JOURNAL OF THE TENNESSEE ACADEMY OF SCIENCE
VOLUME 66, NUMBER 4:153–160, OCTOBER 1991

BIOGEOGRAPHY OF AMPHIBIANS IN TENNESSEE

WILLIAM H. REDMOND
Regional Natural Heritage Project
Tennessee Valley Authority
Norris, TN 37828

ABSTRACT

Distribution maps were completed for 20 species of frogs and 41 species of salamanders. For the purposes of statistical analyses, a grid cell pattern containing 122 sampling units was developed and species were scored present or absent in each cell. The fauna was organized into three groups: frog species, salamander species, and all amphibian species. The results of a G-test for the frequency distribution of range limits fitted to a Poisson distribution suggested a clumped dispersion pattern for each faunal group. Using the coefficient of Jaccard, cluster analyses of distribution data delineated three areas of faunal homogeneity for frogs, nine for salamanders, and six for all amphibians. When compared to frogs, salamander distributions exerted a larger influence on the determination of amphibian areas of homogeneity. An analysis of faunal composition of areas of homogeneity in terms of past dispersal patterns of their component species revealed that frog areas were dominated by species that dispersed from southeastern, southwestern, and southern centers of dispersal, whereas salamander areas were dominated by species with an Appalachian Highland center of dispersal.

INTRODUCTION

Nearly all previous works concerning the amphibians of Tennessee have been descriptive. Early studies included Troost (1843), Cope (1889), Rhoads (1895), Blatchley (1901), Blanchard (1922), Harper (1935), Bailey (1936, 1937), and Burt (1938). Gentry (1937) completed the first state survey and reported 39 species from 124 collecting stations. Gentry (1955-1956) listed 69 species, and later Gentry et al. (1965) noted 47 species and provided distribution maps. This reduction in total number of species (69 to 47) was primarily the result of exclusion of subspecies from the total count in 1965. Apparently Gentry included subspecies in his total count in 1955–1956. Redmond (1985) provided abbreviated accounts and distribution maps for 20 species of frogs and 41 species of salamanders. Redmond et al. (1990) provided the most recent checklist that included 20 species of frogs and 45 species of salamanders.

While most studies have been descriptive, a few attempted to describe and analyze biogeographic patterns. King (1939) noted the geographic affinities of amphibian species in the Great Smoky Mountains National Park. Johnson (1958) provided a biogeographic investigation of the herpetofauna of eastern Tennessee and Sinclair (1968) suggested the Central Basin physiographic region represented a distinct faunal region. The most recent and extensive study of amphibian biogeography in Tennessee was reported by Redmond (1985). This paper is a summary of certain portions of that study.

DISTRIBUTIONS OF SPECIES

Distribution data were accumulated from three major sources. Listed in order of importance, these included (1) the collections of universities, museums, and other institutions, (2) field surveys by the author and University of Tennessee students and faculty, and (3) literature references. Locality data for over 27,000 specimens were obtained from 39 university and other institutional collections. Field surveys were conducted between September 1975 and June 1985. Major emphases during fieldwork were to sample areas of the state where information on amphibians was lacking and to further delineate the ranges of several species whose distributions in Tennessee were poorly defined. All specimens taken were deposited in the University of Tennessee, Knoxville, Vertebrate Zoology Collection. The literature search for data resulted in the review of approximately 660 scientific papers, books, and other articles. Data from literature sources were only used for localities where data from museum specimens were not available, or were questionable. A six-volume, loose-leaf, bound atlas listing all species and locality data utilized in this study was archived at the University of Tennessee, Knoxville, Vertebrate Zoology Collection. Distribution maps for species are provided in Redmond (1985).

DISPERSION PATTERNS

Citing Sokal and Sneath (1963), Hagmeier and Stults (1964) stated that prior to delineation of biogeographic areas, two conditions must be met. The first and most obvious condition is that range limits must occur in the study area. The second condition requires that the distribution of range limits must be clumped or contagious. A visual inspection of maps of Tennessee illustrating the geographic range limits of frog, salamander, and total amphibian species (Figure 1), clearly shows

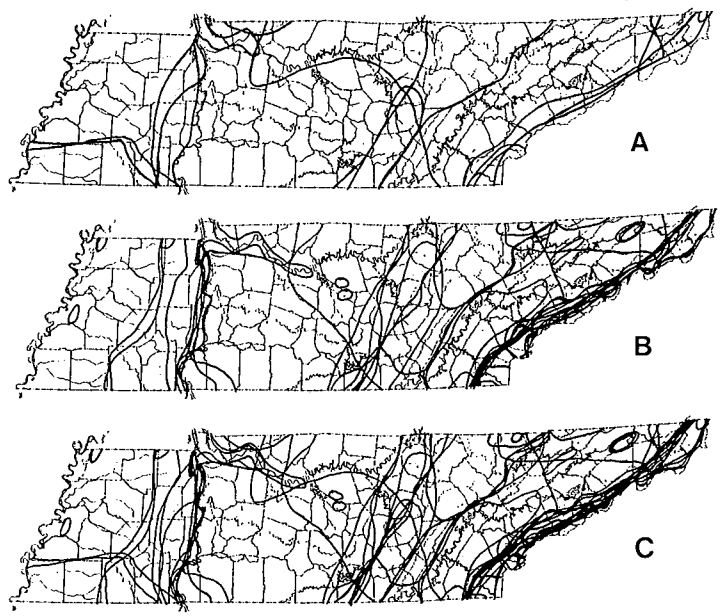

Figure 1. Geographic range limits of frog (A), salamander (B), and all amphibian (C) species in Tennessee.

that the first condition is met. Also, it is evident that range limits tend to be clumped, especially along the western border of the Blue Ridge Mountains and eastern border of the Coastal Plain.

In order to statistically test the type of dispersion pattern exhibited by frog, salamander, and total amphibian faunas, the state was divided into 122 grid cells or sampling units (Figure 2), each approximately 1,024 km^2. For each grid cell, the number of range limits present was tabulated for frog, salamander, and total amphibian species. These data were arranged into three frequency distributions, each of which was compared to a Poisson distribution using an adjusted G-test (Gadj) (Sokal and Rohlf 1981). These procedures allowed a test of the independence of limits of distribution within each faunal group.

For all three faunal groups, the hypothesis that distributional limits within each group are random and occur independently of each other was rejected. Indicating a clumped or contagious dispersion for all three groups, the Gadj values exceeded the expected chi square values at the 0.005 level of significance (Table 1). Also, all three Coefficients of Dispersion (CD) were greater than one and suggest clumped dispersion patterns.

It is interesting to note that frog distributional limits may exhibit less of a clumped nature than do the distributional limits of salamanders or both frogs and salamanders grouped together as amphibians. Due to the small number (four) of frequency classes for frog distributional limits (Table 1), this apparent tendency toward randomness may be an artifact of the test or may indicate a more random dispersion pattern for frog species in Tennessee. Using similar statistical procedures, Hammerson (1981) determined the distributional limits of amphibians in Colorado to be random. Lee (1980) indicated that on the Yucatan Peninsula, frog distributional limits were more weakly clumped than the distributional limits of other groups.

AREAS OF FAUNAL HOMOGENEITY

Areas of faunal homogeneity are often referred to as faunal or biotic provinces. These areas have been determined by both qualitative and quantitative methods; however, most recent studies have stressed the use of quantitative methodologies (Bock et al. 1981, Hagmeier

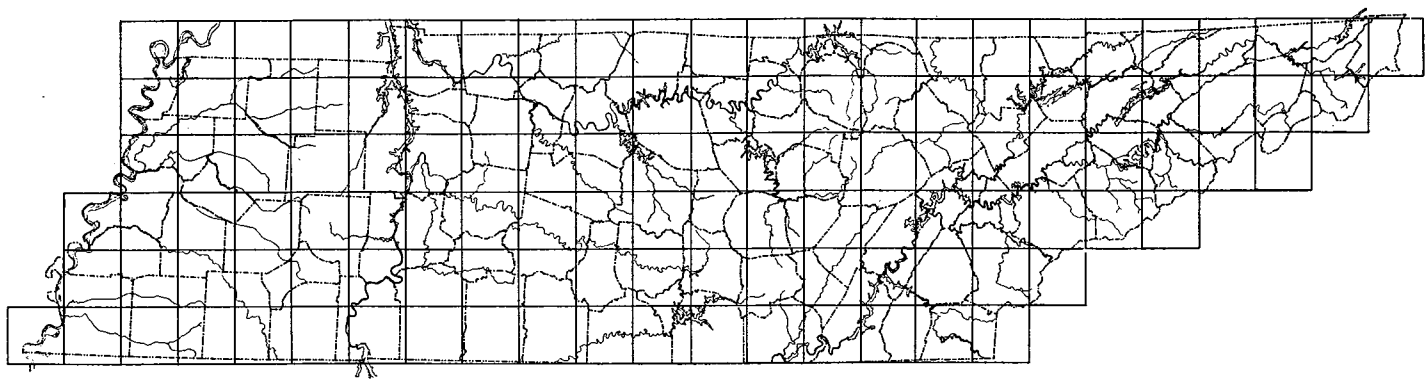

Figure 2. One hundred and twenty-two grid cells used in analysis of distribution patterns of amphibians in Tennessee.

Table 1. Results of G–tests of frequency of geographic distribution limits per grid cell fitted to a Poisson distribution.[a]

Frogs			Salamanders			Amphibians		
No. limits	observed	Expected	No. limits	observed	Expected	No. limits	observed	Expected
0	59	47.5	0	38	10.1	0	31 46	3.9 17.4
1	29	44.8	1	19	25.2	1	15	13.5
2	19	21.1	2	20	31.4	2	15	23.2
3	12 15	6.6 8.2	3	14	26.1	3	16	26.6
4	3	1.6	4	11	16.2	4	12	22.8
			5	2	8.1	5	9	15.7
$\bar{x}$=0.9426	s^2=1.25		6	8	3.4	6	2	9.0
CD=1.33	Gadj=14.35		7	3	1.2	7	7	4.4
X^2 (.005)[2]=10.6			8	1	0.4	8	4	1.9
			9	0 18	0.1 5.1	9	3	0.7
			10	0	0.0	10	1	0.3
			11	3	0.0	11	1 22	0.1 7.4
			12	0	0.0	12	0	0.0
			13	3	0.0	13	0	0.0
						14	2	0.0
			$\bar{x}$=2.4918	s^2=8.71		15	1	0.0
			CD=3.50	Gadj=84.67		16	2	0.0
			X^2 (.005)[5]=16.7			17	1	0.0
						$\bar{x}$=3.4344	s^2=14.34	
						CD=4.18	Gadj=75.60	
						X^2 (.005)[5]=16.7		

[a]Classes with expected frequencies of less than five were pooled with an adjacent class.

1966, Hagmeier and Stults 1964, Hammerson 1981, Lee 1980). To delineate and compare areas of faunal homogeneity for frogs, salamanders, and both combined in Tennessee, the sequential, agglomerative, hierarchic, nonoverlapping (SAHN) clustering techniques described by Sneath and Sokal (1973) were used. Sampling units were the same grid cells shown in Figure 2. To perform the cluster analysis, the TAXON and related programs of the Numerical Taxonomy System of Multivariate Statistical Programs (NT-SYS) were used (Rohlf et al. 1974).

The presence or absence of each species was tabulated for each grid cell. A species presence was denoted by the number one and its absence by a zero. The frog, salamander, and total amphibian species compositions of all pairwise combinations of grid cells were compared using the coefficient of Jaccard (Long 1963). The resultant matrices of coefficients (J values) for frog, salamander, and total amphibian species were each subjected to an unweighted pair-group clustering procedure using arithmetic averages (UPGMA). For each cluster analysis, a cophenetic correlation coefficient was calculated. This value measures the amount of distortion of the original matrix of J values caused by the cluster procedures.

To allow comparisons of results from cluster analyses for frogs, salamanders, and total amphibians, all areas of faunal homogeneity were defined at the 0.80 level of similarity. This level was chosen after a review of the computer generated phenograms showing the hierarchial relationships for all grid cells for the three faunal groupings. Delineation of areas of faunal homogeneity at the 0.80 level allowed the recognition of distinct geographic patterns, and the areas defined were small enough to detect minor differences in species composition.

To quantitatively examine the relationships between the patterns exhibited by frog, salamander, and total amphibian species, coefficients of correlation of similarity matrices (Rss) values were calculated (Sneath and Sokal 1973, Bock et al. 1981) (Table 2). The MXCOMP program of NT-SYS (Rohlf et al. 1974) was used to determine these coefficients. A coefficient of correlation of similarity matrices is a measure of the congruence between two matrices that were determined by different sets of characters (Sneath and Sokal 1973), in this case, matrices of J values for frogs, salamanders, and total amphibians.

Table 2. Correlations (Rss values) of frog, salamander, and amphibian similarity matrices.[a]

	Frogs	Salamanders
Salamanders	0.757	
All amphibians	0.855	0.983

[a]Similarity matrices constructed using coefficients of Jaccard

Frog Faunal Areas

For the frog fauna of Tennessee, three areas of faunal homogeneity were recognized (Figure 3). The hierarchial relationships of these areas are illustrated in Figure 4. For the cluster analysis of frog distribution data, the cophenetic correlation coefficient was 0.892. It is important to note that the phenogram in Figure 4 and the two subsequent phenograms presented in this paper (Figure 6 for salamanders and Figure 8 for all amphibians) are condensed versions of the original phenograms and summarize groupings of grid cells at the 0.80 level of similarity.

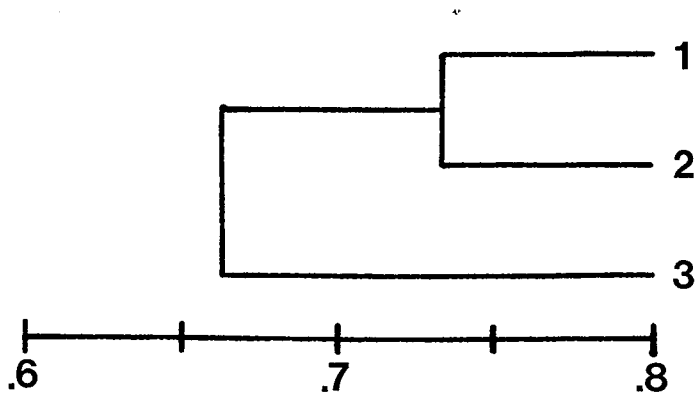

Figure 4. Phenogram showing hierarchial relationships of three major areas of faunal homogeneity based on frog distributions. Areas defined at the 0.80 level of similarity. The cophenetic correlation coefficient is 0.892.

The areas of faunal homogeneity recognized for frog species included: (1) the Coastal Plain of west Tennessee, (2) central and most of east Tennessee, and (3) a small area in the Blue Ridge Mountains of northeastern Tennessee. According to the phenogram in Figure 4, area three is the most distinctive, while areas one and two are more similar in terms of their frog faunas. The number of faunal areas determined for frogs was fewer than the number for salamanders or amphibians. The frequency distribution of the range limits of frog species was shown to possibly tend toward randomness. The fact that almost half of all frog species in Tennessee have statewide distributions and the results of the cluster analysis support this generalization. Species primarily restricted to frog faunal area one include *Acris gryllus*, *Hyla avivoca*, *H. cinerea*, and *Rana areolata*. Species that reach their eastern limits at the eastern border of area two include *Acris*

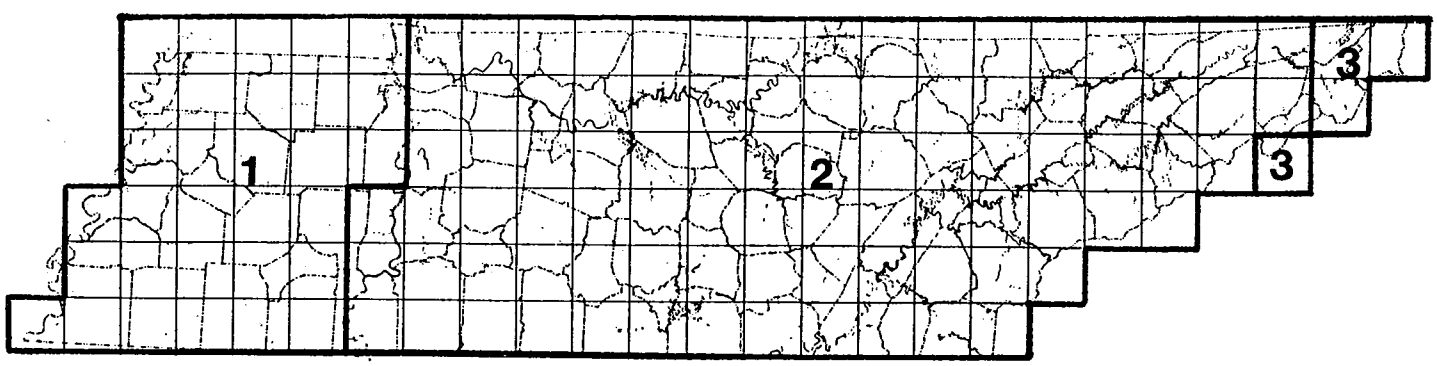

Figure 3. Major areas of faunal homogeneity based on cluster analysis of frog distributions. Areas were defined at the 0.80 level of similarity.

crepitans, *Gastrophryne carolinensis*, and *Scaphiopus holbrookii*. Perhaps the most notable faunal characteristic of frog area three is the apparent absence of *Acris crepitans* and *Rana utricularia*.

Salamander Faunal Areas

Nine areas of faunal homogeneity were recognized for the salamander fauna (Figure 5). Figure 6 depicts the hierarchial relationships of these areas. The cophenetic correlation coefficient was 0.889. Specifically, these areas included (1) the Coastal Plain of west Tennessee, (2) most of central Tennessee including Western and Eastern Highland Rims and Outer and Inner Central Basins, (3) a large part of eastern Tennessee including the Cumberland Plateau, Cumberland Mountains, Sequatchie Valley, and Appalachian Ridge and Valley, (4) a small portion of the Appalachian Ridge and Valley and Blue Ridge Mountains in southeastern Tennessee, (5) the southern Unicoi Mountains, (6) the northern Unicoi Mountains, (7) the Great Smoky Mountains and adjacent parts of the Appalachian Ridge and Valley, (8) the Bald Mountains and adjacent Appalachian Ridge and Valley, and (9) the Blue Ridge Mountains north of Greene County in the northeastern corner of the state.

In terms of geographic size, areas in the easternmost parts of the state tend to be small. A comparison of hierarchial relationships among salamander areas shows area one, the Coastal Plain of west Tennessee, as the most distinctive. Area one is related to all other areas at the 0.45 level of similarity. Areas two, three, and four are grouped together at the 0.67 level of similarity and areas five, six, seven, eight, and nine at the 0.60 level.

The diversity of the salamander fauna of Tennessee is reflected by the large number of faunal areas identified. Of the 41 species present, only seven occur statewide. Two salamander species that are primarily found in the Coastal Plain of west Tennessee reach their eastern range limits near the boundary between areas one and two. These two are *Amphiuma tridactylum*, and *Siren intermedia*. Four species reach the western limits of their distribution in Tennessee near the western boundary of area two. These include *Cryptobranchus alleganiensis*, *Eurycea lucifuga*, *Hemidactylium scutatum*, and *Plethodon dorsalis*. The faunal turnover between areas two and three is due mostly to salamander species reaching the western extents of their ranges along the western boundary of area three. These species include *Aneides aeneus*, *Desmognathus monticola*, *D. ochrophaeus*, and *Gyrinophilus porphyriticus*. However, one species, *Ambystoma texanum*, reaches the eastern extent of its range near the eastern boundary of area two.

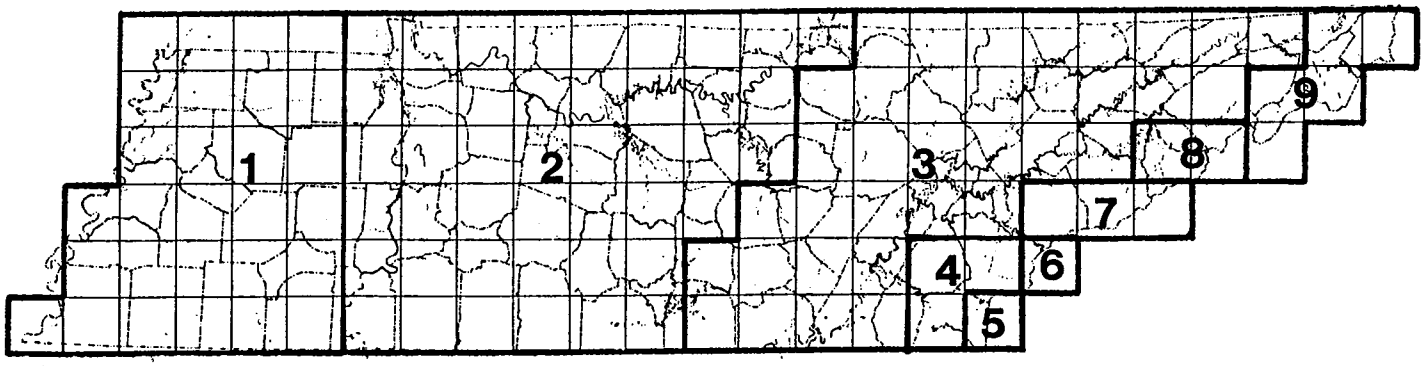

Figure 5. Major areas of faunal homogeneity based on cluster analysis of salamander distributions. Areas were defined at the 0.80 level of similarity.

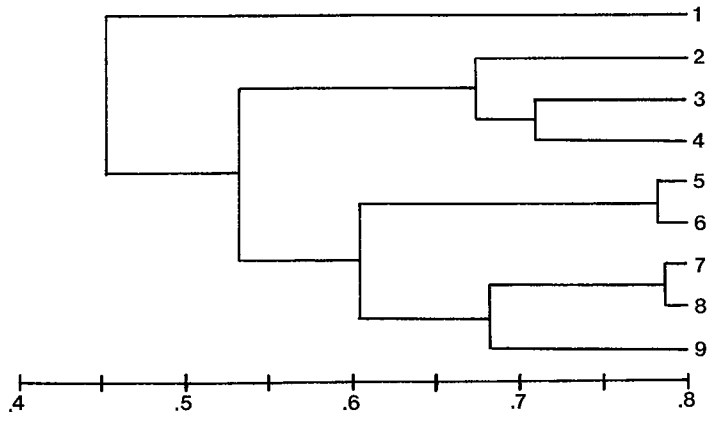

Figure 6. Phenogram showing hierarchial relationships of nine major areas of faunal homogeneity based on salamander distributions. Areas defined at the 0.80 level of similarity. The cophenetic correlation coefficient is 0.889.

The greatest change in salamander faunas occurs in the transition from area three to the six salamander areas centered on the Blue Ridge Mountains in east Tennessee. Species that reach the eastern limits of their distributions near the eastern border of area three include *Ambystoma tigrinum*, *Eurycea lucifuga*, *Gyrinophilus palleucus*, *Plethodon dorsalis*, and *Pseudotriton montanus*. Salamander species that reach the western limits of their distribution near the western borders of areas four, six, seven, eight, and nine include *Desmognathus aeneus*, *D. imitator*, *D. ochrophaeus*, *D. quadramaculatus*, *D. santeetlah*, *D. wrighti*, *Eurycea junaluska*, *Leurognathus marmoratus*, *Plethodon aureolus*, *P. cinereus*, *P. jordani*, *P. serratus*, *P. welleri*, and *P. yonahlossee*.

The number and relative smallness of salamander areas identified in east Tennessee are indicative of the great diversity of species and habitats in the Blue Ridge Mountains. Because of the large number of species and the relatively restricted and overlapping nature of their ranges, a comparison of faunal areas of the Blue Ridge Mountains in terms of north-south faunal changes is difficult. However, a few generalizations are possible. Two species, *Desmognathus aeneus* and *Plethodon aureolus* reach the northern limits of distribution in the northern Unicoi Mountains (area six), whereas the southern range limits of *D. santeetlah* and *P. jordani* occur in the northern Unicois.

Species whose ranges end near the southern terminus of the Great Smoky Mountains (area seven) include *D. imitator, D. wrighti,* and *Leurognathus marmoratus. Desmognathus imitator* is restricted to the Great Smoky Mountains. The range of *D. santeetlah* ends near the northern terminus of the Great Smoky Mountains. The northern limit of distribution of *Plethodon serratus* occurs in area eight in mountains south of the French Broad River. The southern range limit of *P. cinereus* also occurs in area eight, but in the mountains north of the French Broad River. *Plethodon welleri* and *P. yonahlossee* are restricted to faunal area nine.

Amphibian Faunal Areas

For the total amphibian fauna of the state, six areas of faunal homogeneity were delineated (Figure 7), and their hierarchial relationships are shown in Figure 8. The cophenetic correlation coefficient was 0.873. Areas one and six are the most distinctive and are separated from all other areas at the 0.57 and 0.59 levels of similarity, respectively (Figure 8). Areas two, three, four, and five are grouped at the 0.68 level of similarity.

Before discussing areas of homogeneity for all amphibian species and comparing these areas to those defined for frog and salamander species, it is important to review the Rss values presented in Table 2. These values confirm what is self-evident in a comparison of Figures 3, 5, and 7. The distribution of frogs is more closely correlated with the distribution of the total amphibian fauna than with the distribution of salamanders. Also, the distribution of salamanders is more closely correlated with the distribution of total amphibians than with the distribution of frogs. The distribution of total amphibians is more closely correlated with the distribution of salamanders than with that of frogs. Stated differently, salamander distributions exerted a significantly larger influence on the determination of amphibian areas of homogeneity than did frog distributions. This is not surprising since salamander species outnumber frog species by over two to one and salamander distribution patterns are more complex, especially in the Blue Ridge Mountains. Hammerson (1981), Bock et al. (1981), and Lambert and Reed (1981) concluded that the arbitrary lumping of species groups into larger units for biogeographic analyses may obscure the distributional relationships of the component groups. For this reason, areas of faunal homogeneity for amphibians are treated as a summary of the biogeographic patterns of frogs and salamanders and only broad generalizations are discussed.

Major areas of faunal homogeneity for amphibians included (1) the Coastal Plain of west Tennessee, (2) most of central Tennessee including the Western Highland Rim, a small part of the Eastern Highland Rim, and the Outer and Inner Central Basins, (3) a large part of eastern Tennessee including the Cumberland Plateau, Cumberland Mountains, Sequatchie Valley, Appalachian Ridge and Valley, and a small part of the Eastern Highland Rim, (4) the Unicoi Mountains and adjacent parts of the Appalachian Ridge and Valley, (5) the Great Smoky and Bald mountains, and adjacent parts of the Appalachian Ridge and Valley, and (6) the Blue Ridge Mountains north of Greene County in the northeastern corner of the state.

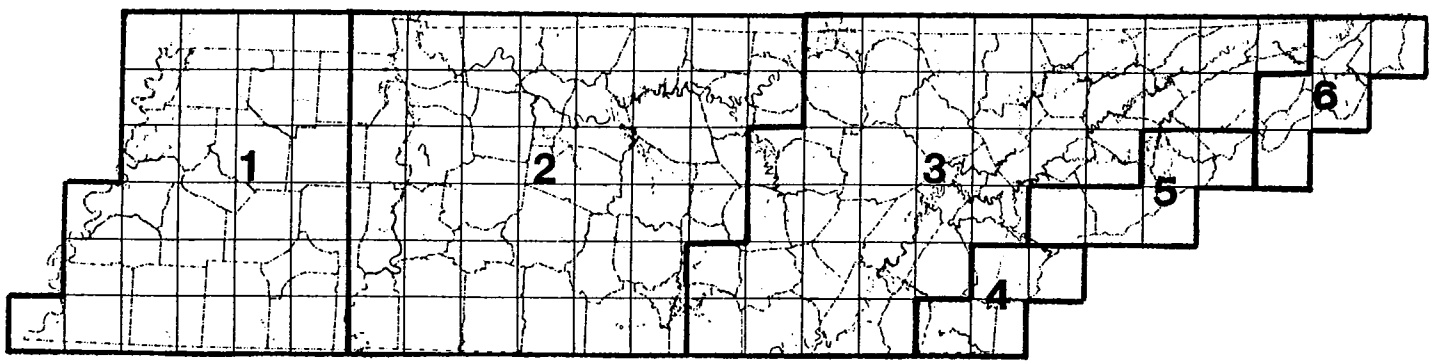

Figure 7. Major areas of faunal homogeneity based on cluster analysis of amphibian distributions. Areas were defined at the 0.80 level of similarity.

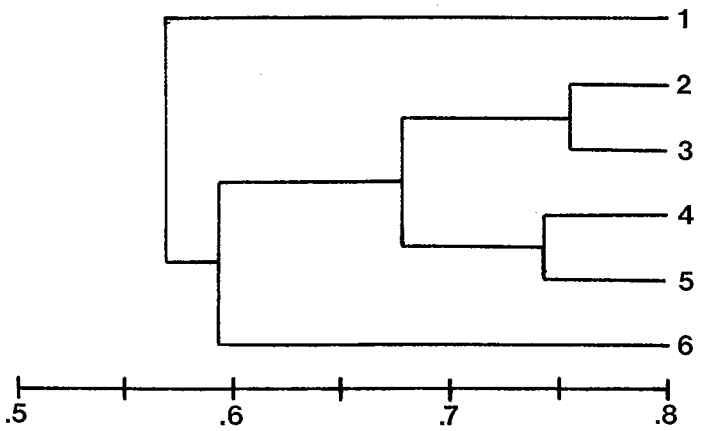

Figure 8. Phenogram showing hierarchial relationships of six major areas of faunal homogeneity based on all amphibian distributions. Areas defined at the 0.80 level of similarity. The cophenetic correlation coefficient is 0.873.

Areas of faunal homogeneity for all amphibians were smaller in the Blue Ridge Mountains. This was primarily due to the presence of a large number of salamander species with relatively complex and restricted distributions. Although there are minor boundary differences, the Coastal Plain of west Tennessee and the Blue Ridge Mountains in northeastern Tennessee are recognized as areas of faunal homogeneity for all three faunal groups. These two areas are on opposite ends of the state and, according to the phenogram in Figure 8, they represent the two most distinctive amphibian faunal areas.

Centers of Dispersal

In an effort to study the faunal composition of areas of faunal

Table 3. Six proposed North American centers of dispersal (cut–in headings) for amphibian species in Tennessee along with literature sources on which they are based.

Species	Source
Southeastern	
Scaphiopus holbrookii, eastern spadefoot	Blair (1965)
Bufo woodhousii, Woodhouse's toad	Blair (1965)
Acris gryllus, southern cricket frog	Blair (1965)
Hyla avivoca, bird-voiced treefrog	Blair (1965)
Hyla cinerea, green treefrog	Blair (1965)
Hyla gratiosa, barking treefrog	Blair (1965)
Gastrophryne carolinensis, E. narrowmouth toad	Blair (1965)
Ambystoma maculatum, spotted salamander	Tihen (1958)
Ambystoma opacum, marbled salamander	Tihen (1958)
Ambystoma talpoideum, mole salamander	Tihen (1958)
Ambystoma texanum, smallmouth salamander	Tihen (1958)
Southwestern	
Acris crepitans, northern cricket frog	Blair (1965)
Pseudacris feriarum, upland chorus frog	Blair (1965)
Rana areolata, crawfish frog	Blair (1965)
Amphiuma tridactylum, three-toed Amphiuma	Blair (1958)
Siren intermedia, lesser siren	Porter (1972)
Ambystoma tigrinum, tiger salamander	Tihen (1958)
Southern	
Hyla versicolor/chrysoscelis, gray treefrogs	Blair (1965)
Rana catesbeiana, bullfrog	Blair (1958)
Rana clamitans, green frog	Blair (1958)
Rana palustris, pickerel frog	Blair (1958)
Eastern Atlantic Coast	
Rana utricularia, southern leopard frog	Pace (1974)
Necturus maculosus, mudpuppy	Sessions & Wiley (1985)
Northern	
Bufo americanus, American toad	Blair (1965)
Pseudacris crucifer, spring peeper	Blair (1965)
Rana sylvatica, wood frog	Porter(1972)
Notophthalmus viridescens, eastern newt	Estes (1970)
Appalachian Highlands	
Pseudacris brachyphona, mountain chorus frog	Blair (1965)
Cryptobranchus alleganiensis, hellbender	Redmond (1985)
Plethodon (all 31 species), woodland salamanders	Wake (1966)

homogeneity in terms of past dispersal patterns of their component species, all species were classified according to their proposed North American center of dispersal. The six proposed North American centers of dispersal for amphibian species in Tennessee are given in Table 3, and are admittedly speculative.

For several species, the sources listed in Table 3 did not specifically propose a North American center of dispersal. For these species, a center of dispersal was arbitrarily assigned based on other evolutionary or biogeographic information provided by the source. For each frog, salamander, and combined amphibian area of faunal homogeneity, total species density was tabulated and the percent species composition from each major North American center of dispersal calculated. Though speculative, it is felt that a description of areas of faunal homogeneity in terms of the past dispersal patterns of species will allow the recognition of some possibly significant trends.

Frog Centers of Dispersal

Frog species with a southeastern center of dispersal dominate all three frog faunal areas (Figure 9). Species with a southeastern center make up 40% of area one, 31% of area two, and 33% of area three. Species associated with a southern center of dispersal rank second in order of dominance and make up 24% of area one, 25% of area two, and 33% of area three. Species with southwestern and eastern Atlantic

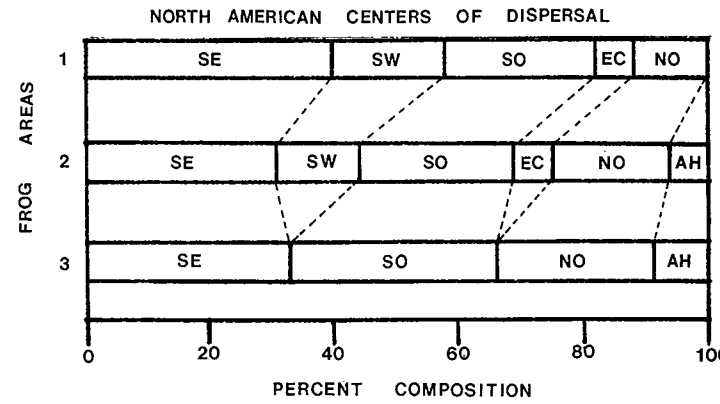

Figure 9. Percent composition of frog species grouped according to their North American centers of dispersal in the three areas of frog faunal homogeneity. SE denotes a southeastern center of dispersal, SW-southwestern, SO-southern, EC-eastern Atlantic Coast, NO-northern, and AH-Appalachian Highlands.

Coast centers are minor faunal components of areas one and two and are entirely absent from area three. Species with a northern center increase in importance from areas one through three making up 12%, 20%, and 25% of the total frog fauna in each, respectively. Frog species with an Appalachian Highlands center are absent from area one and constitute 9% of the fauna of area three.

Frog areas of faunal homogeneity are dominated by species that dispersed from southeastern, southwestern, and southern centers of dispersal. The especially high percent of these species in the Coastal Plain of west Tennessee (frog area one) and the gradual decrease in their importance from west to east, indicates these species probably dispersed into Tennessee via the Mississippi River Valley. Several of these species have successfully dispersed eastward to the base of the Blue Ridge Mountains and others have dispersed throughout the entire state and over most of the eastern United States. While the three previously discussed centers of dispersal are extraneous to Tennessee, the northern and Appalachian Highlands centers are probably intraneous. Of the four frog species thought to have dispersed from a northern or Appalachian Highlands center, only *Bufo americanus* and *Pseudacris crucifer* occur in the Coastal Plain in west Tennessee.

Salamander Centers of Dispersal

Except for area one, all areas of faunal homogeneity for salamander species are dominated by species with an Appalachian Highlands

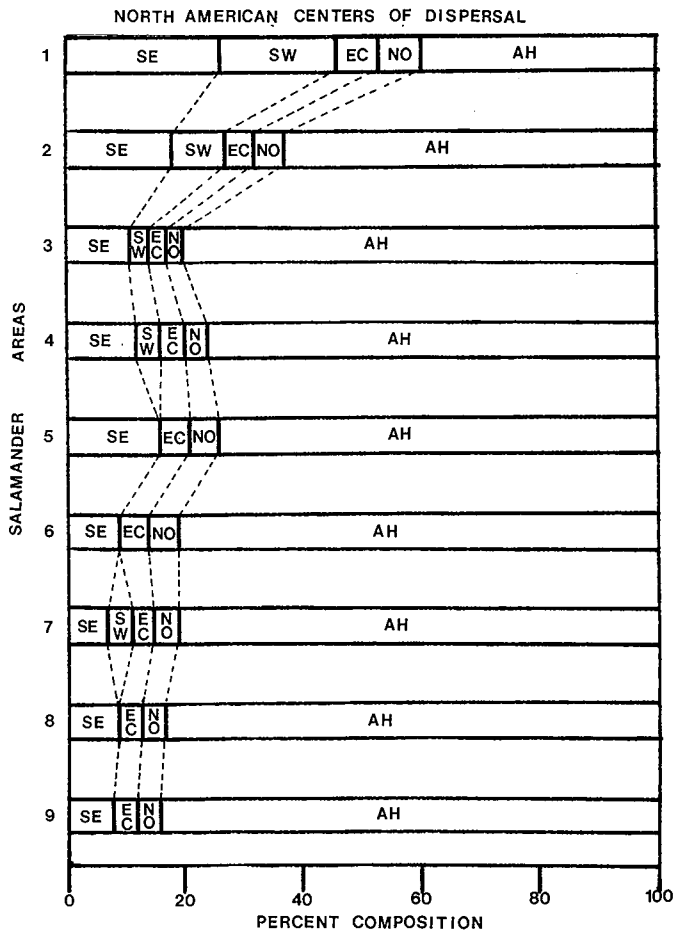

Figure 10. Percent composition of salamander species grouped according to their North American centers of dispersal in the nine areas of salamander faunal homogeneity. SE denotes a southeastern center of dispersal, SW-southwestern, EC-eastern Atlantic Coast, NO-northern, and AH-Appalachian Highlands.

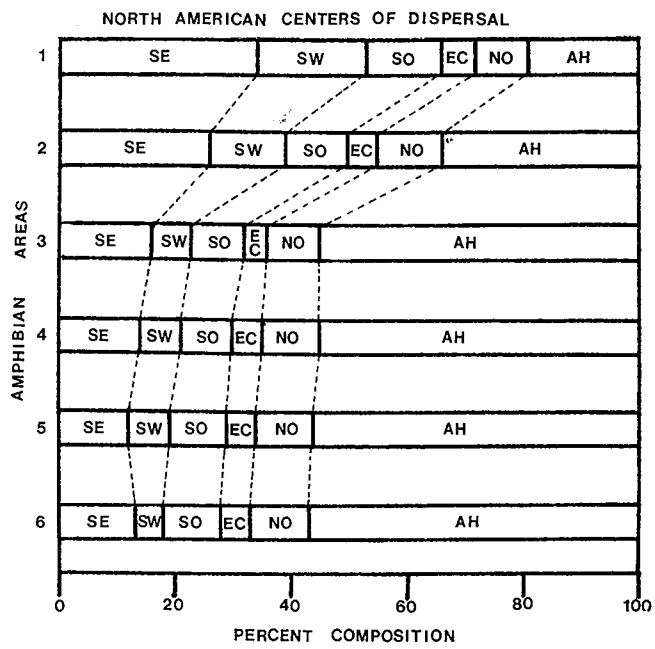

Figure 11. Percent composition of amphibian species grouped according to their North American centers of dispersal in the six areas of amphibian faunal homogeneity. SE denotes a southeastern center of dispersal, SW-southwestern, SO-southern, EC-eastern Atlantic Coast, NO-northern, and AH-Appalachian Highlands.

center of dispersal (Figure 10). Specific percentages include 40% in area one, 63% in area two, 80% in area three, 76% in area four, 74% in area five, 81% in area six, 81% in area seven, 83% in area eight, and 84% in area nine. Salamander species whose centers of dispersal are southeastern or southwestern North America are significant faunal components of areas one (46%) and two (27%), but are minor components of areas three through nine. No salamander species were determined to have a southern center of dispersal.

Seven salamander species, out of 41 total, were proposed to have dispersed from southeastern or southwestern centers of dispersal. Only in west Tennessee do these species outnumber salamander species associated with an Appalachian Highlands center of dispersal. The percent faunal composition from southeastern and southwestern centers in salamander faunal areas decreases from west to east across the state. As discussed for frog species, this trend supports the theory that species from southeastern and southwestern centers of dispersal entered the state via the Mississippi Valley and dispersed eastward. With the exception of area one, the salamander faunas of all areas are dominated by species thought to have an Appalachian Highlands center of dispersal. However, for these species, use of the word dispersal may be misleading, because many species in Tennessee originating from the Appalachian Highlands have not dispersed at all. Most of Tennessee east of the Eastern Highland Rim is considered part of the Appalachian Highlands as defined by Fenneman (1938).

Amphibian Centers of Dispersal

The composition of areas of faunal homogeneity for all amphibians (Figure 11) shows tendencies similar to those for salamander faunal areas. Amphibian species with an Appalachian Highlands center of dispersal constitute 19% of the total amphibian fauna in area one, 34% in area two, and over 50% in areas four, five, and six. Species associated with southeastern, southwestern, and southern centers of dispersal make up 66% of the total fauna in area one, 50% of area two, and approximately 30% of areas three, four, five, and six.

By comparing Figure 9 with Figure 3, Figure 10 with 5, and Figure 11 with 7, the relative importance of North American centers of dispersal can be summarized in geographic terms. Areas of faunal homogeneity in west Tennessee are dominated by species from southeastern, southwestern, and southern centers of dispersal. This is best exemplified by frog and amphibian areas one, but is also evident in salamander area one. From west to east Tennessee, the relative importance of species from these three centers of dispersal decreases. This west to east decrease is smaller for frog areas than in salamander and amphibian areas. Faunas from Appalachian Highlands and northern centers of dispersal contribute the largest number of species to areas of faunal homogeneity in the mountains of east Tennessee. In contrast to species from southeastern, southwestern, and southern centers, their relative importance decreases from east to west Tennessee.

Comparisons with Previous Studies

The areas of faunal homogeneity and dispersal patterns determined during this study, when compared to previously described faunal or biotic regions identified in Tennessee, are for the most part unique.

Dice's (1943) map of biotic provinces of North America shows two provinces in Tennessee. The Mississippi River Valley is regarded as

part of a southern province termed the Austroriparian Biotic Province, while the remainder of Tennessee is included in the Carolinian Biotic Province. Other than recognizing the biota of western Tennessee as more southern than northern in affinity, Dice's scheme bears little resemblance to the faunal patterns determined for frogs, salamanders, and amphibians during this study.

Hagmeier (1966) mapped three mammal provinces in Tennessee. The Louisianian Province (of southern affinity) included a small strip of land along the entire southern border of Tennessee. Most of the rest of the state was included in the Carolinian Province. Only his Alleghenian Province, a small area of northern affinity in the northeastern corner of Tennessee, corresponds closely to any of the areas delineated during this study. These include frog area three, salamander area nine, and total amphibian area six.

Based on a review of amphibian and reptilian distributions, Johnson (1958) proposed two herpetofaunal districts and two zones for eastern Tennessee. The Transition District included the Cumberland Plateau, Sequatchie Valley, Appalachian Ridge and Valley south of Knoxville, the lower slopes (below 760 m elevation) of the Blue Ridge Mountains south of the French Broad River, and all of the Blue Ridge Mountains south of the Hiwassee River. The fauna of the Transition District was characterized as a mixture of species with southern, northern, and western affinities. Johnson's Alleghenian District included the Cumberland Mountains, Appalachian Ridge and Valley north of Knoxville, mid-slopes (up to 912 m elevation) of the Blue Ridge Mountains north of the French Broad River, and mid-slopes (760 to 912 m elevation) of Blue Ridge Mountains south of the French Broad River to the Hiwassee River. The Alleghenian District was characterized as possessing a fauna primarily of northern affinity but with a few species of southern and eastern affinities. The Jordanian Zone was defined as the Blue Ridge Mountains between 1,064 and 1,520 m elevations in the south and between 912 to 1,368 m elevations in the north. This zone was characterized as possessing a northern hardwoods forest and the widespread occurrence of all color morphs of *Plethodon jordani*. The Summit Zone included all peaks of the Blue Ridge Mountains above 1,368 and 1,520 m elevations. Johnson characterized this zone as having a depauperate herpetofauna. The only significant similarity between the faunal areas recognized by Johnson and those determined by this study is that faunal assemblages in the Blue Ridge Mountains are recognized as distinct and tend to form smaller units as compared to faunal assemblages in other parts of the state. Apparently, Johnson did not consider north to south faunal changes as important as elevational changes in the Blue Ridge Mountains and did not recognize separate faunal areas in a north-south direction. His faunal zones in the Blue Ridge Mountains are primarily a reflection of faunal changes associated with increasing elevation.

Sinclair (1968) described the faunal distinctiveness of the Central Basin in Tennessee. Regarding the amphibian fauna, the results of this study do not support recognition of this physiographic region as a distinct faunal area.

LITERATURE CITED

Bailey, J. R. 1936. *Microhyla carolinensis* in northeastern Tennessee. Copeia 1936(2):115.

Bailey, J. R. 1937. Notes on plethodont salamanders of southeastern United States. Occ. Papers Mus. of Zool., Univ. of Mich. No. 364.

Blair, W. F. 1958. Distributional patterns of vertebrates in the southern United States in relation to past and present environments. Pp. 433-468 *in:* Hubbs, C. L. (ed.). Zoogeography. Amer. Assoc. Adv. Sci. Publ. No. 51.

Blair, W. F. 1965. Amphibian speciation. Pp. 543-556 *in:* Wright, H. E., and D. G. Frey (eds.). The Quaternary of the United States. Princeton Univ. Press, Princeton, NJ.

Blanchard, F. N. 1922. The amphibians and reptiles of western Tennessee. Occ. Papers Mus. of Zool., Univ. of Mich. No. 117.

Blatchley, W. S. 1901. On a small collection of batrachians from Tennessee, with descriptions of two new species. 25th Ann. Rept. Dept. Geol. Nat. Resources, Indiana, 1900:759-763.

Bock, J. H., C. E. Bock, and R. J. Fritz. 1981. Biogeography of Illinois reptiles and amphibians. Am. Midl. Nat. 106:258-270.

Burt, C. E. 1938. The frogs and toads of the southeastern United States. Trans. Kans. Acad. Sci. 41:331-360.

Cope, E. D. 1889. Batrachia of North America. Bull. U.S. Natl. Mus. No. 34.

Dice, L. R. 1943. The biotic provinces of North America. Univ. of Mich. Press, Ann Arbor, MI

Estes, R. 1970. Origin of recent North American lower vertebrate fauna: an inquiry into the fossil record. Forma et Functio 3:139-163.

Fenneman, N. M. 1938. Physiography of eastern United States. McGraw-Hill Book Co., New York, NY.

Gentry, G. 1937. A preliminary survey of the Amphibia of Tennessee. M.S. thesis, George Peabody College for Teachers, Nashville, TN.

Gentry, G. 1955-1956. An annotated checklist of the amphibians and reptiles of Tennessee. J. Tenn. Acad. Sci. 30:168-176 and 31:242-251.

Gentry, G., R. M. Sinclair, W. Hon, and B. Ferguson.1965. Amphibians and reptiles of Tennessee. Tenn. Game and Fish Comm., Nashville, TN.

Hagmeier, E. M. 1966. A numerical analysis of the distributional patterns of North American mammals. II. Reevaluation of the Provinces. Syst. Zool. 15:279-299.

Hagmeier, E. M., and C. D. Stults. 1964. A numerical analysis of the distributional patterns of North American mammals. Syst. Zool. 13:125-155.

Hammerson, G. A. 1981. An ecogeographic analysis of the herpetofauna of Colorado. Ph.D. diss., Univ. of Colorado, Boulder.

Harper, F. 1935. Records of amphibians in the southeastern states. Am. Midl. Nat. 16:275-310.

Johnson, R. H. 1958. A biogeographic study of the herpetofauna of eastern Tennessee. Ph.D. diss., Univ. of Florida, Gainesville.

King, W. 1939. A survey of the herpetology of Great Smoky Mountains National Park (Tennessee). Am. Midl. Nat. 21:531-582.

Lambert, S., and W. H. Reid. 1981. Biogeography of the Colorado herpetofauna. Am. Midl. Nat. 106:145-156.

Lee, J. C. 1980. An ecogeographic analysis of the herpetofauna of the Yucatan Peninsula. Univ. of Kans. Mus. Nat. Hist., Misc. Publ. No. 67.

Long, C. A. 1963. Mathematical formulas expressing faunal resemblance. Trans. Kans. Acad. Sci. 66:138-140.

Pace, A. E. 1974. Systematic and biological studies of the leopard frogs (*Rana pipiens* complex) of the United States. Misc. Publ., Mus. of Zool., Univ. of Mich. No. 148.

Porter, K. R. 1972. Herpetology. W. B. Sanders Co., Philadelphia, Penn.

Redmond, W. H. 1985. A biogeographic study of amphibians in Tennessee. Ph.D. diss., Univ. of Tenn., Knoxville.

Redmond, W. H., A. C. Echternacht, and A. F. Scott.1990. Annotated checklist and bibliography of amphibians and reptiles of Tennessee (1835-1989). Misc. Publ. Center for Field Biol., Austin Peay State Univ., Clarksville, Tenn. No. 4.

Rhoads, S. N. 1895. Contributions to the zoology of Tennessee. No. 1. Reptiles and amphibians. Proc. Acad. Nat. Sci. Philadelphia 47:376-407.

Rohlf, F. J., J. Kishpaugh, and D. Kirk. 1974. Numerical taxonomy system of multivariate statistical programs. Computer printout. State Univ. of New York, Stoney Brook, NY.

Sessions, S. K., and J. E. Wiley. 1985. Chromosome evolution in salamanders of the genus *Necturus*. Brimleyana No. 10:37-52.

Sinclair, R. M. 1968. The Central Basin Physiographic Province and its influence on the distribution of Tennessee amphibians and reptiles. J. Herpetology 1:120-121. (Abstract).

Sneath, P. H. A., and R. R. Sokal. 1973. Numerical Taxonomy. W. H. Freeman and Company, San Francisco, CA.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman and Company, San Francisco, CA.

Sokal, R. R., and P. H. A. Sneath. 1963. Principles of numerical taxonomy. W. H. Freeman and Company, San Francisco, CA.

Tihen, J. A. 1958. Comments on the osteology and phylogeny of ambystomatid salamanders. Bull. Flor. State Mus. 3:1-50.

Troost, G. 1843. Pages 39-40 in seventh geological report to the twenty-fifth general assembly of the state of Tennessee. W. F. Band and Co. and B. R. Mckennie Printers, Nashville, TN.

Wake, D. B. 1966. Comparative osteology and evolution of the lungless salamanders, family Plethodontidae. Memoirs Southern Calif. Acad. Sci. 4:1-111.