THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

A NUMERICAL STUDY OF LIATRIS SER. SQUARROSAE

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

BY

ARCHIE DWIGHT THOMAS

Norman, Oklahoma

1974

A NUMERICAL STUDY OF LIATRIS SER. SQUARROSAE

APPROVED BY

DISSERTATION COMMITTEE

ACKNOWLEDGMENT

The author wishes to express his appreciation to those who provided assistance and advice during this study:

Dr. George J. Goodman, the author's major professor, who offered many helpful suggestions and comments as well as providing assistance even to the point of the use of a favorite automobile.

The dissertation committee, Dr. Norman H. Boke, Dr. James R. Estes, Dr. Harry E. Hoy, and Dr. Paul G. Risser, whose comments during the preparation of the manuscript were of immense help.

The curators of the herbaria used for the use of specimens and facilities.

The author's family, especially Judy, who helped in all phases of the work from collecting and pressing plants to copying the manuscript as well as providing encouragement to continue.

Haskell Indian Junior College for the support of fellow faculty members and students and for assistance in terms of released time, travel, and materials.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF ILLUSTRATIONS

A NUMERICAL STUDY OF *LIATRIS* SER. *SQUARROSAE*

CHAPTER I

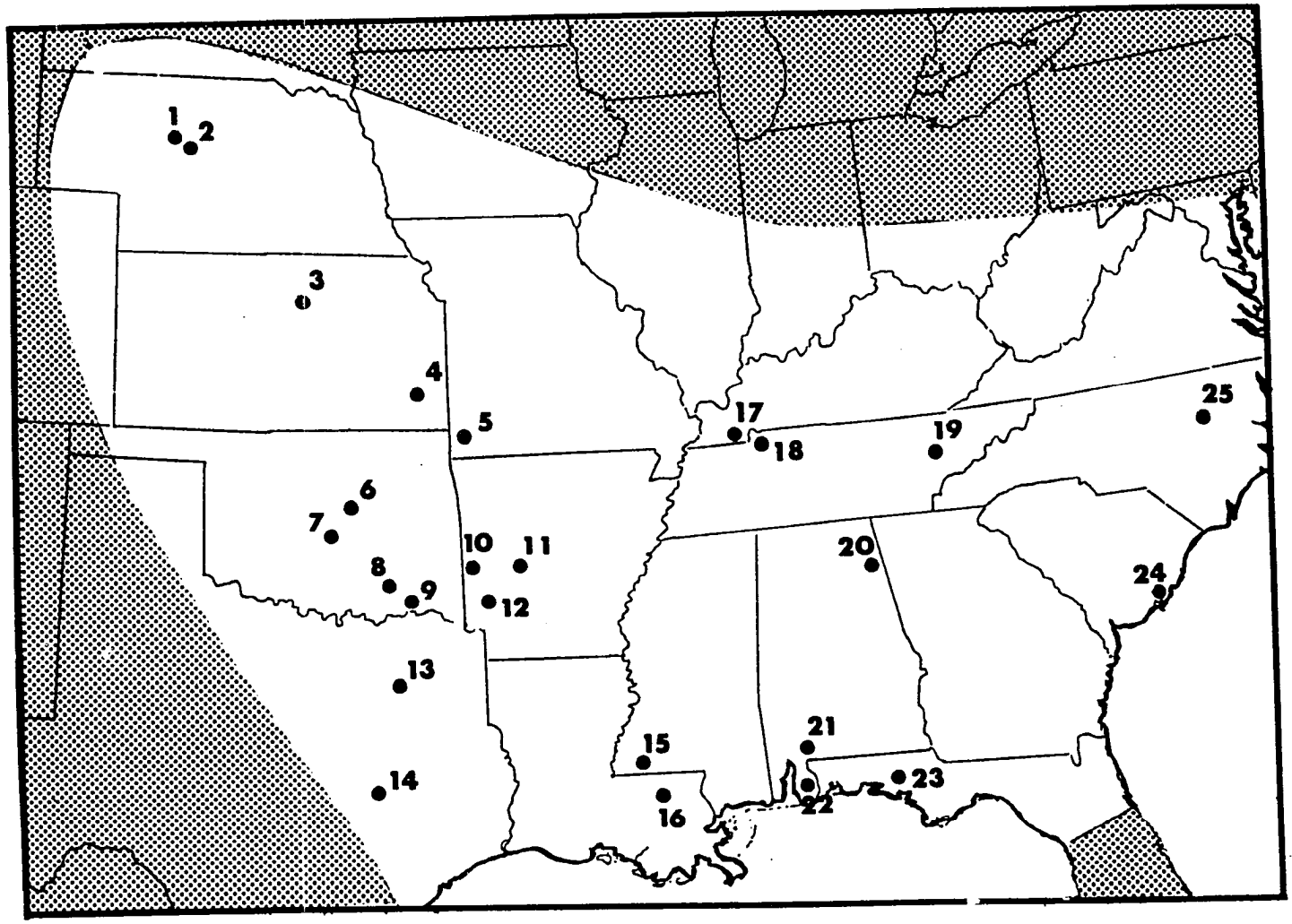
INTRODUCTION

The *Squarrosae* series of *Liatris* has been the subject of much taxonomic study and disagreement. Much of the confusion is due to the wide geographic range and the resulting ecological and morphological variation. The series is restriced to the southeastern two-thirds of the United States (Fig. 1). Habitats range from prairies to coastal forests with the plants usually growing in large populations on disturbed sites that have well-drained sandy or rocky soils.

The taxonomy of the series dates back to 1753 when Linnaeus recognized *Serratula squarrosa* in *Species Plantarum*. He referred to earlier descriptions, the earliest of which was in Morrison's *Plantarum Historia Universalis* in 1680. The generic nomenclature was delineated by Gaiser (1946) in the monograph of the genus *Liatris* with transfers from *Serratula* to *Laciniaria* by Hill in 1762 and to *Liatris* by Michaux in 1803.

Torrey and Gray (1841) added three varieties, *floribunda*, *compacta*, and *intermedia*, collected from the interior of the United States complementing the original collections from the Atlantic coastal regions. Gray (1884) then included the varieties *floribunda* and

Figure 1. The Range of Liatris ser. Squarrosae. The shaded areas represent the areas excluded from the range, and the numbered dots represent the collections used in this study.


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25

compacta in the typical variety retaining only the variety intermedia as a separate taxon.

"Compacta" was then reintroduced and "intermedia" placed in synonomy by Rydberg (1931) with his descriptions of the materials from the western parts of the range of the series. He added three species to the taxonomy of the series: L. compacta, L. glabrata, and L. hirsuta. However, he stated that it was a matter of personal judgment that these were species rather than varieties of L. squarrosa. Two of these species were questioned when Gates (1940) published the collections in Kansas as L. squarrosa hirsuta and L. squarrosa glabrata.

The southern plants also provided variation which was noted with the descriptions of Laciniaria squarrosa alabamensis by Alexander in Small's Manual of the Southeastern Flora (1933) and Liatris squarrosa var. gracilenta by Gaiser (1946).

Based on the extensive, presumed hybridization, Gaiser (1946) considered the entire series to be one species, L. squarrosa, with six varieties: typica, gracilenta, alabamensis, hirsuta, compacta, and glabrata. This treatment was quickly questioned when Shinners (1951) reestablished the species L. glabrata and L. hirsuta and transferred the variety alabamensis to L. glabrata. He stated that he made these changes with some hesitation since the relationships among the taxa were close.

Thus with all of the changes in the taxonomy of the series, there are two problems that are evident. One is that the identity of the groups is in question, and the second is that the relationships among these groups is unclear.

The purpose of this study is to identify the groups that exist within the series and to investigate the affinities among these groups. The outcome of this study is to be a taxonomy based on the observations.

CHAPTER II

MATERIALS AND METHODS

Numerical methods were selected for this study as an attempt to eliminate some of the personal bias that has been the history of the taxonomy of the series. The study was made with new collections, and populations were utilized as the taxonomic units. Data were taken from fresh material as well as from preserved specimens.

Specimens from a number of herbaria (Appendix I) were examined to determine the geographic range of the Squarrosae and to determine the extent of the variation that exists. From these specimens, collection sites were selected to sample the geographic and variation ranges (Table I). Twenty-five populations were used in the study.

To avoid collecting only the most conspicuous plants, population collections were made systematically by establishing a transect across the population with the plant closest to the left foot of the collector on each step being the plant collected. The sizes of the populations varied, so the number of plants collected varied. In small populations a second transect was made parallel to the first to include more material. Since most of the populations were found along roadsides, they were usually linear with an average length of about 25 m.

Soil samples were taken from the holes dug in collecting living plants and were dried and sieved through a USDA Sieve Set to determine the soil particle size. Additional habitat data were obtained from The

TABLE I

POPULATIONS USED IN THIS STUDY

Population Number	Location	Habitat
1	Nebraska: Thomas Co. 9 miles west of Thedford.	South-facing slope on a sand hill above the Middle Loup River.
2	Nebraska: Thomas Co. 15 miles south of Thedford.	North-facing slope of sand hill above the Dismal River.
3	Kansas: Ottawa Co. 3.5 miles east of Bennington.	Sandy roadside along plowed fields.
4	Kansas: Neosho Co. 2.8 miles south of Thayer.	Limestone outcrop along a roadside in prairie.
5	Missouri: Newton Co. .25 miles east of highway I-44 on Reddings Mill Road.	Limestone cliff, oak-hickory forest.
6	Oklahoma: Lincoln Co. 1.5 miles east of Meeker.	Grassy area with sandstone outcrops.
7	Oklahoma: Cleveland Co. 2 miles east and .2 miles south of Franklin.	Open area in oak forest where pipeline disturbance was evident, sandy soils.
8	Oklahoma: Atoka Co. 3 miles west of the intersection of highways US 69 and Ok 3.	Rocky hillside, limestone.

TABLE I--(Continued)

Population Number	Location	Habitat
9	Oklahoma: Choctaw Co. .5 miles east of the intersection of highways US 70 and US 271.	Sandy roadside with sandstone outcrops.
10	Arkansas: Polk Co. Top of Rich Mountain, 2 miles east of Wilhelmena State Park.	Rocky, limestone hilltop, oak-hickory forest.
11	Arkansas: Garland Co. Top of West Mountain in Hot Springs.	Rocky, limestone hilltop, oak-hickory forest.
12	Arkansas: Pike Co. 4.2 miles north of the intersection of highways 19 and 26.	Rocky, steep hillside in pine forest.
13	Texas: VanZandt Co. 3 miles east of Fruitvale.	Sandy roadside between highway and railroad track.
14	Texas: Brazos Co. 6.4 miles southeast of College Station.	Rocky area on and around pond dam.
15.	Mississippi: Amite Co. 1.4 miles north of Coles.	Roadside in pine forest, rocky.
16.	Louisiana: Tangipahoa Pa. .25 miles south of Rt. 22 on Ridgell road in Ponchatoula.	Roadside in pine forest, sandy.
17.	Kentucky: Calloway Co. 2.3 miles southeast of New Concord on Rt. 121.	Rocky roadside in oak-hickory forest.

TABLE I--(Continued)

Population Number	Location	Habitat
18	Tennessee: Stewart Co. 16.6 miles southeast of Dover on Rt. 49.	Rocky roadside in oak-hickory forest.
19	Tennessee: Knox Co. 1.7 miles east of Rt. 441 on Gov. John Sevier Highway in Knoxville.	Rocky roadside in oak-hickory forest.
20	Alabama: Cherokee Co. 5.4 miles north of Piedmont.	Sandy roadside in oak forest at base of a high hill.
21	Alabama: Baldwin Co. 6.4 miles east of Bay Minette.	Rocky roadside in pine forest.
22	Alabama: Mobile Co. 2 miles south of Mon Louis.	Roadside in pine forest, sandy soil, very near coast.
23	Florida: Washington Co. 2 miles south of Chipley.	Rocky, sandy roadside in pine forest.
24	South Carolina: Charleston Co. 2.6 miles south of South Santee River on Rt. US 17.	Rocky, sandy roadside in pine forest, very near coast.
25	North Carolina: Wake Co. 1.1 mile southeast of Morrisville on US 54.	Rocky roadside in oak-hickory forest.

National Atlas, (United States Department of the Interior, 1970). Live plants were transplanted to a garden in Lawrence, Kansas, to determine the influence of the environment on the characters used in the study. Several of the sites were visited again two years after the initial collections had been made to collect additional material for use in evaluating the characters.

Of the various measurements and observations on the preserved material, the fresh material, and the habitat, fifty-five unit characters were finally used in the study (Table II). The characters used were the ones that showed more variation among the populations throughout the range than within the populations. Characters that were not constant in the collections from the same population at different times or from the same population grown in the garden were eliminated from the study. The measurements from all of the plants collected in each population were averaged to establish the population as the Operational Taxonomic Unit (OTU) as described by Sokal and Sneath (1963).

The data were coded into two-state characters by arranging the raw measurements into sequences and making separations into the two states at points where there were natural breaks in the data. If several groups were identified, the data were divided into as many unit characters as there were groups as suggested by Sokal and Sneath (1963).

Each population was compared with every other population to determine the number of similar characters and the number of characters on which comparison could be made. Similarity coefficients were then calculated by using the Simple Matching Coefficient of Sokal and Michener (1958):

TABLE II

CHARACTERS USED IN THIS STUDY

Character Number	Character Description*	Range of Variation	Coding, + Means
1	Plant height	25 - 103 cm.	Greater than 56 cm.
2	Plant height	25 - 103 cm.	Greater than 47 cm.
3	Number of stalks per plant	1 - 40 stalks	Greater than 3
4	Number of heads per stalk	1 - 73 heads	Greater than 13.33
5	Number of heads per stalk	1 - 73 heads	Greater than 6.67
6	Leaf density	0.45 - 1.39/cm.	Greater than 1.03
7	Leaf density	0.45 - 1.39/cm.	Greater than 0.77
8	Corm diameter	15 - 51 mm.	Greater than 40 mm.
9	Leaf thickness		Only midvein prominant
10	Length of lower leaves	50 - 241 mm.	Greater than 117 mm.
11	Length of upper leaves	20 - 78 mm.	Greater than 49 mm.
12	Width of lower leaves	2 - 10 mm.	Greater than 5 mm.

*Discussion about measurement of characters in Appendix II.

TABLE II--(Continued)

Character Number	Character Description	Range of Variation	Coding, + Means
13	Width of upper leaves	1 - 8 mm	Greater than 4 mm.
14	Pubescence type		Long individual hairs
15	Amount of pubescence	0 - 43	Greater than 32.99
16	Amount of pubescence	0 - 43	Greater than 22
17	Amount of pubescence	0 - 43	Greater than 11
18	Amount of pubescence	0 - 43	Greater than 0
19	Length of terminal head	13.5 - 24 mm.	Greater than 21.5 mm.
20	Length of terminal head	13.5 - 24 mm.	Greater than 18.5 mm.
21	Length of terminal head	13.5 - 24 mm.	Greater than 15.5 mm.
22	Width of terminal head	6.5 - 16 mm.	Greater than 14.4 mm.
23	Width of terminal head	6.5 - 16 mm.	Greater than 11.99 mm.
24	Width of terminal head	6.5 - 16 mm.	Greater than 9.4 mm.
25	Phyllary curvature	0 - 3	Greater than 2.99
26	Phyllary curvature	0 - 3	Greater than 1.99
27	Phyllary curvature	0 - 3	Greater than 0.99

TABLE II--(Continued)

Character Number	Character Description	Range of Variation	Coding, + Means
28	Color of stem	0 - 2	Greater than 1
29	Color of phyllaries	0 - 2	Greater than 1
30	Color of phyllaries	0 - 2	Greater than 0.5
31	Length of phyllary tip	0.5 - 18 mm.	Greater than 2 mm.
32	Width of phyllary tip	0.5 - 5 mm.	Greater than 2 mm.
33	Phyllary shape	Lanceolate - mucronate	Lanceolate
34	Phyllary shape		Tip lanceolate
35	Phyllary margin	Callose - membranous	Callose
36	Stem rigidity	36 - 74	Greater than 64.99
37	Stem rigidity	36 - 74	Greater than 54.99
38	Stem rigidity	36 - 74	Greater than 44.99
39	Pappus length	6 - 14 mm.	Greater than 11 mm.
40	Pappus length	6 - 14 mm.	Greater than 8 mm.
41	Corolla tube length	7 - 16 mm.	Greater than 13 mm.

TABLE II--(Continued)

Character Number	Character Description	Range of Variation	Coding, + Means
42	Corolla tube length	7 - 16 mm.	Greater than 9 mm.
43	Corolla tube length	7 - 16 mm.	Greater than 3.99 mm.
44	Style length	12 - 33 mm.	Greater than 28.99 mm.
45	Style length	12 - 33 mm.	Greater than 22.99 mm.
46	Style length	12 - 33 mm.	Greater than 16.99 mm.
47	Length of style branches	6 - 17 mm.	Greater than 12 mm.
48	Length of style branches	6 - 17 mm.	Greater than 8 mm.
49	Length of stigmatic lines	1.5 - 7 mm.	Greater than 5 mm.
50	Length of stigmatic lines	1.5 - 7 mm.	Greater than 2 mm.
51	Soil particle size		Greater than .002 mm.
52	Average amount of sunlight in growing season	1520 - 1810 hr.	Greater than 1700 hr.
53	Average frost-free period length	145 - 270 days	Greater than 225 days
54	Precipitation/Evaporation	0.31 - 1.02 in.	Greater than .70 in.
55	Precipitation/Evaporation	0.31 - 1.02 in.	Greater than .50 in.

$$S_{ab} = \frac{\text{Number of matches in A and B}}{\text{Number of characters compared}} .$$

"A" and "B" represent the two populations being compared. The values derived from these calculations were compiled in a matrix of OTU's for study.

Elementary cluster analysis as described by Sokal and Sneath (1963) was used to determine the groupings of the populations. This technique involved drawing lines connecting the populations represented in a geographic arrangement as the level of similarity was lowered. The major reasons that this clustering method was selected was that it showed the formation and growth of the clusters on a population by population basis as well as the linkages that formed when the clusters began to overlap. Thus it was possible to study the associations that each cluster formed with every other cluster.

The similarity values were rounded to two figures, then in the cluster analysis, 0.01 as the smallest unit of difference among the values was used as the interval for the clustering. Later 0.04 was selected by studying the series of phenograms as the largest interval that described the formation and growth of the clusters. The levels of similarity that described varieties and species were selected at points where no additions had been observed for several successive intervals.

An average similarity value was calculated for each cluster to measure the cohesiveness of the clusters, and average values were calculated between clusters to measure the affinities of the clusters for each other.

A description was written for each cluster based on the measurements made, and this was compared with the descriptions of established taxa. The herbarium material was reclassified with all specimens being placed in one of the clusters, and new distribution maps were drawn.

CHAPTER III

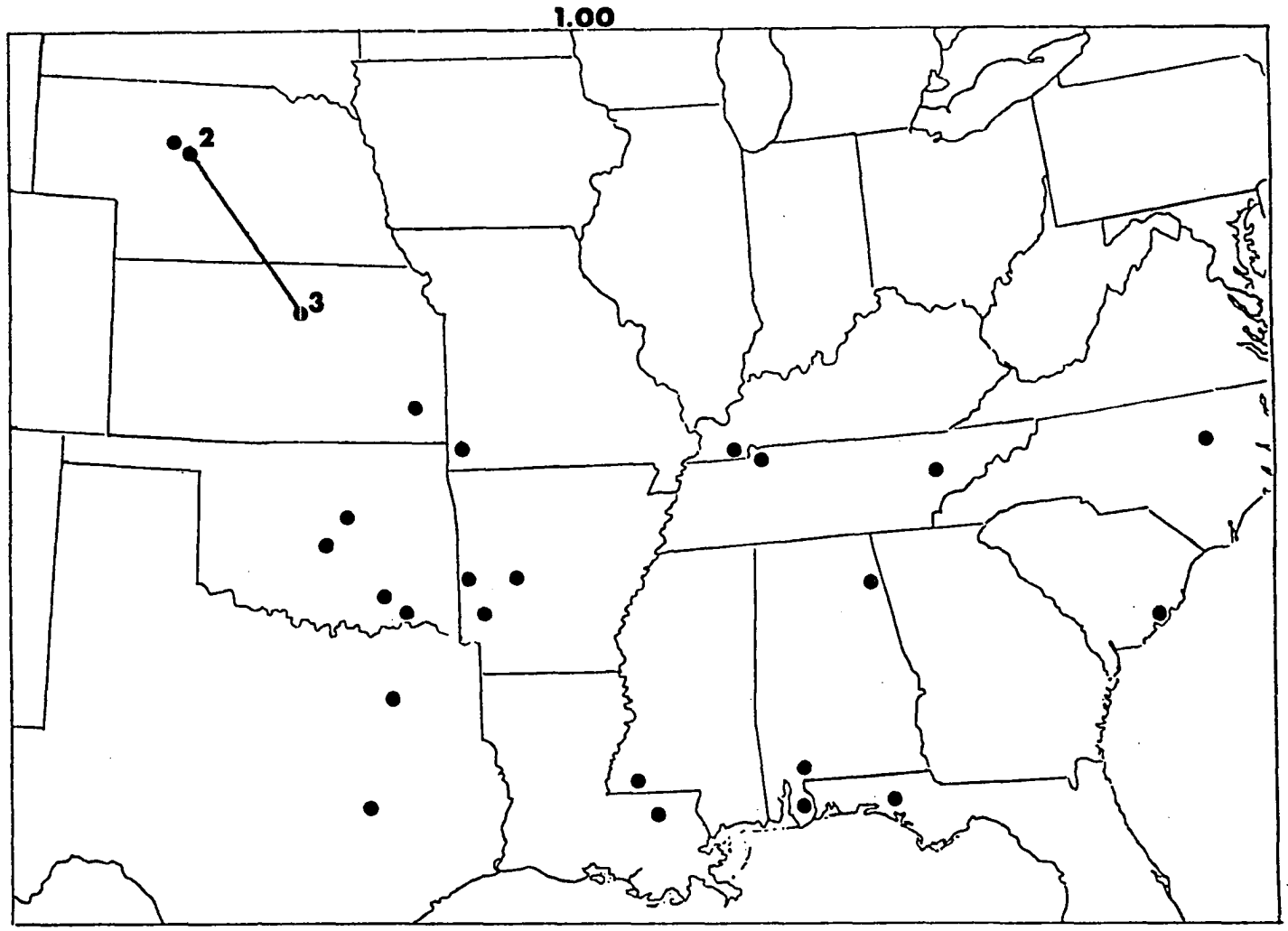
RESULTS

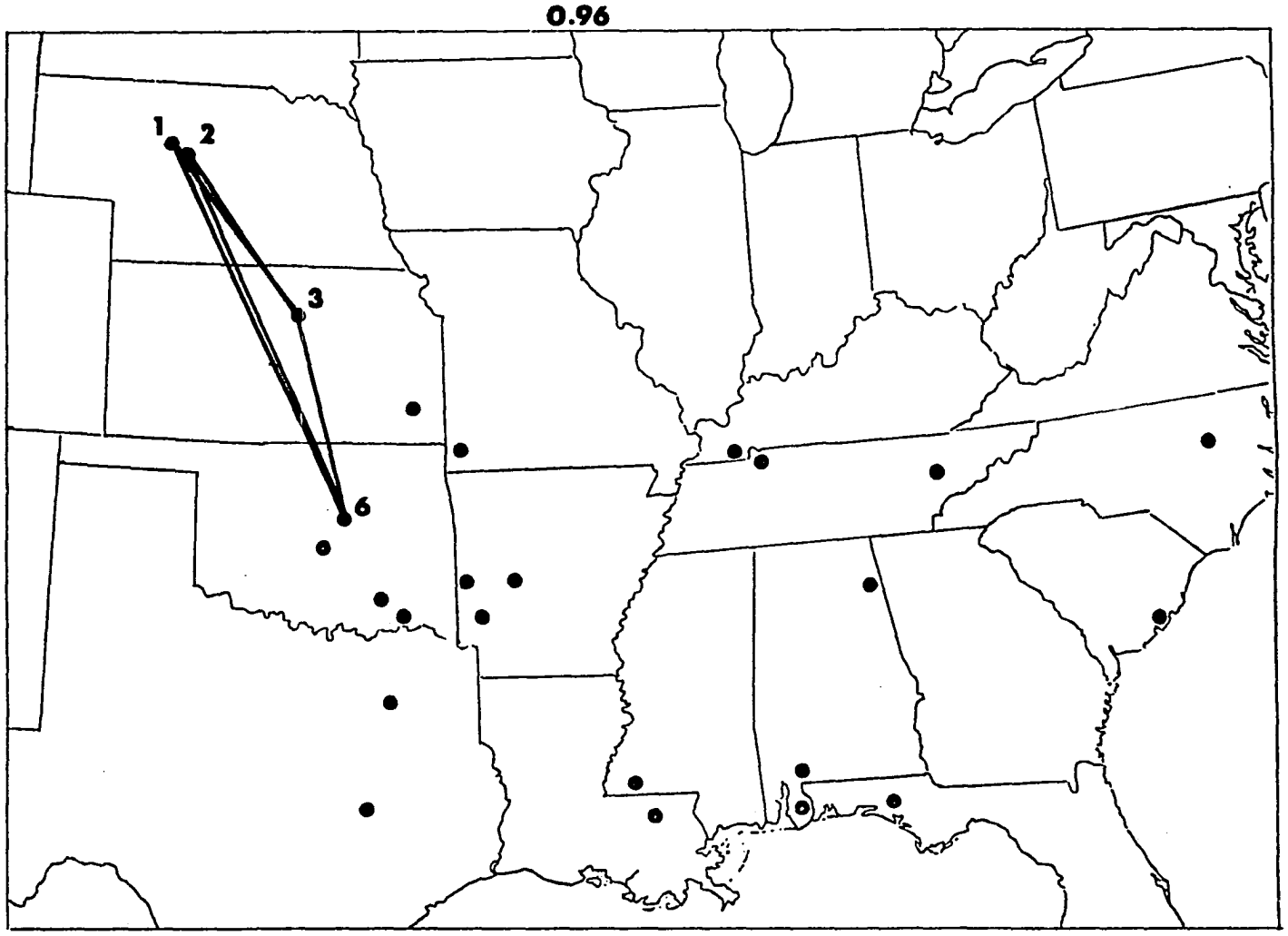
The calculations of similarity coefficients resulted in a matrix of values ranging from a high of 1.00 between populations 2 and 3 and a low of 0.26 between populations 4 and 12. The clustering of these values then resulted in a series of phenograms produced by successively lowering the entry level (Fig. 2). These phenograms illustrate the formation, growth, and disappearance of clusters as well as the linkages that connect the clusters together.

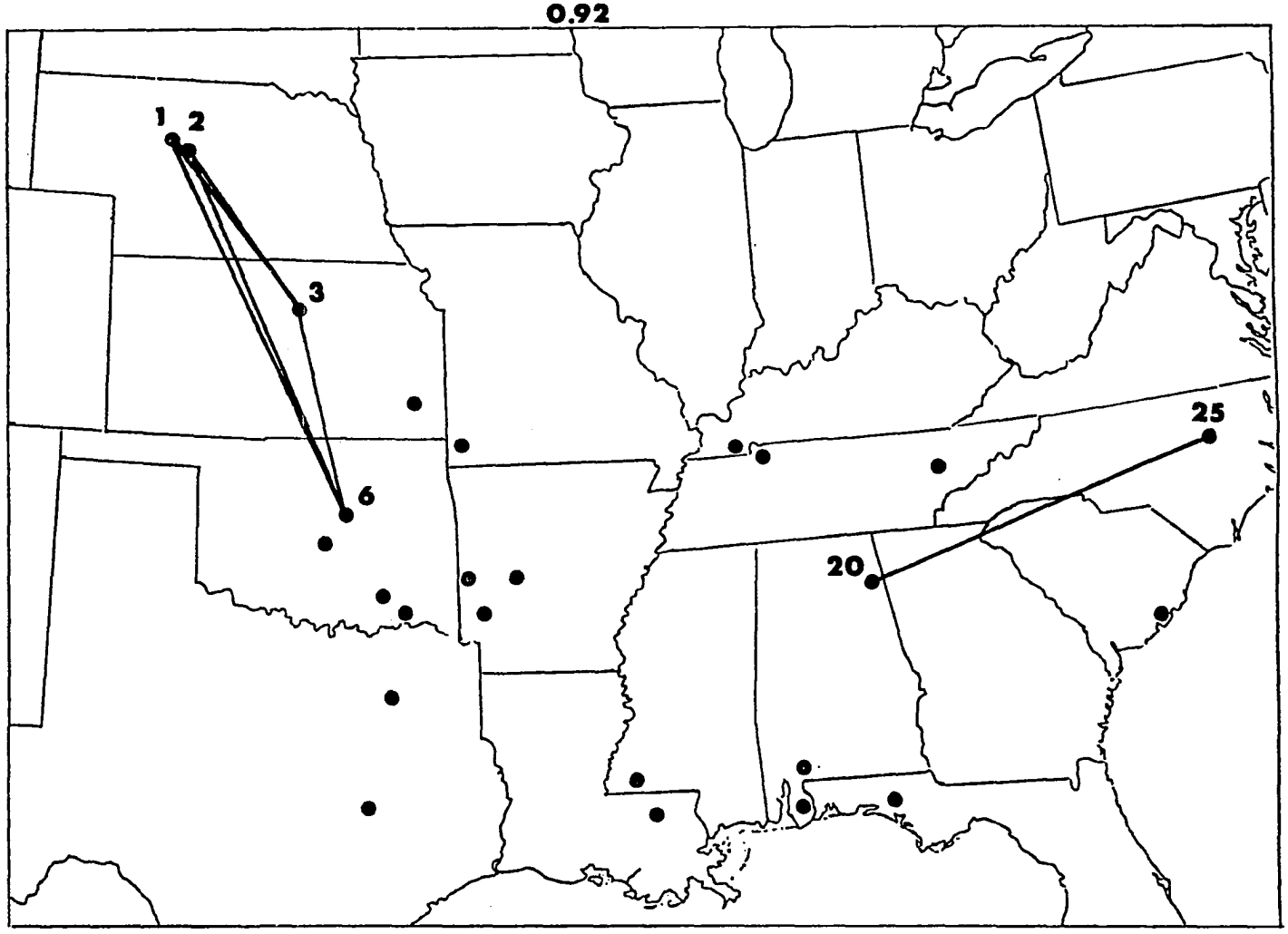
At the 0.84 level five clusters were visible, and every population was associated with a cluster. These five clusters remained completely distinct, adding only internal associations, through an interval of 0.08. Then at 0.76 larger groups began to form with the overlapping of cluster IV with both clusters I and II. At 0.72 clusters III and V joined, and cluster IV was more closely associated with cluster II. Thus the five clusters became parts of three larger groups that were visible until the 0.64 level. Below that level intergroup linkages connected the groups so that there was only one group to be seen.

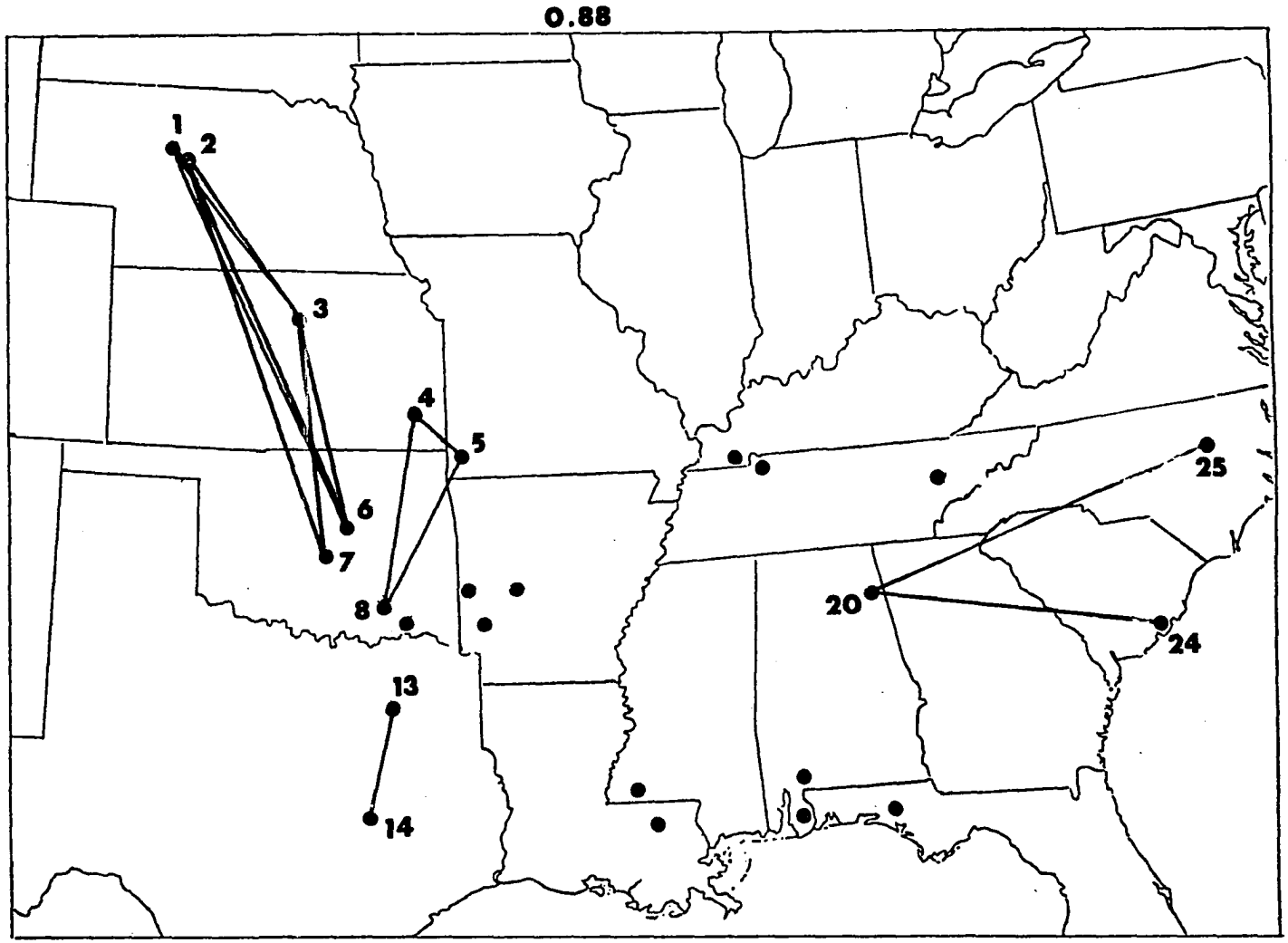
The geographic ends of the range of the series, clusters I and II, remained distinct from each other much lower than any of the other

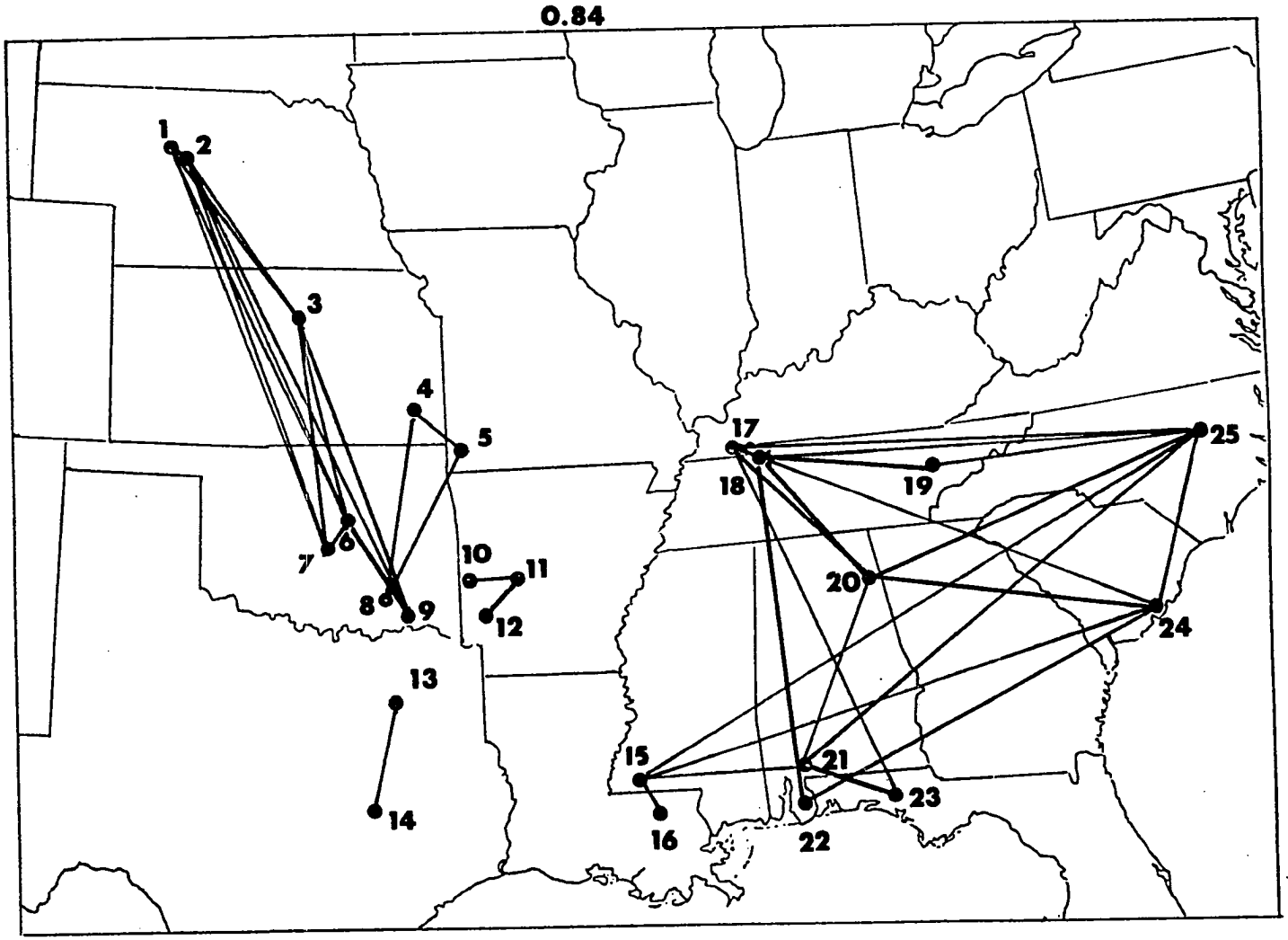
Figure 2. Cluster Phenograms. This series of illustrations represent the formation and growth of clusters as the association level was lowered by an interval of 0.04. The lines are associations at or above the level indicated on each phenogram.

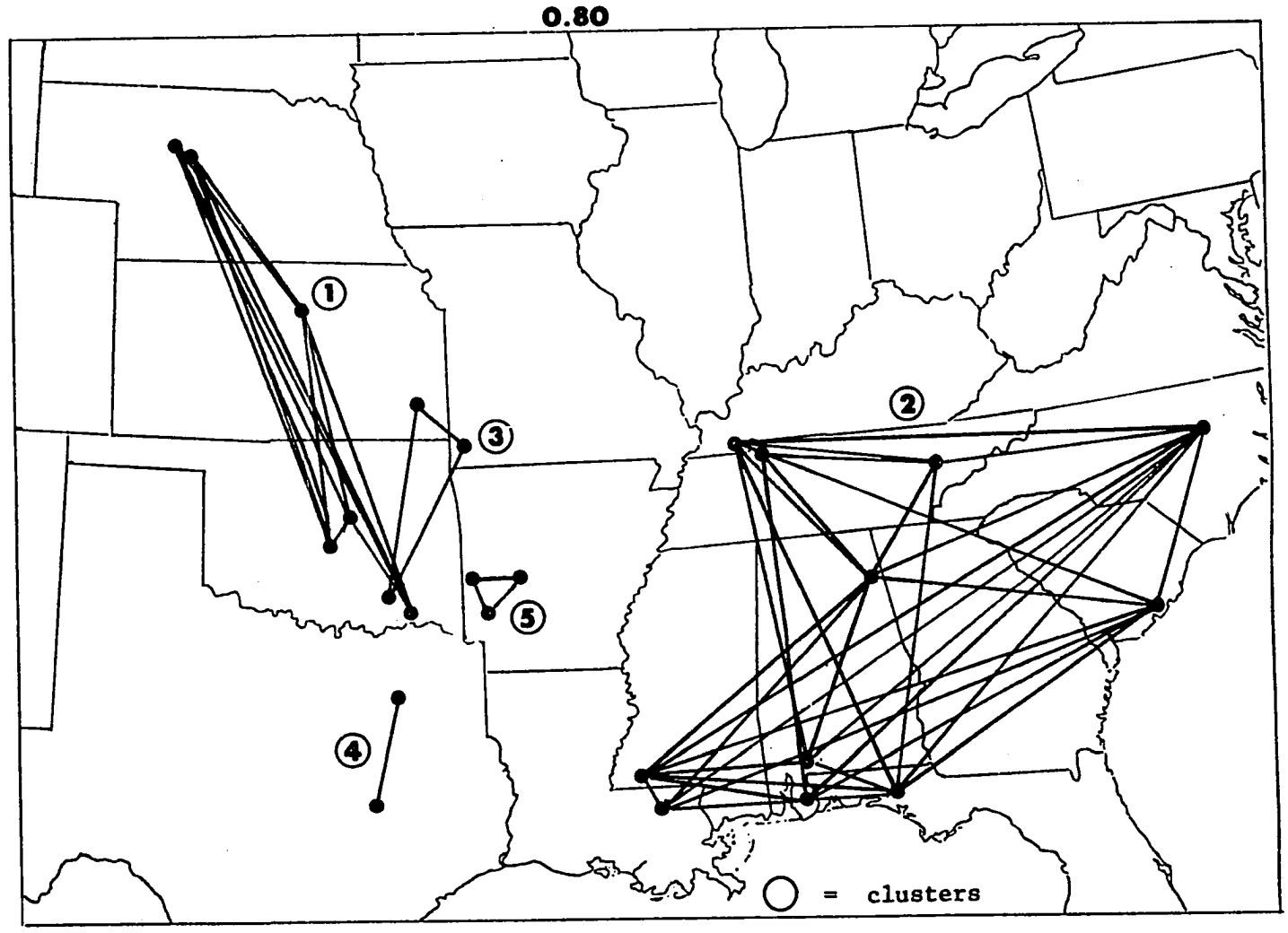

1.00
2
3

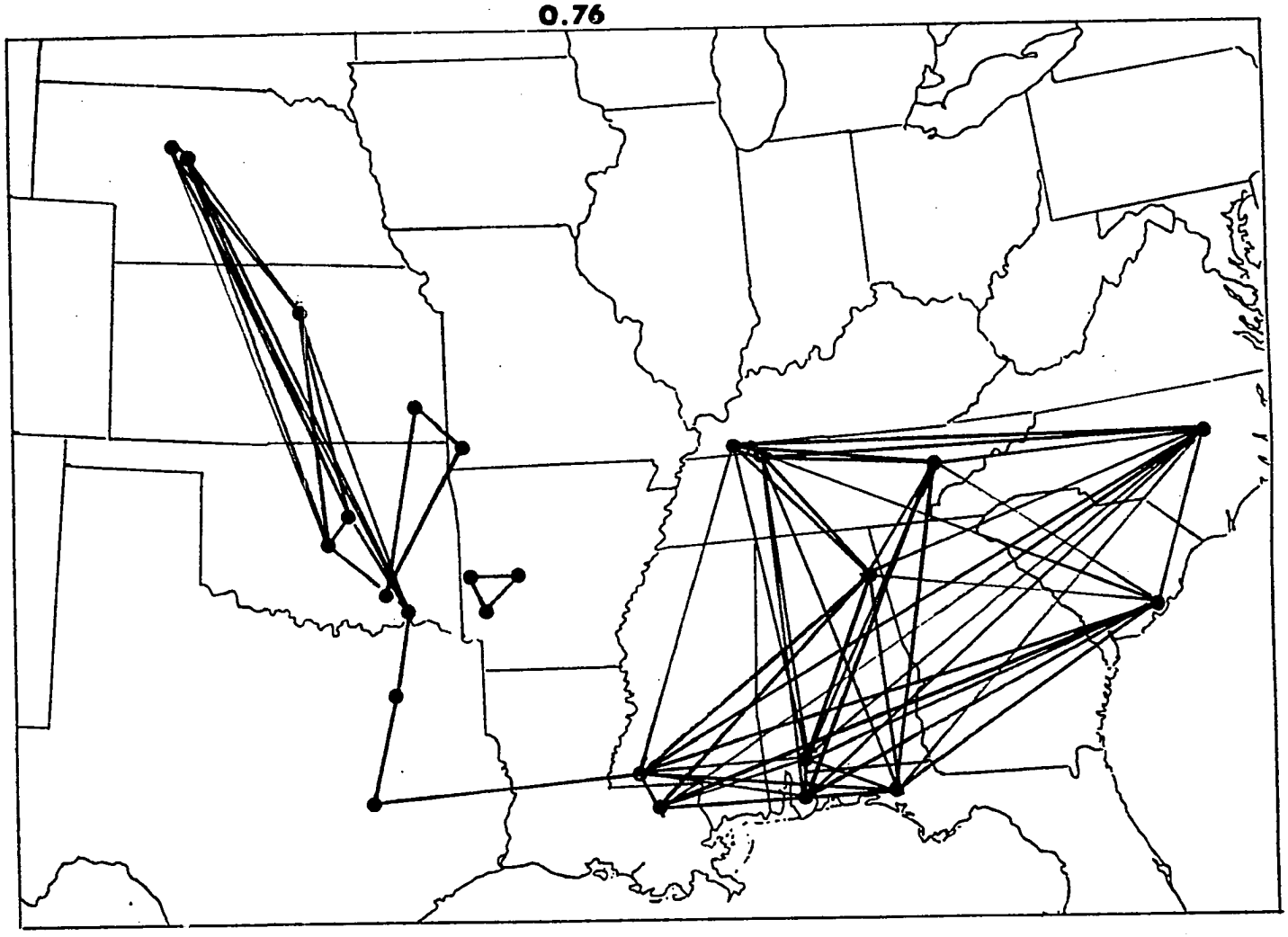

0.96
1
2
3
6

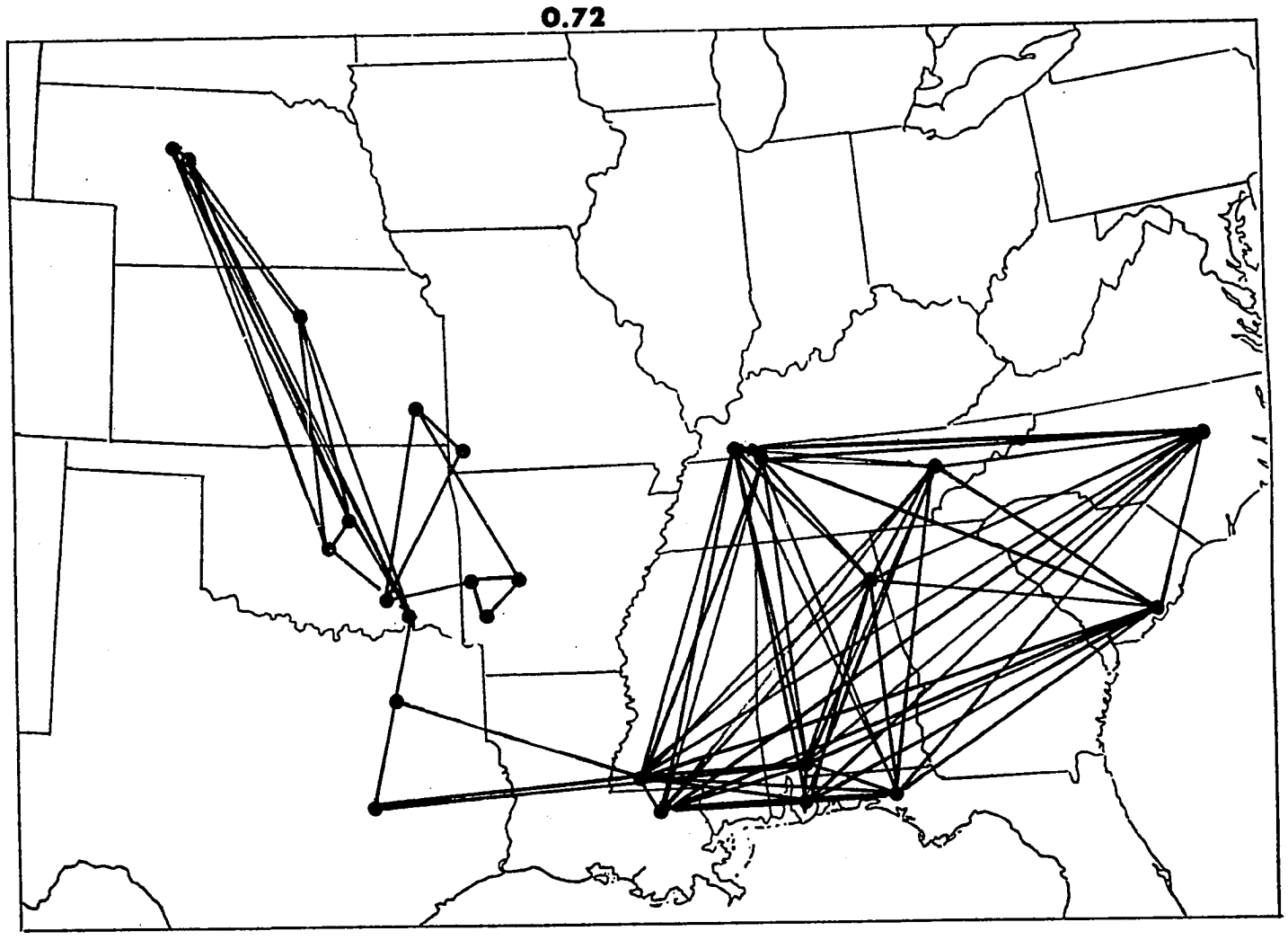

0.92
1
2
3
6
20
25

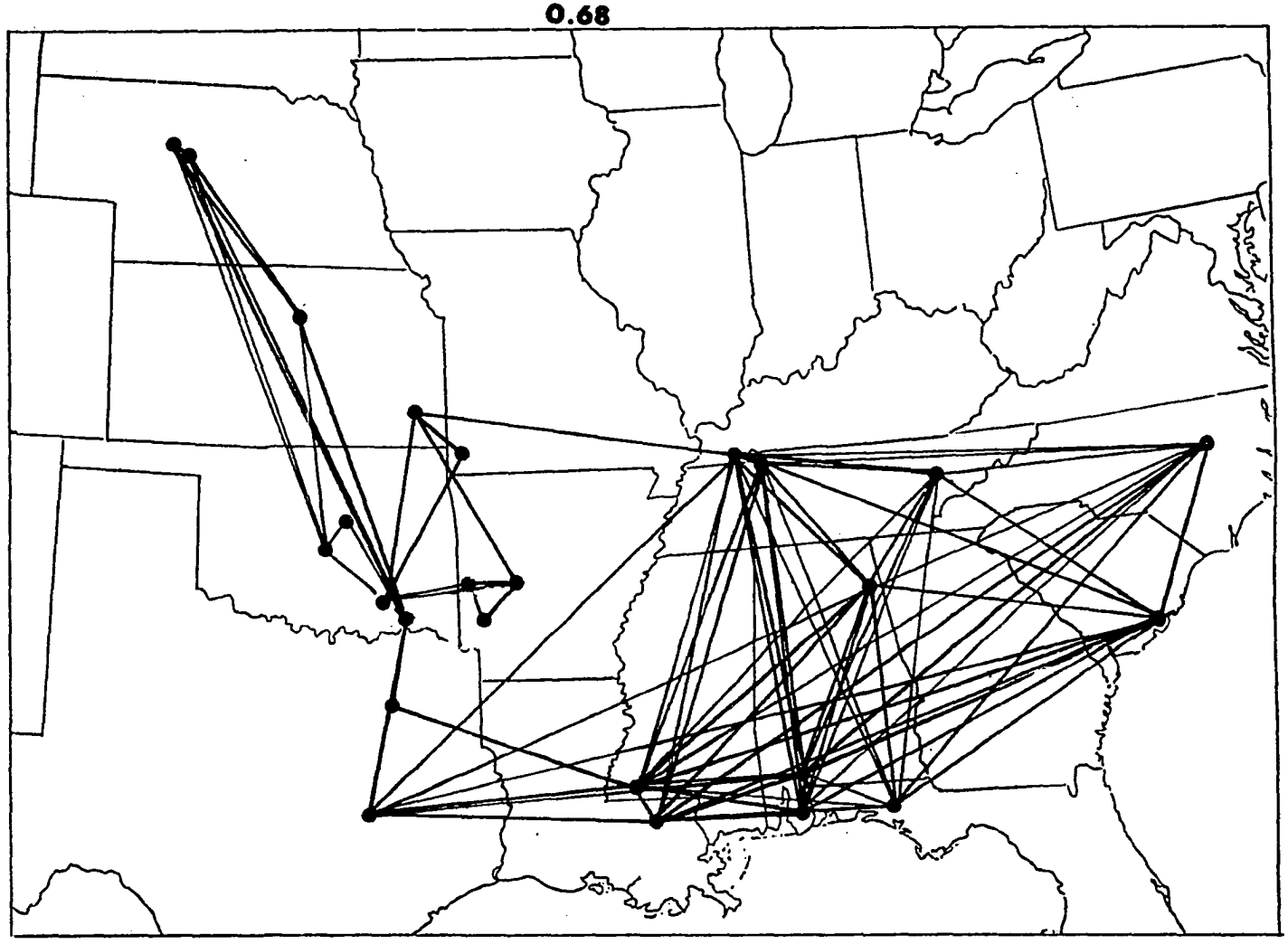

0.88
1
2
3
4
5
6
7
8
13
14
20
24
25

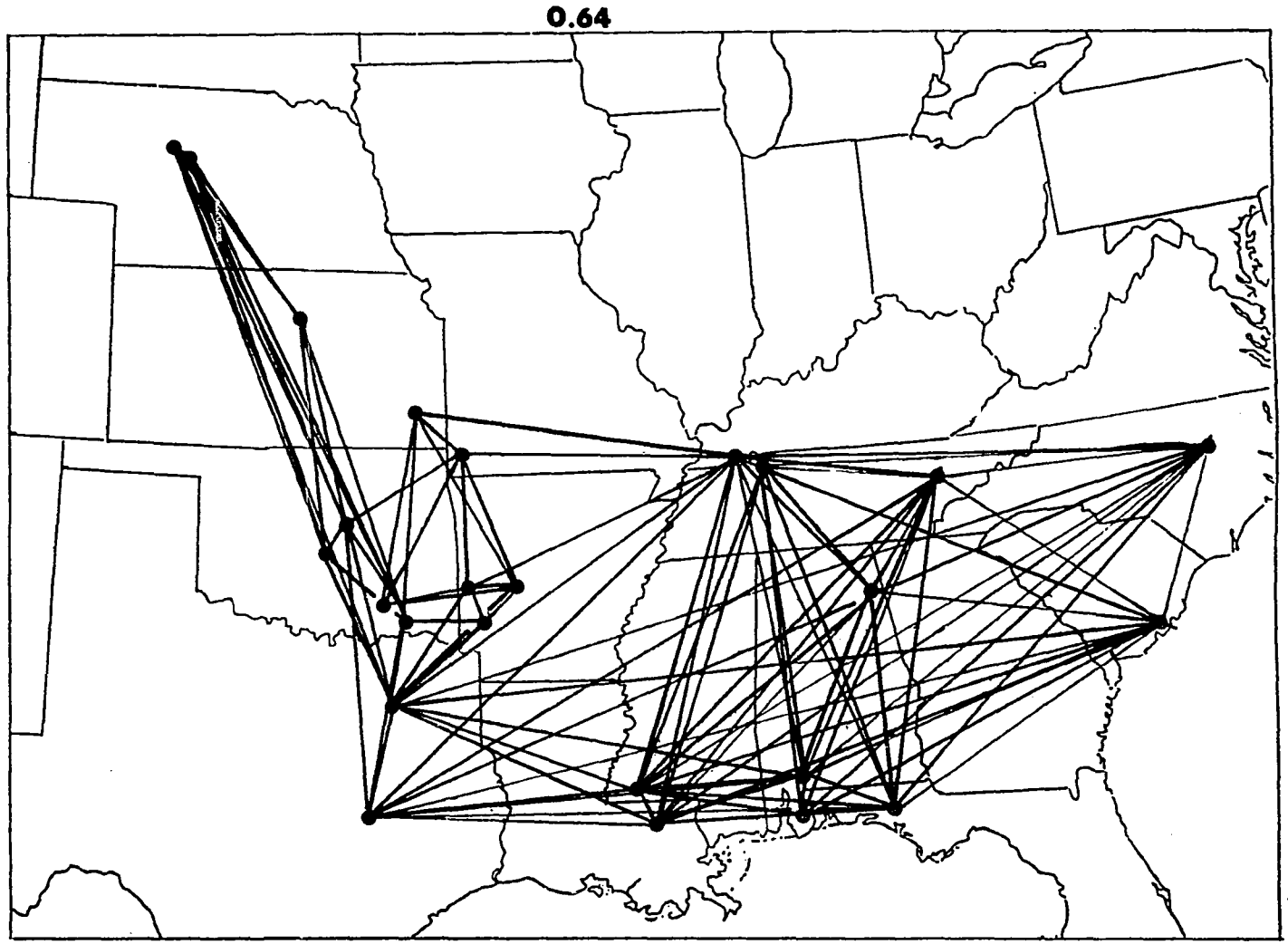

0.84
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25


0.80
1
2
3
4
5
= clusters


0.76


0.72


0.68


0.64

clusters. The first linkage between these two clusters occurred at 0.55, and the lowest was at 0.26.

Thus there were two levels of clusters. The first level was above 0.76, and the second level was above 0.64.

The five clusters that were seen at the 0.80 level were cohesive groups with the average internal association ranging from 0.81 for cluster II, which is a wide-ranging group occurring in a variety of habitats, to 0.91 for cluster I (Table III). The average similarity values between clusters ranged from 0.42 between clusters I and II to 0.67 between clusters III and V (Fig. 3). Cluster IV was almost equally associated with all of the other clusters with values ranging from 0.58 to 0.65, and the 0.65 was shared by two clusters, I and II.

These five clusters were then described and compared with each other on a character by character basis (Table IV). Each was distinct. With placing the herbarium material into the clusters, it was apparent that each cluster had its own geographic range as well (Fig. 4).

TABLE III

AVERAGE SIMILARITY VALUES WITHIN CLUSTERS

Cluster	Average Similarity Value
I	.91
II	.81
III	.89
IV	.88
V	.84

Figure 3. Relationships between the Clusters.

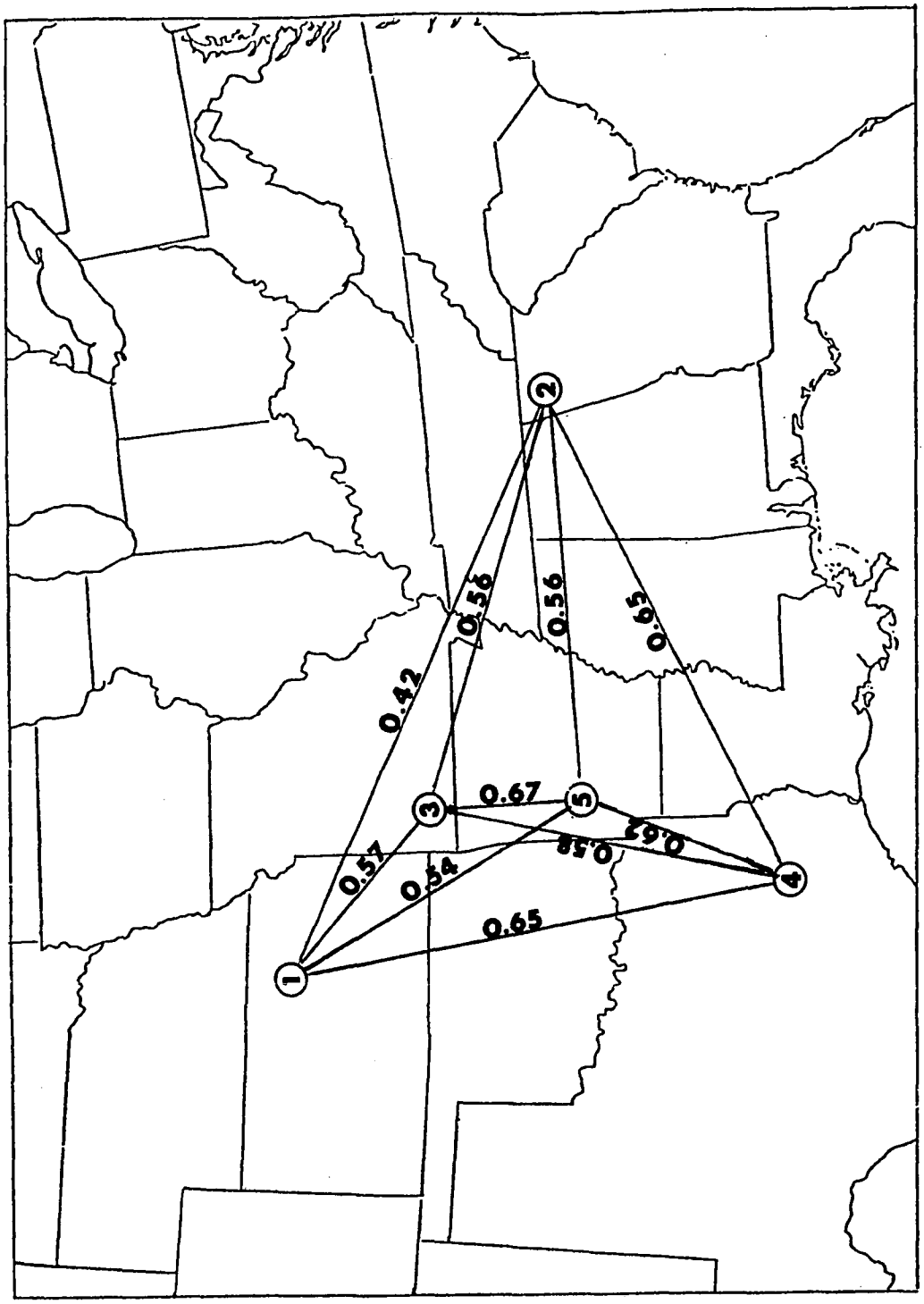

2
0.56
0.56
0.65
0.42
3
0.67
5
0.57
0.54
85.0
79.0
4
0.65
1

TABLE IV

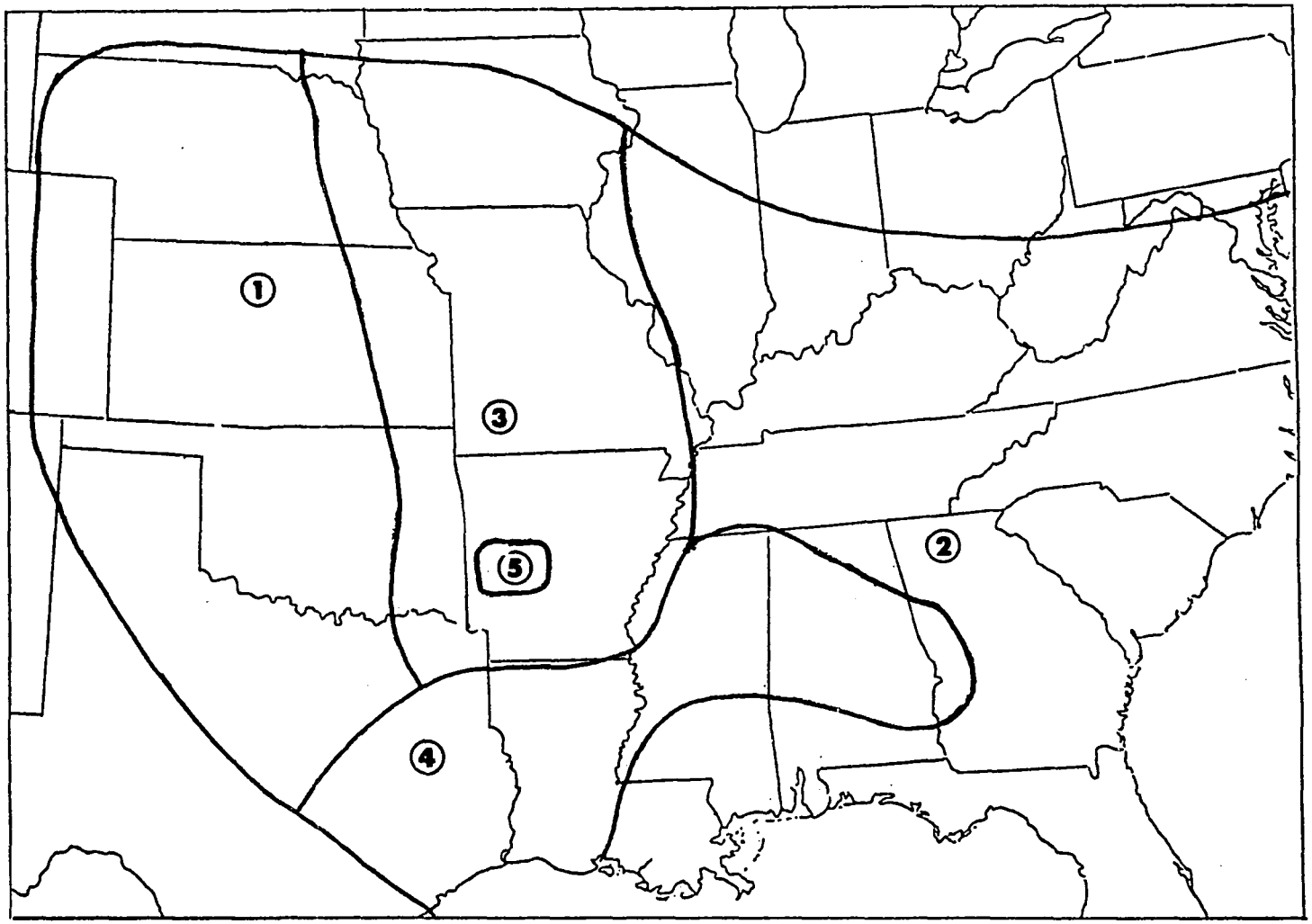
CHARACTER COMPARISON OF THE FIVE CLUSTERS

Character	I	II	III	IV	V
Plant height	< 47 cm.	> 47 cm.	> 47 cm.	< 47 cm.	< 47 cm.
Number of stalks	1-2	1-2	4-many	1-2	4-many
Corm diameter	< 40 mm.	< 40 mm.	> 40 mm.	≤ 40 mm.	> 40 mm.
Number of heads	> 13	< 7	6-13	> 13	1-3
Leaf density	.77-1.03/cm.	< .77/cm.	> 1.03/cm.	.77-1.03/cm.	< .77/cm.
Lower leaf length	< 117 mm.	> 117 mm.	< 117 mm.	< 117 mm.	< 117 mm.
Upper leaf length	< 49 mm.	< 49 mm.	< 49 mm.	< 49 mm.	> 49 mm.
Lower leaf width	> 5 mm.	< 5 mm.	< 5 mm.	> 5 mm.	> 5 mm.
Upper leaf width	< 4 mm.	< 4 mm.	< 4 mm.	< 4 mm.	> 4 mm.
Amount of pubescence	none	dense	dense	medium	sparse
Terminal head length	14.5 mm.	21.3 mm.	17.3 mm.	21.0 mm.	19.5 mm.

TABLE IV--(Continued)

Character	I	II	III	IV	V
Terminal head width	7.9 mm.	10.0 mm.	7.7 mm.	11.5 mm.	15.2 mm.
Phyllary curvature	spreading	spreading	recurved	straight	straight
Phyllary shape	lanceolate	lanceolate	acuminate	triangular	lanceolate
Phyllary margin	callose	membranous	membranous	callose	membranous
Phyllary color	purple	light purple	light purple	purple	green
Pappus length	< 8 mm.	> 11 mm.	< 8 mm.	> 11 mm.	< 8 mm.
Corolla tube length	< 9 mm.	> 13 mm.	< 9 mm.	9-13 mm.	< 9 mm.
Corolla lobe length	< 4 mm.	> 4 mm.	> 4 mm.	> 4 mm.	> 4 mm.
Style length	17-23 mm.	23-29 mm.	17-23 mm.	17-23 mm.	17-23 mm.
Style branch length	< 8 mm.	12-17 mm.	8-12 mm.	8-12 mm.	8-12 mm.
Stigmatic line length	< 2 mm.	2-5 mm.	2-5 mm.	2-5 mm.	2-5 mm.

Figure 4. Distribution of the Clusters. This map includes the Herbarium material used in this study.


1
2
3
4
5

CHAPTER IV

CONCLUSIONS

Five taxa were implied by the cluster analysis, but since they were not all equally distinct, they were not all classified at the same level. These five taxa when compared with the previous taxonomy of the series correspond most closely with what have usually been considered varieties. Thus it appears that the first level of clusters identified at 0.80 represent a varietal separation. The grouping of these clusters into three larger groups indicates the next level of separation, at 0.64, which would be species. Thus I have separated the series into three species, two of which have two varieties each.

Cluster I is the westernmost group farthest removed in geography and similarity from the remainder of the groups. It occurs on sandy prairies such as the Nebraska sandhills and in sandy forests such as the Crosstimbers of Oklahoma. Over the extensive north-south range, it retains a remarkable degree of cohesiveness. However, the southern plants show more variation as they intergrade with clusters III and IV. The description of this group and its range correspond with that of L. glabrata of Rydberg and L. squarrosa var. glabrata of Gaiser. The type specimen for these taxa, Rydberg 1505, seen at the New York Botanical Garden fits well in this cluster. Population 2 of this cluster was

collected at the type locality. Thus this cluster is considered as L. glabrata Rydb.

Cluster II covers the entire eastern half of the range of the Squarrosae, including all of the area east of the Mississippi River except a strip through northern Mississippi into central Alabama where it is hotter and drier in June than the areas around this strip (U. S. Dept. Interior, 1970). The variation included in this cluster is extensive, but the variation within the populations is almost as great as that between populations. For example, the number of heads varies from one to numerous, and the phyllaries vary from almost recurved to straight within every population. The northern populations have a greater preponderance of plants with numerous heads and greater phyllary curvature than the southern ones, where there are more plants with fewer heads and straighter phyllaries. This could have lead to the separation of the cluster into two groups, but there is an overall similarity at high levels. The range and description of this cluster fit that of L. squarrosa (L.) Michx. var. typica, including all of the synonomy listed by Gaiser (1946) and also L. squarrosa var. gracilenta Gaiser, which was originally described to account for the dichotomy explained above. Cluster II is thus represented by the name L. squarrosa (L.) Michx. var. squarrosa. A photograph of the Linnaean type, which was collected in Virginia, was seen at the Gray Herbarium.

Cluster IV is intermediate among the clusters especially between clusters I and II. Its range is reasonable for such a group, being geographically between clusters I and II. Several characters illustrate this point well. The pubescence falls between the heavily pubescent

L. squarrosa and the glabrous L. glabrata. Its phyllary margins are between the callose margins of L. glabrata and the membranous ones of L. squarrosa, and the corolla tube length of 9 - 13 mm is exactly between these two taxa. The Texas plants are the most distinct, and while the eastern extension of this cluster intergrades with L. squarrosa, this extension is still recognizable as part of the cluster. There seems to be a continuum through which cluster IV becomes more distinct to the West. The many associations that this cluster has with L. squarrosa populations have led to the conclustion that it should be considered a variety of L. squarrosa. The range covered by this cluster is that of Laciniaria squarrosa alabamensis of Alexander, Liatris squarrosa var. alabamensis of Gaiser, and L. glabrata var. alabamensis of Shinners. The description and type specimen of these taxa, F. S. Earle and C. F. Baker 1344, seen at the New York Botanical Garden, indicate that cluster IV is coincident with the group represented by these names. The type was collected in Lee County, Alabama, where none were found during the collecting for this study. I have considered it to be L. squarrosa var. alabamensis (Alex.) Gaiser.

Cluster III ranges from the Mississippi River westward into the prairies on limestone outcrops and south from Iowa into Louisiana. This is the range of L. hirsuta of Rydberg and L. squarrosa var. hirsuta of Gaiser. This group shows low associations with both L. glabrata and L. squarrosa, so it has been here designated as the species, L. hirsuta Rydb. It is a variable species with the plants of eastern Missouri, Arkansas, and Louisiana having smaller, more cylindrical heads and fewer, taller stalks than those at the western edge of the range.

However, there is an overall similarity that unites them. The type specimen for L. hirsuta Rydb., E. J. Palmer 32505, seen at the New York Botanical Garden fits well into cluster III. This type was collected in Newton County, Missouri, at the site of population 5 of this study.

Cluster V fits the range and description of L. squarrosa compacta of Torrey and Gray, L. compacta of Rydberg, and L. squarrosa var. compacta of Gaiser. It is associated with L. hirsuta at levels that have been designated as varietal, so it has been named here L. hirsuta var. compacta (T. & G.) Thomas, a new combination.[1] Its range is entirely within that of L. hirsuta, and although it has broader leaves and much less pubescence than L. hirsuta, there are many more similar characters. The Leavenworth specimen designated by Torrey and Gray as the type for this taxon was seen at the New York Botanical Garden. Its location is listed as Arkansas, but accounts of the travels and collections of Leavenworth do not indicate that he was ever in Arkansas. He was stationed at Fort Towson in Oklahoma which

---

[1] Liatris hirsuta var. compacta (T. & G.) Thomas, comb. nov.
Liatris squarrosa compacta Torrey and Gray, Fl. N. Am. 2: 68, 1841.
Liatris compacta Rydberg, Brittonia 1: 98, 1931.
Liatris squarrosa var. compacta (T. & G.) Gaiser, Rhod. 48: 401, 1946.

Plants slightly pubescent; stems weak and thin, less than 47 cm tall; corm large (greater than 40 mm diameter); stalks numberous; leaves sparse, less than 0.77/cm; leaves large (lower leaves less than 117 mm long and greater than 5 mm wide, upper leaves greater than 49 mm long and 5 mm wide); heads one to few per stalk; terminal head ca. 19.5 mm long and 15.5 mm wide; phyllaries lanceolate, spreading, straight, green with membranous margins; pappus less than 8 mm long; corolla tube less than 9 mm long, lobes greater than 4 mm; style length 17-23 mm, branches 8-12 mm, stigmatic lines 2-5 mm.

Range and habitat: Hilltops in central and west-central Arkansas among oaks and hickorys on rocky outcrops.

at that time was Arkansas territory (McVaugh, 1947). Although no specimens have been collected in Oklahoma recently, the type may be from southeastern Oklahoma, which would extend the range of the taxon.

All of these taxa intergrade with each other causing zones of plants that are difficult to place into one or another of them. This led Gaiser to conclude that the entire series is one species. However, this study has shown that the varieties group together to form three larger groups, which I have designated as species. Additional observations that have led to the "splitting" of Gaiser's species are those of habitat differences and flowering time differences. The flowering times range from May to October (Fig. 5), thus there is some reproductive isolation, and the habitats range from the climates of the northern plains to the Gulf coast and from open areas to shaded sites with various soil preferences.

It is recognized that additional collections especially in the ranges of L. hirsuta and L. squarrosa would provide much information in accounting for the variation in these groups, and experiments in breeding as well as chemical analyses would help identify the relationships among the taxa. At this point, the conclusions are that the series can best be described by three species, two of which have two varieties each.

Figure 5. Flowering Times of the Taxa of the Squarrosae.

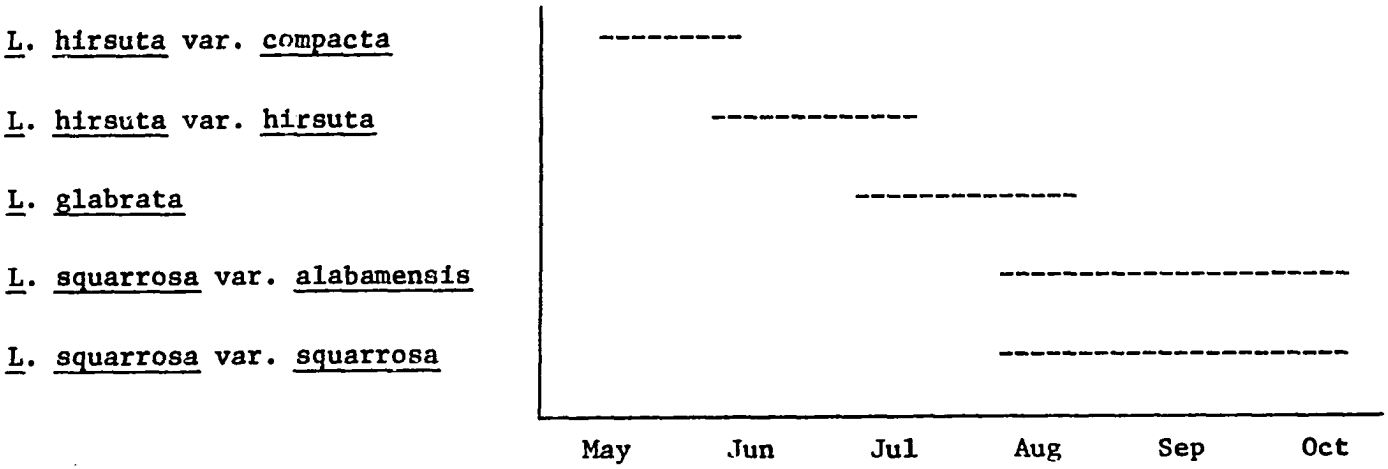
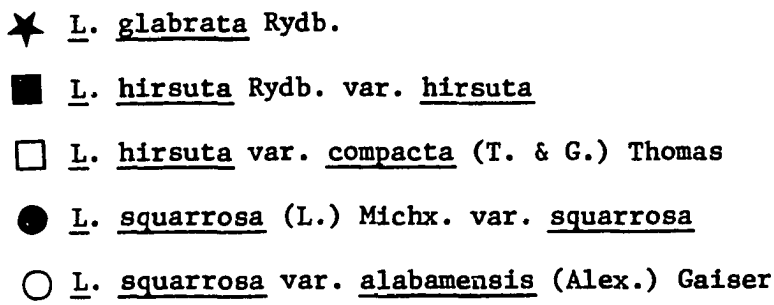
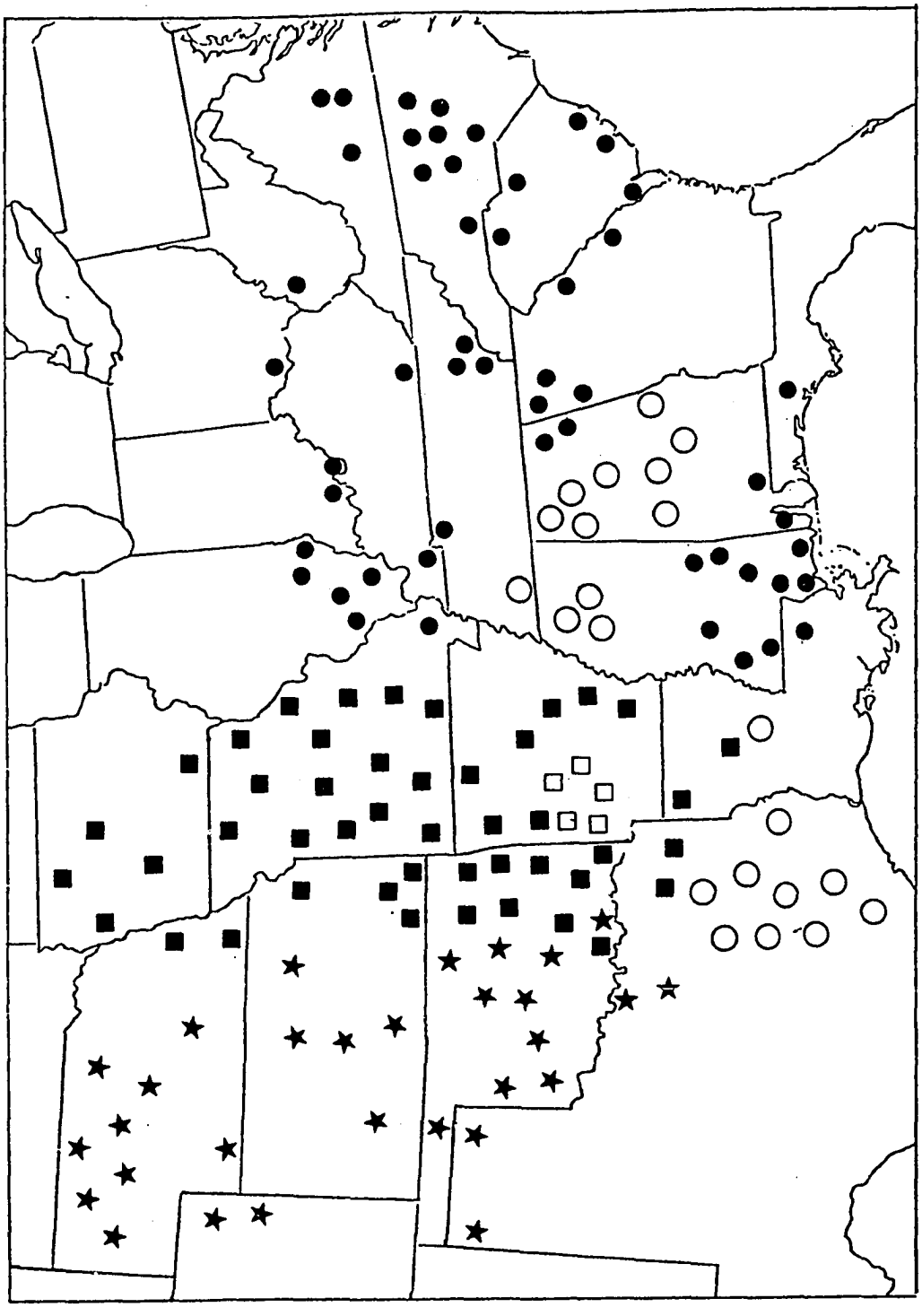

L. hirsuta var. compacta
L. hirsuta var. hirsuta
L. glabrata
L. squarrosa var. alabamensis
L. squarrosa var. squarrosa
May
Jun
Jul
Aug
Sep
Oct

Figure 6. Distribution of the Squarrosae. This map illustrates the distribution of the specimens used in this study.





CHAPTER V

TAXONOMY

Keys to the Squarrosae

Pappus length greater than 11 mm, corolla tube length greater than 9 mm

Style length 23-29 mm, phyllaries lanceolate, margins membranous; number of heads per stalk 1-7 — L. squarrosa var. squarrosa

Style length 17-23 mm, phyllaries triangular, usually straight, margins at least somewhat callose; number of heads per stalk 13 or more. — L. squarrosa var. alabamensis

Pappus length less than 8 mm; corolla tube less than 9 mm.

Phyllary margins membranous; number of stalks usually numerous; number of heads per stalk few (1-4).

Phyllaries recurved; plants densely hirsute; terminal head ca. 21 mm long and 10 mm wide. — L. hirsuta var. hirsuta

Phyllaries straight; plants nearly glabrous; terminal head ca. 19.5 mm long and 15.5 mm wide. — L. hirsuta var. compacta

Phyllary margins callose; stalks few (1-3); number of heads per stalk numerous (more than 13); plants glabrous. — L. glabrata

Descriptions of the Taxa of the Squarrosae

Liatris squarrosa (L.) Michx., Fl. Bor. Am. 2: 92, 1803.

var. squarrosa

Serratula squarrosa L. Sp. Pl. 818, 1753

Laciniaria squarrosa (L.) Hill, Veg. Syst. 4: 49, 1762.

Pteronia caroliniana Walt. Fl. Carol. 202, 1788.

Vernonia hirsutiflora Poiret, Encyc. Meth. Bot. 8: 502, 1803.

Liatris hirsutiflora (Poiret) Kostel, Al. Med. Pharm. Fl. 2: 651, 1833.

Liatris squarrosa β floribunda Torrey and Gray, Fl. N. Am. 2: 68, 1841.

Liatris squarrosa var. gracilenta Gaiser, Rhod. 48: 397, 1946.

Type: Linnaean specimen, collected in Virginia.

Plants often densely pubescent; stalks few, usually 1-3, less than 47 cm tall; corm diameter less than 40 mm; leaves sparse, less than 0.77 per cm; lower leaves longer than 117 mm and wider than 5 mm; upper leaves shorter than 49 mm and narrower than 4 mm; heads few, from 1-7 per stalk; terminal head ca. 21.3 mm long and 1.0 mm wide; phyllaries lanceolate, spreading with tips straight to curved outward as much as 90°, margins membranous, and light purple at anthesis; pappus longer than 11 mm; corolla tube longer than 13 mm, lobes longer than 4 mm; style length 23-29 mm, branches 12-17 mm, stigmatic lines 2-5 mm.

Range and Habitat: Southern Illinois, southern Indiana, southern Ohio, West Virginia, Maryland, Virginia, Kentucky, southeast Missouri, Tennessee, North Carolina, South Carolina, Georgia, northern Florida, northern and southern Alabama but not central, southern Mississippi, eastern and southern Louisiana. Soils rocky to sandy, along roadsides in pine and oak forests.

var. alabamensis (Alex.) Gaiser, Rhod. 48: 394, 1946.

Laciniaria squarrosa alabamensis Alexander, Small Man. S. E. Fl. 1333, 1933.

Liatris glabrata var. alabamensis (Alex.) Shinners, Field Lab. 19: 76, 1951.

Type: F. S. Earle and C. F. Baker 1344, Auburn, Lee Co. Alabama.

Plants lightly pubescent; stalks few, less than 47 cm tall, rigid; corm small, less than 40 mm diameter; heads numerous, more than 13 per stalk; leaf density 0.77-1.03 per cm; lower leaves shorter

than 117 mm and wider than 5 mm; upper leaves shorter than 49 mm and narrower than 4 mm; terminal head ca. 21.0 mm long and 11.5 mm wide; phyllaries triangular, spreading, usually straight, purple at anthesis, margins callose to membranous; pappus longer than 11 mm; corolla tube 9-13 mm long, lobes longer than 4 mm; style length 17-23 mm, lobes 8-12 mm, stigmatic lines 2-5 mm.

Range and Habitat: Southeast Texas, Louisiana, northern Mississippi, northern and central Alabama. Sandy soils along roadsides in pine or oak forests.

Liatris hirsuta Rydberg, Brittonia 1: 98, 1931.

var. hirsuta

Liatris squarrosa hirsuta (Rydb.) Gates, Trans. Kans. Acad. Sci. 42: 138,1940.

Liatris squarrosa var. hirsuta (Rydb.) Gaiser, Rhod. 48: 399, 1946.

Type: E. J. Palmer 32505, Reddings Mill, Newton Co., Missouri. Plants usually densely pubescent with long spreading hairs; corm diameter large, greater than 40 mm, irregular in shape except on young plants where corm is small and spherical; stalks numerous, sometimes only a few on plants growing in wooded areas; heads usually few per stalk, 1-7; leaves dense, greater than 1.03 per cm; lower leaves shorter than 117 mm and narrower than 5 mm; upper leaves shorter than 49 mm and narrower than 4 mm; terminal head ca. 17.3 mm long and 7.7 mm wide; phyllaries lanceolate to mucronate, appressed with tips recurved, margins membranous, light purple at

anthesis; pappus shorter than 8 mm; corolla tube shorter than 9 mm, lobes longer than 4 mm; style length 17-23 mm, branches 8-12 mm, stigmatic lines 2-5 mm.

Range and Habitat: Eastern Nebraska, Kansas, and Oklahoma; northeast Texas; Louisiana; Missouri; Arkansas; and Iowa. Limestone outcrops in oak-hickory forests or prairies.

var. compacta (T. & G.) Thomas, comb. nov. cited on page 40 of this work.

Liatris squarrosa γ compacta Torrey and Gray, Fl. N. Am. 2: 68, 1841.

Liatris compacta (T. & G.) Rydberg, Brit. 1: 98, 1931.

Liatris squarrosa var. compacta (T. & G.) Gaiser, Rhod. 48: 401, 1946.

Type: Leavenworth, collected in Arkansas.

Plants slightly pubescent, at least on phyllary margins; stems thin and weak, less than 47 cm tall; corm diameter large, larger than 40 mm; stalks numerous; leaves sparse, less than 0.77 per cm; lower leaves wider than 5 mm and shorter than 117 mm; upper leaves wider than 4 mm and longer than 49 mm; heads one to few per stalk; terminal head ca. 19.5 mm long and 15.5 mm wide; phyllaries lanceolate, spreading, straight, green, margins membranous, with outer ones longer than the head; pappus shorter than 8 mm; corolla tube shorter than 9 mm, lobes longer than 4 mm; style length 17-23 mm, branches 8-12 mm, stigmatic lines 2-5 mm.

Range and Habitat: Hilltops in central and west-central Arkansas on limestone outcrops among oaks and hickories.

Liatris glabrata Rydberg, Brittonia 1: 98, 1931.

Liatris squarrosa δ intermedia Gray, Syn. Fl. 2: 109. 1884.

Liatris squarrosa glabrata (Rydb.) Gates, Trans. Kans. Acad. Sci. 42: 138, 1940.

Liatris squarrosa var. glabrata (Rydb.) Gaiser, Rhod. 48: 401, 1946.

Type: P. A. Rydberg 1505, Plummer Ford, Thomas Co., Nebraska. Plants glabrous; stems rigid, less than 47 cm tall; stalks few, 1-2; corm diameter small, less than 40 mm; leaves rigid, density of 0.77-1.03 per cm; lower leaves shorter than 117 mm and narrower than 5 mm; upper leaves shorter than 49 mm and narrower than 4 mm; heads numerous, more than 13 per stalk; terminal head ca. 14.5 mm long and 7.9 mm wide; phyllaries lanceolate, spreading with tips curved outward, purple at anthesis, margins callose; pappus shorter than 8 mm; corolla tube shorter than 9 mm, lobes shorter than 4 mm; style length 17-23 mm, branches shorter than 8 mm, stigmatic lines shorter than 2 mm.

Range and Habitat: Southern South Dakota; Nebraska; eastern Colorado; western Kansas and Oklahoma; northwest Texas. Sandy prairies or sandy oak-hickory forests.

LITERATURE CITED

Gaiser, L. O., 1946. The Genus Liatris. Rhodora 48: 393-410.

Gates, F. C., 1940. New Forms and Nomenclatorial Combinations in the Kansas Flora. Transactions of the Kansas Academy of Science 42: 138.

Gray, A., 1884. Synoptical Flora of North America 1: 109. New York.

Linnaeus, C., 1753. Species Plantarum. Stockholm.

McVaugh, R., 1947. The Travels and Botanical Collections of Dr. Melines Conkling Leavenworth. Field and Laboratory 25: 57-70.

Rydberg, P. A., 1931. Taxonomic Notes. Brittonia 1: 98.

Shinners, L., 1951. Notes on Texas Compositae. Field and Laboratory 19: 76.

Small, J. K., 1933. Manual of the Southeastern Flora of the United States. University of North Carolina Press. Chapel Hill, North Carolina.

Sokal, R.R. and C. D. Michener, 1958. A Statistical Method for Evaluating Systematic Relationships. University of Kansas Science Bulletin 38: 1409-1438.

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

Torrey, J. and A. Gray, 1841. Flora of North America 2: 68. New York.

United States Department of the Interior, 1970. The National Atlas. U.S. Printing Office. Washington, D.C.

APPENDIX I

HERBARIA USED IN THIS STUDY

Herbarium	Location
Bebb Herbarium	University of Oklahoma Norman, Oklahoma
Gray Herbarium	Harvard University Cambridge, Massachusetts
Missouri Botanical Garden	St. Louis, Missouri
New York Botanical Garden	Bronx, New York
Oklahoma State University Herbarium	Stillwater, Oklahoma
Southern Methodist University Herbarium	Dallas, Texas
University of Arkansas Herbarium	Fayetteville, Arkansas
University of Georgia Herbarium	Athens, Georgia
University of Kansas Herbarium	Lawrence, Kansas
University of Nebraska State Museum	Lincoln, Nebraska
University of Southwest Louisiana Herbarium	Lafayette, Louisiana

APPENDIX II

EXPLANATION OF CHARACTER MEASUREMENT

Number	Character	Measurement Comments
1-2	Plant height	Plants measured from top of tallest stalk to top of corm.
3	Number of stalks per plant.	Flowering stalks counted.
4-5	Number of heads per flowering stalk	All heads including buds were counted and divided by 3 stalks.
6-7	Leaf density	Nodes were counted and divided by stalk length and averaged for each plant.
8	Corm diameter	Not all plants were measured. Every fifty plant was dug and measured at widest diameter.
9	Leaf thickess	Determined by observing prominance of veins.
10 & 12	Length and width of lower leaves	Leaves at third node from bottom of stalk measured. Averaged for each plant.
11 & 13	Length and width of upper leaves	Leaves at third node from top of each stalk measured and averaged for the plant.
12	Pubescence type	Hirsute or hispid.

APPENDIX II--(Continued)

Number	Character	Measurement Comments
15-18	Amount of pubescence	Scored as follows: a. Thirteen sites were examined including: stem, leaf surface and margins of middle, upper, and lower parts of plant; inner and outer phyllary margins and surface. b. Each site scored as follows: 0 = no pubescence 1 = scattered hairs 2 = regular hairs 3 = complete coverage. c. Scores were totaled.
19-21	Length of terminal head	Measured from base of phyllaries to top of pappus.
22-24	Width of terminal head	Measured at top of phyllaries not including tips.
25-27	Phyllary curvature	Score derived from: 0 = tight and straight 1 = spreading and straight 2 = tips curved out 3 = tips curved out and down
28-30	Color of stem and	Score determined from: 0 = green at anthesis 1 = light purple at anthesis 2 = dark purple at anthesis
31	Length of phyllary tip	Measured from shoulder to tip.
32	Width of phyllary tip	Measured just above shoulder.
33-34	Phyllary shape	Score determined from: 0 = mucronate 1 = accuminate 2 = accuminate to lanceolate 3 = triangular 4 = lanceolate

APPENDIX II--(Continued)

Number	Character	Measurement Comments
35	Phyllary margin	Either callose or membranous.
36-38	Stem rigidity	Diameter of stem at base of stalk measured and divided by height of stalk. Averaged for each plant.
39-40	Pappus length	Measured from tip to top of achene.
41-42	Corolla tube length	Measured from top of achene to base of lobes.
43	Corolla lobe length	Measured from top of tube to tip.
44-46	Style length	Measured from achene to tip.
47-48	Length of style branches	Measured from bifurcation to tip.
49-50	Length of stigmatic lines	Length measured.
51	Soil particle size	Sieved through USDA Set ranging from .002 mm to .2 mm.
52	Sunlight	Taken from National Atlas, 1970.
53	Frost-free period	Taken from National Atlas, 1970.
54-55	Precipitation/ Evaporation	Taken from National Atlas, 1970.