72-9046

RAY, Harold Edwin, 1942-
A BIOSYSTEMATIC STUDY OF ARTEMISIA CARRUTHII.

The University of Oklahoma, Ph.D., 1971
Botany

University Microfilms, A XEROX Company, Ann Arbor, Michigan

THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

A BIOSYSTEMATIC STUDY OF

ARTEMISIA CARRUTHII

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements [illegible]

degree of

DOCTOR OF PHILOSOPHY

BY

HAROLD EDWIN [illegible]

Norman, Oklahoma

1971

A BIOSYSTEMATIC STUDY OF ARTEMISIA CARRUTHII

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ACKNOWLEDGMENT

The author wishes to thank his major professor, Dr. James Estes, for his advice and guidance during the course of research and the critical reading of the manuscript during its preparation. The author also wishes to thank the members of the dissertation committee, Drs. George J. Goodman, Paul G. Risser, John J. Skvarla, and Simon Wender for their comments and advice in the final preparation of the manuscript. The author would like to especially thank Dr. Gary Schnell for his time and assistance in preparation of the numerical taxonomy portion of the manuscript and also Miss Janet Chapman for the excellent drawings that are included in the appendix.

To my family, I wish to express deepest appreciation, particularly to my wife, Shirley, who made it all possible.

Funds for this study were furnished in part by a National Science Foundation Grant.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF ILLUSTRATIONS

A BIOSYSTEMATIC STUDY OF ARTEMISIA CARRUTHII

CHAPTER I

INTRODUCTION

Artemisia carruthii Wood ex Carruth (1877), as defined by David Keck (1946) demonstrates exceptional morphological and ecological diversity. The species is widespread throughout the southwestern United States and northern Mexico (Figure 1), occurring on the treeless plains of the Llano Estacado, under the cover of *Quercus stellata* Wang. and *Juniperus deppeana* Steud., on the lower elevation slopes of mountains throughout the southwest, and under the canopy of mixed coniferous forests in the Rocky Mountains.

The range of morphological variation is illustrated by the number of taxa previously described within the boundaries of *A. carruthii* as established by Keck (Table 1). Five distinct species had been recognized by Gray (1883), Britton and Brown (1898), Osterhout (1898), Greene (1901) and Greenman (1904).

Rydberg (1916) authored the first major treatment of the North American species of *Artemisia*. He grouped *A. carruthii* and five additional species (*A. neomexicana* Greene ex Rydb., *A. prescottiana* Bess., *A. wrightii* Gray, *A. bakeri* Greene and *A. pringlei* Greenman) in the newly established section *Wrightianeae*. Seven years later,

Figure 1. Distribution of *Artemisia carruthii* based on herbarium specimens and collections. Solid dots represent populations used in this study.

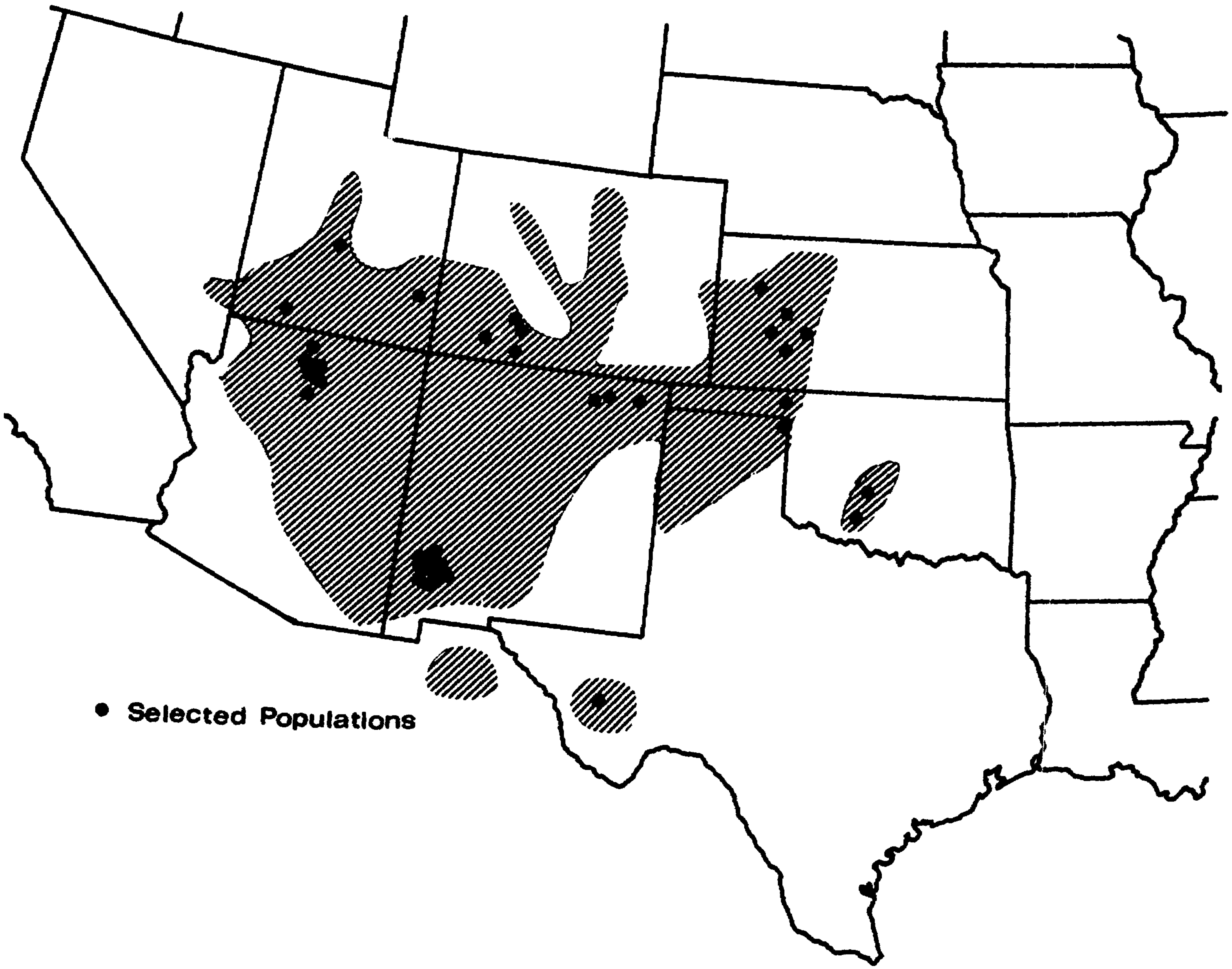

Selected Populations

Table 1. List of Synonymy of _Artemisia carruthii_. Modified from Keck (1946 p. 438).

Taxon	Reference
Artemisia wrightii Gray	Proc. Amer. Acad. 19:48, 1883
Artemisia kansas Britt.	Britt. and Brown, Ill. Fl. 3: 466, 1898
*_Artemisia coloradensis_ Osterh.	Bull. Torr. Club 27: 506, 1898
Artemisia bakeri Greene	Pl. Baker. 3:31, 1901
*_Artemisia pringlei_ Greenm.	Proc. Amer. Acad. 40:50, 1904
Artemisia wrightii coloradensis (Osterh.) A. Nels.	Coult. and Nels., Man. Rocky Mt. 568, 1909
Artemisia mexicana bakeri (Greene) A. Nels	ibid. 569
Artemisia vulgaris ssp. _wrightii_ (Gray) Hall et Clem.	Carn. Inst. Wash. Publ. 326-80, 1923
Artemisia vulgaris var. _wrightii_ (Gray) Palmer et Steyerm.	Ann. Mo. Bot. Gard. 22:677, 1935; Rhodora 40:134, 1938
Artemisia vulgaris carruthii (Wood) F. C. Gates	Trans. Kansas. Acad. Sci. 42: 138, 1940
Artemisia carruthii var. _wrightii_ (Gray) Blake	Jour. Wash. Acad. Sci. 30:472, 1940

*Populations of these taxa not available for inclusion in this study.

Hall and Clements (1923) combined fifty-four of the one-hundred-twenty species recognized by Rydberg as subspecies of *A. vulgaris* L. In doing so they recognized that the resulting species exhibited more variation than any other in the genus, yet they contended that the variation was essentially of a continuous nature and thus conspecific. Section *Wrightianeae* was reduced to the subspecific level.

Clausen, Keck and Hiesey (1940), however, discovered ecotypic and cytologic variation with *A. vulgaris* and in 1946 Keck published his *Revision of the Artemisia vulgaris Complex in North America* in which he resurrected *A. carruthii*.

The taxonomic philosophy employed by Keck appears to be an extension of that presented by Clausen, Keck and Hiesey. The large and variable *A. ludoviciana* was considered tetraploid (2n=4x=36) across its range even though limited chromosome counts were known from only two of the seven included subspecies. He reported *A. carruthii* as 2n=2x=18 (determined from root-tip counts of two plants, both from Springer, New Mexico). Nevertheless he recognized the extreme morphological variation (p. 426) and questioned whether only one chromosome level prevailed throughout the species (p. 440).

Estes (1968) demonstrated that many of Keck's taxa in the Pacific northwest, do in fact include more than one chromosomal level. Additional work by Estes and Ray (1971) has shown the tetraploid and diploid chromosome levels to exist in southwestern taxa of *Artemisia*.

The purpose of this study is to determine the extent of morphological and cytological variability over the range of *A. carruthii*.

CHAPTER II

METHODS AND MATERIALS

During 1969 and 1970, collecting trips were conducted throughout the range of *Artemisia carruthii* to: (1) determine the range of the species in the southwest; (2) note the ecological and environmental conditions which govern the distribution of the species; (3) collect buds for cytological analysis; (4) collect specimens from populations for morphological analysis; (5) collect living material for reproductive experiments.

Bud material and specimens for morphological analysis were randomly selected from each population of *A. carruthii*. Voucher specimens are on deposit in the Bebb Herbarium, University of Oklahoma (OKL).

Field notes were made concerning soil conditions, exposure, moisture and associated species. Live specimens were excavated and placed in 6 inch plastic pots for transplant in the University of Oklahoma greenhouse.

Cytology

Buds were collected and fixed in chloroform, 95% ethanol and glacial acetic acid (6:3:1) for a minimum of 24 hours, washed and stored in 70% ethanol until staining. Buds were stained at 55°C in

HCl-alcohol-carmine stain (Snow, 1963) for 48 hours, washed with 70% ethanol to remove excess stain and dissected in 45% glacial acetic acid. Excess material was removed and the anthers mounted in a drop of Hoyer's medium (Alexopoulis and Beneke, 1952) and squashed. Analysis of meiotic figures were conducted with Zeiss bright-field optics.

Morphology

Thirty-three morphological characters (Table 2) were selected and measured from 5 to 15 plants from each of 37 populations (Table 3). Measurements of characters 17 and 25-30 were to the nearest 1.0 mm, while characters 7, 8, 11-16 and 18-24 were measured to the nearest .015 mm using a Wild Heerbrugg stero microscope. Characters 31-33 were measured using a Hayashi Automatic Area Meter to the nearest .01 mm^2.

The 33 character by 37 OTU (operational taxonomic unit; Sokal and Sneath, 1963) basic data matrix was analyzed using R-type (Rohlf, 1968) and Q-type analysis (Cattell, 1952). Processing of data was carried out on the IBM 360-50 computer at the University of Oklahoma, Merrick Computing Center. The NT-SYS programing package (Numerical Taxonomy System of Multivariate Statistical Programs, III) developed by James Rohlf, John Kishbaugh and David Kirk of the State University of New York at Stony Brook, was used for data analysis.

R-type analysis results in a three-dimensional model such as shown in figure 4. This figure represents the first three principal components extracted by factor analysis from a matrix of correlations. The horizontal axis is rigidly rotated so that it accounts for the maximum variation among characters. Each succeeding axis, that explains a major

Table 2. List of morphological character measurements of *Artemisia carruthii*.

Character Number		Character Number	
1	Leaflet number	16	Height of plant
2	Lower leaf surface pubescence	17	Leaf width at base
		18	Width of terminal leaflet
3	Upper leaf surface pubescence	19	Bract length
		20	Bract width
4	Bract pubescence	21	Length of opaque areas of bract
5	Degrees of panicle branching	22	Disk corolla length
6	Length of hyaline bract tip	23	Ray style length
		24	Number of heads per lower panicle
7	Width of opaque area of bract	25	Length of inflorescence
8	Number of ray florets	26	Width of inflorescence
9	Number of disk florets	27	Length of upper leaf
10	Disk corolla width	28	Length of lowest panicle
11	Disk achene length	29	Length of middle leaf
12	Corolla limb length	30	Length of lowest leaf
13	Ray corolla length	31	Area of top leaf
14	Ray stigma length	32	Area of middle leaf
15	Ray achene length	33	Area of bottom leaf

Table 3. Location of populations of *Artemisia carruthii*.

OTU Code No.	Collection Number	Locality	Ecological Notes
1	1109	Kansas: Hodgeman Co. 3 miles south of Jetmore.	Dry, rocky, limestone-sided wash east-west direction, open short-grass pasture.
2	1116	Kansas: Gray Co. 5 miles north and 2 miles east of Montezuma.	Dry, rocky, limestone hillside, east exposure, open short-grass pasture.
3	1111	Kansas: Lane Co. 1.4 miles east and 1.8 miles south of Dighton.	Dry, rocky, limestone hillside west exposure, open short-grass pasture.
4	1115	Kansas: Finney Co. 6 miles north of Garden City.	Dry, sandy rolling short-grass pasture.
5	1113	Kansas: Logan Co. 21 miles north of Scott City.	Dry, loam, rolling short-grass pasture, east exposure.
6	1031	New Mexico: Colfax Co. 12 miles north of Springer.	Dry, loam rolling short-grass pasture, plants in low area between low hills.
7	1094	Utah: San Juan Co. 4.5 miles east of La Sal.	Dry, along top of north-south rocky ridge, scattered in a lumbered oak-pine forest.

Table 3 (Continued)

OTU Code No.	Collection Number	Locality	Ecological Notes
8	1090	Arizona: Coconino Co. 4 miles west of Jacob Lake.	Rocky mountain side with little slope, scattered under a stand of mature pines.
9	1086	Arizona: Coconino Co. 6. 5 miles east on East Rim Road, Grand Canyon.	Rocky mountain side with slight south slope, scattered between groups of mature and younger pines.
10	1039	Arizona: Coconino Co. 3. 5 miles east of Grandview Overlook, Grand Canyon.	Rocky, steep mountain slope, southeast exposure, scattered in open areas of mature pine stand.
11	1097	Colorado: LaPlata Co. 5 miles south of Hesperus.	Dry wash between low mountains, plants along edge of wash and scattered among pines on hill-side.
12	1041	Arizona: Coconino Co. 16. 7 miles north of Sedona.	Dry rock mountain top, scattered among mature pines.
13	1100	Colorado: Archuleta Co. 8 miles south and 2 miles east of Pagosa Springs.	Rocky mountain slope, east exposure, scattered under mature stand of pines.

Table 3 (Continued)

OTU Code No.	Collection Number	Locality	Ecological Notes
14	1101	Colorado: Mineral Co. 5 miles east of Wagon Wheel Gap.	Rocky steep mountain slope, south exposure, scattered in open area below pine forest.
15	1118	Texas: Lipscomb Co. 13 miles south of Booker.	Dry, loam, rolling short-grass pasture, southern exposure.
16	1092	Utah: Kane Co. 10 miles west of Long Valley Junction.	Rocky mountain top, scattered under mature pines and small spruces and firs.
17	1053	Oklahoma: Caddo Co. 8 miles west and 1.2 miles north of Cogar.	Sandy, steep banks of canyon under juniper trees.
18	1068	Texas: Jeff Davis Co. .1 mile west of McDonald Observatory entrance.	Dry, loam short-grass meadow between mountains.
19	1082	New Mexico: Grant Co. 4.6 miles north of Silver City.	Dry, sandy foothill, scattered under juniper trees.
20	1106	Oklahoma: Comanche Co. 3 miles south of Wichita Mountain Wildlife Refuge Headquarters.	Dry, rocky wash, growing under oaks.

Table 3 (Continued)

OTU Code No.	Collection Number	Locality	Ecological Notes
21	1093	Utah: Sevier Co. 12 miles northeast of Fremont on Elkhorn Mountain.	Rocky ridge, scattered in open area on top above aspens, spruce and firs.
22	1085	Arizona: Coconino Co. 2 miles east of Flagstaff.	Rocky, level area, scattered in open areas and under pines.
23	1022	Oklahoma: Beaver Co. 2.8 miles east and .7 miles south of Slapout.	Dry, loam, limestone wash, in short-grass pasture, growing along banks and in bottom.
24	1040	Arizona: Coconino Co. 2.6 miles north of Flagstaff.	Rocky ridge, scattered among rocks and between scattered mature pines.
25	1103	New Mexico: Colfax Co. east of Red River, 7 miles south of Colfax-Taos county line.	Deep loam soil in an open valley between spruce, fir covered peaks.
26	1029	New Mexico: Union Co. 8.4 miles east of Des Moines.	Dry, rolling short-grass pasture, on north facing slope.
27	1088	Arizona: Coconino Co. Hull Tanks, Kaibab National Forest.	Sandy, growing in valley between mountains under pines.

Table 3 (Continued)

OTU Code No.	Collection Number	Locality	Ecological Notes
28	1081	New Mexico: Grant Co. 11.5 miles north of Silver City.	Rocky mountain slope, western exposure. Near lower limits of coniferous forest under pines.
29	1047	New Mexico: Grant Co. 11. 8 miles north of Silver City.	Rocky, east slope of mountain, scattered under spruce and fir.
30	1080	New Mexico: Grant Co. 12.8 miles north of Silver City.	Rocky, east slope of mountain, large numbers in open areas, scattered under spruce and firs.
31	1075	New Mexico: Grant Co. Emory Pass.	Rocky, south slope of mountain, scattered under spruce-fir-pine forest.
32	1074	New Mexico: Grant Co. 5.4 miles east of Emory Pass.	Rocky, scattered on south facing mountain slope and along dry stream bed. Dense stands of pines.
33	1077	New Mexico: Grant Co. 8.8 miles west of Emory Pass.	Rocky, north facing slope of mountain. Plants scattered in open areas in pine forest.
34	1052	New Mexico: Grant Co. 3.2 miles east of Santa Rita.	Rocky mountain slope, south exposure, transition zone between oak-juniper forest.

Table 3 (Continued)

OTU Code No.	Collection Number	Locality	Ecological Notes
35	1079	New Mexico: Grant Co. 14 miles north and 6 miles east of Silver City.	Rocky mountain top, clumps in open areas of spruce, fir, pine forest.
36	1076	New Mexico: Grant Co. 7.3 miles west of Emory Pass.	Rocky mountain slope, south exposure, growing under pines and scattered along dry creek.
37	1102	Colorado: Mineral Co. 2 miles north of Creede.	Rocky cliff, plants in crevices in face of mountain.

portion of the remaining variation, is placed perpendicularly to the preceding axis.

Q-type analysis requires that product moment correlation coefficients and average distance coefficients be calculated for all pairs of OTUs by the standard formulae of Sokal and Sneath (1963). Phenograms are then extracted by the unweighted pair group method using averages (UPGMA; Sokal and Sneath, 1963). Cophenetic correlations (Sokal and Rohlf, 1962) are calculated between each matrix and its resulting phenogram to give an indication of how well the phenogram expresses its data matrix. Coefficients of correlation of cophenetic matrices and of basic similarity matrices were computed as described by Crovello (1969). Further explanation of the methods of analysis used can be found in Sokal and Sneath (1963), Schnell (1970a, 1970b) and Robins and Schnell (1971).

CHAPTER III

RESULTS

Cytology

Chromosome counts and meiotic analysis were determined, using diakinesis, metaphase I and anaphase I in microsporocytes. Results of this analysis are shown in Table 4. Only the diploid condition (2n=2x=18) was found in the population samples and only bivalents (9_{II}) were observed at metaphase I. Only one plant (Estes 206A, OKL) was found to have irregular meiosis. This plant is believed to be either asynaptic or desynaptic. No correlation was found between chiasmata frequency and morphological variation.

Morphology

A phenogram (Figure 2) was extracted from the matrix of correlation between OTUs. The clusters of each phenogram will be referred to throughout by the upper and lower OTUs of each cluster: e.g., cluster 1-18 will indicate the large cluster containing smaller clusters 1-20, 6-22 and 11-18.

The correlation phenogram shows two major clusters, one large (1-24) and the other smaller (29-33). Within the larger cluster are two major subclusters (1-18, 7-24) that appear to differ almost as much as they differ from cluster 29-33. The first subcluster, contain-

Table 4. Chiasmata frequency of selected populations of *Artemisia carruthii*.

Population	Number of Cells	Minimum	Mean	Maximum	Standard Deviation	Standard Error
1047	31	8.00	9.7128	12.00	0.95618	0.20866
1048A	9	9.00	9.11111	10.00	0.33333	0.11111
1048B	11	8.00	9.63636	11.00	0.92442	0.27872
1049	12	9.00	9.50000	11.00	0.79772	0.23028
1050	14	9.00	9.64286	10.00	0.49724	0.13289
1052	37	9.00	9.90000	12.00	0.85224	0.19057
1079	38	8.00	9.84210	12.00	1.01451	0.23275
1028	1	10.00	10.00000	10.00	0.00000	0.00000
1029	16	9.00	10.33333	11.00	0.70711	0.23570
1088	20	8.00	9.80000	12.00	0.89443	0.20000
1103	19	9.00	10.57895	12.00	1.01739	0.23341
1104	19	7.00	9.84210	12.00	1.01451	0.23275
1106	4	11.00	13.00000	16.00	2.16025	1.08012
1022	8	10.00	10.75000	12.00	0.88641	0.31339

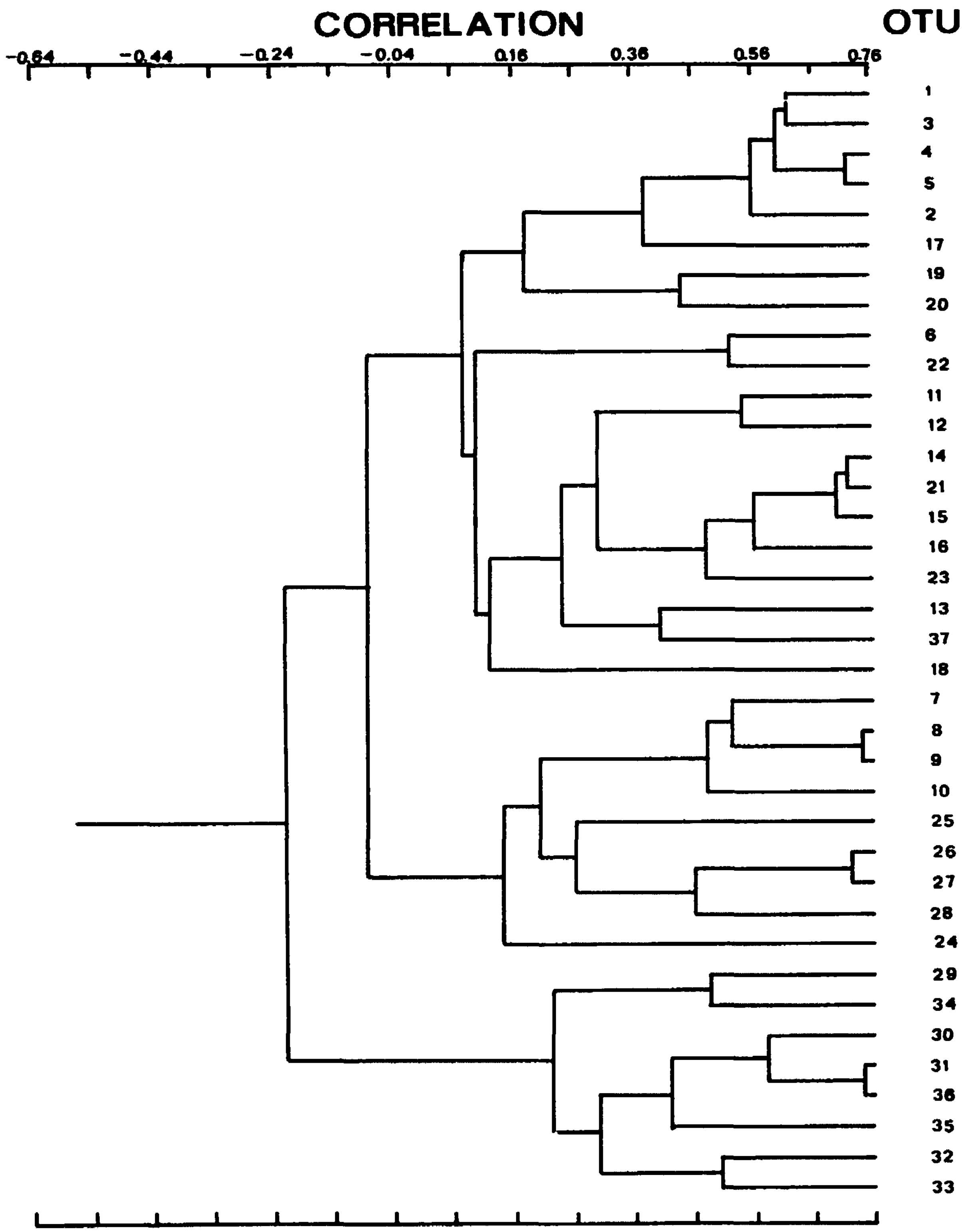
Table 4 (Continued)

Population	Number of Cells	Minimum	Mean	Maximum	Standard Deviation	Standard Error
1031	10	9.00	10.60000	12.00	0.96609	0.30550
1033	7	9.00	10.14286	12.00	1.21499	0.45922
1036	10	10.00	12.30000	17.10	1.88856	0.59721
1039	10	9.00	9.90000	11.00	0.73786	0.23333
1040	24	9.00	9.82353	11.00	0.80896	0.19620
1041	20	9.00	10.55000	13.00	0.88704	0.19835
1053		7.00	9.84210	12.00	1.01451	0.23275
1066	19	9.00	11.15789	14.00	1.25889	0.28881
1068	8	9.00	10.37500	11.00	0.74402	0.26305
1082	18	9.00	9.94444	11.00	0.72536	0.17097
1085	39	9.00	9.0500	11.00	0.82558	0.18460
1086	20	9.00	10.95000	13.00	1.31689	0.29447
1092	20	9.00	11.70000	14.00	1.49032	0.33325
1094	20	9.00	11.15000	13.00	1.22582	0.27410

Table 4 (Continued)

Population	Number of Cells	Minimum	Mean	Maximum	Standard Deviation	Standard Error
1096	18	9.00	10.16667	11.00	0.70711	0.16667
1100	18	11.00	13.05556	15.00	1.05564	0.24882
1101	13	9.00	11.76923	15.00	1.73944	0.48243
1106	19	9.00	10.68421	13.00	1.49267	0.34244
1108	8	10.00	11.00000	12.00	0.75593	0.26726
1109	3	11.00	12.00000	13.00	1.00000	0.57735
1110	18	9.00	11.72222	15.00	1.60167	0.37752
1111	7	10.00	12.14286	15.00	1.57359	0.59476
1112	12	9.00	10.40000	12.00	0.96609	0.30550
1102	16	9.00	12.43750	15.00	2.6458	0.51615

Figure 2. Correlation phenogram of 37 OTUs based on unweighted pair group of cluster analyses using arithmetic averages (UPGMA) for 33 character measurements. Cophenetic correlation is 0.705.


CORRELATION
OTU
-0.64
-0.44
-0.24
-0.04
0.16
0.36
0.56
0.76
1
3
4
5
2
17
19
20
6
22
11
12
14
21
15
16
23
13
37
18
7
8
9
10
25
26
27
28
24
29
34
30
31
36
35
32
33

ing 20 OTUs has two groups of very closely related OTUs (1-17 and 14-23). Groups 19-20, 6-22, 11-13 and 13-37 consist of OTUs not closely related to other clusters, showing a low degree of correlation between the two OTUs contained in each. OTU 18 is contained in the larger cluster 1-18 but shows a degree of correlation that almost separates it as a third subcluster.

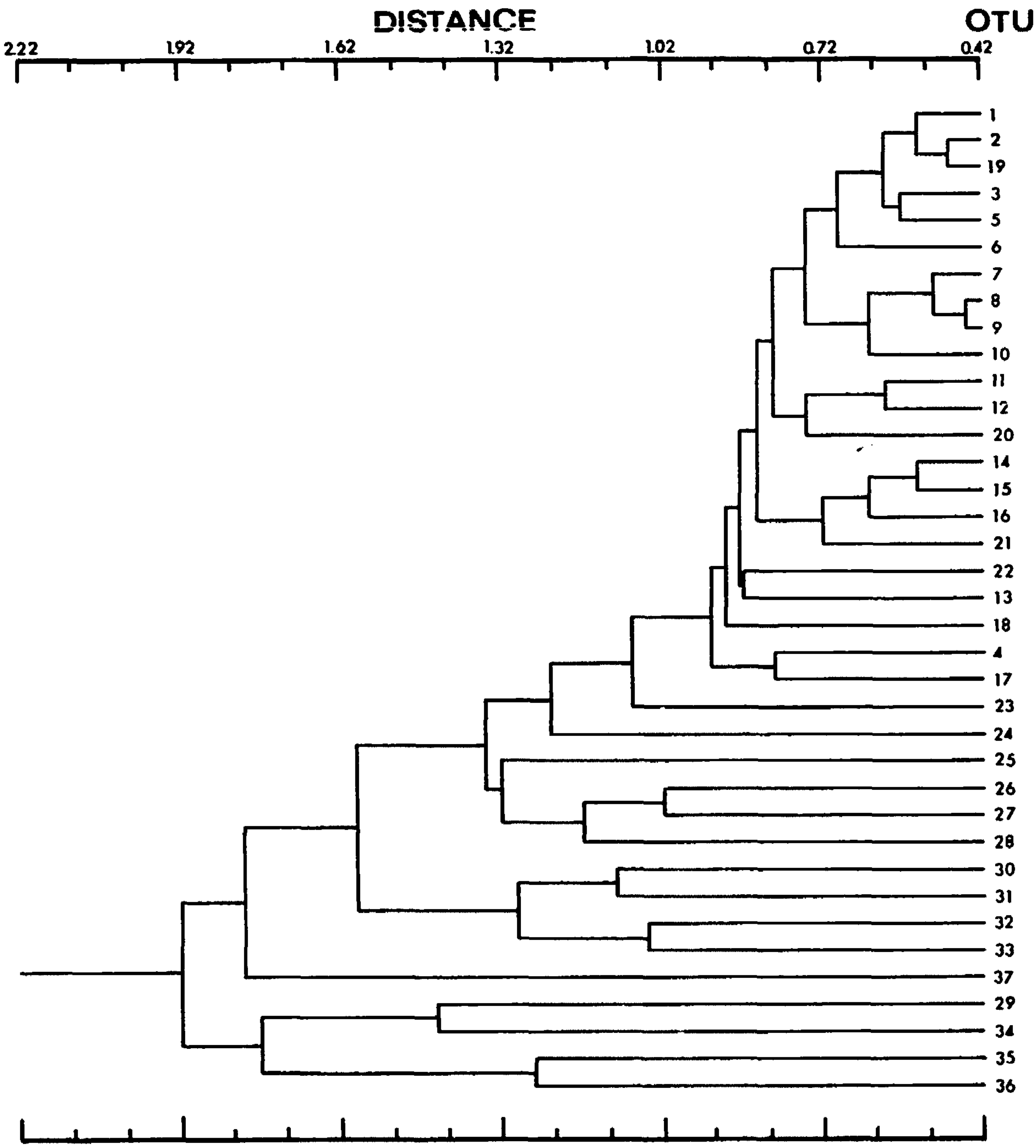
Subcluster, 7-28 has only two closely related pairs of OTUs (8-9 and 26-27). These pairs are contained in the more poorly correlated clusters of 7-10 and 26-28. Again in this subcluster, we have two OTUs (24, 25) that are very poorly correlated with other members of the cluster.

Cluster 29-33 contains only one pair of closely related OTUs (31-36). The remaining OTUs appear to be a very loose aggregation having low correlation with other members of the cluster.

The phenogram extracted from a matrix of distances between OTUs (Figure 3) contains three major clustering groups (1-28, 30-33 and 29-36) plus OTU 37 that is segregated from the remainder. Clusters 29-36 and 30-33 are not tight clusters, but they correspond to cluster 29-33 of the previous figure.

In the large cluster (1-28), the closely related group (1-5) is similar to group 1-17 of the correlation phenogram with OTU 19 replacing OTUs 4 and 17. Groups 7-10 and 14-21 appear to group in almost exactly the same manner as groups 7-10 and 14-16 of the previous phenogram. The distances involved in the relationship of OTUs 18, 23, 24, 25 and 28 with other OTUs indicates that, as noted in the correlation phenogram, they are not closely related to any

Figure 3. Distance phenogram of 37 OTUs based on unweighted pair group of cluster analyses using arithmetic averages (UPGMA) for the 33 character measurements. Cophenetic correlation coefficient is 0.899.


DISTANCE
OTU
2.22
1.92
1.62
1.32
1.02
0.72
0.42
1
2
19
3
5
6
7
8
9
10
11
12
20
14
15
16
21
22
13
18
4
17
23
24
25
26
27
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31
32
33
37
29
34
35
36

of the other OTUs. Groups 4-17 (from the 1-17 cluster of the correlation phenogram) and 26-27 form loose pairs of OTUs as in the correlation phenogram while OTUs 13 and 22 now form the same type of pair. OTU 20 is joined to group 11-12, but the relationship is not good.

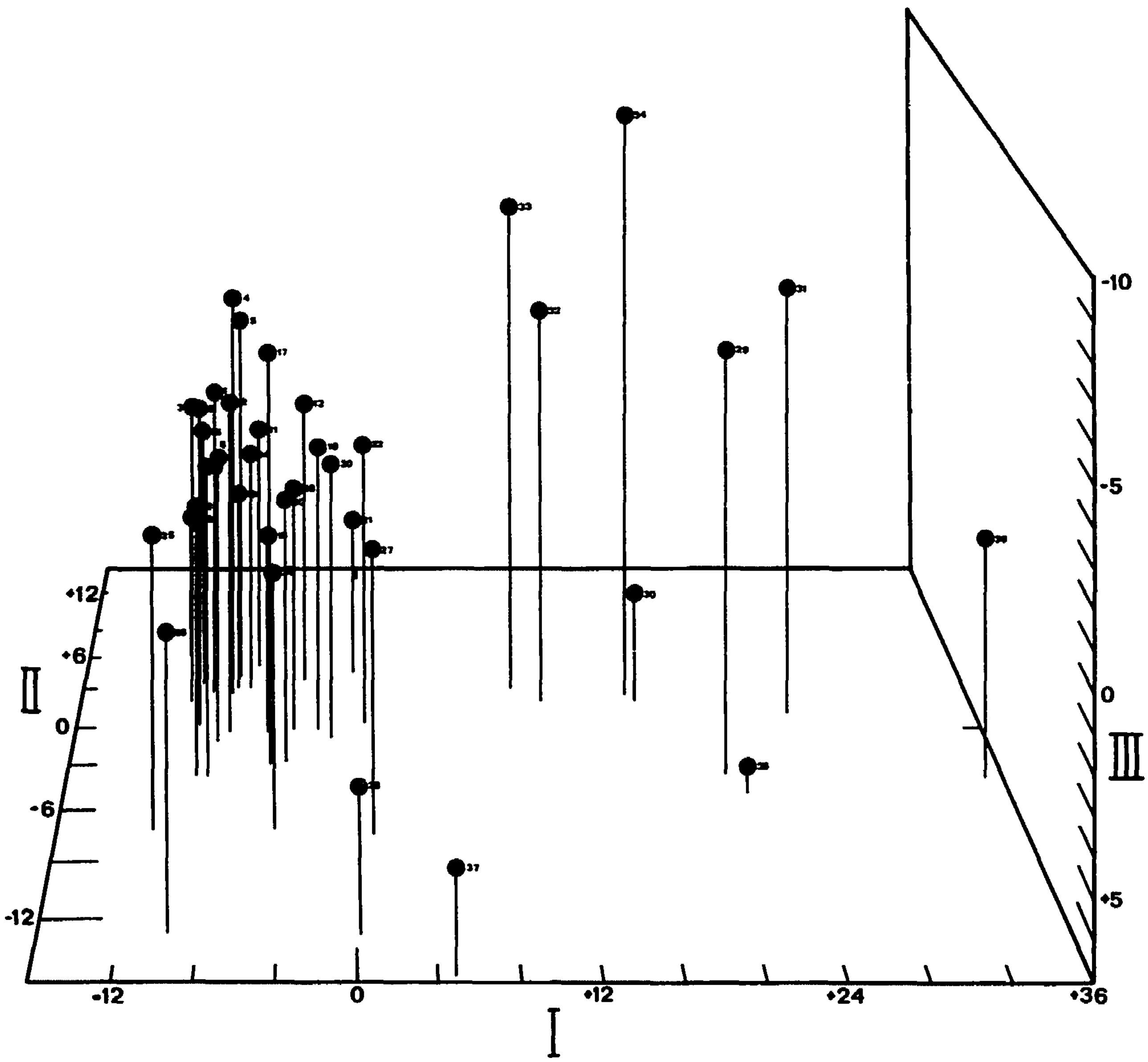
The three dimensional diagram (Figure 4) of projections of OTUs on the first three principal components reduces possible distortion in the major branches of the previous phenograms. This diagram may be used to demonstrate why some OTUs changed positions in the phenograms and explain why the expressed relationships between other OTUs was weak.

There are two groupings separated in the model. The left cluster (L-cluster) is one tightly associated grouping of OTUs only loosely associated with OTUs 24, 25, 26, 27 and 28. This lack of association is noted in the phenograms: these populations are always more closely related to each other than to the remainder of the OTUs found in L-cluster. This is shown in both the correlation and distance phenograms by cluster 26-28 and OTUs 23, 24 and 25. The members of L-cluster appear to group closely in both phenograms.

The right group (R-cluster) appears as a widely scattered aggregate with no tight groupings. This is indicated in the loose subclusters of the correlation phenogram (29-33) and the distance phenogram (30-33 and 29-36).

The movement of OTU 37 from the large subcluster (1-18) of the correlation phenogram to an independent or intermediate position between subclusters 30-33 and 29-36 of the distance phenogram is explained by this figure. OTU 37 is an intermediate position between

Figure 4. Projections of the 37 OTUs onto the first three principal components based on a matrix of correlations among characters.



-10
-5
0
III
+5
+12
+6
II
0
-6
-12
-12
0
+12
+24
+36
I

the L-cluster and R-cluster when ploted in multidimensional space.

The cophenetic correlation coefficient between the correlation matrix and the phenogram generated from it is 0.705. This correlation is not particularly high, but represents 49.70% of the variation presented by the characters in the matrix. The coefficient between the distance matrix and the representative phenogram is 0.899 and presents 80.82% of the character variation.

Cophenetic correlation coefficient values between the correlation and distance matrices is -0.648 while the value calculated between the representative phenograms is -0.534. The negation of the correlation values is explained by the fact that OTUs with high correlation values are closely related and OTUs with low distance values are closely related.

CHAPTER IV

DISCUSSION

The clustering of OTUs 29, 30, 31, 32, 33, 34, 35 and 36 in all three analytic methods is of significance. These plants represent populations from the Gila National Forest of southern New Mexico. These populations were growing on the moist, upper slopes of the Black and Pinos Altos Ranges under the closed canopy of the mixed coniferous forest.

Subcluster 1-24 of the correlation phenogram (Figure 2) is an aggregation of populations from over the total range of *A. carruthii*. Several interesting associations of OTUs are to be found. Group 1-17 is composed of populations from the open plains of western Kansas and one (OTU 17) is from Caddo County, Oklahoma, growing under *Juniperus virginiana* L. The association of OTUs 19-20 is of particular interest because OTU 19 was collected in the dry foothills of the Pinos Altos Range, growing under *Juniperus deppeana*, and OTU 20 was collected in the Wichita Mountains of Oklahoma, growing under the canopy of *Quercus stellata*. OTU 19 was only a few miles removed from the location of group 29-33, yet it is morphologically more similar to a population growing under similar ecological conditions 550 air miles to the east.

The large grouping 11-37 contains one large closely related group (14-23) and three pairs of OTUs. This grouping of OTUs represents populations from the same approximate latitude across southern Colorado and Utah and northern Arizona, New Mexico and Texas. All of these populations, with exception of the Lipscomb County, Texas and Beaver County, Oklahoma populations (OTUs 15 and 23) were growing in open stands of pines on mountain slopes. The Texas and Oklahoma populations were however, collected from an open grassland.

OTU 18 is from the Davis Mountains of Trans Pecos region of southwestern Texas. This population appears to be disjunct from the distribution (Figure 1) of the species.

Subcluster 7-24 shows the correlation of populations from Coconino County, Arizona with populations of the same ecological habitat (scattered pine forest) in southeastern Utah (OTU 7) and New Mexico (OTUs 25 and 28). There is a very close correlation between one Arizona population (OTU 27) and the population collected in the grasslands of Union County, New Mexico. OTUs 19, 28, 29, 30 and 35 were all collected along a transect from the lower foothills of the Pinos Altos Mountains to the upper spruce-fir-pine belt. OTU 19, from the juniper covered foothills, clustered with OTU 20 (previous page). OTUs 29, 30, and 35 were at the upper end of the transect. OTU 28 occurred in an apparently intermediate ecological site on a dry mountain slope near the lower elevational extent of the coniferous forest.

The distance phenogram (Figure 3) shows the grouping of the Kansas populations in cluster 1-6 along with a northern New Mexico population of similar habitat and the foothill population from Grant County, New Mexico. The Caddo County, Oklahoma (OTU 17) and one Kansas population (OTU 4) have moved into a position showing greater relative distance between them. Cluster 7-10 appears nearly the same as in the correlation phenogram, grouping three populations from Coconino County, Arizona with the morphologically and ecologically similar population from Utah. OTUs 11 and 12 (from southern Colorado and northern New Mexico) again pair but this time showing more similarity to the Wichita Mountain population. The populations contained in cluster 14-21 maintain their close relationship in this analysis as in the previous method.

The remainder of the populations in cluster 1-28 show no definite patterns of clustering. The groupings are poor, as previously pointed out, and all the populations appear essentially random in their association.

The first three principal components of Figure 4 explain 34.59, 16.05 and 8.86 per cent of the total character variation. Principal component I (horizontal axis) is highly loaded (over 0.70) with characters concerning size and vegetative morphology. Leaf length, width and area, plant height, inflorescence length and width, length and number of heads on lower panicle branch and lower leaf pubescence all tend to aggregate the smaller plants with more compact panicles and smaller leaves into a tight cluster on the left and to scatter the larger plants with spreading panicles and large leaves in almost a linear fashion on the right.

Principal component II (axis into page) is mainly floral and achene characters, which are disk corolla length and width, ray stigma, style and corolla length and disk and ray achene length. Smaller character values are toward the front of the figure (negative axis values) and larger values toward the back (positive axis values). Separation of OTUs 24, 25, 26, 27 and OTU 28 (from the intermediate site in Grant County, New Mexico), from the L-cluster is due to reduced size of flowers and achenes. This difference, however, may be due to the immaturity of florets in these populations. OTU 37 (Creede, Colorado) shows a great difference in floral morphology from the members of the L-cluster and the R-cluster.

Principal component III (verticle axis) expresses bract length, length of the opaque area of the bract, degrees of panicle branching, number of heads per panicle and width of panicle. The character having the greatest weight on this component is the increase in total length and reduced size of the hyaline tip of bracts (positive axis values). The reduction in the number of heads per lower panicle branch is closely correlated to the reduction in the degrees of branching in the panicle and also has a positive component value. This component has little effect on the L-cluster, but shows a great deal of effect in separating the Gila National Forest populations and the Creede, Colorado population.

The populations from the Gila National Forest do not appear to be morphologically similar to any of the taxa listed in the synonymy of _A. carruthii_ by Keck (Table 1). Examination and comparison with the type of _A. neomexicana_ (NY) (placed under synonymy of _A. ludovicana_ ssp. _mexicana_ (Willd.) Keck) demonstrates these populations correspond to that segregate. These populations (OTUs 29, 30, 31, 32, 33, 34, 35 and 36) cluster together in a loose arrangement in each of the methods of analysis.

Similar comparison of collections, herbarium specimens and type specimens of A. wrightii (G), A. pringlei (G) and A. bakeri (NY) has not clarified the clustering of OTUs in the phenograms and three dimensional drawing. These populations tend to group together in an arrangement that appears to be a continuum from what is regarded as typical A. carruthii (type specimen unavailable) in Kansas to the typical A. wrightii in Utah and Arizona.

The Creede, Colorado population (OTU 37) most resembles A. bakeri. Both the sample population and the type collection are morphological anomalies, however, a taxonomic decision as to their status must await additional collections from Colorado.

The R-cluster from the mountains of southwestern New Mexico also presents a significant taxonomic difficulty. They are not tightly clustered, differing among themselves to the extent that they cannot be clearly distinguished satisfactorally from the L-cluster. Interestingly, the extreme variability of these OTUs is in spite of the fact that all occur in a limited geographical region and under similar ecological situations.

Keck (1946) considered A. neomexicana to be approaching A. carruthii (p. 452) while Hall and Clements (1923) considered it to be intermediate between A. vulgaris ssp. mexicana and A. vulgaris ssp. wrightii. A satisfactory solution cannot be attained until this group and the L-cluster are compared to A. ludoviciana ssp. mexicana.

LITERATURE CITED

Alexopoulos, C. J. and E. S. Beneke, 1952. Laboratory Manual for Introductory Mycology. Minneapolis, Minnesota, Burgess Publishing Co. pp. 199.

Blake, S. F., 1940. New Species and New Names Among Arizona Asteraceae. Jour. Wash. Acad. Sci. 30:467-472.

Britton, Nathaniel L. and Hon. Addison Brown, 1898. An Illustrated Flora of the Northern United States, Canada and the British Possessions. Charles Scribner's Sons, New York 3:466.

Carruth, James H., 1877. Centennial Catalogue of the Plants of Kansas. Trans. Kans. Acad. Sci. 5:40-59.

Cattell, R. B., 1952. Factor Analysis. New York, Harper and Bros.

Clausen, J., David D. Keck and William M. Hiesey, 1940. Experimental Studies in the Nature of Species. I. Effect of Varied Environments on Western North American Plants. Carn. Inst. of Wash. Publ. 520 pp. 452.

Coulter, John M., 1909. New Manual of Botany of the Central Rocky Mountains. American Book Company, New York. pp 565-570.

Crovello, T. J., 1969. Effects of Change of Characters and of Numbers of Characters in Numerical Taxonomy. Amer. Midl. Naturalist 81:68-86.

Estes, J. R., 1968. In: IOPB Chromosome Numbers Reports. Taxon 17: 101-103.

Estes, James R. and H. E. Ray, 1971. Chromosome Counts of Southwestern Species of Artemisia (in preparation).

Gates, Frank C., 1939. New Forms and Nomenclatorial Combinations in the Kansas Flora. Trans. Kans. Acad. Sci. 42:135-138.

Gray, A., 1883. Contribution to North American Botany. Proc. Amer. Acad. 19:48.

Greene, E. L., 1901. Plantae Bakerianae 3:31.

Greenman, M., 1904. Proc. Amer. Acad. 40:50.

Hall, Harvey M. and Frederic E. Clements, 1923. The Phylogenetic Method in Taxonomy. Carn. Inst. of Wash. Publ. 326 pp. 355.

Keck, David D., 1946. A Revision of the Artemisia vulgaris Complex in North America. Cal. Acad. of Sci. 55:421-468.

Osterhout, George E., 1898. New Plants from Colorado. Bull. Torr. Club 27:506-508.

Palmer, Ernest J. and Julian A. Steyermark, 1935. An Annotated Catalogue of the Flowering Plants of Missouri. Ann. Mo. Bot. Gard. 22: 676-677.

Robins, Jerome D. and Gary D. Schnell, 1971. Skeletal Analysis of the Ammodramas-Ammospiza Grassland Sparrow Complex: A Numerical Taxonomic Study. Auk 88:567-590.

Rohlf, F. J., 1968. Sterograms in Numerical Taxonomy. Syst. Zool. 17:246-255.

Rydberg, Per Axel, 1916. Carduales. North American Flora 34:244-285.

Schnell, Gary D., 1970a. A Phenetic Study of the Suborder Lari (Aves) I. Methods and Results of Principal Components Analysis. Syst. Zool. 19:35-37

________. 1970b. A Phenetic Study of the Suborder Lari (Aves) II. Phenograms, Discussion and Conclusions. Syst. Zool. 19:264-302.

Snow, R., 1963. Alcoholic Hydrochloric Acid - Carmine as a Stain for Chromosomes in Squash Preparations. Stain Tech. 38:9-13.

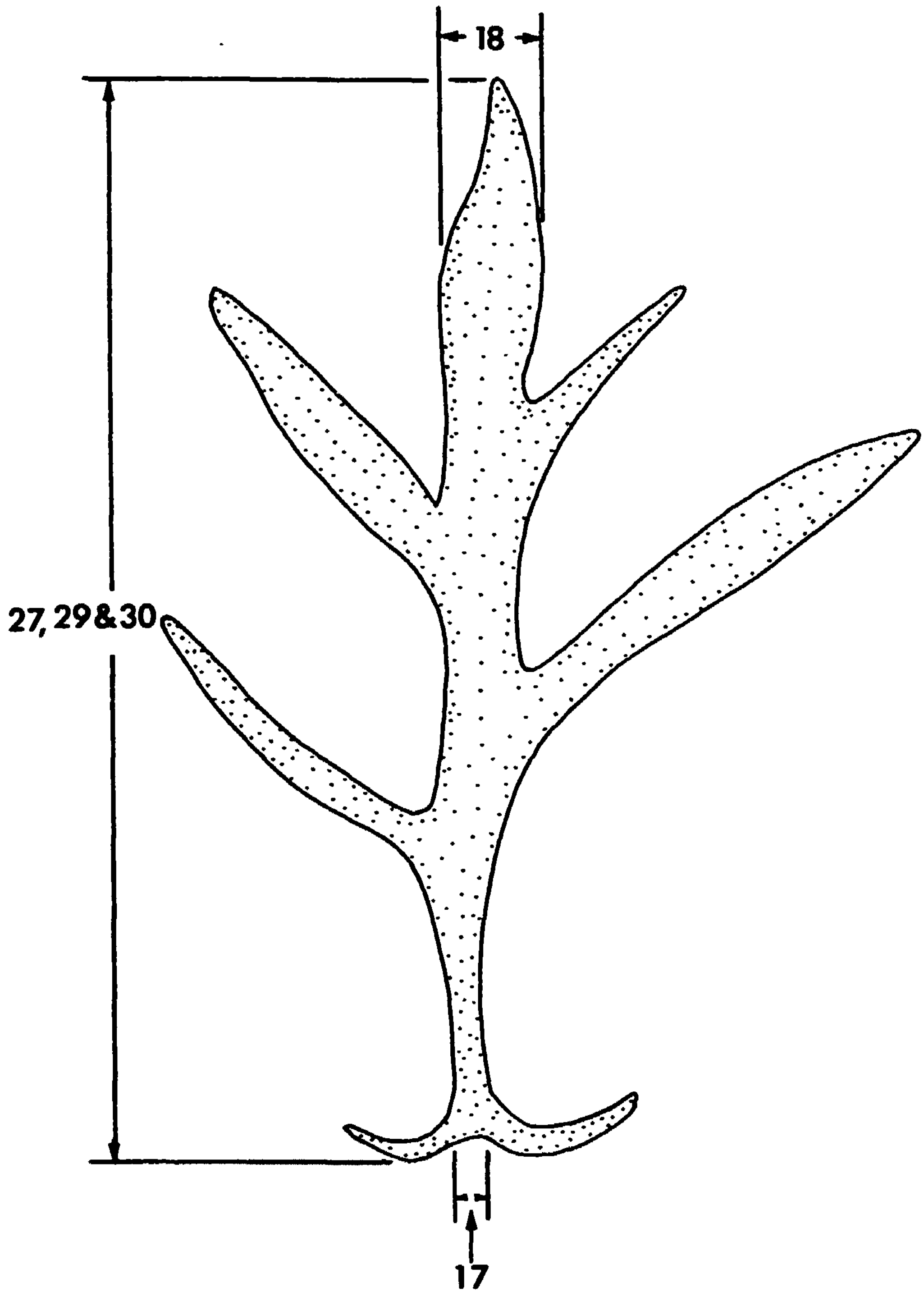
Sokal, R. R., and F. J. Rohlf, 1962. The Comparison of Dendrograms by Objective Methods. Taxon 11:33-40.

Sokal, R. R. and P. H. A. Sneath, 1963. Principles of Numerical Taxonomy. San Francisco, W. H. Freeman and Co.

Steyermark, Julian A., 1938. Validation of Combinations in Palmer and Steyermark's Annotated Catalogue of the Flowering Plants of Missouri. Rhodora 40:131-134.

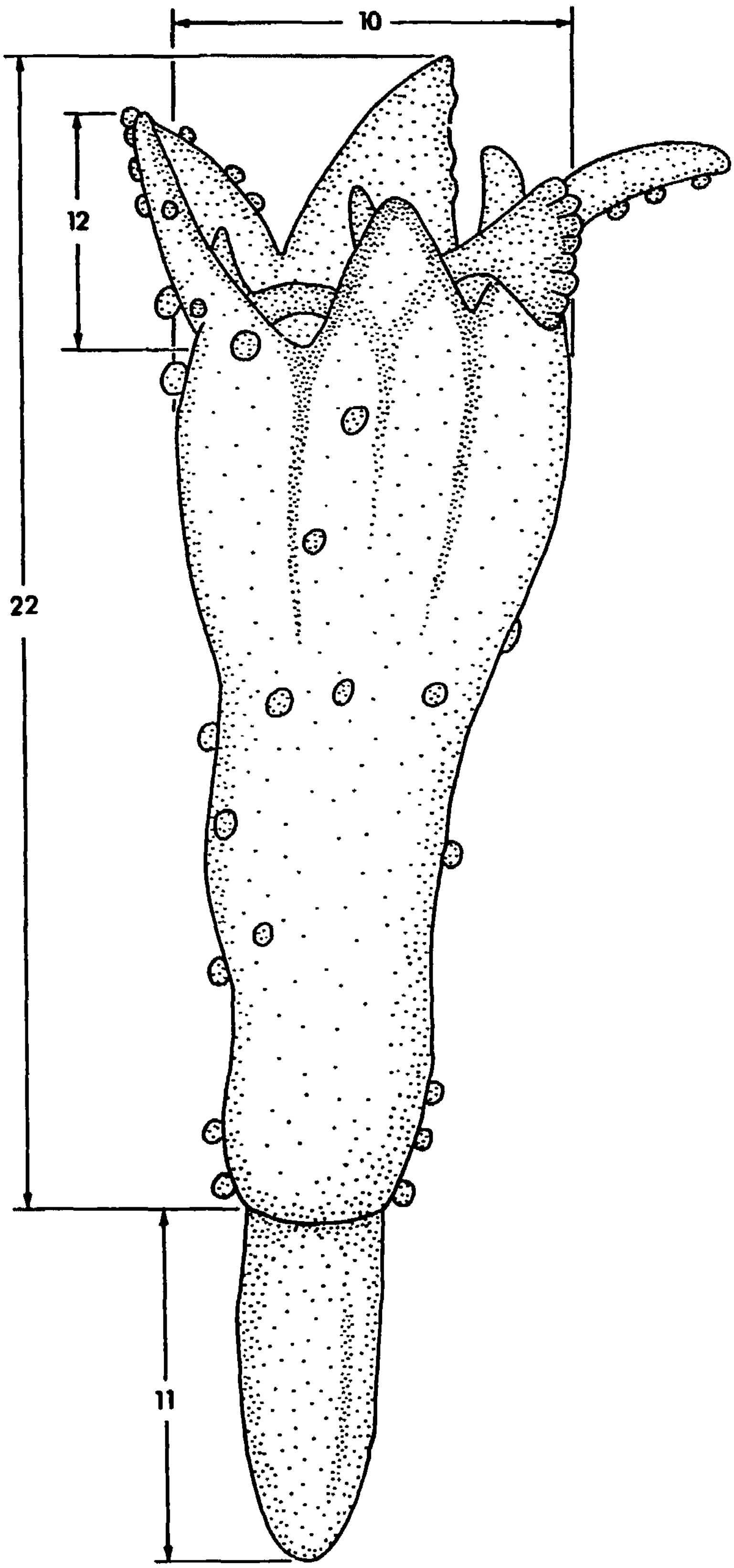
Appendix 1. Drawing A shows how leaf characters 17, 18, 27, 29 and 30 were measured. Measurements 17 and 18 were to the nearest .015 mm and 27, 29 and 30 to the nearest mm.

A



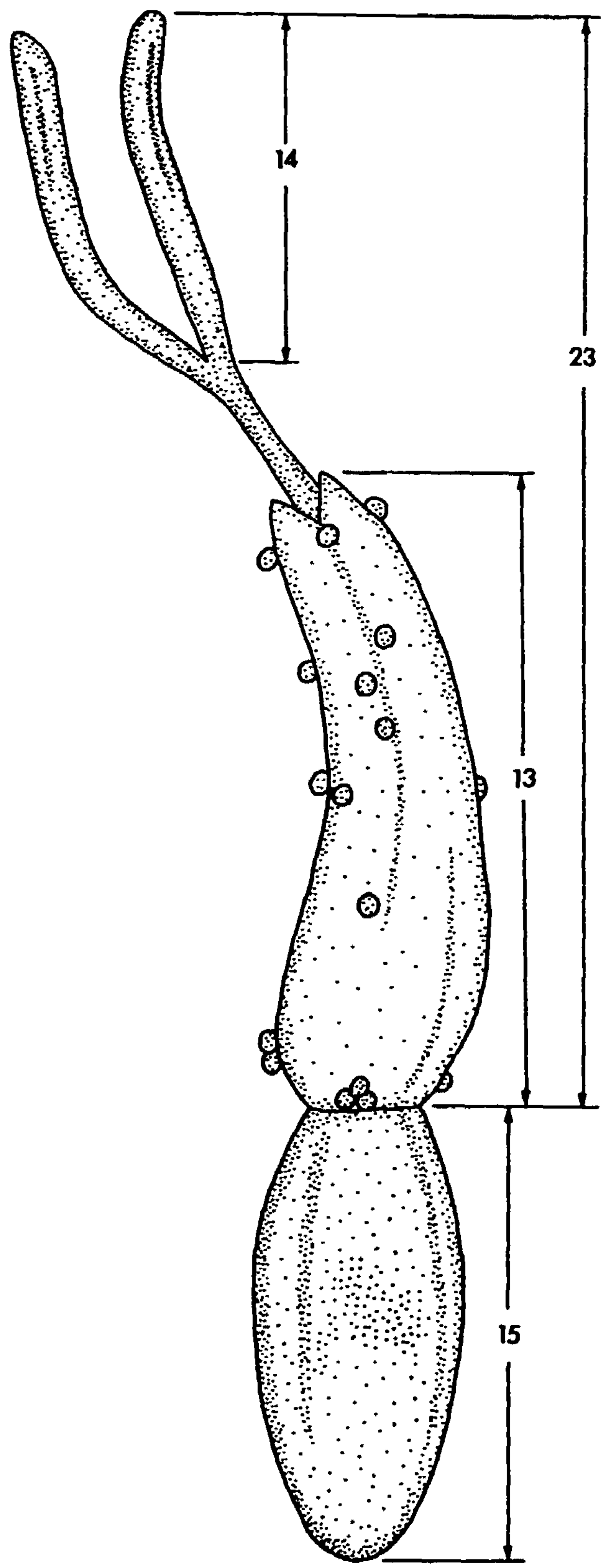
Appendix 1 (Continued). Drawing B shows how disk floret characters 10, 11, 12 and 22 were measured. All measurements were to the nearest .015 mm.

B



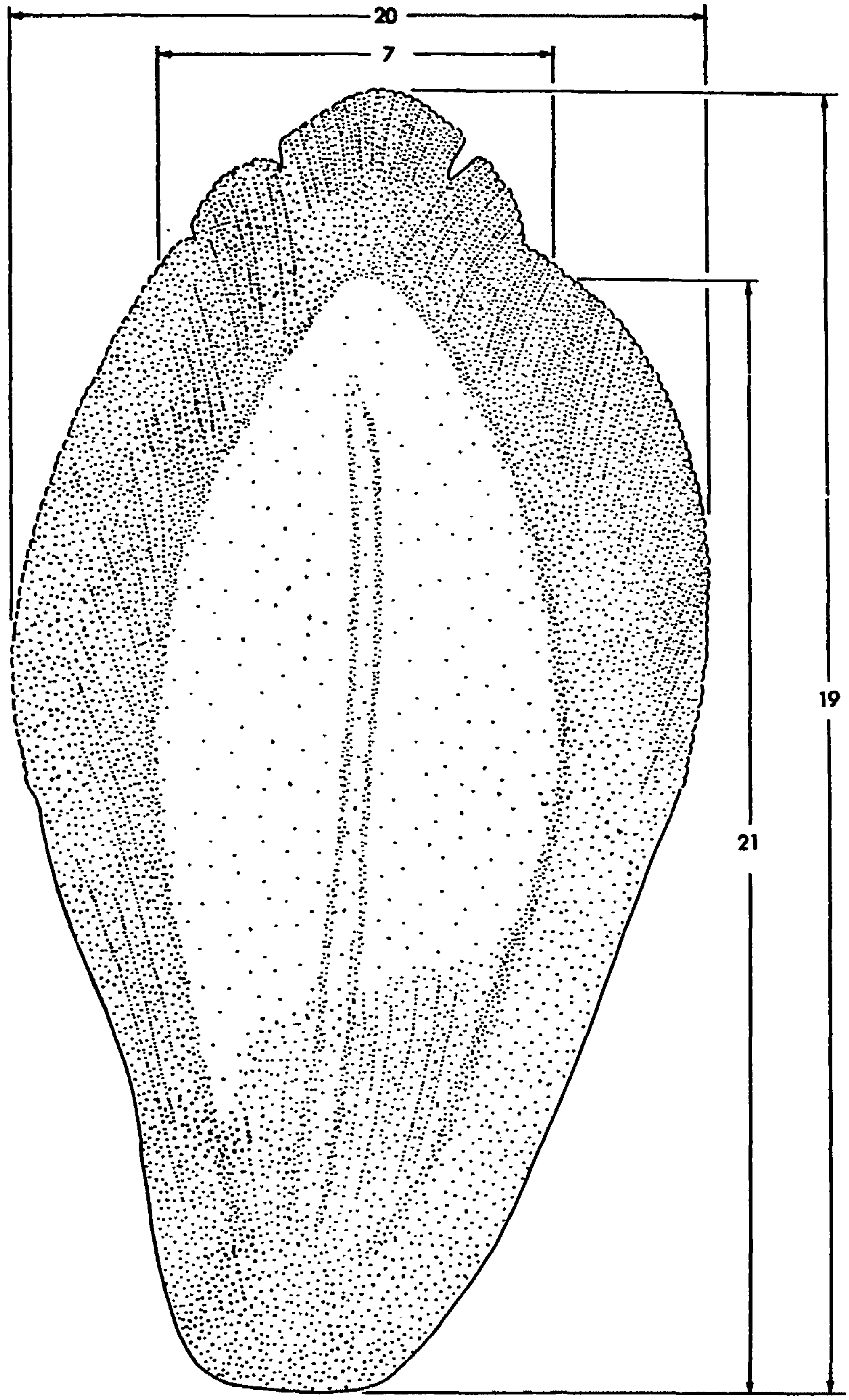
Appendix 1 (Continued). Drawing C shows how ray floret characters 13, 14, 15 and 23 were measured. All measurements were to the nearest .015 mm.

C



Appendix 1 (Continued). Drawing D shows how bract characters 7, 19, 20 and 21 were measured. All measurements were to the nearest .015 mm.

D



Appendix 2. Populations of Artemisia carruthii collected.

Collection Number	Location
1000	Oklahoma: Caddo Co. 8 miles west of Cogar.
1004	Oklahoma: Caddo Co. 8 miles west and 1.2 miles north of Cogar.
1006	Oklahoma: Caddo Co. 8 miles west and 2.3 miles north of Cogar.
1008	Oklahoma: Caddo Co. 8 miles west and 2.0 miles north of Cogar.
1011	Oklahoma: Canadian Co. Canyon wall above the Methodist Campground.
1022	Oklahoma: Beaver Co. 2.8 miles east and .7 mile south of Slapout.
1024	Oklahoma: Texas Co. 8.4 miles northwest of Guymon.
1028	New Mexico: Union Co. 7.4 miles east of Mt. Dora.
1029	New Mexico: Union Co. 8.4 miles east of Des Moines.
1031	New Mexico: Colfax Co. 12 miles north of Springer.
1036	New Mexico: San Miguel Co. 10.4 miles north of Pecos.
1037	New Mexico: McKinley Co. 8 miles north and 13.4 miles west of Gallup.
1039	Arizona: Coconino Co. 3.5 miles east of Grand View Overlook, Grand Canyon.
1040	Arizona: Coconino Co. 2.6 miles north of Flagstaff.

Appendix 2 (Continued)

Collection Number	Location
1041	Arizona: Coconino Co. 16.7 miles north of Sedona.
1047	New Mexico: Grant Co. 11.8 miles north of Silver City.
1048	New Mexico: Grant Co. 14.3 miles north of Silver City.
1049	New Mexico: Grant Co. 13.3 miles north of Silver City.
1050	New Mexico: Grant Co. 12.8 miles north of Silver City.
1052	New Mexico: Grant Co. 3.2 miles east of Santa Rita.
1053	Oklahoma: Caddo Co. 8 miles west and 1.2 miles north of Cogar.
1055	Oklahoma: Canadian Co. Canyon wall above the Methodist Campground.
1066	Texas: Jeff Davis Co. .3 miles south of McDonald Observatory entrance.
1068	Texas: Jeff Davis Co. .1 mile west of McDonald Observatory entrance.
1069	Texas: Jeff Davis Co. 11.4 miles west of McDonald Observatory entrance.
1074	New Mexico: Grant Co. 5.4 miles east of Emory Pass.
1075	New Mexico: Grant Co. Emory Pass.
1076	New Mexico: Grant Co. 7.3 miles west of Emory Pass.

Appendix 2 (Continued)

Collection Number	Location
1077	New Mexico: Grant Co. 8.8 miles west of Emory Pass.
1078	New Mexico: Grant Co. 9.5 miles west of Emory Pass.
1079	New Mexico: Grant Co. 14 miles north and 6 miles east of Silver City on Signal Peak.
1080	New Mexico: Grant Co. 12.8 miles north of Silver City.
1081	New Mexico: Grant Co. 11.5 miles north of Silver City.
1082	New Mexico: Grant Co. 4.6 miles north of Silver City.
1085	Arizona: Coconino Co. 2 miles east of Flagstaff.
1086	Arizona: Coconino Co. 6.5 miles east on East Rim Road, Grand Canyon.
1088	Arizona: Coconino Co. Hull Tanks, Kaibab National Forest.
1089	Arizona: Coconino Co. 5 miles east of Jacob Lake.
1090	Arizona: Coconino Co. 4 miles west of Jacob Lake.
1091	Utah: Kane Co. 7 miles west of Long Valley Junction.
1092	Utah: Kane Co. 10 miles west of Long Valley Junction.
1093	Utah: Sevier Co. 12 miles northeast of Fremont on Elkhorn Mountain.

Appendix 2 (Continued)

Collection Number	Location
1094	Utah: San Juan Co. 4.5 miles east of La Sal.
1095	Utah: San Juan Co. 5 miles east and 7 miles north of La Sal on Mt. Peale.
1096	Utah: San Juan Co. 4 miles west of Monticello on Abajo Peak.
1097	Colorado: LaPlata Co. 5 miles south of Hesperus.
1099	Colorado: Archuleta Co. 25 miles west of Pagosa Springs.
1100	Colorado: Archuleta Co. 8 miles south and 2 east of Pagosa Springs.
1101	Colorado: Mineral Co. 5 miles east of Wagon Wheel Gap.
1102	Colorado: Mineral Co. 2 miles north of Creede.
1103	New Mexico: Colfax Co. East of Red River, 7 miles south of Colfax-Taos county line.
1105	New Mexico: Colfax Co. .8 mile east of Springer.
1106	Oklahoma: Commanche Co. 3 miles south of Wichita Mountain Wildlife Refuge Headquarters.
1108	Kansas: Ford Co. 6.3 miles north of Ford.
1109	Kansas: Hodgeman Co. 3 miles south of Jetmore.
1110	Kansas: Ness Co. 5 miles south of Ness City.

Appendix 2 (Continued)

Collection Number	Location
1111	Kansas: Lane Co. 1.4 miles east and 1.8 miles sourth of Dighton.
1112	Kansas: Grove Co. 23 miles north of Dighton.
1113	Kansas: Logan Co. 21 miles north of Scott City.
1114	Kansas: Scott Co. 10 miles north of Scott City.
1115	Kansas: Finney Co. 6 miles north of Garden City.
1116	Kansas: Gray Co. 5 miles north and 2 miles east of Montezuma.
1117	Kansas: Meade Co. 9 miles north of Meade.
1118	Texas: Lipscomb Co. 13 miles south of Booker.

Appendix 3. List of herberia used in study.

Herbarium	Location	Number of Specimens
University of Arizona (ARIZ)	Tucson, Arizona	74
Arizona State University (ASC)	Tempe, Arizona	18
Brigham Young University (BRY)	Provo, Utah	8
*California Academy of Science (CAS)	San Francisco, California	17
*University of California (UC)	Berkeley, California	60
*Carnegie Institute of Washington (CI)	Stanford, California	3
University of Colorado (COLO)	Boulder, Colorado	39
Gray Herbarium (GH)	Cambridge, Massachusetts	39
University of Kansas (KANU)	Lawrence, Kansas	14
Kansas State University (KSC)	Manhattan, Kansas	86
Missouri Botanical Garden (MO)	St. Louis, Missouri	111
University of New Mexico (UNM)	Albuquerque, New Mexico	39
New Mexico State University (NMC)	Las Cruces, New Mexico	77
Northern Arizona University (ASU)	Flagstaff, Arizona	8
*New York Botanical Garden (NY)	Bronx Park, New York	176

Appendix 3 (Continued)

Herbarium	Location	Number of Specimens
*Philadelphia Academy (PH)	Philadelphia, Pennsylvania	20
*Rancho Santa Ana Botanical Garden (RSA) and	Claremont, California	33
Herbarium of Pomona College (POM)	Claremont, California	
Southern Methodist University (SMU)	Dallas, Texas	25
*Dudley Herbarium (DS)	Stanford, California	26
University of Texas (TEX)	Austin, Texas	148
Texas A&M University (TAES)	College Station, Texas	8
Texas Tech University (TTC)	Lubbock, Texas	20
University of Utah (UT)	Salt Lake City, Utah	10
Utah State University (UTC)	Logan, Utah	12
*University of Wyoming (RM)	Laramie, Wyoming	60
Herbario Nacional del Instituto de Biologia (MEXU)	Mexico, D. F.	15

*Denotes herbaria containing material examined by Keck (1946).