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A TAXIMETRIC STUDY OF INFRASPECIFIC VARIATION IN AUTOGAMOUS *LIMNANTHES FLOCCOSA* (LIMNANTHACEAE)

MARY T. KALIN ARROYO

Arroyo, Mary T. Kalin (New York Botanical Garden, Bronx). A taximetric study of intraspecific variation in autogamous *Limnanthes floccosa* (Limnanthaceae). *Brittonia* **25**: 177-191, 1973.—*Limnanthes floccosa* Howell is a variable autogamous species of recent origin. The phenetic relationships of a large number of populations of *L. floccosa* were studied using taximetric techniques. Five subspecies are recognized in *L. floccosa* on the basis of the taximetric results. *Limnanthes floccosa* ssp. *californica* and *L. floccosa* ssp. *grandiflora* are described as new, and *L. floccosa* ssp. *pumila* and *L. floccosa* ssp. *bellingermaniana* are proposed as new combinations. Aspects of autogamy responsible for the highly discrete pattern of variation in *L. floccosa* are discussed.

INTRODUCTION

In a monograph of the genus *Limnanthes* R. Br., Mason (1952) recognized the relationship of *L. floccosa* Howell to *L. bellingermaniana* Peck and *L. pumila* Howell. *L. floccosa* was described from pubescent plants occurring on the Medford Plains, *L. bellingermaniana* from small-flowered glabrous plants from Mountain View, and *L. pumila* was described from a single population of larger-flowered, glabrous plants occurring on the summit of Lower Table Rock on the Medford Plains, all in Jackson County, Oregon. He treated each of these species as varieties of *L. floccosa*. *Limnanthes floccosa* sensu Mason is a highly polymorphic vernal annual occurring throughout northeastern California and south-central Oregon, populations of which are characterized by various amounts of autogamy (Kalin, 1971). The pattern of variation in this species, however, is far more complex than suggested by Mason's treatment. This paper outlines a taximetric approach to intraspecific variation in *L. floccosa* and presents a taxonomic revision of *L. floccosa* based on this approach.

METHODS AND MATERIALS

Selection and treatment of populations. The OTUs of this analysis are 26 populations drawn from throughout the geographical range of the species (Fig. 1). All data were obtained from 15 to 30 plants per population grown in growth chambers with similar conditions of light, temperature, and humidity. With the exception of a few plants that originated from field transplants at an early stage of development, the plants were grown from seed collected in the field. The 26 populations used (Table I) were selected on the basis of two seasons of field work covering the geographical range of the species. They represent approximately 50% of all populations of *Limnanthes floccosa* (including all those from which type collections were made) known to date from herbarium records (Fig. 1). Populations were selected to represent all obvious morphological variation at approximately 20-mile intervals. Two areas were notably more complex than others in their variation. In the Medford Plains area (Jackson County, Oregon) two morphologically distinct plant types (differing in pubescence patterns, flower size, and a number of other floral characteristics) were found to be marginally sympatric over a large area of the plains. The same two morphological types occur together on the type sheet of *L. floccosa*, which contains a number of separate plants. Because of the complexity of the varia-

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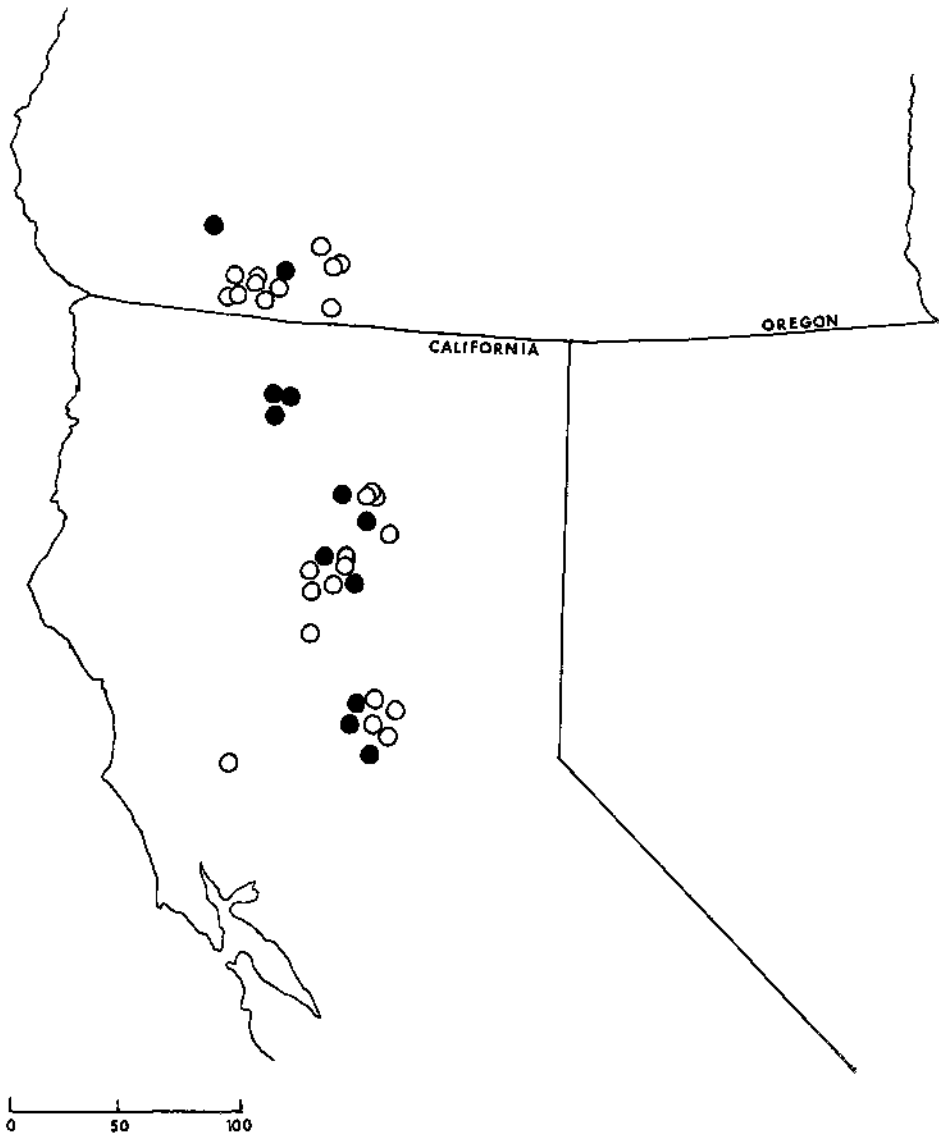


FIG. 1. The distribution of *Limnanthes floccosa* based on localities from herbarium specimens and all field populations known to the author. Open circles: populations used in the taximetric analysis.

tion, five populations were selected from this area (OTUs Antioch-1, Tresham Lane-1, Agate Road-1, Modoc Road-2, Camp White-1). The two morphologically distinct plant types have been considered as separate OTUs. A second area of complexity occurs on the eastern upland margin of the distribution of the species on the northwestern flanks of the Sierra Nevada of California and the Cascade Mountains in California and Oregon. In two localities in this area there occur sympatric populations of the glabrous plants referable to *L. floccosa* var. *bellingeriana* (Peck) Mason (OTUs Butte Falls-2, Ingot-3) and pubescent plants referable to *L. floccosa* var. *floccosa* (OTUs Butte Falls-1, Ingot-2). The glabrous plants and pubescent plants

TABLE I

LOCALITIES, HABITATS, AND LEVELS OF AUTOGAMY OF POPULATIONS OF *Limnanthes floccosa* FORMING THE BASIS OF OTUs IN THE TAXIMETRIC ANALYSIS

Population	Locality	Habitat	Level of Autogamy*
OREGON			
Jackson Co.:			
Butte Falls-1	3.7 mi W of Butte Falls	Dry edge of meadow	highly autogamous
Butte Falls-2	3.7 mi W of Butte Falls	Shaded damp meadow	highly autogamous
Crowfoot-1	Crowfoot Road, 5 mi N of Butte Falls Road jct.	Roadside embankment	highly autogamous
Mountain View-1	Mountain View	Damp stony meadow	highly autogamous
Camp White-1	Outside Camp White, Medford Plains	Vernal pool	partially autogamous
Agate-1	Agate Desert, Medford Plains	Vernal pool	partially autogamous
Modoc Road-2	Modoc Road, Medford Plains	Vernal pool	partially autogamous
Upper Table Rock-1	Upper Table Rock, Medford Plains	Vernal pool	partially autogamous
Lower Table Rock-1	Lower Table Rock, Medford Plains	Vernal pool	partially autogamous
Antioch-1	Antioch Road, Medford Plains	Roadside water channel	highly autogamous
Tresham Lane-1	Tresham Lane, Medford Plains	Cultivated field	highly autogamous
CALIFORNIA			
Shasta Co.:			
Cayton-2	0.3 mi S Cayton Creek Bridge Hwy. 89	Rocky outcrops	highly autogamous
Cayton-3	0.8 mi S Cayton Creek Bridge Hwy. 89	Stony flat	highly autogamous
Cayton-4	0.5 mi S Cayton Creek Bridge Hwy. 89	Damp meadow edge	highly autogamous
Pit-1	Pit Road No. 1, near jct. with Hwy. 89	Roadside embankment	highly autogamous
Ingot-1	6.7 mi W of Ingot	Stony flat	highly autogamous
Ingot-2	5.4 mi SW of Ingot	Stony flat	highly autogamous
Ingot-3	5.4 mi SW of Ingot	Shaded damp stony flat	highly autogamous
South Cow-1	Jct. South Cow Creek Rd. and Hwy. 44	Roadside clearing	highly autogamous
Bear Creek-1	1.3 mi W of Bear Creek Bridge Hwy. 44	Dry stony flat	highly autogamous
Tehama Co.:			
Mineral-1	5 mi E of Mineral	Roadside embankment	highly autogamous
Butte Co.:			
Chico-1	8 mi NW of Oroville	Vernal pool	partially autogamous
Oroville-1	1 mi W of Oroville	Vernal pool	partially autogamous
Shippe-1	Hwy. 99E, 0.5 mi S jct. with Shippe Rd.	Vernal pool	partially autogamous
Table-1	Table Mountain	Vernal pool	partially autogamous
Lake Co.:			
Lake Co.-1	Jct. Hwy. 175 & Hwy. 29	Old dry lake bed	highly autogamous

* Levels of autogamy are based on degree of floral adaptation toward autogamy, greenhouse selfing ability, and the degree to which populations are visited by bees in the field. Populations described as partially autogamous are large-flowered, having nectar guides and protandry, and over 50% of their flowers visited by bees in the field in years of abundant insect activity. Populations described as highly autogamous are small-flowered and lack nectar guides and protandry; less than 30% of their flowers are visited by bees in the field. All populations are automatically self-pollinated in the greenhouse.

TABLE II
CHARACTERS USED IN TAXIMETRIC ANALYSIS

	Measured from	Coding method*
1. Petiole length	1st flower	actual value
2. Leaflet length	1st leaf	actual value
3. Leaflet width	1st leaf	actual value
4. Sepal length	1st flower	actual value
5. Sepal width	1st flower	actual value
6. Petal length	1st flower	actual value
7. Petal width	1st flower	actual value
8. Petal:sepal ratio		actual value
9. Pistil length	2nd flower	actual value
10. Style branch length	2nd flower	actual value
11. Filament length	1st flower	actual value
12. Anther length	1st flower	actual value
13. Anther width	1st flower	actual value
14. Staminal nectary width	1st flower	actual value
15. Height of stamens above receptive stigma	2nd flower	actual value
16. Angular position of stamens relative to receptive stigma		actual value
17. Anther movement after dehiscence (in degrees)		actual value
18. Length of receptive stigma	2nd flower	actual value
19. Width of receptive stigma	2nd flower	actual value
20. Diameter of open flower	2nd flower	actual value
21. Average petal vein number		actual value
22. Life span of flower in days		actual value
23. Number of days from anthesis to anther dehiscence		actual value
24. Number of days from anther dehiscence to stigma receptivity		actual value
25. Foliage pubescence		3 states
26. Inner-surface sepal pubescence		present/absent
27. Outer-surface sepal pubescence		present/absent
28. Basal sepal pubescence		present/absent
29. Sepal margin pubescence		present/absent
30. Oblique rows of hairs at base of petals		present/absent
31. Surface petal hairs		present/absent
32. Color of ageing petals		2 states
33. Pubescence of leaves immediately subtending first flower		present/absent
34. Floral odor		2 states
35. Fruiting calyx length	3rd flower	actual value
36. Fruiting calyx width	3rd flower	actual value
37. Fruiting calyx abscission zone		present/absent
38. Mode of nutlet dehiscence		2 states
39. Average number of nutlets produced per flower		actual value
40. Nutlet length	3rd flower	actual value
41. Nutlet width	3rd flower	actual value
42. Nutlet tuberculation		2 states

* Actual values are averages of measurements for 15-30 plants per OTU.

have been considered as separate OTUs. Voucher specimens from each population are deposited at UC with duplicates in several cases at NY.

Character choice and assessment. The analysis employed 42 characters derived from all stages of the life cycle (Table II). These include all characters used in previous taxonomic treatments of *Limnanthus floccosa* (e.g., flower size, pubescence patterns) as well as many additional characters. Most of the characters are from the flowering and fruiting stages of the life cycle. In the absence of good qualitative differences, moreover, the number of quantitative characters used is relatively large. For all quantitative characters, data were averaged for 15 to 30 plants per population. Distributions of the values obtained for quantitative characters were always approximately normal, which facilitated the use of average population values. Qualitative characters were considered either as multistate or presence/absence characters (the latter were coded as 2-state characters).

All characters were measured directly from living plants while growing in the growth chambers or from preserved material collected at specified stages (Table II) in the development of the plants. Most of the leaf characters were measured from the first leaf appearing on the plant. Corolla, calyx, and stamen characters were measured from preserved specimens of the first flower on the plant. Characters of the gynoecium were measured from preserved specimens of the second flower of the plant. The time-dependent characters (e.g., degree of protandry, length of the life of the flower) were measured by following the phenological development of flowers daily.

Taximetric techniques and methods of data presentation. Computations were performed using Program NT 11 of a system of numerical programs developed by Wayne W. Moss, Department of Entomology, University of California, Berkeley for use with the CDC-6400 computer facilities. Input data were in the form of a rectangular OTU-by-character matrix. In preliminary runnings the data were standardized using three types of standardization: range standardization, cophenetic correlation coefficient 0.910; condensation, cophenetic correlation coefficient 0.910; standardization by variance, cophenetic correlation coefficient 0.899. In further runnings only the range standardization and condensation techniques were employed. As the phenograms generated by these two types of standardization were identical, only the results of one method of standardization by range are presented here. The correlation coefficient used was Gower's Association Coefficient, and clustering for phenogram construction was performed by the Unweighted Pair Group Method with Average Linkage (Sokal & Sneath, 1963).

The results of the taximetric analysis are presented by two methods: 1. THE PHENOGRAM (Fig. 2), which was constructed directly from the cluster analysis in the conventional way; and 2. DIAGRAM OF RELATIVE OTU SIMILARITIES (DROS: Fig. 3). The latter 2-dimensional representation of OTU similarities is constructed by using line linkages (vectors that are proportional to the values of the association coefficients between pairs of OTUs). The technique consists of ranking in descending order (by computer) the association coefficients obtained for every combination of pairs of OTUs in the analysis. Relative positions of the OTUs in the diagram are then established by a process of trial and error, using vectors proportional to the three highest association coefficients appearing in each list. Relative positions of OTUs that do not join according to their first three orders of similarity are estimated by taking fourth order vectors into consideration. These vectors are not depicted in Fig. 3 since they tend to clutter the diagram. Due to the distortion that results when attempting to portray a multidimensional space in two dimensions, it is clear that it is not always possible to position all OTUs at distances from one another that are exactly proportional to their similarity values; however, the amount of distortion is

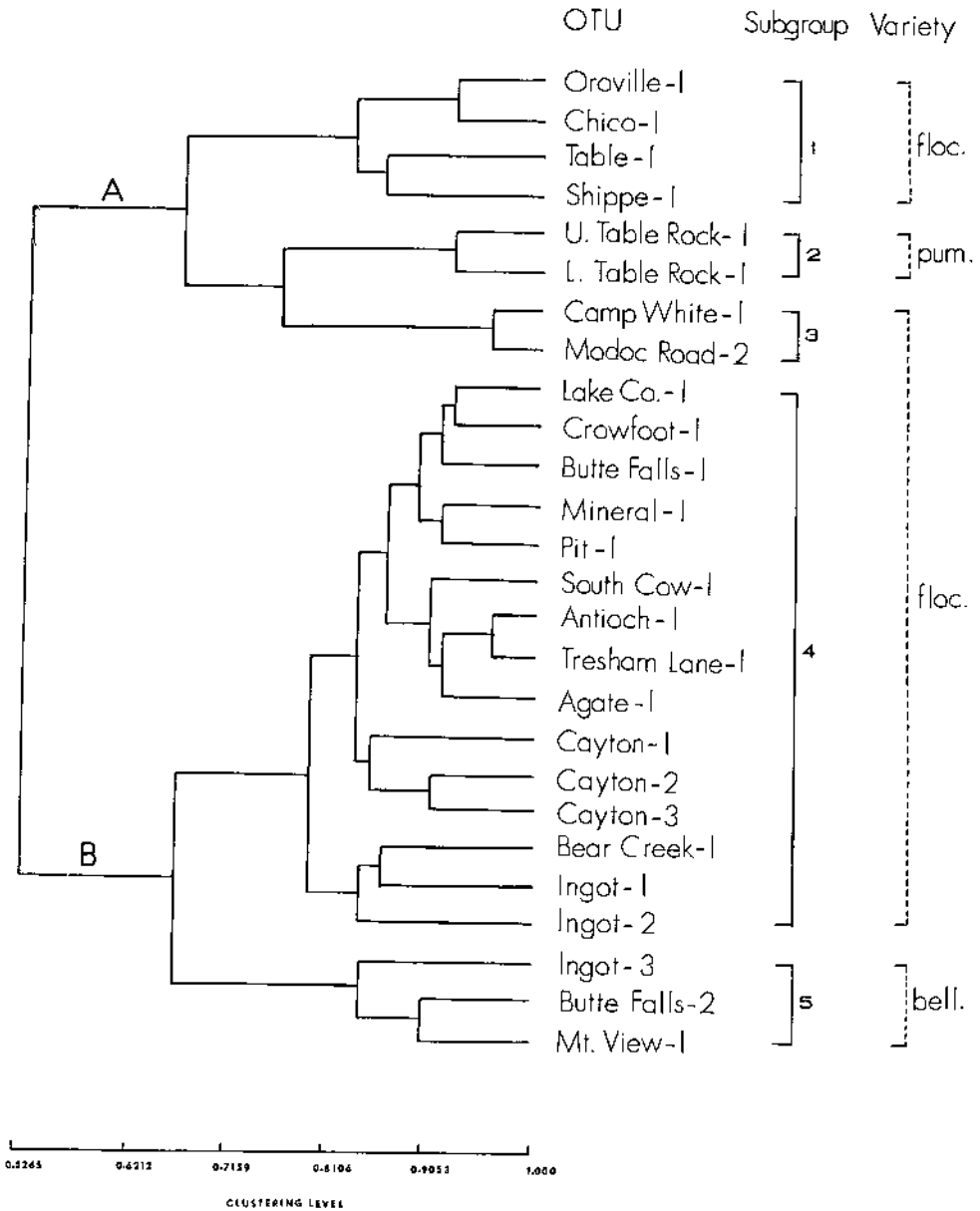


FIG. 2. Phenogram of overall similarities for 26 populations of *Limnanthes floccosa* based on comparisons of 42 characters. Cluster A: partially autogamous populations; Cluster B: highly autogamous populations. Placement of populations in Mason's varieties appears on the right on the phenogram. Subgroups 1-5 are groups of populations referred to in the text.

probably insufficient to alter the basic conclusions. The method for portraying OTU similarities presented here is similar in principle to that developed by Moss (1967) but differs in its mode of construction. With Moss's method, independent pairs of OTUs are joined according to their first order similarity coefficients. When all pairs are formed, second order coefficients are used to join the existing pairs. In the present

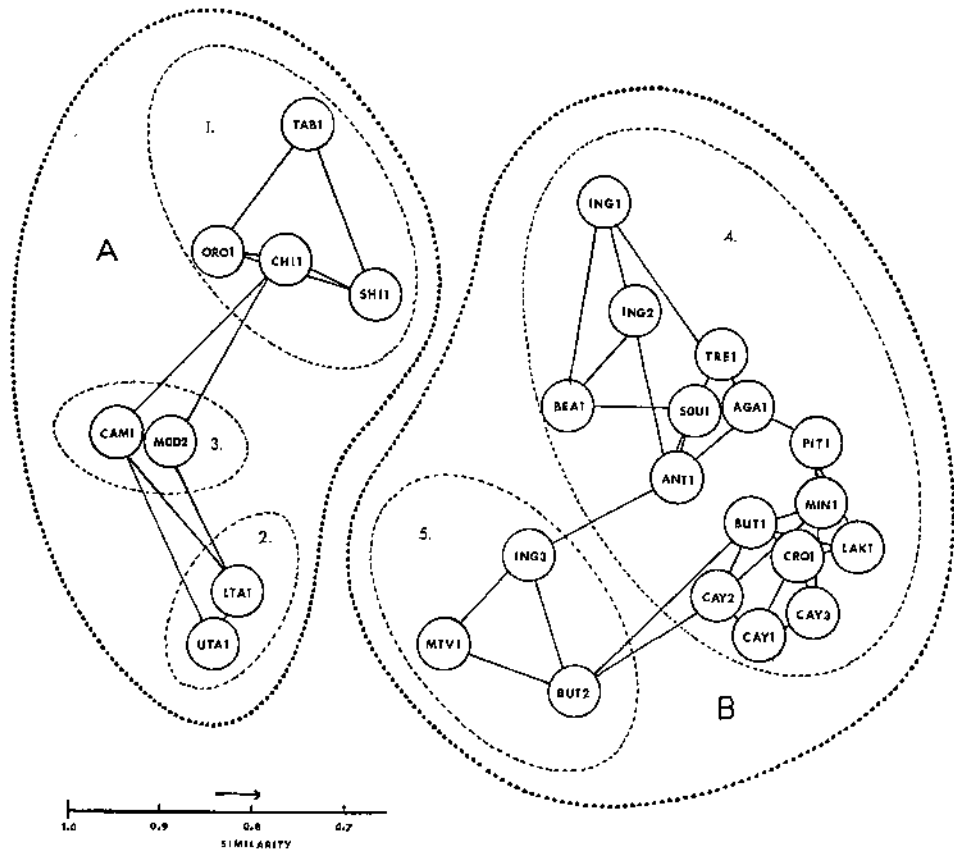


FIG. 3. Diagram of Relative OTU Similarities (DROS) based on the association coefficients of OTUs according to their first three orders of similarity. Distances between OTUs proportional to the scale given. Cluster A: partially autogamous populations; Cluster B: highly autogamous populations. Subgroups 1-5 are groups of populations referred to in the text. OTU name abbreviated to first three letters and numbers.

method chains of OTUs are built up by empirical positioning and repositioning of the joined OTUs until all OTUs of the analysis are added.

RESULTS

Phenetic relationships of populations of *Limnanthes floccosa*. The phenogram and DROS indicate that there are several discontinuities in the variation pattern of *Limnanthes floccosa*. The most conspicuous of these is the separation of OTUs Oroville-1 through Modoc Road-2 (Cluster A) from OTUs Lake Co.-1 through Mt. View-1 (Cluster B). The overall level of similarity of the two clusters is low (0.5265), indicating that the two groups of populations differ for almost 50% of the characters used. The composition of the two major clusters, moreover, has little relation to Mason's varietal delineations. Cluster A includes populations of *L. floccosa* var. *pumila* (Howell) Mason (Lower Table Rock-1 and Upper Table Rock-1), and five populations referred to *L. floccosa* var. *floccosa* (Oroville-1 through Shippe-1, Camp White-1, Modoc Road-2). The phenetic separation of the two clusters is due primarily to floral differences relating to different levels of autogamy. All populations of

L. floccosa are structurally adapted for self-pollination with the stigma maturing directly below the level of the dehiscent anthers. The flowers of populations occurring in Cluster A, however, have relatively large corollas, anthers, sepals, and nectaries; they are protandrous and retain nectar guides. Following pollination three to five of the five ovules mature to seed. Such populations, which are described as *partially autogamous*, are still visited by pollinators and have large amounts of self-pollination only in years of pollinator stress (Kalin, 1971). There is limited retention of floral features associated with outcrossing in populations of Cluster B, however. All populations of this cluster have very small flowers that lack nectar guides and protandry and have poorly developed nectaries. Of the five ovules only one or two develop to seed. These populations, which undergo large amounts of self-pollination, are described as *highly autogamous*.

In addition to the separation of populations of *Limnanthes floccosa* on the basis of their different levels of autogamy, several other discontinuities are present in *L. floccosa*. In the partially autogamous cluster (Cluster A) three separate subgroups of populations are evident (subgroups 1-3). The subgroups are geographically separated from one another, at least on a local basis. Subgroup 2 is made up of the only two known populations of *L. floccosa* var. *pumila* from Lower and Upper Table Rock respectively, on the Medford Plains in southern Oregon. This subgroup includes glabrous plants that may be easily distinguished from the pubescent plants of subgroups 1 and 3. A second division in the partially autogamous cluster is indicated by OTUs Camp White-1 and Modoc Road-2 (subgroup 3). Partially autogamous populations of subgroup 3 were referred to *L. floccosa* var. *floccosa* by Mason (1952). Like those of subgroup 2, populations of this subgroup are also vernal pool plants of the Medford Plains. Subgroups 2 and 3, however, never occur in mixed populations, since populations of subgroup 3 are found only on the rolling plains some 1000 ft below the two Table Rocks to which subgroup 2 is restricted. OTU Camp White-1 originates from the type locality of *L. floccosa* and represents the occasional large-flowered plant that occurs on the type sheet of that species along with several other plants. Populations of the third subgroup of Cluster A (subgroup 1; OTUs Oroville-1 through Shippe-1) all occur at the southern edge of the distribution of *L. floccosa*. They inhabit the edges of vernal pools on the eastern margin of the Sacramento Valley and may be distinguished from the pubescent plants of subgroup 3 by the pubescence patterns of their sepals (Table III).

Two subgroups are evident in the highly autogamous Cluster B. Subgroup 4 is made up of populations of densely pubescent plants, while subgroup 5 includes populations of glabrous plants. Subgroup 5 contains three populations that are referable to *L. floccosa* var. *bellingermana* (OTUs Ingot-3 through Mt. View-1). All derive from the eastern margin of the distribution of *L. floccosa*. Two of the populations (Ingot-3 and Butte Falls-2) occurred in damp meadows in habitats resembling that occupied by the population from which the type collection of *L. floccosa* var. *bellingermana* was made, but also occurred adjacent to populations of pubescent plants, which in this study cluster in the highly autogamous subgroup 5 (Butte Falls-1 and Ingot-2). The morphological differences separating subgroups 4 and 5 appear to be maintained through genetic isolation stemming from the very high levels of self-pollination in such marginal populations of *L. floccosa*. The second subgroup of highly autogamous populations (subgroup 4), OTUs Lake Co.-1 through Ingot-2, includes the largest proportion of populations of *L. floccosa*. Such populations occur from Shasta County, California (with two outlying stations in Tehama County and Lake County, California) as far north as the Medford Plains in southern Oregon.

TABLE III
DISTINGUISHING FEATURES OF THE SUBSPECIES OF *Limnanthes floccosa*

Character	ssp. <i>californica</i>	ssp. <i>grandiflora</i>	ssp. <i>pumila</i>	ssp. <i>floccosa</i>	ssp. <i>bellingerriana</i>
Habit	erect	erect	decumbent	erect-decumbent	erect-decumbent
Foliage pubescence	dense	sparse	absent	dense	absent
Perianth shape	crateriform	crateriform	crateriform	campanulate-urceolate	urceolate
Sepal length (mm)	7.5-8.5	8.5-9	7.5-8	4-7.5	5.5-7.5
Sepal pubescence: inner surface	dense	dense	absent	dense	absent
outer surface	dense	sparse-absent	absent	dense	absent
Petal length (mm)	8-9	7.5-9	7.5-8	4.5-8.4	5.5-7.5
2 rows of hairs on claws of petals	present	present	present	absent	absent
Filament length (mm)	5-7	4.5-5	4.2-4.7	2-4.5	2-3.5
Anther length (mm)	1-1.5	.75	1	.4-.74	.5
Direction of anther dehiscence	extorse	extorse	extorse	mostly introrse	mostly introrse
Pistil length (mm)	3.5-4	3.2-4	3-3.5	1.5-3	2.3-2.5
Style branch length (mm)	1-1.5	1-1.5	1-1.5	1-2	1.4-1.5
No. of nutlets produced per flower	3-5	3-5	3-5	1-2(3)	1-2(3)
Mode of nutlet dehiscence	with calyx	with calyx	without calyx	with calyx	with calyx
Protandry (in days)	1	1	0-1	0	0
Breeding system	partially autogamous	partially autogamous	partially autogamous	highly autogamous	highly autogamous
Chromosome number	$n = 5$ (Kalin 7014)	$n = 5$ (Kalin 7048)	$n = 5$ (Kalin 7034)	$n = 5$ (Kalin 7045, 7020, 7032; Ornduff 6890)	$n = 5$ (Kalin 7031; Ornduff 6911b)

They inhabit ecologically marginal situations (dry stony flats, roadsides; Table I). Over a large part of the Medford Plains, plants of this subgroup, which are identical to the small-flowered plants on the type sheet of *L. floccosa*, are marginally sympatric with plants of subgroup 2. Only occasional plants intermediate between the two subgroups are found. As plants of subgroup 4 flower almost one month in advance of those of subgroup 2, lack of intergradation is probably maintained through seasonal isolation in combination with high levels of self-pollination in subgroup 4.

Taxonomic revision of *Limnanthes floccosa*. On the basis of the results of the taximetric analysis, five subspecies are recognized in *Limnanthes floccosa*. *Limnanthes floccosa* var. *pumila* and *L. floccosa* var. *bellingermana* are elevated in rank to subspecies (ssp. *pumila* and ssp. *bellingermana*, respectively). *Limnanthes floccosa* var. *floccosa* sensu Mason is a complex taxon including three distinct entities (ssp. *floccosa*, ssp. *grandiflora*, and ssp. *californica*) with two of the subspecies differing from the third by the same constellation of characters that separates *L. floccosa* ssp. *pumila* from *L. floccosa* ssp. *bellingermana*. Differences between Mason's treatment of *L. floccosa* and that given herein are the results of differing taxonomic approaches. Mason (1952) emphasized pubescence differences, whereas I emphasize differences in floral morphology related to levels of autogamy as well as pubescence differences. The five subspecies of *L. floccosa* are listed below and are compared in Table III.

1. LIMNANTHES FLOCCOSA ssp. FLOCCOSA

Limnanthes floccosa Howell, Fl. NW Amer. 1: 108. 1897. TYPE: UNITED STATES: OREGON: Jackson Co.: On gravelly plains near Medford, 15 Apr 1887, T. Howell s.n. (GRE).
Limnanthes floccosa var. *floccosa* (Howell) Mason, Univ. Calif. Publ. Bot. 25: 455-506. 1952, pro parte.

Distribution: Common in Shasta Co., California and Jackson Co., Oregon. Local in Siskiyou Co., Tehama Co., California and Josephine Co., Oregon.

Habitat: Dry stony flats on tops of bluffs, roadsides, cultivated fields, and meadow edges.

Representative specimens:

OREGON: Josephine Co.: Grants Pass, 1912, Prescott s.n. (GH, WILLU). Jackson Co.: Crow-foot Rd., 5 mi N jct. with Butte Falls Rd., Kalin 7059 (NY, UC); 31.7 mi W of Butte Falls, Kalin 7060B (NY, UC); Central Point, Peck 24855 (WILLU); N of Medford, Thompson 10303 (WILLU); Upper Sams Valley, Delling 12352 (ORE); Agate Desert, Delling 395 (ORE); Wheeler Rd., Medford Plains, Kalin 7051 (NY, UC); Modoc Rd., Medford Plains, Kalin 7054 (UC), 7058 (UC), 7030B (NY, UC); Jct. Agate Rd. & Hwy. 234, Kalin 7029 (NY, UC); Antioch Rd., Medford Plains, Kalin 7032 (NY, UC); Tresham Lane, Medford Plains, Kalin 7036 (UC). CALIFORNIA: Siskiyou Co.: Yreka, Greene 705 (F, GH, MO); Yreka Creek, Wheeler 3501 (GH). Shasta Co.: The Bench, Fall River Valley, M. S. Baker 111 (UC); Cayton Creek, Hwy. 89, Ornduff 6890 (UC), Kalin 7063 (NY, UC); 6 mi N of the entrance of MacArthur-Burney State Park, Kalin 7043 (NY, UC); Ingot, Mason 1264 (UC); 6 mi W of Ingot, Mason 1260 (UC); 6.7 mi W of Ingot, Niehaus 645 (UC); 5.4 mi SW of Ingot, Ornduff 6911a (UC), Kalin 7045 (UC); Jct. Pit Rd. no. 1 & Hwy. 299, Kalin 7044 (NY, UC); Jct. South Cow Creek Rd. & Hwy. 44, Kalin 7066 (UC); 1.3 mi W of Bear Creek Bridge, Hwy. 44, Kalin 7024 (NY, UC), Niehaus 649 (UC). Tehama Co.: 5 mi E of Mineral, Kalin 7067 (UC). Lake Co.: Jct. of Hwy. 175 & Hwy. 29, Ornduff 6881 (UC), Kalin 7020 (UC).

The type collection of *Limnanthes floccosa* Howell is a mixture of small-flowered plants lacking hairs on the claws of the petals and large-flowered plants having two rows of hairs on the claws of the petals. In a handwritten description of *L. floccosa* appended to the type specimen, Howell writes ". . . the pubescent lines at the base obscure. . . ." In the published description of *L. floccosa* this reference to hairs on the

claws of the petals was omitted. As it reads, the published description of *L. floccosa* best fits the small-flowered plants on the type sheet. These accordingly are designated as lectotype of *L. floccosa*.

2. *Limnanthes floccosa* ssp. *bellingermana* (M. E. Peck) Arroyo, comb. nov.

Limnanthes bellingermana M. E. Peck, Proc. Biol. Soc. Wash. **50**: 93. 1937. TYPE: UNITED STATES: OREGON: Jackson Co.: Stony flat near Pinehurst, 15 Apr 1936, G. C. Bellingerman s.n. (WILLU).

Limnanthes floccosa var. *bellingermana* (M. E. Peck) Mason, Univ. Calif. Publ. Bot. **25**: 455. 1952.

Distribution: Local on the eastern margin of the distribution of *L. floccosa* in Shasta Co., California and Jackson Co., Oregon.

Habitat: Shaded edges of damp rocky meadows.

Representative specimens:

OREGON: Jackson Co.: Mountain View, *Mason 1210* (US), *Ornduff 6925* (UC), *Kalin 6927* (UC), *7031* (UC); Pinehurst, *Thompson 103040 1/2* (MO, NY); 1 mi E of Lincoln, *Bacigalupi & Holmgren 3195* (UC); 3.7 mi W of Butte Falls, *Kalin 7060A* (NY, UC). CALIFORNIA: Shasta Co.: 4.5 mi SW of Ingot, *Ornduff 6911b* (UC).

Limnanthes floccosa ssp. *bellingermana* is a rare plant that has been collected on few occasions. Since the collections cited from "Mountain View," "Pinehurst," and "1 mi W of Lincoln" all appear to be from the same population, from which the type gathering was also made, this subspecies is known only from a total of three populations.

3. *Limnanthes floccosa* ssp. *pumila* (Howell) Arroyo, comb. nov.

Limnanthes pumila Howell, Fl. NW Amer. **1**: 108. 1897. TYPE: UNITED STATES: OREGON: Jackson Co.: Top of (Lower) Table Rock, *T. Howell 635* (ORE).

Limnanthes floccosa var. *pumila* (Howell) Mason, Univ. Calif. Publ. Bot. **25**: 455. 1952.

Distribution: Known only from the summits of Lower Table Rock and Upper Table Rock (ca. 1300 ft), Jackson Co., Oregon.

Habitat: Common along the edges of deep vernal pools.

Representative specimens:

OREGON: Jackson Co.: (Lower) Table Rock, *Howell 635* (GH, MO), *1532* (ORE, US), *Henderson 5759* (MO, ORE), *Mason 1270* (UC), *Ornduff 6924* (UC), *Kalin 7034* (NY, UC); Upper Table Rock, *Kalin 7033* (NY, UC).

Limnanthes floccosa ssp. *pumila* is known only from the two ancient elevated lava flows forming Upper and Lower Table Rocks, respectively, in Jackson Co., Oregon. Although *L. floccosa* ssp. *grandiflora* and *L. floccosa* ssp. *floccosa* occur immediately below the rock formations inhabited by this subspecies, ssp. *pumila* has never been found at lower elevations.

4. *Limnanthes floccosa* ssp. *californica* Arroyo, ssp. nov.

Caulis et folia dense pubescentia. Sepala petalis breviora utrinque dense pubescentia; petala 8–9 mm longa seriebus pilis in unguibus 2; filamenta 5–7 mm longa; antherae 1–1.5 mm longae; pistillum 3.5–4 mm longum. Nuculae maturae in quoque flore 3–5. Chromosomatum numerus, $n = 5$ (*Kalin 7014*).

TYPE: UNITED STATES: CALIFORNIA: Butte Co.: On Hwy. 99E 0.5 mi S of jct. with Shippe Road, 29 Mar 1970, *M. T. Kalin 7014* (UC).

Distribution: Local on the eastern edges of the Sacramento Valley and also on Table Mountain, Butte Co., California.

Habitat: Edges of deep vernal pools in undisturbed areas.

Representative specimens:

CALIFORNIA: Butte Co.: Chico, *Heller 15002* (MO, NY); 10 mi N of Chico, *Heller 12672* (F, GH, MO, NY, US); 8 mi NW of Oroville, *Mason 1255* (UC); 1 mi W of Oroville on Hwy. 70, *Ornduff 6885* (UC); Table Mountain, *Mason 1254* (UC), *Niehaus 371* (UC).

Limnanthes floccosa ssp. *californica* is a rare plant of the eastern edge of the Sacramento Valley in Butte Co., California, which from herbarium specimens appears to have been considerably more common in earlier times. Today ssp. *californica* may only be found in undisturbed sites, and it is evident that this subspecies is in danger of extinction.

5. *Limnanthes floccosa* ssp. *grandiflora* Arroyo, ssp. nov.

Caulis et folia sparse pubescentia. Sepala petalis longiora vel paulo breviora, intus dense pubescentia, extus sparse pubescentia vel glabra; petala 7.5–9.5 mm longa seriebus pilis in unguibus 2; filamenta 4.5–5 mm longa; antherae 7.5–9.5 mm longae; pistillum 3.2–4 mm longum. Nuculae maturae in quoque flore 3–5. Chromosomatum numerus, $n = 5$ (*Kalin 7048*).

TYPE: UNITED STATES: OREGON: Jackson Co.: Modoc Road, 0.8 mi S of jct. with Hwy. 234, 23 Apr 1970, *M. T. Kalin 7030A* (HOLOTYPE: NY; ISOTYPE: UC).

Distribution: Known only from the Medford Plains, Jackson Co., Oregon.

Habitat: Edges of vernal pools.

Representative specimens:

OREGON: Jackson Co.: Agate Desert, *Deiling 3951* (ORE); 10 mi N of Medford, *Thompson 2177* (WILLU); Camp White, *Ornduff 6950* (UC), *Kalin 7028* (UC); Kirtland Road, Medford Plains, *Ornduff 6793* (UC), *Kalin 7048* (UC); Modoc Rd., Medford Plains, *Kalin 7053* (NY, UC), *7057* (UC).

Limnanthes floccosa ssp. *grandiflora* occurs abundantly over the Medford Plains beneath Lower and Upper Table Rock, in Jackson Co., Oregon. Over much of this area ssp. *grandiflora* is sympatric with ssp. *floccosa*, the two subspecies forming concentric rings around vernal pools with ssp. *floccosa* always on the drier, outer fringes of the pool and with ssp. *grandiflora* on the wetter, inner fringes of the pool. The flowering times of the two subspecies are distinct (ssp. *grandiflora* tending to flower one month later than ssp. *floccosa*), a factor that presumably allows the two subspecies to coexist without significant intergradation.

DISCUSSION

Feature of the analysis. The phenetic approach to infraspecific variation presented herein has many similarities to other analyses that have appeared in the taxonomic literature in recent years but differs in other respects. In this analysis, populations rather than already-established infraspecific taxa have formed the basis of OTUs. The existing varieties of *Limnanthes floccosa* were rejected as OTUs because any taxonomic changes resulting from their comparison would only result in the same, or a more inclusive taxonomic scheme, which would do little to resolve the basic variation pattern evident in *L. floccosa*. A second way in which this study differs from more conventional taximetric approaches is in the strong emphasis given to reproductive characters. Of the 42 characters employed, 88.1% concern flower and

fruit characters. In view of this fact, the taxonomic revision resulting from the analysis might be considered artificial. The use of a large number of floral characters is primarily a reflection of large numbers of morphological differences associated with the evolution of two different levels of autogamy in *L. floccosa*. The lack of vegetative characters, on the other hand, is due to the remarkable uniformity this species displays in vegetative characters throughout its geographical range. The use of invariant vegetative characters would lead to considerable redundancy in the data, whereas reduction in the number of floral characters would de-emphasize the importance of self-pollination in the infraspecific differentiation of *L. floccosa*. The emphasis on reproductive characters in the analysis, therefore, is due to the exaggerated effect that the evolution of autogamy has had on floral characters rather than to bias in character choice. The third way in which this study differs from the majority of taximetric studies is in the use of live plants grown under standardized growth conditions for data extraction. Most taximetric studies, for pragmatic reasons, are conducted with data taken from herbarium sheets (see, however, Rhodes et al., 1968; Ornduff & Crovello, 1968, in which some living material was used). The procedure of using living plants grown under similar conditions of light, temperature, and humidity in growth chambers was considered essential because of the high degree of phenotypic flexibility displayed by *L. floccosa*. The stature and yield of plants of *L. floccosa* depends greatly upon seasonal and local variation in the dryness of its vernal habitat. Differences in measurements obtained from plants grown in the field, especially for quantitative characters, could represent different phenotypic expressions of the same genotype rather than differences in the genotype. In using uniform growing conditions, the amount of phenotypic variation both within populations and between populations is standardized. Any differences in measurements obtained from plants growing under standardized growth conditions thus can be presumed to have a genetic basis. The use of live plants for data extraction also facilitated obtaining measurements of individual characters at a specified stage of development for all plants.

Taxonomic conclusions based on the taximetric analysis. On the basis of the phenetic similarities of its populations, *Limnanthes floccosa* is subdivided into five subspecies. Although the taxonomic revision of *L. floccosa* has been based entirely on the phenetic analysis, it is felt that such subspecies will be accepted by many taxonomists who consider phenetic studies as having no value in plant taxonomy. The rejection of taximetric studies in making taxonomic revisions, as pointed out by several authors (e.g., Ornduff & Crovello, 1968; Fryxell, 1971), relates to the difficulty of determining whether phenetic similarities are due to common ancestry or to convergence. Four of the subspecies of *L. floccosa* are probably monophyletic (ssp. *californica*, ssp. *pumila*, ssp. *grandiflora*, ssp. *floccosa*). These subspecies have internally continuous ranges, which might indicate that the individual populations of each subspecies are related through descent rather than through convergence. In the one case of range overlap, between ssp. *grandiflora* and ssp. *floccosa* on the Medford Plains in southern Oregon, the two subspecies are strongly differentiated ecologically (ssp. *floccosa* occurring on dry exposed sites and flowering early in the spring; ssp. *grandiflora* occurring only along the edges of vernal pools and flowering late in the spring), and their distinctiveness cannot be doubted. The monophyletic nature of ssp. *floccosa* is also supported by cytogenetic data (Kalin, 1971). Chiasma frequencies obtained for four populations of ssp. *floccosa* (1.81–2.04) were all higher than those obtained from a single population of each of the three partially autogamous subspecies (1.48–1.78). The fifth subspecies, *L. floccosa* ssp. *bellingermana*, nevertheless is probably polyphyletic. It is known from only three widely separated popula-

tions, in two of which pubescent plants of ssp. *floccosa* also occur. As the glabrous plants of ssp. *bellingermana* and pubescent plants of ssp. *floccosa* are otherwise identical, the glabrous plants have probably arisen as variants in populations of ssp. *floccosa* on different occasions. The phenetic similarity of these two independently derived populations of ssp. *bellingermana* is due to the parallel development of glabrousness in populations of ssp. *floccosa* in combination with the fact that the ancestral pubescent populations have reached a similar level of autogamy. I have chosen to include the glabrous populations in a single subspecies, as no taxonomic purpose would be served in regarding morphologically indistinguishable populations as distinct taxa.

The taxonomic implications of autogamy in *Limnanthes floccosa*. Autogamy is a well-known cause of taxonomic difficulties in a large number of plant groups. Autogamous complexes are notorious for large amounts of discrete variation ranging from that associated with entities having diverse ecological and geographical characteristics, to morphologically discrete intra-population variants of a sporadic nature and of often dubious adaptive value. The taxonomic treatment of these variation patterns presents many problems. Two aspects of autogamy that have had an important effect on the infraspecific variation pattern in *Limnanthes floccosa* are the effects on floral morphology resulting from changes in level of autogamy and the genetic effect on population structure of high levels of self-pollination. Differences in the pubescence patterns between the two highly autogamous subspecies of *L. floccosa* are probably the result of genetic isolation through high levels of self-pollination. In two localities the glabrous ssp. *bellingermana* is sympatric with pubescent plants of ssp. *floccosa*. Insofar as the glabrous and pubescent plants occur together in the same populations and are otherwise morphologically indistinguishable, the most reasonable explanation is that the difference has a simple genetic basis that is maintained by the high levels of self-pollination characterizing these populations. Many taxonomists may argue that the recognition of taxa on the basis of such minor pubescence differences is unwarranted. Ecological evidence indicates, however, that such pubescence differences have a good adaptive basis. Without exception, the glabrous plants in both localities are restricted to shaded, damp edges of the meadows inhabited by the populations. The pubescent plants in contrast are restricted to the upper dry, exposed edges of the meadows. Clearly, to include such glabrous and pubescent plants in one subspecies would be to neglect an important capacity of autogamous *L. floccosa*: rapid adaptation to ecologically marginal conditions on the edge of its range.

In *Limnanthes floccosa* changes in floral morphology resulting from changes in levels of autogamy have had a far greater impact on infraspecific variation patterns than the genetic effect of autogamy has had on population structure. Increases in autogamy are invariably accompanied by losses of floral features associated with outcrossing (Lloyd, 1965; Ornduff, 1969). In many instances residual floral features associated with outcrossing that remain in autogamous taxa are lost in a sporadic fashion due to lack of selection for their maintenance. Although this source of variation in autogamous entities undoubtedly contributes to the greater amount of floral variation displayed by autogamous entities in relation to outcrossers, it is rarely likely to be of taxonomic significance. The loss of features associated with outcrossing in autogamous entities, however, may occur in a coordinated fashion through the effect of natural selection. In *L. floccosa* the large number of floral differences separating the highly autogamous and partially autogamous subspecies appear to have resulted from catastrophic selection (Lewis, 1962; Moore & Lewis, 1965). The partially autogamous subspecies are late-flowering vernal-pool dwellers. The highly autogamous

subspecies, in contrast, are early-flowering plants of dry, marginal, and weedy habitats, and there is little doubt that the highly autogamous subspecies of *L. floccosa* evolved from a partially autogamous ancestor through rapid selection for small-flowered, rapidly maturing, highly self-pollinating genotypes (Kalin, 1971)). Clearly the effect of the combination of autogamy and catastrophic selection on taxonomic patterns can be very great. Evolutionarily closely related taxa may appear to be distantly related on the basis of morphological characteristics. The phenetic differences separating the relatively closely related partially and highly autogamous subspecies are such that their conspecificity may be questioned, but since they display some fertility, both in the field and in the greenhouse, they are probably best considered conspecific.

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