate with apically few teeth [165], to approximately pinnate with highly dissected leaflets [168]. As Hooker says, "and indeed all the deviations now specified offer such insensible transitions, that it quite impossible to fix any where the limits of a variety" (Hooker 1832, p. 190).

The type of *Potentilla campestris* Nuttall at PH [166] is digitate and moderately strigose, illustrating the transitional characters which have been ascribed to *P. glaucophylla* Lehmann. Indeed, several specimens labeled *P. campestris* by Nuttall (e.g., NY) have the locality data cited by Lehmann for *P. glaucophylla*; however, the specimens of *P. campestris* available are quite variable from specimen to specimen, not unlike the variation in authentic specimens of *P. diversifolia*. In fact, one of them (GH) is *P. plattensis*! Perhaps one of these specimens of *P. campestris* was used to describe *P. glaucophylla*.

Potentilla intermittens is a larger specimen, but in every way is within the range of characters of *P. diversifolia*; some of the specimens annotated by Rydberg as *P. intermittens* have some tomentum and are more consistently subdigitate, suggesting possible hybridization with *P. subjuga* Rydberg. *Potentilla vreelandii* is typical *P. diversifolia*.

REPRESENTATIVE SPECIMENS. ARIZONA. Apache Co., meadow near Oak Creek, base of Mt. Baldy, 9000 ft, *Isaak* on 18 August 1965 (MNA! [101]). CALIFORNIA. Mono Co., Hall Natural Area, Slate Creek Valley, 10300 ft, *Keck* 4924 on 16 August 1938 (US! [003]); Tuolumne Co., west slope Mt. Dana, 10000 ft, *Sharsmith* 357A on 9 August 1933(UC! [115]). COLORADO. Chaffee Co., just below Cottonwood Pass. open gravelly meadow, 11600 ft, *Haber and Given* 2077 (CAN! [111]); Clear Creek-Summit Cos., ridge 0.5-0.9 mi southwest of Loveland Pass, S33-34 T4S R76W, 12350 ft, *Johnston* 2224 & 2227 on 19 August 1979 (COLO!); Gunnison Co., Cottonwood Pass, S14 T14S R81W, 12100 ft, *Johnston* 2241 on 22 August 1979 (COLO!); Gunnison Co., west summit Mt. Bellview, S17 T12N R86W, 12250 ft, *Johnston* 2218 on 16 August 1979 (COLO!); Gunnison Co., 0.8-1.3 mi WSW of Cumberland Pass, S14-15 T51N R4E, 12150 ft, *Johnston* 2242 & 2248 on 23 August 1979 (COLO!); Larimer Co., Cameron Pass, 10000 ft, *Baker s.n.* on 13 July 1896 (NY! [063]); Park Co., Hoosier Ridge, ca. 12500 ft, *Thorne* 34142 on 26 August 1964 (RSA! [109]). IDAHO. Lemhi Co., grassy slope, summit of Moccasin Creek, *Hitchcock and Muhlick* 14288 on 1 July 1946 (CAS! [113]); near Sawtooth, *Evermann* 540 on 9-10 July 1896 (US! [002]). MONTANA. Beaverhead Co., Monida, *Jones s.n.* on 20 June 1922 (POM! [110]); Madison Co., limestone outcrop 1 mi south of Crockett Lake, Gravelly Range, 8700 ft, *Hitchcock and Muhlick* 12498a on 19 July 1945 (WS! [076]); mountains near Indian Creek, 8000 ft, *Rydberg and Bessey* 4391 on 22 July 1897 (NY! [030]). NEVADA. Elko Co., Ruby Mts., rocky slope above Liberty Lake, 10100 ft, *Mills and Beach* 1329 on 13-18 August 1941 (CAS! [036]); Elko Co., cirque above Island Lake, S36 T32N R58E, ca. 10600 ft, *Johnston* 2273 on 27 August 1979 (COLO!); Nye Co., Toquima Range, Pine Creek Canyon, T11N R45E, ca. 10900 ft, *Reveal* 630 on 23 July 1964 (WS! [106]). NEW MEXICO. Sandoval Co., Los Conchas, 9000 ft, *Weissenborn* 78 on 20 August 1962 (UNM! [112]). UTAH. Duchesne Co., Long Park, upper Hells Canyon, S2 T2N R5W, 10150 ft, *Johnston* 2249A on 24 August 1979 (COLO!); Grand Co., Mt. Tomasaki, La Sal Mts., S31 T26S R25E, 11200 ft, *Johnston* 2147 on 18 July 1979 (COLO!); Uintah Co., Oaks Park, S1 T1S R20E, 9350 ft, *Johnston* 2253 on 25 August 1979 (COLO!); Wayne Co., Flat Top, Thousand Lake Mtn., S21 T27S R4E, 11100 ft, *Cronquist and Holmgren* 9347 on 24 June 1961 (WS! [102]). WASHINGTON. Clallam Co., open slopes of Mt. Angeles, 5500 ft, *Thompson* 8043 on 18 June 1932 (WTU! [103]); Okanogan Co., meadowland at Brown Meadow, S29 T37N R23E, *Hitchcock and Muhlick* 21649 on 1 July 1958 (NY! [029]). WYOMING. Park Co., Clay Butte, S1 T57N R106W, 9800 ft, *Johnston* 2283 on 29 August 1979 (COLO!); Teton Co., along trail in South Teton Canyon, ca. 4 mi above Teton Forest Camp, *Anderson* 605 on 1 August 1956 (UTC! [038]). CANADA. ALBERTA. Lake Louise, *Farr s.n.* on 28 July 1903 (PENN! [037]); vicinity of Banff, open woods near summit of Sulphur Mtn., 7000 ft, *McCalla* 2079 on 18 July 1899 (ALTA! [105]); wet meadows, valley below Mt. Aylmer, 6700 ft, *McCalla* 2080 on 4 August 1899 (ALTA! [104]);

Banff National Park, Bow River Valley, south slope of Cascade Mtn., 4700-8000 ft, *Porsild and Breitung* 12393 on 30 June 1945 (CAN! [032]). BRITISH COLUMBIA. Vancouver Island, trail to summit of Mt. Albert Edward, Forbidden Plateau, 49°41'N 125°25'W, *Calder and McKay* 32180 on 6 August 1961 (DAO! [108]). MACKENZIE. Mackenzie Mts., Backbone Ridge, Grizzly Bear Lake, 62°41'N 127°50'W, *Cody and Spicer* 17963 on 10 August 1967 (DAO! [013]). YUKON. Canol Road, mile 95, Upper Rose River Valley, 3600 ft, *Porsild and Breitung* 10540 on 17 June 1944 (CAN! [100]).

11. *POTENTILLA OVINA* J. M. Macoun, Canad. Record Sci. 6:464 (1895). CANADA. ALBERTA. "High slopes of Castle Mountain," Silver City, on earth on mountain summits, *Macoun* "634,7242" on 8 August 1885 (Holotype CAN! [178], isotypes NY! GH!).

11a. *POTENTILLA OVINA* J. M. Macoun var. *DECURRENS* (S. Watson) B. C. Johnston, *comb. nov.* *Potentilla dissecta* Pursh var. *decurrens* S. Watson, Proc. Amer. Acad. Arts Sci. 8:557,565 (1873). *Potentilla decurrens* (S. Watson) Rydberg, Bull. Torrey Bot. Club 23:396 (1896). *Potentilla diversifolia* Lehmann var. *decurrens* (S. Watson) Th. Wolf, Bibl. Bot. 16(71):502 (1908). UTAH. "Peaks of the" Uinta Mountains, 12000 ft, *Watson* 329 in August 1869 (Holotype GH!, isotype US! [174]).

Potentilla nelsoniana Rydberg, North Amer. Flora 22(4):344 (1908). *Potentilla pinnatisecta* A. Nelson, Wyoming Experiment Sta. Bull. 28:104 (1896), *non P. diversifolia* var. *pinnatisecta* S. Watson (1871). WYOMING. Albany Co., La Plata Mines, *A. Nelson* 1819 on 23 August 1895 (Holotype NY! fragment UC!). Possible isotypes: WYOMING. Albany Co., La Plata Mines, *A. Nelson* 1819 on 21 August 1895 (RM!); La Plata Mines, 11500 ft, *A. Nelson* 1819 on 24 August 1895 (GH! [175]).

Medium-height to small plants, with decumbent to erect stems 10-35(-50) cm long; basal leaves usually erect with rachis 3-12 cm long, pinnate with (5-)9-18 leaflets occupying (20-)40-70% of rachis, petioles glabrous or sparsely strigose; terminal leaflet pinnate or more commonly narrow and apically few-toothed; lower leaflets apically few-toothed or rarely digitate, with 2-12 teeth cutting 50-80% to midrib, glabrous to sparsely strigose, rarely also with sparse tomentum on lower surface, usually appearing dark green and glabrescent to the naked eye; midstem stipules (7-)8-14(-20) mm long and (2-)3-5 mm wide; stem with 3-15 flowers on erect or ascending pedicels; calyx 6-8(-10) mm high (including lobes); styles 1.8-2.7 mm long.

Moist open meadows and rocky slopes, upper montane to the lower alpine, characteristic and most abundant in the Uinta Mountains of Utah and the Front Range of Colorado, but also scattered on the other mountains of Utah, southern Wyoming, Colorado, and eastern Nevada; at scattered localities northward in the Rocky Mountains to ca. lat. 55°N; 5500 ft (Alberta) to 12300 ft (central Colorado). Map, Fig. 31.

Potentilla nelsoniana is a better representative of this variety than var. *decurrens*, but *decurrens* has priority in the rank of variety. The two varieties of this species are almost distinct in geographical area; in the Uinta Mts. they are distinct ecologically as well, since *decurrens* is predominantly a species of montane meadows, *ovina* being alpine in that range, growing on frost-scarred talus slopes.

REPRESENTATIVE SPECIMENS. COLORADO. Boulder Co., Niwot Ridge, 11000-12600 ft, *Komarkova s.n.* on 28 August 1971 (COLO! [099]); Gunnison Co., west summit Mt. Bellview, S17 T12N R86W, 12250 ft, *Johnston* 2219 on 16 August 1979 (COLO!); Gunnison Co., ridge 0.8-1.3 mi WSW Cumberland Pass, S14-15 T51N R4E, 12100 ft, *Johnston* 2243 & 2247 on 23 August 1979 (COLO!); Moffat Co., summit of Zenobia Peak, S33 T8N R102W, 2730 m, *Johnston* 2058 on 15 June 1979 (COLO!). UTAH. Duchesne Co., south fork Log Hollow, S31 T2N R7W, 11100 ft, *Johnston* 2186 on 21 July 1979 (COLO!); Duchesne Co., near BM Blind Stream, S36 T2N R8W, 11250 ft, *Johnston* 2185 on 21 July 1979 (COLO!); Duchesne Co., Long Park, upper end Hells Canyon, S2 T2N R5W, 10150 ft, *Johnston* 2249 on 24 August 1979 (COLO!); Grand Co., La Sal Mts., Mt. Tomasaki, S31 T26S R25E, 11350 ft, *Johnston* 2160 on 18 July 1979 (COLO! [093]); Grand Co., saddle below Manns Pk., S25 T26S R24E, 11600 ft, *Johnston* 2161 on 18 July 1979 (COLO!); Juab Co., Mt. Ibapah, 10500 ft, *Jones s.n.* on 17 July 1903 (GH! [124]); Salt Lake Co., head of Little Cottonwood Canyon, near top of Albion Lift, ca. 9000 ft, *Neese* 1550 on 29 July 1975 (BRY! [069]); San Pete Co., Horseshoe Summit, Wasatch Mts., 3330 m, *Eggleston* 10580 on 17-18 August 1914 (US! [095]); Summit Co., 1 mi northwest of La Motte Pk., S36 T1N R10E, ca. 12000 ft, *Johnston* 2257 on 26 August 1979 (COLO!); Uintah Mts., Dyer Mine, dead timber, *Goodding* 1235 on 2 July 1902 (POM! [097]); Uintah Co., Oaks Park, S1 T1S R20E, 9350 ft, *Johnston* 2252 on 25 August 1979 (COLO!). WYOMING. Albany Co., Telephone Mines, dry rocky ridges, *Nelson* 7917 on 2 August 1900 (COLO! [098]); Albany Co., ridge northwest of Glacier Lake, Snowy Range, S3 T16N R79W, 11500 ft, *Johnston* 2285 on 30 August 1979 (COLO!); Lincoln Co., Sheep Mtn., Snake River Range, rocks at summit, *Payson and Armstrong* 3460 on 11 July 1923 (RM! [070]). CANADA. ALBERTA. Crowsnest Pass, Summit of Turtle Mtn., *Macoun* 16729 on 12 August 1897 (CAN! [082]); Porcupine Hills, *Malte and Watson* 605 on 25 June 1925 (CAN! [065]); vicinity of Banff, rocky ledges, east face of Tunnel Mtn., 5000 ft,

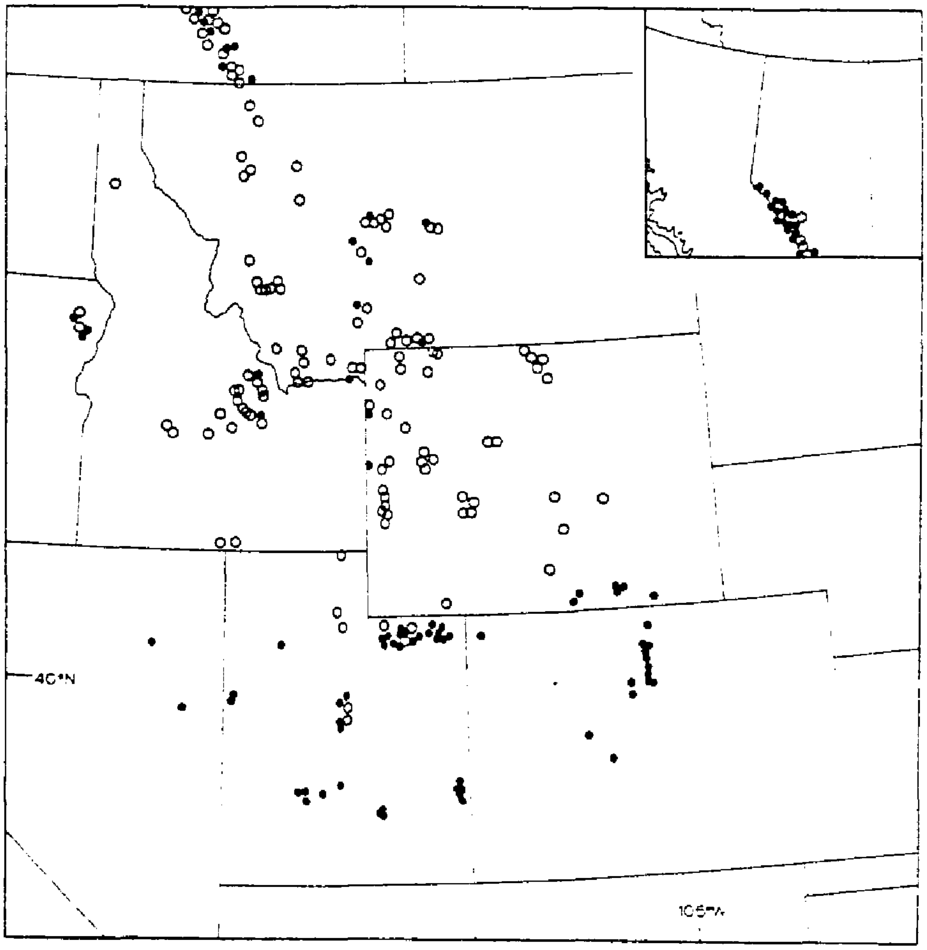


FIG. 31. Rocky Mountains states; inset: central and northern Alberta and adjacent provinces. Distribution of *Potentilla ovina* var. *ovina* (open circles) and *Potentilla ovina* var. *decurrens* (closed circles).

McCalla 2083 on 23 June 1899 (ALTA! [077]); Elbow River, Forget-Me-Not Mtn., *Macoun* 16728 on 14 July 1897 (CAN! [067]); Waterton Lakes National Park, Mt. Crandell, 7800 ft, *Breitung* 17346 on 9 August 1953 (NY! [064]); Mountain Park, Mt. Harris, *Malte and Watson* 2154 on 13 August 1925 (CAN! [071]); Prospect Mtn., 10 mi southwest of Cadomin, 52°55'N 117°20'W, 2085 m, *Mortimer* 238 (ALTA! [072]).

11b. *POTENTILLA OVINA* J. M. Macoun var. *OVINA*

Potentilla diversifolia Lehmann var. *pinnatisecta* S. Watson, Bot. King's Explor. 87 (1871). *Potentilla pinnatisecta* (S. Watson) A. Nelson, Wyoming Experiment Sta. Bull. 28:104 (1896), *excl. descript. et spm. cit.* *Potentilla plattensis* Nuttall var. *pinnatisecta* (S. Watson) Th. Wolf, Bibl. Bot. 16(71):494 (1908). UTAH. Uinta Mountains, more alpine [than 331], 12000 ft, *Watson* 332 in August 1869 (Lectotype [Rydberg 1898, p. 107] GH!, isotype US! [189]). Other specimens cited in protologue: UTAH. Uinta Mountains, 10000 ft, *Watson* 331 in August 1869 (GH! NY! US! [188]). NEVADA. Clover Mts., 10000 ft, alpine, *Watson* 332 in September 1868 (NY!). See discussion below.

Potentilla wyomingensis A. Nelson, Bull. Torrey Bot. Club 27:32 (1900). *Potentilla plattensis* Nuttall var. *pinnatisecta* (S. Watson) Th. Wolf fma. *wyomingensis* (A. Nelson) Th. Wolf, Bibl. Bot. 16(71):495 (1908). WYOMING. Yellowstone National Park, on the rocky summits of the higher ridges, Druid Peak, *A. Nelson* 5781 on 12 July 1899 (Holotype RM!, isotypes NY! US! [181]).

Horkelia seminolensis A. Nelson, *nom. herbariorum provis. pro Potentilla wyomingensis* A. Nelson. WYOMING. Seminoe ("Seminole") Mountains, *E. Nelson* 4916 on 21 July 1898 (NY! RM! US! [086]).

Potentilla monidensis A. Nelson, Bull. Torrey Bot. Club 27:266-267 (1900). MONTANA. [Beaverhead Co.], "plentiful on the high, open slopes among the sagebrush, near Monida," gravelly and stony slopes, *Nelson and Nelson* 5414 on 16 June 1899 (Holotype RM!, isotypes NY! GH! CAS! POM! [160]).

Potentilla caespitosa A. Nelson, *nom. herbariorum provis. pro P. monidensis* A. Nelson, *non P. cespitosa* Rafinesque (1840).

Small plants, stems prostrate to less commonly ascending to erect, 5-20 cm long; basal leaves relatively short, 2-6(-9) cm long, pinnate with (7-)9-20 leaflets occupying (20-)40-80% of rachis, petiole glabrous or strigose, sometimes with a little tomentum in addition; terminal leaflet usually deeply pinnately divided into narrow segments; lower leaflets usually also pinnate, often grading into the digitate lowest ones, moderately to densely strigose, sometimes in addition sparsely tomentose, usually appearing grayish-green; midstem stipules 3-11(-17) mm long and 1-5 mm wide, not divided; stem with 1-15 flowers on erect or ascending pedicels; calyx 4-8 mm long (including lobes); styles 1.5-3.0 mm long.

Dry rocky meadows and exposed slopes and ridges, often on calcareous or basic soil, northern Rocky Mountains at ca. lat. 54° southward to northeastern Oregon, central Idaho, west-central and central Wyoming; Wasatch Mountains and the north slopes of the Uinta Mountains of northern Utah. Nearly always alpine, but in southwestern Montana, Idaho, and around the rim of the Wyoming basin becoming submontane. Map, Fig. 31.

Typification of *Potentilla diversifolia* var. *pinnatisecta* is difficult. There are at least six specimens cited by Watson in the protologue under his collection numbers 331 and 332, one each of the two numbers in herbaria GH, NY, and US. Watson 332 (GH!) is selected by Rydberg (1898, p. 107) as the type, although he inexplicably does not mention the US specimens, in spite of his own pre-1898 annotations on them. Watson 332 (GH!) consists of two plants: one plant (much like the single plant Watson 332 [US!]) is the apparently-hairy short-leaved form [189] which is very close to *P. ovina*; the other plant (which someone has separated from the first plant and the label with a light pencil line) apparently belongs to what I am calling here var. *decurrens*, with its more erect leaves, subglabrous surfaces, and apically few-toothed leaflets. The two varieties both occur in the Uintas, in different habitats, var. *ovina* in frost-scarred rocky slopes and var. *decurrens* in more protected grassy tundra on ridgetops. Var. *decurrens* is at the top of its altitudinal range in the alpine of the Uintas, being a characteristic plant of montane and subalpine meadows there.

Watson 331(GH), collected at 10000 ft in the Uinta Mountains, is clearly var. *decurrens*, as are the closely similar specimens Watson 331 (NY US [188]).

Watson 332(NY), collected in the Clover Mountains, Nevada, in a different year, is clearly *Potentilla breweri* var. *breweri*, which species Watson named in 1873, two years after *pinnatisecta* was written.

Rydberg (as shown by his 1898 synonymy and annotations on the specimens) believed from 1898 on, that *P. ovina* and var. *pinnatisecta* were synonymous; this makes it possible to take the first plant (with the label) of Watson 332 (GH) as the type of *P. diversifolia* var. *pinnatisecta* S. Watson.

Var. *pinnatisecta* antedates var. *decurrens*, and should be chosen as the name for the characteristic montane plant of the Uintas, if the majority of the plants cited in the protologue (4 of 7) are brought to bear on the problem. However, to do so would contradict Rydberg's lectotypification, which was done correctly in every way, since he chose a specimen apparently before Watson when the type description was written. Therefore, I follow Rydberg.

Potentilla wyomingensis is typical *P. ovina* var. *ovina*, except for its stature in the large end of the range, and its more dissected leaflets (characters shared by *P. monidensis*). *Potentilla monidensis* is submontane but otherwise indistinguishable from the *wyomingensis* phase of var. *ovina*, except in its caespitose habit, which is shared by the other submontane plants of this variety in central Idaho and the Wyoming Basin; it has fewer leaflets than in the *wyomingensis* phase. It is tempting to recognize these submontane plants as another variety, but the reduced mat-form of this is very close to the type of *P. ovina*.

REPRESENTATIVE SPECIMENS (TYPICAL FORM). MONTANA. Lewis and Clark Co., Scapegoat Mtn., rocky south slope, 7900 ft, *Craighead* 75 on 8 August

1975 (MONTU! [088]). NEVADA. Nye Co., Toquima Range, head of Pine Creek, 11000 ft, *Maguire and Holmgren* 25808a on 16 July 1945 (UTC! [050]). OREGON. High ridges of the Wallowa Mts., 9000 ft, *Cusick* 2300 on 31 July 1899 (UC! [084]); granite cliffs, extreme source of the Imnaha, 3000 m, *Cusick* 3225 on 27 August 1907 (ORE! [083]). UTAH. Juab Co., Wasatch Range, Mt. Nebo, north Peak, 11000 ft, *Cottam and Rowland* 15120 on 16 July 1958 (BRY! [094]); Summit Co., dry rocky slopes, La Motte Peak, 12000 ft, *Payson and Payson* 5098 on 24 August 1926 (CAS! [090]); Summit Co., summit of La Motte Peak, S36 T1N R10E, ca. 12450 ft, *Johnston* 2260 on 26 August 1979 (COLO!); Summit Co., alpine meadow, divide between East Fork Bear River and Blacks Fork, 10000 ft, *Goodman and Hitchcock* 1528 on 9-13 July 1930 (UC! [034]); Weber Co., Ben Lomond, near peak, 9000 ft, *Call* 55 on 28 June 1940 (RSA! [066]). WYOMING. Park Co., Clay Butte, S1 T57N R106W, 9800 ft, *Johnston* 2282 on 29 August 1979 (COLO!). CANADA. ALBERTA. Sheep Mountain, Waterton Lake, *Macoun* 10488 on 31 July 1895 (US! [087] CAN! [091]); west of Banff, rock ledges, limestone, *Lewis s.n.* in July 1915 (ALTA! [078]); Sheep Mountain, Waterton Lake, crevices of rocks, *Macoun* 10489 on 31 July 1895 (CAN!); Cheviot Mtn., 5 mi south of Cadomin, alpine slope, *Dumais, Packer, and Scott* 5606a on 7 July 1971 (ALTA! [079]); Waterton Lakes National Park, summit of Mt. Richards, 7500 ft, *Breitung* 17478 no date (ALTA! [081]); Banff National Park, east slope of Sulphur Mtn., 7350 ft, *Porsild and Breitung* 12429 on 1 July 1945 (CAN! [073]); Rocky Mtn. Forest Reserve, mountain west of Highwood Pass road, rocky slopes and ledges, 7200 ft, *Porsild and Lid* 18377 & 19378 (CAN! [085] CAN! [001]).

(MONIDENSIS FORM). IDAHO. Bingham Co., Blackfoot Mts., Wolverine Creek, 2 mi above mouth of canyon, S9 T2S R38E, 4950 ft, *Holmgren and Marttala* 5401 on 13 July 1971 (NY! [119]). WYOMING. Carbon Co., S10 T16N R88W, 8000 ft, rocky calcareous ridge, *Dorn* 2891 on 24 May 1977 (RM!); Carbon Co., limestone ridge ca. 25 mi south of Rawlins, ca. S30 T17N R87W, 8000 ft, *Johnston* 2051 on 14 June 1979 (COLO!); Fremont Co., east of South Pass City, 8100 ft, *Ripley and Barneby* 7958 on 14 June 1946 (CAS! [045]); Hot Springs Co., north flank of Owl Creek Range, Grass Creek, 7100 ft, *Fisser* 513 on 21 June 1961 (RM! [089]); Sweetwater Co., 45 mi south of Green River, 5500 ft, *Ripley and Barneby* 7907 on 12 June 1946 (CAS! [044]); Rattlesnake Mts., *E. Nelson* 4995 on 29 July 1898 (RM! [068]); Seminoe ("Seminole") Mts., *E. Nelson* 4916 on 21 July 1898 (US! [086]).

CHAPTER VIII

RESULTS AND DISCUSSION: SECT. CONCINNAE AND SECT. SUBJUGAE

Part of the results of program CHARANAL are shown in Fig. 32. The characters fall into three rough groups: I. the measurement, number, and arrangement characters (characters 2,3,4,6,7,9,10,11,16,19,23); group II. the pubescence characters (12,13,14,18,21,22); and group III. other characters (1,8,15,17,20). The characters used for character analysis and classification in this chapter are different from those used in the classification of sect. Multijugae, as shown in Table 15.

The characters in group I share much information with one another, and will therefore be retained, following Bisby's (1970) finding that the choice of well-correlated characters will improve the classification. Many of the pubescence characters (group II) have a high proportion of information shared with others, although it is surprising that character 12, pubescence of upper leaf surface, is better correlated that no. 13, that of the lower. Lower leaflet pubescence and petiole pubescence (5 and 13) will be retained, partly because of their (admittedly low) correlations, and partially because they have been used often in past classifications of these species.

Characters in group III are less certain: stem branching (no. 17) bridges the gap between groups I and II, as does calyx lobe form (no. 20). These share information with a moderate portion of other characters, and probably should be retained. Character 8 (terminal leaflet shape), on the other hand, shares little information with any other character; the

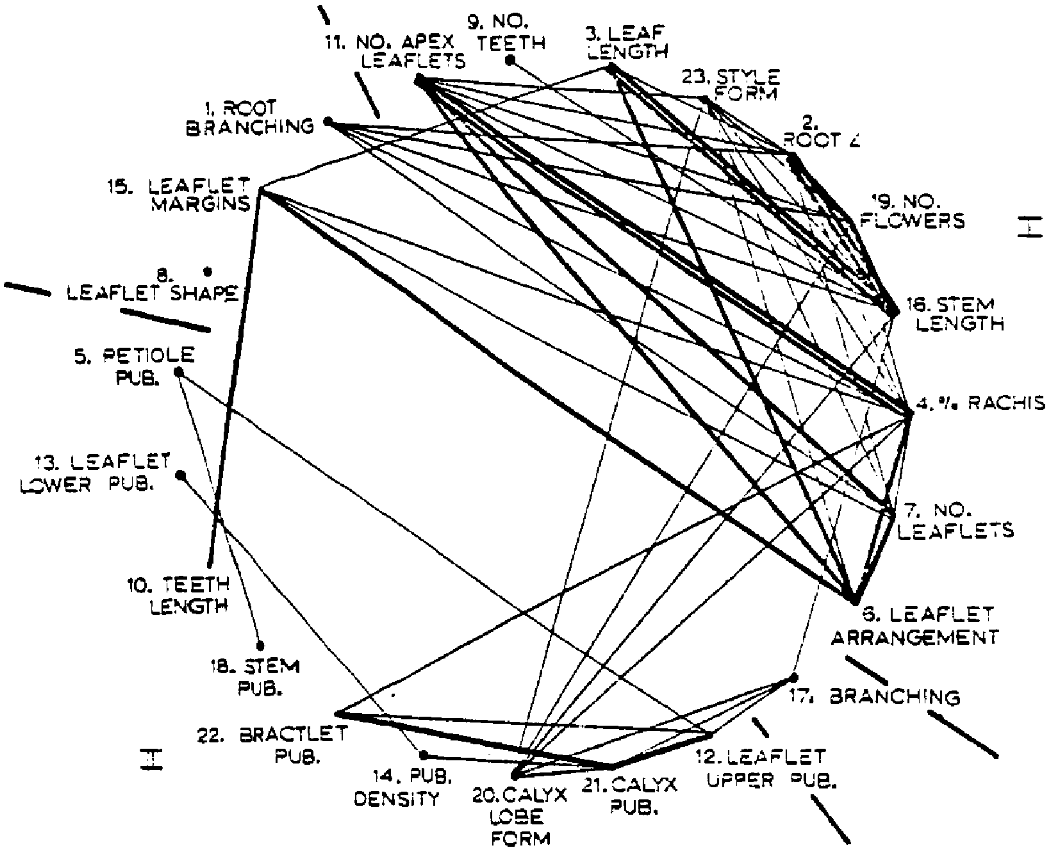


FIG. 32. Results of CHARANAL for the 23 characters in Table 15. Shown are proportion of information shared between pairs of characters: proportion 0.4 or greater (double-thick lines); 0.3-0.4 (single-thick lines); 0.2-0.3 (thin lines). Values of the proportion of shared information less than 0.2 are not shown.

TABLE 15. Characters used in classification of sect. Concinnae and sect. Subjugae.

Character number and description[a]	States
1 (-). Root branching	1 branched, caespitose
	2 erect, unbranched
2 (1). Root-stem angle	1 indeterminate, stem shorter than leaves
	2 decumbent
	3 arched-ascending
	4 erect-ascending
	5 stiffly erect
3 (2). Length of longest basal leaf rachis	1-6 x 4 cm[b]
4 (3). Per cent of rachis <u>not</u> occupied	1-A x 10%[b]
5 (4). Petiole pubescence	1 hispid/tomentose[c]
	2 hispid/- or glandular
	3 strigose/tomentose
	4 strigose/- or glandular
	5 -/tomentose scattered
	6 -/tomentose covering
6 (5). Leaflet arrangement	1 digitate-subdigitate: confluence not visible
	2 opposite confluent
	3 opposite not confluent
	4 scattered confluent
	5 scattered not confluent
7 (6). Number of leaflets	1 1-4
	2 5-6
	3 7-8
	4 9-10
	5 11-12
	6 13-
8 (-). Terminal leaflet shape	1 oblanceolate-lanceolate
	2 ovate-obovate
	3 linear-deltoid
	4 lobed
9 (7). Number of teeth along one side of leaflet	1 2-3
	2 4-5
	3 6-9
	4 10-15
	5 15-
10 (8). Relative length of teeth	1 1/3 or less
	2 1/2
	3 2/3
	4 greater than 2/3

TABLE 15. (Continued).

Character number and description[a]	States
11 (9). Number of leaflets at apex of rachis	1 1, petioluled
	2 2-3
	3 4-5
	4 6-7
12 (10). Leaflet pubescence, upper surface (lamina)	1 sericeous/tomentose[c]
	2 sericeous/- or glandular
	3 strigose/tomentose
	4 strigose/- or glandular
	5 -/tomentose
	6 glabrous
13 (11). Leaflet pubescence, lower surface (lamina)	1 sericeous/tomentose, gray
	2 sericeous/tomentose, silvery or white
	3 sericeous/-
	4 -/tomentose, gray
	5 -/tomentose, silvery or white
	6 glabrous
14 (12). Pubescence coverage	1 lower sparse, not bicolored
	2 lower sparse, lightly bicolored
	3 lower dense, not bicolored
	4 lower dense, lightly bicolored
	5 lower dense, strongly bicolored
	6 lower glabrous, not bicolored
15 (-). Leaflet margins	1 revolute, leaf coplanar
	2 revolute, noncoplanar
	3 not revolute, coplanar
	4 not revolute, noncoplanar
16 (13). Stem length	1-B x 5 cm[b]
17 (14). Stem branching	1 openly in upper 1/3, not leafy
	2 tightly in upper 1/3, not leafy
	3 in upper 2/3. leafy
	4 in upper 2/3, not leafy
	5 upper 1/2, leafy
	6 upper 1/2, not leafy
18 (15). Midstem pubescence	1 hispid/tomentose[c]
	2 hispid/- or glandular
	3 strigose/tomentose
	4 strigose/- or glandular
	5 -/tomentose scattered
	6 -/tomentose covering
	7 glabrous

TABLE 15. (Continued).

Character number and description[a]		States
19 (16). Number of flowers	1	1-3
	2	4-6
	3	7-10
	4	10-20
	5	20-
20 (17). Calyx lobes	1	rounded-obtuse, bractlets 1/2
	2	rounded-obtuse, =
	3	acute-deltoid, 1/2
	4	acute-deltoid, =
	5	acuminate, 1/2
	6	acuminate, =
21 (18). Calyx pubescence	1	strigose/tomentose[c]
	2	sericeous/tomentose
	3	strigose-sericeous/- or glandular
	4	tomentose-scattered
	5	tomentose-covering
22 (19). Bractlet adaxial pubescence	1	glabrous
	2	sericeous-ciliate
	3	tomentose
	4	glandular
23 (20). Style form	1	equally thickened 1/2 or more
	2	uniform-filiform
	3	club-shaped
	4	conical

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a. The first number shown is that used for CHARANAL (Fig. 32); the number in parenthesis shows the number used for GRAPH (following figures). Three characters have been rejected; see text.

b. See Table 11, footnote a.

c. The slash (/) divides upper and lower layers of pubescence; a dash (-) indicates absence of that layer.

matrix of values of information shared (not shown) revealed that this character shared a slight amount of information with each of the other characters. Since character 8 had been included as a trial to determine its usefulness and had not been used in any previous classifications, it will be dropped from use in the classification to follow.

Character 1, root branching, and no. 15, leaflet margins, were both trial characters; although Fig. 32 shows them both to have a certain amount of information in common with other characters, they are an example of how this diagram may be misleading. The matrix of values of information shared shows that each of these characters has a large proportion of itself in common with others (i.e., SAMRAT is high), but shares a small proportion of any other character (SUMRAT is low; see Fig. 1[A]). This means that these characters actually have very little information in them, and will be rejected.

Thus three characters have been selected for removal from the classification to follow; the data set was adjusted, and new character numbers were used for the rest of the results (numbers in parenthesis in Table 15). These resulting 20 characters were then used for the 174 herbarium specimens selected, as an input for GRAPH, in the manner described above for sect. Multijugae. As before, a complete set of subgraphs was drawn, and one of the levels was selected as most representative of the clusters that formed, shown in Fig. 33. The named clusters on this diagram were then redrawn separately, as before, and all connections shown. There were, however, two distinct linkage groups that formed early, but remained apart until late in the clustering; one of them is shown in Fig. 33, and is *Potentilla* sect. Subjugae.

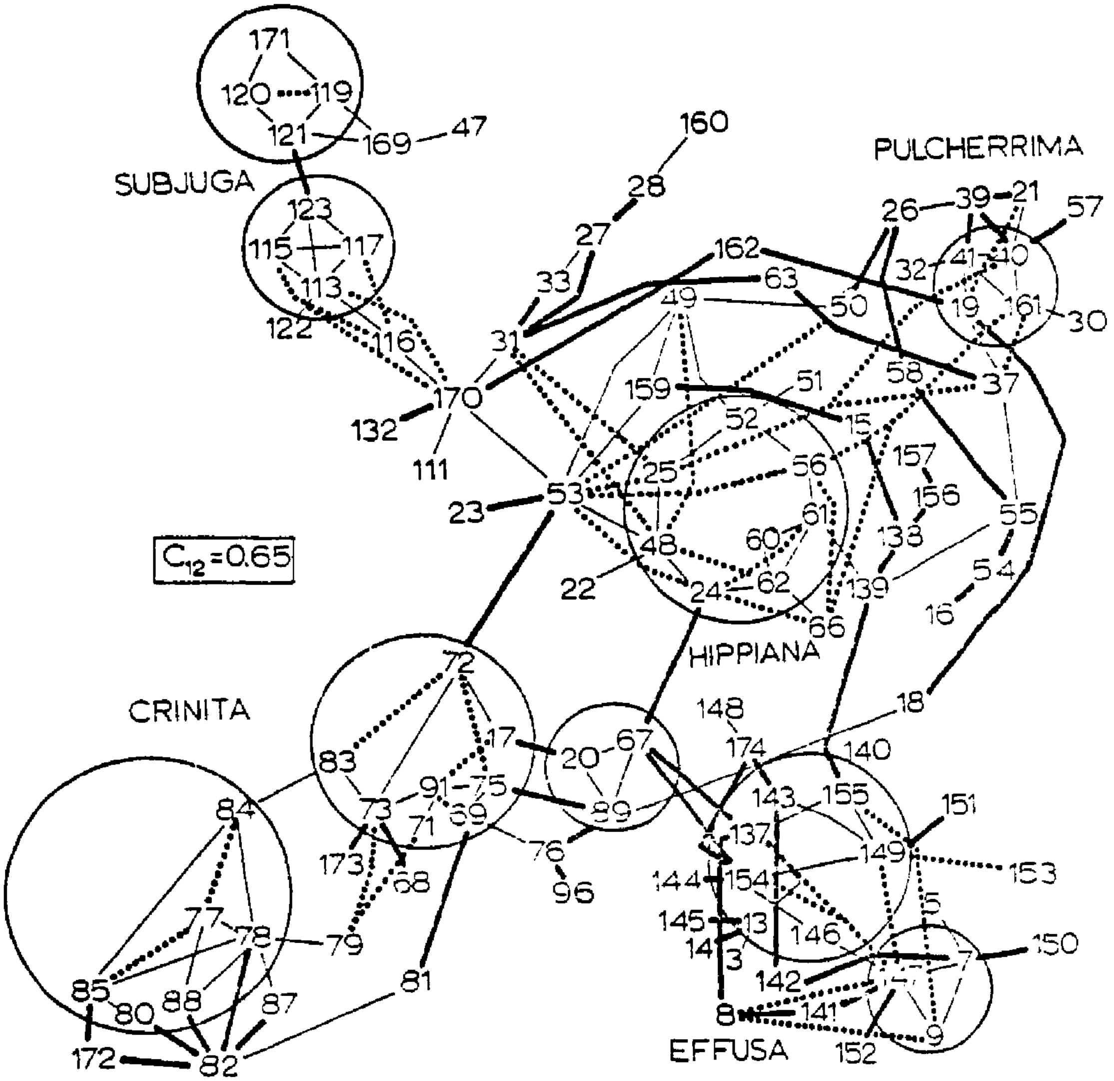
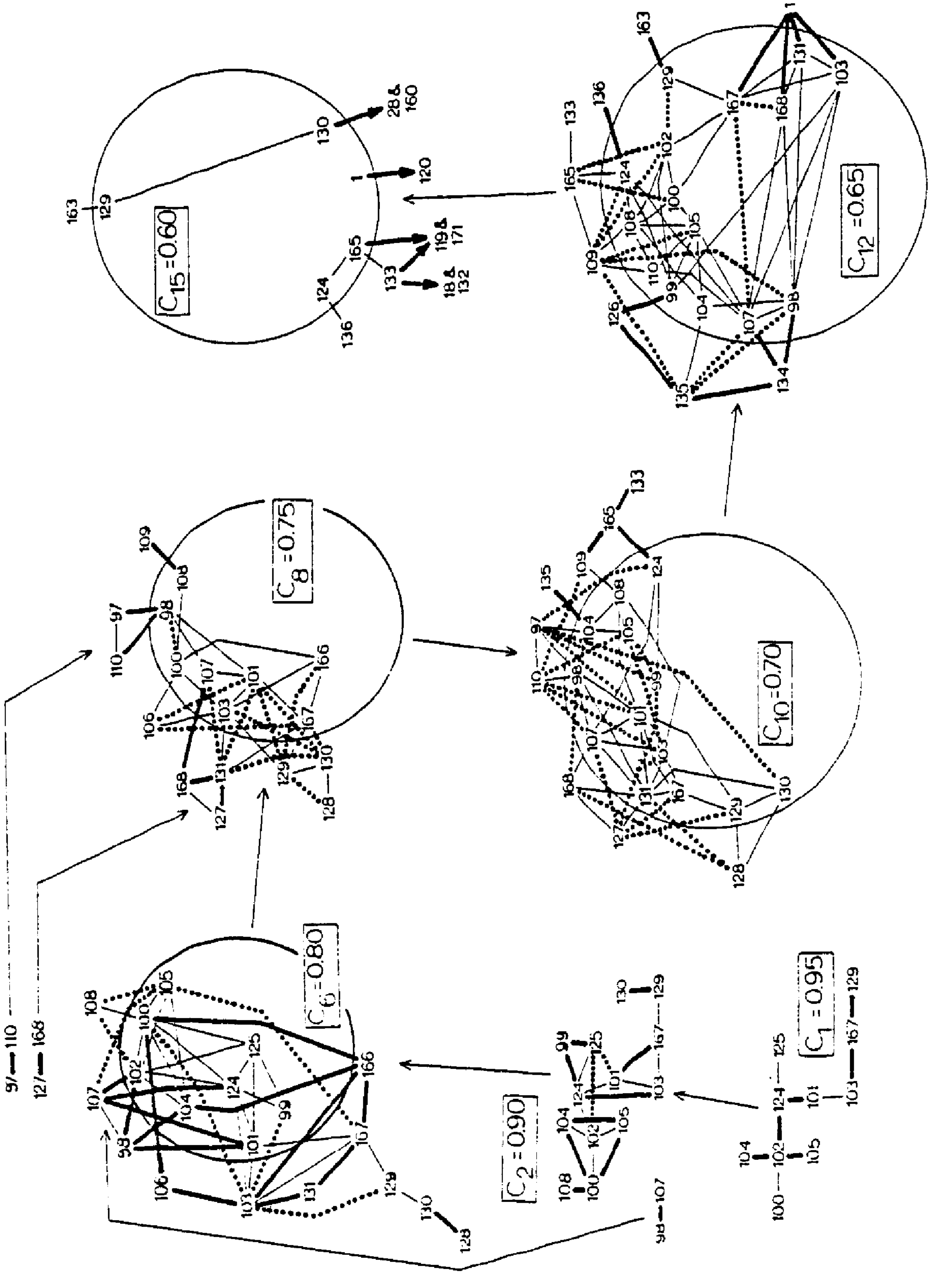


FIG. 33. Subgraph for the 12th level, showing *Potentilla* sect. Subjugae; the clusters shown separately in following figures are named. Conventions and symbols as in Fig. 17 and the text.

The other linkage group is shown in a different way in Fig. 34, and is sect. Concinnae. Because sect. Concinnae formed a tight cluster very early in the clustering (and so by level 12, when Fig. 33 was drawn, would show very little internal structure), it was decided to show a series of several different levels in the same diagram (Fig. 34) as an example of the usefulness of the GRAPH output in showing the progress of clustering. The same *P. concinna* cluster is shown in Fig. 35. Both of these figures show that this cluster is very tight at an early level, including an authentic specimen of *P. concinna* [167] and the type of var. *divisa* [166]. Another early cluster forms close to the type of *P. bicrenata* [168]. Several items, including a type of *P. beanii* [165] attach more loosely at lower left, and become intermediate between this cluster and *P. hippiana*. Items 158 and 163 (type of *P. oblanceolata*) attach later at upper right; in light of their disjunct distribution in Chihuahua and the paucity of collections, these will be tentatively maintained at species rank. Item 1 attaches late and is somewhat intermediate between *P. concinna* and its var. *bicrenata*; it is closer to *bicrenata*. The plants are disjunct geographically from var. *bicrenata* and distinctive morphologically, and will therefore be described as a new variety.

Fig. 36 shows the subgraph for *Potentilla subjuga* and *P. macounii*; *P. subjuga* forms a tight cluster with its type [170] early in clustering, although it is very close to the *P. hippiana* and *P. pulcherrima* clusters. Nonetheless, *P. subjuga* has a consistently subdigitate leaf that is subglabrous above; it is distinct from *P. pulcherrima* ecologically and in its smaller stems, with more subdigitate leaves. *P. subjuga* var. *minutifolia* forms a looser cluster including the types of *P. minutifolia* [171] and *P. tenerrima* [169]; this variety occupies the same geographical

FIG. 34. Complete subgraphs for the *Potentilla* sect. Concinnae cluster, using simple character states only. The diagram flows from lower left to upper right, following the arrows. New cluster connections at a level (solid thick lines); internal connections at a level (dotted lines); previously made connections (thin lines). The dark arrows at the last level shown are connections to numbers in the cluster shown in Fig. 33.


C1 = 0.95
C2 = 0.90
C6 = 0.80
C8 = 0.75
C10 = 0.70
C12 = 0.65
C15 = 0.60
28 & 160
119 & 171
18 & 132

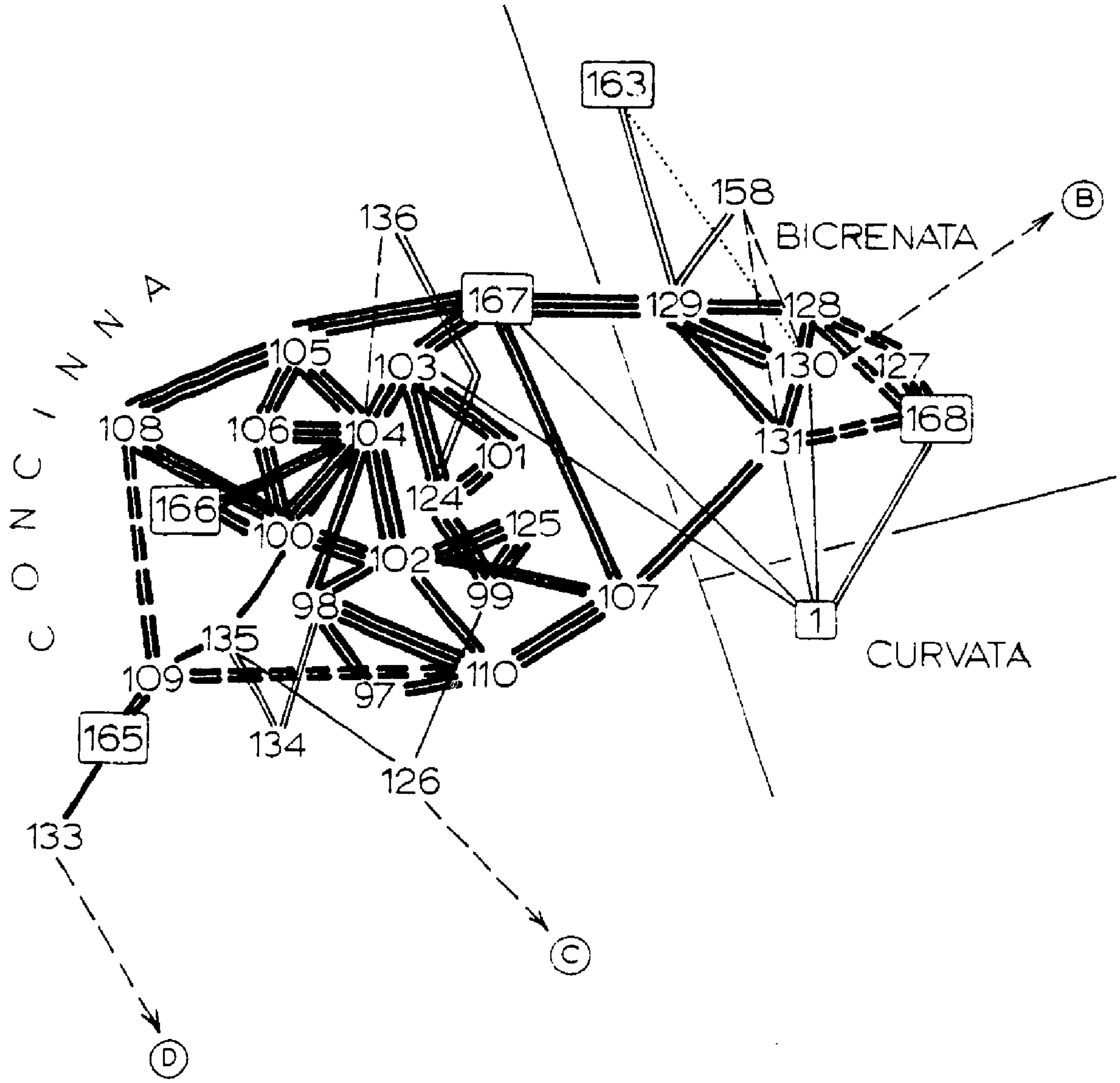
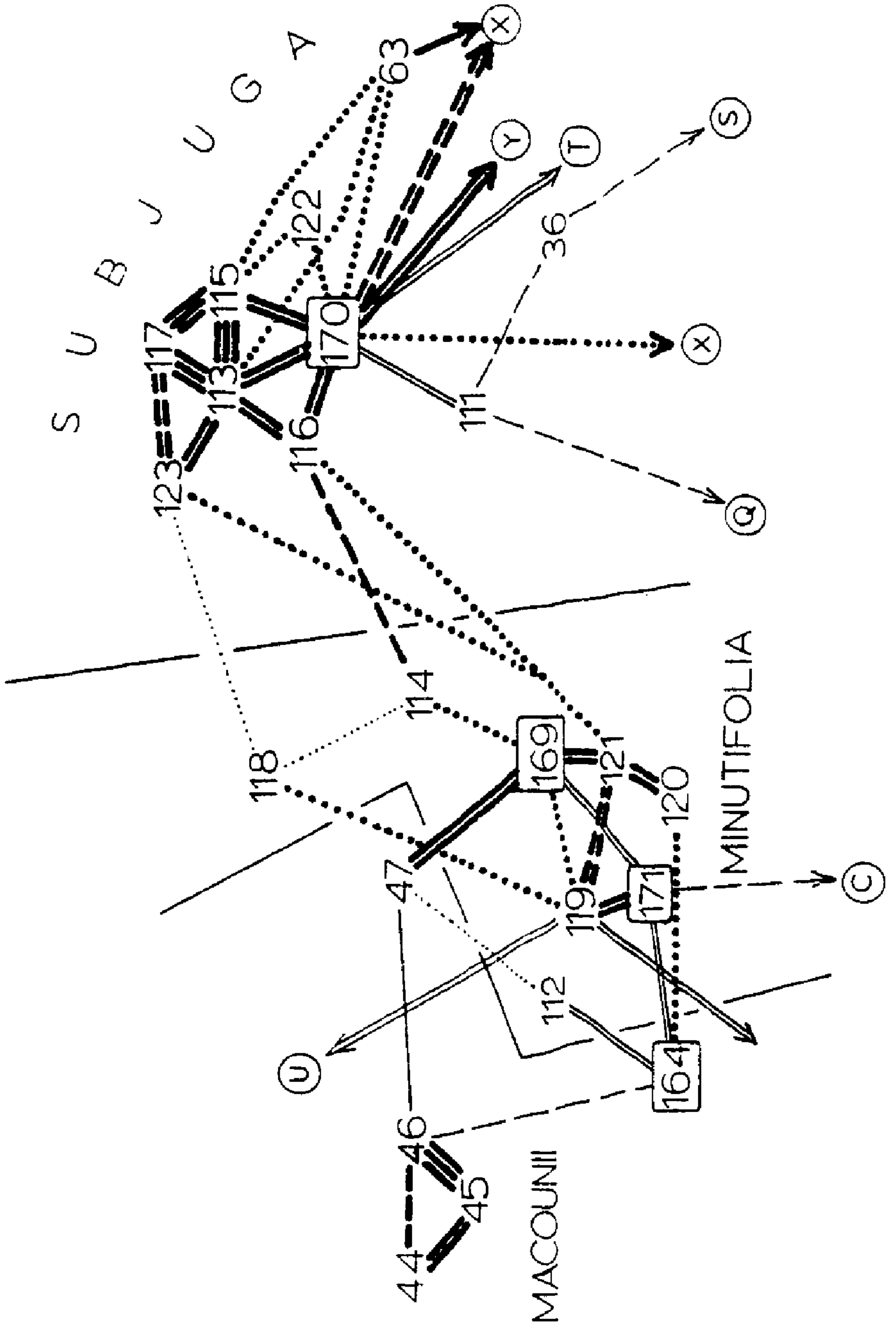


FIG. 35. Subgraph showing the clusters for *Potentilla concinna* and its vars. *bicrenata* and *curvata*. Symbols as in Table 12.

FIG. 36. Subgraph showing the clusters of *Potentilla subjuga*, its var. *minutifolia*, and *P. macounii*. Symbols as in Table 12.


SUBJUGA
MINUTIFOLIA
MACOUNII
170
169
171
164
117
115
113
116
123
122
63
36
111
114
118
121
120
119
47
112
46
45
44
X
Y
T
S
X
Q
C
U

range as *P. subjuga* var. *subjuga*. However, *P. macounii* [164], while being related to *P. subjuga*, is morphologically distinctive in its highly dissected leaflets with tomentose upper surfaces, and geographically disjunct in the northern Rocky Mountains, whereas *P. subjuga* is concentrated in the southern Rocky Mountains.

Fig. 37 shows the subgraph for *Potentilla ambigens*, the most distinct species in its section. Item no. 92 is somewhat transitional between *P. ambigens* and *P. crinita*, and may represent a hybrid.

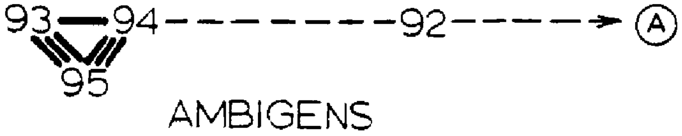


FIG. 37. Subgraph for the *Potentilla ambigens* cluster. Symbols as in Table 12.

In Fig. 38 is shown *Potentilla crinita*; on the right is the typical cluster, including the type of *P. crinita* [172] and a topotype [87]. This cluster forms early and remains loosely attached to var. *lemmonii*, shown at left; the interesting fact is that *P. crinita* var. *crinita* does not connect with any other cluster at any level, except through var. *lemmonii*. Var. *lemmonii*'s cluster includes its type [173] and is connected through several intermediates to *P. effusa* (top left) and through several other intermediates to *P. hippiana* (bottom). There are several specimens which bridge *P. crinita* and its var. *lemmonii*; these are cited in the taxonomic revision, Chapter IX.

Fig. 39 shows the subgraph for *Potentilla effusa* and its var. *rupincola*. This cluster is diffuse, and is connected to the *P. hippiana*

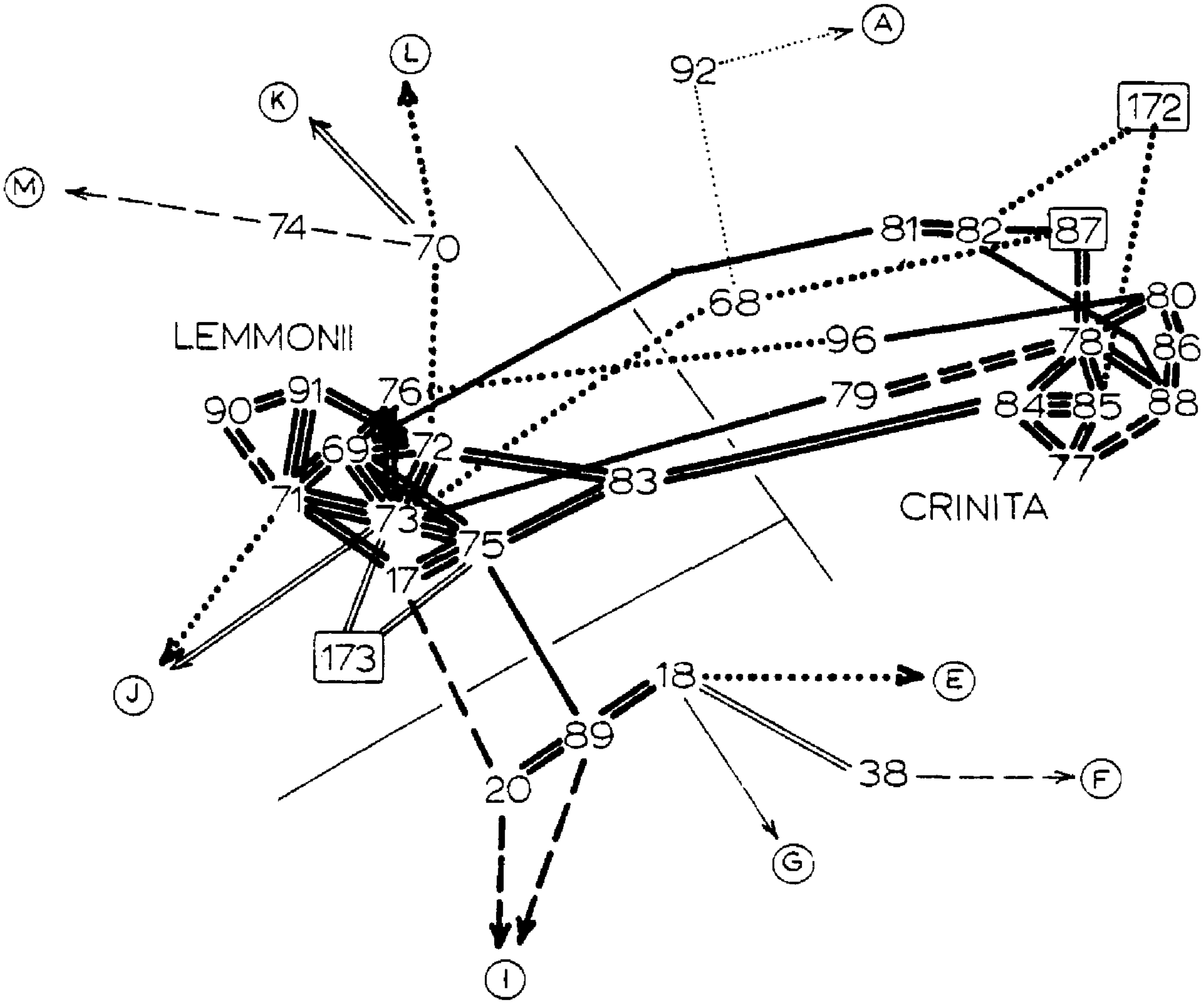


FIG. 38. Subgraph showing the clusters for *Potentilla crinita*, its var. *lemmonii*, and intermediates between var. *lemmonii* and the *P. hippiana* cluster (bottom). Symbols as in Table 12.

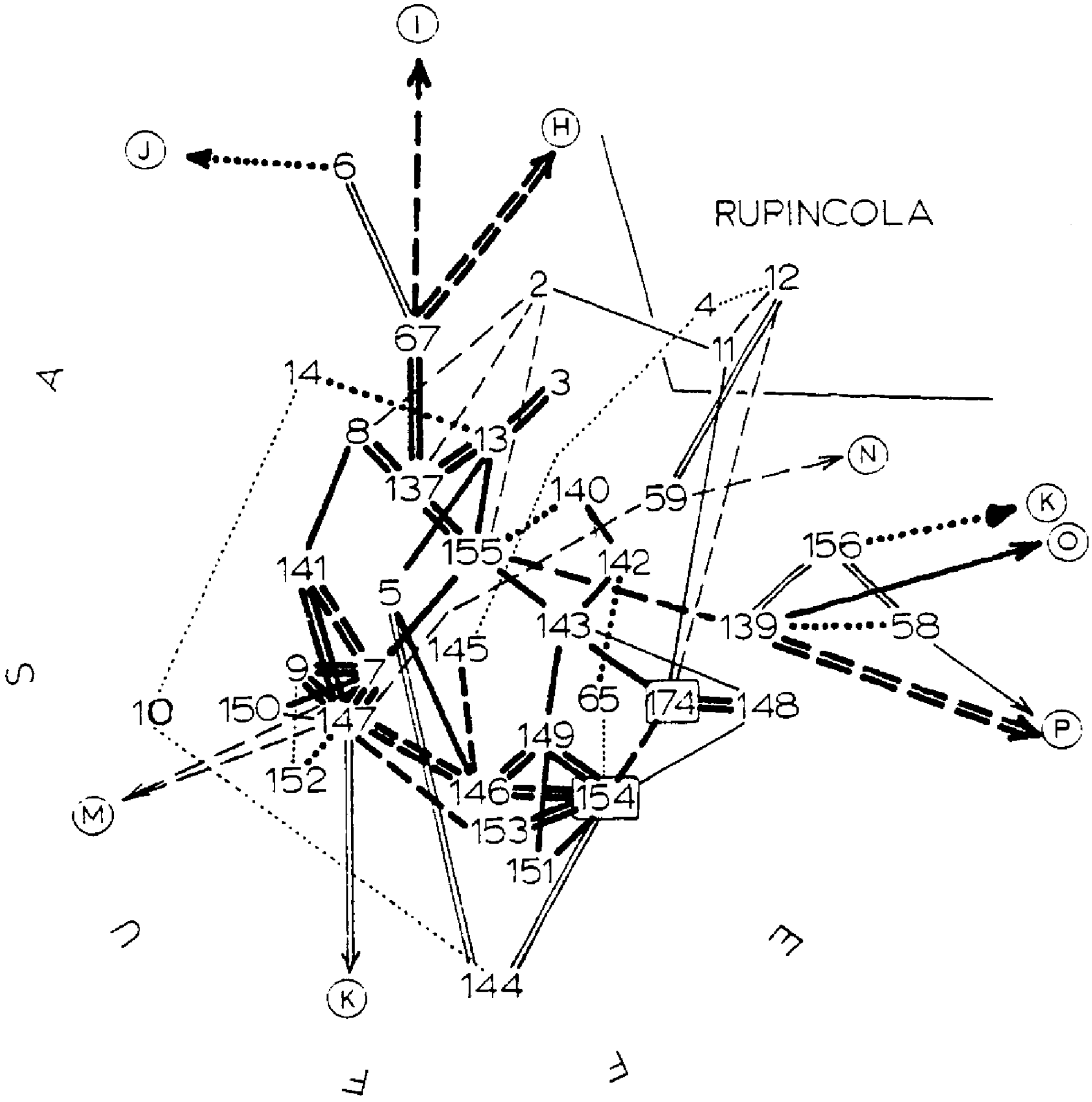
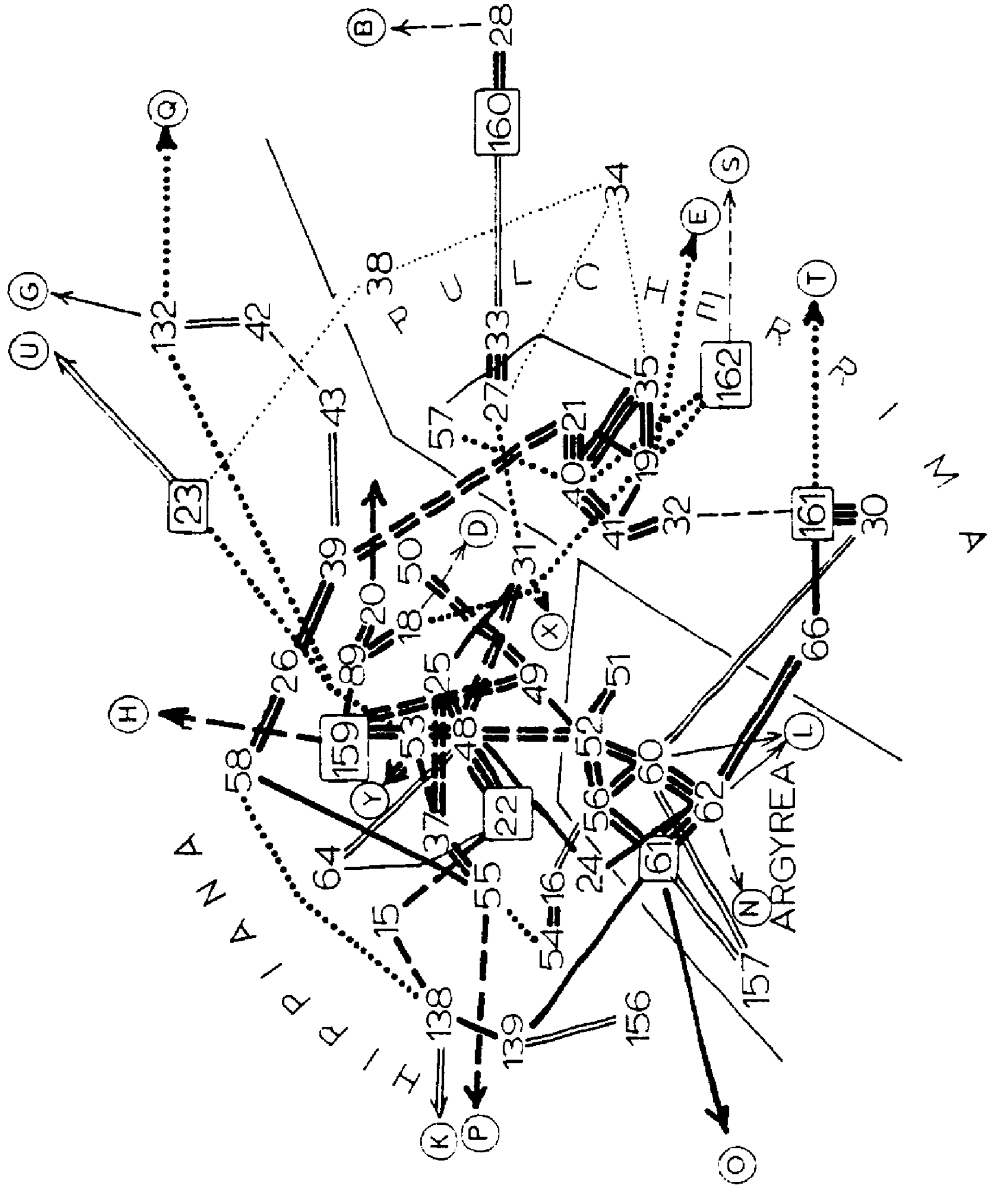


FIG. 39. Subgraph showing the clusters for *Potentilla effusa* and its var. *rupincola*. Symbols as in Table 12.

cluster through several sets of intermediates, as well as to *P. crinita* var. *lemmonii*, as mentioned above. *P. effusa* is disjunct geographically from *P. crinita*; it differs from *P. hippiana* in its small, tomentose calyx with contrasting bractlets, and finer tomentum on the leaves.

The subgraph for *Potentilla hippiana* and *P. pulcherrima* is shown in Fig. 40. This is a complex diagram, and shows a diffuse cluster for *P. hippiana*, including the types of *P. hippiana* [22], *P. diffusa* A. Gray [159], and *P. mogollonica* [23]; this last is transitional to *P. crinita* var. *lemmonii* and may represent a hybrid. The *P. hippiana* cluster is connected loosely to *P. pulcherrima*, which consists of three units: one, close to an authentic specimen of *P. pulcherrima* [162]; another, transitional to *P. hippiana* and including the type of *P. wardii* [161]. This last group has been observed by the author in the field to comprise a hybrid swarm between *P. hippiana* and *P. pulcherrima*. The third unit centers around no. 160, the type of *P. obovatifolia*, a poorly known central-Mexican species that is probably not in this section of *Potentilla*.

FIG. 40. Subgraph showing the clusters of *Potentilla hippiana*, *P. pulcherrima*, and their interconnections. Symbols as in Table 12.


HIPPIANA
PULCHERRIMA
ARGYREA
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CHAPTER IX

TAXONOMY OF *POTENTILLA* SECT. CONCINNAE AND SECT. SUBJUGAE

POTENTILLA SECT. CONCINNAE Rydberg, Bull. Torrey Bot. Club 23:431 (1896); Mem. Dept. Bot. Columbia Univ. 2:24 (1898). Type species: *Potentilla concinna* Richardson.

Key to species: sect. Concinnae

1. Leaflets oblanceolate, finely toothed about 1/3 of way to midrib, digitate; flowers 7-10; calyx-lobes and bractlets acuminate. Chihuahua . . . . 1. *P. oblanceolata*

1. Leaflets obovate to rarely oblanceolate, often toothed 1/2 to midrib or more, digitate to subdigitate; flowers 1-10; calyx lobes and bractlets acute to blunt. Widespread in western North America . . . . (2)

2. Leaflets with more than three teeth, incised 1/2 to midrib or more, digitate or subdigitate; flowers 1-6; leaflets sometimes with tomentum on upper surface in addition to strigae . . . . 2a. *P. concinna* var. *concinna*

2. Leaflets with three small teeth at very apex, often narrow and conduplicate, only strigose on upper surfaces; flowers 2-10. New Mexico, southern Colorado, southern Utah, and Nevada; very rarely northward . . . . (3)

3. Plant without tomentum, uniformly strigose and glandular throughout. Nye Co., Nevada . . . . 2b. *P. concinna* var. *curvata*

3. Lower leaf surfaces tomentose, leaflets bicolored. Southern Utah, northern New Mexico, and southern Colorado, very rarely northward; not known from Nevada . . . . 2c. *P. concinna* var. *bicrenata*

1. *POTENTILLA OBLANCEOLATA* Rydberg, Mem. Dept. Bot. Columbia Univ. 2:53 (1898). MEXICO. CHIHUAHUA. Southwestern part, *Palmer s.n.* in 1885 (US! [163]).

These plants have the characteristic leaf pubescence of *P. concinna*: strigose and glandular above, white-tomentose below; while having the large flowers with acuminate calyx-lobes of *P. pulcherrima*. The stems seem to be decumbent, although the three small individual plants seen are all somewhat fragmentary. The number of flowers per stem in these specimens is larger than that usually found in *P. concinna*, while not approaching that of *P. pulcherrima*, which is many-flowered with an erect stem.

OTHER SPECIMENS SEEN. MEXICO. CHIHUAHUA. Vicinity of Madera, ca. 2250 m, *Palmer* 296 in 1908 (NY! [158]).

2. *POTENTILLA CONCINNA* Richardson, Bot. Append., in Franklin, Narr. Journey Shores Polar Sea 7:739 (1823). [CANADA. ALBERTA.] "Sandy plains in the neighborhood of Carlton, strongly resembling the plains of the Missouri...," *Richardson* 192 no date (Type K photo CAN!, isotype GH!, authentic specimens from same expedition PH! [167] NY!).

2a. *POTENTILLA CONCINNA* Richardson var. *CONCINNA*

Potentilla humifusa Nuttall, Gen. Plant. 1:310 (1818), *non P. humifusa* Willdenow (1813). *Potentilla concinna* Richardson var. *humifusa* Lehmann, Stirp. Pugillus 9:49 (1851). *Potentilla concinna* Richardson var. *humistrata* Rydberg, Contrib. U. S. Natl. Herb. 3:497 (1896), *nom. superfl. subst. pro P. concinna* var. *humifusa* Lehmann. "On high gravelly hills near Fort Mandan, Missouri." Specimen not located.

Potentilla quinquefolia Rydberg, Mem. Dept. Bot. Columbia Univ. 2:76-77 *t.*30 (1898), as to description and specimens cited, but excluding basionym.

Potentilla concinna Richardson var. *divisa* Rydberg, Bull. Torrey Bot. Club 23:431 (1896). *Potentilla divisa* (Rydberg) Rydberg, North Amer. Flora 22(4):330 (1908). "Rocky Mountains," *Douglas s.n.* no date (Type GH! [166]).

Potentilla proxima Rydberg, North Amer. Flora 22(4):339 (1908). UTAH. [Beaver-Piute Cos.], divided between Sevier and Beaver Rivers, south of Belknap Peak, *Rydberg and Carlton* 7369 on 28 July 1905 (Holotype NY! photo UC!).

Potentilla beanii Clokey, Bull. Southern California Acad. Sci. 38:4 (1939). NEVADA. Clark Co., ridge to Charleston Peak, Charleston Mts., grassy slope with *Pinus aristata*, alt. 3280 m, *Clokey* 7974 on 22 July 1938 (Holotype UC!, isotypes COLO! RM! NY! DAO! WS! ORE! US! PH! [165] CAN! POM!).

Low, prostrate plants, caespitose from a branched caudex; basal leaf petioles usually 4 cm or smaller, leaves digitate to subdigitate, usually strigose and often also glandular; leaflets 5-7(-9), from few-toothed to deeply parted into many narrow lobes, strigose and glandular (sometimes also tomentose) above, densely tomentose below; stems usually decumbent, less than 10 cm long (sometimes shorter than the basal leaves), 3-7-flowered, not leafy; flowers medium-sized, calyx crateriform, with broad acute (not acuminate) lobes, strigose and sessile-glandular on outer surfaces; bractlets relatively broad, approaching the size and shape of the calyx lobes; stamens 20; style claviform or uniformly-thickened, 1.6-2.4 mm long.

Sandy prairies, rocky hills on the plains, gravelly foothills, and ridgetops into the alpine zone, often on calcareous soil or shale; southern Alberta and southwestern Manitoba, southwestward to northeastern New Mexico; northern Arizona, southern and central Nevada. Map, Fig. 41.

This species is remarkably uniform, considering its large range and wide range of elevations. The two varieties listed below are the only variants that seem to have geographical integrity. Within var. *concinna* there are, however, two minor variants of note. In the northern portion of the range the plants with leaflets more dissected have been called var. *divisa*, but such plants occur throughout the range. (This is *not* the same as *P. nivea* var. *dissecta*, from which it was justifiably separated by Rydberg).

In southern Utah and in Nevada, a form with long-trailing stems, subdigitate leaves, and sparser pubescence occurs (*P. proxima*, *P. beanii*): it is the only form of var. *concinna* so far reported from Nevada. Plants with this combination of characters have also been collected on the northern Great Plains. Occasional plants with larger leaves, more deeply and irregularly dissected into obtuse-rounded lobes, are found throughout the range of this variety; they represent second-growth after flowering, and are therefore never found with young flowers (e.g., Barr 949-950 [RM!] with comments by C. L. Porter).

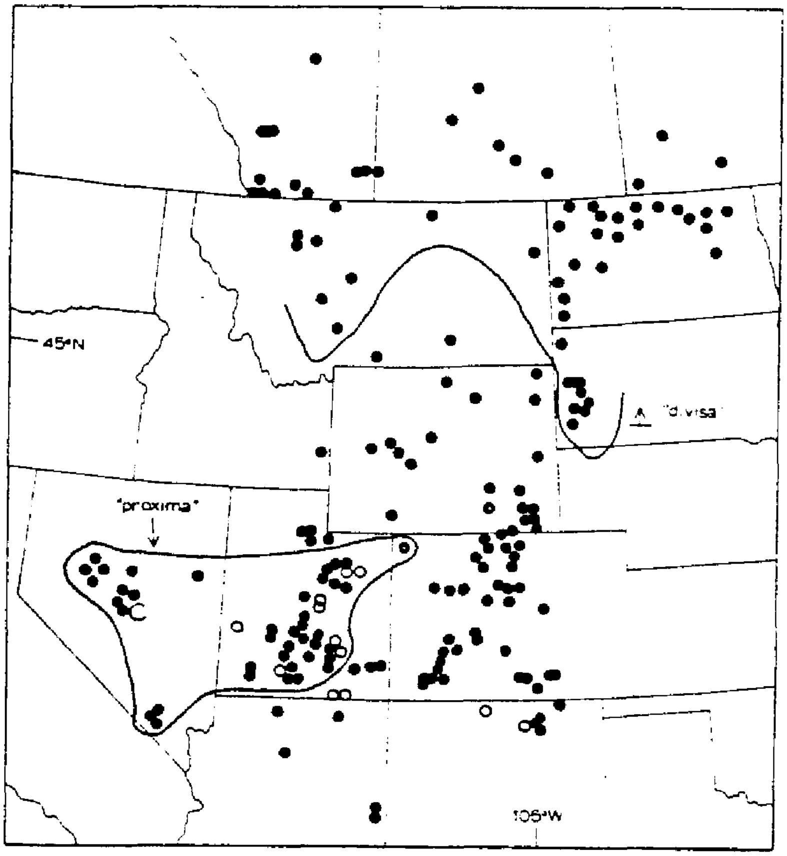

FIG. 41. Rocky Mountains and Great Basin states. Distribution of *Potentilla concinna* var. *concinna* (closed circles); var. *bicrenata* (open circles); and var. *curvata* (C). Solid lines show approximate limits of two forms of var. *concinna*.

Potentilla quinquefolia in the sense of Rydberg and most later authors, is included in *P. concinna* var. *concinna*. *P. nivea* var. *pentaphylla* Turczaninow, upon which *P. quinquefolia* and its basionym *P. nivea* var. *quinquefolia* Rydberg (*nom. superfl.*) are based, is a quinate form of *P. nivea* L. It is not related to sect. Concinnae, and is very rare in North America. I have seen two specimens from northern Alaska and Yukon.

Potentilla leonina Standley (Field Mus. Publ. Bot. 17:260 [1937]) is unknown to me except as the type specimens, collected on Cerro Potosi, Nuevo Leon; these seem to be closely similar to alpine forms of *P. concinna* var. *concinna* from southern Colorado. More material is needed to resolve its relationships.

REPRESENTATIVE SPECIMENS. COLORADO. Larimer Co., Chambers Lake, *Osterhout* 3701 on 29 June 1908 (RM! [101]); Moffat Co., summit of Zenobia Peak, S33 T8N R102W, 2730 m, *Johnston* 2057 on 15 June 1979 (COLO! [097]); San Juan Co., Noname Basin, valley floor, 10800 ft, *Michener* 749 on 29 August 1962 (COLO! [100]); Park Co., Hoosier Pass, ridge flanking Mt. Bross, 11800-12100 ft, *Willard and Zwinger* 7172 on 10 July 1971 (COLO! [099]). NEVADA. Clark Co., head of Lee Canyon, Charleston Mts., 9800 ft, *Heller* 11069 on 5 August 1913 (NY! [109]). NORTH DAKOTA. Benson Co., Leeds, *Lunell s.n.* on 14 May 1906 (NY! [134]). SOUTH DAKOTA. Custer Co., Gobblers Knob, Wind Cave National Park, limestone, *Barr* 949-950 on 7 May 1965 (RM! [135]); Custer Co., near Pringle, rocky slope, *Wiegand and Wiegand* 962 (GH! [104]). UTAH. Emery Co., east edge of East Mtn., 9600 ft, *Lewis* 4708 on 22 June 1977 (BRY! [126]); Emery Co., Mohagany Point, S18 T18S R7E, ca. 8400 ft, *Johnston* 2183 on 20 July 1979 (COLO!); Garfield Co., Aquarius Plateau, S20 T32S R2E, 8600 ft, *Holmgren, Reveal, and LaFrance* 2074 on 28 June 1965 (BRY! [125]); Garfield Co., Aquarius Plateau, 2 mi north of Posey Lake, 10000 ft, *Maguire* 19212 on 29 June 1940 (UTC! [110]); Garfield Co., ridge just north of Bull Creek Pass, Henry Mts., S27 T31N R10E, 10500 ft, *Johnston* 2123 on 22 June 1979 (COLO!); Garfield Co., upper end of Pearl Flat, Henry Mts., S26 T31N R10E, 10000 ft, *Johnston* 2122 on 22 June 1979 (COLO! [098]); San Juan Co.?, La Sal Mts., *Jones s.n.* on 13 June 1913 (NY! [107]); Wayne Co., 12 mi south of Torrey, S10 T31S R4E, 11000 ft, *Neese and White* 3273 on 21 June 1977 (NY! [108]); Wayne Co., Flat Top of Thousand Lake Mtn., S21 T27S R4E, 11100 ft, *Cronquist and Holmgren* 9351 on 24 June 1961 (NY! [124]). WYOMING. Albany Co., Chug Creek, *E. Nelson* 4348a on 10 June 1898 (RM! [105]); Crook Co., gravelly hilltop 7 mi northwest of Hulett, 4500 ft, *Ownbey* 566 on 21 May 1935 (WS! [103]). CANADA. ALBERTA. Cypress Lake, *Macoun* 10470 on 1 July 1895 (RM! [102]); Craigmyle Dist., dry prairie, *Brinkman* 5352 on 3 May 1943 (GH!

[106]); Banff, rocky slopes of Tunnel Mountain, 5000 ft, *McCalla* 2081 on 16 June 1899 (NY! [136]).

2b. *POTENTILLA CONCINNA* Richardson var. *CURVATA* B. C. Johnston in ed. Varietas nova *P. concinnae* var. *concinnae* affinis, a qua differt pubescentia foliolorum non tomentosa, ergo folia non bicolorato; foliolis breviter tri-dentatis, angustis et plerumque conduplicatis. A *P. concinnae* var. *bicrenatae* absentia tomenti differt.

TYPE. NEVADA. Nye Co., Quinn Canyon Range, summit above Cherry Creek, *B. Maguire and A. H. Holmgren* 25352 on 8 June 1945 (Holotype UTC! [1], isotypes UC! CAS! WS! NY!).

OTHER SPECIMENS SEEN. NEVADA. Same locality, *Lewis* 3399 on 6 June 1975 (RM!); same locality, *Sharsmith* 4819 on 25 May 1960 (UTC! NY! RM!).

Habitat in declivitatibus saxosis humilium montium Juniperinis Pininis monospermis Artemisinis in terram calcaream in elevatione 2460 m. s. m. (7500 ped.). Varietato distributio in tabulo 41 depicta.

Low perennial herb, caespitose from a thick, branched caudex; basal leaves erect to ascending, digitately divided (neither subdigitate not approximate) on petioles about twice as long as the leaflets; petioles 2.0-5.0 cm long, strigose and sessile-glandular; leaflets 5-7, linear or narrowly deltoid, with three blunt teeth at the very apex (the adaxial pair often entire), often folded and gently curved away from the petiole, sparsely and uniformly strigose on upper and lower surfaces, often in addition sessile-glandular on upper surface; stems decumbent, equal to twice as long as basal leaves, branched above the middle, with 2-9 flowers; calyx 3.8-7.1 mm high (including lobes), with acute (not acuminate) ovate lobes; bractlets ovate, acute (not acuminate), of same shape, texture, and color as the calyx lobes at fruit maturity, strigose and glandular on adaxial surfaces; stamens 20; styles 1.9-2.3 mm long, uniformly-thickened below (neither incrassate nor papillose), moniliform or more commonly claviform (thickened just below stigma).

This variety resembles *P. multisecta* (Chapter VII), similar in absence of tomentum, geographical range, habitat, and habit; however, var. *curvata* differs in its much shorter teeth on the leaflets, many fewer teeth, and the glandular pubescence. In division of the leaves and leaflets var. *curvata* differs from var. *concinna* but approaches var. *bicrenata*, from which it differs in the absence of tomentum; var. *curvata* also appears to be out of the range of var. *bicrenata*. In pubescence and curving of the leaflets var. *curvata* resembles *P. crinita* var. *crinita*, but differs in its digitate leaves, few-flowered decumbent stem, and larger flowers; var. *crinita* is not known from Nevada.

2c. *POTENTILLA CONCINNA* Richardson var. *BICRENATA* (Rydberg) Welsh and Johnston in ed. *Potentilla bicrenata* Rydberg, Bull. Torrey Bot. Club 23:431 (1896). NEW MEXICO. Agua Fria, *Walcott* 66 in 1883 (Holotype US! [168]).

Rocky slopes, lower foothills or low mountains, often with Pinons and junipers, northeastern New Mexico, southern and central Utah, very rarely northward; not seen from Nevada, but possibly to be expected there. Map, Fig. 41.

The typical form is only found in New Mexico. The plants in Utah tend to be larger, with longer petioles and more upright leaflets, and sparser tomentum. Plants from Nevada representing the extreme expression of these characters have been described above as var. *curvata*.

REPRESENTATIVE SPECIMENS. COLORADO. Costilla Co., near La Veta Pass, *Ramaley* 12016 on 14 June 1928 (COLO! [131]). NEW MEXICO. Rio Arriba Co., hills southwest of Tierra Amarilla, 2300 m, *Eggleston* 6503 in 1911 (GH! [127]). UTAH. Duchesne Co., north rim of Nine Mile Creek, S10 T11S R14E, 8200 ft, *Holmgren, Reveal, and LaFrance* 1952 on 18 June 1965 (GH! [128]); Emery Co., Mohagany Point, S18 T18S R7E, ca. 8400 ft, *Johnston* 2184 on 20 July 1979 (COLO!); Garfield Co., Henry Mts., Granite Ridges, S26 T31S R10E, 9200 ft, *Johnston* 2131 (COLO!). WYOMING, Albany Co., Sherman and Buford, meadow edge, *Macbride* 2491 on 27 July 1913 (RM! [130]).

POTENTILLA SECT. SUBJUGAE Rydberg, Bull. Torrey Bot. Club 23:397 (1896); Mem. Dept. Bot. Columbia Univ. 2:27 (1898). Type species: *Potentilla subjuga* Rydberg.

Potentilla sect. Hippianae Rydberg, Bull. Torrey Bot. Club 24:1 (1897); *Potentilla* sect. Leucophyllae Rydberg, Mem. Dept. Bot. Columbia Univ. 2:31 (1898). Type species: *Potentilla hippiana* Lehmann (*Potentilla leucophylla* Torrey *non* Pallas).

Key to species: sect. Subjugae

1. Leaves pinnate, usually with 50-60% of rachis occupied, moderately to densely long-strigose throughout, sometimes also with tomentum as a secondary layer below; leaflets narrowly oblanceolate to narrowly linear-deltoid, entire or with 3-5(-7) shallow teeth on each side, these usually in the upper 1/3, sometimes conduplicate; inflorescence usually branched from about the middle of the stem, often with long pedicels. Four Corners states and Nevada . . . . (2)

1. Leaves pinnate to subdigitate or rarely digitate, usually with (0-)10-40% of rachis occupied, short-strigose, glabrous, or tomentose below, sometimes long-sericeous, but then densely tomentose below as well; leaflets relatively broadly oblanceolate to obovate, with 4-20 teeth on each side, soemtimes deeply incised, flat; inflorescence various. Widespread in Rocky Mountains, Great Plains, and Great Basin . . . . (3)

2. Leaflets 11 or more, uniformly long-strigose, not bicolored, with 2-9 teeth on each side of the leaflet, often small, curled, and conduplicate; petioles, stems, and lower surface of leaflets usually without any tomentum; 30-60% of rachis occupied. Not in Nevada . . . . 3a. *P. crinita* var. *crinita*

2. Leaflets 7-12, long-strigose below, often tomentose above and slightly bicolored, with 2-5 teeth on one side of the leaflet, sometimes larger and flat; petioles, stems, and lower surface of leaflets usually with some tomentum; 40-60% of rachis occupied. Rare in New Mexico . . . . 3b. *P. crinita* var. *lemmonii*

3. Leaves subdigitate to rarely truly digitate; leaflets 5-7(-10), without tomentum above (or if tomentose above then rare plants of northwest Montana and southwest Alberta), densely tomentose below, usually strongly bicolored; stems erect to ascending, not leafy, 30 cm or more long, or if lower then plants of the eastern slope of the Front Ranges from Wyoming to New Mexico or on the eastern slope of the northern Rocky Mountains; petioles not tomentose, strigose or sometimes glandular and/or hirsute . . . . (4)

3. Leaves apparently pinnate to subdigitate, when subdigitate the pinnae evenly spaced (though crowded), with or without tomentum above, densely tomentose below, bicolored or not; stems decumbent to erect, leafy or not, 15-50(-70) cm long; petioles hirsute, or else strigose and tomentose . . . . (7)

4\. Leaflets with 4-9 teeth on each side, incised (1/2-)2/3 or more to midrib, these sometimes crenate; stems 4-35 cm tall; leaves subdigitate with 10-30(-40)% of rachis occupied; petioles strigose and glandular; flowers 4-20. Central Colorado, southern Wyoming and northern New Mexico; rarely in northwestern Montana and southwestern Alberta; mostly subalpine . . . . (5)

4\. Leaflets with 10-15 teeth on each side incised 1/3-1/2 of way to midrib, usually acute; stems 30-60(-80) cm tall; leaves subdigitate or rarely digitate, with (0-)10% of rachis occupied; petioles strigose or hirsute with or without glandular pubescence; flowers 10-30 . . . . 5. *P. pulcherrima*

5\. Style 1.4-2.5 mm long; stems 20-35 cm long; leaflets dissected 1/2-1/3 of way to midrib, conspicuously bicolored with upper surface not tomentose; calyx with some tomentum under sericae . . . . 4b. *P. subjuga* var. *subjuga*

5\. Style 1.1-2.1 mm long; stems 5-15 cm long; leaflets dissected 2/3 or more to midrib, moderately bicolored, or if conspicuously bicolored then with upper surface tomentose; calyx tomentose or not . . . . (6)

6\. Lower surface of leaflets densely snow-white tomentose, upper surface often tomentose, leaves grayish-green in appearance; leaflets 7-10, the upper pairs often not opposite; flowers 4-6; stems 3-15 cm long, decumbent to ascending. Southwestern Alberta and western Montana . . . . 9. *P. macounii*

6\. Lower surface of leaflets more sparsely grayish-tomentose, upper surface not tomentose, leaves green in appearance; leaflets 5-8, the upper pairs opposite; flowers 4-20; stems 10-18 cm long, ascending. Central Colorado . . . . 4a. *P. subjuga* var. *minutifolia*

7\. Calyx densely tomentose at anthesis, with bractlets that are darker in color and often much smaller than the calyx-lobes; leaflets always with some tomentum above (except when whole plant glabrescent), never strongly bicolored, the tomentum often in patchy tufts and sometimes sparse, with 4-9 teeth on each side and these often in upper 1/2 of leaflet; stems leafy. Mostly east of the Continental Divide and north of the Arkansas River; rare in Utah, western Colorado, and New Mexico; absent in Nevada and Arizona . . . . . (8)

7\. Calyx sericeous at anthesis with or without additional tomentum, with bractlets that are usually of the same color and texture as the calyx lobes and often acuminate; leaflets tomentose or not on upper surface, often strongly bicolored, with 6-18 teeth on each side, often toothed in the lower 1/2 of leaflet; stems leafy or not. Mostly west of the Continental Divide and south of Wyoming . (9)

8\. Tomentum sparse to dense, leaf appearing light-green to gray . . . . 6a. *P. effusa* var. *effusa*

8\. Tomentum absent or very sparse, leaf appearing dark-green and glabrescent to the naked eye. Larimer Co., Colorado . . . . 6b. *P. effusa* var. *rupincola*

9. Longest basal leaf rachis 20-30 cm long, 40-60% occupied with leaflets; petioles and stems conspicuously hirsute; leaflets large, coarsely toothed with 10-30 teeth on each side, short-hirsute or slightly tomentose below, green and not bicolored . . . . . 7. *P. ambigens*

9. Longest basal leaf rachis 8-16 cm long, 20-50% occupied; petioles strigose and tomentose; leaflets medium-sized or small, toothed with 6-15 teeth on each side, densely tomentose below and often also strigose, bicolored or not, but if not bicolored then grayish-white . . . . (10)

10. Upper stem densely white-pubescent, usually sericeous and tomentose; inflorescence glomerate with short pedicels, stem leafy; leaflets 7-11, occupying 10-40% of rachis, confluent with the rachis or not, always with some tomentum above, often with an olive-greenish cast . . . . 8a. *P. hippiana* var. *argyrea*

10. Upper stem sparsely pubescent, usually scattered-tomentose; inflorescence openly branched with mostly medium-length to long erect pedicels, stem not leafy; leaflets 7-15, occupying 20-50% of rachis, confluent with the rachis, usually bicolored and grayish in color, sometimes without tomentum above . . . . 8b. *P. hippiana* var. *hippiana*

3. *POTENTILLA CRINITA* A. Gray, Mem. Amer. Acad. Arts Sci. II 4:41 (1849). NEW MEXICO. "Along Santa Fe Creek, and at the foot of hills, in sunny places," *Fendler* 199 in 1847 (Holotype GH!, isotypes NY! PH! US! [172]).

3a. *POTENTILLA CRINITA* A. Gray var. *CRINITA*

Potentilla vallicola Greene, Leafl. Bot. Observ. Crit. 2:137-138 (1911). ARIZONA. Coconino Co., Fort Valley, wet park, 7250 ft, *Burrall s.n.* on 4 September 1909 (Type MNA!).

Moderately-large plants, multicipital from an unbranched caudex; basal leaves pinnate with 11-15 leaflets, uniformly strigose and sessile-glandular thoughout; leaflets narrow oblanceolate to more commonly narrowly linear-deltoid, with 3-9 teeth on each side; stems (10-)20-45 cm tall, not leafy, openly branched above the middle, with 10-30 flowers on long thin pedicels; calyx campanulate, strigose and sessile-glandular, with acuminate lobes; bractlets acuminate, more or less glandular on adaxial surfaces; styles filiform, 1.6-2.6 mm long. Map, Fig. 42.

This species is not closely related to any other, as shown by the subgraph (Fig. 38), and is usually immediately recognizible; however,

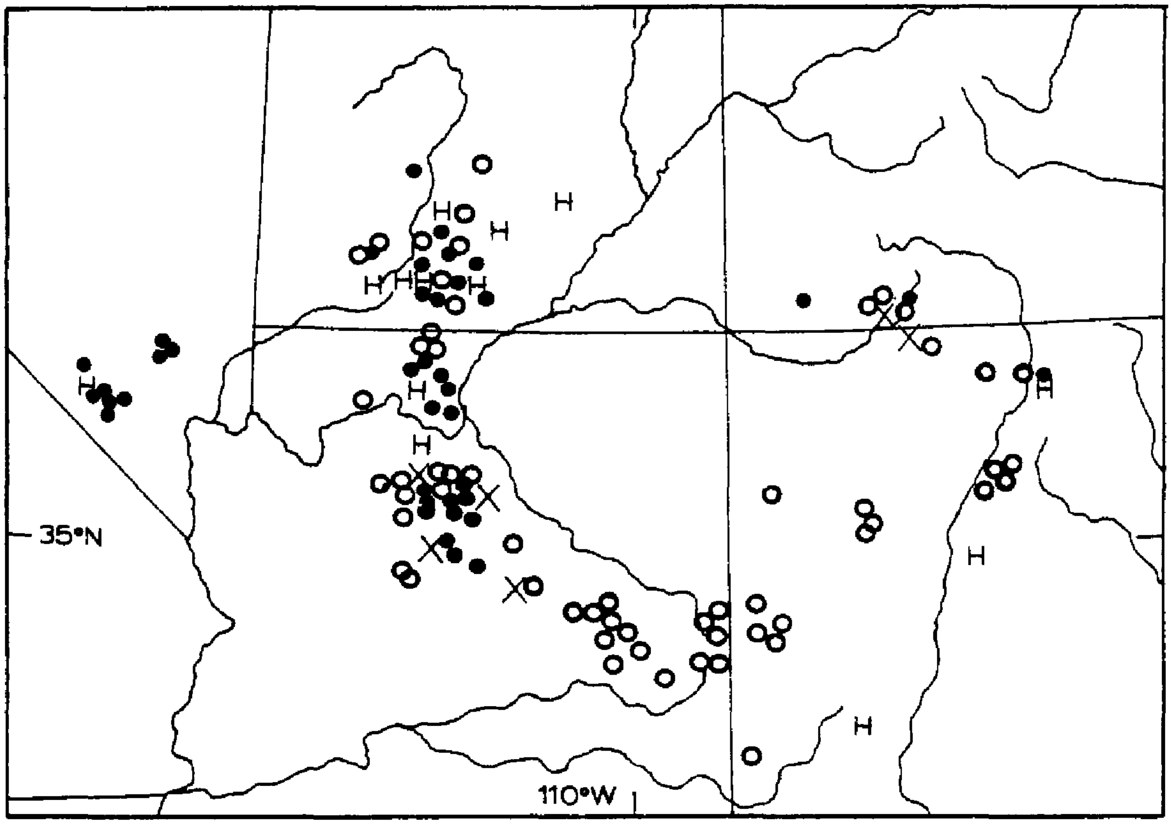

FIG. 42. Four Corners states and southern Nevada. Distribution of *Potentilla crinita* var. *crinita* (open circles); and var. *lemmonii* (closed circles). Intermediates between the two varieties (X); and between *P. crinita* var. *lemmonii* and *P. hippiana* (H).

some gradation occurs to var. *lemmonii*, and through it to *P. hippiana*.

REPRESENTATIVE SPECIMENS. ARIZONA. Coconino Co., Navajo Ordnance Dept, open pine woods, 7200 ft, *Schallert s.n.* on 13 September 1943 (RM! [088]); Coconino Co., 2 mi west of Flagstaff, 7000 ft, *Genelle and Fleming* 1391 on 2 July 1972 (ASC! [084]); Coconino Co., Flagstaff, north of Armory, 7000 ft, *Deaver s.n.* on 11 August 1945 (RM! [082]); Coconino Co., Flagstaff, between sawmill and old city dump, 7000 ft, *Demaree* 42862 on 27 July 1960 (CAS! [080]); Navajo Co., 3 mi south of Showlow, 6225 ft, *Hutchinson* 7125 on 14 August 1936 (COLO! [085]). COLORADO. Archuleta Co., Piedra, *Baker s.n.* on 12 July 1899 (ND-G! [077]). NEW MEXICO. Catron Co., ca. 10 mi east of Beaverhead, ca. 8000 ft, *Dunn* 7710 on 28 September 1951 (RSA! [086]); Catron Co., Datil Mts., Chavez Spring, S6 T1S R9W, ca. 8200 ft (UNM!); Santa Fe Co., Santa Fe Canyon, *Eastwood* 15620 on 15 October 1928 (CAS! [087]). UTAH. Garfield Co., 14.7 mi north of Escalante on Bicknell road, S22 T33S R2E, 8000 ft, *Higgins* 1114 on 19 August 1977 (BRY! [078]).

3b. *POTENTILLA CRINITA* A. Gray var. *LEMMONII* (S. Watson) Kearney and Peebles, J. Wash. Acad. Sci. 29:480 (1939). *Ivesia lemmonii* S. Watson ("*Lemmoni*"), Proc. Amer. Acad. Arts Sci. 20:365 (1885). *Potentilla lemmonii* (S. Watson) Greene, Pittonia 1:104 (1887). ARIZONA. "On vertical rocks bordering Oak Creek, near Flagstaff," *Lemmon and Lemmon* 3202 on 23 August 1884 (September?) (Holotype GH!, 3 isotypes UC! [173]).

Moderately-large plants multicipital from an unbranched caudex; basal leaves pinnate with 7-12 leaflets, apparently strigose at least below and on petioles, in addition with some tomentum below, often also tomentose above, the pubescence appearing much softer and the leaflets more bicolored than in var. *crinita*; leaflets oblanceolate to narrowly oblanceolate to linear-deltoid, with 1-5 shallow teeth on each side; stems 15-40 cm tall, not leafy, openly branched above the middle, with 7-30 flowers on thin pedicels; calyx campanulate, strigose or sericeous, often also with some tomentum, usually also with glandular hairs, with acuminate lobes; bractlets acuminate, more or less glandular on adaxial surfaces; styles filiform, 1.6-2.6 mm long. Map, Fig. 42.

This variety, while being part of *P. crinita*, is transitional in morphology between var. *crinita* and the *P. hippiana* complex. There are a few transitional forms between var. *crinita* and var. *lemmonii* as well. The transitions to *P. hippiana* (cited under that species) have the more open inflorescence, smaller flowers, more pinnate leaves with more leaflets, and glandular pubescence of *P. crinita* var. *lemmonii*, and the denser tomentum and broader leaflets with more and broader teeth of *P. hippiana*.

REPRESENTATIVE SPECIMENS. (VAR. LEMMONII). ARIZONA. Coconino Co., vicinity of Jacobs Lake, *Collom s.n.* on 22 June 1938 (ASC! [091]). NEW MEXICO. Taos Co., 4 mi west of Santa Barbara campground, *Garcia* 733 on 26 July 1969 (UNM! [069]). NEVADA. Clark Co., Charleston Mts., Lee Canyon, 8000 ft, *Heller* 10983 on 25 July 1913 (CAS! [076]). UTAH. Garfield Co., Pine Lake near Table Cliff Plateau, S24 T35S R2W. 8100 ft, *Neese and White* 3807 on 27 July 1977 (BRY! [075]); Garfield Co., 0.5 mi south of Tropic Reservoir, S18 T37S R4W, 7850 ft, *Foster and Foster* 4393 on 30 June 1977 (BRY! [073]); Garfield Co., Henry Mts., McMillan Springs Campground, S31 T31S R10E, 8400 ft, *Neese, Rogers, and White* 2109 (BRY! [071]); Kane Co., 4 mi east of Duck Creek Lake, 8000 ft, *Maguire* 20238 on 17 July 1940 (UTC! [072]); Wayne Co., Singletree Campground, *Harrison* 1245 on 23 July 1973 (BRY! [090]).

(INTERMEDIATES BETWEEN VAR. CRINITA AND VAR. LEMMONII). ARIZONA. Coconino Co., 27.1 mi south of junction of hwys. 160 and 64, *Cooke, Pinkava, Keil, and Weber* on 14 September 1969 (ASC! [068]); Coconino Co., Wild Bill Study Area, 7200 ft, *Kruse* 2594 on 21 August 1967 (MNA! [079]); Navajo Co., Raibow Lake, 6800 ft, *Lehr* 1808 on 22 July 1976 (BRY!). NEVADA. Clark Co., Charleston Park, 2270 m, *Clokey* 5514 on 30 July 1935 (CAS! [083]). NEW MEXICO. Rio Arriba Co., Chama, *Baker* 392 on 3 September 1899 (RM! [081] POM!).

4. *POTENTILLA SUBJUGA* Rydberg, Bull. Torrey Bot. Club 23:397-398 *t*.274 (1896). COLORADO. Clear Creek Co., mountains about the headwaters of Clear Creek, near Empire, 9500 ft, *Patterson* 192 on 28 July-6 September 1892 (Holotype NY!, isotypes GH! BRY! [170]).

4a. *POTENTILLA SUBJUGA* Rydberg var. *MINUTIFOLIA* (Rydberg) B. C. Johnston in ed. *Potentilla minutifolia* Rydberg, Bull. Torrey Bot. Club 23:399 *t*.275 *f*.6-10 (1896). *Potentilla rubripes* Rydberg var. *minutifolia* (Rydberg) Th. Wolf, Bibl. Bot. 16(71):205 (1908). COLORADO. El Paso Co., Pikes Peak, alpine, *Canby s.n.* on 27 August 1895 (Holotype US! [171], isotypes GH! UC!).

Potentilla tenerrima Rydberg, Bull. Torrey Bot. Club 23:398 *t*.275 *f*.1-5 (1896). COLORADO. Fremont Co., Bergens Park, *Brandegee* 950 in 1874 (Lectotype [the only specimen with notes by Rydberg] GH!, isotypes NY! [not seen by Rydberg] UC! PH! [169]).

Potentilla rubripes Rydberg, Bull. Torrey Bot. Club 33:143 (1906); Rydberg, North Amer. Flora 22(4):337 (1908). *Potentilla rubricaulis* Rydberg, Mem. Dept. Bot. Columbia Univ. 2:101 (1898), as to specimens cited and description, not *P. rubricaulis* Lehmann. *Potentilla concinna* Richardson var. *rubripes* (Rydberg) C. L. Hitchcock, Vasc. Plants Pacific Northwest 3:136 (1961). COLORADO. El Paso Co., Pikes Peak, *Biltmore Expedition* 1425 on 25 June 1896 (Holotype NY!).

Low plants with erect-ascending to decumbent stems 8-15 cm long, multicipital from an unbranched caudex; basal leaves with rachis about 4 cm long, pinnate or loosely subdigitate with 5-7 leaflets, petioles strigose without tomentum; leaflets obovate, the upper 1-2 pairs opposite and the lower 1-3 pairs scattered, not confluent, with 4-9 narrow, blunt teeth on each side, incising leaflet 2/3 or more to midrib, strigose above, silky-sericeous and tomentose below, slightly bicolored to not bicolored; stems not leafy, with 4-20 flowers; calyx campanulate, strigose and not tomentose, sometimes also glandular, with acuminate lobes; bractlets of same size and shape as calyx lobes, acuminate, sericeous on adaxial surface; styles filiform with slightly incrassate base, (1.1-)1.4-2.1 mm long.

Open rocky meadows and protected recesses on rocky ridges, subalpine and alpine, Front Range, Sawatch Range, and La Garita Range of central Colorado, possibly also on the Wet Mountains. Map, Figs. 43 and 48.

This variety is closely related to var. *subjuga*, as shown by the subgraph (Fig. 36), morphological similarities of the leaf, and common habitats. The variety is probably better represented by the type specimens of *P. tenerrima* cited above, with *P. minutifolia* and *P. rubripes* being somewhat transitional to var. *subjuga*; but *minutifolia* has priority in the rank of variety.

P. rubripes is not related to *P. concinna*, contrary to the proposal of C. L. Hitchcock; *P. subjuga* and its var. *minutifolia* form a natural

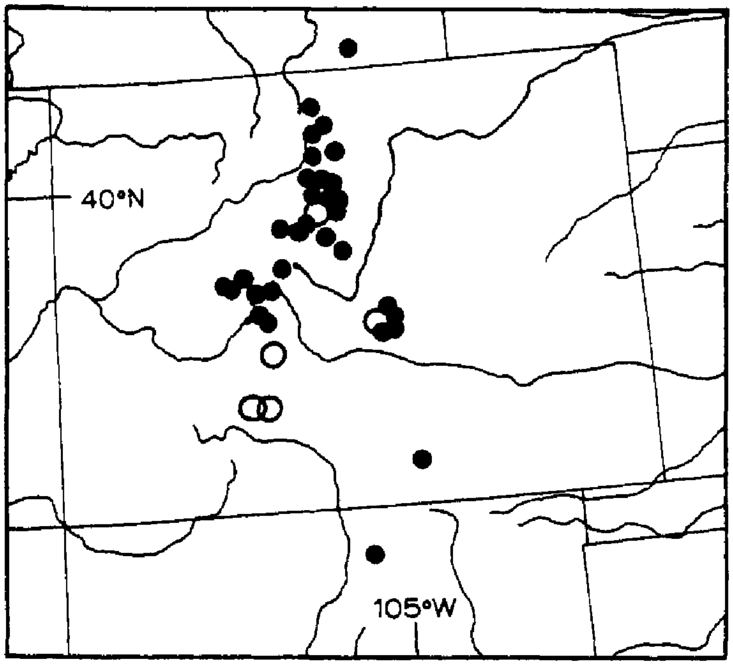

FIG. 43. Colorado and adjoining states. Distribution of *Potentilla subjuga* var. *subjuga* (closed circles) and var. *minutifolia* (open circles).

geographical entity, easily recognized in the field, and evidently distinct from *P. concinna* with its prostrate habit. Within the range of *P. subjuga*, *P. concinna* is rarely subalpine, prostrate, always digitate or very slightly subdigitate, and short-toothed.

P. saximontana Rydberg, supposed by Hitchcock to be related to his *P. concinna* var. *rubripes*, is actally a disjunct outlier of the arctic-alpine *P. rubricaulis* Lehmann (*non P. rubricaulis* Rydberg), as evidenced by its pubescence, style form and length, which are characteristic of *Potentilla* sect. Niveae.

REPRESENTATIVE SPECIMENS. COLORADO. Gilpin Co., slope of the cirque on the northeast side of James Peak, 12000 ft, *Komarkova s.n.* on 4 July 1972 (COLO! [120]); Gilpin Co., Eldora to Baltimore, 8500-9500 ft, *Tweedy* 5752 in 1903 (NY! [119]); Mineral Co., gentle north slope, La Garita Range, head of Bellows Creek and Saguache Creek, 12400 ft, *Murdock* 4690 on 9 July 1911 (GH! [112]); alpine, lat. 39°-41°, *Hall and Harbour* 160 *p.p.* in 1862 (GH! [114]).

4b. *POTENTILLA SUBJUGA* Rydberg var. *SUBJUGA*

Potentilla rubricaulis fma. *nana* Clements and Clements, Sched. Exsicc. Herb. Format. Coloradensis 507 (*post* 1901). COLORADO. El Paso Co., Saddle, 4000 m, *Clements and Clements* 507 on 30 July 1901 (RM! NY!). The label reads: "*Potentilla rubricaulis nana* (est P. rubricaulis forma depauperata prostrata). Rosula endemica, Colorado, species principalis aspectus prioris Paronychia-Silene- chalicodio."

Potentilla osterhoutiana Th. Wolf, Bibl. Bot. 16(71):200-201 (1908). COLORADO. Larimer Co., "Estes Park, leg. Geo. *Osterhout*, 20 Jul. 1903." Specimen not located in Osterhout's herbarium at RM; the data may be a misprint.

Potentilla viridior Rydberg, North Amer. Flora 22(4):342 (1908). COLORADO. Larimer Co., Estes Park, mountains, *Osterhout s.n.* on 12 July 1897 (Type NY!). Since Osterhout did not number his specimens for distribution, it is uncertain to which specimen at RM this corresponds; the number "12" that appears on the NY specimen is probably tne number of duplicates made.

Low to medium-sized plants with ascending stems 15-35 cm long, multicipital from an unbranched caudex; basal leaves with rachis 4-10 cm long, loosely subdigitate with 5-7 leaflets, petioles strigose without tomentum; leaflets obovate, usually with all pairs opposite, sometimes with 5 leaflets digitate at the apex of the rachis, not confluent, with 6-9 narrow blunt teeth on each side, incising leaflet 1/2-2/3 to midrib, strigose above, tomentose below, moderately to strongly bicolored; stems not leafy, with 10-20 flowers; calyx campanulate, strigose with some tomentum in addition, sometimes also glandular, with acuminate lobes; bractlets of same size and shape as calyx lobes, acuminate, sericeous on adaxial surfaces; styles filiform with slightly incrassate base, 1.5-2.4 mm long.

Open rocky meadows and protected recesses on rocky ridges, subalpine and alpine, southern Rocky Mountains of Colorado, northern New Mexico, and southern Wyoming, usually on the eastern slope; disjunct on the eastern slope of the northern Rocky Mountains in Alberta. Map, Figs. 43 and 48.

The specimens cited below from Alberta are usdoubtedly *P. subjuga* var. *subjuga*. However, Garton 1219 [123], from Sibley Peninsula, Ontario, while being roughly like *P. subjuga* in leaf dissection and pubescence, is a much larger plant in all proportions, with leafy stems and considerably out of range for *P. subjuga*; it probably represents *P. hippiana* var. *argyrea* with smaller basal leaves.

REPRESENTATIVE SPECIMENS. COLORADO. Clear Creek Co., high mountains about Grays Peak, near timber line, *Patterson s.n.* in August 1885 (GH! [115]); Clear Creek Co., ridge 0.9 mi northwest of Loveland Pass, S28 T4S R76W, 12000-12200 ft, *Johnston* 2230 on 19 August 1979 (COLO!); El Paso Co., Peak Slope, 3900 m, *Clements and Clements* 419 on 12 July 1901 (RM! [118]); El Paso Co., shore of Dead Lake, Pikes Peak, 10000 ft, *Ewan* 15162 on 1 August 1943 (COLO! [111]); Gunnison Co., flat ridgetop 0.8 mi WSW of Cumberland Pass, *Johnston* 2244 on 23 August 1979 (COLO!); Gunnison Co., Cottonwood Pass, S14 T14S R81W, 12150 ft, *Johnston* 2240 on 22 August 1979 (COLO!); Larimer Co., mountains of Estes Park, Windy Gulch, *Osterhout* 1502 on 12 July 1897 (RM! [117]; is this *P. osterhoutiana*?); Larimer Co., Estes Park, Windy Gulch, nearly alpine, *Osterhout s.n.* on 12 July 1897 (RM! [116]); alpine, lat. 39°-41°, *Hall and Harbour* 160 *p.p.* in 1862 (GH! [113]). CANADA. ALBERTA. Mount Forget-Me-Not, 7500 ft, *Macoun* 16734 on 16 July 1897 (NY!); Banff National Park, Sundance Canyon, *Malte and Watson* 873 on 4 July 1925 (CAN! WTU!); Elbow River, 49°40'N, *Macoun* 16734 in 1897 (GH!).

5. *POTENTILLA PULCHERRIMA* Lehmann, Strp. Lehm. Prim. Descript. Pugillus 2:10-11 (1830); in Hooker, Flora Bor.-Amer. 1(4):190-191 (1832). *Potentilla pensylvanica* Linnaeus var. *pulcherrima* (Lehmann) Torrey and Gray, Flora North Amer. 1:438 (1840). *Potentilla hippiana* Lehmann var. *pulcherrima* (Lehmann) S. Watson, Proc. Amer. Acad. Arts Sci. 8:555 (1893). *Potentilla gracilis* Douglas var. *pulcherrima* (Lehmann) Fernald, Rhodora 42:213 (1940). "In the prairies, as well as dry banks, in the Rocky Mountains between lat. 52° and 56°. *Drummond*." (Hooker). Type not seen; authentic specimens, ex herb. Hooker and from the same expedition (PH! GH! [162]).

Potentilla filipes Rydberg, Bull. Torrey Bot. Club 28:174-175 (1901). *Potentilla pulcherrima* Lehmann var. *filipes* (Rydberg) Th. Wolf, Bibl. Bot. 16(71):209-210 (1908). COLORADO. Huerfano Co., Spanish Peaks, Wahatoya Canyon, 2400 m, *Rydberg and Vreeland* 6039 on 13 June 1900 (Holotype NY!, isotype RM!).

Potentilla pulcherrima Lehmann var. *subpinnata* Th. Wolf, Bibl. Bot. 16(71):209 (1908). "...in europaischen Garten gezogenen Kulturformen."

Potentilla pulcherrima Lehmann var. *condensata* Th. Wolf, Bibl. Bot. 16(71):210 (1908). Two specimens cited, from Silverton, Colorado, at 2900 m, and Cloudcroft, New Mexico, at 2650 m. Specimens fitting Wolf's localities and description have not been seen.

Potentilla camporum Rydberg, North Amer. Flora 22(4):319 (1908). SOUTH DAKOTA. Black Hills, *Pratt* 93 no date (Holotype NY!).

Potentilla wardii Greene, Leafl. Bot. Observ. Crit. 2:138-139 (1911). UTAH. Wayne Co., Thousand Lake Mountain, 11100 ft, *Ward* 387 on 14 July 1875 (Holotype US! [161]).

Large plants, multicipital from an unbranched caudex, 30-80 cm tall, erect to ascending; longest basal leaf rachis 8-25 cm long, petioles strigose or less often hirsute, often also tomentose; leaves with 7(-9) leaflets, subdigitate or uncommonly truly digitate, with 10-15 coarse teeth along each side cutting 1/3-1/2 to midrib, sericeous or strigose above without tomentum, densely white-tomentose below, strongly bicolored; stem branching in upper 1/2 or 1/3, leafy or not, with 10-40 flowers; calyx large, to 12 mm high including lobes, the lobes acuminate, bractlets of same shape and texture as lobes, acuminate, often glandular on adaxial surfaces; style filiform, slightly thickened at base, 1.6-3.0 mm long.

Moist meadows of plains and montane valleys, sometimes in disturbed soil, central British Columbia, Alberta, and Saskatchewan, sough through North and South Dakota to southeastern New Mexico, central Arizona, and eastern Nevada. Scattered localities in southern Ontario and Quebec; surely cultivated in St. Louis, Missouri. Map, Fig. 44.

P. pulcherrima is distinct in its characteristically large plants with erect stems, large flowers, and toothy, bicolored, slightly subdigitate leaves. Hybrid swarms of *P. pulcherrima* and *P. hippiana* var. *hippiana* occur in the Rocky Mountains and Black Hills, usually giving every variation in the 6-8 differential characters within the populations, in addition to the distinctly different extreme forms. The large plants of the typical form are characteristic of the Great Plains; the Great Basin and western Colorado plants present a complex, intricate array of

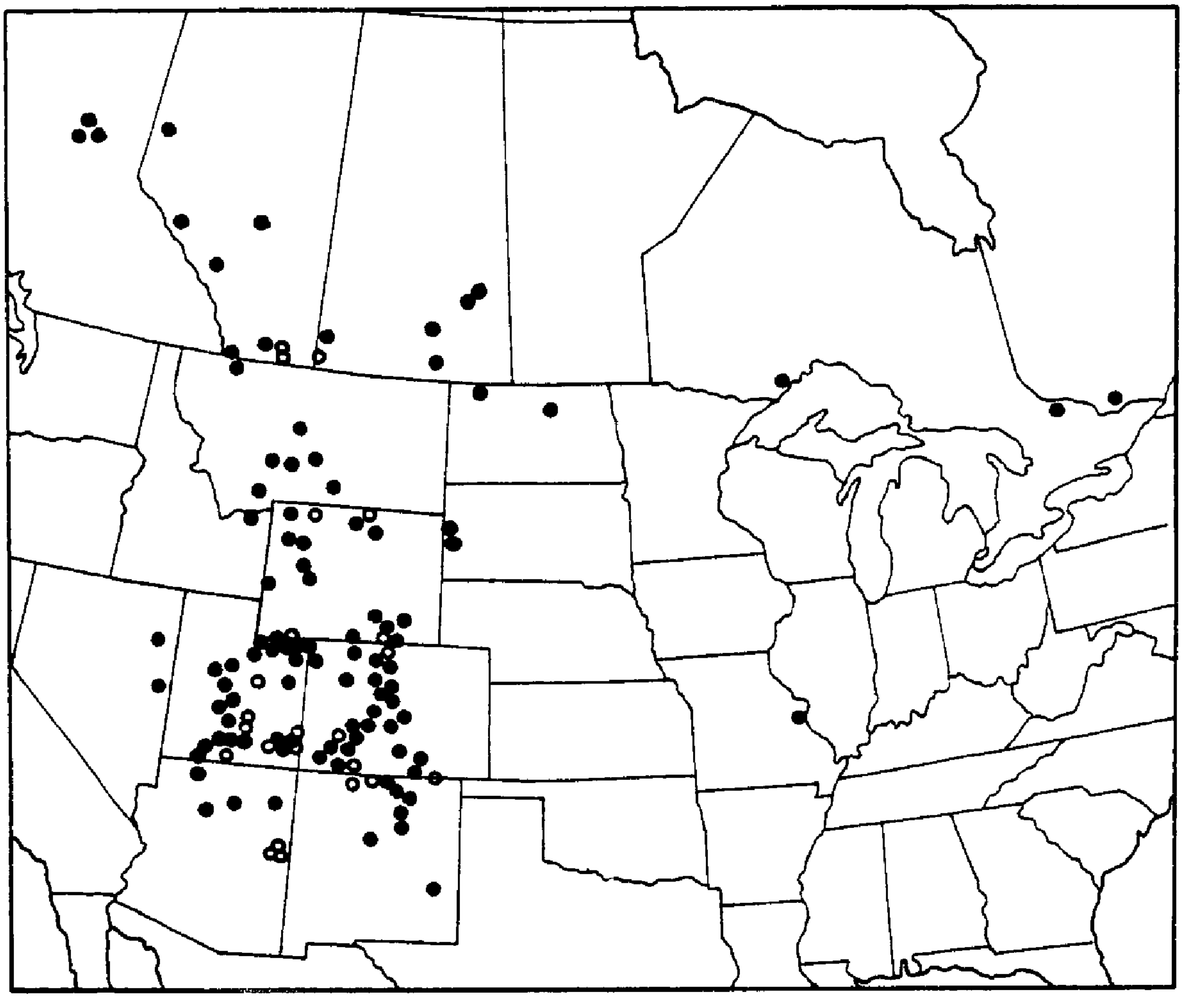

FIG. 44. United States and southern Canada. Distribution of *Potentilla pulcherrima* (closed circles), and intermediates to *P. hippiana* (open circles).

small-leaved forms, some of which are truly digitate. This species has been associated with *Potentilla gracilis* Douglas, by Keck (1940) as a species, and by Fernald (cited above) as a variety. In the Rocky Mountains and Colorado Basin, the distributional range of *P. pulcherrima*, the latter species is clearly different from the forms of *P. gracilis* there. The best character is the characteristic style of *P. gracilis*, which is uniformly thickened to about half its length, then abruptly tapered to a filiform tip; whereas that of *P. pulcherrima* is uniformly filiform and usually slightly thickened at the very base. The leaflets of *P. gracilis* are usually oblanceolate, whereas *P. pulcherrima* obovate. The only form of *P. gracilis* that is conspicuously bicolored is found from northwestern California to west-central British Columbia, completely disjunct from *P. pulcherrima*; the forms of *P. gracilis* in the Rocky Mountains and Great Basin either completely lack tomentum (*brunnescens*), have leaflets that are narrowly divided almost to the midrib (*flabelliformis, pectinisecta, elmeri*) or are variously pubescent with no tomentum or tomentulose (*nuttallii, glabrata*).

REPRESENTATIVE SPECIMENS. COLORADO. Archuleta Co., Chimney Rock Mesa, Piedra, *Schmoll* 1349 on 31 June 1924 (RM! [021]); Hinsdale Co., La Garita Range, head of Cochetopa Creek, above tree limit, *Willard* 6886 on 11-13 August 1971 (COLO! [027]); Larimer Co., Longs Peak Valley, 9000 ft, *Kiener* 2756 on 20 July 1931 (GH! [031]). MONTANA. Madison Co., north form Mill Creek, Tobacco Root Mts.,2 mi south of Brandon Lakes, *Hitchcock* 16947 on 29 July 1947 (COLO! [034]). NORTH DAKOTA. Leeds, prairies, *Lunell* 43 on 16 June 1900 (GH! [030]). UTAH. San Juan Co., Dickson Pass, Abajo Mts., ca. S13 T34S R22E, 10450 ft (NY! [033]); San Pete Co., alpine station, Ephraim Canyon, 10000 ft, *Maguire and Richards* 20237 on 15 August 1934 (UTC! [040]); San Pete Co., 6.5 mi up Manti Canyon, 7000 ft, *Holmgren* 219 on 11 July 1962 (NY! [028]); Summit Co., 1/4 mi on road to Dead Horse Pass, west fork of Blacks Fork, Uinta Mts., *Holmgren, Anderson, and Witte* 10988 on 20 August 1955 (UTC! [041]); Uintah Co., Dinosaur National Monument, Doug Chew's Cabin, 7400 ft, *Welsh* 474 on 2 June 1956 (BRY! [038]); Uintah Co., East Tavaputs Plateau, along the road to Hill Creek Ranger Station, *Vickery and Wiens* 1600 on 13-15 July 1956 (GH! [035]). CANADA. ONTARIO. Perry's Bay, Sibley Peninsula, *Love and Love* 6919 (COLO! [036]). SASKATCHEWAN. Cypress Hills Park, *Breitung* 4805 on 15 July 1947 (COLO! [C32]).

INTERMEDIATE BETWEEN P. PULCHERRIMA AND P. HIPPIANA VAR. ARGYREA. CANADA. ALBERTA. Waterton Lakes National Park, Camp Columbus, 49°04'N 113°53'W, 4400 ft, *Nagy and Blais* 1084 on 16 June 1969 (CAS! [063]).

6. *POTENTILLA EFFUSA* Douglas ex Lehmann, Stirp. Lehm. Prim. Descript. Pugillus 2:8 (1830); Lehmann ex Hooker, Flora Bor.-Amer. 1(4): 187 (1832). *Pentaphyllum effusum* (Douglas) Lunell, Amer. Midl. Nat. 4:416 (1916). "On elevated grounds of the Assinaboyne, and the higher waters of the Red Rivers" (Hooker), *Douglas s.n.* no date (Type K photo CAN!).

6a. *POTENTILLA EFFUSA* Douglas ex Lehmann var. *EFFUSA*

Potentilla effusa Douglas var. *filicaulis* Nuttall ex Torrey and Gray, Flora North Amer. 1:437 (1840). *Potentilla filicaulis* (Nuttall) Rydberg, Bull. Torrey Bot. Club 24:2 (1897). *Potentilla hippiana* Lehmann var. *filicaulis* (Nuttall) Boivin, Natural. Canad. 93: 435 (1966). "Rocky Mountains towards the sources of the Platte," *Nuttall s.n.* no date (NY! GH!; BM photos NY! WS! US!).

Potentilla effusa Douglas var. *gossypina* Nuttall ex Torrey and Gray, Flora North Amer. 1:437 (1840). *Potentilla gossypina* (Nuttall) Hooker, J. Bot. 6:219 (1847), excluding specimens cited and synonyms. "Rocky Mountains," *Nuttall s.n.* no date (BM photos NY! US!).

Potentilla coloradensis Rydberg, Mem. Dept. Bot. Columbia Univ. 2:115 (1898). *Potentilla effusa* Douglas var. *coloradensis* (Rydberg) Th. Wolf, Bibl. Bot. 16(71):199 (1908). COLORADO. Park Co., South Park, *Porter s.n.* on 24 July 1872 (Holotype NY!, isotypes GH! [174] NY! PH!).

Potentilla effusa Douglas var. *filiformis* Torrey and Gray ex Th. Wolf, Bibl. Bot. 16(71):203 (1908). *Err. sphalm. pro P. effusa* var. *filicaulis* Nuttall ex Torrey and Gray.

Plants of medium height, multicipital from an unbranched caudex, stems 20-55 cm high, usually branched below the middle and conspicuously leafy, upper leaves subdigitate or pinnate; leaves pinnate with scattered or opposite leaflets, often not confluent or very slightly so; leaflets 5-15, with 4-9 teeth on each side cutting about 1/2 to midrib, sericeous and tomentose above, tomentose below, not strongly bicolored, tomentum sometimes sparse and patchy when color grayish-green, otherwise greenish-gray; stem with 7-30 flowers; calyx small, about 4 mm high including lobes, densely covered with tomentum; bractlets 1/2 length of calyx lobes or less, in young flowers of darker color from calyx, usually tomentose on adaxial surface; styles filiform or slightly thickened at base, 1.5-2.1 mm long.

Open rocky slopes and meadows, or in open forest, on shelves or niches of cliffs, mostly montane to subalpine, southcentral Alberta to southern Manitoba, northwestern Minnesota, south across Montana, Wyoming, and western South Dakota and Nebraska, to north-central New Mexico, principally on the eastern slope of the Continental Divide, but escaping westward through the Wyoming gap to the north slope of the Uinta Mountains. Map, Fig. 45.

The typical variety, with ascending to decumbent stems, many and very small flowers, leafy stems, and leaves white-tomentose on both surfaces, is best represented in this study by Boivin and Dore 8021 [154] or Booth 56965 [144], both cited below; the other principal form of var. *effusa* has larger, more pinnate leaves that are moderately bicolored, and taller stems; it has a tendency to occur north of Wyoming. Grayish-green plants, with sparse, patchy tomentum (usually not bicolored) similarly occur throughout the larger range of var. *effusa*, but are most common in Colorado and southern Wyoming (var. *coloradensis*).

The sheet at BM bearing the type of *P. effusa* var. *gossypina* Nuttall has two plants and two labels; one large plant (specimen of *P. pensylvanica* L. in fruit) fits the label for Geyer 119, since the small plant is obviously that "of which Mt. Nuttall collected but a single specimen, not quite in flower," described by Torrey and Gray in the protologue of var. *gossypina*. This situation was misinterpreted by Hooker (1847), who cites as a synonym of *P. gossypina* (Nuttall) Hooker, Douglas' manuscript-name *P. arachnoidea*, finally published by Rydberg in 1908, which is a synonym of one or another of the varieties of *P. pensylvanica*. The two

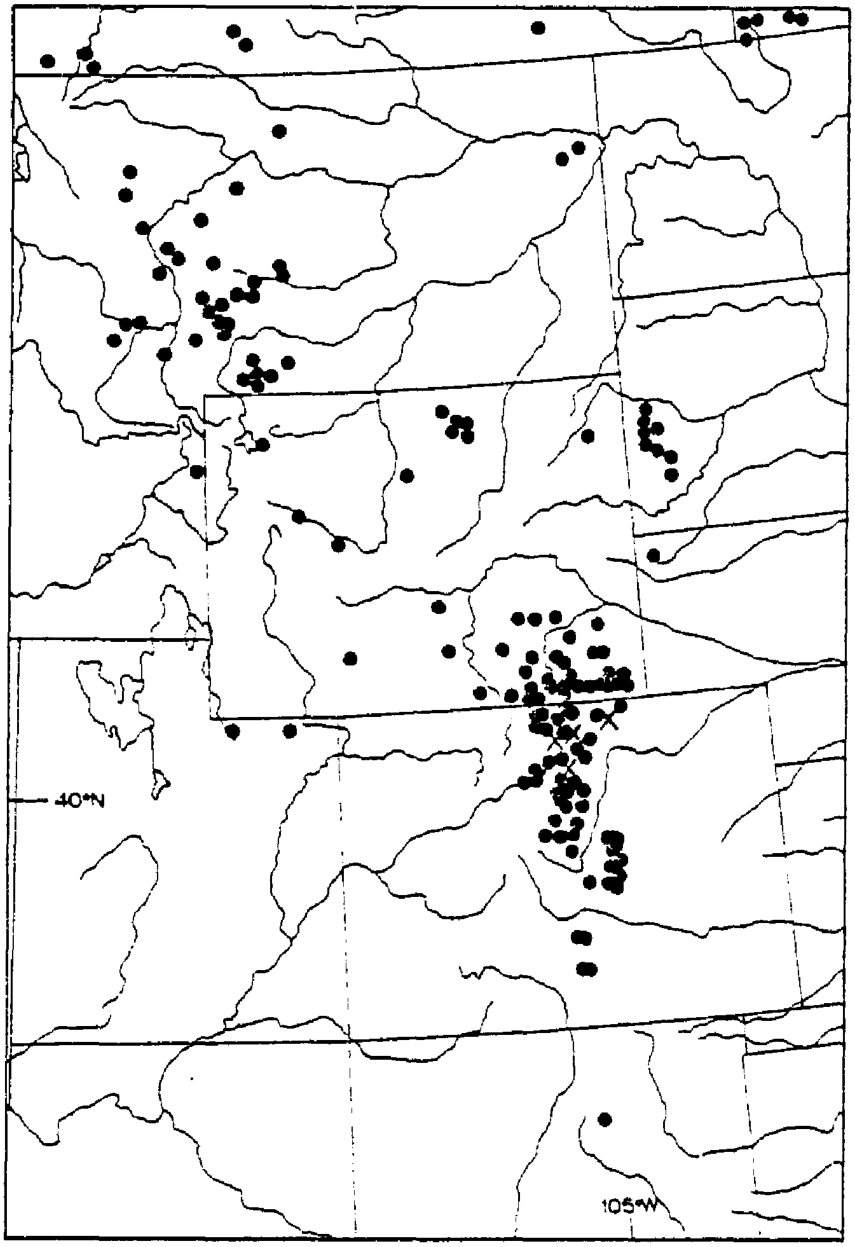

FIG. 45. Rocky Mountain states. Distribution of *Potentilla effusa* var. *effusa* (closed circles); and var. *rupincola* (X).

species are this nomenclaturally entangled, but not to my knowledge biologically.

REPRESENTATIVE SPECIMENS. COLORADO. Boulder Co., near Boulder, *Ramaley* A82 on 20 June 1900 (RM! [002]); Clear Creek Co., mountain sides near Georgetown, *Patterson* 27 in 1885 (PH! [148]); El Paso Co., Minnehaha, 2600 m, *Clements and Clements* 260 on 21 July 1901 (GH! [014]); Jefferson Co., Rocky Flats, Church Ditch west of plant site, *Kunkel and Shultz* 165 (COLO! [013]); Larimer Co., Estes Park near Eagle Cliff Camp, 8000 ft, *Baker* 4459b on 4 August 1930 (CAS! [008]); Larimer Co., dry upland, Estes Park, *Knowlton s.n.* on 27 June 1937 (GH! [006]); Larimer Co., Moraine Park, *Osterhout* 5628 on 10 July 1917 (RM! [005]); Larimer Co., Estes Park, Moraine, *Osterhout* 1498 on 15 July 1897 (RM! [009]). MONTANA. Lewis and Clark Co., Helena, *Butler* 891 on 22 June 1908 (NY! [145]); Lewis and Clark Co., 1 mi north of Wolf Creek, *Hitchcock* 17950 on 2 July 1948 (GH! [142]); Meagher Co., open field 15 mi northwest of White Sulphur Springs, *Hitchcock* 16233 on 8 July 1947 (CAN! [151]); Powell Co., ca. 15 mi south of Deer Lodge, *Booth* 56965 on 20 June 1956 (NY! [144]); Wheatland Co., juniper scabland 20 mi south of Harlowtown, *Hitchcock* 16306 on 10 July 1947 (GH! [146] UC! [153]); central Montana, Cottonwood Creek, 5000 ft, *Flodman* 557 on 30 July 1896 (ND-G! [143]). MINNESOTA. Polk Co., Melvin, *Stevens* 251 (GH! [147]). NORTH DAKOTA. Cutler, sandy soil, *Bergman* 2619 on 28 July 1909 (RM! [141]). WYOMING. Albany Co., Upper Grade, *Willits* 272 on 9 July 1909 (RM! [007]); Albany Co., 5 mi east of Laramie, *Porter* 3105 on 28 June 1942 (RM! [010]); Sheridan Co., Tongue Dist. experimental pastures, 8000 ft, *Hurd* 309 (RM! [149]); Jaw-Bone Gulch, *E. Nelson* 2017 (RM! [003]). CANADA. ALBERTA. 10 mi south of Cardston, grassland of Rocky Mountain foothills, *Dore and Breitung* 12330 on 4 August 1950 (GH! [150]). MANITOBA. Steep Rock, east coast of Lake Manitoba, *Scoggan* 9366 on 11 July 1951 (MAN! [152]); Winnipeg, Birds Hill, *Hart* 753 on 15 July 1939 (NY! [059]). SASKATCHEWAN. Assiniboia, Roche Percee, sandstone cliffs bordering the valley of the Souris River, *Boivin and Dore* 8021 (MAN! [154]).

6b. *POTENTILLA EFFUSA* Douglas ex Lehmann var. *RUPINCOLA* (Osterhout) Th. Wolf, Bibl. Bot. 16(71):199-200 (1908). *Potentilla rupincola* Osterhout, Bull. Torrey Bot. Club 26:256 (1899). COLORADO. Larimer Co., Dale Creek, *Osterhout* 1780 on 21 July 1898 (Holotype RM!, isotypes NY! PH! US!).

Potentilla saxialis Osterhout, *nom. herbariorum provis. pro P. rupincola* Osterhout.

Short to medium-height plants, multicipital tufted from an unbranched caudex, glabrous and green or subglabrous; stems 15-30 cm high, brittle, usually branched about the middle and leafy; leaves pinnate with scattered or opposite leaflets, not confluent with the rachis; leaflets 5-10, with 3-5 teeth along each side cutting about 1/2 to midrib, very sparsely strigose above and without tomentum, glabrous to sparsely-patchy tomentose below, not bicolored, but dark green and shining throughout; petiole sparsely strigose and tomentose; stem with 7-30 flowers; calyx small, about 4 mm high including lobes, with acuminate lobes, sparsely tomentose; bractlets 1/2 length of calyx lobes or less, in young flowers contrasting with calyx (or not contrasting when calyx glabrous), glabrous or tomentose on adaxial surface; styles filiform or slightly thickened at base, 1.6-1.9 mm long.

Shelves or niches of cliffs, often on granite, montane of northcentral Colorado, eastern slope of the Front Range. Map, Fig. 45.

Except for the near lack of tomentum or other pubescence, var. *rupincola* greatly resembles in all other characters the typical form of *P. effusa* var. *effusa*; it represents the end of a series in pubescence density from the typical form through the light-green form (*coloradensis*) to *rupincola*. However, the light-green form is found throughout the range of var. *effusa* with a southern flavor, whereas the glabrous-subglabrous plants are restricted to three counties along the Front Range in northcentral Colorado. It should also be noted that *rupincola* represents the end of a series leading to rockier, better-drained habitats.

7. *POTENTILLA AMBIGENS* Greene, Erythea 1:5 (1893). "Moist meadows along Bear Creek above Morrison, Colorado, July, 1889." Specimen not located at ND-G or other herbaria.

Large, coarse plants, perennial, multicipital from an unbranched caudex, stems (20-)30-80 cm tall; longest leaf rachis 20-25 cm long, conspicuously hirsute without tomentum, pinnate with 11-12 leaflets occupying 40-60% of rachis, the leaflets confluent with the rachis forming a toothed wing between upper leaflets; leaflets large, coarsely toothed with 10-18 teeth on each side, cutting about 1/3 to midrib, sparsely sericeous or glabrous above, short-hirsute below on veins but usually glabrous-subglabrous on lamina; stems with 20-30 flowers, not leafy; calyx large, the largest 10-15 mm long (including lobes), the lobes acuminate, sericeous; bractlets acuminate and about equalling the calyx-lobes, glandular on adaxial surfaces; styles filiform, thickened at base, 1.8-3.0 mm long.

Montane woods, eastern slope of the Front Ranges from southeastern Wyoming south through Colorado to the Sacramento Mountains of New Mexico. Map, Fig. 46.

Although I have not seen the type, Rydberg (1898) apparently cites it and gives a very full description and plate characterizing this unique species; Wolf (1908) gives an even better description. The plants resemble a gigantic *P. hippiana* var. *hippiana*, but differ from that species in the unique pubescence on lower leaf-surfaces, pubescence of the petioles, the winged leaf-rachis, and the absence of tomentum. *Shultz and Shultz* 1447 [092] is somewhat transitional to *P. hippiana*, as shown on the subgraph (Fig. 37). *P. ambigens* is the most distinct species in this section.

REPRESENTATIVE SPECIMENS. COLORADO. Rocky Mountains, lat. 39°-41°, *Hall and Harbour* 158 *p.p.* in 1862 (GH! [095], mixed with *P. effusa* var. *effusa*); Rocky Mountains, lat. 39°-41°, *Hall and Harbour* 162 in 1862 (GH!). NEW MEXICO. Catron Co., Mogollon Mts., S33 T1N R17W, 8200 ft, *Shultz and Shultz* 1447 on 5 September 1974 (BRY! [092]); Otero Co., Sacramento Mts., Cloudcroft, east side of town, S5 T16S R12E, 8500 ft, *Worthington* 4785 on 28 July 1979 (COLO! [093]). WYOMING. Albany Co., Halleck Canyon, *A. Nelson* 7438 on 4 July 1900 (COLO! [094]).

8. *POTENTILLA HIPPIANA* Lehmann, Stirp. Lehm. Prim. Descrpt. Pugillus 2: 7-8 (1830); ex Hooker, Flora Bor.-Amer. 1(4):188-189 t.64 (1832). *Potentilla leucophylla* Torrey, Ann. Lyc. New York 2:197-198 (1827), *non Potentilla leucophylla* Pallas (1815). *Potentilla pensylvanica* Linnaeus var. *hippiana* (Lehmann) Torrey and Gray, Flora North Amer. 1:438 (1840). COLORADO. "Sources of the Platte," *James* 130 in 1820 (NY! ex herb. Torrey [022]).

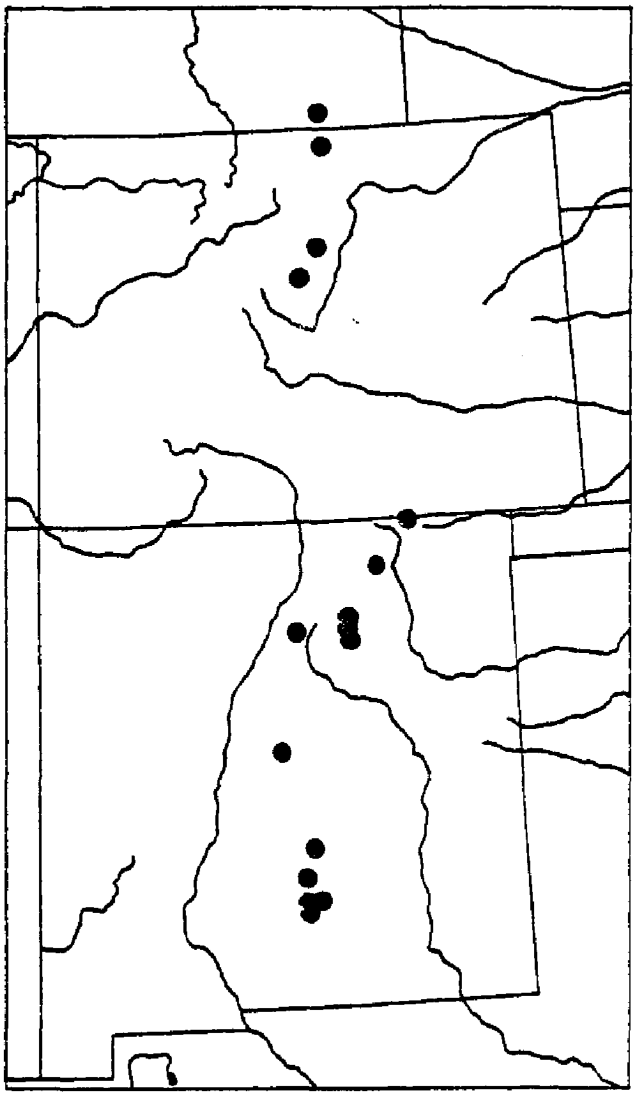

FIG. 46. Colorado, New Mexico, and portions of adjoining states. Distribution of *Potentilla ambigens*.

Potentilla leneophylla Torrey and James ex Eaton, Manual V 344 (1829). *Err. sphalm. pro P. leucophylla* Torrey.

8a. *POTENTILLA HIPPIANA* Lehmann var. *ARGYREA* (Rydberg) Boivin, Phytologia 4:90 (1952). *Potentilla argyrea* Rydberg, North Amer. Flora 22(4):341 (1908). CANADA. SASKATCHEWAN. Moose Jaw, on open prairie, *Macoun* 14441 on 20 June 1896 (Holotype NY!, isotype CAN! [061]).

Medium-height to tall perennial plants, multicipital from an unbranched caudex, stems (15-)25-50 cm tall; basal leaves pinnate to subdigitate, occupying 10-40% of rachis, petioles strigose and tomentose; leaflets 7-12, opposite, more or less confluent with the rachis, with 6-18 teeth on each side cutting about 1/2 to midrib, these often blunt, strigose or sericeous above with tomentum in addition, densely tomentose below, moderately bicolored and grayish-olive in color; stems conspicuously leafy with upper leaves subdigitate, tightly-branched (often glomerate) in upper 1/3. densely white-tomentose at least above, with 10-25 flowers; calyx medium-sized, 5-8 mm high including lobes, densely sericeous and also tomentose, with lobes acuminate to acute; bractlets not contrasting with calyx-lobes (or slightly so in early anthesis), usually about equal with calyx-lobes, sericeous on adaxial surfaces; style filiform, moderately incrassate at base, 1.7-2.0 mm long. Map, Fig. 47.

This is the most marked intermediate between *P. hippiana* and *P. effusa*; it has the leafy stems and leaf-pubescence of *P. effusa*, with the calyx form and leaf-dissection of *P. hippiana*. The calyx pubescence combines that of both species. It could as well be a variety of *P. effusa*, but contradicting Boivin's decision to place it with *P. hippiana* would serve no purpose, and would make the key more difficult.

Palmer 37614 [157], cited below, may represent another form of *hippiana-effusa* intermediate, and perhaps should better belong with var. *hippiana*.

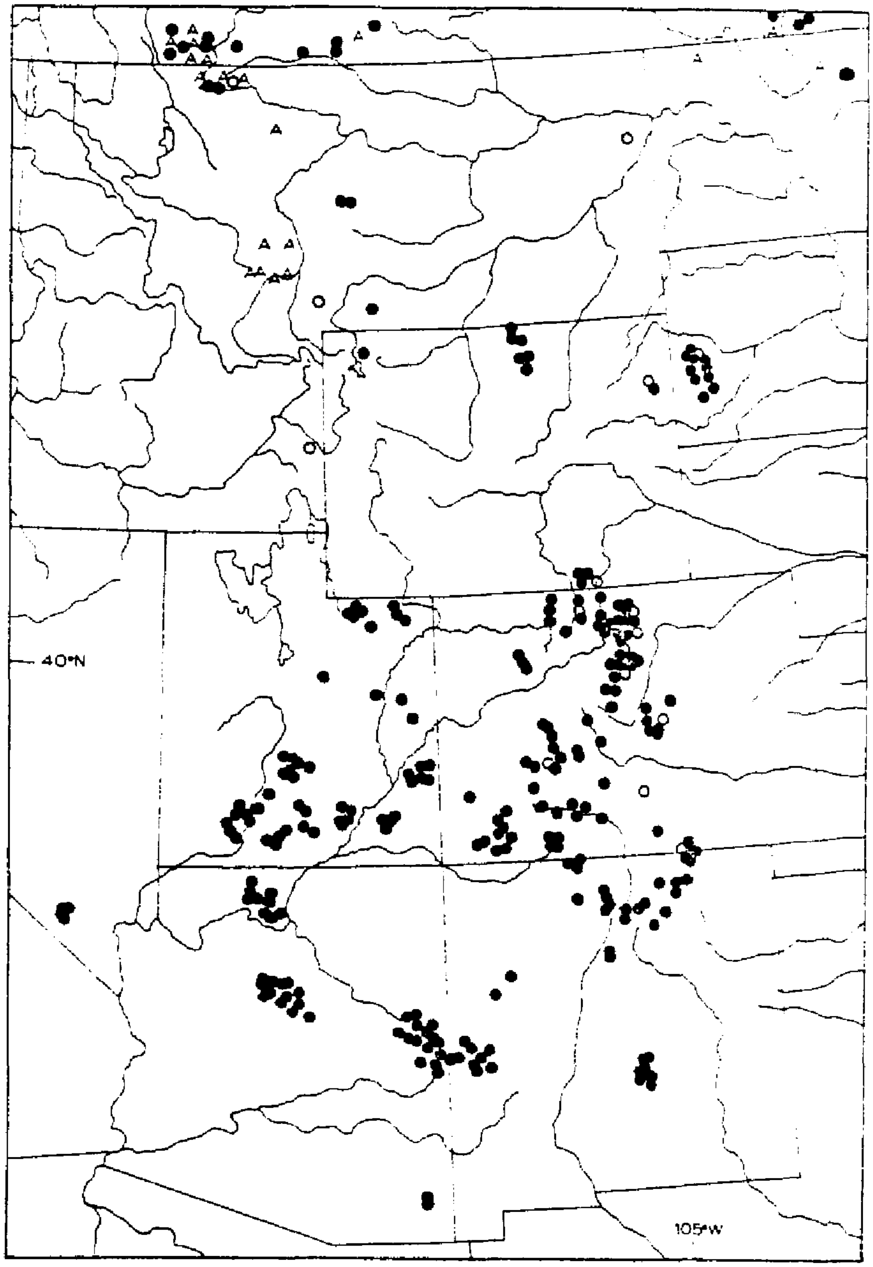

FIG. 47. Rocky Mountain states. Distribution of *Potentilla hippiana* var. *hippiana* (closed circles) and var. *argyrea* (A). Transitions between var. *hippiana* and *P. effusa* (open circles).

REPRESENTATIVE SPECIMENS. MONTANA. Midvale, *Umbach* 471 on 21 July 1903 (GH! [140]); Powell Co., Deer Lodge, along Cottonwood Creek, 4500 ft, *Kirkwood* 1772 on 28 June 1924 (MONTU! [056]). SOUTH DAKOTA. Lawrence Co., rocky bluffs near Deadwood, *Palmer* 37614 on 28 June 1929 (GH! [157]). NORTH DAKOTA. Burke Co., Lostwood Wildlife Refuge, *Stevens* 865 on 30 June 1946 (GH! [060]). CANADA. ALBERTA. Waterton Lakes National Park, dry prairie north of Waterton Lake, 4300 ft, *Breitung* 15926 on 14 July 1953 (NY! [062]). MANITOBA. Melita, *Scoggan* 11072 on 2 July 1953 (MAN! [058]).

8b. *POTENTILLA HIPPIANA* Lehmann var. *HIPPIANA*

Potentilla diffusa A. Gray, Mem. Amer. Acad. Arts Sci. II 4:41 (early 1849), *non Potentilla diffusa* Willdenow (1809). *Potentilla hippiana* Lehmann var. *diffusa* Lehmann, Del. Sem. Hort. Hamburg 8 (late 1849). *Potentilla hippiana* Lehmann var. *propinqua* Rydberg, Bull. Torrey Bot. Club 24:3 (1897), *nom. superfl. pro P. hippiana* var. *diffusa* Lehmann. *Potentilla propinqua* Rydberg, Bull. Torrey Bot. Club 28:176-177 (1901). NEW MEXICO. [Santa Fe Co.], "moist soil along Santa Fe Creek; June," *Fendler* 198 in 1847 (Holotype GH!, isotypes NY! GH! PH! [159]).

Potentilla dealbata Douglas, "Mss. in herb. soc. hort. London (non Bunge)," cited in synonymy under *P. hippiana* Lehmann by Lehmann (1856).

Potentilla pinetorum Greene, *nom. herbariorum non publ., non Potentilla pinetorum* Wiggins (1933). NEW MEXICO. Grant Co., top of Hillsboro Peak, 10200 ft, *Metcalfe* 1208 on 3 August 1904 (NY! CAS! [096]).

Potentilla lupina Rydberg, North Amer. Flora 22(4):240 (1908). WYOMING. Sheridan Co., eastern slope of Big Horn Mts., near the headwaters of Clear Creek and Crazy Woman River, 7000-9000 ft, *Tweedy* 3215 on 20 July-15 August 1900 (Holotype NY!).

Potentilla mogollonica Greene, Leafl. Bot. Observ. Crit. 2:138 (1911). NEW MEXICO. Socorro Co. [now Catron Co.], on or near the west fork of the Gila River, Mogollon Mts., *Metcalfe* 594 on 25 August 1903 (Holotype US!, isotypes RM! NY! ND-G! [023]).

Medium-sized to tall perennial plants, multicipital from an unbranched caudex, stems (20-)30-60 cm tall; basal leaves pinnate or subdigitate, occupying 20-50% of rachis, petioles strigose and tomentose; leaflets 7-15, opposite and confluent with the rachis, with 6-15 teeth on each side cutting 1/2-2/3 to midrib, sericeous and sometimes also glandular above, densely (or rarely sparsely) tomentose below, usually moderately to strongly bicolored, grayish or silvery-grayish; stems not leafy, with upper leaves rudimentary or represented by stipules only, openly-branched with pedicels of moderate length and thickness, stem usually scattered-tomentose above, with 10-30 flowers; calyx medium- to large-sized, 6-12 mm high including lobes, sericeous and sometimes also sparsely tomentose, with acuminate lobes; bractlets equal to calyx lobes, acuminate, sericeous on adaxial surfaces; style filiform with moderately-thickened base, 1.6-3.0 mm long.

Wide diversity of habitats; mostly in dry open meadows of high plains and mountain valleys, and on low mountain ranges or damp valleys of the Great Basin; central Alaska and northwestern British Columbia (reports) to southeastern British Columbia, across southern and central Alberta and Saskatchewan into southwestern Manitoba, scattered southward on the eastern slope of the central Rocky Mountains (but uncommon in Wyoming), most abundant and characteristic in Utah (outside the Great Salt Desert), the western two-thirds of Colorado and New Mexico, and in northern, east-central, and southeastern Arizona. Also less commonly in Nevada and the eastern slope of Colorado and New Mexico. Map, Fig. 47.

The typical form, a relatively large erect-ascending plant with large, confluent, moderately-bicolored leaves, is found throughout the total range. A common form in drier habitats through the southwest has smaller leaves with folded, overlapping, thicker leaflets that are moderately bicolored to densely silky-sericeous and tomentose on both surfaces. Either of these two forms may contribute to hybrid swarms with *P. pulcherrima*. In the Mogollon Mountains of Arizona and New Mexico may be found (among other things) a form with long, narrow leaflets with large, triangular-deltoid, deeply-incised teeth and leaves on long petioles. The form with decumbent stems, subdigitate leaves strigose above and strongly bicolored (*P. diffusa* A. Gray) is very close to the typical form, and is the usual form involved in the various intermediates between var. *hippiana* and *P. crinita* var. *lemmonii*. This last form has also apparently been involved in a putative hybrid with *P. diversifolia* in the San Francisco Mountains of Arizona (*Collom s.n.* and *Cannon and Lloyd s.n.* [132], cited below), which are subdigitate, prostrate, but without tomentum, approaching what Rydberg called *P. concinnaeformis* (a synonym of *P. diversifolia*).

Intermediates between var. *hippiana* and *P. crinita* var. *lemmonii* usually combine the shallowly few-toothed leaflets with more rachis coverage, open inflorescence, and sparse strigose and glandular pubescence of *P. crinita*, with the softer tomentum and larger leaves of *P. hippiana*. Forms in the Mogollon Mountains (e.g., *Metcalfe* 1208 [096], cited above under *P. mogollonica*), are glabrous to subglabrous on lower leaf surfaces, and seem to combine characters of the toothy form of *P. hippiana* and var. *lemmonii*.

Intermediates between var. *hippiana* and *P. effusa* usually combine the tomentose calyx, contrasting bractlets, softer pubescence, and moderately bicolored leaves of *P. effusa*, with the greater number of leaflet-teeth, less stem branching, sericeous calyx, and confluent leaflets of var. *hippiana*. A different form from Idaho and western Montana has the light pubescence and leafy stems of some forms of *P. effusa* and the calyx and larger flowers of *P. hippiana*; the color and subdigitate leaves are somewhat reminiscent of *P. hippiana* var. *argyrea* (*Payson and Armstrong* 3586 [057], *Williams s.n.* in 1897 [037]).

Hybrid swarms between *P. hippiana* and *P. pulcherrima* are fairly common in the southwestern portion of the range and scattered elsewhere.

In most of these (e.g., *Johnston* 2177), the extremes are the ascending-erect, large-leaved, subdigitate, strongly-bicolored *P. pulcherrima* on one hand, and the decumbent-ascending, small-leaved, pinnate, white-tomentose on both surfaces *P. hippiana* var. *hippiana*. Individual plants in such a population may show any combination in these characters between the extremes.

REPRESENTATIVE SPECIMENS (VAR. HIPPIANA). ARIZONA. Coconino Co., San Francisco Peaks, *Collom s.n.* on 3 August 1941 (ASC!); Coconino Co., Kaibab National Forest, *Eastwood and Howell* 1119 on 24 June 1933 (CAS! [056]); Coconino Co., San Francisco Mts., south slope, *Cannon and Lloyd s.n.* in August 1904 (NY! [132]); Coconino Co., Kaibab Forest, 8000 ft, *Goodman and Hitchcock* 1627 (CAS! [054]). COLORADO. Archuleta Co., Pagosa Springs, *Baker* 390 on 26 July 1899 (NY! [026]); Chaffee Co., Buena Vista, *Sheldon s.n.* on 7 July 1892 (NY! [048]); El Paso Co., Ruxton Dell, 2950 m, *Clements and Clements* 141 on 24 July 1901 (CAS! [066]); Gunnison Co., Gunnison, 7680 ft, *Baker* 560 on 23 July 1901 (RM! [015]); Gunnison Co., Blue Mesa west of Dayton, *Tidestrom* 1614 on 27 July 1908 (NY! [053]); Montezuma Co., West Mancos Canyon, 9000 ft, *Baker, Earle, and Tracy* 301 on 3 July 1898 (RM! [025]); Rocky Mountains, lat. 40°-41°, *Vasey* 161 in 1868 (GH!). MONTANA. Bear Lodge, *Williams s.n.* on 8 August 1897 (MONTU! [037]). NEW MEXICO. Catron Co., Gilita Campground, 20 mi northeast of Mogollon, *Hitchcock, Rethke, and Raadshooven* 4402 on 1 August 1938 (CAS! [050]); Catron Co., near Snow Lake, T1N R16W, 8000 ft, *Shultz and Shultz* 1493 on 6 September 1974 (GH! [049]). NORTH DAKOTA. Benson Co., Butte, *Lunell s.n.* on 4 July 1906 (RM! [051]); Eddy Co., Sheyenne, *Lunell s.n.* on 4 July 1908 (NY! [052]). SOUTH DAKOTA. Pennington Co., 12 mi west of Deerfield, *Hayward* 2302 on 22 July 1927 (RM! [024]). UTAH. Garfield Co., Aquarius Plateau, *Rydberg and Carlton* 7479 on 6 August 1905 (NY! [016]); Summit Co., snowslide west of La Motte Peak, S1 T1S R10E, ca. 10900 ft, *Johnston* 2265 on 26 August 1979 (COLO! [020]); Uintah Co., Oaks Park Campground, S12 T1S R20E, 9250 ft, *Johnston* 2251 on 24 August 1979 (COLO! [039]). WYOMING. Albany Co., Medicine Bow Mts., slopes of open parks, *A. Nelson* 7794 on 28 July 1900 (GH! [055]).

(INTERMEDIATES BETWEEN VAR. HIPPIANA AND P. CRINITA VAR. LEMMONII). NEVADA. Clark Co., Charleston Mts., Lee Canyon, 2670 m, *Clokey* 8395 on 26 July 1939 (UTC! [089]). NEW MEXICO. (See *P. pinetorum* Greene, cited above). UTAH. Garfield Co., vicinity of Panguitch Lake Camp, 8300 ft, *Maguire* 19049 on 24 June 1940 (WS! [074]); Garfield Co., Aquarius Plateau, Posy Lake, 15 mi north of Escalante, S17 T22S R2E, 8800 ft, *Holmgren, Reveal, and LaFrance* 2501 on 16 August 1965 (NY! [070]).

(INTERMEDIATES BETWEEN P. EFFUSA AND P. HIPPIANA). COLORADO. Clear Creek Co., Empire, 8500 ft, *Tweedy* 5747 on 15-25 July 1903 (NY! [067]); El Paso Co., meadow, Colorado Springs, *Shear* 1137 on 6 July 1896 (RM! [065]); Gunnison Co., Gunnison, *Baker s.n.* in July no year (UC! [138]); Larimer Co., Poudre Flats above Fort Collins, *Cowen* 599 on 12 July 1895 (MONTU! [137]); Larimer Co., Bosworth's Ranch, 7500 ft, *State Agric.*

College Colo. 597 on 14 July 1898 (WS! [064] CAN! [155]). IDAHO. Bonneville Co., Caribou Mtn., *Payson and Armstrong* 3586 (PH! [057]). WYOMING. Weston Co., forest near Newcastle, *Porter* 3961 on 4 July 1946 (GH! [139]).

(INTERMEDIATE-HYBRID SWARMS BETWEEN P. HIPPIANA AND P. PULCHERRIMA). ARIZONA. Greenlee Co., Sheep Crossing, White Mts., *Goodding* 1164 on 12 July 1912 (NY!). NEW MEXICO. Rio Arriba Co., Chama, *Eastwood s.n.* in August 1892 (GH!). COLORADO. Gunnison Co., Quartz Creek meadows 1.5 mi SSW of Pitkin, S17 T50N R4W, ca. 10000 ft, *Johnston* 2216 on 15 August 1979 (COLO!); Gunnison Co., Gothic, *Higgins* 2064 on 7 July 1969 (BRY!); Larimer Co., 8 mi east of Longs Peak, roadside, 7500-8000 ft, *Maguire and Maguire* 36 on 7 August 1931 (UTC!); Las Animas Co., Wootton Ranch, 1 mi south of Morley, 7300 ft, *Ewan* 13202 (CAS!); Montezuma Co., West Mancos Canyon, 9000 ft, *Baker, Earle, and Tracy* 301 on 3 July 1898 (RM! GH!); locality unknown, *Brandegee* 127 in 1871 (NY!). UTAH. Duchesne Co., lower end of Long Park, S2 T2N R5W, 10150 ft, *Johnston* 2250 on 24 August 1979 (COLO!); Garfield Co., Posy Lake, *Beck s.n.* on 22 June 1938 (BRY!); Grand Co., La Sal Mts., 11000 ft, *Payson and Payson* 3999 on 23 July 1924 (RM!); Piute Co., mountains north of Bullion Creek, near Marysvale, *Rydberg and Carlton* 7129 on 23 July 1905 (NY! GH!); Summit Co., 1/4 mi on road to Dead Horse Pass, west fork of Blacks Fork, Uinta Mts., *Holmgren, Anderson, and Witte* 10983 on 20 August 1955 (UTC!); Wasatch Co., Soldier Summit, *Eastwood* 7684 on 24 June 1918 (CAS!); Wayne Co., Thousand Lake Mtn., S21 T27S R4E, 11200 ft, *Johnston* 2177 on 20 July 1979 (COLO! [018, 019]). WYOMING. Albany Co., La Plata Mines, *A. Nelson* 1789 on 22 August 1895 (NY!); Park Co., Beartooth Mts., Crazy Woman Creek, 7000 ft, *Williams and Williams* 3523 on 12 July 1937 (GH! NY!); Sheridan Co., headwaters of Tongue River, *Tweedy* 98 in July 1898 (NY!). CANADA. ALBERTA. Craigmyle, pasture, 2750 ft, *Brinkman* 274 on 27 July 1921 (NY!). SASKATCHEWAN. Cypress Hills Park, *Breitung* 4927 on 20 July 1947 (RM!).

9. *POTENTILLA MACOUNII* Rydberg, Mem. Dept. Bot. Columbia Univ. 2:101 *t.*41 *f.*1-2 (1898). *Potentilla concinna* Richardson var. *macounii* (Rydberg) Hitchcock, Vasc. Plants Pacific Northwest 3:136 (1961). CANADA. ALBERTA. Crows Nest Pass, on dry rocks, 4000 ft, *Macoun* 16709 on 4 August 1897 (Holotype NY!, isotypes CAN! [164] GH!).

Medium-sized to small plants, decumbent to ascending, multicipital from an unbranched caudex, stems 5-15 cm long; leaves subdigitate to less commonly pinnate, leaflets occupying 20-30% of rachis; leaflets 7-10, not confluent with the rachis, narrowly 4-9-toothed along each side, incising 2/3 or more to midrib, strigose and sometimes also tomentose above, densely sericeous and densely white-tomentose below, conspicuously bicolored; stem branching in upper 1/2, not leafy, with 4-6 flowers;

calyx medium-sized, 6-9 mm high including lobes, lobes acute or sometimes acuminate, sericeous and often also tomentose, bractlets usually about equal to the calyx lobes, sericeous on adaxial surfaces; styles filiform or slightly thickened at base, 1.8-2.2 mm long.

Rocky slopes at relatively low elevations, eastern slope of the northern Rocky Mountains in western Alberta, and slopes of the Little Belt and Bridger Mountains, Montana. Map, Fig. 48.

Some forms of *P. macounii* have the prostrate stems of *P. concinna* var. *concinna*, but the two species are amply distinct in style form, distinctly different pubescence, and calyx form; the dissection and form of the leaflets of *P. macounii*, as well as their pinnateness, suggest relationships with *P. ovina*, as Rydberg supposed in the protologue.

REPRESENTATIVE SPECIMENS. MONTANA. Gallatin Co., Bridger Mts., 10000 ft, *Rydberg and Bessey* 4395 on 10 June 1897 (NY! [046]); Teton Co., East Front Mountains, foothills, Indian Head Rock, 5790 ft, *Lackschewitz* 3561 on 9 June 1972 (NY!); Little Belt Mts., 9 mi from Barker, 6000 ft, *Flodman* 556 on 18 August 1896 (NY!); Cedar Mountain, 10000 ft, *Rydber and Bessey* 4396 on 16 July 1897 (NY! [047]). CANADA. ALBERTA. Banff, 4521 ft, *Schaffer s.n.* on 30 May 1904 (PH!); Waterton Lakes National Park, near north park entrance, 4300 ft, *Breitung* 17068 on 4 August 1953 (NY! [045]); Rocky Mountain Forest Reserve, Wind Mountain, among rocks on scree, 6000-7000 ft, *Porsild and Lid* 19306 on 3 July 1956 (CAN! [044]).

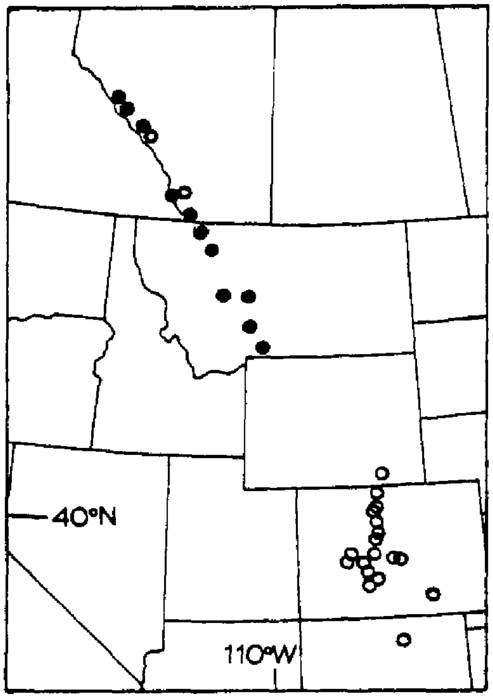

FIG. 48. Rocky Mountain states and provinces. Distribution of *Potentilla subjuga* (open circles) and *Potentilla macounii* (closed circles).

CHAPTER X

CONCLUSIONS

Potentilla sect. Multijugae is restricted to North America, inhabiting rocky slopes of temperate to subarctic mountains, or low moist meadows of the Pacific coastal plain and intermontane valleys of western North America, with disjunct populations on the mountains of Mexico and on the coasts of Greenland and Labrador. Sect. Multijugae is classified into eleven species; subspecific units have been classified where appropriate, in three of these species.

Statistical analysis of variation, and analysis of correlation, of population samples from these species, and information-theoretical character analysis were used to improve the set of characters to be used. Single-linkage clustering with subgraph representation facilitated the classification by allowing comparison of a large number of characters simultaneously. Morphological characters were used throughout, so that the results would be applicable to taxonomic theories of classification, and so that use could be made of a large number of herbarium specimens.

In this study, most of the metric characters used varied significantly among populations, even within the same taxonomic variety. For any character, there was often significant variation among plants within populations, and the frequency distributions of different populations overlapped; no character was found which could distinguish a majority of plants of any population from those of other populations. Statistical tests on means of the populations showed that no character was capable of separating populations into taxonomically meaningful sets. In a few cases, a character was found which would separate the population means of one taxon from all others, the remainder being divided with no taxonomic meaning; even in these cases, however, the frequency distributions overlapped, leaving certain individuals of any population unclassified.

When pairs of metric characters were used, no pair was found that classified the populations into taxonomic sets; this was true even when correlated characters were paired. Although a large number of character-pairs showed significant correlations in the total sample of all populations, there were great differences in the pattern of correlations from population to population. These differences between populations were notable within the same variety of a species, and also in one case between two populations from the same site. Choice of a set of characters for classification which are intercorrelated for the total sample, may bias the results of the classification in favor of those taxa whose populations share the same pattern of correlation as the total sample.

Taxonomic classification of this section (at least) must be based on simultaneous consideration of at least three characters, and probably more. A set of intercorrelated characters was chosen for classification, but the number of them (around 20) required the use of a numerical method, because consideration of all of them simultaneously over a large set of specimens is otherwise very difficult. Results of the clustering method chosen were found to be very useful, because they allowed the steps in the process of clustering to be seen in sequence. Subsequent analysis of the characters responsible for the formation of clusters showed that for any cluster, certain characters were better for distinguishing it from others. This comprises a new, objective method for determining which characters are more useful for distinguishing taxa, and hence are most useful in identification and keys. A set of characters found useful in distinguishing one taxon is not necessarily the same set as that for another taxon.

This discussion suggests that classification based on one or two characters is unlikely to lead to accurate identification of subsequently encountered individuals. The classification produced here has the purpose of providing as broad a basis as possible for identification, to be easily adaptable to manuals and floras, and so uses a larger number of characters simultaneously. Comparison of these results with previous taxonomic treatments of this section shows that the unaided intuition of competent taxonomists is not always sufficient to decide which characters produce the best classification.

Aided by information-theoretical character analysis and single-linkage clustering as used for sect. Multijugae, a new classification was produced for two other, related sections of *Potentilla*: sect. Concinnae, with two species, and sect. Subjugae, with seven species.

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APPENDIX

```
      PROGRAM PORE (INPUT,OUTPUT,TAPE3=INPUT)
      DIMENSION C(20,500),X(500),Y(500),N(100),S(20,20),F(4)
      K=1
      NR=0
      IX=0
      NP=0
      READ 1,(F(I),I=1,4),NC
    1 FORMAT (4A10,1X,1I3)
      IF (EOF(3)) 17,2,17
    2 KP=K
      NR=NR+1
      READ F,K,(C(I,NR),I=1,NC)
      IF (EOF(3)) 4,3,4
    3 IF (K.EQ.KP) GO TO 2
   31 NP=NP+1
      N(NP)=NR-1
      IF (IX.EQ.1) GO TO 5
      GO TO 2
    4 IX=1
      GO TO 31
    5 DO 13 I=1,NP
      IF (I.EQ.1) GO TO 6
      NA=N(I)-N(I-1)
      MA=N(I-1)
      GO TO 7
    6 NA=N(I)
      MA-0
    7 DO 9 J=1,NC
      DO 9 L=1,NC
      DO 8 M=1,NA
      NB=MA+M
      X(M)=C(J,NB)
    8 Y(M)=C(L,NB)
      CALL COR(X,Y,R,NA)
      S(J.L)=R
    9 CONTINUE
      PRINT 10,I
   10 FORMAT (8H1POP.NO.,1I2,2X,2H 1,4X,2H 2,4X,2H 3,4X,2H 4,4X,2H 5,4X,
     +2H 6,4X,2H 7,4X,2H 8,4X,2H 9,4X,2H10,4X,2H11,4X,2H12,4X,2H13,4X,2H
     +14,4X,2H15,4X,2H16,4X2H17,4X,2H18,4X,2H19,4X,2H20)
      DO 12 J=1,NC
      PRINT 11,J,NC,(S(J,L),L=1,NC)
   11 FORMAT (3X,1I2,4X,=(1X,1F5.3))
   12 CONTINUE
      PRINT 101,NA
  101 FORMAT (1H0,*SAMPLE SIZE =*,1I3)
   13 CONTINUE
      DO 15 I=1,NC
      DO 15 J=1.NC
      NNP=N(NP)
      DO 14 L=1,NNP
      X(L)=C(I,L)
   14 Y(L)=C(J,L)
      CALL COR(X,Y,R,NNP)
```

```
 15   S(I,J)=R
      NN=99
      PRINT 10,NN
      DO 16 I=1,NC
      PRINT 11,I,NC,(S(I,J),J=1,NC)
 16   CONTINUE
      PRINT 101,NNP
 17   CONTINUE
      END


      SUBROUTINE COR(X,Y,R,N)
      DIMENSION X(500),Y(500)
      RN=N
      SA=0.
      SA2=0.
      SB=0.
      SB2=0.
      SAB=0.
      DO 1 I=1,N
      SA=SA+X(I)
      SA2=SA2+X(I)*X(I)
      SB=SB+Y(I)
      SB2=SB2+Y(I)*Y(I)
  1   SAB=SAB+X(I)*Y(I)
      SSA=SA2-SA*SA/RN
      SSB=SB2-SB*SB/RN
      SP=SAB-SA*SB/RN
      R=SP/SQRT(SSA*SSB)
      RETURN
      END


      PROGRAM POST (INPUT,OUTPUT,TAPE3=ONPUT)
      INTEGER T
      DIMENSION C(100),F(4),T(10),S(100),S2(100),R(100),R2(100),Q(100),
     +Q2(100),SA(100),SB(100),SC(100)
      NP=0
      IX=0
      NR=0
NO=0
      NN=0
      N=0
      NT=0
      IZ=0
      DO 1 I=1,100
      C(I)=0.
      S(I)=0.
      S2(I)=0.
      R(I)=0.
      R2(I)=0.
      Q(I)=0.
      Q2(I)=0.
```

```
      SA(I)=0.
      SB(I)=0.
      SC(I)=0.
    1 CONTINUE
      K=1
      L=1
      READ 3,(F(I),I=;,4).NC,(T(J),J=1,10)
    3 FORMAT (4A10,1X,1I3/10I3)
      IF (EOF(3)) 22,4,22
    4 IF (NC.GT.100) GO TO 22
    5 KP=K
      LP=L
      NT=NT+1
      IX=0
      IZ=0
      READ F,K,L,M,(C(I),I=1,NC)
      IF (EOF(3)) 17,7,17
    7 IF (K.GT.KP) GO TO 12
      IF (L.GT.LP) GO TO 10
   97 DO 9 I=1,NC
      DO 100 J=1, 10
      IF (I.EQ.T(J)) GO TO 99
      RC=C(I)
      GO TO 100
   99 IF (C(I).NE.0.) GO TO 98
      RC=C(I)
      GO TO 101
   98 RC=ALOG10(C(I))
      GO TO 101
  100 CONTINUE
  101 S(I)=S(I)+RC
      S2(I)=S2(I)+RC*RC
      R(I)=R(I)+RC
      R2(I)=R2(I)+RC*RC
      Q(I)=Q(I)+RC
    9 Q2(I)=Q2(I)+RC*RC
      GO TO 5
   10 DO 11 I=1,NC
      RNT=NT
      SA(I)=SA(I)+S(I)*S(I)/(RNT-1.)
   11 S(I)=0.
      NN=NN+1
      N=N+NT-1
      NT=1
      IF (IZ.EQ.1) GO TO 13
      IF (IX.EQ.1) GO TO 13
      GO TO 97
   12 IX=1
      GO TO 10
   13 RN=N
      RNN=NN
      NA=NN-1
```

```
      NB=N-NN
      NK=N-1
      NO=NO+N
      NR=NR+NN
      NN=0
      N=0
      DO ;6 I=1,NC
      A=S2(I)-R(I)*R(I)/RN
      B=SA(I)-R(I)*R(I)/RN
      X=A-B
      SB(I)=SB(I)+R(I)/RN
      Z=R(I)/RN
      SC(I)=SC(I)+SA(I)
      SA(I)=0.
      R(I)=0.
      S2(I)=0.
      D=B/(RNN-1.)
      E=X/(RN-RNN)
      Y=D/E
      IF (I.EQ.1) PRINT 14
   14 FORMAT (1H1,15X,56H     SS      DF      MS      F(S)      ME
     +AN CHAR.)
      PRINT 15,B.NA,D,Y,Z,I,X,NB,E,KP,A,NK
   15 FORMAT (1H0,15H    AMONG PLANTS,1F12.4,1X,1I4,1X,1F12.4,1X,1F12.4,
     +1F7.3,2X,1I2/16H   WITHIN PLANTS,1F12.4,1X,1I4,iX,;F;2/4/13H     TOT
     +AL POP.,1I2,1Z,1F12.4,1X.1I4)
   16 CONTINUE
      NP=NP+1
      IF (IZ.EQ.1) GO TO 18
      KP=K
      LP=L
      GO TO 97
   17 IZ=1
      GO TO 10
   18 PRINT 19
   19 FORMAT (14H1TOTAL SAMPLE./)
      PRINT 14
      RNP=NP
      RNR=NR
      RNO=NO
      NA=NP-1
      NB=NR-NP
      NK=NO-NR
      ND=NO-1
      DO 21 I=1,NC
      X=R2(I)-Q(I)*Q(I)/RNO
      A=SB(I)-Q(I)*Q(I)/RNO
      B=A/(RNP-1.)
      D=SC(I)-SB(I)
      E=D/(RNP-RNR)
      G=R2(I)-SC(I)
      H=G/(RNO-RNR)
```

```
      Y=B/E
      W=E/H
      Z=Q(I)/RNO
      PRINT 20,A,NA,B,Y,Z,I,D,NB,E,W,G,NK,H,X,ND
   20 FORMAT (1H0,15H    POPULATIONS,1F12.4,1X,1I4,1X,1F12.4,1X,1F12.4,1
     +F7.3,2X,1I2/16H          PLANTS,1F12.4,1X,1I4,1X,1F12.4,1X,1F12.4/
     +16H   MEASUREMENTS,1F12.4,1X,1I4,1X,1F12.4/16H           TOTAL,1F1
     +2.4,1X,1I4)
   21 CONTINUE
   22 CONTINUE
      END
```