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A Biogeographic Study of Amphibians in Tennessee

William H. Redmond Jr.
University of Tennessee, Knoxville

To the Graduate Council:

I am submitting herewith a dissertation written by William H. Redmond Jr. entitled "A Biogeographic Study of Amphibians in Tennessee." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

Arthur C. Echternacht, Major Professor

We have read this dissertation and recommend its acceptance:

H. R. DeSelm, D. A. Etnier, D. L. Bunting, C. C. Amundsen

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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A BIOGEOGRAPHIC STUDY
OF
AMPHIBIANS IN TENNESSEE

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

William H. Redmond, Jr.

December 1985

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ABSTRACT

Range maps and descriptive, taxonomic, and habitat information are provided for 20 species of frogs and 41 species of salamanders. The environmental setting of Tennessee is described in terms of geology, physiography, climate, drainages, soils, vegetation, and ecoregions. For the purposes of the analyses, a grid cell pattern containing 122 sampling units is used, and the amphibian fauna is organized into three faunal groups. These groups are frog species, salamander species, and all species grouped together as amphibians. The results of a G-test for the frequency distribution of range limits fitted to a Poisson distribution suggest a clumped dispersion pattern for each faunal group. Using the coefficient of Jaccard, cluster analyses of distribution data delineate three areas of faunal homogeneity for frogs, nine for salamanders, and six for all amphibians. Coefficients of correlation of similarity matrices are calculated and indicate that (1) the geographic distribution patterns of both frogs and salamanders are most closely correlated with the patterns of climate, soils, and physiography; and (2) when compared to frogs, salamander distributions exert a larger influence on the determination of amphibian areas of homogeneity. An analysis of the faunal composition of areas of homogeneity in terms of past dispersal patterns of their component species reveals that frog areas are dominated by species that dispersed from southeastern, southwestern, and southern centers of dispersal while salamander areas are dominated by species with an Appalachian Highland center of dispersal. Simple correlation and stepwise multiple regression analyses of the relationships between frog, salamander, and amphibian species densities and values for 17 environmental variables indicate that frogs and salamanders exhibit diametrically different responses to a majority of the environmental gradients studied. Modified by historical factors, aspects of the evolutionary time, ecological time, and spatial heterogeneity theories are used to tentatively explain these density gradients. Frog and salamander faunas of Tennessee exhibit significantly different biogeographic patterns. This is evident in both a study of areas of faunal homogeneity and an analysis of species densities. Results from analyses of total amphibian fauna obscure the unique characteristics of each faunal group.

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CHAPTER I

INTRODUCTION

Nearly all previous works concerning the amphibians of Tennessee have been descriptive. Early studies referring to the amphibian fauna of Tennessee include Troost (1844), 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 of amphibians from Tennessee, and later Gentry, Sinclair, Hon, and Ferguson (1965) noted 47 species and provided distribution maps.

County surveys have been conducted in Knox (Taylor, 1938), Davidson (Ashton, 1966), Montgomery (Scott and Snyder, 1968), and Hardeman (Norton and Harvey, 1975) counties. Also, there have been numerous surveys of selected ecological areas of the state. Parker (1937, 1939) studied the amphibian and reptilian fauna of Reelfoot Lake. Numerous authors have worked in the Great Smoky Mountains National Park. Some of their more important works include Hassler (1929), McClure (1931), Weller (1931), Necker (1934), King (1939, 1944), Huheey and Brandon (1961), Huheey and Stupka (1965, 1967), and Huheey (1966). A survey of amphibians and reptiles of a central Tennessee cedar glade was provided by Jordan, Garton, and Ellis (1968), and Harris (1967) studied the herpetofauna on Davies Island in Center Hill Reservoir. Phillips and Richmond (1971) listed amphibians found on islands of Boone and Watauga reservoirs in northeastern Tennessee. Snyder (1972) provided a handbook of amphibians and reptiles for Land Between The Lakes Recreation Area in northwestern Tennessee and adjacent Kentucky.

Additional studies of importance include Shoup, Peyton, and Gentry's (1941) survey of counties in the vicinity of the Obey River; Johnson's (1964) survey of the Oak Ridge area; Parker's (1948) and Endsley's (1954) studies in western Tennessee. Many other authors have published information concerning amphibians of Tennessee in distributional, taxonomic, and ecological studies. Shoup (1974) provided an extensive bibliography of publications dealing with the herpetofauna of Tennessee and the Tennessee Valley Region.

While most studies have been descriptive, a few have attempted to describe and analyze biogeographic patterns. King (1939) described the geographic affinities of amphibian species in the Great Smoky Mountains National Park. The faunal distinctiveness of the Central Basin of Tennessee was recognized by Sinclair (1968). Perhaps the most thorough biogeographic investigation was Johnson's (1958) analysis of the herpetofauna of east Tennessee.

The primary goals of this study are to (1) determine amphibian species present and delineate their distributions in Tennessee; (2) review species origins and dispersal patterns as they occurred in the geological past; (3) delineate amphibian faunal regions; and (4) analyze current distribution patterns and species densities with respect to topography, drainage systems, soils, climate, vegetation, and past geological and environmental conditions.

CHAPTER II

ENVIRONMENTAL SETTING

A. Geology

Major geological deposits are shown in Figure 1. Unless otherwise noted, strata categories, designations, and descriptions were taken from Miller (1974). The major exception involves deposits in west Tennessee where geological age designations and boundaries follow Hardeman (1966). Deposit descriptions proceed from oldest to youngest.

Precambrian surface deposits occur in eastern Tennessee along the North Carolina border and form the backbone of the Blue Ridge Mountains. Precambrian deposits include rocks of igneous origin and rocks of sedimentary origin and range between 600 million and one billion years old. Luther (1977) described how these sediments filled a large geosyncline about one billion years ago. Possibly as a result of colliding continents, these deposits were folded, broken, pushed to the northwest and buried very deeply. They have undergone varying degrees of metamorphism and have endured several cycles of uplift and erosion. Rock types include slate, schist, quartzite, granite, gneiss, and lava. No fossil remains are known from Precambrian deposits in Tennessee.

Cambrian deposits form several mountain ranges west of the high Precambrian deposits along the Tennessee-North Carolina border. Rocks include quartzite, sandstone, shale, siltstone, limestone, and dolomite. Like Precambrian deposits, Cambrian strata are the result of a long period of sedimentation that began approximately 600 million

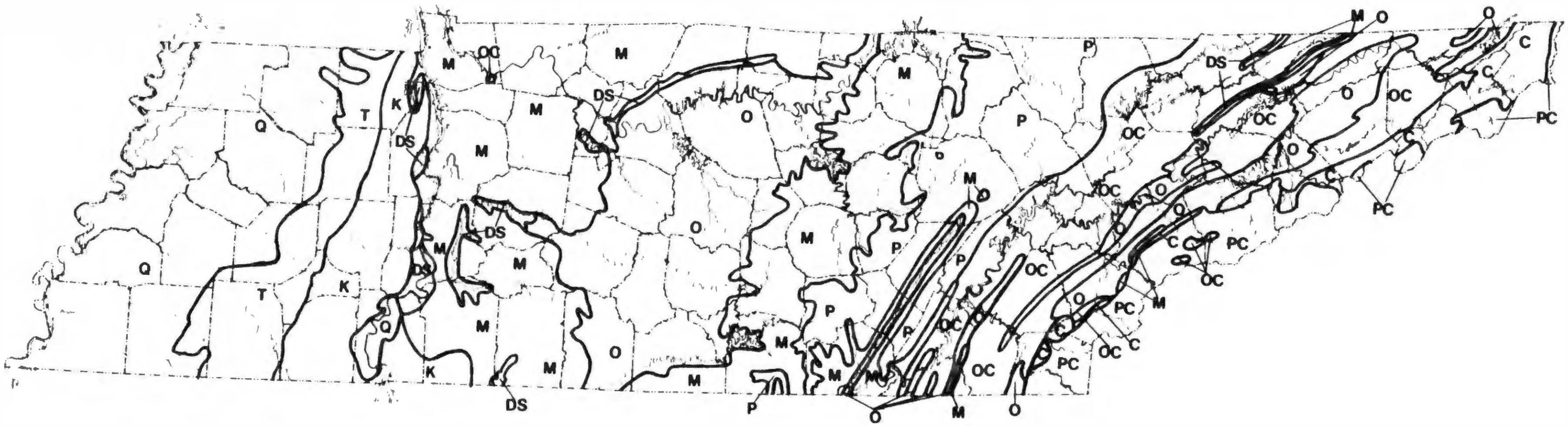

Figure 1. Major geological strata (modified from Miller, 1974). Areas labeled Q denote Quaternary deposits, T-Tertiary deposits, K-Cretaceous deposits, P-Pennsylvanian deposits, M-Mississippian deposits, DS-Devonian and Silurian deposits, O-Ordovician deposits, OC-Ordovician and Cambrian deposits, C-Cambrian deposits, and PC-Precambrian deposits.

years ago. This was followed by folding, faulting, burial, metamorphism, and subsequent cycles of uplift and erosion. In Tennessee, Cambrian deposits contain invertebrate and algal fossils associated with marine environments. Ostracods, trilobites, brachiopods, gastropods, graptolites, and the borings and trails of worms have been found.

Ordovician strata are commonly found in the Appalachian Ridge and Valley and Central Basin. Rocks are primarily metamorphic and include dolomite and limestone. Ordovician deposits are the result of at least two episodes of marine sedimentation and are as old as 500 million years. In east Tennessee, Ordovician strata have undergone severe folding and faulting. Coral fossils are found for the first time in Tennessee, and many other marine invertebrates are represented. These include bryozoans, brachiopods, cephalopods, graptolites, ostracods, and trilobites.

Silurian deposition is considered a continuation of marine sedimentation of the Ordovician. Silurian strata range in age from 430 to 410 million years old and include limestone, shale, dolomite, and sandstone. Silurian outcrops are most common along the Tennessee River in west Tennessee, along stream valleys of the Western Highland Rim, and along the northwestern border of the Central Basin. Silurian sandstones form several high ridges in the Ridge and Valley of east Tennessee. Invertebrate fossils of this period are similar to those of the Ordovician and include corals, brachiopods, cephalopods, gastropods, trilobites, sponges, and crinoids.

Devonian marine deposition began approximately 410 million years ago and ended approximately 350 million years ago. Several episodes of emergence and erosion occurred; however, by late Devonian, these deposits covered most of Tennessee west of the Blue Ridge Mountains. In Tennessee, Devonian rocks are predominately shale. Erosion has removed these shales from most of Tennessee with outcrops now present along the border of the Central Basin, Tennessee River Valley in west Tennessee, and several areas of east Tennessee. Marine invertebrates, especially brachiopods, continued to abound. In Tennessee, the first land plant fossil, driftwood, and the first vertebrate remains, an armor-plated fish, are found in Devonian strata.

Mississippian deposits range from 350 to 325 million years old and include chert, shale, siltstone, limestone, and dolomite. During the Mississippian, shallow seas covered most of the state. Presently, deposits are found throughout the Eastern and Western Highland Rims, on hilltops in the Central Basin and on some ridges in east Tennessee. Fossils found in Mississippian deposits include fish bones and teeth, crinoids, foraminifera, corals, brachiopods, and bryozoans.

Conditions during the Pennsylvanian were apparently very similar to those of the Mississippian and, in Tennessee, a distinct boundary between the two is often absent. Pennsylvanian sedimentation began 325 million years ago and ended 285 million years ago. The most common rocks are sandstone and shale. Pennsylvanian strata form the Cumberland Mountains and Cumberland Plateau. The complexity of deposits indicates numerous advances and retreats of shorelines and their ecosystems. Fossil remains indicate a warm tropical environment with large stands of swamp forests where scale trees, ferns, and rushes were common. Fossil fish scales are the only vertebrate remains known from the

Pennsylvanian in Tennessee. Also, in Tennessee, the end of the Pennsylvanian marked the end of active deposition of sediments during the Paleozoic and the beginning of events that lifted the landscape above sea level and built the foundations of the Appalachian Mountains.

During the Permian, which lasted from 230 to 285 million years before present, sediments that had accumulated for millions of years were buckled, folded, subjected to intense pressures, pushed to the northwest, and lifted to form the Appalachian Mountain Range. Evidence of these events occurs as far west as the Cumberland Plateau in Tennessee. During the Permian all areas of the state were lifted above sea level and, with the exception of the Coastal Plain of west Tennessee, no subsequent periods of marine deposition have occurred. The present topography of areas east of the Tennessee River Valley in west Tennessee is the result of weathering and eroision of this newly uplifted landscape. These processes continued through the Triassic, Jurassic, and early Cretaceous Periods.

About 70 million years ago, during the late Cretaceous, a shallow sea returned to west Tennessee to begin another episode of marine sedimentation (Luther, 1977). This sea is commonly called the Mississippi Embayment and extended as far north as southern Illinois. Cretaceous deposits in Tennessee are predominately sands, clay, and silt. Fossils include remains of marine fish and reptiles, cephalopods, pelecypods, and gastropods. The Mississippi Embayment continued to cover west Tennessee and possibly parts of middle Tennessee until mid-Tertiary times. Luther (1977) estimated its retreat to have occurred about 40 million years ago. Tertiary deposits in Tennessee are mostly sand, clay, and silt. Fossils from Tertiary deposits include leaves, flowers, and stems of plants that are similar to present day species. Animal fossils include whale bones and turtle remains.

The Quaternary began approximately 2.5 million years ago and, in North America, this period has been marked by four major glacial advances and retreats. Even though none of these ice sheets are thought to have extended as far south as Tennessee, their effect on climate and stream flows had profound consequences for the Tennessee landscape, especially in west Tennessee. Perhaps the most notable depositional feature is the large deposits of loess in west Tennessee. Loess beds are thick in some areas and were formed by the accumulation of wind-blown powdered rock material that was pulverized by the movement of ice sheets north of Tennessee. With each major glacial advance, sea levels were lowered and continental stream gradients increased. Alternately, each glacial retreat resulted in higher sea levels and less severe stream gradients. Thus, during the Quaternary, streams and drainage systems in Tennessee were subjected to alternating cycles of gorge development during times of low sea levels and floodplain development during times of high sea levels. Fossil evidence indicates the Quaternary fauna of Tennessee included mastodons, wooly mammoths, large cats, ground sloths, and camels. These forms became extinct approximately 10,000 years ago, at about the time of the last glacial retreat. The climatic and other events of the Quaternary have had a direct influence in determining present-day amphibian distribution patterns in Tennessee. These events and other fossil faunas of the Quaternary are discussed in greater detail in Chapter IV.

B. Physiography

Physiographic features of Tennessee are illustrated in Figure 2. With several modifications, descriptions of these features and their boundaries were taken from Miller (1974). In terms of the physiographic provinces of Fenneman (1938), the features of Tennessee may be catagorized as follows. The Mississippi River Valley, Loess Plain, and Coastal Plain Uplands make up the Gulf Coastal Plain Province. The Interior Low Plateaus Province includes the Western and Eastern Highland Rims and the Outer and Inner Central Basins. The Cumberland Plateau, Cumberland Mountains, and Sequatchie Valley make up the Appalachian Plateaus Province. No subdivisions are recognized for the Appalachian Ridge and Valley and Blue Ridge Mountains provinces.

The Blue Ridge Mountains extend along the entire border of eastern Tennessee. The highest elevations in Tennessee are found here with several peaks rising above 1830 m. Major high mountain ranges near the North Carolina border vary from 1477 to 2025 m in peak elevations and include the Stone Mountains, Roan Mountain, Unaka Mountains, Bald Mountains, Great Smoky Mountains, and Unicoi Mountains. Mountains to the west of these high ranges are typically oriented in a northeast-southwest direction and include Holston Mountain, Iron Mountains, Doe Mountain, Meadow Creek Mountains, English Mountain, Chilhowee Mountain, Starr Mountain, Bean Mountain, Big Frog Mountain, and Little Frog Mountain. Peak elevations range from 654 to 1321 m. The Blue Ridge Mountains are characterized by a steep topography that is heavily forested. Valleys tend to be narrow and found only along large creeks and rivers. However, several isolated limestone valleys with valley

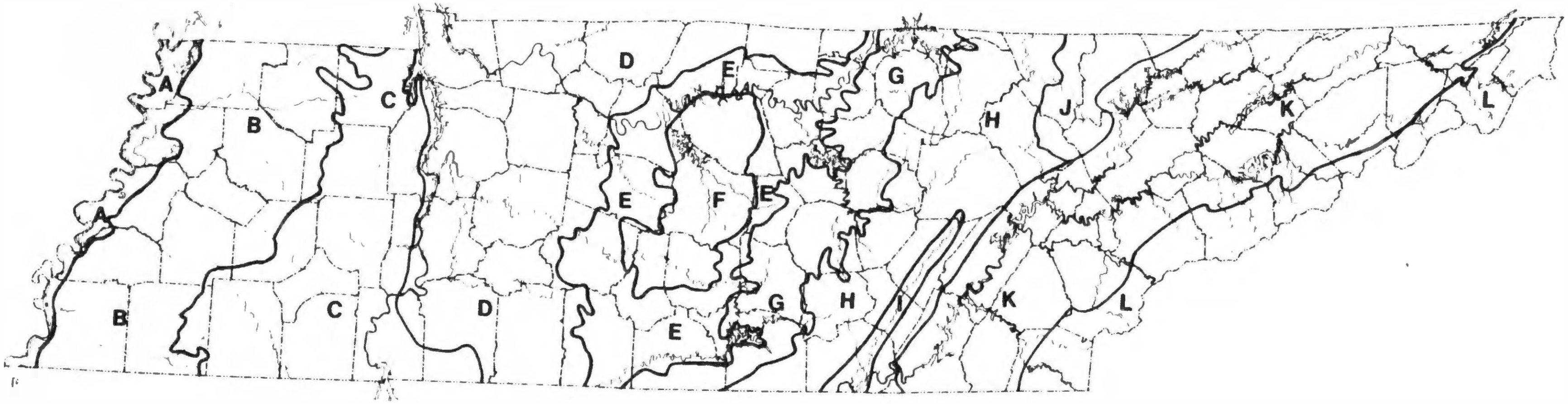

Figure 2. Physiographic features (modified from Miller, 1974). Area labeled A denotes Mississippi River Valley, B-Loess Plain, C-Coastal Plain Uplands, D-Western Highland Rim, E-Outer Central Basin, F-Inner Central Basin, G-Eastern Highland Rim, H-Cumberland Plateau, I-Sequatchie Valley, J-Cumberland Mountains, K-Appalachian Ridge and Valley, and L-Blue Ridge Mountains.

floor elevations ranging from 335 to 854 m are present. The most notable of these are Shady Valley, Bumpass Cove, Wear Cove, Cades Cove, and Tuckaleechee Cove.

Immediately west of the Blue Ridge Mountains is the Appalachian Ridge and Valley Province. This area possesses a topography marked by long, narrow, steep-sided ridges with interposed valleys, both of which are oriented in a northeast-southwest direction. Major ridges include Clinch Mountain, Powell Mountain, and the Bays Mountains in the northern portions and Whiteoak Mountain in the southern portion. Elevation of these prominent ridges ranges from 944 m on Bays Mountains to 456 m on Whiteoak Mountain. Average valley elevations range from 305 m in the north to 229 m in the south. Also, valleys tend to be larger and more numerous in the southern part of the Appalachian Ridge and Valley Province.

The topography of the Cumberland Mountains is similar to the steep terrain of the Blue Ridge Mountains. Several peaks reach over 915 m elevation. The elevation of the highest peak, Cross Mountain, is 1077 m. The border between the Cumberland Mountains and Appalachian Ridge and Valley Province is formed by a distinct escarpment. To the west and south, the Cumberland Mountains blend gradually into the tableland of the Cumberland Plateau.

South of its border with the Cumberland Mountains, the Cumberland Plateau is bordered on the east by a distinct escarpment that stands about 274 m above the Appalachian Ridge and Valley Province. To the west, the boundary between the Cumberland Plateau and Eastern Highland Rim is irregular and less distinct. Elevations of the Plateau's tableland average 518 to 579 m. Topography is essentially flat with a few hilly areas. Several streams flowing off the Cumberland Plateau have cut large gorges along both its eastern and western margins.

The Sequatchie Valley is a large anticlinal valley bordered on each side by an escarpment averaging 305 m elevation. In Tennessee, this valley is 96 km long and ranges from 6.4 to 8 km wide. Its topography is flat to gently rolling with northern elevations averaging approximately 280 m and southern elevations 198 m.

The Eastern and Western Highland Rims cover a large land area in Tennessee and together they encircle the Outer Central Basin. The Eastern and Western Rim areas are separated by the Cumberland River Valley in the north and Elk River Valley in the south. The Eastern Highland Rim averages about 305 m elevation and possesses gently rolling to nearly level terrain. Highest elevation is 632 m on Short Mountain, which is an outlier of the Cumberland Plateau. Another notable feature on the western margin of the Eastern Highland Rim is an extremely flat area called the barrens. The Western Highland Rim covers more land area than the Eastern Highland Rim and has a more rolling and dissected terrain. According to Luther (1977), elevations average about 274 m in the eastern portions and 213 m in the western portions. Highest elevations are found in Giles, Lawrence, and Wayne counties. DeSelm (1959) studied the topography of the Central Basin and adjacent areas in middle Tennessee and further subdivided the Highland Rims into dissected and undissected portions.

Enclosed by the Eastern and Western Highland Rims, the Central Basin is divided into two regions based on topography and elevation. The

Outer Basin has a hilly terrain with elevations averaging 229 m. However, some hilltops may reach elevations of up to 396 m. The Inner Basin possesses a flatter topography with several almost level areas. Elevations average approximately 183 m. Karst features, such as underground drainages and sinkholes, are common.

Miller (1974) and Luther (1977) recognized the Tennessee River Valley in west Tennessee as a distinct physiographic unit. In this area, events of the geological past have created a mosaic of strata and a diverse topography with characteristics of both the Cenozoic and Mesozoic strata of the Coastal Plain Province and the Paleozoic strata of the Interior Low Plateaus Province. This transition zone is commonly called the Fall Line in other areas of the southeastern United States. However, in Tennessee this transitional area has been extensively modified by the erosive and depositional activities of the Tennessee River. Even though the western Tennessee River Valley can be recognized as distinct because of its geological and topographic complexity, it is essentially a transition zone and is considered as such in this study.

The Coastal Plain Hills occupy approximately the eastern half of west Tennessee and include the divide between the Mississippi and Tennessee River Drainages. Although a few areas are over 213 m in elevation, average elevation is about 152 m. Topography is moderately hilly.

The Loess Plain forms a wide belt across western Tennessee and includes the area of loess deposits delineated by Hardeman (1966). The topography is predominately flat and gently slopes to the west. Average elevation is approximately 122 m. Rivers and creeks have developed broad floodplains. The western boundary is formed by the Mississippi River bluffs. Although he did not delineate the Loess Plain on his generalized physiographic map of Tennessee, Miller (1974) called this area the West Tennessee Plains. Fink and Elder (1982) recognized it as the Loess Belt Ecosystem.

West of the Mississippi River bluffs, which are approximately 30 m in height, is the Mississippi River Valley. This alluvial valley is essentially flat with an average elevation of about 77 m. Flooding is frequent, and the landscape possesses typical features of a low gradient, mature river valley. These features include oxbow lakes, backswamps, cutoffs, and natural levees. The most notable feature is Reelfoot Lake. This shallow, elongated lake was formed by the New Madrid earthquakes of 1811 and 1812.

C. Climate

Amphibians are poikilothermic and most require moist conditions. Temperature and moisture variables play an important role in their growth and reproduction. Climatic descriptions presented were primarily taken from Tennessee Department of Finance and Administration (1966) and Dickson (1960). Both of these sources and the U.S. Department of Commerce (1968) provide maps that show temperature and precipitation trends that are useful for characterizing general climatic variations in Tennessee.

Tennessee has a humid mesothermal climate. Located between 35° 00' to 36° 30' north latitudes and 81° 45' to 90° 15' west longitudes, the state is in the path of warm, moist air currents from the Gulf of Mexico and cold, relatively dry air currents from Canada. Normally there are four distinct seasons of about equal length. Typical spring weather includes periods of cool temperatures interrupted by warmer periods. Precipitation occurs as scattered showers and a few general rains. Due to the influx of air from the Gulf of Mexico, summers are warm and humid. Thundershowers are the main form of precipitation. Fall weather includes mild temperatures, low humidities, and light to moderate precipitation. Winters are moderately cold and may have moderate to heavy amounts of precipitation.

According to the U.S. Department of Commerce (1968) four climatic divisions are recognized in Tennessee (Figure 3). Climatic trends within the state are directly related to topographic characteristics, especially elevation. On the average, temperatures drop approximately 1.7°C for every 305 m increase in elevation. The mean annual temperature ranges from about 17°C near Memphis to under 7°C atop the highest peaks in the Great Smoky Mountains (Figure 4). Mean annual temperatures of the Cumberland Plateau and Cumberland Mountains vary from 13° to 14°C. To emphasize the effect of elevation, the mean July temperature in the Great Smoky Mountains is similar to the mean July temperature along the southern end of the Hudson Bay in Canada. Several other temperature variables and their trends illustrate the influence of elevation on the climate of Tennessee. These variables include mean maximum temperatures for January (Figure 5), mean minimum temperatures for January (Figure 6), mean maximum temperatures for July (Figure 7), mean minimum temperatures for July (Figure 8), mean annual number of days maximum temperature at or above 32°C (Figure 9), and mean annual number of days minimum temperature at or below 0°C (Figure 10).

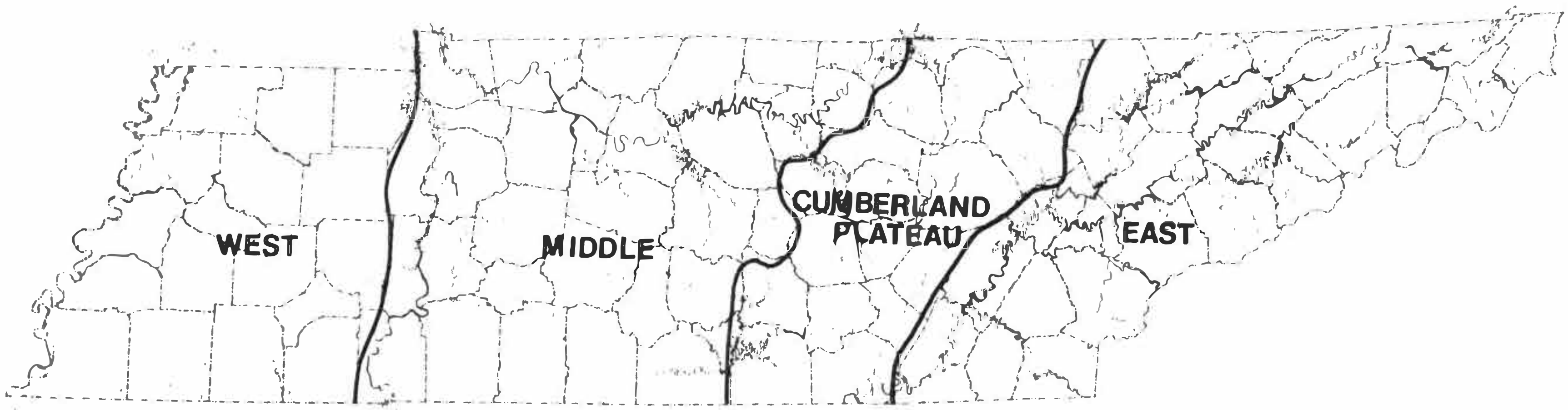

Figure 3. Climatic divisions (U.S. Department of Commerce, 1968).

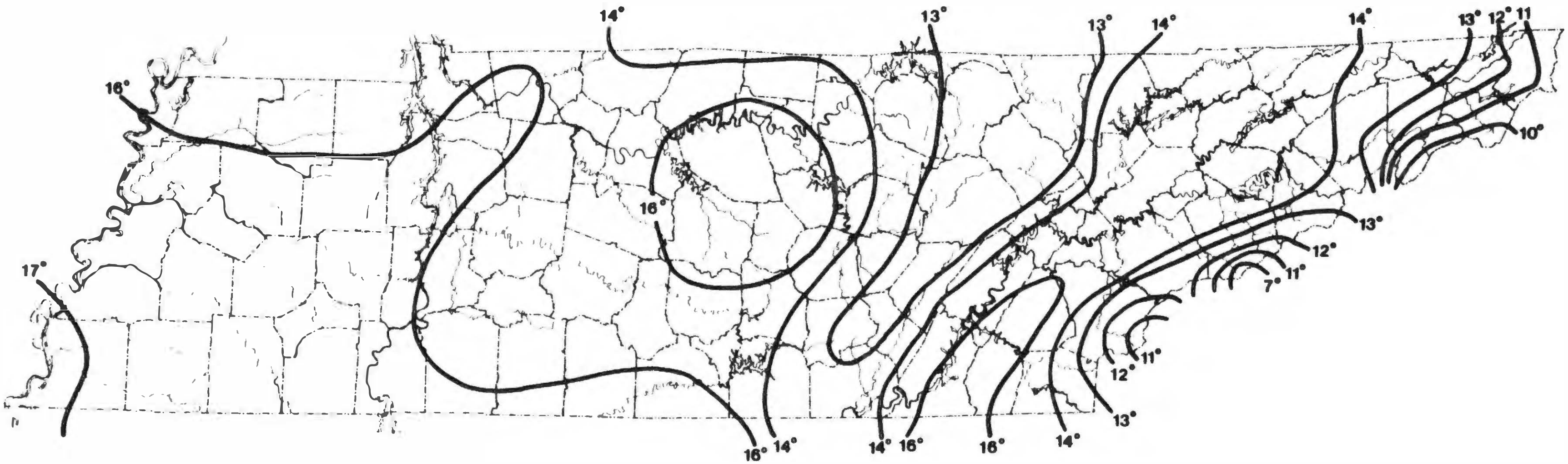

Figure 4. Mean annual temperatures (Tennessee Department of Finance and Administration, 1966). Temperature values converted from fahrenheit to centigrade units. Isolines connect points of approximately equal value. Based on period 1931-1960.

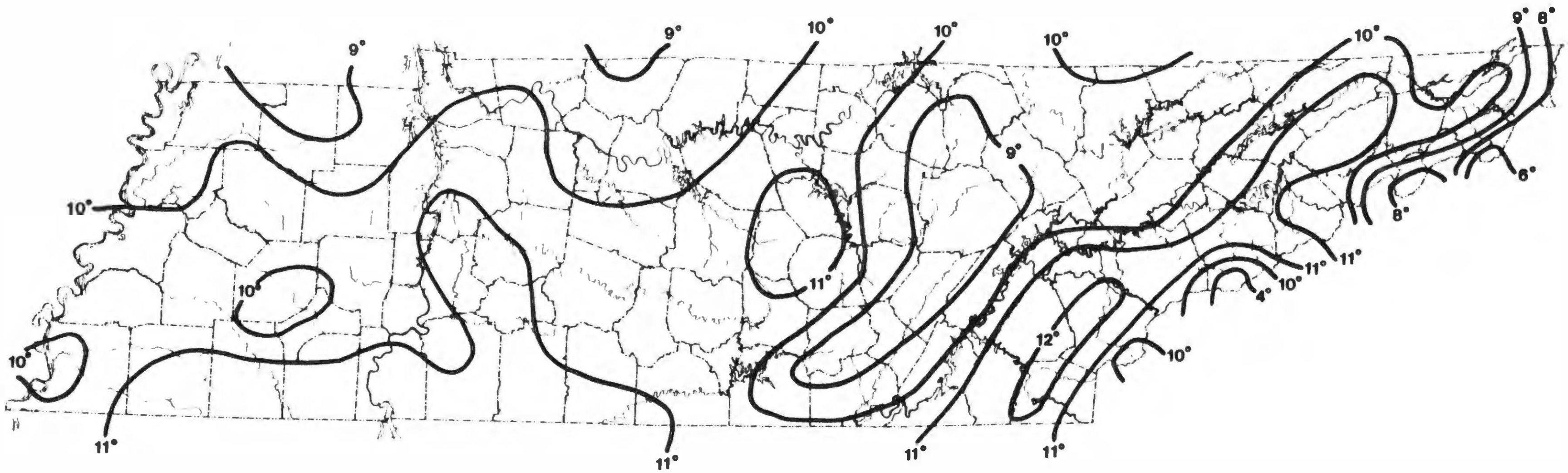

Figure 5. Mean maximum temperatures for January (Dickson, 1960). Temperature values converted from fahrenheit to centigrade units. Isolines connect points of approximately equal value. Based on period 1931-1952.

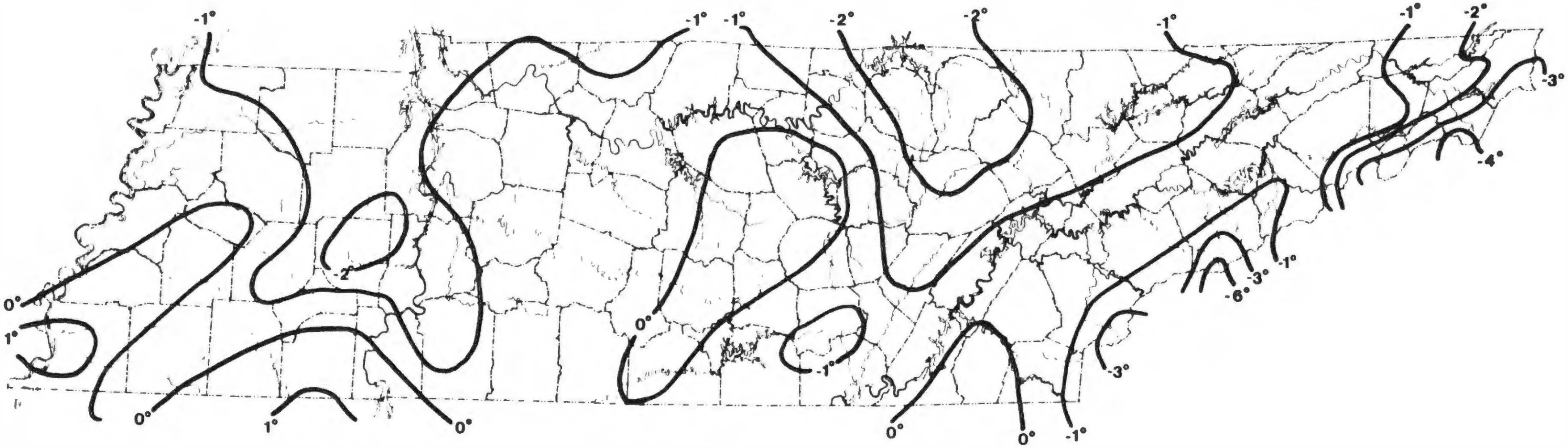

Figure 6. Mean minimum temperatures for January (Dickson, 1960). Temperature values converted from fahrenheit to centigrade units. Isolines connect points of approximately equal value. Based on period 1931-1952.

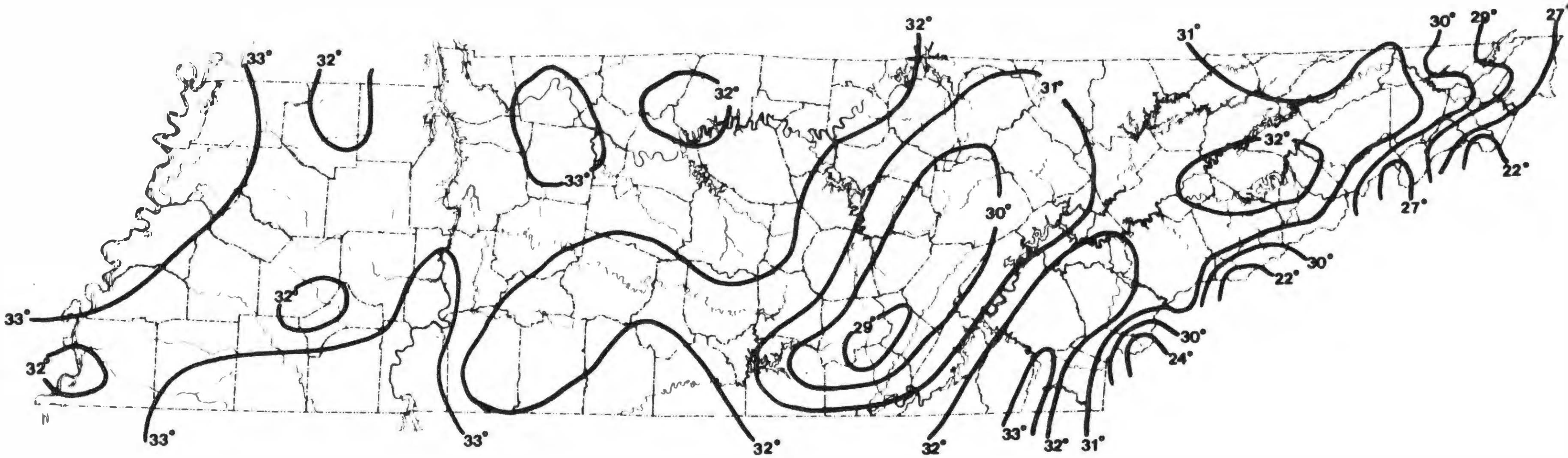

Figure 7. Mean maximum temperatures for July (Dickson, 1960). Temperature values converted from fahrenheit to centigrade units. Isolines connect points of approximately equal value. Based on period 1931-1952.

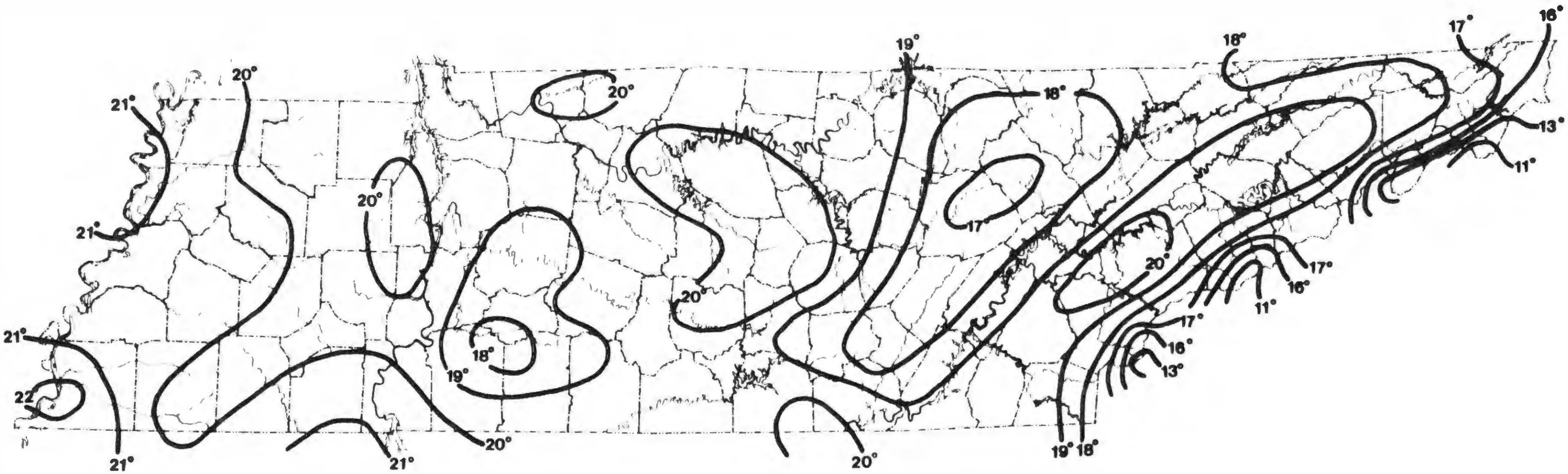

Figure 8. Mean minimum temperatures for July (Dickson, 1960). Temperature values converted from fahrenheit to centigrade units. Isolines connect points of approximately equal value. Based on period 1931-1952.

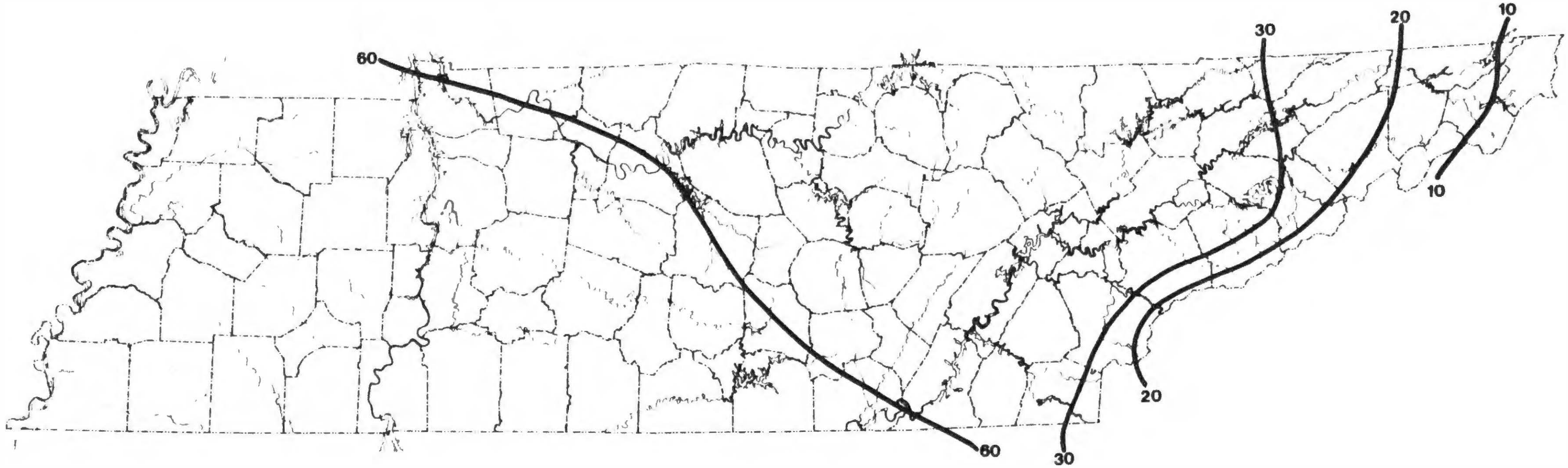

Figure 9. Mean annual number of days maximum temperature at or above 32° C (U.S. Department of Commerce, 1968). Isolines connect points of approximately equal value. Based on period through 1960.

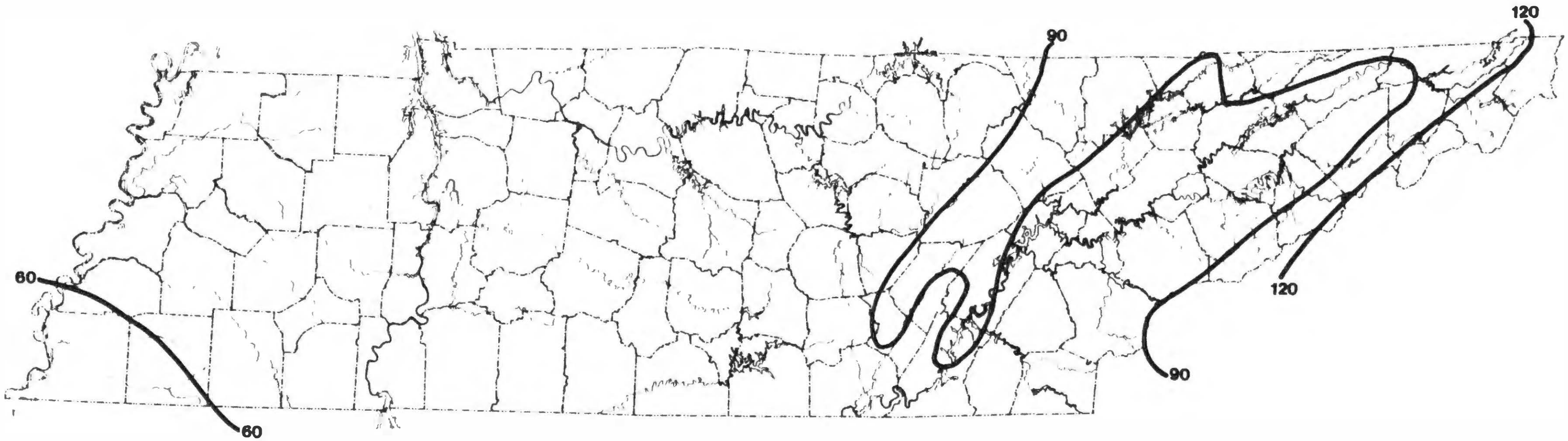

Figure 10. Mean annual number of days minimum temperature at or below 0^{o} C (U.S. Department of Commerce, 1968). Isolines connect points of approximately equal value. Based on period through 1964.

Another important climatic variable, particularily important in regards to the reproductive success of amphibians, is the length of the yearly freeze-free period. For Tennessee, Figure 11 shows the average dates of first killing freeze in the fall, and Figure 12 shows the average dates of last killing freeze in the spring. The mean lengths in days of freeze-free periods are illustrated in Figure 13. Again, the cooling effects of high elevations of the Blue Ridge Mountains, Cumberland Plateau, and Cumberland Mountains are obvious.

Most of the state annually receives approximately 114 to 140 cm of precipitation (Figure 14). However, high elevation areas of the Cumberland Plateau and Cumberland Mountains may receive an average of over 142 cm, and the peaks of the Blue Ridge Mountains may receive in excess of 193 cm. Heaviest rains and often flooding normally occur during late winter and early spring. Extended drought periods are normally limited to summer and fall.

D. Drainages

Streams and their associated valleys and floodplain habitats can either act as barriers or corridors for amphibian dispersal. Like other southeastern states, Tennessee has an abundance of surface water. Names of major streams and drainage area boundaries were taken from Kernodle (1972) and are shown in Figure 15. Most rivers have been modified by channelization in west Tennessee and by impoundment in middle and east Tennessee. The largest natural lake is Reelfoot Lake in the northwest corner of the state. Five major drainage areas occur in Tennessee. Statistics in the following descriptions of drainage areas were taken from Kernodle (1972). Area values were converted to hectares.

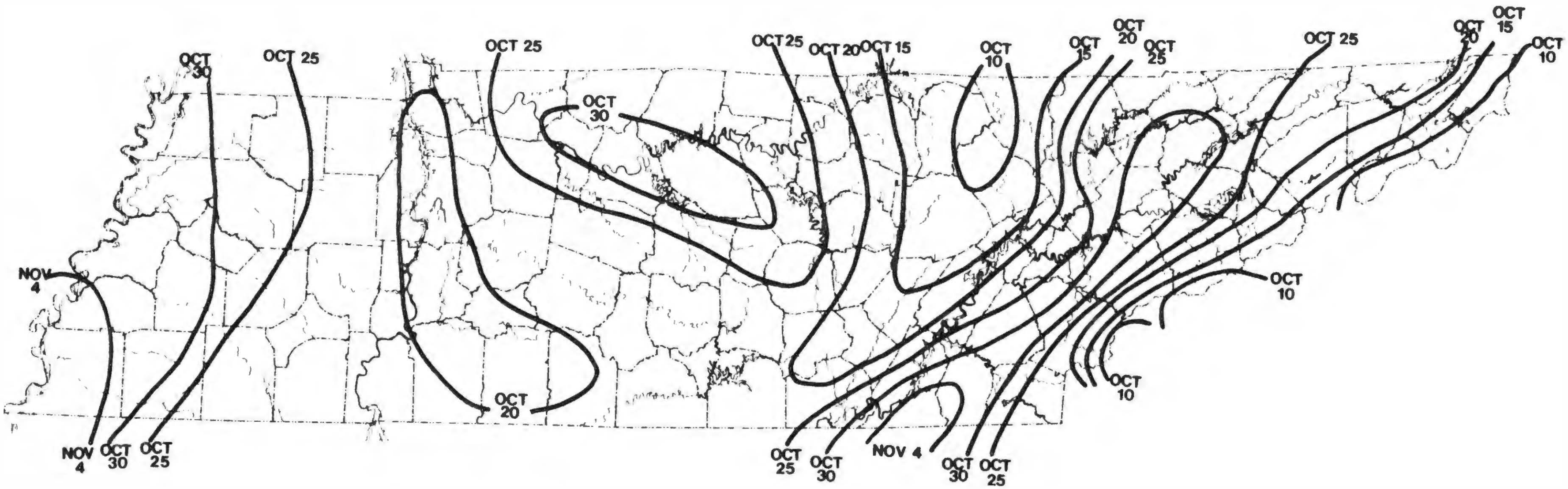

Figure 11. Average dates of first killing freeze in fall (Tennessee Department of Finance and Administration, 1966). Isolines connect points of approximately equal value. Based on period 1921-1950.

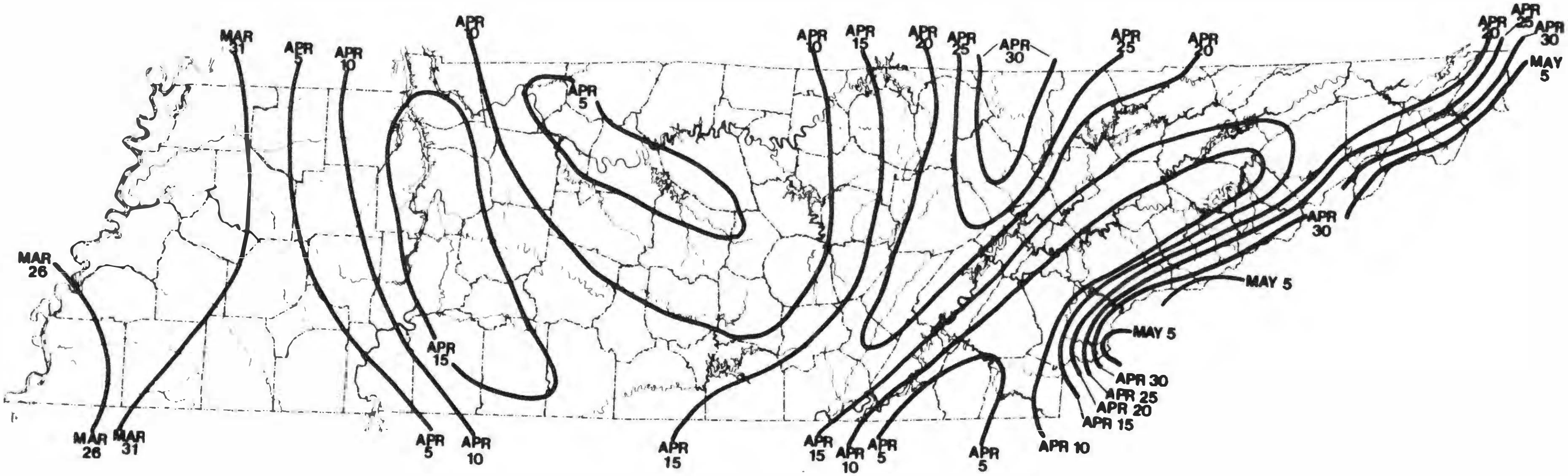

Figure 12. Average dates of last killing freeze in spring (Tennessee Department of Finance and Administration, 1966). Isolines connect points of approximately equal value. Based on period 1921-1950.

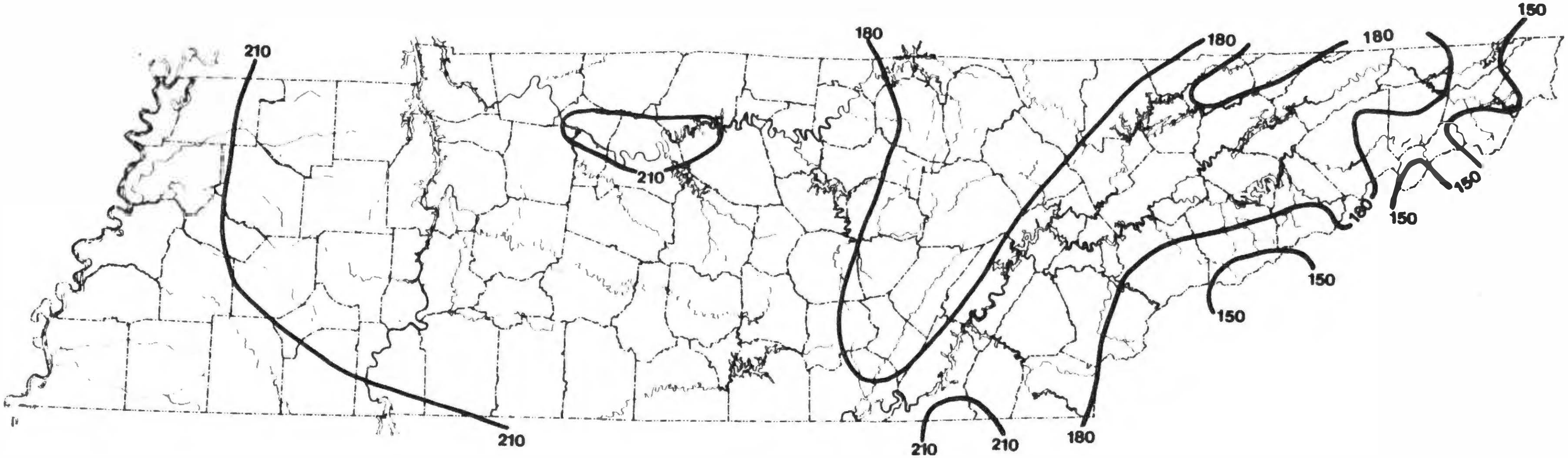

Figure 13. Mean length in days of freeze-free periods (U.S. Department of Commerce, 1968). Isolines connect points of approximately equal value. Based on period 1921-1950.

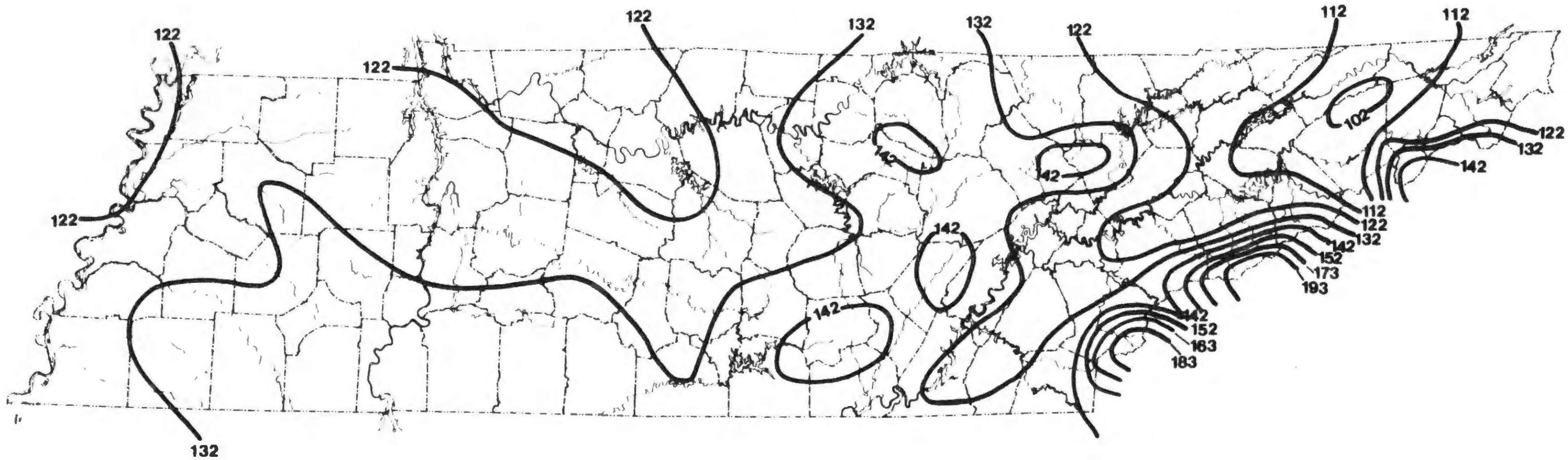

Figure 14. Mean annual precipitation (Tennessee Department of Finance and Administration, 1966). Precipitation values converted from inches to centimeters. Isolines connect points of approximately equal value. Based on period 1931-1960.

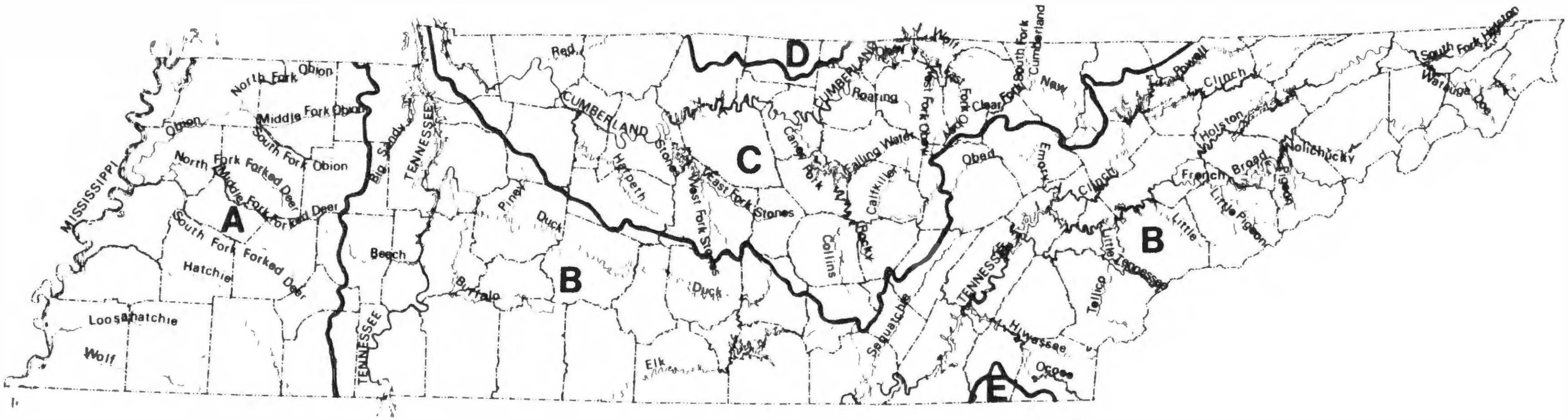

Figure 15. Rivers and major drainage systems (Kernodle, 1972). Area labeled A depicts Mississippi River Drainage, B-Tennessee River Drainage, C-Cumberland River Drainage, D-Barren River Drainage, and E-Conasauga River Drainage.

The Mississippi River Drainage area includes approximately 2,171,234 ha. Major tributaries include the Obion, Forked Deer, Hatchie, Loosahatchie, and Wolf rivers. Most exhibit characteristics of low gradient, mature streams. Features such as broad alluvial floodplains, meandering channels, natural levees, oxbow lakes, and sloughs are common. The Tennessee River Drainage is the largest in the state and covers about 5,842,881 ha. Major tributary streams include the Big Sandy, Duck, Buffalo, Beech, Elk, Sequatchie, Hiwassee, Ocoee, Clinch, Emory, Powell, Little Tennessee, Tellico, Little, Holston, Watauga, French Broad, Little Pigeon, Pigeon, and Nolichucky rivers. Tennessee River tributaries occur in the Coastal Plain Hills of west Tennessee and in every physiographic region in middle and east Tennessee. As a result, stream characteristics are diverse and range from the mature, meandering streams of the Coastal Plain in west Tennessee and valleys of middle and east Tennessee to the swift, cool, high gradient streams draining the escarpments of the Highland Rim, Cumberland Plateau, Cumberland Mountains, and Blue Ridge Mountains. The Cumberland River Drainage includes about 2,765,909 ha. Major tributaries are the Red, Harpeth, Stones, Caney Fork, Falling Water, Calfkiller, Collins, Rocky, Roaring, Obey, Wolf, South Fork Cumberland, New, and Clear Fork rivers. As in the Tennessee Drainage, streams are relatively mature with floodplain development in lowland areas and are young, swift, with steep gradients in the uplands of the Highland Rim, Cumberland Plateau, and Cumberland Mountains. In north-central Tennessee, the Barren River Drainage is small and encompasses approximately 106,710 ha. There are no major riverine tributaries in Tennessee. This drainage area includes headwater creeks flowing northward off the level to rolling terrain of the Western Highland Rim. These creeks drain into the Barren River in Kentucky, which joins with the Green River and ultimately flows into the Ohio River near Henderson, Kentucky. The Conasauga River Drainage area is the smallest and includes about 32,894 ha. The Conasauga River originates in north Georgia, flows north into Tennessee, and then south back into Georgia. Only a small stretch of river occurs in Tennessee where it receives small creeks from both the Appalachian Ridge and Valley and Blue Ridge Mountains. The Conasauga River is a headwater tributary of the Alabama River Drainage which eventually empties into the Gulf of Mexico near Mobile, Alabama.

E. Soils

Compared to most other terrestrial vertebrates, amphibians are more limited in their dispersal capabilities and are probably more dependent on substrate characteristics. Many forms are predominately fossorial and are directly influenced by soil characteristics. Others are indirectly affected by the soil's influence on vegetation and biotic communities. The soils of Tennessee are diverse and major soil areas closely approximate geologic and physiographic boundaries (Figure 16). General soil areas and their descriptions were taken from Springer and Elder (1980). They recognized nine major soil areas.

The soils of the major stream bottoms occur in the floodplains of the mainstreams and larger tributaries of the Mississippi, Tennessee, and Cumberland Rivers. Major soil orders present include Entisols, Inceptisols, Mollisols, Alfisols, and Ultisols. These soils are heavily

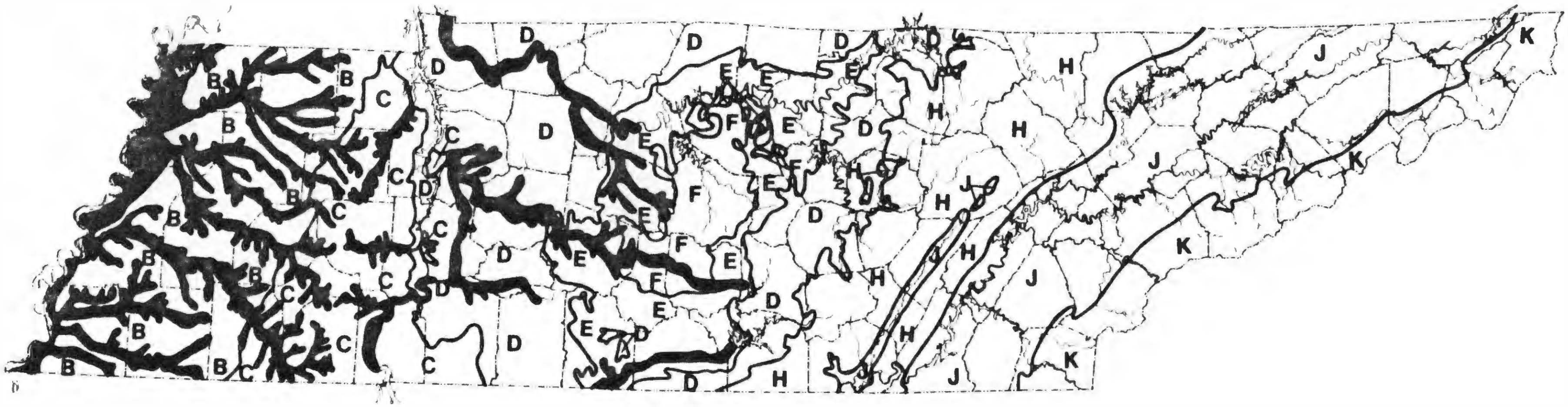

Figure 16. General soil areas (Springer and Elder, 1980). Darkened areas denote soils of major stream bottoms. Areas labeled B denote loess region, C-Coastal Plain, D-Highland Rim, E-Outer Nashville Basin, F-Inner Nashville Basin, H-Cumberland Plateau and Mountains, J-ridges and valleys, and K-Unaka Mountains.

used for agriculture. Loamy, well drained soils typically occur along streams, and clayey, poorly drained soils are usually found in backwater swamps. Springer and Elder subdivide this general soil area into (1) loamy, silty, and sandy soils of the Mississippi River bottoms; (2) clayey soils of the Mississippi River bottoms; (3) silty and loamy soils of the bottoms in the Loess and Coastal Plain regions; and (4) loamy, silty, and clayey soils of the bottoms and terraces in the Highland Rim and Nashville Basin.

The soils of the Loess Region include the orders Alfisols, Entisols, and Ultisols. Soils are mostly silty and range from poorly drained on level areas to well drained in hilly areas. Fragipans are common. This soil area is subdivided into four groupings that include (1) rolling to steep, well drained and moderately well drained, silty soils from thick loess; (2) level to rolling, moderately well drained and well drained, silty soils from thick loess; (3) level and undulating, poorly drained to moderately well drained, silty soils from thick loess; and (4) undulating and rolling, well drained and moderately well drained, silty and loamy soils from loess and coastal plain sediment.

The Coastal Plain Region comprises loamy or sandy, and in some areas, clayey soils. These soils are mostly very acid and well drained to moderately well drained. Poorly drained soils occur in some creek bottoms and other level areas. Ultisols, Alfisols, and Entisols are the major soil orders. Major soil groupings in the Coastal Plain Region are (1) hilly, loamy soils from coastal plain sediment and undulating and rolling, silty soils from thin loess; (2) hilly, clayey soils from coastal plain sediment and rolling and undulating, silty soils from thin loess; and (3) undulating and rolling, silty soils from alluvium and loess.

Soil orders of the Highland Rim include Ultisols, Inceptisols, and Alfisols. Soils in areas underlain by limestone have clayey and cherty subsoils. In general, soils are strongly acid. Subgroupings of soils of the Highland Rim include (1) hilly and steep cherty, clayey, and loamy soils and narrow strips of silty soils from limestone, thin loess, and shale; (2) hilly and rolling, cherty and clayey soils and undulating, silty soils from limestone and thin loess; (3) undulating and rolling, silty and loamy soils from thin loess, coastal plain sediment, and limestone; (4) undulating and rolling, silty and clayey soils from thin loess, alluvium, and limestone; and (5) rolling and undulating, clayey, loamy, and silty soils from alluvium and thin loess.

Soils of the outer part of the Nashville Basin range from deep to shallow, are well drained, and are very rocky in some areas. Alfisols, Ultisols, Mollisols, and Inceptisols are the major soil orders present. Soil subgroupings are (1) hilly and steep, cherty and clayey soils from colluvium and limestone; (2) rolling and hilly, clayey and loamy soils from phosphatic limestone, shale, and alluvium; and (3) undulating and rolling, clayey and silty soils from phosphatic limestone and alluvium.

Soil orders of the inner part of the Nashville Basin are Alfisols and Mollisols. Soils along larger streams may be 2 to 3 m deep while in cedar glades soils may only be a few centimeters in depth. Soils in this area have less phosphorus and are redder than those in the outer part of the Nashville Basin. Subgroupings include (1) undulating and rolling, clayey soils from limestone; (2) undulating, clayey and silty soils from limestone and alluvium; and (3) level and undulating, clayey soils from alluvium and limestone.

The soils of the Cumberland Plateau and Mountains are mostly loamy, well drained, strongly acid, and about 1 m deep. Sandstone outcroppings are frequent. Soil orders present are Ultisols and Inceptisols. Subgroupings include (1) undulating to hilly, loamy soils from sandstone and shale; and (2) steep and hilly, stony and loamy soils from sandstone, shale, and limestone.

The soils of the ridges and valleys are the most diverse in the state. Soil formation boundaries closely follow geological boundaries, are narrowly elongate in shape, and are oriented in a northeast-southwest direction. Soils are usually deep over limestone strata and shallow over shales and sandstone. Upland soils are typically strongly acid. Soil orders include Ultisols, Alfisols, and Inceptisols. Subgroupings are (1) rolling to steep, cherty and clayey soils from dolomitic limestone; (2) rolling and hilly, clayey soils from dolomitic limestone; (3) undulating to hilly, clayey and loamy soils from alluvium and limestone; (4) steep and hilly, shaly, clayey and loamy soils from calcareous shale; (5) undulating to hilly, clayey and loamy soils from shale and limestone; (6) steep ridges and rolling valleys with stony, loamy and clayey soils; and (7) hilly and steep, dark red, clayey and loamy soils from calcareous sandstone.

Soils of the higher elevations of the Unaka Mountains are typically a meter or less in depth, loamy, and rocky. At lower elevations, soils range from about 1 to 2 m in depth, are loamy, and may be rocky.

North-facing slopes usually have a deeper, richer, and more productive soil than south-facing slopes. Valley soils are deep, well drained, and loamy. Soil orders include Inceptisols, Utilisols, and Spodosols. Major subgroupings include (1) steep and very steep, loamy and stony soils at high elevations from metamorphic and igneous rocks and colluvium; (2) steep and very steep, loamy and channery soils from phyllite, sandstone, quartzite, and colluvium; (3) hilly and steep, loamy and stony soils from metamorphic and igneous rocks; and (4) undulating to hilly, loamy and clayey soils from colluvium, alluvium, shale, and limestone.

A soil characteristic important to the distribution and ecology of amphibians is temperature. Springer and Elder (1980) provided a state map showing average annual soil temperatures and soil temperature classes (Figure 17). Temperature classes were delineated based on average temperature of soil series present. Soils with an average annual temperature above 16^{o} C are considered thermic; 15^{o} to 16^{o} C - mainly thermic; 14^{o} to 15^{o} C - mainly mesic or mesic depending on geographic location; and 9^{o} to 14^{o} C - frigid.

F. Vegetation

Vegetative features of Tennessee are discussed in both this subchapter and the next subchapter on ecoregions. This arrangement was adopted somewhat arbitrarily after an examination and comparison of available information on the vegetative regions of Tennessee. Major studies include Braun (1950), Shanks (1958), Kuchler (1964), Bailey (1976), and Fink and Elder (1982). Although these authors used different

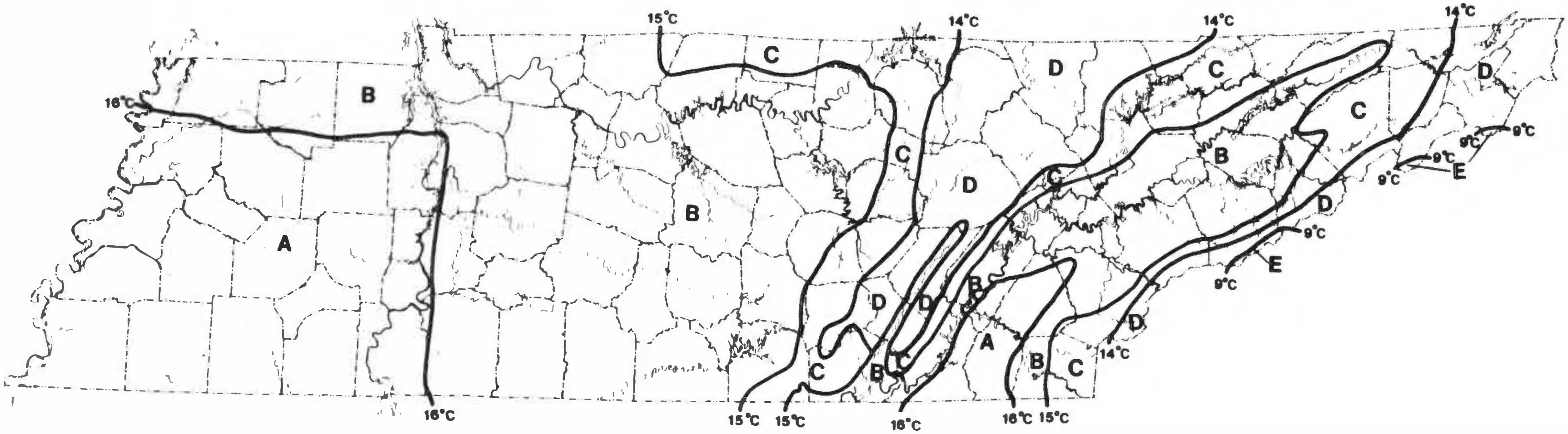

Figure 17. Average soil temperatures and soil temperature classes (Springer and Elder, 1980). Temperature values converted from fahrenheit to centigrade units. Areas labeled A depict thermic soils, B-mainly thermic, C-mainly mesic, D-mesic, and E-frigid.

terminology, they recognized many common boundaries. With the exception of Kuchler (1964), they delineated vegetative boundaries that were usually coincident with physiographic boundaries in Tennessee. Because Kuchler's study of potential natural vegetation appears significantly different from the other four studies and relies more on purely vegetative characteristics, its content was used to provide an overview of the vegetative features in Tennessee (Figure 18). Due to the overall similarity of the other four studies, they are included together and serve as the sources for describing the ecoregions of Tennessee in the following subchapter.

Kuchler recognized nine vegetative types in Tennessee. The Spruce-Fir Forest is limited to higher elevations of the Great Smoky Mountains and, although not shown on Kuchler's map, an area occurs near the peak of Roan Mountain in Carter County. This vegetation type reaches a low to medium height and the understory may be shrubby. Dominant tree species are *Abies fraseri* and *Picea rubens.* Small areas of Northern Hardwoods-Hemlock Forests occur along the slopes of the Great Smoky Mountains, Unicoi Mountains, Roan Mountain, Cumberland Plateau in Morgan County, and in the northeastern corner of the state. This tall broadleaf deciduous forest may also contain needleleaf evergreen species. Dominant species are *Acer saccharum, Betula allegheniensis, Fagus grandifolia,* and *Tsuga canadensis.* Covering most of east Tennessee is the Appalachian Oak Forest. Dominant species of this tall broadleaf deciduous forest include *Quercus alba, Q. rubra,* and *Q. prinus.* According to Kuchler, another tall broadleaf deciduous forest called the Mixed Mesophytic Forest extends in a belt across most of the Cumberland

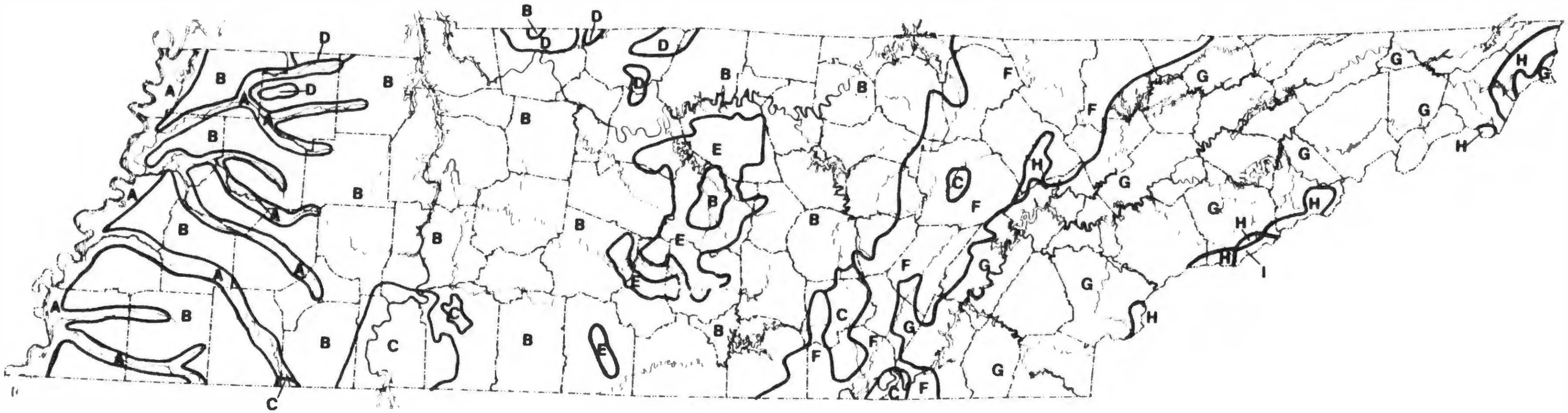

Figure 18. Vegetative features (Kuchler, 1964). Areas labeled A denote Southern Floodplain Forest, B-Oak-Hickory Forest, C-Oak-Hickory-Pine Forest, D-Mosaic of Bluestem Prairie and Oak-Hickory Forest, E-Cedar Glades, F-Mixed Mesophytic Forest, G-Appalachian Oak Forest, H-Northern Hardwoods, and I-Southeastern Spruce-Fir Forest.

Mountains and Cumberland Plateau. Dominant species are Acer saccharum, Aesculus octandra, Fagus grandifolia, Liriodendron tulipifera, Quercus alba, Q. rubra, and Tilia heterophylla. Hal R. DeSelm, University of Tennessee (pers. comm.), suggested that Kuchler's Mixed Mesophytic Forest is actually restricted to coves, north sloping ridges, and other upland areas on the Cumberland Plateau, while most of the Plateau is covered by oak, oak-pine, and swamp forests. Cedar Glades are found mainly in the central part of the state, but also occur in the Appalachian Ridge and Valley west of the Tennessee River. This vegetation type is characterized by low to medium height scattered forbs and areas of annual and perennial grasses that may have patches of evergreen shrubs and clumps of small to medium height trees. Dominant species are Celtis laevigata, Juniperus virginiana, Sporobolus vaginiflorus, and Ulmus alata. Kuchler identified five isolated areas in north-central and northwestern Tennessee as possessing vegetation characteristic of Bluestem Prairie and Oak-Hickory Forest. Bluestem Prairie is a dense grassland composed of tall grasses and numerous forbs. Dominant grass species include Andropogon gerardi, A. scoparius, Panicum virgatum, and Sorghastrum nutans. Besides being a component of these five isolated areas, the Oak- Hickory Forest blankets most of the state west of the Cumberland Plateau. Dominant species of this medium tall to tall broadleaf deciduous forest include Carya tomentosa, C. ovata, Quercus alba, Q. coccinea, and Q. velutina. Three areas on the Cumberland Plateau, one large and an adjacent small area along the Tennessee River in western Tennessee, and another small area along the Hatchie River near the Mississippi border possess an Oak-Hickory-Pine Forest.

Vegetation consists of a mixture of medium tall to tall broadleaf deciduous and needleleaf evergreen tree species. Dominant species are Carya spp., Pinus echinata, P. taeda, Quercus alba, and Q. stellata. The Southern Floodplain Forest occurs in the alluvial floodplains of the Mississippi River and tributary drainages in west Tennessee. These forests include medium tall to tall broadleaf and needleleaf deciduous trees. Dominant species are Nyssa aquatica, Quercus spp., and Taxodium distichum.

G. Ecoregions

The ecoregion concept for classifying and mapping ecosystems in the United States was developed by Bailey (1976, 1978) and consisted of a nine-level classification hierarchy. Bailey and Cushwa (1980) produced a map of ecoregions at the district level for the Appalachian and Tennessee Valley Regions. Modifying Bailey and Cushwa's map, Fink and Elder (1982) utilized a physiographic approach to develop a district level ecoregion map for the Tennessee Valley Region. In Tennessee, they recognized 18 districts (Figure 19).

A comparison of Fink and Elder's ecoregion boundaries with the forest and floristic boundaries of Braun (1950) and Shanks (1958) reveals a high degree of similarity. This is evident even though each classification scheme differs in the number of units delineated and the level of detail considered. For example, Fink and Elder's Blue Ridge High Mountains and Blue Ridge Valleys and Low Mountains districts are essentially identical to Braun's Southern Appalachian Section and Shanks' Unaka Region. A summary of the classification scheme used by Fink and Elder is provided

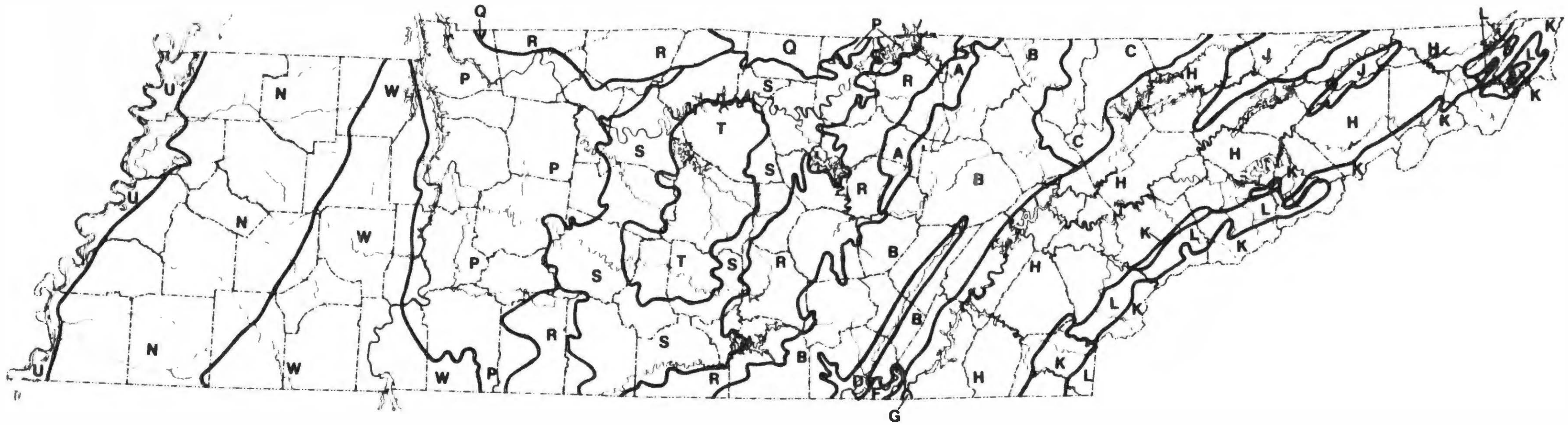

Figure 19. Ecoregions (Fink and Elder, 1982). Area labeled A denotes Cumberland Benches and Escarpment, B-Cumberland Plateau, C-Cumberland Mountains, D-Sequatchie Valley, F-Sand Mountain, G-Lookout Mountain, H-Great Appalachian Valley, J-Appalachian Sandstone Capped Ridges, K-Blue Ridge High Mountains, L-Blue Ridge Valleys and Low Mountains, N-Loess Belt, P-Highland Rim (Pennyroyal) Cherty Hills, Q-Pennyroyal (Highland Rim) Low Limestone Hills, R-Highland Rim (Pennyroyal) Plains, S-Outer Nashville Basin, T-Inner Nashville Basin, U-Mississippi Bottomland, and W-Coastal Plain Hills.

in Table 1. A comparison of this scheme with Braun's (1950) forest sections is provided in Table 2 and with Shanks' (1958) floristic regions in Table 3. Fink and Elder's classification is the most detailed and recognizes nearly all the areas identified by Braun and Shanks. Thus, any effects of ecoregions on the distribution of amphibians can also be described in terms of the forest and floristic regions of Braun and Shanks. Another feature of the ecosystem approach is that it combines physiographic, geologic, climatic, hydrologic, edaphic, and floristic data to delineate ecogeographic units which should prove useful in any analysis of animal distribution patterns.

According to Fink and Elder (1982), all of Tennessee lies within the Humid Temperate Domain, and two divisions, the Hot Continental and Subtropical, are recognized (Table 1). The Hot Continental Division is described as having cold winters and hot summers. Average temperature during coldest month is below 0° and above 22° C during the warmest month. Heaviest precipitation occurs in summer. Soils are predominately Alfisols with Ultisols in southern latitudes. Dominant vegetation is deciduous forests with sparse understories. The Subtropical Division is defined as having mild winters and hot summers. Average temperature during the coldest month varies from 18° to -3° C and are above 22° C during the warmest month. Most common soils are heavily leached Ultisols. Coniferous and mixed coniferous-deciduous forests are the dominant vegetation. Divisions are subdivided into provinces which are defined as broad vegetation regions with the same type or types of soils. In Tennessee, the Eastern Deciduous Forest Province is the only province of the Hot Continental Division. The Subtropical Division is subdivided

Table 1. Summary of hierarchial classification of ecoregions in Tennessee according to Fink and Elder (1982).

- LEVEL I - HUMID TEMPERATURE DOMAIN
  - LEVEL II - HOT CONTINENTAL DIVISION
    - LEVEL III - EASTERN DECIDUOUS FOREST PROVINCE
      - LEVEL IV - MIXED MESOPHYTIC FOREST SECTION
        - LEVEL V - Cumberland Benches and Escarpment District
          - Cumberland Plateau District
          - Cumberland Mountains District
          - Sequatchie Valley District
          - Sand Mountain District
      - LEVEL IV - APPALACHIAN OAK FOREST SECTION
        - LEVEL V - Lookout Mountain District
          - Great Appalachian Valley District
          - Appalachian Sandstone-Capped Ridges District
          - Blue Ridge High Mountains District
          - Blue Ridge Valleys and Low Mountains District
      - LEVEL IV - OAK-HICKORY FOREST SECTION
        - LEVEL V - Loess Belt District
          - Highland Rim (Pennyroyal) Cherty Hills District
          - Pennyroyal (Highland Rim) Low Limestone Hills District
          - Highland Rim (Pennyroyal) Plains District
          - Outer Nashville Basin District
          - Inner Nashville Basin District
  - LEVEL II - SUBTROPICAL DIVISION
    - LEVEL III - OUTER COASTAL PLAIN FOREST PROVINCE
      - LEVEL IV - SOUTHERN FLOODPLAIN FOREST SECTION
        - LEVEL V - Mississippi Bottomland District
    - LEVEL III - SOUTHEASTERN MIXED FOREST PROVINCE
        - LEVEL V - Coastal Plain Hills District

Table 2. A comparison of Braun's (1950) forest sections and Fink and Elder's (1982) ecoregions in Tennessee.

Braun's Sections	Equivalent Ecoregion(s) of Fink and Elder
Cumberland Mountains	Cumberland Mountains
Cumberland and Allegheny Plateaus	Cumberland Benches and Escarpment Cumberland Plateau Sequatchie Valley Sand Mountain Lookout Mountain
Nasvhille Basin	Outer Nashville Basin Inner Nashville Basin
Mississippian Plateau	Highland Rim (Pennyroyal) Cherty Hills Pennyroyal (Highland Rim) Low Limestone Hills Highland Rim (Pennyroyal) Plains
Mississippi Embayment	Loess Belt Coastal Plain Hills
Southern Appalachians	Blue Ridge High Mountains Blue Ridge Valleys and Low Mountains
Ridge and Valley	Great Appalachian Valley Appalachian Sandstone-Capped Ridges
Gulf Slope	None
Mississippi Alluvial Plain	Mississippi Bottomland

Table 3. A comparison of Shanks' (1958) floristic regions and Fink and Elder's (1982) ecoregions in Tennessee.

Shanks' Regions	Equivalent Ecoregion(s) of Fink and Elder
Mississippi Alluvial Plain	Mississippi Bottomland
Mississippi Embayment	Loess Belt Coastal Plain Hills
Mississippi River Bluffs	None - Forms western boundary of Loess Belt
Coastal Plain Uplands	Coastal Plain Hills
Highland Rim	Highland Rim (Pennyroyal) Cherty Hills Pennyroyal (Highland Rim) Low Limestone Hills Highland Rim (Pennyroyal) Plains
Kentucky Prairie Barrens	None[a]
Barrens of the Southwestern Rim	None
Barrens of the Southeastern Rim	None
Central Basin	Outer Nashville Basin Inner Nashville Basin
Cedar Barrens	Inner Nashville Basin
Cumberland Plateau	Cumberland Benches and Escarpment Cumberland Plateau Cumberland Mountains Sequatchie Valley Sand Mountain Lookout Mountain
Appalachian Valley	Great Appalachian Valley Appalachian Sandstone-Capped Ridges
Oak-Pine Region	None - Equivalent to Braun's Gulf Slope
Unakas	Blue Ridge High Mountains Blue Ridge Valleys and Low Mountains

[a]Shanks' Kentucky Prairie Barrens are roughly equivalent to Kuchler's Bluestem Prairie/Oak-Hickory Forest Region (Figure 17).

into the Outer Coastal Plain Province and Southeastern Mixed Forest Province. Provinces are subdivided into sections that are the equivalent of Kuchler's (1964) potential natural vegetation types. In Tennessee, the Eastern Deciduous Forest Province is subdivided into the Mixed Mesophytic Forest Section, Appalachian Oak Forest Section, and Oak Hickory Forest Section. The Outer Coastal Plain Forest Province is represented by the Southern Floodplain Forest Section. There are no sections recognized for the Southeastern Mixed Forest Province.

Sections are subdivided into districts. Fink and Elder's districts as shown in Figure 19 were defined in terms of geomorphic setting, climate, geology, hydrology, soils, and land use/land cover.

The Mixed Mesophytic Forest Section comprises the Cumberland Benches and Escarpment, Cumberland Plateau, Cumberland Mountains, Sequatchie Valley, and Sand Mountain districts. The Cumberland Benches and Escarpment district forms the western boundary of the northern portion of the Cumberland Plateau. Elevations vary from 305 to 549 m. Annual precipitation averages 137 to 142 cm and average annual temperature is 14^{o} C. On the average a freeze-free period of 188 days extends from approximately April 15 to October 20. Bedrock is sandstone at higher elevations and limestone at lower elevations. Surface water is sparse, and there are few permanent streams. Higher elevation soils are shallow, loamy, and may possess outcrops of sandstone. Soils of the lower elevations consist of red plastic clays with outcrops of limestone. Higher elevation forests are mostly hardwood while lower slopes have a mixed hardwood-red cedar forest.

The Cumberland Plateau District is characterized as a rolling plateau with elevations ranging from 518 to 579 m. A few hills reach

610 m elevation. An average of 132 to 142 cm of precipitation occurs annually. Average annual temperature varies from 13^{o} to 14^{o} C. Freeze-free period in the northern portion averages 163 days and normally occurs from about April 30 to October 10. Freeze-free period in the southern portion averages 195 days and typically occurs between April 15 and October 25. Bedrock is mostly sandstone with some limestone along lower slopes of escarpments. Permanent streams are present in gorges along escarpments but are uncommon on the plateau. Soils are acidic, well drained, and have a loamy composition. In areas not cut over or cultivated, hardwood forests predominate. Hemlock and white pine may occur in the gorges along the escarpment.

Possessing a steep topography, the Cumberland Mountains District is actually a deeply dissected plateau. Several mountain peaks are above 915 m. Annual precipitation averages 102 to 132 cm and average annual temperature varies from 11^{o} to 13^{o} C. Bedrock includes shale, sandstone, siltstone, and coal. Permanent surface water is common and drainages exhibit a dendritic pattern. Soils at high elevations are usually rocky loams or silt loams while soils of lower slopes are silt loams, loams, or channery and stony loams. Dominant forests are mixed pine-hardwood and hardwood.

The Sequatchie Valley District is an elongate anticlinal valley bordered on both sides by the Cumberland Plateau. Elevations vary from 183 to 244 m. Annual precipitation averages 137 to 142 cm and average annual temperature ranges from 13^{o} to 16^{o} C. The average last spring freeze occurs from April 10 to April 25, and first fall frost occurs around October 5 to October 30. The average freeze-free period is 183 days. Bedrock is mostly limestone with some shale or cherty limestone underlying a few narrow ridges. Permanent surface streams are common. Soils are deep, well drained, and consist of alluvium with surface loams and clayey loam subsoils. Land use and cover is mostly agriculture with only a few remnants of the original hardwood forest.

Only a small part of the Sand Mountain District occurs in Tennessee. This small area is similar to the Cumberland Plateau and in many respects can be considered a southern extension of Walden's Ridge south of the Tennessee River. Annual precipitation averages 137 cm and average annual temperature ranges from 16^{o} to 17^{o} C. Number of freeze-free days averages from 200 to 210 on the plateau and 240 days at lower elevations along the escarpment. Sandstone is the most common bedrock. Permanent streams are common. Well drained, acidic, loamy soils predominate, especially on the plateau. Land use and cover consists of about half forest and half agriculture.

Fink and Elder recognize five districts in the Appalachian Oak Forest Section of Tennessee. These include the Lookout Mountain, Great Appalachian Valley, Appalachian Sandstone-Capped Ridges, Blue Ridge High Mountains, and Blue Ridge Valleys and Low Mountains districts. The Lookout Mountain District includes a very small area in southeastern Tennessee. Elevations on this plateau bordered by distinct escarpments range from 549 to 610 m. Annual temperature averages near 14^{o} C and annual precipitation averages 127 cm. A freeze-free interval lasts about 190 days. Bedrock is mostly sandstone with a few shale lenses. Low elevations along escarpments are underlain by limestone. Intermittent streams are common. Soils on the plateau are loamy and very acid. Soils along escarpments are thin near the top and are often composed of thick colluvium near the base. This small area in Tennessee is covered by residential development. Escarpment forests are mostly mixed pine-hardwood.

The topography of the Great Appalachian Valley District consists of long parallel ridges and valleys oriented in a northeast-southwest direction. Valleys vary in elevation from 183 m in the south to 305 m in the north. Ridges tend to be narrow and may reach elevations of 610 to 915 m. Annual precipitation averages 89 to 140 cm. Annual temperature averages 11° to 16° C. Both average annual temperature and precipitation increase from north to south. A freeze-free period averages near 220 days in the southern part and 160 days in the northern part. The bedrock of ridges is mostly sandstone, cherty dolomite, and hard shale. Valley bedrocks include soft shale and clayey limestone. Both permanent and intermittent streams are present. In limestone areas. karst features such as subterranean streams are common. Soil formations are complex and vary with the bedrock geology. The most common soils are leached and very acid and have clayey subsoils. Agricultural lands predominate with areas of hardwood forests mostly restricted to ridges.

In Tennessee, the Appalachian Sandstone-Capped Ridges District includes two areas of high ridges. The most prominent ridges are Clinch Mountain, Powell Mountain, and the Bays Mountains. Average elevation of ridges ranges from about 610 to 915 m. Climate is generally moist and cool with annual precipitation averaging 102 to 127 cm. Annual temperature averages 12° to 14° C. A freeze-free period typically varies from 150 to 190 days in length. The bedrock of mountain ridges is mainly sandstone with shales and carbonates along slopes. Lower elevation valleys are very narrow and underlain by limestone. Small permanent streams and springs are common. Soils of high elevations are shallow, rocky, and acid. Deep colluvial soils are common in coves. Mixed pine-hardwood forest cover most of the area with a few valley areas utilized for agriculture.

The high mountains along the Tennessee-North Carolina border form the Blue Ridge High Mountains District. Elevations vary from 915 to above 1829 m. Climatic patterns are diverse, but in general, higher elevations have a cooler, wetter climate than lower elevations. Annual average precipitation ranges from around 122 cm at lower elevations to 203 cm at higher elevations. Annual average temperature varies from about 12^{o} C at lower elevations to 7^{o} C at higher elevations. Bedrocks include phyllite, slate, sandstone, quartzite, granite, and gneiss. Surface water in the form of permanent streams is especially abundant and evenly distributed. Rocky loams are the predominant soils. Vegetation types include mixed oak-pine forests, oak forests, and hemlock-northern hardwoods. Grass balds, heath slicks, and spruce-fir forests occur near the top of some of the higher peaks.

The Blue Ridge Valleys and Low Mountains District includes the low mountains and broad valleys adjacent to the Blue Ridge High Mountains. Elevations range from 366 to 915 m. Annual temperature averages 12^{o} to 14^{o} C and annual precipitation averages 107 to 140 cm. The freeze-free interval ranges from 170 to 190 days. Bedrock consists of gneiss, schist, granite, phyllite, and slate. Low valleys are underlain by dolomite. Permanent streams are plentiful and evenly distributed. The most common soils are loamy with clay loam subsoils. Most valleys are utilized for agriculture and mountain areas are covered by hardwood forests.

The Oak-Hickory Forest Section is subdivided into six districts. The Loess Belt District is characterized by a gently rolling topography with wide floodplain development along major streams. Its western border is formed by the prominent Mississippi River bluffs. Elevations range from 61 m to 183 m. Precipitation and temperature increase from north to south. Annual temperature averages 14^{o} to 17^{o} C and annual precipitation averages 122 to 132 cm. The freeze-free period normally lasts 195 days in the north and 220 days in the south. Loess beds are the predominant geological formation. Permanent streams are low gradient and evenly distributed. Intermittent streams are also common. Soils are silty and range from poorly to well drained. Fragipans are common in upland areas. Most of the area is in row crop agriculture. Large tracts of hardwood forests mainly occur along a few large streams.

The Highland Rim (Pennyroyal) Cherty Hills District includes the western part of the Highland Rim physiographic region and is characterized by a hilly, steep, heavily dissected topography. Elevations range from 122 to 305 m. Annual precipitation averages 114 to 137 cm and annual average temperature varies from 13^{o} to 16^{o} C. The average last spring freeze occurs around April 10 and first fall frost about October 20. Average freeze-free period last 193 days. Bedrock includes cherty limestone and clayey limestone. Some highland areas lack permanent surface drainages; however, permanent streams are common elsewhere. Most soils are cherty or gravelly, acidic, and well to excessively well drained. In some areas, soils are silty with a fragipan. Forested areas are extensive and include hardwoods, mixed pine-hardwoods, and pine plantations.

The Pennyroyal (Highland Rim) Low Limestone Hills District possesses a landscape composed of rolling hills with wide level valleys. Karst features are common. Elevations vary from 152 to 244 m. Annual temperature averages 14^{o} C and annual precipitation averages 114 to 127 cm. A freeze-free period usually lasts around 188 days. First fall frost occurs about October 20 and last spring freeze occurs about April 15. Limestone is the predominant bedrock along with some sandstone, shale, and loess. Permanent surface and subsurface drainages are present. Soils are acid, silty loams with fragipans common on level upland areas. Poorly drained soils occur in the floodplains. Agricultural lands occupy about half of this district and hardwood forest the other half.

The Highland Rim (Pennyroyal) Plains District is characterized as a weakly dissected limestone plateau. Limestone sinks and other karst features are common. Average elevation is approximately 305 m. Annual precipitation averages 114 to 137 cm and annual temperature averages from 13^{o} to 16^{o} C. The first fall frost normally occurs about October 20 and last spring freeze near April 10. Average freeze-free period extends 193 days. Bedrock is limestone. Loess deposits occur in several level areas. Permanent surface streams are not common, especially in karst areas. Soils vary from poorly to moderately well drained and have reddish clayey subsoils on slopes and brownish or yellowish silty subsoils on level areas. Fragipans are found on level areas. Land use and cover is mostly agriculture with a few hardwood forests remaining in woodlots and along steep slopes.

The topography of the Outer Nashville Basin District is deeply dissected with steep valleys between rolling ridge tops. Elevations of ridges range from 274 to 366 m. Annual temperature averages 14^{o} to 16^{o} C and average annual precipitation varies from 114 to 137 cm. First fall frost occurs approximately October 21 and last spring freeze about April 21 giving the area a freeze-free period of about 192 days. Bedrock is phosphatic limestone. Some hilltops are capped with cherty limestone. Only a few large permanent streams are present and most small streams are intermittent. Soils have thin loamy surface layers, clayey subsoils, and are well drained. Forests cover about one-fourth of the area and are mostly hardwood with some red cedar present.

The Inner Nashville Basin District has karst features and a relatively flat to rolling topography. Although a few hilltops reach 366 m, elevations normally range from 152 to 229 m. Annual precipitation averages 122 to 132 cm and average annual temperature about 16^{o} C. The average freeze-free interval lasts approximately 192 days and extends from near April 12 to October 21. Clayey limestone is dominant bedrock. Small streams are mostly intermittent. Soils are shallow to moderately deep. Glade areas have shallow, dark clayey soils formed over flat limestone strata. Approximately one-fourth of area is forested, some parts of which are pure stands of red cedar.

The Mississippi Bottomland District is the only district of the Southern Floodplain Forest Section in Tennessee. Shaped by the meandering Mississippi River, the topography is flat. Natural levees, oxbows, and bayous are common. Annual temperature averages 14^{o} to 21^{o} C and annual precipitation averages 114 to 165 cm. Both average annual temperature and precipitation increase from north to south. The freeze-free period usually lasts 230 days and normally extends from near March 15 to November 1. Surface water is abundant in the form of streams, swamps, and bayous. Soils are alluvial in origin and are sandy and loamy near streams and clayey elsewhere. Most of this area is heavily cultivated. However, hardwood bottomland forests still occur along several of the largest streams.

No sections are recognized for the Southeastern Mixed Forest Province and only one district is found in Tennessee. The Coastal Plain Hills District consists of wide, level bottomlands with broad rolling terraces and hills. Elevations range from 91 to 244 m. Annual precipitation averages 122 cm in the north and 137 cm in the south. Annual temperature averages 16^{o} to 18^{o} C. A freeze-free period lasts for about 200 days in the north and 230 days in the south. The area is underlain by sands, clays, shales, and some gravel. Permanent streams are common. Soils of the uplands are well drained, acid loams, sands, and clays. Bottomland soils may be poorly to well drained. Bottomlands are extensively cultivated. Forests are mostly cut-over hardwood and pine.

CHAPTER III

DISTRIBUTION OF SPECIES

A. Methods

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; and (3) literature references. Locality data for over 27,000 specimens were obtained from 39 university and other collections (Table 4). Twenty-nine of these were visited, specimens from Tennessee examined, and locality data recorded. Information from the remaining 10 collections was provided by correspondence; however, unusual records or questionable identifications were checked by correspondence with the resident curator or by a loan of specimens. Field surveys were conducted between September 1975 and June 1985. A major emphasis during fieldwork was to sample areas of the state where information on amphibians was lacking. These areas were identified by a review of existing data from collections and the literature. Another goal of fieldwork was to further delineate the ranges of several species whose distributions in Tennessee were poorly defined. All specimens taken in the field were deposited in the University of Tennessee, Knoxville, Vertebrate Zoology Collection. The literature search for distribution 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. A six-volume, loose-leaf bound atlas listing all species and locality data utilized in this study has

Table 4. List of university and other institutional collections from which locality data were obtained and commonly accepted abbreviations.

Institution	Abbreviation
American Museum of Natural History	AMNH
Austin Peay State University	APSU
Auburn University Museum	AUM
Bays Mountain City Park	BMCP
Chicago Academy of Sciences	CAS
Carnegie Museum of Natural History	CMNH
Chattanooga State Technical Community College	CSTCC
East Tennessee State University	ETSU
Field Museum of Natural History	FMNH
Great Smoky Mountains National Park	GSMNP
Illinois State Natural History Survey	INHS
Indiana State University	ISU
University of Kansas Museum of Natural History	KU
Louisiana State University Museum of Zoology	LSUMZ
Museum of Comparative Zoology	MCZ
Murray State University	MSU
Memphis State University Museum of Zoology	MSUMZ
Middle Tennessee State University	MTSU
North Carolina State Museum	NCSM
Northeast Louisiana University Museum of Zoology	NLU
Savannah Science Museum	SSM
Tennessee Technological University	TTU
Tulane University	TU
University of Alabama Museum of Natural History	UANH
University of Tennessee, Chattanooga	UTC
Florida State Museum	UF
University of Georgia	UGA
University of Illinois Museum of Natural History	UIMNH
University of Kentucky	UK
University of Louisville	UL
University of Michigan Museum of Zoology	UMMZ
University of North Carolina, Charlotte	UNC
University of the South, Sewanee	US
United States National Museum	USNM
University of Tennessee, Knoxville, Vertebrate Zoology Collection	UTKVZC
University of Tennessee, Martin	UTM
Virginia Commonwealth University	VCU
Virginia Polytechnic Institute and State University	VPI
Webb High School Amphibian and Reptile Collection	WSARC

been deposited in the University of Tennessee, Knoxville, Vertebrate Zoology Collection.

In the following 60 species accounts, descriptive, taxonomic, distribution, and habitat information are presented in a uniform manner. Species names are followed by their author's name. Common names are listed and, in most cases, follow the suggestions of Collins, Huheey, Knight, and Smith (1978). A description for each species summarizes only those characteristics found useful in differentiating species in Tennessee, especially closely related forms. Unless stated otherwise, length measurements listed were taken from Conant (1975). The taxonomic treatment discusses subspecific variation reported in Tennessee and, where appropriate, taxonomic and nomenclatural usage adopted. By plotting locality data, distribution maps were developed and range limits determined for each species. A conservative approach was taken in delineating ranges and, in most instances, boundaries were based primarily on available locality data. Other considerations included known distributions in adjacent states, physiography, and habitat availability. During field surveys, habitat data were recorded for each species observed and, coupled with references from the literature, a habitat sketch is provided for each species.

B. Accounts of Species

In the following accounts, species are arranged alphabetically by genus, genera alphabetically by family, and families alphabetically by order. For reference purposes, a map showing the county names of Tennessee is provided in Figure 20.

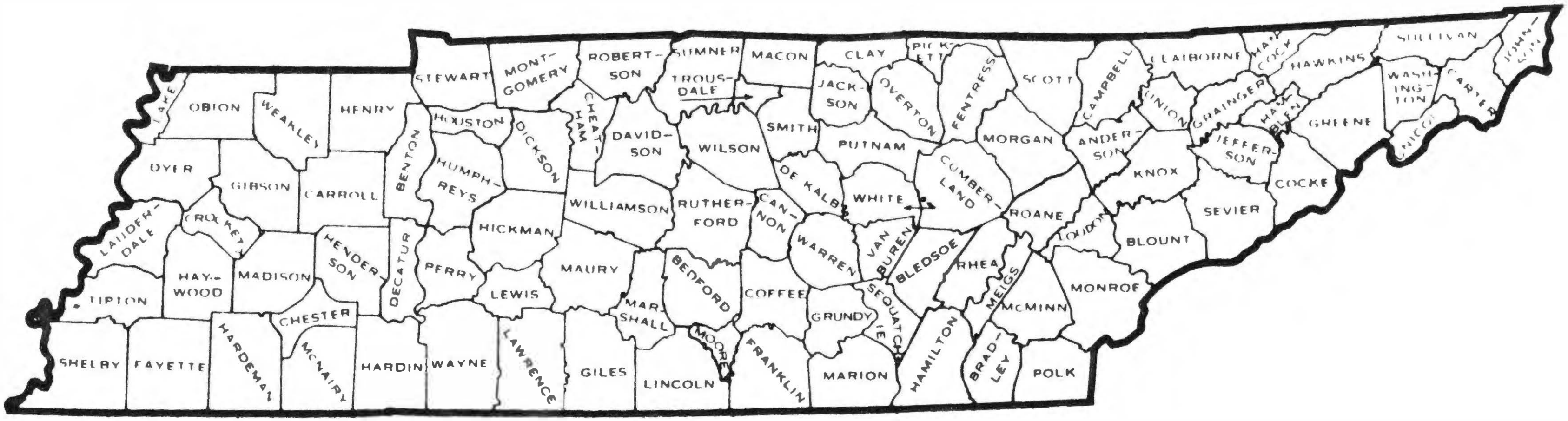

Figure 20. Maps of Tennessee showing county names.

1. Order Anura - Frogs and Toads

a. Family Bufonidae - Toads

(1.) Bufo americanus Holbrook - American Toad

(a.) Description. Bufo americanus is a medium-sized toad with adult head-body lengths ranging from 5.1 to 8.9 cm. Ground color may be gray, brown, or reddish and, when present, dorsal dark spots usually possess only one or two large warts. The venter is usually light with chest and upper abdomen dark spotted. Parotid glands are not in contact with postorbital ridges but are usually connected to them by a spur.

(b.) Taxonomic Considerations. Two subspecies are currently recognized in Tennessee. Bufo a. americanus ranges over most of the state (Conant, 1975) with B. a. charlesmithi Bragg occurring in extreme northwestern Tennessee (Conant, 1975; Lynch, 1964; Smith, 1961). Hybridization of B. americanus with B. woodhousei fowleri has been reported in eastern Tennessee by Johnson (1958), in Montgomery County by Scott and Snyder (1968), in Stewart County by Snyder (1972), and in Hardeman County by Norton and Harvey (1975). In contrast, King (1939) mentions no interbreeding even though he found both species breeding in the same pond.

(c.) Distribution and Habitat. The American toad is most often encountered during its early spring breeding season and is found statewide (Figure 21). It occurs in a wide variety of woodland and openland habitats that provide either permanent or temporary shallow water areas for breeding. Mathews and Echternacht (1984) reported this toad from above 1650 m in the Great Smoky Mountains National Park.

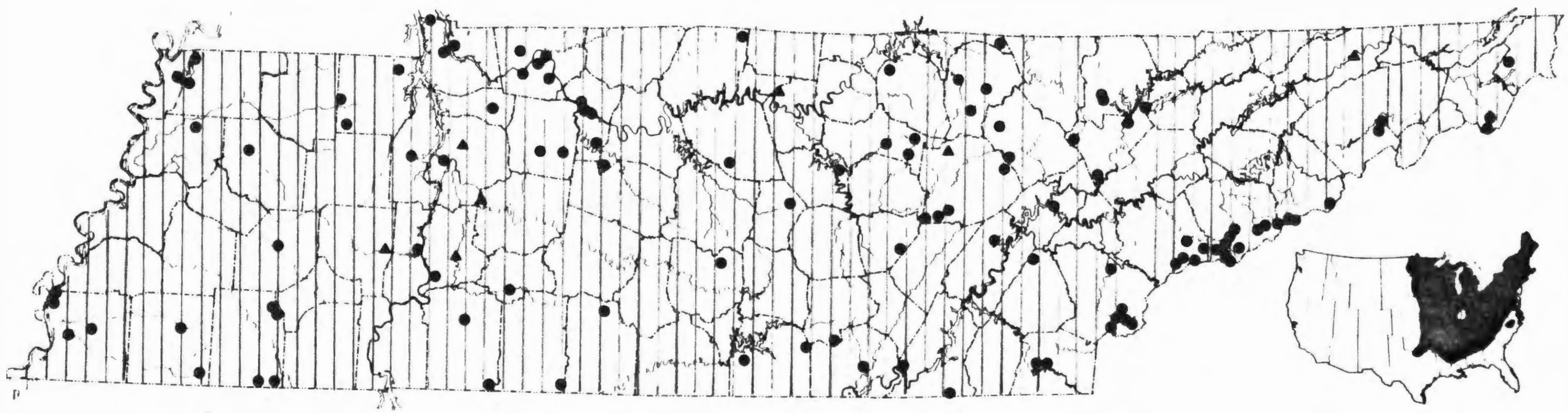

Figure 21. Distribution of <u>Bufo americanus</u>. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Smaller map depicts range in conterminous United States (Conant, 1975).

(2.) Bufo woodhousei Girard - Woodhouse's Toad

(a.) Description. Mature individuals range from 5.1 to 7.6 cm in head-body length. Ground color is variable and ranges from light gray to brick red. When present, each large dorsal dark spot usually possesses three or more small warts. Venter is usually light, however, breast may have a single, central dark spot. Anterior edge of parotoids is usually in direct contact with interorbital crests.

(b.) Taxonomic Considerations. Only one subspecies, B. w. fowleri Hinckley has been reported from Tennessee (Conant, 1975).

(c.) Distribution and Habitat. Bufo woodhousei is a very common species that occurs in a wide array of natural and urban habitats throughout the state (Figure 22). The species may occur as high as 1494 m in the Blue Ridge Mountains of eastern Tennessee (Stevenson, 1959). Breeding typically occurs in permanent aquatic sites including reservoirs, ponds, rivers, and sloughs.

b. Family Hylidae - Treefrogs

(1.) Acris crepitans Baird - Northern Cricket Frog

(a.) Description. This species is a small hylid whose adult head-body length varies from 1.6 to 3.8 cm. Dorsal ground color is highly variable and ranges from light gray to dark brown. A dorsal median green stripe may extend from head to rump. Snout is blunt and a dorsal dark triangle usually occurs between the eyes. A dark longitudinal stripe with ragged edges is present on rear of thigh. There are typically a pair of prominent anal warts. Tips of toes are only slightly rounded. Fourth toe on hind foot has 1.5 to 2 phalanges free of webbing.

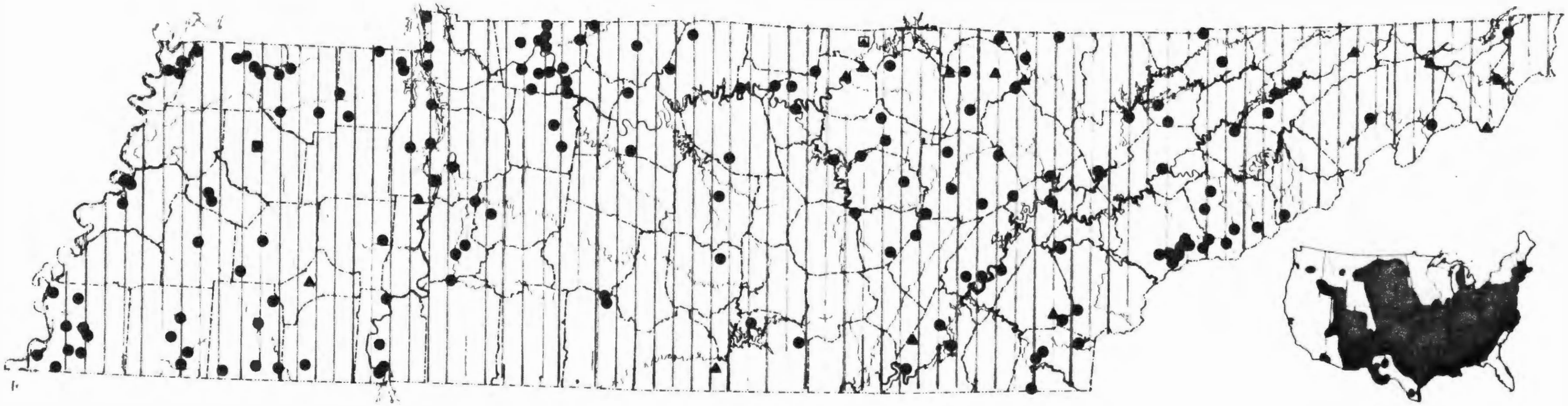

Figure 22. Distribution of Bufo woodhousei. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Solid circle in square denotes county record based on museum specimen without exact locality data. Solid triangle in square denotes county literature record without exact locality data. Smaller map depicts range in conterminous United States (Conant, 1975).

(b.) Taxonomic Considerations. Two subspecies have been listed from Tennessee. According to Conant (1975), *A. c. crepitans* ranges in the southeastern two-thirds of Tennessee while *A. c. blanchardi* Harper occupies the northwestern one-third.

(c.) Distribution and Habitat. *Acris crepitans* is known to occur throughout most of Tennessee, but, based on current data, the species is apparently absent from the northeastern corner of the state (Figure 23). Also, the species is probably absent from elevations above 335 m in the Great Smoky Mountains (Huheey and Stupka, 1967). The northern crickett frog is most often found near permanent bodies of water such as ponds, reservoirs, sloughs, and streams.

(2.) *Acris gryllus* (Le Conte) - Southern Cricket Frog

(a.) Description. *Acris gryllus* is a small frog very similar to *A. crepitans.* Head-body length for adults ranges from 1.6 to 3.2 cm. Dorsal ground color varies from gray to almost black. A dorsal median green, yellow, or brown stripe may extend from head to rump. As compared to *A. crepitans,* the snout of *A. gryllus* is more pointed and the body more slender. A dorsal dark colored triangle may occur between the eyes. A distinct dark longitudinal stripe with smooth edges is present on rear of thigh. Scattered warts in anal region are without a prominent pair near vent. Tips of toes are only slightly rounded. Fourth toe on hind foot has at least 2.5 phalanges free of webbing.

(b.) Taxonomic Considerations. As illustrated by Conant (1975), only the nominate subspecies occurs in Tennessee. Mount (1975) indicated hybridization with *A. crepitans* in Alabama. No evidence of this cross was found in Tennessee populations.

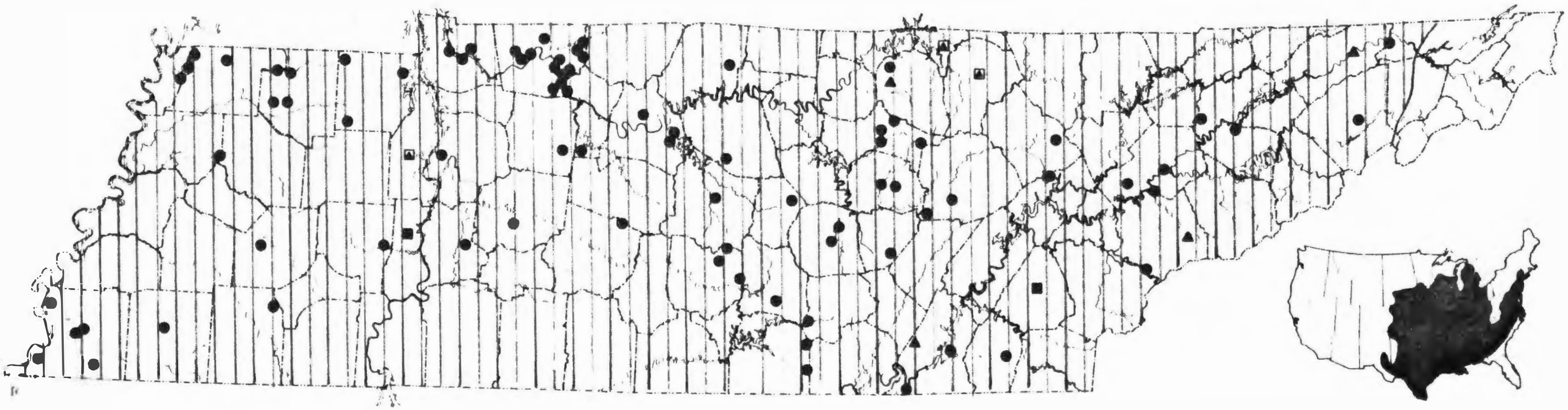

Figure 23. Distribution of Acris crepitans. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Solid circles within squares denote county records based on museum specimens without exact locality data. Solid triangles within squares denote county literature records without exact locality data. Smaller map depicts range in conterminous United States (Conant, 1975).

(c.) Distribution and Habitat. The southern cricket frog is known from five counties in extreme southwestern Tennessee (Figure 24). Like A. crepitans, A. gryllus occurs near permanent aquatic sites and may occur sympatrically with A. crepitans. However, A. gryllus may also utilize temporary pools. Norton and Harvey (1975) noted that where they occurred together, A. crepitans was usually found near the shoreline of a reservoir while A. gryllus typically occurred in well drained areas and near roadside pools.

(3.) Hyla avivoca Viosca - Bird-voiced Treefrog

(a.) Description. Hyla avivoca is a typical treefrog with ends of digits expanded into adhesive discs. Head-body length in mature specimens varies from 2.9 to 4.4 cm. Dorsal ground color may be green, various shades of gray, or nearly black. A dark irregularly shaped blotch is usually present on dorsum. Dark dorsal markings are usually present between the eyes and limbs are usually marked with dark crossbars. A small light spot is present on each side of head below the eyes. Dorsal surface of skin is mostly smooth. Inner surface of thighs are washed with light green or pale yellow.

(b.) Taxonomic Considerations. Only the nominate subspecies is recorded for Tennessee (Smith, 1966). Mount (1975) and, to a lesser degree, Smith (1966) question the validity of subspecific designations for this species.

(c.) Distribution and Habitat. The bird-voiced treefrog is known from the Coastal Plain of west Tennessee and along the lower Cumberland River in middle Tennessee (Figure 25). Based on a preserved specimen, Dunn (1927a) reported H. phaeocrypta Cope from Nashville. The specimen

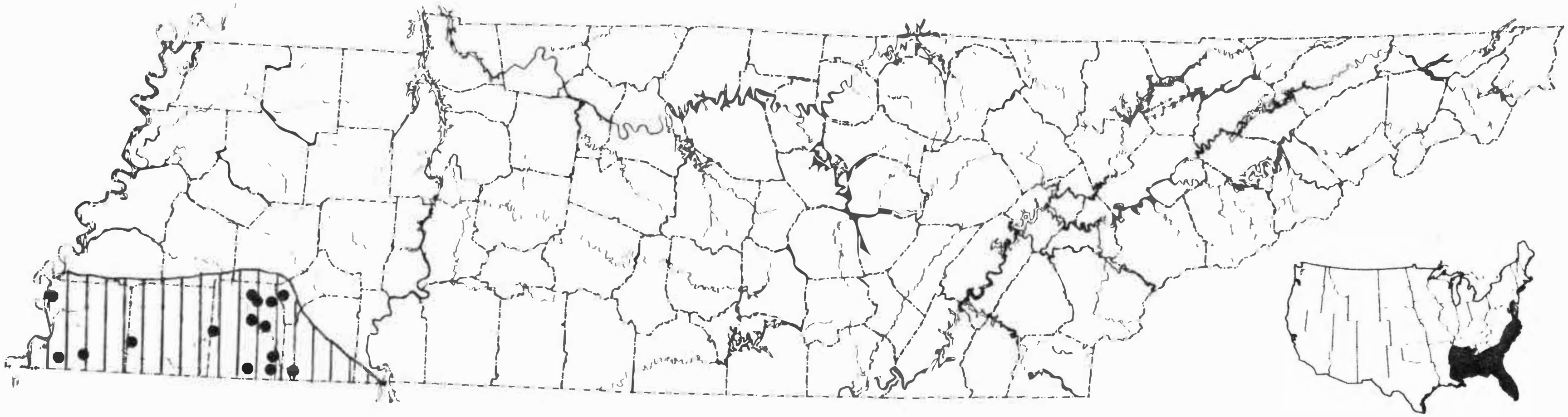

Figure 24. Distribution of *Acris gryllus*. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Smaller map depicts range in conterminous United States (Conant, 1975; Mount, 1975).

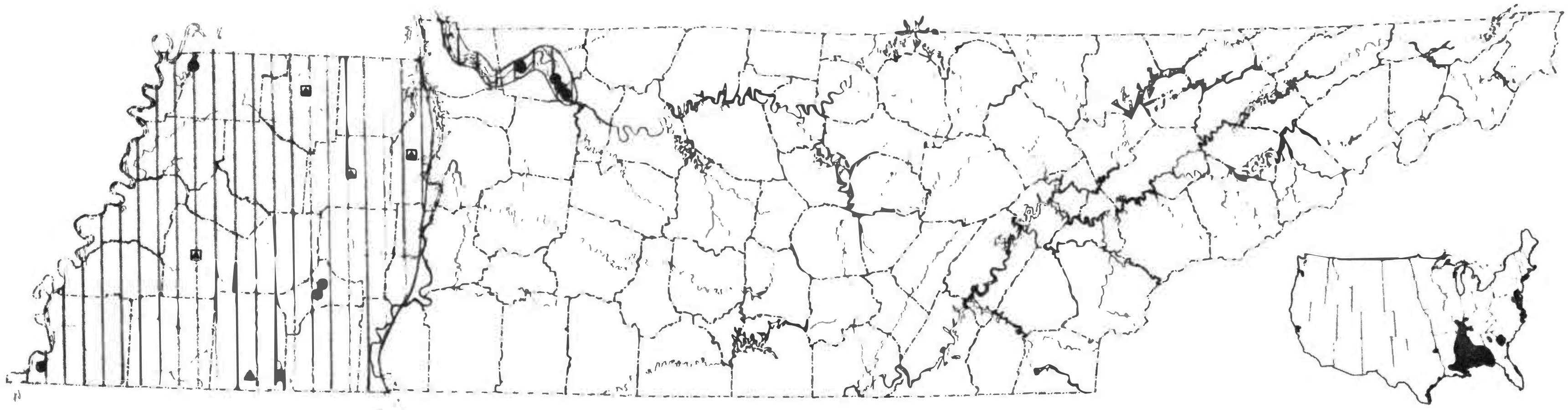

Figure 25. Distribution of Hyla avivoca. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Solid triangles within squares denote county records based on literature records without exact locality data. Smaller map depicts distribution in conterminous United States (modified from Smith, 1966; Conant, 1975).

was sent to the Museum of Comparative Zoology (MCZ) and has apparently been lost. Before Viosca (1928) described *H. avivoca*, *H. phaeocrypta* was the name applied to what are now known as two species, *H. avivoca* and *H. versicolor*. Thus, Dunn's record from Nashville remains questionable but probably refers to *H. versicolor*. In Tennessee, this hylid occurs in bottomland sloughs and swamps along major rivers and large creeks. It is especially abundant around Reelfoot Lake.

(4.) *Hyla cinerea* (Schneider) - Green Treefrog

(a.) *Description.* Adult size ranges from 3.2 to 5.7 cm in head-body length. Tips of toes are expanded to form adhesive discs. Dorsal surface is smooth. Dorsal color ranges from light to dark green and may have a few scattered small gold flecks. A lateral, sharply defined light stripe (usually white) extends from upper lip to about mid-body. Body form is slender.

(b.) *Taxonomic Considerations.* No subspecies are currently recognized (Conant, 1975). Hybridization with *H. gratiosa* has been reported in Florida by Lee (1968) and in Alabama by Mount (1975). No evidence of this hybrid cross was observed in Tennessee.

(c.) *Distribution and Habitat.* The green treefrog is primarily an inhabitant of bottomland swamps and sloughs of the Coastal Plain in west Tennessee (Figure 26). Like *H. avivoca*, *H. cinerea* is especially common around Reelfoot Lake. *Hyla cinerea* and *H. gratiosa* have often been confused in past literature reports for Tennessee. Burt (1938) reported *H. cinerea* from Clarksville, Montgomery County, and listed the collector and date as Howell, 1910. According to Burt (1937), all specimens taken during this study were deposited in the United States

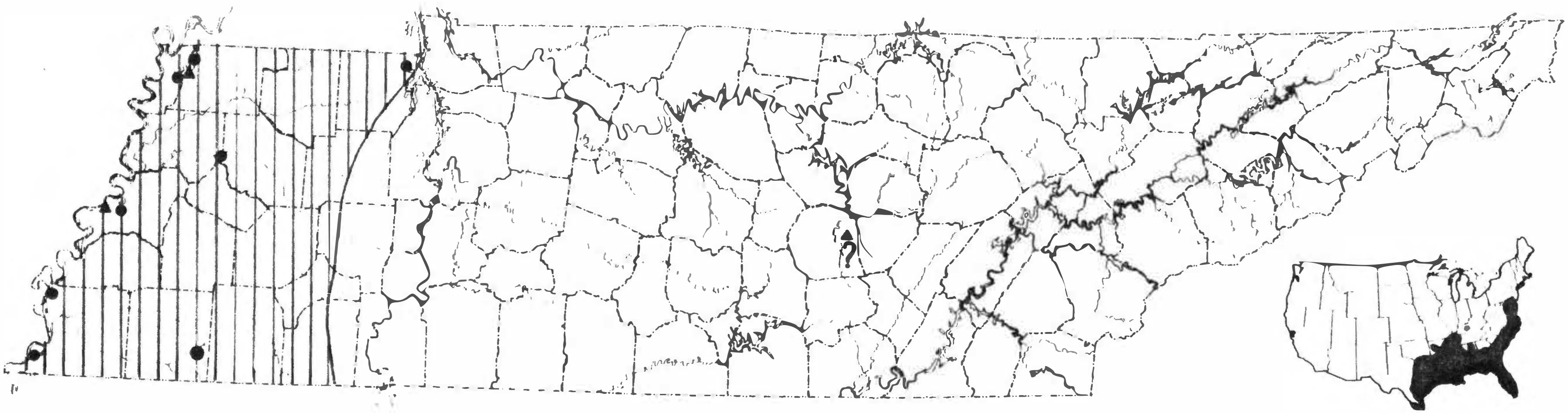

Figure 26. Distribution of Hyla cinerea. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Question mark adjacent to Warren County locality indicates questionable record. Smaller map depicts range in conterminous United States (modified from Conant, 1975; Mount, 1975).

National Museum (USNM). A study of the holdings at the USNM revealed an individual (USNM No. 48194) of H. gratiosa collected from Clarksville, Montgomery County, in 1910. In the USNM catalogue, this specimen was listed as H. cinerea. Thus, Burt's (1938) record is probably invalid. Based on a specimen at the Memphis State University Museum of Zoology (MSUMZ No. A2142) from Hardeman County, Jacob (1980) provided a new distribution record for H gratiosa that was originally labeled and reported by Norton and Harvey (1975) as H. cinerea. Another Montgomery County specimen of H. cinerea in the Illinois State Natural History Survey collection (INHS No. 9527) is correctly identified; however, the locality data is suspect. According to the INHS catalogue, this specimen was taken near Clarksville during the summer of 1960 by Floyd Ford. Dr. Ford is now a faculty member at Austin Peay State University and was questioned by A. Floyd Scott about this record. According to Scott (pers. comm.), Ford does not recall where he collected the specimen. However, during the summer of 1960, he was conducting fieldwork at Reelfoot Lake, and it is likely that the specimen was taken there. Scott (pers. comm.) has over 10 years field experience in the Montgomery County area and has never observed H. cinerea. Gentry (1955-1956) reported H. cinerea from temporary sinkhole lakes in Warren County. This report is also considered questionable (Figure 26) and is probably invalid. As clearly indicated by past literature reports, H. cinerea and H. gratiosa are easily confused. Also, their calls are somewhat similar and can be confused. Considering these similarities, the documented presence of H. gratiosa in adjacent White and Van Buren counties, and the occurrence of H. gratiosa in sinkhole ponds elsewhere in Tennessee (see H. gratiosa account), it is likely that Gentry's record is actually H. gratiosa.

(5.) Hyla crucifer Wied - Spring Peeper

(a.) Description. The spring peeper is a small hylid species. Average adult size varies from 1.9 to 3.2 cm in head-body length. Tips of toes possess adhesive discs. Dorsal skin surface is smooth. Dorsal ground color ranges from light tan with a pinkish tinge to dark brown. Distinct dark brown markings in the form of an X are usually present on dorsum, and a dorsal dark mark typically forming a transverse bar is present between the eyes.

(b.) Taxonomic Considerations. Conant (1975) lists all populations in Tennessee as H. c. crucifer.

(c.) Distribution and Habitat. Hyla crucifer is an early spring breeder that occurs statewide (Figure 27). In Tennessee, the species is very common near almost any type of woodland or brushland aquatic habitats, and breeding individuals especially favor sites bordered by dense vegetation. The species does not appear to be limited by elevational factors in Tennessee and has been reported from above 1650 m in the Great Smoky Mountains National Park (Mathews and Echternacht, 1984).

(6.) Hyla gratiosa Le Conte - Barking Treefrog

(a.) Description. Hyla gratiosa is often confused with H. cinerea. Adults vary in head-body length from 5.1 to 6.7 cm. Tips of toes are expanded into adhesive discs. Dorsal surface is more rugose and body form stockier than H. cinerea. Dorsal ground color ranges from light to dark green. Round dark dorsal spots may either be distinct or barely detectable and are often lost in preservative. A lateral white line may extend from upper lip to mid-body; however, in contrast to H. cinerea, its borders are broken and irregular.

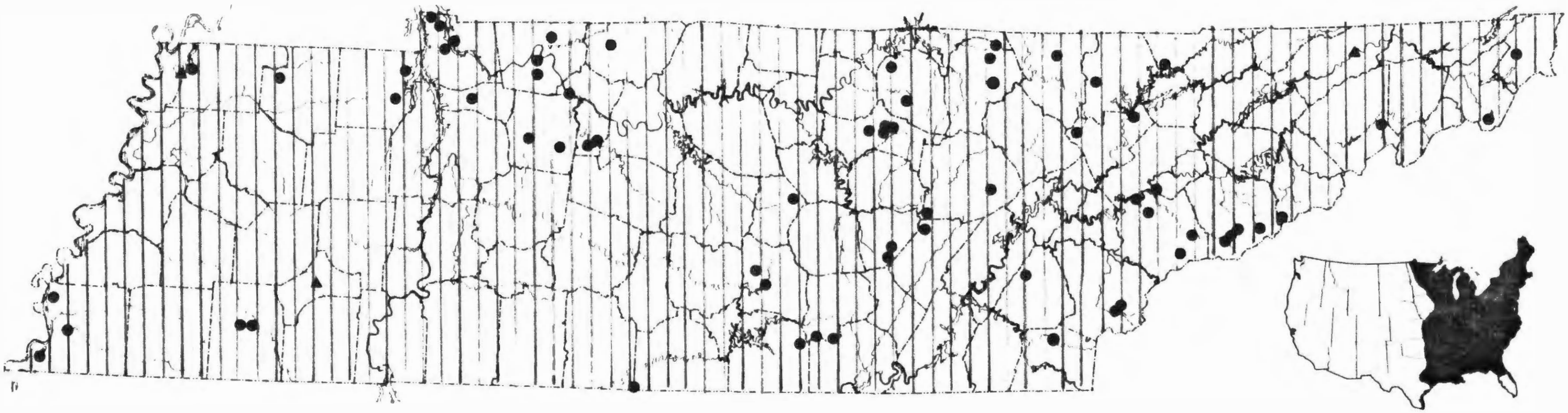

Figure 27. Distribution of Hyla crucifer. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Smaller map indicates range in conterminous United States (Conant, 1975).

(b.) Taxonomic Considerations. No subspecies are recognized (Caldwell, 1982).

(c.) Distribution and Habitat. In Tennessee, distribution and habitat requirements are poorly known, and the species is currently known from three disjunct areas (Figure 28). Recently, Jacob (1980) and Heineke and Heineke (1984) reported specimens from the Coastal Plain in southwestern Tennessee. Jacob's (1980) record from Hardeman County was based on a specimen taken by Norton (1971) at night "in a honeysuckle thicket above a ravine." Norton (1971) and Norton and Harvey (1975) incorrectly identified this specimen as *H. cinerea.* Heineke and Heineke (1984) found a specimen after a brief rainfall on a patio in suburban Bartlett, Shelby County. Coastal Plain populations are tentatively considered continuous with those from northwestern Alabama (Mount, 1975). The presence of *H. gratiosa* from limestone sinkponds on the Western Highland Rim in north-central Tennessee has been well documented by Scott and Harker (1968), Scott and Snyder (1967, 1968), and VanNorman (1985). VanNorman's study indicates that populations of *H. gratiosa* in north-central Tennessee and south-central Kentucky form a continuous geographic unit that is probably disjunct from the southern portion of the species range. Rossman (1958) found a female on a motel porch in White County. This locality is near the transition from Eastern Highland Rim to Cumberland Plateau. On the Cumberland Plateau, populations are known from upland swamps and stripmine ponds in Van Buren County and a limestone sinkpond in Franklin County. These Cumberland Plateau and Eastern Highland Rim populations are regarded as continuous with those reported from northeastern Alabama by Mount (1975).

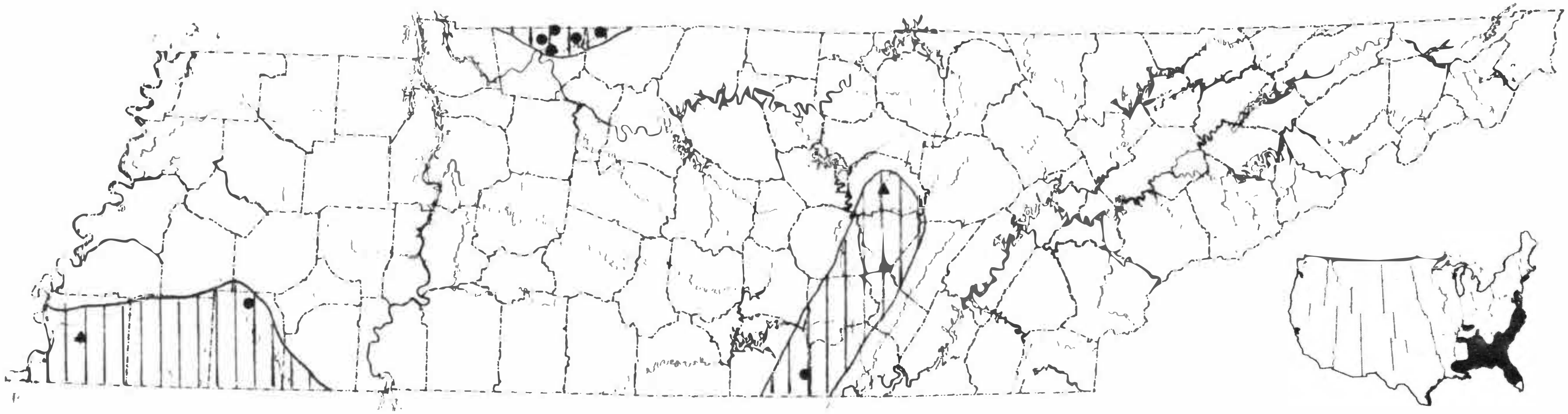

Figure 28. Distribution of Hyla gratiosa. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Smaller map indicates range in conterminous United States (modified from Caldwell, 1982).

(7.) Hyla versicolor Le Conte - Gray Treefrog and Hyla chrysoscelis Cope - Cope's Gray Treefrog

(a.) Description. Because these two species cannot be reliably separated based on external morphology and the range of each has not been determined in Tennessee, they are treated together as a sibling species pair. In addition, members of this species pair are also easily confused with H. avivoca. The following characteristics are shared by both members of the species pair. Adult head-body lengths range from 3.2 to 5.1 cm. Tips of toes have adhesive discs. Dorsal ground color varies from light gray or light green to dark brown. Large dark blotches of irregular size and shape may occur on dorsum. Limbs are usually marked with dark crossbars. A small light spot is present on each side of head below the eyes. Dorsal skin surface is more rugose than H. avivoca. Also, inner surface of thighs are washed with bright yellow or orange in contrast to the greenish or pale yellowish color present in H. avivoca.

(b.) Taxonomic Considerations. Based on breeding experiments that revealed a high degree of incompatibility between the two species and the existence of different mating call trill rates, Johnson (1966) recognized H. chrysoscelis as a cryptic species. Johnson described a fast trill rate for the mating call of H. chrysoscelis and a slower trill rate for H. versicolor. Other studies have reinforced Johnson's conclusions and characteristics found useful in separating the two species include chromosome number, cell size, and cell nucleus size and composition. Bogart and Wasserman (1972) showed that H. versicolor is tetraploid (4N=48) while H. chrysoscelis is diploid (2N=24). They also noted that blood and sperm cells were larger in H. versicolor. Green

(1984) reported larger epidermal cells in the toe-pads of H. versicolor. The cell nuclei of H. versicolor were found to be larger and contain more nucleoli than the nuclei of H. chrysoscelis (Cash and Bogart, 1978).

(c.) Distribution and Habitat. The composite range of the species pair is statewide (Figure 29). The distribution of each species is unknown. The majority of references in the literature fail to distinguish the two species, and available museum specimens could not be separated without extensive laboratory studies. Ralin's (1968) distribution map shows the range of H. chrysoscelis to include west Tennessee and H. versicolor in central and east Tennessee. Hyla chrysoscelis has been identified from Reelfoot Lake (Bushnell, Bushnell, and Parker, 1939; Wasserman, 1970) and Cumberland and Wilson counties (Wiley, 1982). Based on these scant data, it appears that H. chrysoscelis may occur as far east in Tennessee as the Cumberland Plateau and may be sympatric with H. versicolor in the central part of the state. During the course of this study, individuals were observed in a wide variety of aquatic habitats in both woodland and open areas. Breeding was observed in small ponds, along the edges of large reservoirs, flooded fields, roadside ditches, and swamps. Individuals have been reported from above 1650 m in the mountains of extreme eastern Tennessee (Mathews and Echternacht, 1984).

(8.) Pseudacris brachyphona (Cope) - Mountain Chorus Frog

(a.) Description. The mountain chorus frog is a small stocky hylid with adult head-body length varying from 2.5 to 3.2 cm. Toe tips are slightly expanded to form adhesive discs. Dorsal ground color is usually

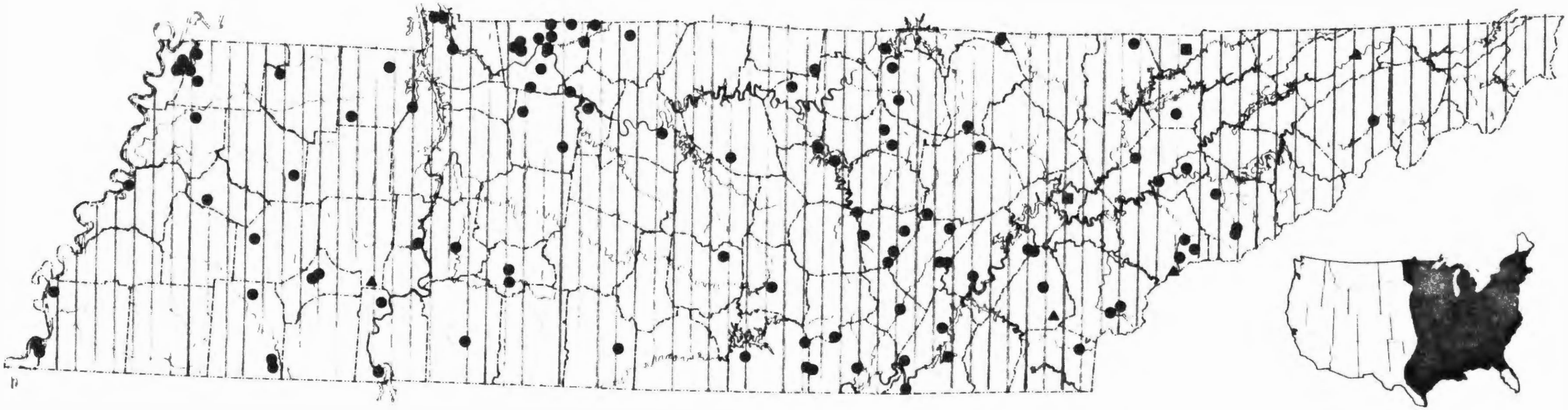

Figure 29. Composite range of Hyla versicolor and Hyla chrysoscelis. Vertical hatching indicates composite range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Solid circles within squares denote county records based on museum specimens without exact locality data. Smaller map depicts composite range in conterminous United States (Conant, 1975).

brown or gray. A dorsal dark triangle typically occurs between the eyes. Dark colored bars on dorsum may form a reverse parenthesis or H-shaped pattern. However, these markings may be broken into irregularly shaped spots and in some individuals may be absent. A light stripe is present on the upper lip.

(b.) Taxonomic Considerations. Hoffman (1980) does not recognize any subspecific variation.

(c.) Distribution and Habitat. This small hylid is seldom encountered except during its early spring breeding season. On the Cumberland Plateau, *P. brachyphona* and *Bufo americanus* often utilize the same breeding sites. Breeding activity typically occurs in wooded seepage pools, shallow flooded ditches along roads and railroads, small puddles, and shallow ponds. In Tennessee, the mountain chorus frog is known from the Cumberland Mountains, Cumberland Plateau, and Blue Ridge Mountains in extreme northeastern and southwestern Tennessee (Figure 30). Distributional limits depicted for Tennessee follow Hoffman (1980).

(9.) *Pseudacris triseriata* (Wied) - Striped Chorus Frog

(a.) Description. This species is similar in size to *P. brachyphona* but is somewhat more slender in appearance. Mature individuals attain head-body lengths ranging from 1.9 to 3.5 cm. Toe-tips are slightly expanded to form adhesive discs. Light stripe is present on upper lip. A lateral dark line originates on snout and extends through the eye to the groin area. Dorsal ground color varies from gray to dark brown. A dorsal dark triangle generally occurs between the eyes. Dorsal markings are variable but usually consist of a median and two lateral dark stripes.

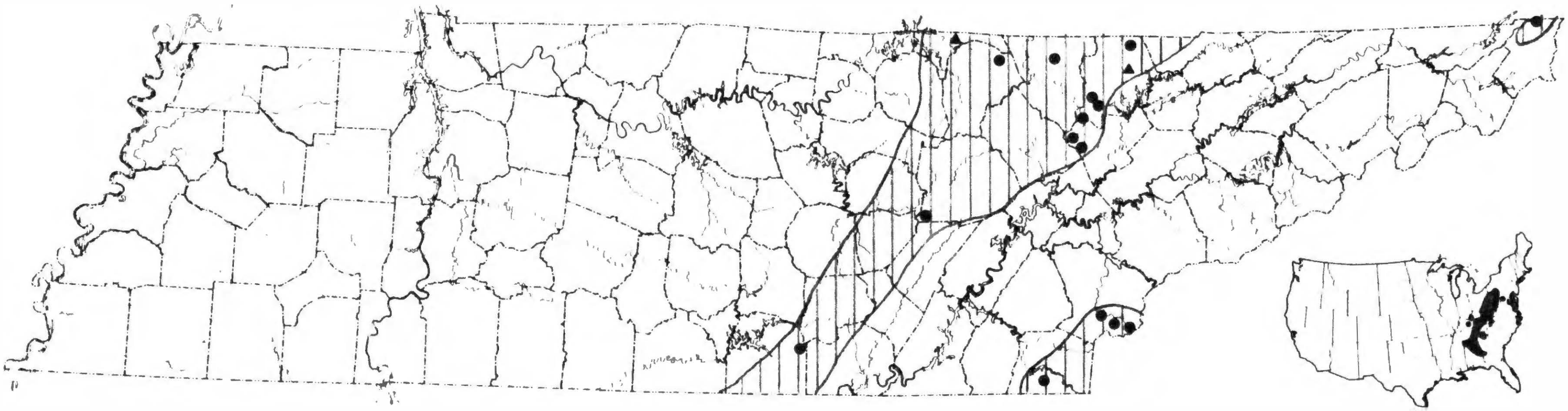

Figure 30. Distribution of Pseudacris brachyphona. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Smaller map depicts range in conterminous United States (Hoffman, 1980).

(b.) Taxonomic Considerations. *Pseudacris t. feriarum* (Baird) is the only subspecies currently recognized in Tennessee (Conant, 1975).

(c.) Distribution and Habitat. *Pseudacris triseriata* occurs statewide (Figure 31) and occupies woodland and openland habitats that provide suitable breeding sites. Preferred breeding sites include shallow water ponds, flooded woodlands and pastures, and roadside ditches.

c. Family Microhylidae - Narrowmouth Toads

(1.) *Gastrophryne carolinensis* (Holbrook) - Eastern Narrowmouth Toad

(a.) Description. *Gastrophryne carolinensis* is a small stocky anuran with a distinctly pointed snout and small head. Adult head-body lengths range from 2.2. to 3.2 cm. Legs are short and webbing is absent between toes. Skin is smooth and dorsal ground color may be gray, brown, or rust. Broad, light colored dorsolateral stripes are usually present.

(b.) Taxonomic Considerations. According to Nelson (1972), no subspecies are recognized.

(c.) Distribution and Habitat. *Gastrophryne carolinensis* is widespread in Tennessee but is apparently limited in the east by the high elevations of the Blue Ridge Mountains (Figure 32). Martof, Palmer, Bailey, and Harrison (1980) and Nelson (1972) provide distribution maps that show *G. carolinensis* absent from most of the Blue Ridge Mountains in Virginia, North Carolina, Tennessee, and Georgia. Available records for Tennessee indicate the species occurs as high as 549 m in Cades Cove in the Great Smoky Mountains National Park (Huheey and Stupka, 1967). This burrowing species is found near reservoirs, ponds, drainage ditches, and sloughs.

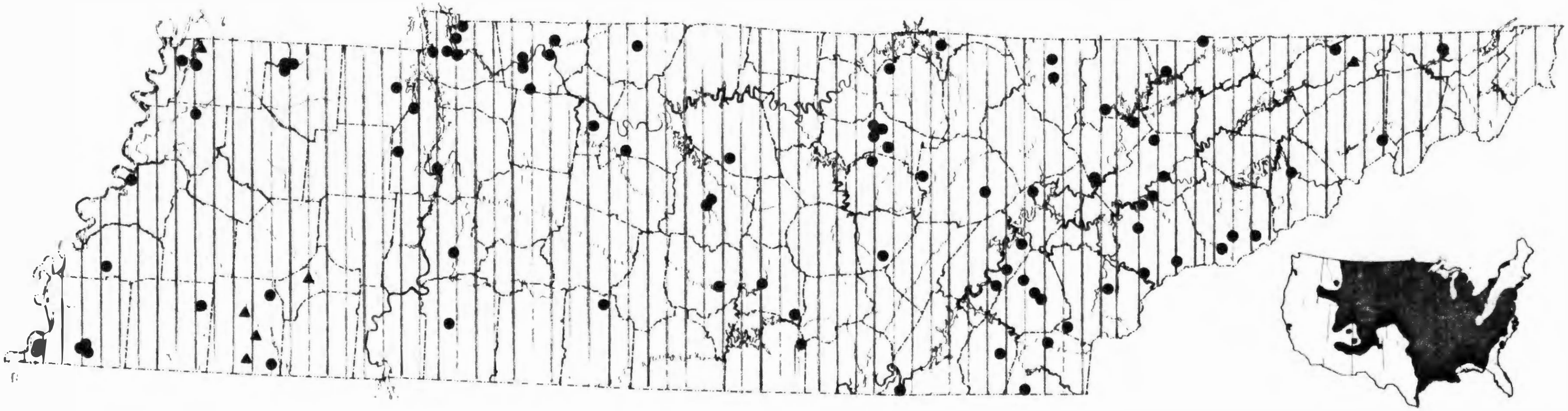

Figure 31. Distribution of <u>Pseudacris triseriata.</u> Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Smaller map depicts range in conterminous United States (Conant, 1975).

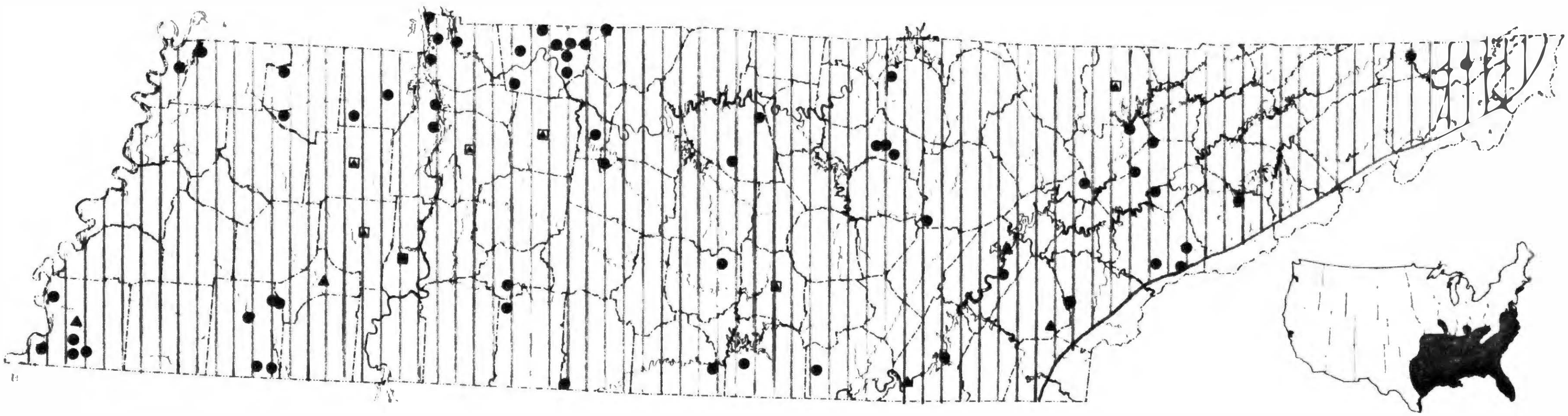

Figure 32. Distribution of <u>Gastrophryne carolinensis.</u> Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Solid circle within square denotes county record based on museum specimens without exact locality data. Solid triangles within squares denote county literature records without exact locality data. Smaller map depicts range in conterminous United States (Nelson, 1972).

d. Family Pelobatidae - Spadefoot Toads

(1.) Scaphiopus holbrooki (Harlan) - Eastern Spadefoot

(a.) Description. The eastern spadefoot is toad-like in appearance. Average adult head-body length varies from 4.4 to 5.7 cm. Cranial crests are absent. Pupils of eyes are vertically elliptical in shape. A dark, elongate, horny spade is present on heel of each foot. Dorsal ground color varies from yellowish brown to dark brown. Lyre shaped light markings are usually present on dorsum.

(b.) Taxonomic Considerations. Only the nominate subspecies is known to occur in Tennessee (Wasserman, 1968).

(c.) Distribution and Habitat. Museum records for Tennessee and range map for North Carolina provided by Martof, Palmer, Bailey, and Harrison (1980) indicate that S. holbrooki occurs throughout Tennessee with the exception of the Blue Ridge Mountains (Figure 33). Although Wasserman's (1968) map shows the species as absent from the Cumberland Plateau of Tennessee and Alabama, museum records indicate its presence there. The eastern spadefoot is a secretive burrowing species that breeds in temporary pools formed by heavy rains.

e. Family Ranidae - True Frogs

(1.) Rana areolata Baird and Girard - Crawfish Frog

(a.) Description. The crawfish frog is a stocky ranid with adults varying in head-body length from 5.7 to 7.6 cm. Dorsolateral folds are present along each side of body. Snout is conical in shape and upper jaw is mottled with dark and light markings. Dorsal ground color varies from light gray to off-white. Dorsal markings are profuse consisting of

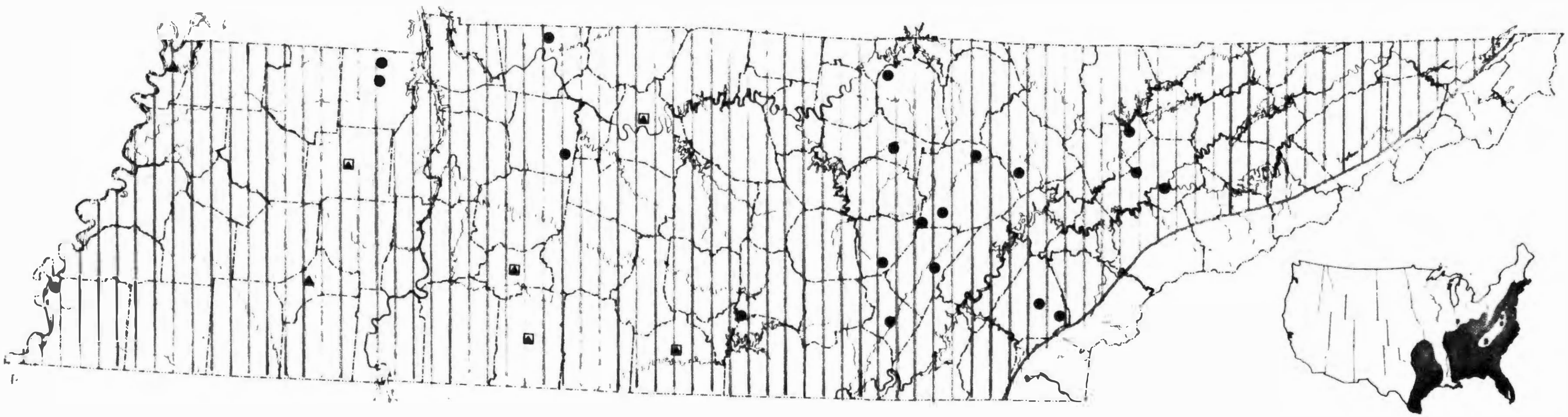

Figure 33. Distribution of <u>Scaphiopus holbrooki.</u> Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Solid triangles within squares denote county literature records without exact locality data. Smaller map depicts range in conterminous United States (Conant, 1975; Martof, Palmer, Bailey, and Harrison, 1980; Mount, 1975; Barbour, 1971).

many round dark spots interspersed with smaller dark markings of varying shapes.

(b.) Taxonomic Considerations. Five subspecies are currently recognized. However, only *R. a. circulosa* Rice and Davis, is known from Tennessee (Altig and Lohoefener, 1983).

(c.) Distribution and Habitat. *Rana aerolata* is found in the Coastal Plain of western Tennessee (Figure 34). Although records are lacking for a large area in the Hardeman-McNairy county area, the species is known from just across the state line near Corinth, Mississippi (George Folkerts, pers. comm.). The crawfish frog is very wary and difficult to approach. It breeds in flooded pastures and woodlands, farm ponds, and small reservoirs and often takes refuge in abandoned crawfish burrows.

(2.) *Rana catesbeiana* Shaw - Bullfrog

(a.) Description. The bullfrog is a large ranid. Mature specimens average 9.0 to 15.0 cm in head-body length. Dorsolateral ridges are absent. Dorsal color is typically light to dark green with a highly variable pattern of faint dark markings. Mottling is not present on the upper lip. The tympanic fold is well developed.

(b.) Taxonomic Considerations. No subspecies are currently recognized (Conant, 1975).

(c.) Distribution and Habitat. The bullfrog is common throughout Tennessee and occurs near most all permanently aquatic habitats including creeks, rivers, ponds, reservoirs, sloughs, and drainage ditches (Figure 35).

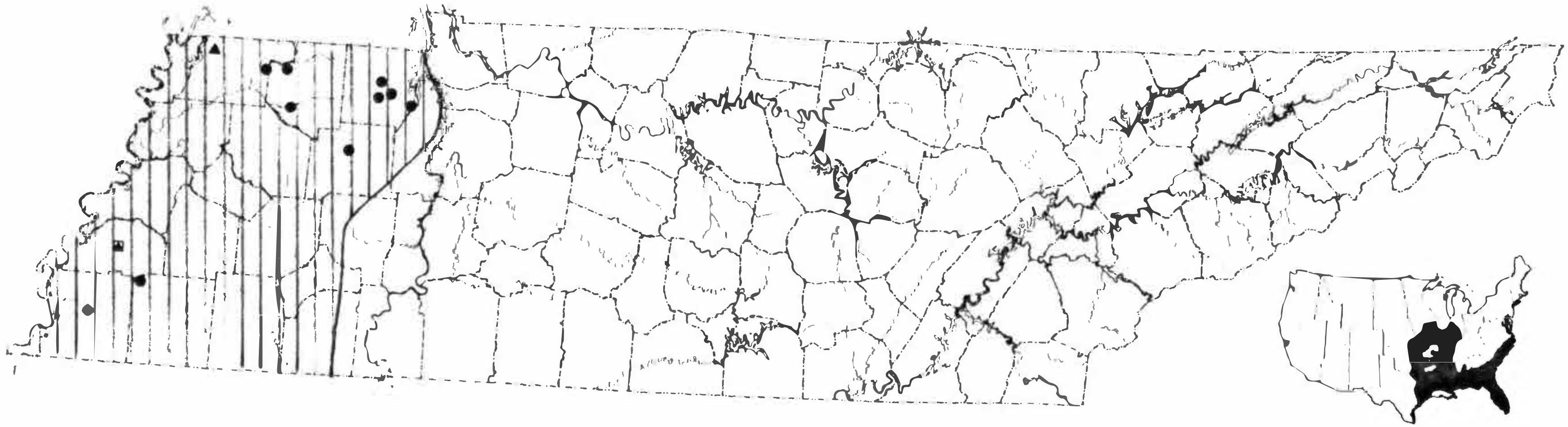

Figure 34. Distribution of <u>Rana areolata.</u> Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangle denotes literature record believed valid. Solid triangle within square denotes county literature record without exact locality data. Smaller map depicts range in conterminous United States (Altig and Lohoefener, 1983).

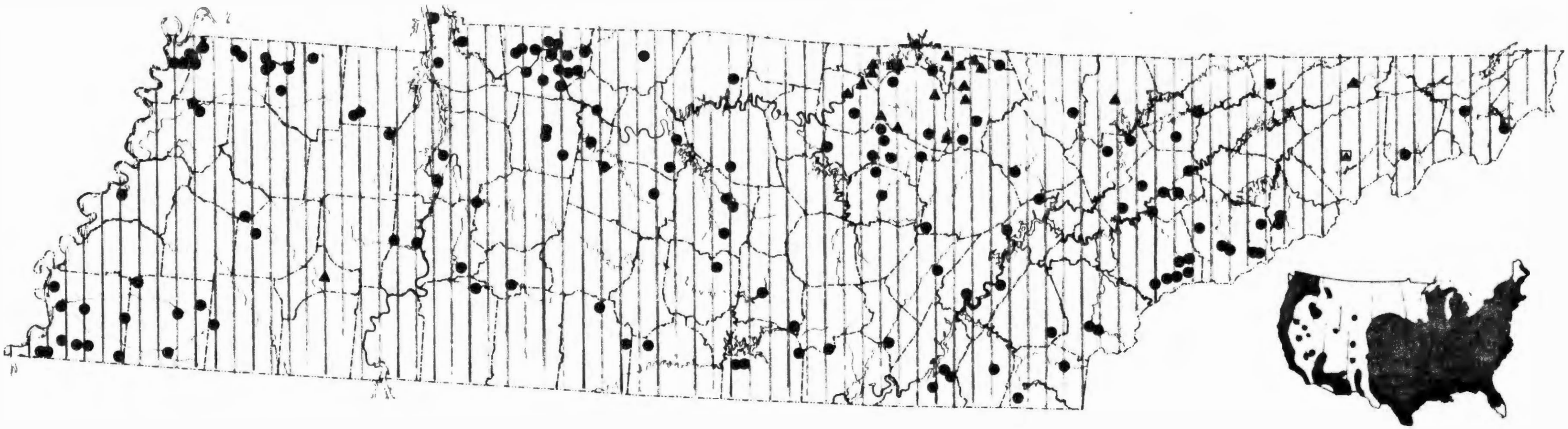

Figure 35. Distribution of Rana catesbeiana. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Solid triangle within square denotes a county literature record without exact locality data. Smaller map depicts range in conterminous United States (Conant, 1975).

(3.) Rana clamitans Latreille - Green Frog

(a.) Description. Rana clamitans is a medium size frog with adult head-body lengths ranging from 5.4 to 8.9 cm. Dorsolateral folds are present, but distinct only from head to mid-body. Dorsal ground color may be green, brown, or bronze. Dark dorsal markings are usually absent; however, indistinct spots, blotches, or worm-like markings may be present.

(b.) Taxonomic Considerations. According to Stewart (1983), R. c. melanota (Rafinesque) occurs in the eastern two-thirds of Tennessee and R. c. clamitans ranges in the Gulf Coastal Plain of western Tennessee. There appears to be a broad zone of intergradation between these two subspecies and in some areas subspecific variation is poorly defined (Stewart, 1983; Mount, 1975; Ferguson, 1961).

(c.) Distribution and Habitat. This species is a common inhabitant of creeks, rivers, swamps, sloughs, reservoirs, and ponds and occurs throughout Tennessee (Figure 36).

(4.) Rana palustris Le Conte - Pickerel Frog

(a.) Description. The pickerel frog is similar in size to R. clamitans. Head-body lengths of adults range from 4.4 to 7.6 cm. Dorsolateral ridges are well developed and extend from just behind the eyes to groin area. Dorsal ground color ranges from light gray to light brown with distinct rectangular or square-shaped, paired dark markings. In a few individuals, these markings may fuse to form longitudinal bars. Dark spot is typically present on snout. Inner surfaces at hind legs and groin area are tinged with yellow.

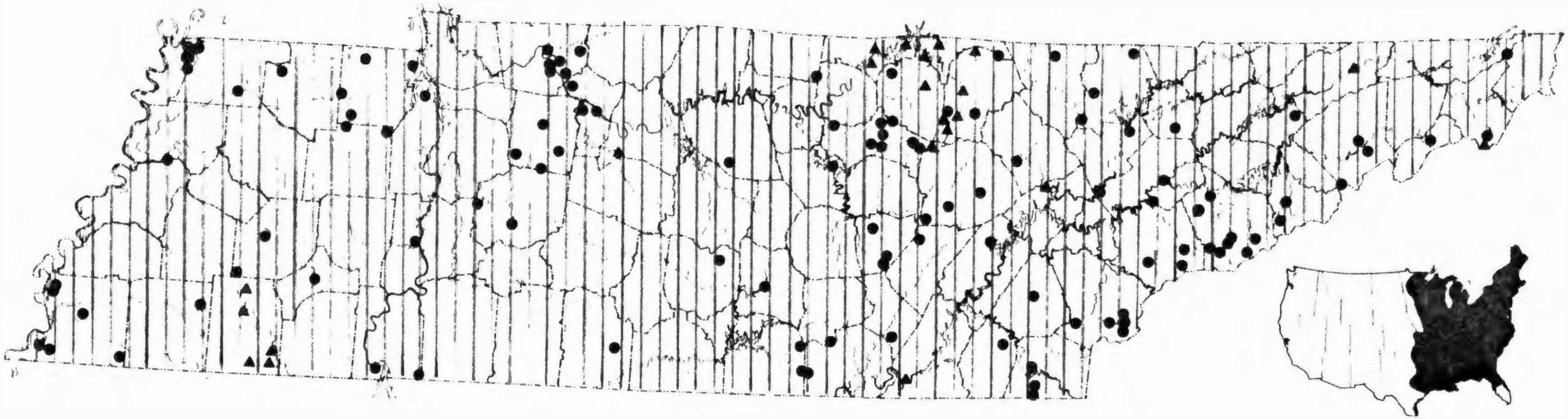

Figure 36. Distribution of *Rana clamitans*. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Smaller map depicts range in conterminous United States (Stewart, 1983).

(b.) Taxonomic Considerations. Currently, no subspecies are recognized (Schaff and Smith, 1971).

(c.) Distribution and Habitat. Although usually considered to occur statewide, *R. palustris* appears to be uncommon in the Coastal Plain of west Tennessee (Figure 37). It is usually found in and near woodland creeks, ponds, and reservoirs.

(5.) *Rana sylvatica* Le Conte - Wood Frog

(a.) Description. This species is a medium-sized ranid with adult head-body length 3.5 to 7.0 cm. Dorsolateral folds are present and extend from just behind eyes to groin area. Dorsal coloration varies from light tan to brown. Scattered dark markings may occur on dorsum. Light stripe is present on upper lip. Lateral brown to blackish markings extend from the snout to behind tympanum and form a distinct facial mask.

(b.) Taxonomic Considerations. No subspecific designations are recognized (Martof, 1970).

(c.) Distribution and Habitat. A species usually found near upland woodland streams and flooded depressions, *R. sylvatica* is presently known from approximately the northeastern one-third of Tennessee (Figure 38).

(6.) *Rana utricularia* Harlan - Southern Leopard Frog

(a.) Description. *Rana utricularia* is a medium-sized frog that as an adult ranges from 5.1 to 8.9 cm in head-body length. Dorsal ground color varies from light green to brown. Dorsal spotting is highly variable, but usually includes scattered, distinctly rounded large dark spots. On some individuals, spots may be elongate and on others dorsal

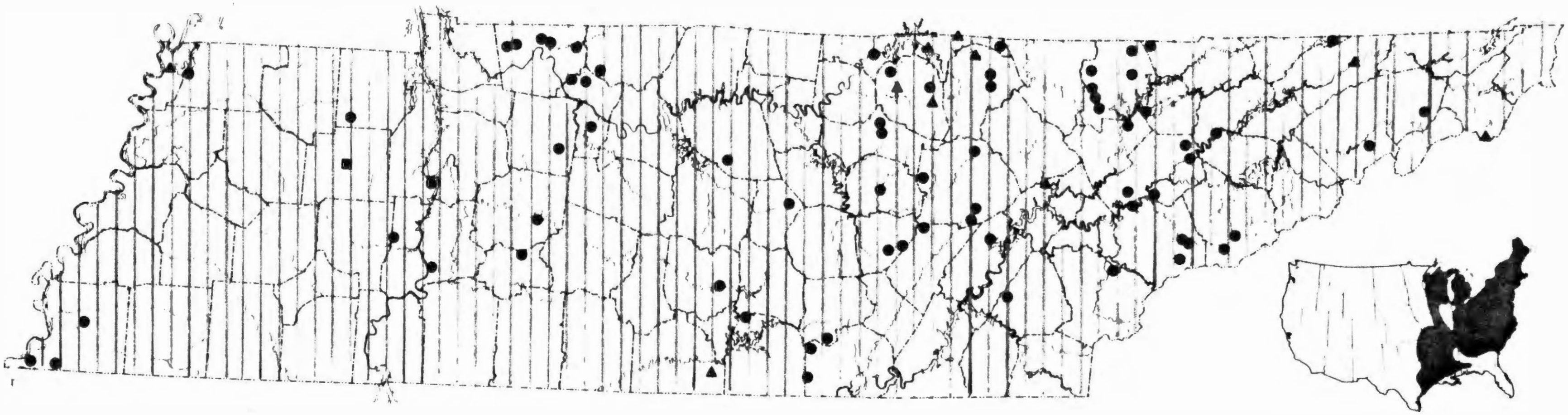

Figure 37. Distribution of Rana palustris. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Solid circle within square denotes county record based on museum specimens without exact locality data. Smaller map depicts range in conterminous United States (Conant, 1975; Mount, 1975; Martof, Palmer, Bailey, and Harrison, 1980).

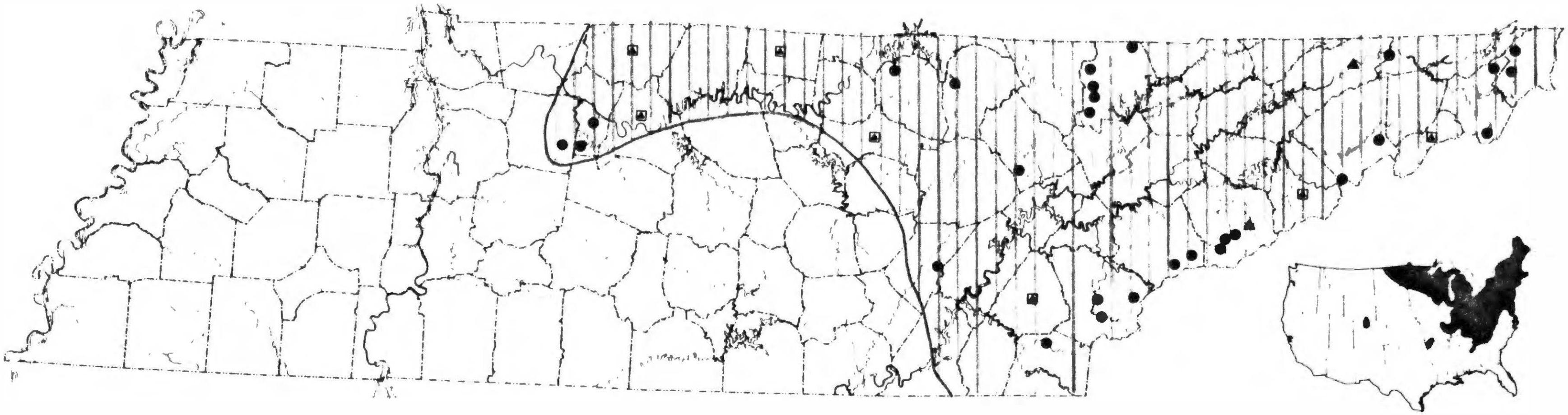

Figure 38. Distribution of Rana sylvatica. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Solid triangles within squares denote county literature records without exact locality data. Smaller map depicts range in conterminous United States (Conant, 1975; Mount, 1975).

spotting may be indistinct or absent. Distinct dorsolateral folds extend from just behind eyes to groin area. Lateral surfaces usually have a few dark spots. Light line is present on upper lip. Venter is typically white and a white spot usually occurs in center of tympanum.

(b.) Taxonomic Considerations. The *Rana pipiens* complex has a confusing taxonomic history. Following the recent treatment of Pace (1974), populations in Tennessee are considered *R. u. utricularia.* This species is often referred to as *R. sphenocephala* Cope or *R. pipiens sphenocephala* in the literature.

(c.) Distribution and Habitat. Like *Gastrophryne carolinensis, R. utricularia* is common throughout most of Tennessee, but is apparently limited in the east by the higher elevations of the Blue Ridge Mountains. *Rana utricularia* is also possibly absent from a small area of upper northeastern Tennessee (Figure 39). Conant's (1975) distribution map for the species shows it absent from the Blue Ridge Mountains of Virginia, North Carolina, northeastern Tennessee, South Carolina, and Georgia. In the Great Smoky Mountains of Tennessee, Huheey and Stupka (1967) recorded the species from Cades Cove near 549 m elevation. Southern leopard frogs are common near farm ponds, reservoirs, creeks, rivers, sloughs, and swamps.

2. Order Caudata - Salamanders

a. Family Ambystomatidae - Mole Salamanders

(1.) *Ambystoma maculatum* (Shaw) - Spotted Salamander

(a.) Description. *Ambystoma maculatum* is a large burrowing species with adults reaching total lengths of 15 to 20 cm. Dorsal coloration

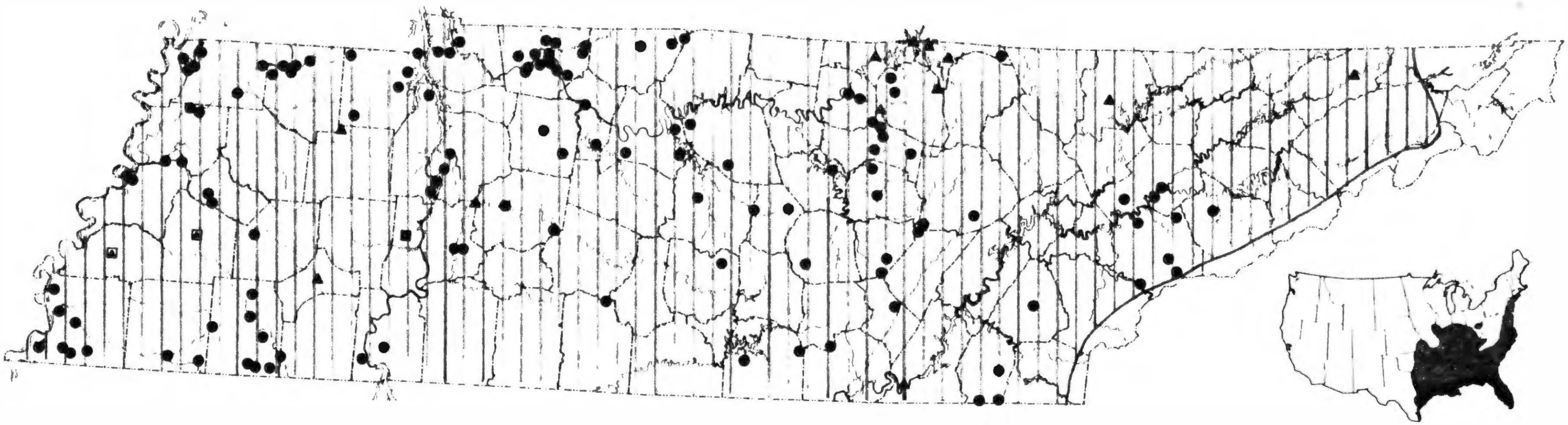

Figure 39. Distribution of Rana utricularia. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Solid circle within square denotes county record based on museum specimen without exact locality data. Solid triangles within squares denote county literature records without exact locality data. Smaller map depicts range in conterminous United States (Pace, 1974; Conant, 1975).

ranges from gray to dark brown with several pair of rounded yellow to orange spots forming two irregular rows from eyes to near the end of the tail. Adults typically possess 12 costal grooves.

(b.) Taxonomic Considerations. Anderson (1967a) does not list subspecies.

(c.) Distribution and Habitat. The spotted salamander occurs statewide (Figure 40) and is most often found in hardwood or mixed pine-hardwood forests near both permanent and temporary pools.

(2.) *Ambystoma opacum* (Gravenhorst) - Marbled Salamander

(a.) Description. The adult marbled salamander is chunky and medium-sized, varying in total length from 9 to 11 cm. Dorsal ground color varies from dark gray to black. Light gray or white dorsal markings form crossbands that are often complete, but sometimes broken. Costal groove count varies from 11 to 13.

(b.) Taxonomic Considerations. No subspecies are currently recognized (Anderson, 1967b).

(c.) Distribution and Habitat. Even though distribution records are lacking for much of northeastern Tennessee, *A. opacum* is considered to occur statewide (Figure 41). Northeastern Tennessee is included in the range of the species on the basis of distribution information provided for Kentucky by Barbour (1971) and North Carolina and Virginia by Martof, Palmer, Bailey, and Harrison (1980). The marbled salamander is known from a wide variety of habitats ranging from bottomland hardwood forests to relatively xeric, upland pine forests.

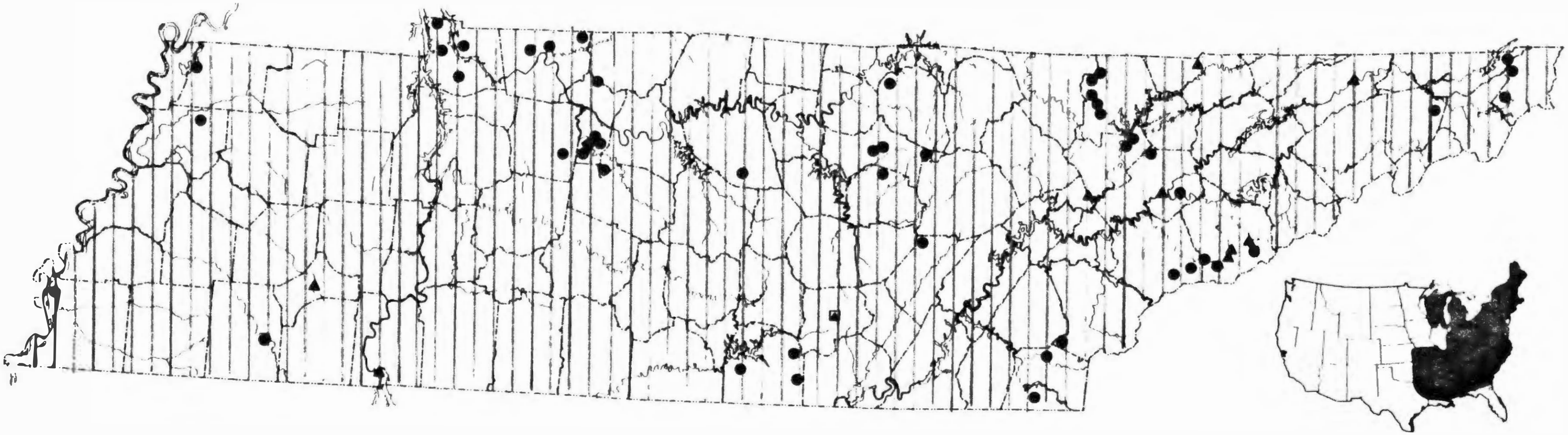

Figure 40. Distribution of <u>Ambystoma maculatum.</u> Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Solid triangle within square denotes county literature record without exact locality data. Smaller map depicts range in conterminous United States (Conant, 1975; Anderson, 1967a).

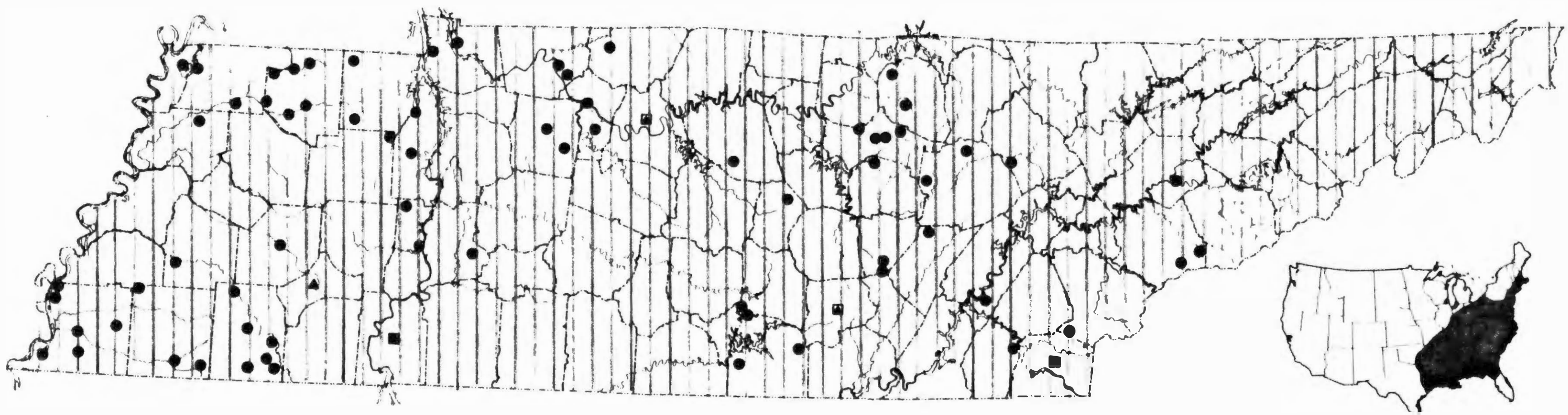

Figure 41. Distribution of Ambystoma opacum. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangle denotes literature record believed valid. Solid circles within squares denote county records based on museum specimens without exact locality data. Solid triangles within squares denote county literature records without exact locality data. Smaller map depicts range in conterminous United States (Conant, 1975; Anderson, 1967b).

(3.) Ambystoma talpoideum (Holbrook) - Mole Salamander

(a.) Description. Ambystoma talpoideum is a medium-sized, short, stocky salamander with relatively large head and legs. Adults reach total lengths of 8 to 10 cm. Dorsal ground color varies from gray to black. Dorsal markings may be absent or, if present, consist of light colored flecks. Costal groove count is typically 11.

(b.) Taxonomic Considerations. No subspecific variation has been recognized for this species (Shoop, 1964).

(c.) Distribution and Habitat. The mole salamander is known from forested and shrubby swamps and flooded depressions from the Coastal Plain, northern portions of Western Highland Rim, eastern edge of Eastern Highland Rim, Cumberland Plateau west of the Sequatchie Valley and the extreme southeastern Blue Ridge (Figure 42). Distributional boundaries follow those suggested by Redmond, Scott, and Roberts (1982). Populations in the southeastern portion of the Blue Ridge Mountains in Tennessee and those reported by Braswell and Murdock (1979) from southwestern North Carolina are considered to form a continuous geographic unit that is disjunct from other portions of the range of the species. Also, Cumberland Plateau and Eastern Highland Rim populations in Tennessee and Alabama (Mount, 1975) are regarded as a continuous unit that is disjunct. Populations in the northern Western Highland Rim appear to be continuous with those in the Coastal Plain in west Tennessee.

(4.) Ambystoma texanum (Matthes) - Smallmouth Salamander

(a.) Description. As compared to other ambystomatid species in Tennessee, the body form of A. texanum is more elongate in appearance

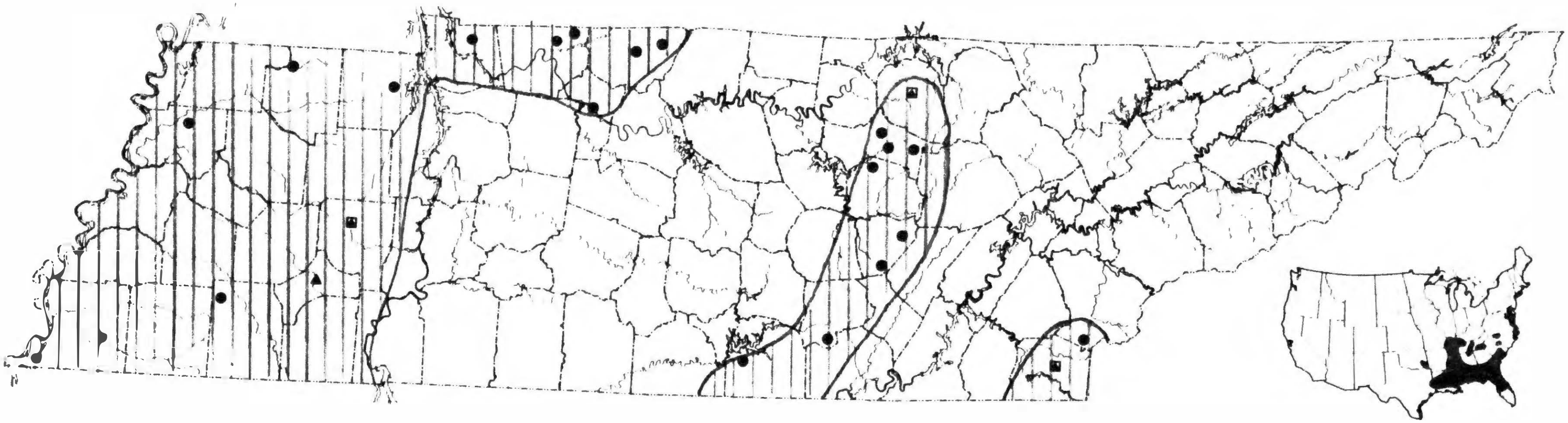

Figure 42. Distribution of Ambystoma talpoideum. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangle denotes literature record believed valid. Solid triangles within squares denote county literature records without exact locality data. Smaller map depicts range in conterminous United States (modified from Conant, 1975; Mount, 1975; Martof, Palmer, Bailey, and Harrison, 1980).

with a narrower head and smaller mouth. Adults attain total lengths ranging from 11 to 14 cm. Dorsal coloration ranges from dark gray to black. Distinct dorsal markings are usually absent but, when present, usually consist of scattered light colored flecks. Costal groove count ranges from 13 to 15.

(b.) Taxonomic Considerations. According to Anderson (1967c), there are no subspecies. Petranka (1982) provided evidence that the species may include a pair of sibling species, including a pond form and a stream form. He found only the pond form in Tennessee.

(c.) Distribution and Habitat. *Ambystoma texanum* occurs in the western half of the state (Figure 43). Its distribution outside the Coastal Plain, especially in south-central Tennessee, needs further study. The species is usually found in bottomland forests near swamps, ponds, and small streams. However, in middle Tennessee, it has been found along woodland creeks and rivers.

(5.) *Ambystoma tigrinum* (Green) - Tiger Salamander

(a.) Description. The tiger salamander is the largest ambystomatid species in Tennessee. Adults range from 18 to 21 cm in total length. Dorsal ground color varies from gray to black with irregularly shaped yellow spots or blotches. Costal groove count is typically 12 to 13.

(b.) Taxonomic Considerations. Only the nominate subspecies is reported from Tennesee (Gehlbach, 1967).

(c.) Distribution and Habitat. Except for north-central Tennessee, locality data for *A. tigrinum* is sparse, and many specimens taken have been the result of chance encounters during or just after heavy rainfall in late winter or early spring. For example, Parker (1948)

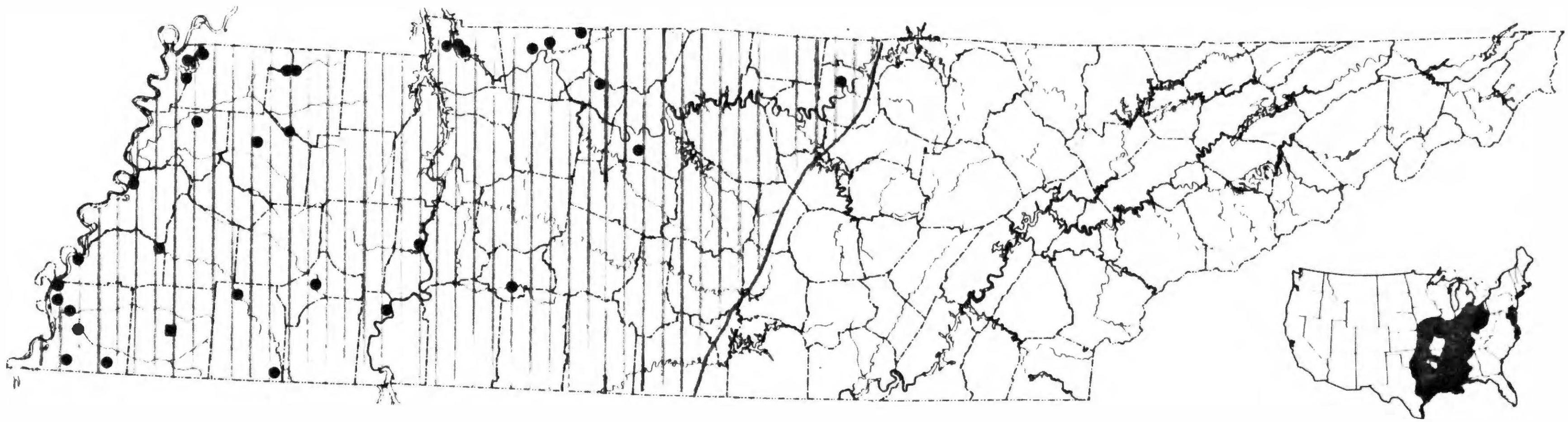

Figure 43. Distribution of Ambystoma texanum. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid circle within square denotes county record based on museum specimen without exact locality data. Smaller map depicts range in conterminous United States (Conant, 1975; Petranka, 1982; Mount, 1975).

reported a specimen found on a sidewalk in Memphis. Two records from Knox County were reported by residents who found specimens roaming their premises following heavy rains. The distribution in Tennessee as shown in Figure 44 is based on both the available data for Tennessee and data for surrounding states (Mount, 1975; Martof, Palmer, Bailey, and Harrison, 1980; Barbour, 1971; Conant, 1975; Gehlbach, 1967). The species is apparently absent from the Blue Ridge Mountains and a large area of northeastern Tennessee. Breeding habitats in Tennessee include flooded woodlands (Taylor, 1938), farm ponds (Gentry, 1955-1956; Ashton, 1966), shallow temporary ponds (Snyder, 1972), and a limestone quarry pond (Owen and Yeatman, 1954).

b. Family Amphiumidae - Conger Eels

(1.) *Amphiuma tridactylium* Cuvier - Three-toed Amphiuma

(a.) Description. This species has an eel-like body form, is relatively large, and attains total lengths of 46 to 76 cm. External gills are absent. Three toes are typically present on each of four very small limbs. Dorsal coloration ranges from dark gray to black and is distinctly separated from a light gray venter. The species has a distinct bicolored appearance when viewed laterally.

(b.) Taxonomic Considerations. No subspecies are currently recognized (Salthe, 1973).

(c.) Distribution and Habitat. The three-toed amphiuma is an inhabitant of sluggish Coastal Plain streams, oxbow lakes, and flooded ditches in Mississippi River drainages in west Tennessee (Figure 45). Parker (1948) provided a sight record from the Tennessee River drainage in Benton County that is considered questionable.

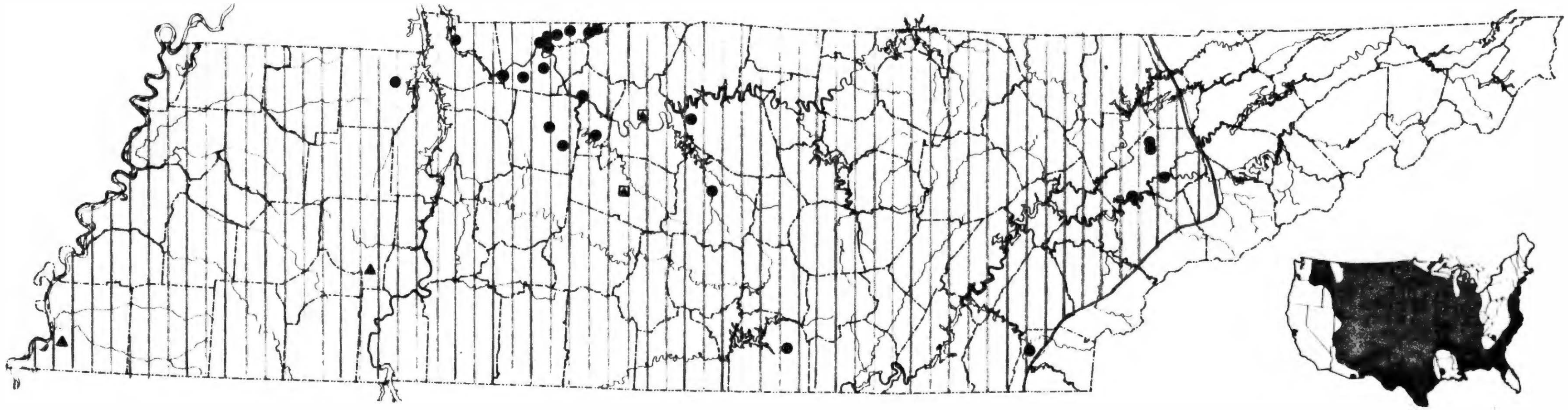

Figure 44. Distribution of <u>Ambystoma tigrinum.</u> Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Solid triangles within squares denote county literature records without exact locality data. Smaller map depicts range in conterminous United States (Conant, 1975; Martof, Palmer, Bailey, and Harrison, 1980).

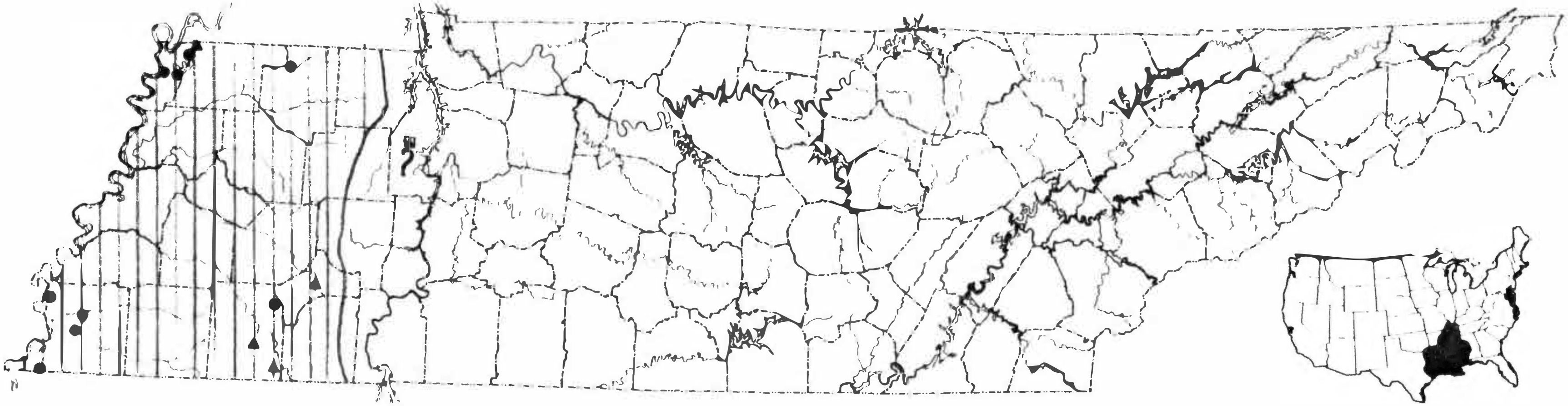

Figure 45. Distribution of Amphiuma tridactylium. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Solid triangle within square and adjacent question mark indicate questionable county literature record without exact locality data. Smaller map depicts range in conterminous United States (Conant, 1975; Salthe, 1973; Mount, 1975).

c. Family Cryptobranchidae - Hellbenders

(1.) Cryptobranchus alleganiensis (Daudin) - Hellbender

(a.) Description. The hellbender is a very large aquatic salamander and reaches total lengths of up to 74 cm. Average adults range from 29 to 51 cm in total length. Trunk and head are dorso-ventrally flattened, and the tail muscular, well developed, and laterally compressed. Between front and hind limbs are extensively vascularized lateral skin folds. External gills are absent in adults, and adults have a single pair of gill openings. Eyes are small and without eyelids. Ground color varies from olive-brown to rusty orange. Irregularly shaped gray to black spots may occur on dorsum.

(b.) Taxonomic Considerations. According to Dundee (1971), only C. a. alleganiensis occurs in Tennessee.

(c.) Distribution and Habitat. Although a few specimens have been reported for reservoirs, C. alleganiensis primarily occurs in medium-sized to large free-flowing streams in the Tennessee and Cumberland River drainages (Figure 46). Inhabited streams possess large rocks or logs that serve as shelters and breeding sites. In the Coastal Plain of west Tennessee, no records are known from western tributaries of the Tennessee River.

d. Family Necturidae - Mudpuppies

(1.) Necturus maculosus (Rafinesque) - Mudpuppy

(a.) Description. The mudpuppy is another aquatic species somewhat similar in appearance to Cryptobranchus alleganiensis. Adults reach total lengths ranging from 20 to 33 cm. External gills are present and well

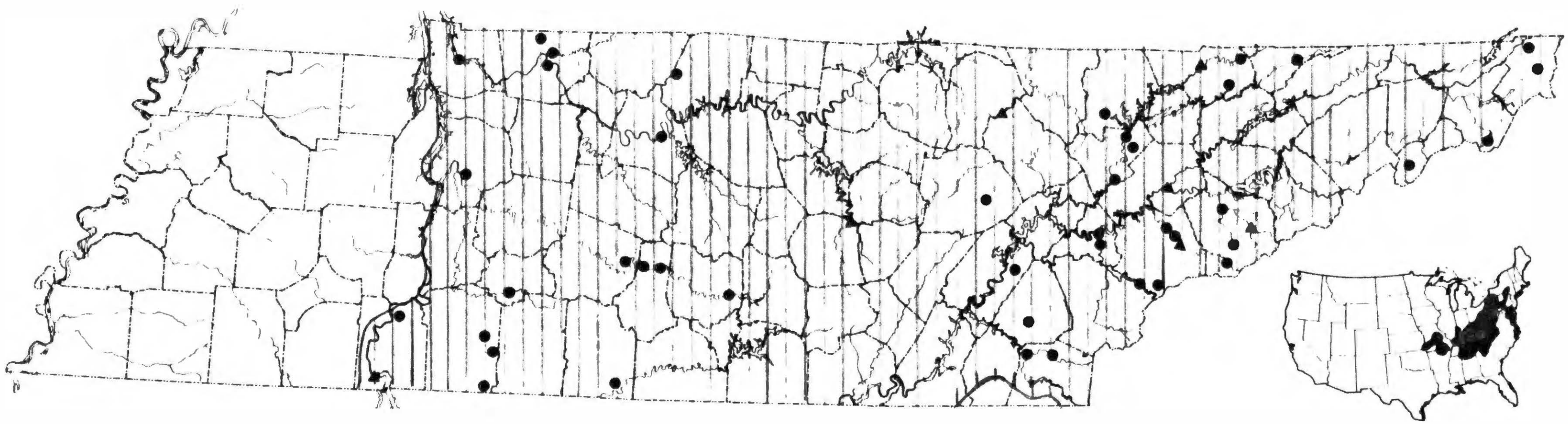

Figure 46. Distribution of Cryptobranchus alleganiensis. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Smaller map depicts range in conterminous United States (Conant, 1975; Dundee, 1971).

developed. Four toes are present on each of four well developed limbs. Dorsal ground color varies from pink to brown. Dorsal markings may be absent but usually consist of scattered dark blotches. Venter may be immaculate or possess several large dark spots.

(b.) Taxonomic Considerations. Species groups in the genus *Necturus* are poorly understood. Several authors (Hecht, 1958; Neill, 1963a; Brode, 1969; Mount, 1975) have proposed conflicting taxonomic schemes. However, most of these taxonomic problems have been reported for areas south of Tennessee and most accounts assign populations in Tennessee to *N. maculosus*. According to Conant (1975), two subspecies are found in Tennessee. The subspecies, *N. m. louisianensis* Viosca, occurs in Coastal Plain drainages of west Tennessee, while *N. m. maculosus* ranges eastward in drainages of upland provinces in central and east Tennessee.

(c.) Distribution and Habitat. This salamander occurs statewide (Figure 47) in streams, reservoirs, and other permanent bodies of water. No specimens were available from the Obion River drainages; however, Parker (1939) reported specimens caught by commercial fishermen in the Obion River.

e. Family Plethodontidae - Lungless Salamanders

(1.) *Aneides aeneus* (Cope and Packard) - Green Salamander

(a.) Description. Adults of this species attain total lengths of 8 to 13 cm. Toe tips are expanded to form adhesvie discs. Dorsal ground color is dark brown with profuse green to greenish yellow lichen-shaped blotches.

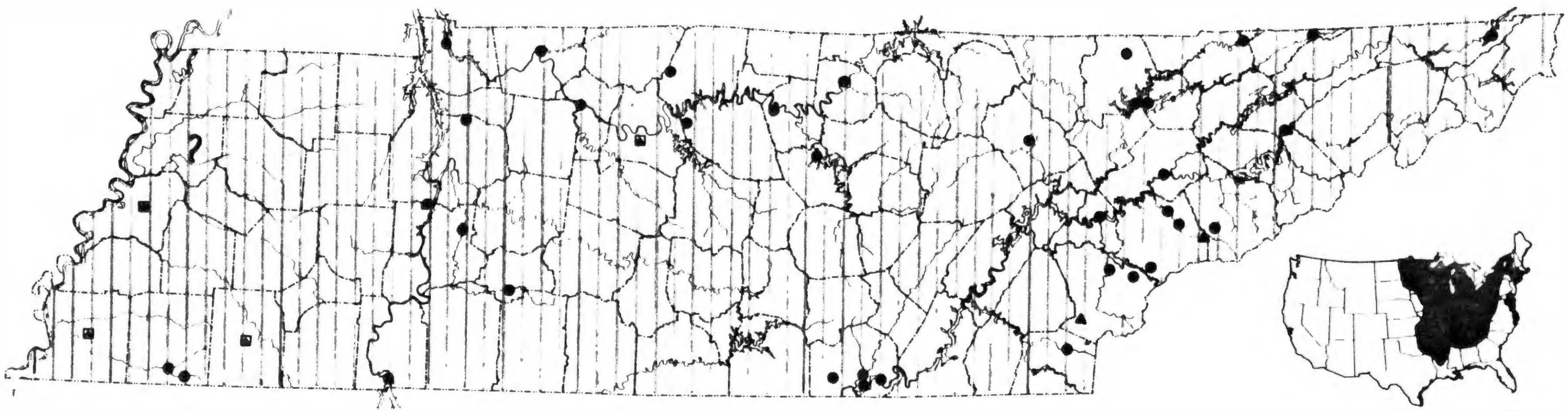

Figure 47. Distribution of <u>Necturus maculosus.</u> Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Solid circle within square denotes county record based on museum specimen without exact locality data. Solid triangles within squares denote county literature records without exact locality data. Question mark refers to literature reference to presence in Obion River drainage. Smaller map depicts range in conterminous United States (Conant, 1975).

(b.) Taxonomic Considerations. No subspecific variation recognized (Gordon, 1967). Type locality is mouth of Nickajack Cave, Marion County, Tennessee.

(c.) Distribution and Habitat. *Aneides aeneus* is primarily found in the Cumberland Mountains, Cumberland Plateau, and Eastern Highland Rim (Figure 48). Presumably isolated populations occur in the Bays Mountains area and on Clinch Mountain in the Appalachian Ridge and Valley and a cedar glade area in the Inner Central Basin. Weller (1931) reported a specimen from the eastern slope of Mt. LeConte in the Great Smoky Mountains National Park. King (1939) verified the identification of this specimen. Since 1931, the herpetofauna of the Great Smoky Mountains has been studied extensively by numerous scientists and Weller's report remains the only account for the species. For this reason, the present occurrence of *A. aeneus* in the Great Smoky Mountains National Park is considered questionable. Suitable habitats include rock crevices on shaded sandstone cliff faces and mesic upland hardwood forests.

(2.) *Desmognathus aeneus* Bishop and Brown - Seepage Salamander

(a.) Description. *Desmognathus aeneus* is a small, slender desmognathine salamander with adult total lengths ranging from 4.4 to 5.7 cm. A light line extends from just behind the eye to angle of jaw. Tail is rounded and without a keel. Hind limbs are noticeably larger than forelimbs. Dorsal color is usually reddish brown or bronze with irregularly shaped dark spots that sometimes form a mid-dorsal dark stripe. Lateral surfaces usually have dark mottling that forms wide irregularly bounded dorsolateral stripes. These may extend from the

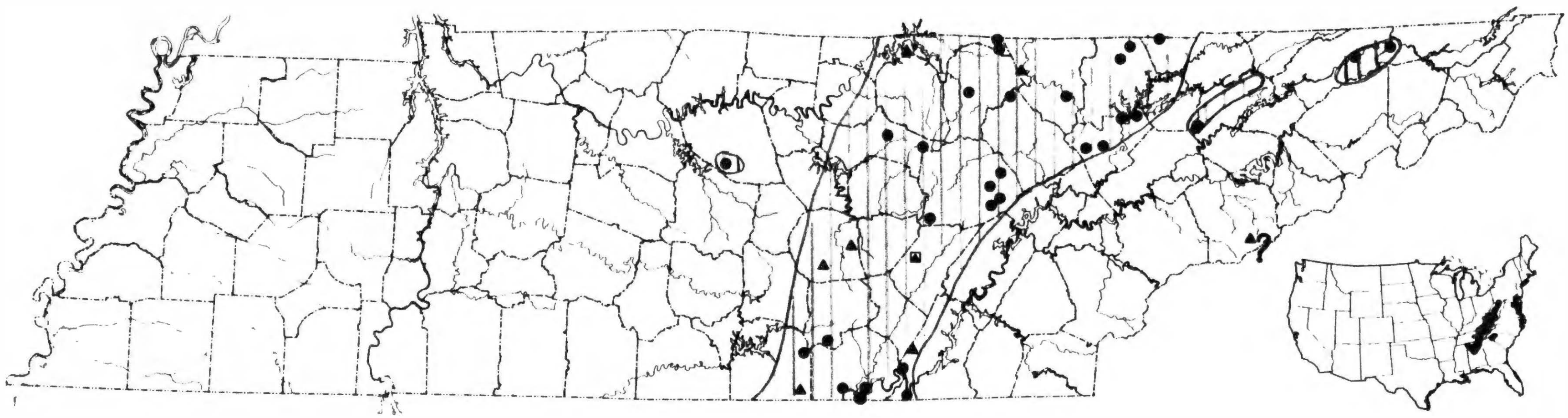

Figure 48. Distribution of Aneides aeneus. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Question mark refers to problematical literature record. Solid triangle within square denotes county literature record without exact locality data. Solid triangle within circle indicates type locality. Smaller map depicts range in conterminous United States (modified from Conant, 1975; Gordon, 1967; Mount, 1975).

forelimbs to the tip of tail. Dorsal surface of thighs usually has a light reddish or tan spot. Venter may be immaculate or lightly mottled with dark melanophores.

(b.) Taxonomic Considerations. No subspecies are currently recognized (Conant, 1975).

(c.) Distribution and Habitat. The seepage salamander is restricted to the Blue Ridge Mountains, specifically the Unicoi Mountains, in southeastern Tennessee (Figure 49). Jones (1982a) studied the ecology and distribution of the species in Tennessee and characterized its habitat as leaf litter near small streams and seepage areas between 280 and 1000 m elevation.

(3.) *Desmognathus fuscus* (Rafinesque) - Dusky Salamander

(a.) Description. The dusky salamander is a medium-sized salamander that exhibits extremely variable color patterns. Adult total length ranges from 6 to 12.7 cm. A light line extends from just behind the eye to angle of jaw. Hind limbs are noticeably larger than forelimbs. Tail is triangular in cross section and is moderately keeled. Jaw line of mature individuals is slightly sinuous. Dark friction pads on toes are absent. Jaw teeth have blunt crowns. Dorsal ground color ranges from light gray to dark brown. Dorsal color pattern is highly variable. Dorsal dark markings may be indistinct, randomly arranged, or consist of several light tan, yellowish, or red pairs of dorsal spots bordered by wavy or sometimes straight dark dorsolateral stripes. Dorsal color blends gradually with ventral color. Venter is usually mottled with dark melanophores. Older individuals may become

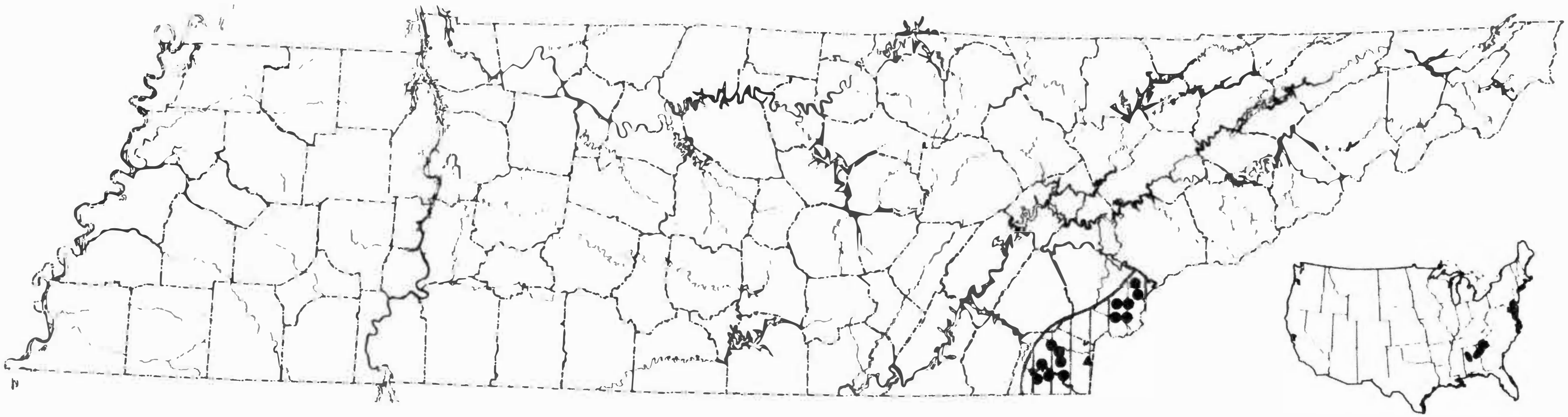

Figure 49. Distribution of Desmognathus aeneus. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangle denotes literature record believed valid. Smaller map depicts range in conterminous United States (Conant, 1975; Mount, 1975; Jones, 1982a).

melanistic. *Desmognathus fuscus* and *D. santeetlah* can often be separated using external characteristics, but for some populations a biochemical analysis is required (Tilley, 1981).

(b.) Taxonomic Considerations. In Tennessee, Conant (1975) noted a relatively wide zone of intergradation between *D. f. fuscus* which occurs in the eastern one-half of the state and *D. f. conanti* Rossman which ranges in the western one-half of Tennessee. Hybridization with *D. santeetlah* has been reported in Cocke (Tilley, 1981) and Monroe (Jones, 1982b) counties.

(c.) Distribution and Habitat. Excluding the Mississippi River Lowlands and Loess Plain of west Tennessee and high elevations in extreme east Tennessee, *D. fuscus* is common along small to large-sized streams in Tennessee (Figure 50). An apparently isolated population occurs on the Mississippi River Bluffs near Ripley, Tennessee (Brandon and Huheey, 1979; Brandon, pers. comm.). Its occurrence in the Great Smoky Mountains National Park and at high elevations along the Tennessee-North Carolina border has been the subject of debate. King (1939) reported *D. fuscus* up to 1677 m in the Great Smoky Mountains National Park. Martof and Rose (1963) noted that *D. ochrophaeus* was morphologically similar to *D. fuscus* in the Great Smoky Mountains and that *D. fuscus* is rare in the southern Appalachian Mountains. Huheey (1966) and Huheey and Stupka (1967) believed *D. fuscus* was absent in the National Park and previous reports were based on incorrect identifications. Tilley (1981) described *D. santeetlah* from high elevations along the Tennessee-North Carolina border and stated that past reports of *D. fuscus* in the Park probably referred to *D. santeetlah.* He also found evidence of hybridization between

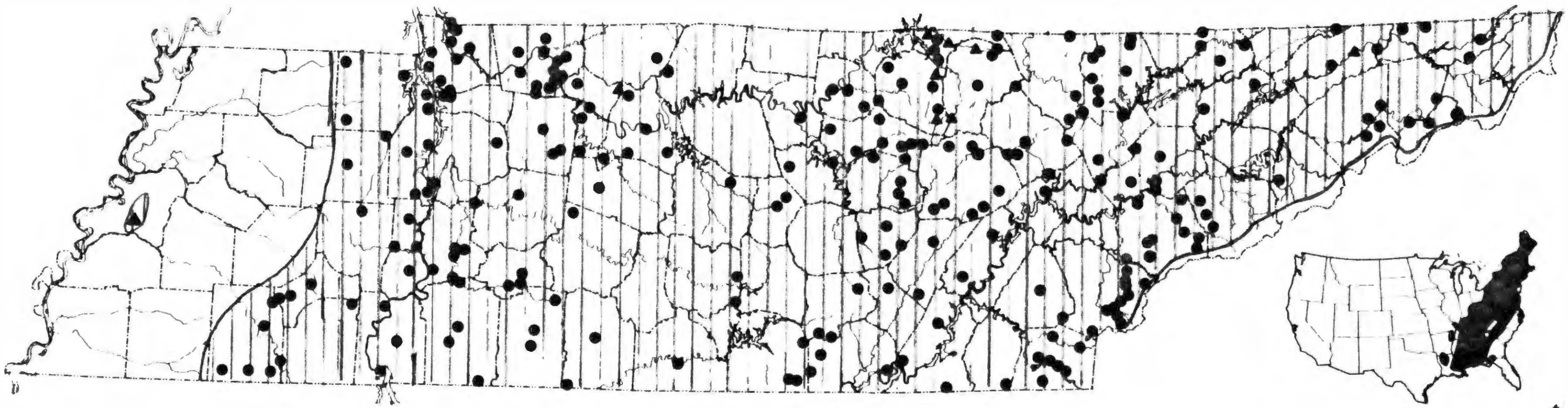

Figure 50. Distribution of Desmognathus fuscus. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Smaller map depicts range in conterminous United States (Conant, 1975; Tilley, 1981; Martof, Palmer, Bailey, and Harrison, 1980).

D. fuscus and D. santeetlah at 518 m elevation in the Cosby Creek watershed. Tilley (1985) subsequently identified D. fuscus from Whiteoak Sinks in the Park. The status of D. fuscus at low elevations in the Park is poorly known and needs further study. Tilley's studies are primarily based on electrophoretic analysis of proteins and identification of preserved specimens is at best tentative. Thus, past literature references and locality data for museum specimens from the Great Smoky Mountains National Park were not included on the distribution map for D. fuscus (Figure 50). In the Blue Ridge Mountains south of the Park, the distribution of D. fuscus has been adequately documented by Tilley (1981) and Jones (1982b). Both authors note that D. fuscus and D. santeetlah are essentially parapatric with D. santeetlah replacing D. fuscus along the high elevations of the Tennessee-North Carolina state line. The distribution of D. fuscus and D. santeetlah along the Tennessee-North Carolina border north of the Great Smoky Mountains National Park is virtually unknown (Tilley, 1981; Tilley, pers. comm.).

(4.) Desmognathus imitator Dunn - Imitator Salamander

(a.) Description. A medium-sized species, D. imitator is morphologically very similar to D. ochrophaeus. In areas of sympatry, the only sure method of distinguishing the two is an electrophoretic analysis of proteins. However, in many instances, morphological characteristics may be useful. Adult females may attain 5.0 cm and males 5.7 cm in snout-vent length (Tilley, 1985). A light line extends from eye to angle of jaw. Hind limbs are noticeably larger than forelimbs. Tail is round in cross-section and keel is absent. Jaw line of mature individuals is strongly sinuous. Individuals in the Great Smoky Mountains National Park often have yellow, orange, or red cheek patches. Melanistic specimens with red cheek patches mimic the red-cheeked Jordan's salamander, Plethodon jordani. In contrast to the usually straight edged dorsolateral dark bands of D. ochrophaeus, D. imitator typically has wavy dorsolateral bands that may be broken and extend onto the dorsum to enclose irregularly shaped light spots. Venter is usually gray.

(b.) Taxonomic Considerations. This form was originally described by Dunn (1927b) as a subspecies of D. fuscus. Most subsequent authors considered it a color morph of D. ochrophaeus. Based on genetic studies using electrophoretic techniques, Tilley, Merritt, Wu, and Highton (1978) provided evidence that D. imitator deserved species status. According to Tilley (1985), D. imitator is a monotypic species. Type locality is Indian Pass, Great Smoky Mountains, Sevier County, Tennessee.

(c.) Distribution and Habitat. Because of the likelihood of confusing preserved specimens of D. imitator and D. ochrophaeus, locality data presented in Figure 51 were taken exclusively from Tilley, Merritt, Wu, and Highton (1978) and Tilley (1985). Desmognathus imitator is restricted to the Great Smoky Mountains National Park and is found at or above 900 m elevation along small creeks and seepages, in moist leaf litter, and on wet rock faces (Tilley, 1985).

(5.) Desmognathus monticola Dunn - Seal Salamander

(a.) Description. Adult D. monticola range from 8 to 13 cm in total length. A light line extends from just behind the eye to angle of jaw. Hind limbs are noticeably larger than forelimbs. Tail is triangular in

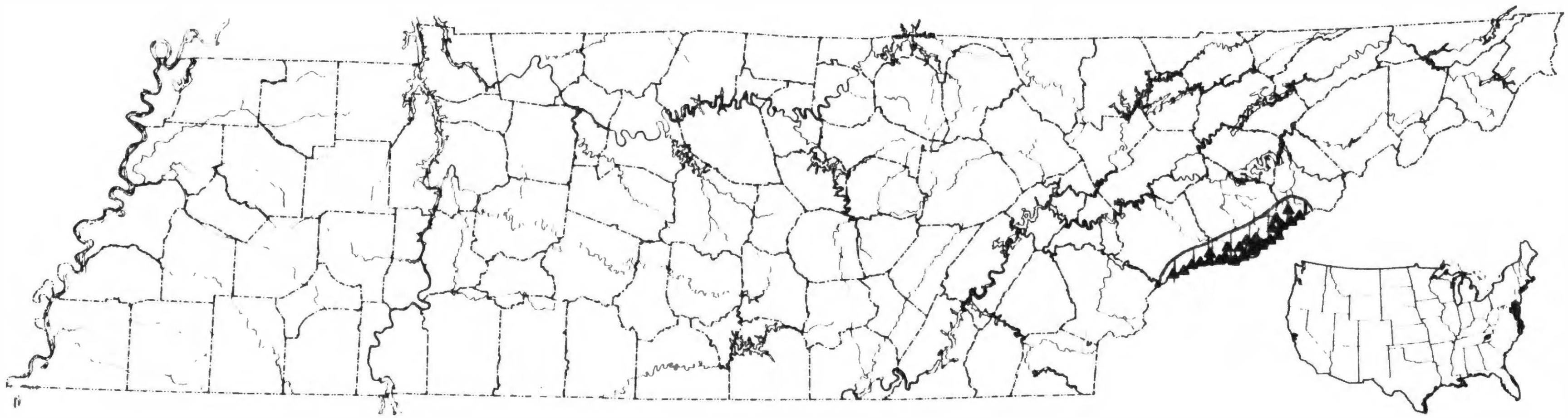

Figure 51. Distribution of <u>Desmognathus imitator</u>. Vertical hatching indicates range. Solid triangles denote literature records believed valid. Solid triangle within circle indicates type locality. Smaller map depicts range in conterminous United States (Tilley, 1985).

cross-section and is moderately keeled. Dark friction pads may be present on tips of toes. Jaw teeth have pointed crowns. Dorsal ground color ranges from light tan to dark brown. Dorsal dark markings are often distinct and form vermiculate shaped blotches. Blotches may enclose several pair of light tan or reddish brown light spots. Old individuals may become completely dark brown. On lateral surfaces, the transition from dorsal to ventral color is abrupt. Venter may be immaculate or lightly pigmented with melanophores.

(b.) Taxonomic Considerations. Two subspecies are recognized, and only *D. m. monticola* occurs in Tennessee (Conant, 1975).

(c.) Distribution and Habitat. The range of *D. monticola* in Tennessee is considered to include approximately the eastern one-quarter of the state (Figure 52). Its presence in the Blue Ridge Mountains and Cumberland Mountains is well documented. However, its presence in the Appalachian Ridge and Valley and Cumberland Plateau is represented by a few widely scattered localities. Seal salamanders occur along permanent, small to medium-sized rocky bottom woodland streams. The species seems to prefer streams with a moderate to steep gradient. Mathews and Echternacht (1984) reported *D. monticola* above 1305 m in the Great Smoky Mountains National Park.

(6.) *Desmognathus ochrophaeus* Cope - Mountain Dusky Salamander

(a.) Description. *Desmognathus ochrophaeus* is a medium-sized desmognathine. Adults attain total lengths ranging from 7 to 10 cm. A light line extends from eye to angle of jaw. Hind limbs are noticeably larger than forelimbs. Tail is round in cross-section and keel is absent. Jaw line of mature individuals is strongly sinuous. Dorsal

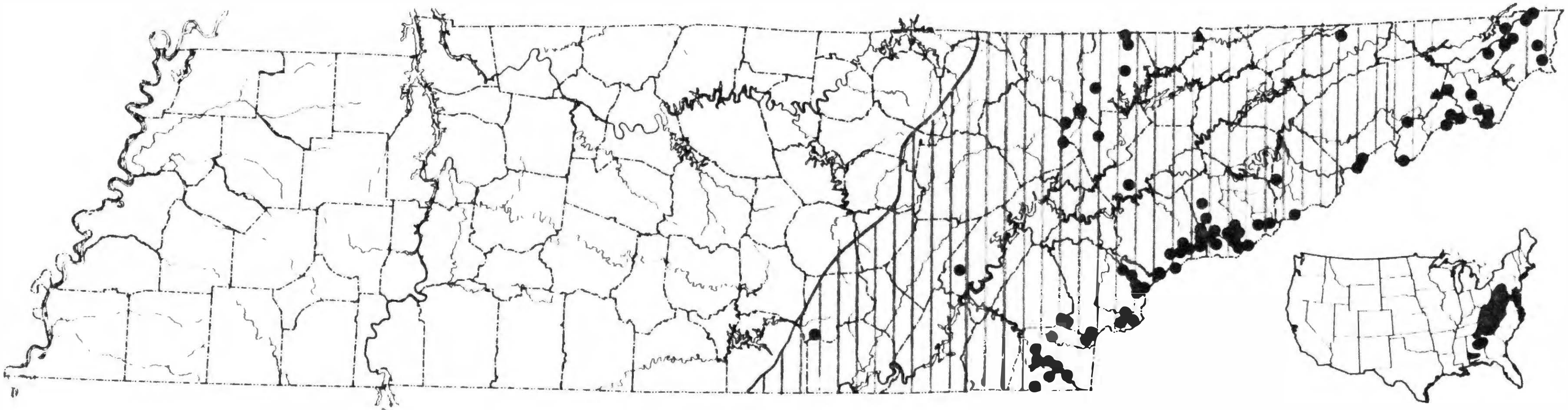

Figure 52. Distribution of Desmognathus monticola. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Smaller map depicts range in conterminous United States (Conant, 1975; Martof, Palmer, Bailey, and Harrison, 1980).

ground color ranges from light gray to dark brown. Some individuals may be melanistic. Dorsal markings are highly variable. Dorsum may be relatively plain with only a few scattered small dark spots or flecks, or dark markings may be concentrated to form a mid-dorsal line. Dark pigment on sides form dorsolateral bands that may have wavy or straight dorsal edges, or lateral dark pigment may extend onto dorsum to enclose several light irregularly shaped spots. Ventral color varies from light gray to brown with dark melanophores usually present.

(b.) Taxonomic Considerations. No subspecies are recognized (Martof and Rose, 1963; Tilley, 1973). Also, D. ocoee Nicholls, a species described from Ocoee Gorge, Polk County (Nicholls, 1949), is considered a local variant of D. ochrophaeus (Martof and Rose, 1963). As described in the account for D. imitator, in the Great Smoky Mountains, D. ochrophaeus and D. imitator are often similar in morphology and color pattern, and a biochemical analysis is often necessary to separate the two.

(c.) Distribution and Habitat. The mountain dusky salamander is known from the Blue Ridge Mountains, Cumberland Mountains, Cumberland Plateau, and Bays Mountain area in the Appalachian Ridge and Valley (Figure 53). For reasons discussed in the account for D. imitator, locality data for D. ochrophaeus from the Great Smoky Mountains National Park was taken exclusively from Tilley, Merritt, Wu, and Highton (1978). At high elevations in the Blue Ridge Mountains, D. ochrophaeus inhabits mesic forests where it may be found in leaf litter or under rocks and logs. At lower elevations and elsewhere in Tennessee, the species occurs along small streams, seepage areas, and on moist cliff faces.

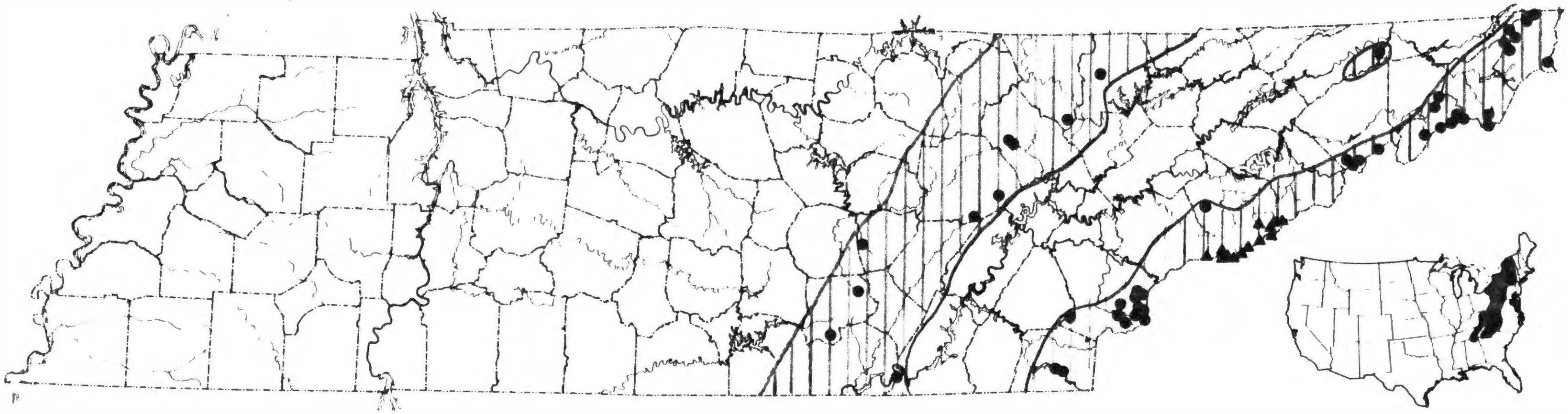

Figure 53. Distribution of <u>Desmognathus ochrophaeus.</u> Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Smaller map depicts range in conterminous United States (modified from Conant, 1975; Tilley, 1973; Tilley, Merritt, Wu, and Highton, 1978).

(7.) Desmognathus quadramaculatus (Holbrook) - Blackbelly Salamander

(a.) Description. This is the largest species of Desmognathus in Tennessee. Adults attain total lengths of 10 to 17 cm. A light line extends from eye to angle of jaw. Hind limbs are noticeably larger than forelimbs. Tail is triangular in cross-section and is strongly keeled. Internal nares are round and distinct. Dorsal color is usually dark brown or black with lighter brown or rusty brown blotches. A double row of light spots normally exists on lateral surfaces between front and hind limbs. Venter of adults is heavily pigmented and may be completely
black.

(b.) Taxonomic Considerations. Valentine (1974) did not recognize subspecies; however, he did note color pattern differences between northern and southern populations. Hinderstein (1971) noted these color differences and described biochemical differences. He found two variants, one from north and one from south of the French Broad River. He suggests these may represent two separate forms; however, he refrained from assigning taxonomic ranks.

(c.) Distribution and Habitat. Desmognathus quadramaculatus is found along permanent, rocky woodland streams in the Blue Ridge Mountains and in the Bays Mountain area in the Appalachian Ridge and Valley (Figure 54). Inhabited streams usually have a moderate to steep gradient. The species has been reported above 1650 m in the Great Smoky Mountains National Park (Mathews and Echternacht, 1984).

(8.) Desmognathus santeetlah Tilley - No common name available.

(a.) Description. This species is closely related to and resembles D. fuscus. According to Tilley (1981), adults attain snout-vent lengths

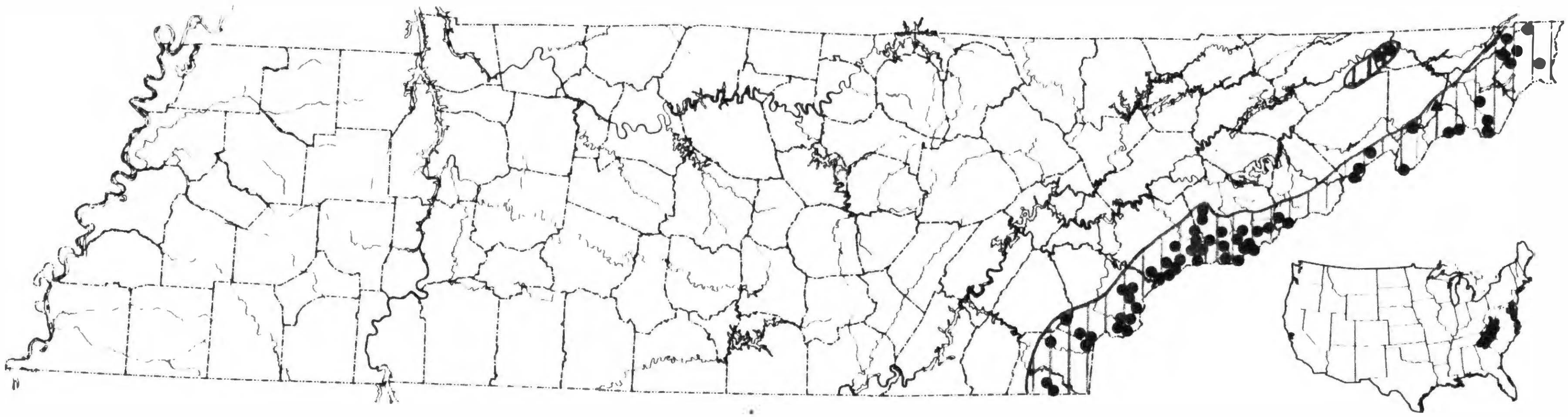

Figure 54. Distribution of Desmognathus quadramaculatus. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangle denotes literature record believed valid. Smaller map depicts range in conterminous United States (modified from Conant, 1975; Valentine, 1974).

of 3.0 to 5.5 cm. A light line extends from just behind the eye to angle of jaw. Hind limbs are noticeably larger than forelimbs. Tail is triangular in cross-section and is moderately keeled. Jaw line of mature individuals is slightly sinuous. Dark friction pads on tips of toes are absent. Body form is smaller and more slender with a shorter tail than D. fuscus. Dorsal coloration is usually less bright and more indistinct than D. fuscus. Dorsal ground color may be light brown or greenish brown. Typical dorsal color patterns include (1) dark markings coalescing to enclose light spots, (2) scattered dark markings forming worm-like blotches, and (3) indistinct small dark flecks widely scattered over dorsum. Lateral surfaces and venter usually have scattered patches of melanophores and may have a yellowish tint. A row of light is spots usually present on lower sides between front and hind limbs. In some instances, the use of external characteristics, such as color pattern and body measurements, may not allow separation of D. fuscus and D. santeetlah (Tilley, pers. comm.). As described by Tilley (1981), the most reliable method of distinguishing the two is an electrophoretic analysis of proteins.

(b.) Taxonomic Considerations. Type locality is near crest of Unicoi Mountains in Monroe County, Tennessee (Tilley, 1981). No subspecies are recognized. Desmognathus santeetlah hybridizes with D. fuscus (see account of D. fuscus).

(c.) Distribution and Habitat. As shown by Tilley (1981) and Jones (1982b), the distribution of D. santeetlah includes high elevation seepage areas in the Unicoi and Great Smoky Mountain ranges in eastern Tennessee (Figure 55). As discussed in the account for D. fuscus, most

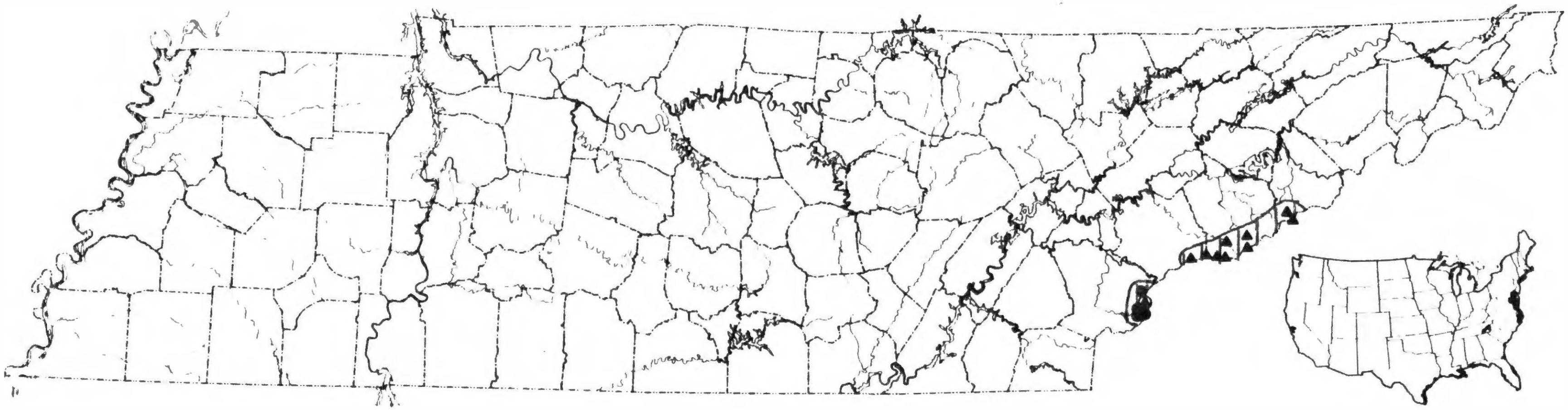

Figure 55. Distribution of Desmognathus santeetlah. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Solid triangle within circle indicates type locality. Smaller map depicts range in conterminous United States (Tilley, 1981; Jones, 1982b).

previous reports from the Great Smoky Mountains of D. fuscus probably refer to D. santeetlah.

(9.) Desmognathus welteri Barbour - Black Mountain Salamander

(a.) Description. Desmognathus welteri is a large species similar in appearance to both D. fuscus and D. monticola. Adults attain total lengths of 8 to 13 cm. A light line usually extends from just behind the eye to angle of jaw. Hind limbs are noticeably larger than fore-limbs. Tail is triangular in cross-section and is strongly keeled. Dark friction pads are present on tips of toes. Jaw teeth possess blunt crowns. Dorsal ground color varies from light to dark brown. Dorsal dark markings usually consist of numerous dark flecks or small spots that are seldom arranged into a distinct pattern. Dark markings on sides may be concentrated to form wide, indistinct dorsolateral stripes. Dorsal ground color blends gradually with ventral color. Venter is usually mottled with dark melanophores. Old individuals may become melanistic.

(b.) Taxonomic Considerations. Desmognathus welteri was originally described as a subspecies of D. fuscus (Barbour, 1950); however, Barbour (1971) later elevated it to species rank. Subsequent studies by Caldwell (1977, 1980), Caldwell and Trauth (1979), and Juterbock (1975, 1978, 1984) support Barbour's proposal. None of the aforementioned authors or Conant (1975) recognized subspecies.

(c.) Distribution and Habitat. Redmond (1980) determined the distribution of D. welteri to include the Cumberland Mountains and northern half of the Cumberland Plateau (Figure 56). The species is typically encountered along small to medium-sized permanent streams in

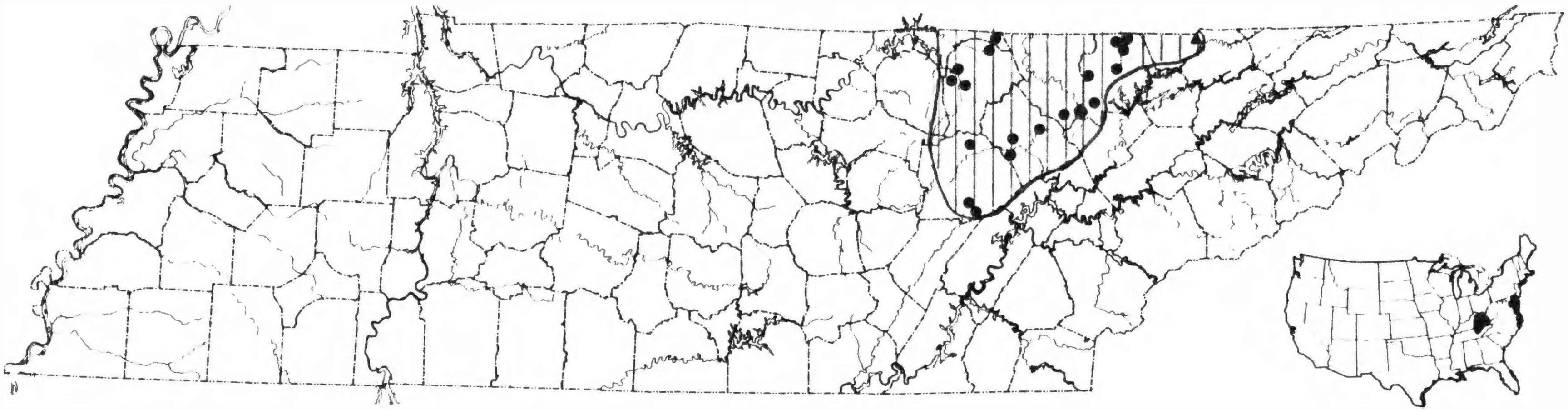

Figure 56. Distribution of <u>Desmognathus welteri.</u> Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangle denotes literature record believed valid. Smaller map depicts range in conterminous United States (Conant, 1975; Caldwell, 1977; Redmond, 1980).

mesic upland hardwood forests. This species is strongly aquatic, and its apparent absence on the southern Cumberland Plateau may be due to the seasonal nature of most small streams in the region.

(10.) Desmognathus wrighti King - Pygmy Salamander

(a.) Description. The pygmy salamander is a small salamander similar in body size and form to D. aeneus. Adults may reach total lengths of 3.8 to 5.1 cm. A light line extends from just behind the eye to angle of jaw. Tail is rounded in cross-section and is not keeled. Hind limbs are noticeably larger than forelimbs. Dorsal ground color ranges from light gray to rusty brown. Dorsal markings typically consist of narrow dark lines forming a herringbone pattern. Dark markings with scattered silver flecks occur on lateral surfaces to form dorsolateral bands. Dorsal surface of head and snout is rugose. Venter is usually immaculate.

(b.) Taxonomic Considerations. No subspecies have been reported (Conant, 1975). King (1936) described D. wrighti from Mt. LeConte, Sevier County, Tennessee.

(c.) Distribution and Habitat. Desmognathus wrighti is restricted to high elevation habitats in the Blue Ridge Mountains along the Tennessee-North Carolina border (Figure 57). Most authorities (Huheey, 1966; Huheey and Stupka, 1967; Tilley and Harrison, 1969; Mathews and Echternacht, 1984) regard this species as characteristic of spruce-fir forests. However, it has been found in moist hardwood forests as low as 838 m (Huheey, 1966). Tilley and Harrison (1969) believe these lower elevation populations in hardwood forest habitats represent relicts from the past when spruce-fir habitats were more widespread in the southern

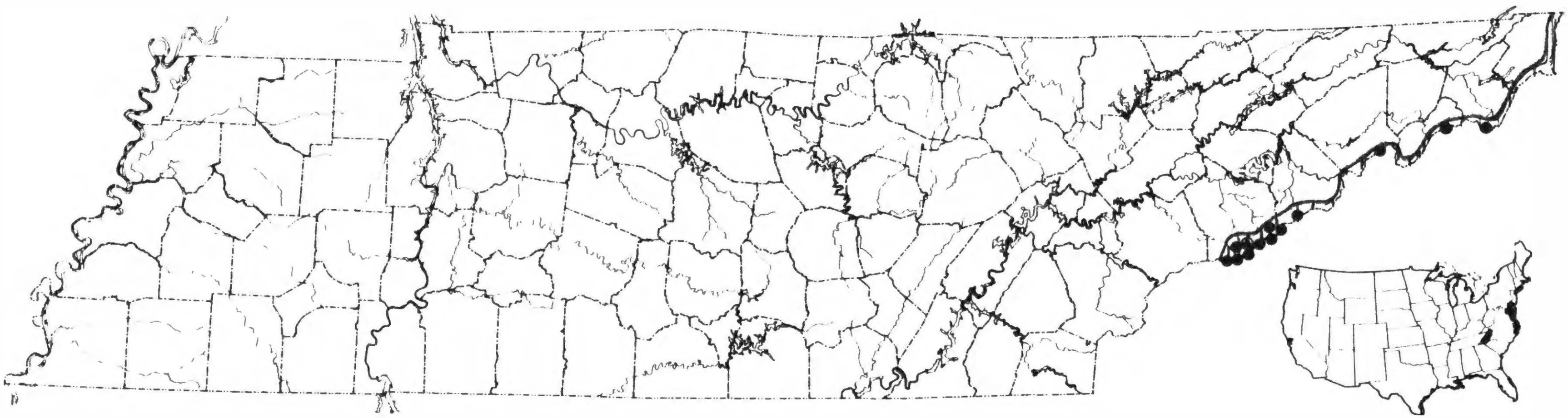

Figure 57. Distribution of Desmognathus wrighti. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangle within circle indicates type locality. Smaller map depicts range in conterminous United States (Conant, 1975).

Appalachians. Desmognathus wrighti is the most terrestrial of all desmognathine species and may occur great distances away from streams and seepages. Adults are found under and within rotting logs, under rocks, and just beneath leaf litter.

(11.) Eurycea bislineata (Green) - Two-lined Salamander

(a.) Description. The two-lined salamander is a slender species. Adults reach total lengths of 6.4 to 11 cm. Ground color ranges from yellow to orange and occasionally light brown. A dark lateral stripe occurs on each side of the body and extends from eye to either mid-tail or all the way to tip of tail. Small black or brown spots may occur on dorsum between lateral dark stripes.

(b.) Taxonomic Considerations. Conant (1975) lists three subspecies in Tennessee. As shown on his distribution map, E. b. cirrigera (Green) occurs in the Coastal Plain of west Tennessee, E. b. bislineata ranges from Tennessee River in west Tennessee eastward to the foot of the Blue Ridge Mountains, and E. b. wilderae Dunn occurs in the Blue Ridge Mountains of extreme east Tennessee. However, examination of approximately 1,650 specimens from Tennessee indicates that currently accepted subspecific designations and the ranges of subspecies in the state are poorly understood and in need of further study. Included in synonymy with E. bislineata in Tennessee is E. aquatica. Rose and Bush (1963) described E. aquatica from a spring in central Alabama. Based on personal communication with Richard Johnson, they indicated this new species possibly occurred in Tennessee. Ashton (1966) reported E. aquatica from Davidson County, Tennessee. Mount (1975) sampled several populations near the type locality and observed numerous specimens with characteristics intermediate with E. bislineata. In Alabama, Mount concluded E. aquatica was merely an ecotype of E. bislineata. Wallace (1975) studied the biochemical genetics of E. bislineata and E. aquatica in Davidson County, Tennessee, and reached the same conclusion.

(c.) Distribution and Habitat. Eurycea bislineata is a very common streamside inhabitant along woodland creeks and rivers throughout Tennessee (Figure 58). It is known from bottomland habitats in west Tennessee to the highest elevation forests in the Blue Ridge Mountains.

(12.) Eurycea junaluska Sever, Dundee, and Sullivan - Junaluska Salamander

(a.) Description. This recently described species is morphologically very similar to E. bislineata. According to Sever (1983a), adults attain snout-vent lengths of 3.4 to 5.0 cm. In comparison with E. bislineata, E. junaluska has a relatively shorter tail and longer limbs. Dorsal coloration is usually a light yellow with dorsolateral brown stripes absent or broken into narrow wavy lines. Scattered small dark spots or flecks may occur on dorsum.

(b.) Taxonomic Considerations. No subspecies are reported (Sever, 1983a).

(c.) Distribution and Habitat. Eurycea junaluska is known from medium to large-sized streams in a small area of east Tennessee (Figure 59). Sever (1976) reported an individual from Fighting Creek in Sevier County and later (Sever, 1983b) found the species along the Tellico River in Monroe County. He collected individuals under rocks along stream borders and from wet roads adjacent to streams during or just after a rainfall. On the night of September 12, 1976, eight specimens

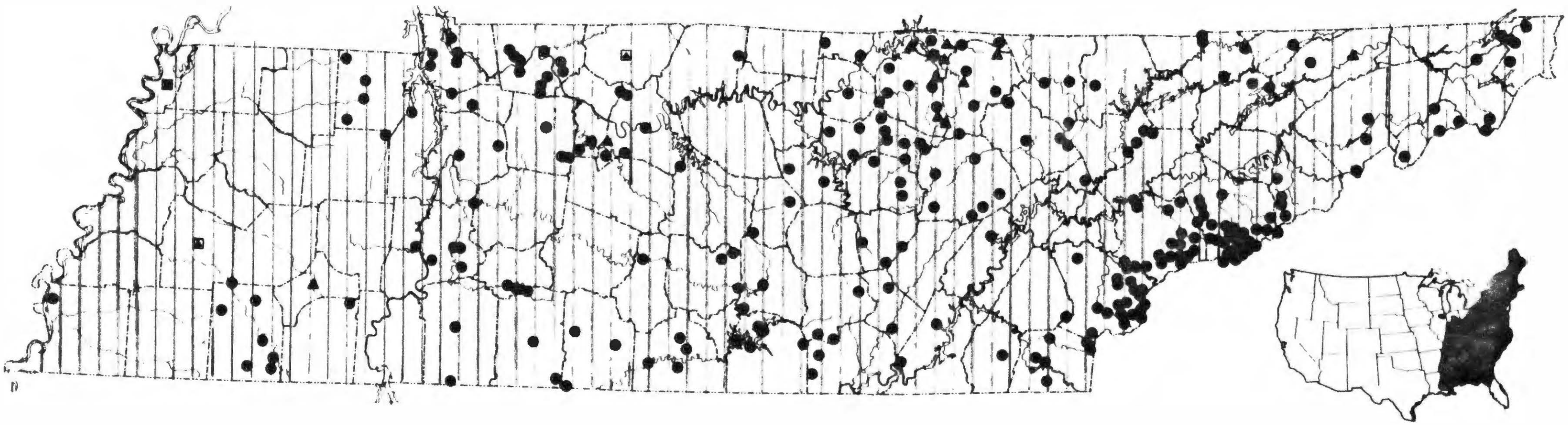

Figure 58. Distribution of <u>Eurycea bislineata.</u> Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Solid circle within square denotes county record based on museum specimens without exact locality data. Solid triangles within squares denote county literature records without exact locality data. Smaller map depicts range in conterminous United States (Conant, 1975; Mittleman, 1966).

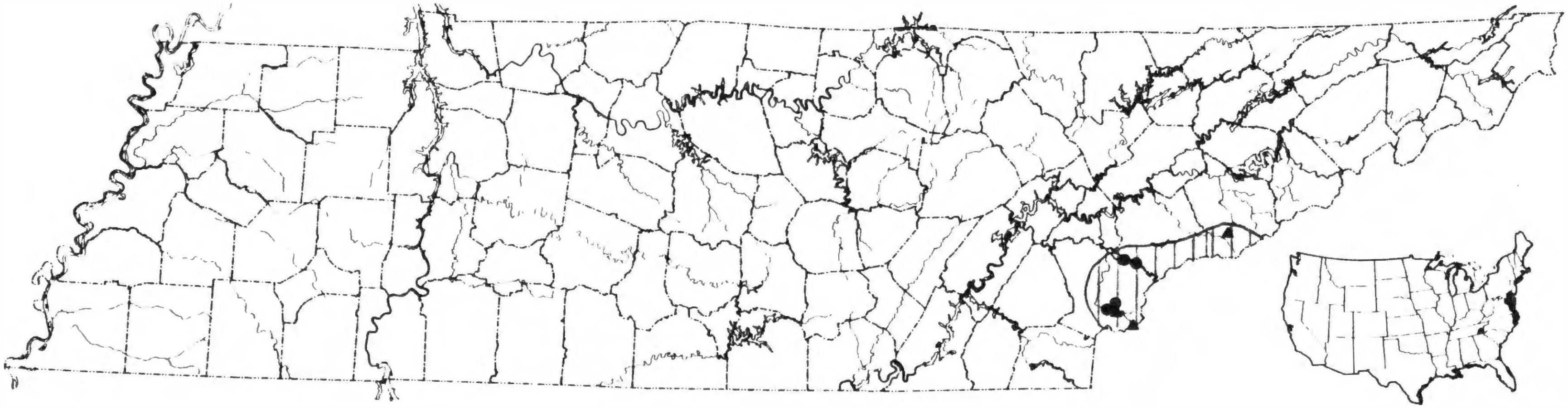

Figure 59. Distribution of <u>Eurycea junaluska</u>. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Smaller map depicts range in conterminous United States (Sever, 1983a).

(UTKVZC Nos. 2375-2381, 2462) were found perched on boulders in the Little Tennessee River along the Blount-Monroe County line. This area has since been inundated to form Tellico Reservoir.

(13.) Eurycea longicauda (Green) - Longtail Salamander

(a.) Description. Eurycea longicauda possesses a slender body form with a long tail. Adults range from 10 to 16 cm in total length. Dorsal ground color varies from light yellow to yellowish brown. In Tennessee, two distinct dorsal color patterns occur representing two subspecies. One type consists of a mid-dorsal and two dorsolateral dark stripes. The mid-dorsal stripe originates near the eyes and extends to base of tail. Dorsolateral stripes begin just behind the eyes and may extend to tip of tail. This form, commonly called the three-lined salamander, also possesses dark spots or a mottled pattern on the venter. The other pattern type typically has numerous irregularly shaped dark spots on dorsum and lateral surfaces. Arrangement of markings on lateral surfaces may form indistinct dorsolateral stripes. Venter is usually immaculate. Sides of tail have vertical dark markings that form a distinctive herringbone pattern.

(b.) Taxonomic Considerations. Two subspecies are found in Tennessee (Ireland, 1979). Eurycea l. guttolineata (Holbrook), the three-lined salamander, occurs in the Coastal Plain of west Tennessee and has been found from a few scattered localities in the mountains of east Tennessee. Eurycea l. longicauda ranges from the Tennessee River in west Tennessee eastward throughout the state. Also, Parker (1937, 1939) reported this subspecies from the Coastal Plain of west Tennessee in the hills east of Reelfoot Lake. Ireland (1979) comments that along the Blue Ridge escarpment these two subspecies appear to be reproductively isolated. Examination of over 650 specimens during this study revealed no evidence of interbreeding between these two forms in extreme eastern Tennessee. Along both sides of the Tennessee River in west Tennessee (i.e., Stewart, Henry, Perry, Henderson, Hardin, and Lawrence counties) specimens from several populations possessed color patterns indicating some degree of interbreeding. These intergrade specimens typically had a distinct mid-dorsal dark stripe which is a characteristic of E. l. guttolineata. However, many had reduced amounts of dark pigmentation on the venter indicating genetic influence from E. l. longicauda. Also, the mid-dorsal dark stripe was broken and indistinct on a few specimens. Further studies are needed to quantify and determine the extent of intergradation between these two subspecies in Tennessee.

(c.) Distribution and Habitat. Eurycea longicauda occurs statewide (Figure 60) but may be absent from higher elevations in the Blue Ridge Mountains. Suitable habitats include woodlands along creeks and rivers, mesic woodland hillsides, and the twilight zone of caves.

(14.) Eurycea lucifuga Rafinesque - Cave Salamander

(a.) Description. Like E. longicauda, the cave salamander is a slender species with a long tail. Total length measurements in adults range from 10 to 15 cm. Dorsal ground color may be yellowish orange, orange, or reddish orange. Markings include numerous irregularly shaped dark spots over the entire dorsal surface, including the tail. Herringbone dark pattern is absent on sides of tail.

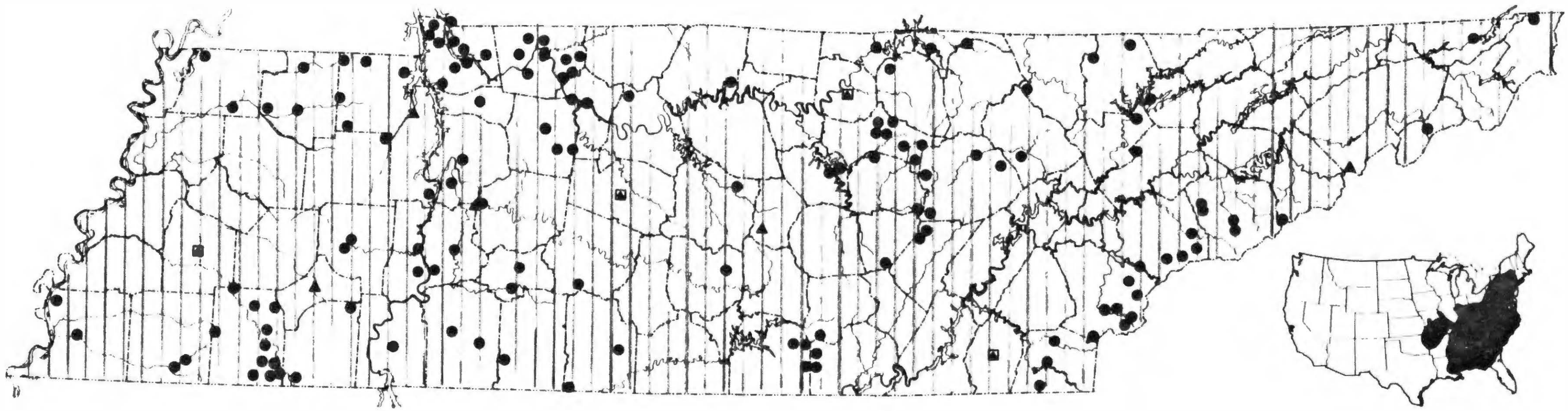

Figure 60. Distribution of Eurycea longicauda. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Solid triangles within squares denote county literature records without exact locality data. Smaller map depicts range in conterminous United States (Conant, 1975; Ireland, 1979).

(b.) Taxonomic Considerations. Hutchison (1966) does not recommend subspecific designations for this species. Grobman (1943) and Sinclair (1965) reported unusually large, dark, dusky colored specimens from several localities within and near the Nashville Basin of central Tennessee. However, neither author proposed taxonomic recognition for these aberrent individuals. Also, Merkle and Guttman (1977) studied genetic variation using electrophoretic techniques and noted allelic differences between Nashville Basin and other populations.

(c.) Distribution and Habitat. The range of E. lucifuga includes the Western Highland Rim and extends eastward to the Blue Ridge Mountains (Figure 61). Two cave localities are known from western portions of the Blue Ridge Mountains. Eurycea lucifuga occurs near cave entrances and the twilight zone of caves. It also inhabits mesic upland woodlands, especially near bluffs and limestone outcrops.

(15.) Gyrinophilus palleucus McCrady - Tennessee Cave Salamander

(a.) Description. The Tennessee cave salamander is a pale colored troglobite. Adults range from 8 to 18.4 cm in total length. External gills are normally present throughout life. Eyes are very small and poorly developed. Snout is flat and head broad. Dorsal ground color varies from pale white to brown. Dark dorsal spots may occur, and a dark stripe may be present on throat. Occasional individuals naturally lose their external gills and undergo metamorphosis. In Tennessee, naturally metamorphosed individuals have been reported from Knox County (Simmons, 1976) and Franklin County (Yeatman and Miller, 1985).

(b.) Taxonomic Considerations. Three subspecies have been reported for Tennessee. These include G. p. palleucus, G. p. necturoides

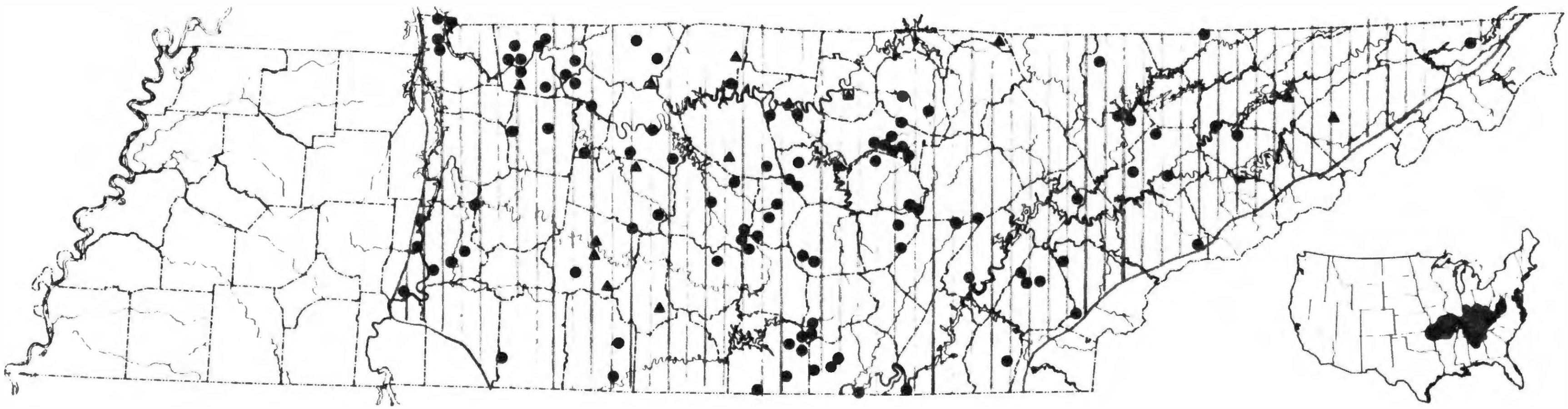

Figure 61. Distribution of Eurycea lucifuga. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Solid triangle within square denotes county literature record without exact locality data. Smaller map depicts range in conterminous United States (modified from Conant, 1975; Hutchison, 1966).

Lazell and Brandon, and G. p. gulolineatus Brandon (Brandon, 1967a). Type locality for the species is Sinking Cove Cave in Franklin County, Tennessee. Using electrophoretic techniques, Addison Wynn and Jeremy Jacob, U.S. National Museum, (pers. comm.) are currently studying biochemical variation within G. palleucus and have found evidence of a new species in Tennessee and possible hybridization of G. palleucus and G. porphyriticus.

(c.) Distribution and Habitat. In Tennessee, this troglobite is currently known from subterranean waters of the Tennessee River drainage in Knox, Roane, McMinn, Hamilton, Marion, Grundy, and Franklin counties and from the Cumberland River drainage in Rutherford County (Figure 62). Very little is known about the habitat requirements of this species.

(16.) Gyrinophilus porphyriticus (Green) - Spring Salamander

(a.) Description. The spring salamander is a large species. Total length measurements of adults range from 12 to 19 cm. The canthus rostralis, a light line from each eye to nostril, may be indistinct or distinctly bordered with black pigment. Ground color is usually yellowish pink, red, reddish brown, or tan. Dorsal dark markings are extremely variable. Dorsal markings may be virtually absent consisting only of small black spots or flecks or dorsum may be heavily mottled with dark reticulations, sometimes forming chevron-shaped markings. Venter may be plain or possess numerous melanophores.

(b.) Taxonomic Considerations. Within the species, four subspecies with wide zones of intergradation are recognized. According to Brandon (1962, 1967b), populations in Tennessee from the Eastern Highland Rim

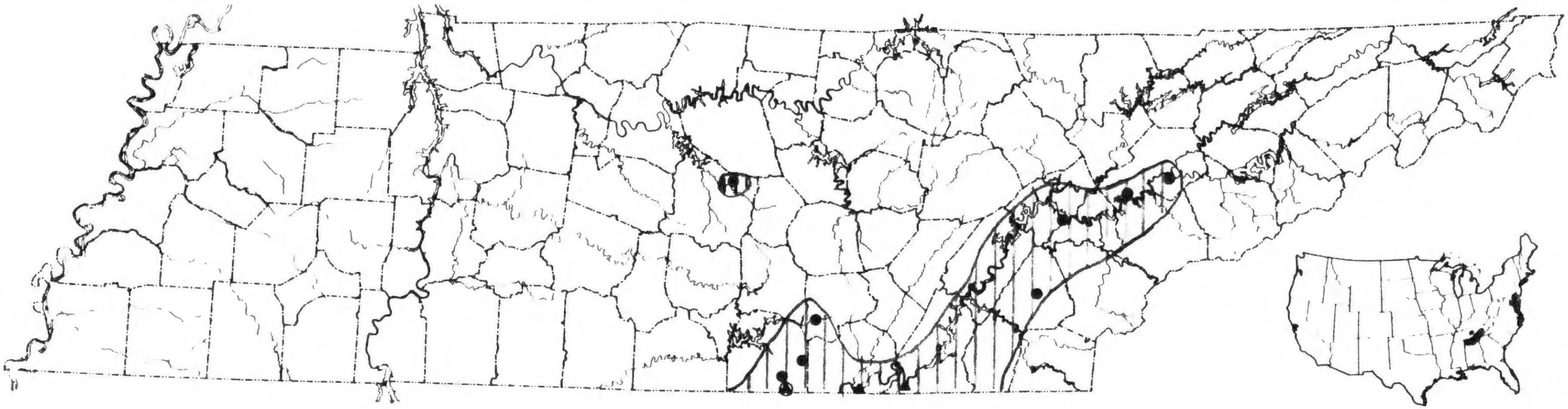

Figure 62. Distribution of Gyrinophilus palleucus. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Solid triangle within circle indicates type locality. Smaller map depicts range in conterminous United States (modified from Conant, 1975; Simmons, 1975; Brandon, 1967a).

to the western edge of the Blue Ridge Mountains are intergradient between G. p. porphyriticus and G. p. duryi Mittleman and Jopson. Populations in the Blue Ridge Mountains are considered G. p. danielsi (Blatchley). Sinclair (1953, 1955) proposed the recognition of G. warneri as a new species from middle Tennessee. His comments are available as abstracts from papers presented at an annual meeting of the Tennessee Academy of Science. A formal description was never published. Brandon (1962) studied specimens made available by Sinclair and concluded that they were not members of the genus Gyrinophilus, but were probably Pseudotriton montanus.

(c.) Distribution and Habitat. The spring salamander occurs along shaded, small to medium-sized streams east of the Outer Central Basin (Figure 63). In areas of karst topography where permanent surface habitats are scarce, the species is known to occur in cave streams and pools.

(17.) Hemidactylium scutatum (Schlegel) - Four-toed Salamander

(a.) Description. The four-toed salamander is a small species with adult total lengths ranging from 5.1 to 8.9 cm. Four toes are present on hind feet. A distinct constriction at the base of the tail separates body from tail region. Dorsal coloration varies from gray to a rusty brown with indistinct small dark markings. Lateral surfaces are often heavily mottled with black or dark brown markings. Venter is bright white with distinct scattered black spots.

(b.) Taxonomic Considerations. As reported by Neill (1963b) no subspecies ranks have been designated. The type locality is listed as Nashville, Davidson County, Tennessee.

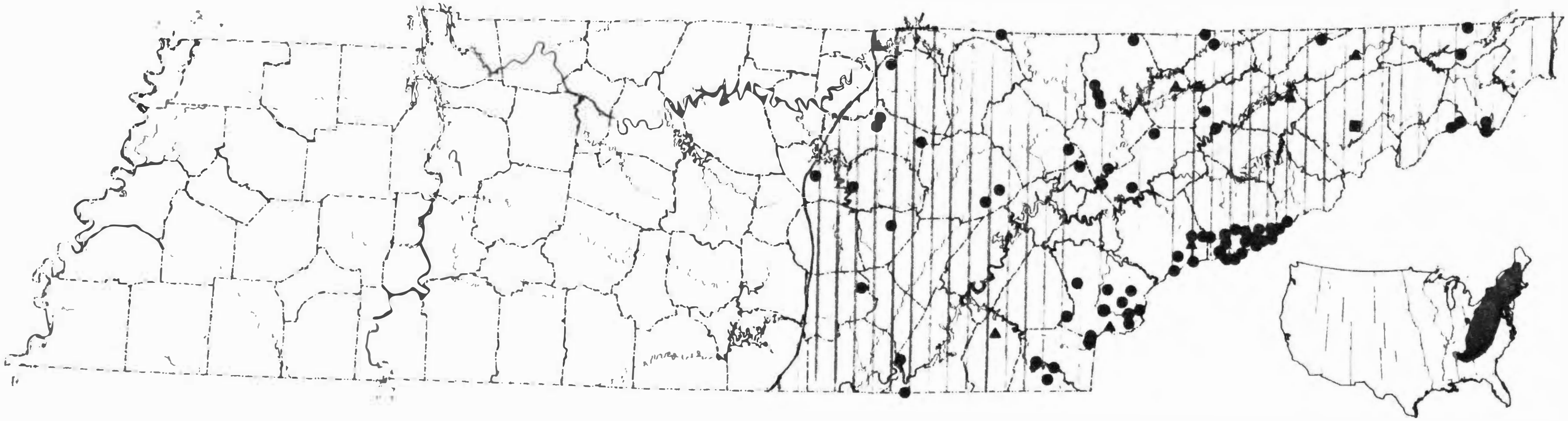

Figure 63. Distribution of Gyrinophilus porphyriticus. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Solid circle within square denotes county record based on museum specimen without exact locality data. Smaller map depicts range in conterminous United States (Conant, 1975; Brandon, 1967b; Mount, 1975).

(c.) Distribution and Habitat. As evidenced by the limited locality data provided in Figure 64, the distribution of *H. scutatum* in Tennessee is poorly known. The range as shown in Figure 64 is considered provisional and its determination relied heavily on distribution information available for adjacent states (Conant, 1975; Neill, 1963b; Mount, 1975; Martof, Palmer, Bailey, and Harrison, 1980; Barbour, 1971). Habitats include woodland swamps, shallow ponds, and sphagnum bogs.

(18.) *Leurognathus marmoratus* Moore - Shovelnose Salamander

(a.) Description. *Leurognathus marmoratus* is a permanently aquatic species that is often confused with *D. quadramaculatus.* Adults vary in total length from 9 to 13 cm. Although often difficult to see, a light line extends from eye to angle of jaw. Hind limbs are noticeably larger than forelimbs. Tail is laterally compressed and strongly keeled. Snout is flatter in appearance than in *D. quadramaculatus.* Internal nares are slit-like and obscure. Dorsal coloration is typically dark brown or black with two rows of irregularly shaped light blotches. Venter is usually dark gray and may possess a lighter center.

(b.) Taxonomic Considerations. No subspecies are currently recognized (Martof, 1963).

(c.) Distribution and Habitat. The shovelnose salamander is found in drainages of the Blue Ridge Mountains north of the Little Tennessee River (Figure 65). The species is typically found in rocky, small to medium-sized woodland streams with steep to moderate gradient. Mathews and Echternacht (1984) recorded *L. marmoratus* above 1650 m elevation, and Huheey and Stupka (1967) noted its apparent absence below 457 m.

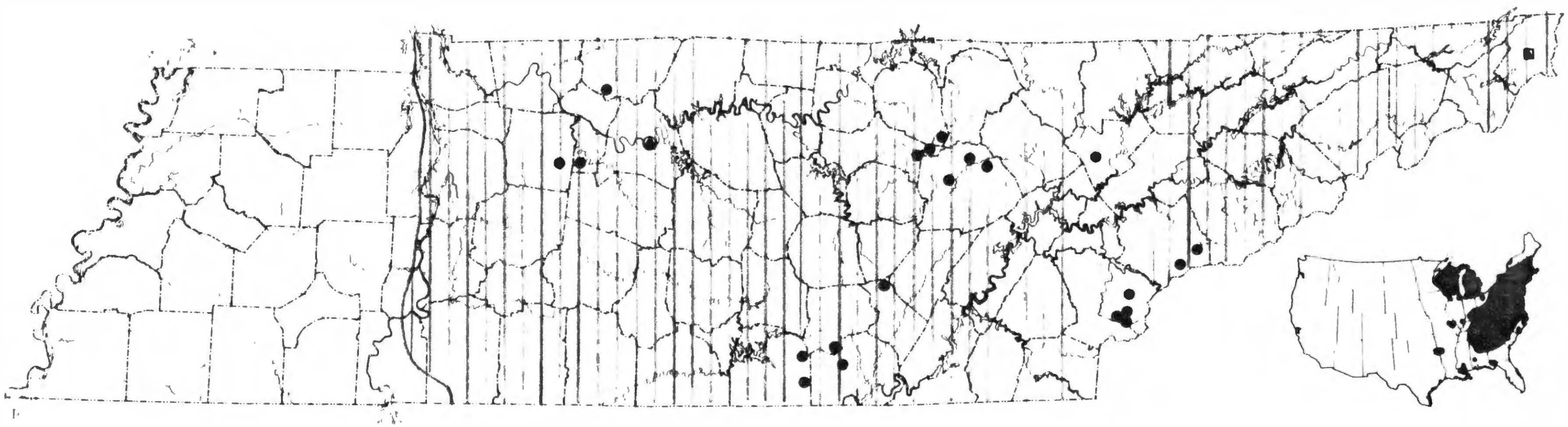

Figure 64. Distribution of <u>Hemidactylium scutatum.</u> Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangle within square denotes county literature record without exact locality data. Solid triangle within circle indicates type locality. Smaller map depicts range in conterminous United States (Conant, 1975; Neill, 1963b; Martof, Palmer, Bailey, and Harrison, 1980).

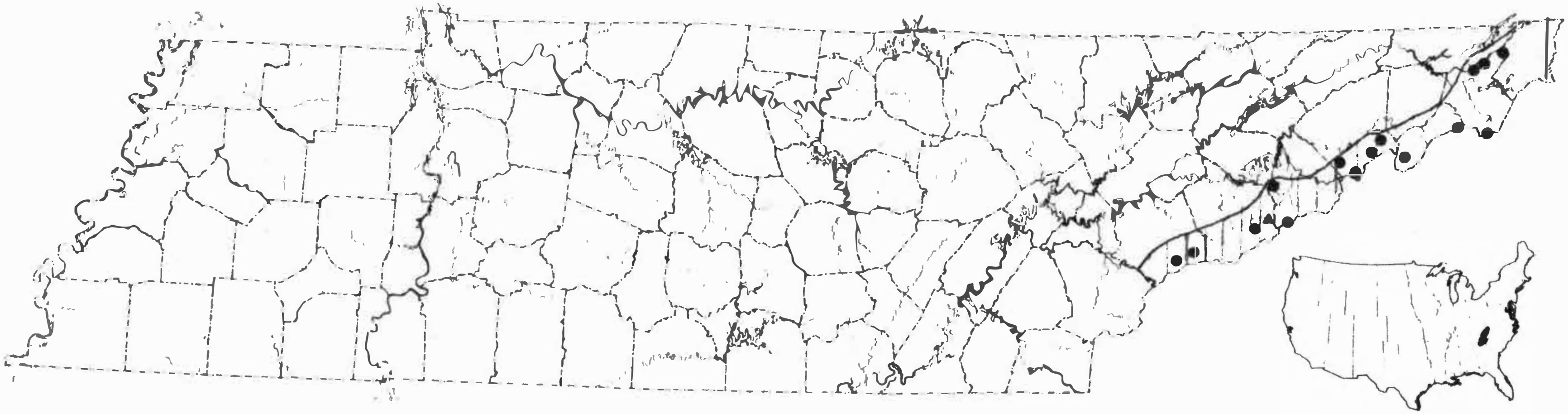

Figure 65. Distribution of Leurognathus marmoratus. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangle denotes literature record believed valid. Smaller map depicts range in conterminous United States (Martof, 1963; Conant, 1975).

(19.) Plethodon aureolus Highton - Tellico Salamander

(a.) Description. The Tellico salamander is a large, recently described species very similar in external morphology to P. glutinosus (Highton, 1983). Morphological differences are often inadequate in separating the two species; however, they may be consistently separated using biochemical characteristics. According to Highton, P. aureolus is smaller than P. glutinosus. Holotype was 5.4 cm in snout-vent length, and largest specimen measured by Highton had a snout-vent length of 6.7 cm. Dorsal and lateral ground color is dark gray to black with numerous, large brassy colored spots. Venter is dark gray to black, and chin is typically lighter color than venter.

(b.) Taxonomic Considerations. No subspecies are currently recognized (Highton, 1983). As described by Highton, P. aureolus is sympatric with typical P. glutinosus on the western edge of the Unicoi Mountains and sympatric throughout its range with the teyahalee morph of P. glutinosus (see account for P. glutinosus). Highton provided evidence of hybridization of P. aureolus and P. jordani. Type locality is Farr Gap, Unicoi Mountains, Monroe County, Tennessee.

(c.) Distribution and Habitat. All locality data plotted in Figure 66 was taken from Highton (1983). Highton defined the species range to include the western slopes of the Unicoi Mountains and adjacent lowlands between the Little Tennessee and Hiwassee Rivers. Even though Highton did not provide habitat data, he did note that P. aureolus was commonly sympatric with the white spotted teyahalee form of P. glutinosus. Typical habitat for P. glutinosus in this area includes both upland and stream valley woodlands.

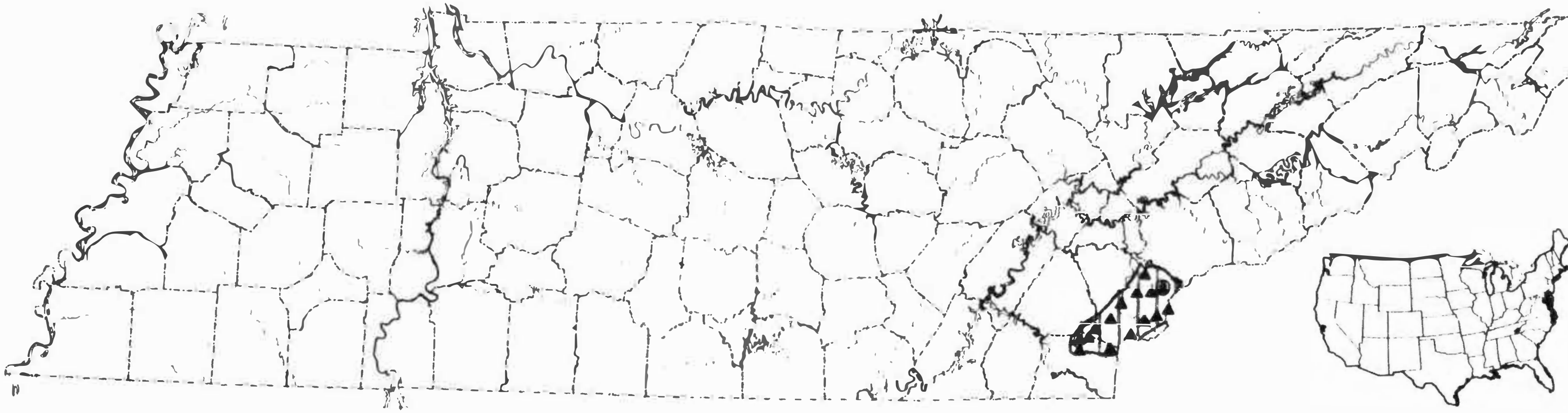

Figure 66. Distribution of Plethodon aureolus. Vertical hatching indicates range. Solid triangles denote literature records believed valid. Solid triangle within circle indicates type locality. Smaller map depicts range in conterminous United States (Highton, 1983).

(20.) Plethodon cinereus (Green) - Redback Salamander

(a.) Description. Plethodon cinereus is small, similar to P. dorsalis and, based on external morphology, is virtually indistinguishable from P. serratus. Adults attain total lengths of 5.7 to 9.2 cm. Dorsal coloration consists of a straight-edged light red stripe that extends from neck well onto tail. This stripe appears to become narrower at base of tail. Some individuals lack dorsal stripe, and dorsum is dark brown or black with scattered light flecks. Dorsal red pigment is usually absent. Venter is mottled with equal amounts of black and white. Ventral red markings are typically absent. Costal groove count varies from 18 to 20.

(b.) Taxonomic Considerations. No subspecific taxa are recognized (Highton and Webster, 1976). Prior to Highton and Webster's study, populations in the Blue Ridge Mountains of Tennessee were considered one species, P. cinereus. Using biochemical differences, Highton and Webster recognized two species, P. cinereus and P. serratus.

(c.) Distribution and Habitat. As determined by Highton and Webster, the range of P. cinereus in Tennessee includes the Blue Ridge Mountains north of the French Broad River (Figure 67). The redback salamander is found under logs and rocks and under leaf litter in upland forests. One Tennessee record of P. cinereus from outside the Blue Ridge Mountains was determined invalid by Grobman (1944). He provided substantial evidence that a specimen in the U.S. National Museum (USNM No. 57106), listed from Franklin County, Tennessee, was actually taken in Franklin County, Missouri.

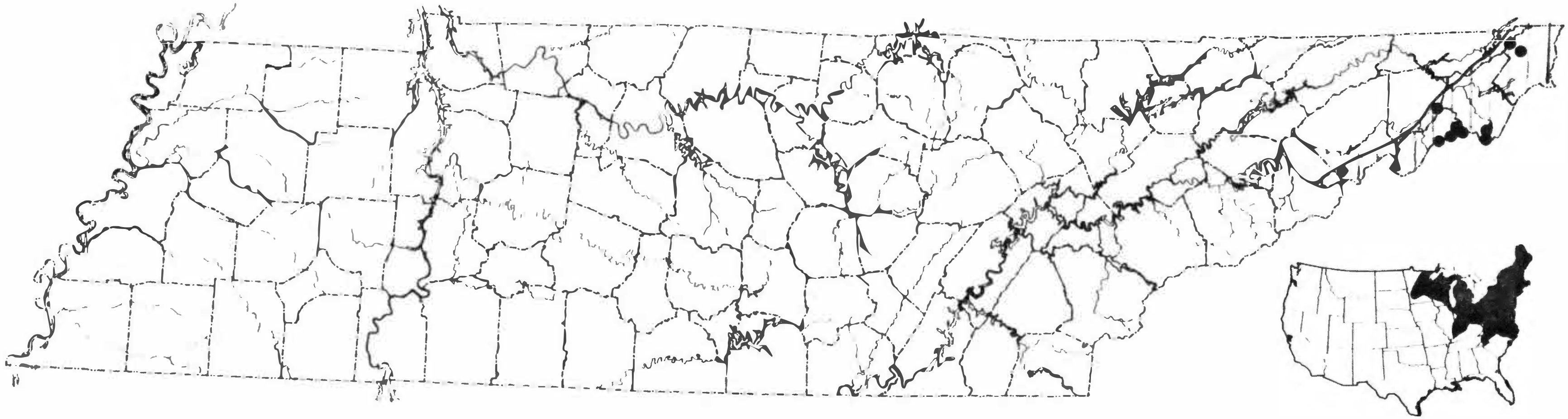

Figure 67. Distribution of <u>Plethodon cinereus.</u> Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangle denotes literature record believed valid. Smaller map depicts range in conterminous United States (Highton and Webster, 1976; Martof, Palmer, Bailey, and Harrison, 1980).

(21.) Plethodon dorsalis Cope - Zigzag Salamander

(a.) Description. The zigzag salamander is small. Total length of adults varies from 6.4 to 8.9 cm. A dorsal light red, brown, or yellowish stripe, which has lobed or wavy margins, extends from neck well onto the tail. Stripe may appear to widen at base of tail. In some individuals, dorsum may be uniformly dark brown or black. Ventral surfaces are light with profuse black or black and reddish mottling. Costal groove count is usually 18.

(b.) Taxonomic Considerations. According to Thurow (1966) and Conant (1975), only the nominate subspecies occurs in Tennessee.

(c.) Distribution and Habitat. The distribution of P. dorsalis as shown in Figure 68 was slightly modified from the range provided by Highton (1979). The species appears to be absent from elevations above 762 m in the Blue Ridge Mountains (King, 1939) and from most of the Coastal Plain in west Tennessee. Two localities are known from the Coastal Plain. Parker (1939) described an Obion County site as wooded hills east of Walnut Log and Reelfoot Lake. He found specimens in leaf mats and near springs. Thurow (1966) characterized this area as bluffs composed of consolidated loess that provided rock shelter habitats. Ecological data for a Henry County locality are lacking. Two specimens were taken from the Obion River area, Highway 69, north of Jones Mill (NLU Nos. 45756-45757). Elsewhere in Tennessee, the species is most often found under leaf litter, rocks, and logs in mesic upland woodlands. The status of P. dorsalis in the Cumberland Mountains is poorly known and needs futher study.

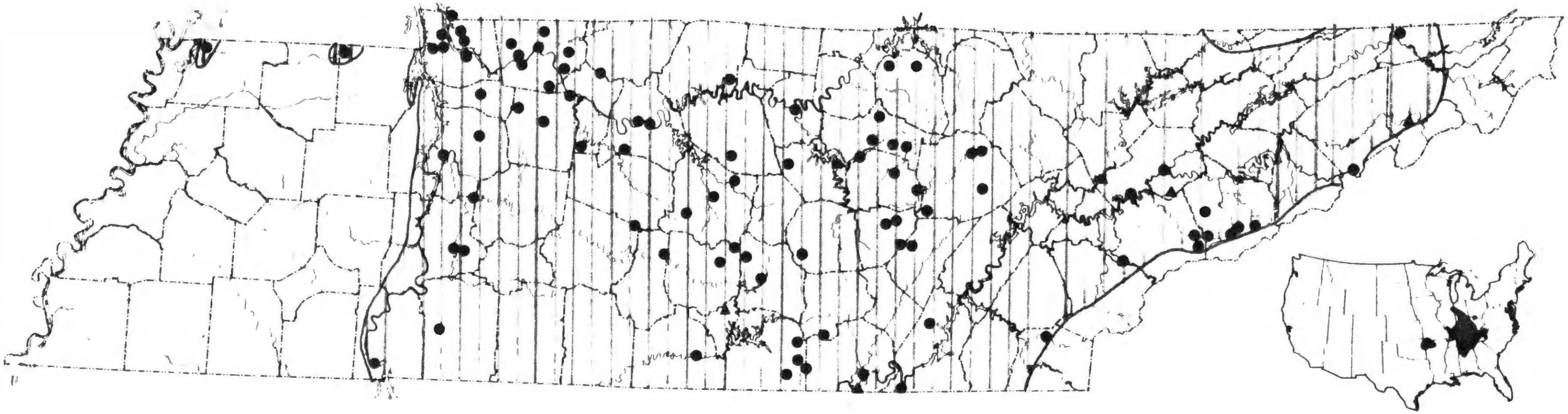

Figure 68. Distribution of Plethodon dorsalis. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Smaller map depicts range in conterminous United States (modified from Conant, 1975; Highton, 1979; Thurow, 1966).

(22.) Plethodon glutinosus (Green) - Slimy Salamander

(a.) Description. The slimy salamander is a large plethodontid. Adults range from 12 to 17 cm in total length. Dorsal ground color may be dark gray or black. Dorsum and lateral surfaces are lightly to heavily marked with white, light gray, or brassy spots and flecks. Light markings on lateral surfaces may be concentrated and form large irregularly shaped spots or blotches. Venter is dark gray or black, and chin color not lighter than venter.

(b.) Taxonomic Considerations. Following Conant (1975), one subspecies, P. g. glutinosus, is recognized from Tennessee. Highton (1973) considered P. jordani teyahalee Hairston synonymous with P. glutinosus. Based on biochemical data, Highton (1983) subsequently suggested that the teyahalee morph should be considered a separate species. He described P. teyahalee as a large species with small dorsal white spots. He also reported numerous localities in the Unicoi Mountains in Monroe and Polk counties, but did not provide a detailed account of its total distribution. He stated that a detailed account of this species will be provided in a future paper. Because available distribution and taxonomic information is insufficient to delineate the range of P. teyahalee in Tennessee, P. teyahalee and P. glutinosus are tentatively treated together as a cryptic species pair. In Tennessee, P. glutinosus occurs sympatrically with the cryptic species P. aureolus in the Unicoi Mountains and P. kentucki in the Cumberland Mountains. For further information, see accounts for P. aureolus and P. kentucki.

(c.) Distribution and Habitat. Plethodon glutinosus occurs statewide (Figure 69). Mathews and Echternacht (1984) reported the species above 1305 m in the Great Smoky Mountains National Park.

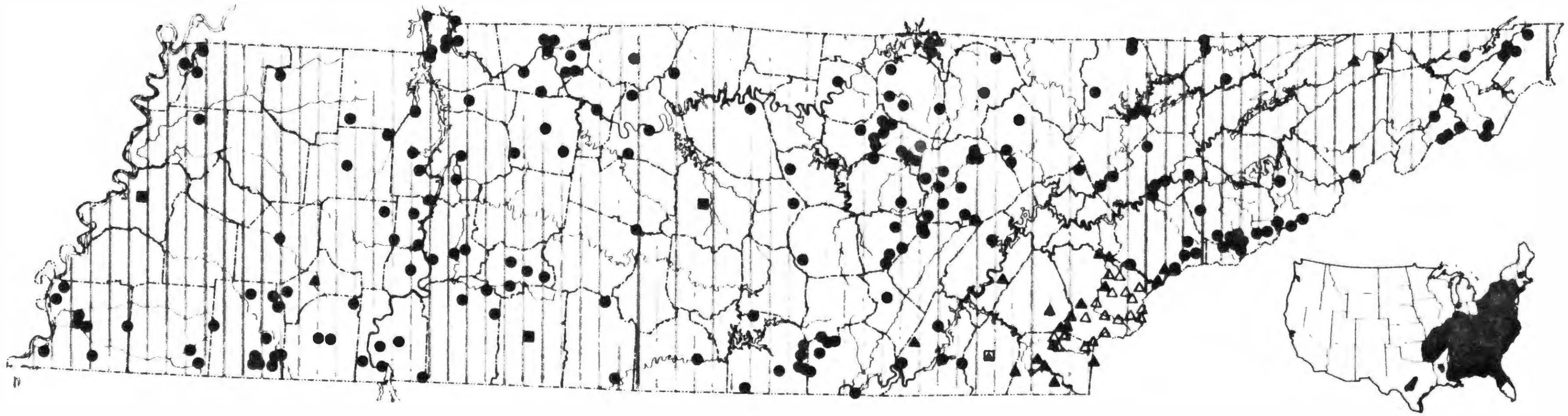

Figure 69. Distribution of Plethodon glutinosus. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Hollow triangles denote teyahalee morph of Highton (1983). Solid circles within squares denote county records based on museum specimens without exact locality data. Solid triangle within square denotes county literature record without exact locality data. Smaller map depicts range in conterminous United States (Conant, 1975; Highton, 1971; Martof, Palmer, Bailey, and Harrison, 1980).

Because of the difficulty in separating preserved specimens of P. aureolus, typical P. glutinosus, and the teyahalee form of P. glutinosus, locality data plotted for Monroe and Polk counties were taken exclusively from Highton (1983). The slimy salamander exploits a wide vareity of woodland habitats ranging from mesic bottomland hardwood to relatively dry hillside forests.

(23.) Plethodon jordani Blatchley - Jordan's Salamander

(a.) Description. Jordan's salamander is a large plethodontid. Adults attain total lengths ranging from 9 to 13 cm. In most adults, dorsal ground color is dark gray or black without white or brassy markings. However, individuals from the Unicoi Mountains in southeastern Tennessee typically have lateral white spots and flecks. Populations from Great Smoky Mountains usually possess red cheek patches while other Tennessee populations have cheeks essentially the same color as dorsum. Venter is usually lighter than dorsum and chin is usually lighter than rest of venter.

(b.) Taxonomic Considerations. In the past, two races were recognized from Tennessee. These included the uniformly black metcalfi race, and the red-cheeked jordani race (Conant, 1958). Highton (1962, 1973) studied variation in this species complex and concluded subspecific ranks were unwarranted. Highton and Henry (1970) reported slight evidence of hybridization between P. jordani and P. glutinosus in the Great Smoky Mountains and substantial hybridization with P. glutinosus in the Unicoi Mountains. He later (Highton, 1983) described P. aureolus and P. teyahalee, two biochemically defined cryptic species of P. glutinosus, from the Unicoi Mountains of Tennessee and adjacent western North Carolina and cited evidence of hybridization of both with P. jordani. Highton (1971) found no indication of hybridization of P. glutinosus and P. jordani east of the French Broad River. The type locality is near the divide along the Tennessee-North Carolina border in the Great Smoky Mountains National Park.

(c.) Distribution and Habitat. The range of P. jordani includes high elevation habitats in the Blue Ridge Mountains along the Tennessee-North Carolina border (Figure 70). It occurs in moist woodlands on mountain summits and down to 762 m elevation (Huheey and Stupka, 1967). Highton (1983) noted that what appeared to be P. jordani from several localities north of Jones Knob in the Unicoi Mountains in Monroe County were actually P. aureolus. He determined that Jones Knob was the northernmost locality for P. jordani in the Unicoi Mountains.

(24.) Plethodon kentucki Mittleman - Cumberland Plateau Woodland Salamander

(a.) Description. Plethodon kentucki is a large plethodontid very similar to P. glutinosus and, in areas of sympatry, biochemical characteristics may be the only criteria useful in separating the two (Highton, 1985). Adult P. kentucki are typically smaller than P. glutinosus. Mittleman (1951) found snout-vent lengths ranging from 3.4 to 6.0 cm. Dorsal and lateral color is black with scattered white spots that are smaller and less numerous than those of P. glutinosus. Also, white spots of P. kentucki have less brassy color than P. glutinosus. Mental gland of adult male P. kentucki is larger than that of P. glutinosus. Venter is black and chin is a noticeably lighter color than venter.

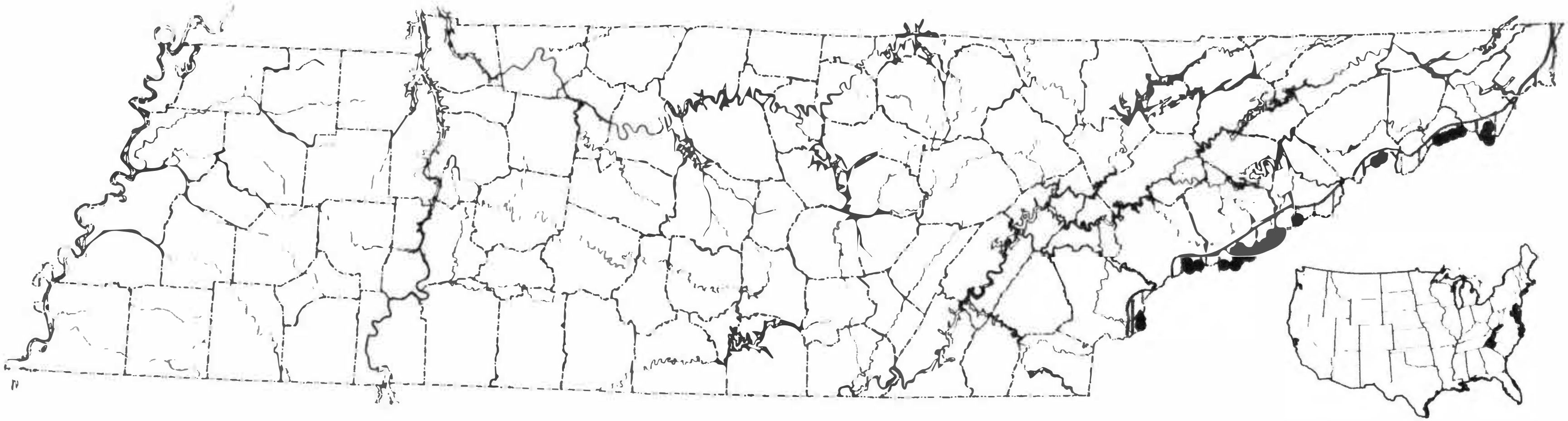

Figure 70. Distribution of Plethodon jordani. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangle denotes literature record believed valid. Solid triangle within circle indicates type locality. Smaller map depicts range in conterminous United States (Highton, 1973; Conant, 1975).

(b.) Taxonomic Considerations. Plethodon kentucki was originally described by Mittleman (1951) from eastern Kentucky. Clay, Case, and Cunningham (1955) reduced P. kentucki to synonymy with P. glutinosus. After an analysis of both morphological and biochemical characteristics, Highton and MacGregor (1983) reinstated P. kentucki to species rank. No subspecies are currently recognized (Highton, 1985).

(c.) Distribution and Habitat. The distribution of P. kentucki as shown in Figure 71 was taken from Highton (1985) and must be considered tentative. MacGregor and Stephens (1985) collected the only specimen known from Tennessee and briefly described its habitat as a shale outcrop bordering a gravel road. MacGregor (pers. comm.) feels the species probably occurs elsewhere in the Cumberland Mountains in Tennessee. His unpublished data indicate that P. kentucki is often sympatric with P. glutinosus, and he characterizes optimum habitat for P. kentucki as mature hardwood forests on steep slopes underlain by sandstone or shale.

(25.) Plethodon richmondi Netting and Mittleman - Ravine Salamander

(a.) Description. Plethodon richmondi is a small, slender worm-like plethodontid with relatively short limbs. Adults attain adult total lengths of 8 to 11 cm. Dorsal and lateral color is dark brown or black with scattered silver, white, or brassy colored flecks. Plethodon richmondi differs from other small plethodontids in possessing a predominantly dark brown or black venter. Costal groove count ranges from 19 to 22.

(b.) Taxonomic Considerations. No subspecies are recognized (Conant, 1975). Thurow (1969) reported evidence of hybridization of

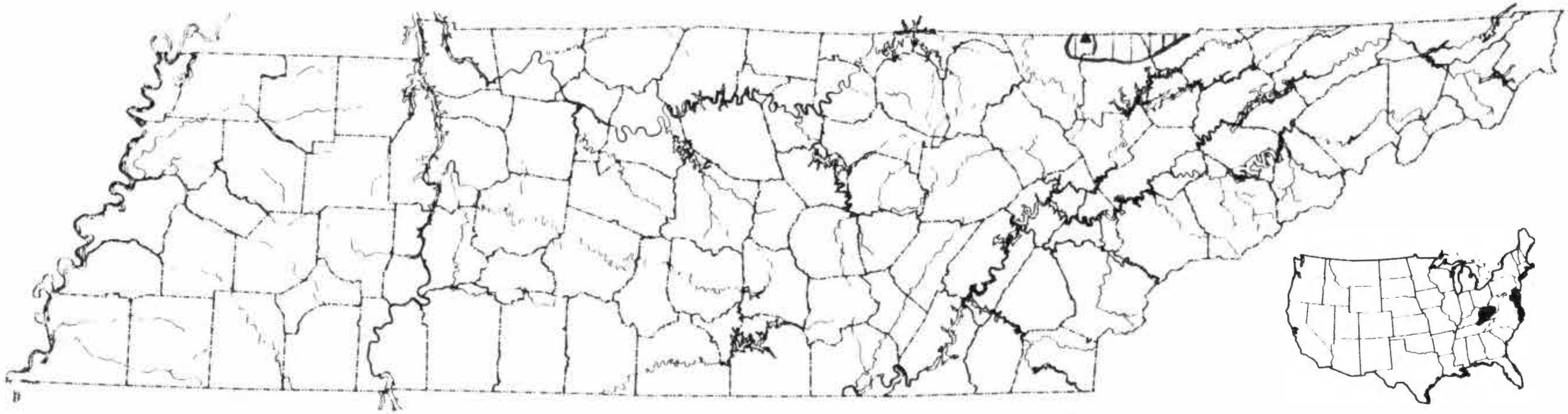

Figure 71. Distribution of Plethodon kentucki. Vertical hatching indicates range. Solid triangle denotes literature record believed valid. Smaller map depicts range in conterminous United States (Highton, 1985; MacGregor and Stephens, 1985).

P. richmondi and P. cinereus on Iron and Holston Mountains in northeastern Tennessee.

(c.) Distribution and Habitat. Plethodon richmondi is known from northern portions of the Blue Ridge Mountains, Appalachian Ridge and Valley, and Cumberland Mountains (Figure 72). Typical habitats are mesic upland forests where individuals are usually found under rocks, logs, and leaf litter.

(26.) Plethodon serratus Grobman - Southern Redback Salamander

(a.) Description. Plethodon serratus is a small plethodontid similar to P. dorsalis and cannot be reliably separated from P. cinereus based on external characteristics. Total lengths of adults range from 5.7 to 9.2 cm. Dorsal color pattern includes a straight-edged light red stripe that extends from neck well onto the tail. Stripe appears to become narrower at base of tail. Although rare, a few individuals may lack stripe and have a dark brown or black dorsum with scattered light flecks. Dorsal red pigment is typically present. Venter is mottled with equal amounts of black and white. Ventral red pigment is usually present. Costal groove count varies from 18 to 20.

(b.) Taxonomic Considerations. No subspecies are recognized (Highton and Webster, 1976). Highton and Webster elevated this form to species status based on biochemical characteristics.

(c.) Distribution and Habitat. Following Highton and Webster's proposals, P. serratus is considered to occur in the Blue Ridge Mountains south of the French Broad River (Figure 73). Like P. cinereus, P. serratus is terrestrial in habits and occurs in upland forests.

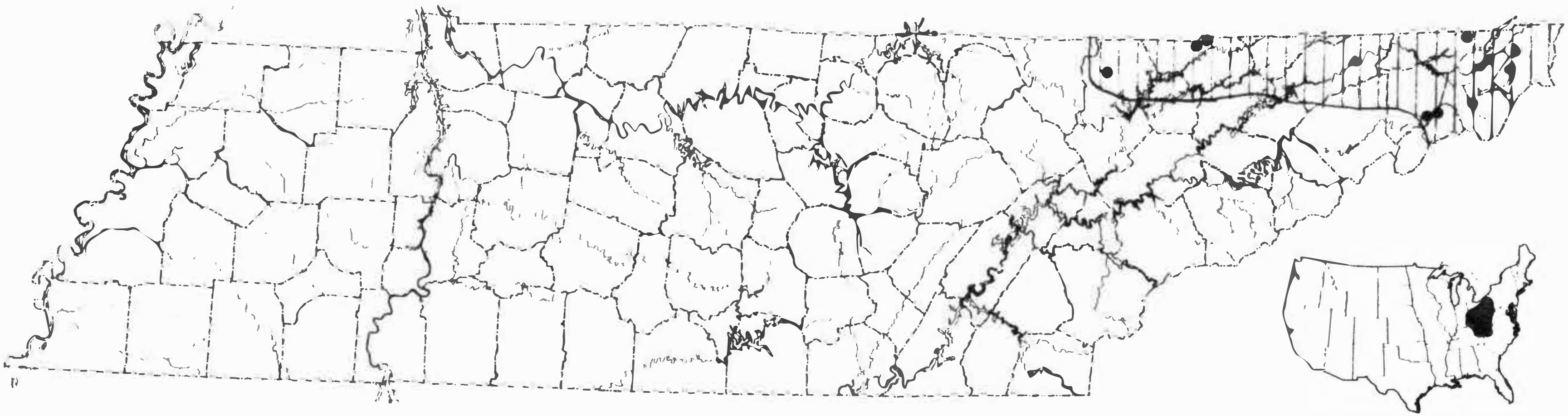

Figure 72. Distribution of Plethodon richmondi. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangle denotes literature record believed valid. Smaller map depicts range in conterminous United States (modified from Conant, 1975).

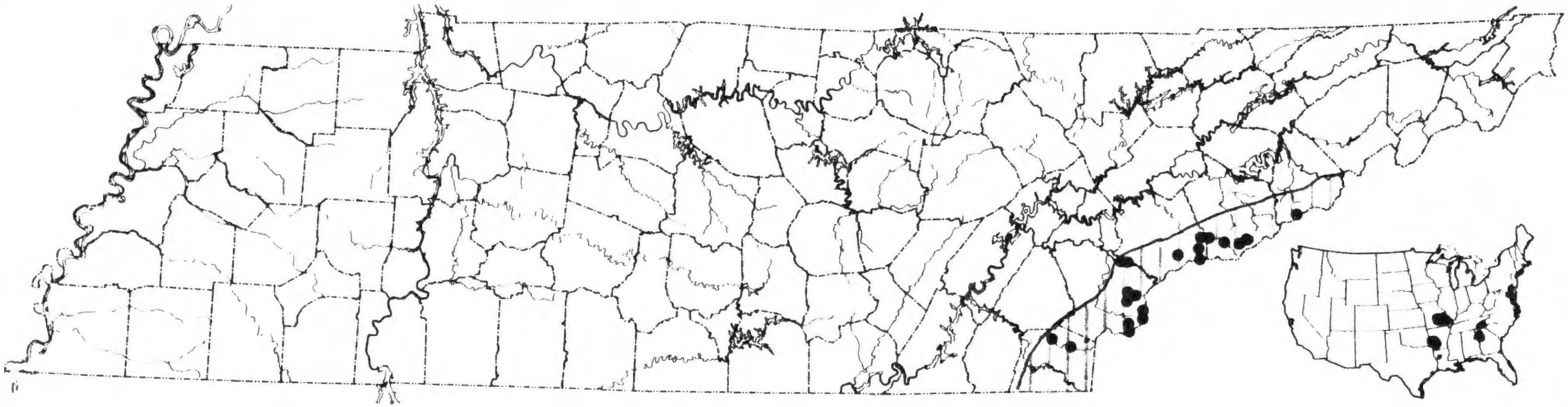

Figure 73. Distribution of Plethodon serratus. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Smaller map depicts range in conterminous United States (Highton and Webster, 1976).

(27.) Plethodon wehrlei Fowler and Dunn - Wehrle's Salamander

(a.) Description. There are only two specimens, one adult and one juvenile, available from Tennessee (Redmond and Jones, 1985). Adult specimen has a total length of 9.1 cm and a snout-vent length of 4.8 cm. Juvenile total length is 5.7 cm and snout-vent length is 3.1 cm. On both specimens, dorsal ground color is dark brown with 8 to 10 irregularly shaped yellow spots. Venter is gray. Distinct webbing is present between toes.

(b.) Taxonomic Considerations. According to Conant (1975) no subspecies are recognized. Within the range of P. wehrlei, the yellow spotted morph is rare and has been reported from only three localities (Cupp and Towles, 1983; Redmond and Jones, 1985). Richard Highton (pers. comm.) does not believe these populations deserve formal taxonomic recognition.

(c.) Distribution and Habitat. In Tennessee, Wehrle's salamander is known from one locality, a gorge with a mesic hardwood forest, in the Cumberland Mountains (Figure 74). Adult specimen was found in a rock crevice in a rock shelter on a shaded sandstone cliff face. Juvenile was taken along path adjacent to sandstone cliff face approximately 20 m from rock shelter where adult was taken. Both specimens were collected on warm misty nights.

(28.) Plethodon welleri Walker - Weller's Salamander

(a.) Description. Weller's salamander is a small plethodontid species that as adults reach 6.4 to 7.9 cm in total length. Dorsal ground color is black and washed with gold or brassy colored irregularly shaped blotches. Venter is usually black with numerous small white flecks or spots.

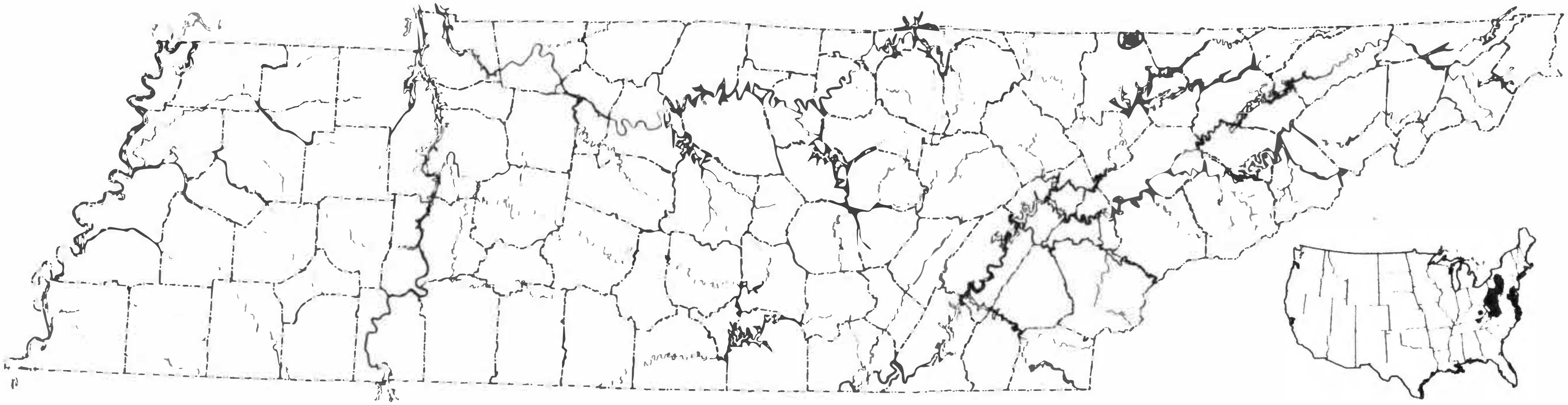

Figure 74. Distribution of Plethodon wehrlei. Vertical hatching indicates range. Solid circle denotes locality based on museum specimens. Smaller map depicts range in conterminous United States (Conant, 1975; Cupp and Towles, 1983; Redmond and Jones, 1985).

(b.) Taxonomic Considerations. Thurow (1964) lists one subspecies, *P. w. ventromaculatus* Thurow, from Tennessee.

(c.) Distribution and Habitat. *Plethodon welleri* is restricted to the Blue Ridge Mountains in northeastern Tennessee (Figure 75). Populations are usually found above 762 m elevation on forested mountain summits, mesic woodland talus slopes, and in cove hardwood forests. Thurow (1963) noted a population at 700 to 732 m in a limestone cove forest dominated by hemlock and yellow birch.

(29.) *Plethodon yonahlossee* Dunn - Yonahlossee Salamander

(a.) Description. *Plethodon yonahlossee* is a large plethodontid species. Adults reach total lengths ranging from 11 to 17 cm. A wide irregularly shaped dorsal red stripe extends from near the head onto the tail. This stripe may be partially interrupted by black spots or blotches. Lateral surfaces are heavily marked with white or light gray. Throat is light in color. Venter is dark gray and usually has numerous scattered light spots.

(b.) Taxonomic Considerations. No subspecies are recognized (Pope, 1965; Conant, 1975).

(c.) Distribution and Habitat. The range of *P. yonahlossee* in Tennessee (Figure 76) is strikingly similar to that of *P. welleri*. Yonahlossee salamanders inhabit mature woodlands, and populations are currently known from elevations ranging from 732 to 1433 m.

(30.) *Pseudotriton montanus* Baird - Mud Salamander

(a.) Description. The mud salamander is a relatively large species with a slender body form. Adults attain total lengths of 9 to 15 cm.

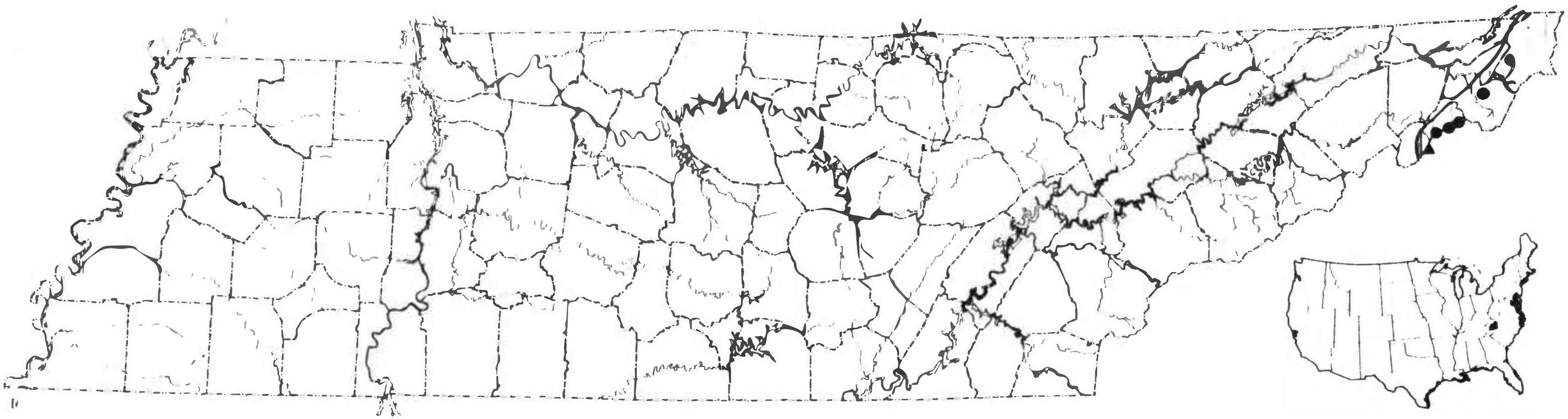

Figure 75. Distribution of Plethodon welleri. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangle denotes literature record believed valid. Smaller map depicts range in conterminous United States (Conant, 1975; Thurow, 1964).

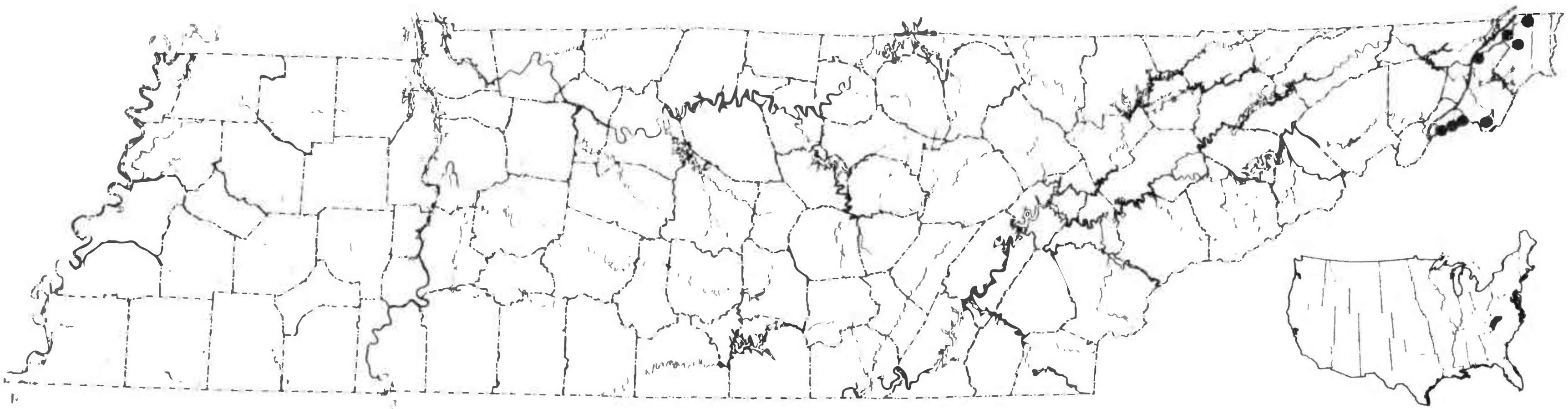

Figure 76. Distribution of Plethodon yonahlossee. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Smaller map depicts range in conterminous United States (Conant, 1975; Pope, 1965).

Dorsal and ventral ground color may be coral-pink, red, or reddish brown. A few well defined, rounded black spots are usually present on dorsum. Venter is usually immaculate.

(b.) Taxonomic Considerations. Martof (1975a) followed the recommendation of Bruce (1968a) and did not recognize subspecific subdivisions. Conant (1975) apparently disagreed and recognized four subspecies. Conant's range map shows one subspecies, *P. m. diastictus* Bishop, in Tennessee.

(c.) Distribution and Habitat. Excluding the high elevations of the Blue Ridge Mountains, the range of *P. montanus* includes the eastern one-half of the state (Figure 77). Highest reported locality in the Great Smoky Mountains National Park is 477 m, and several localities in the Cumberland Mountains and Cumberland Plateau occur above 550 m elevation. The mud salamander inhabits muddy areas of floodplain woodland streams, swamps, and seepage areas.

(31.) *Pseudotriton ruber* (Sonnini) - Red Salamander

(a.) Description. *Pseudotriton ruber* is a large stout-bodied species that reaches adult total lengths of 7 to 15 cm. This species is very similar to *P. montanus*, but has a stockier body and smaller head. Dorsal and ventral ground color range from bright red to a dull purplish brown. Dorsal markings typically consist of many small irregularly shaped dark spots that may fuse in older individuals. Ventral surface of chin may be lightly flecked or heavily pigmented with black. Venter may be immaculate or spotted with dark markings.

(b.) Taxonomic Considerations. Disagreement exists regarding the existence of valid subspecies. Martof (1975b) cites Bruce (1968a) and

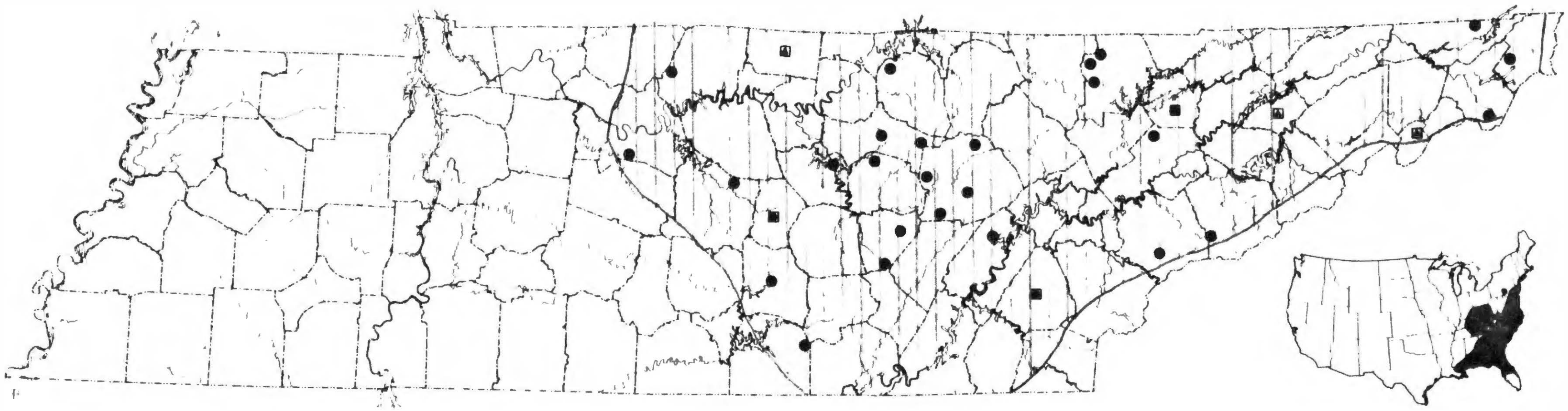

Figure 77. Distribution of <u>Pseudotriton montanus.</u> Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid circles within squares denote county records based on museum specimens without exact locality data. Solid triangles within squares denote county literature records without exact locality data. Smaller map depicts range in conterminous United States (modified from Conant, 1975; Martof, 1975a; Mount, 1975; Martof, Palmer, Bailey, and Harrison, 1980).

did not recognize subspecific designations. However, Conant (1975) lists four subspecies, all of which occur in Tennessee. According to Conant, P. r. vioscai Bishop occurs in the eastern two-thirds of the Coastal Plain in west Tennessee, P. r. ruber from the Tennessee River in west Tennessee to the western edge of the Blue Ridge Mountains, P. r. nitidus Dunn in the northern half of the Blue Ridge Mountains, and P. r. schencki (Brimley) in the southern half of the Blue Ridge Mountains.

(c.) Distribution and Habitat. Pseudotriton ruber is found throughout Tennessee east of the Loess Plain of west Tennessee (Figure 78). Available data indicate the species may be rare in the Inner and Outer Central basins. The red salamander has been reported above 1524 m in the Great Smoky Mountains National Park (Huheey and Stupka, 1967). Pseudotriton ruber occurs near many woodland aquatic habitats including creeks, springs and spring runs, and seepage areas. It may occasionally be found in mesic to relatively dry woodlands.

f. Family Salamandridae - Newts

(1.) Notophthalmus viridescens (Rafinesque) - Eastern Newt

(a.) Description. Notophthalmus viridescens has a distinct terrestrial larval form and an aquatic adult form. Neither form typically has external gills. The terrestrial stage is commonly called an eft and is bright red or orange with dorsal red or black spots. Total length ranges from 3.5 to 8.6 cm. Skin of eft is very spinose. Adults are aquatic and attain total lengths of 6 to 10.2 cm. Adult dorsal coloration ranges from yellowish green to brown with either numerous red spots bordered by black or with only small black spots.

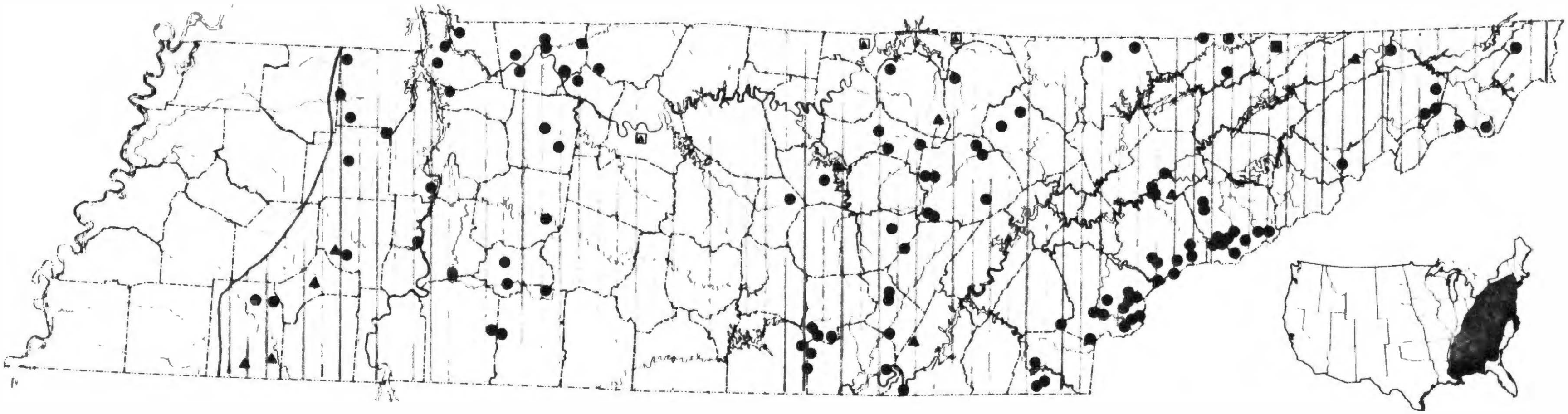

Figure 78. Distribution of Pseudotriton ruber. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Solid circle within square denotes county record based on museum specimen without exact locality data. Solid triangles within squares denote county literature records without exact locality data. Smaller map depicts range in conterminous United States (Martof, 1975b; Conant, 1975).

(b.) Taxonomic Considerations. Two subspecies are reported in Tennessee. *Notophthalmus v. viridescens* occurs in the eastern two-thirds of the state and *N. v. louisianensis* (Walterstorff) occurs in the Coastal Plain in the western one-third (Mecham, 1967).

(c.) Distribution and Habitat. The eastern newt occurs throughout the state (Figure 79). Adults inhabit ponds, pools along and within streams, oxbows, and flooded ditches. Efts are most often encountered under rocks and logs in upland woodland habitats.

g. Family Sirenidae - Sirens

(1.) *Siren intermedia* Le Conte - Lesser Siren

(a.) Description. A permanently aquatic species that is eel-like in appearance, *S. intermedia* possesses well-developed external gills. Adults reach total lengths of 18 to 68.6 cm. Front limbs are present. Hind limbs are absent. Dorsal coloration varies from gray, brown, or black and may include small diffuse light spots. Lateral body surfaces and venter may have light colored flecks.

(b.) Taxonomic Considerations. Only one subspecies, *S. i. nettingi* Goin is found in Tennessee (Martof, 1973).

(c.) Distribution and Habitat. The lesser siren occurs in sluggish streams, oxbows, and flooded ditches in the Coastal Plain of west Tennessee (Figure 80). It has also been found in Cumberland River bottoms in Davidson County (Gentry, 1955-1956; Ashton, 1966). Snyder (1972) noted its occurrence in a small impoundment adjacent to Barkley Reservoir just north of the Stewart County, Tennessee-Trigg County, Kentucky boundary line.

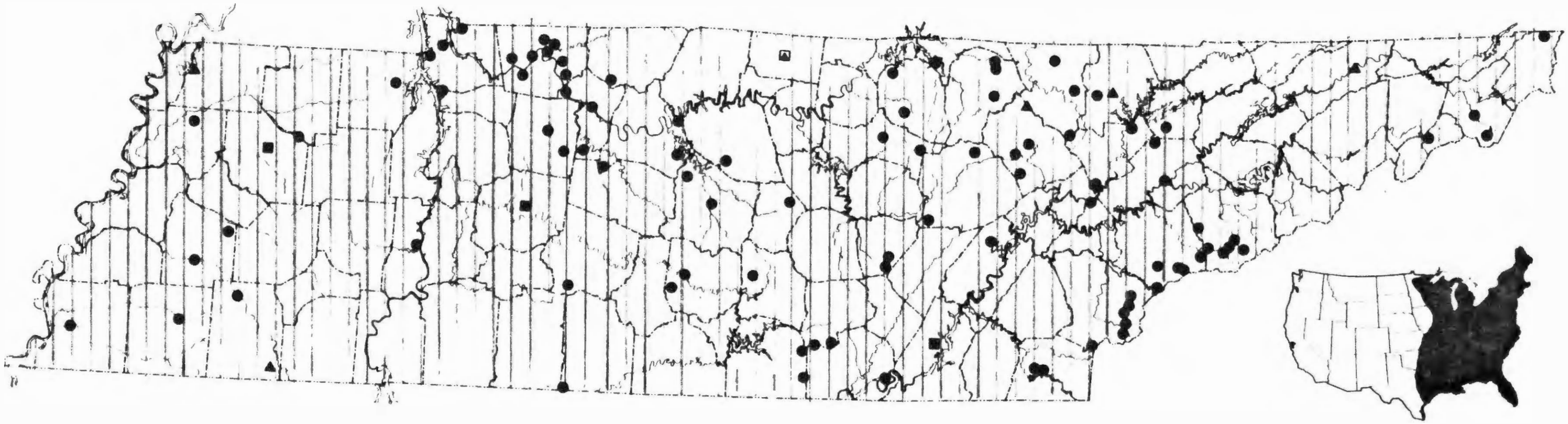

Figure 79. Distribution of Notophthalmus viridescens. Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangles denote literature records believed valid. Solid circles within squares denote county records based on museum specimens without exact locality data. Solid triangle within square denotes county literature record without exact locality data. Smaller map depicts range in conterminous United States (Conant, 1975; Mecham, 1967).

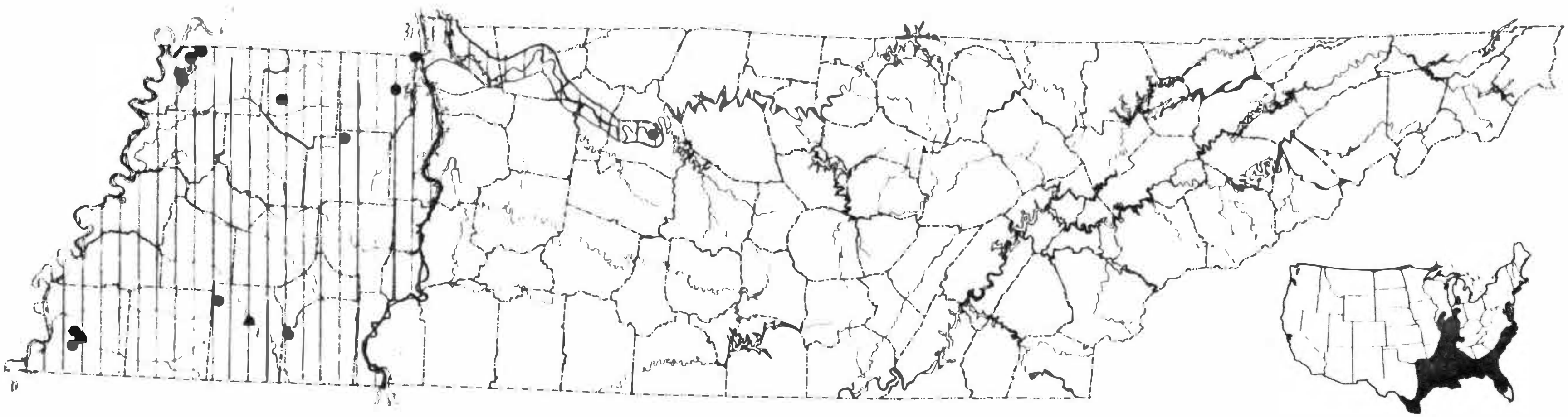

Figure 80. Distribution of <u>Siren intermedia.</u> Vertical hatching indicates range. Solid circles denote localities based on museum specimens. Solid triangle denotes literature record believed valid. Smaller map depicts range in conterminous United States (Conant, 1975; Martof, 1973; Martof, Palmer, Bailey, and Harrison, 1980).

C. Erroneous Species Report

Questionable and erroneous records of species presently known from Tennessee and those considered taxonomically invalid are discussed in the preceeding accounts. The following comments are limited to reports of species that have probably never occurred in the state.

Rhoads (1895) noted the southern toad, Bufo lentiginosus, from Davidson and Hamilton counties. He commented on the similarity of specimens from Tennessee and those from the more southern Gulf states. Bufo lentiginosus is a junior synonym of B. terrestris, and in all likelihood, Rhoads was referring to what is now known as B. terrestris. Based on his experiences, Gentry (1955-1956) concluded that B. terrestris does not occur in Tennessee, and Blem (1979) illustrated the species as occurring only as far north as northern Mississippi. During this study, no specimens of B. terrestris from Tennessee were observed.

Wright and Wright (1949) provided a distribution map that showed Hyla squirella ranging as far north as the mid-Mississippi and lower Ohio River valleys in west Tennessee, west Kentucky, and southern Illinois. Following Wright and Wright, Gentry (1955-1956) and Gentry, Sinclair, Hon, and Ferguson (1965) included H. squirella as a part of the state's herpetofauna, but noted that they were unaware of valid records for Tennessee. Wright and Wright (1949) probably based their inclusion of west Tennessee on literature references and museum specimens reported from southern Illinois and Kentucky. Smith (1961) reviewed these reports and examined specimens from Kentucky. He found the specimens were actually Pseudacris triseriata and concluded that

H. squirella is not present in Illinois and Kentucky. The most recent account of the range of H. squirella excludes Tennessee (Martof, 1975c).

Bishop's (1943) distribution map for Necturus beyeri included Tennessee River drainages in extreme eastern Tennessee. Gentry (1955-1956) could not verify its presence, but listed N. beyeri from east Tennessee. Hecht (1958), Gentry, Sinclair, Hon, and Ferguson (1965), and Conant (1975) did not consider N. beyeri to occur in Tennessee. During this study, all specimens examined from Tennessee River drainages in east Tennessee were assignable to N. maculosus. Mount (1975) summarized the confusing and often conflicting nature of past taxonomic treatments for the genus. If the taxonomy adopted by Mount is accepted, then populations of Necturus in the Conasauga River System (Mobile Drainage) of southeastern Tennessee might prove to be N. beyeri. However, no specimens are available from this area.

Several authors (Rhoads, 1895; Bishop, 1943; Maldonado-Koerdell and Firschein, 1947; Gentry, 1955-1956; Gentry, Sinclair, Hon, and Ferguson, 1965) reported Ambystoma jeffersonianum from Tennessee. Most recent accounts (Uzzell, 1967; Conant, 1975) do not consider the species to occur in the state. No specimens from Tennessee were collected or examined from museum collections, and the older reports are considered erroneous. Rhoads (1895) gave an account of 13 individuals collected from Roan Mountain in Carter County. He found specimens very numerous under logs at elevations ranging from 1220 to 1585 m. He noted that A. jeffersonianum seemed to replace Plethodon glutinosus at higher elevations and described A. jeffersonianum as "bluish black above, dusky below, with a brownish yellow chin and throat." He further stated "there is no spotting, but a close examination shows a light blue pitting along the sides and tail and over the chest and abdomen." Rhoads' specimens were not available for verification. However, his ecological observations and description of specimens indicate he probably collected Plethodon jordani. Maldonado-Koerdell and Firschein (1947) reported two specimens (KU Nos. 2642-2643) taken in 1926 from Decatur County. Currently, KU No. 2643 is identified as A. texanum and KU No. 2642 has apparently been lost. There are also three specimens of A. opacum (KU Nos. 2639-2641) taken from the same locality on the same date. Considering these facts, the report for Decatur County is considered erroneous. Gentry (1955-1956) and Gentry, Sinclair, Hon, and Ferguson (1965) record A. jeffersonianum from Hardeman County. This appears to be based on one larval specimen (Gentry, 1955-1956) that is now unavailable for verification. Norton and Harvey (1975) acknowledge Gentry's record, but were unable to collect the species in Hardeman County. They somewhat subtly agree with Bishop (1943) that records south of the general range of the species are possibly A. texanum or some other species.

CHAPTER IV

ORIGINS AND PAST DISPERSAL PATTERNS OF MODERN AMPHIBIAN GROUPS

Geologic, climatic, and evolutionary events of the past have played a basic role in determining Tennessee's current amphibian fauna and their distribution patterns. Insights into the origin, dispersal, and evolution of modern amphibian faunas have come from paleontological, morphological, biochemical, behavioral, and geographic distribution studies. Examples of such studies include Estes (1970), Hecht (1963), Wake (1966), Lynch (1973), Highton and Larson (1979), Guttman (1973), Rabb (1973), Savage (1973), and Cracraft (1974). Savage (1973) and Cracraft (1974) emphasized the role of continental drift in determining distributions. A review of these studies and others revealed a significant degree of disagreement in regard to the classification of fossil forms, specific dates of origin of several modern families, and the make-up of taxonomic lineages. Despite the disagreement over details, there are three generally accepted premises. These are: (1) most modern families of amphibians can be traced back to the Mesozoic or early Tertiary (Hecht, 1963; Estes, 1970), (2) most modern North American genera and species groups were present at the beginning of the Pleistocene (Porter, 1972; Hecht, 1963), and (3) Pleistocene and post-Pleistocene climatic and vegetation shifts were major factors in determining current distributions (Porter, 1972; Blair, 1958, 1965; Smith, 1957). Utilizing these three premises as organizational concepts and incorporating information from published studies, a historical account of the amphibian fauna of Tennessee is provided in the following subchapters. Because of insufficient fossil data for Tennessee (Corgan, 1976) and the general lack of knowledge regarding the origin, dispersal, and evolution of amphibians, the following accounts should be viewed as speculative.

A. Mesozoic Events

Continental drift was an important factor influencing the early evolution and dispersal of Mesozoic ancestors of modern amphibian families (Cracraft, 1974; Savage, 1973). During the early Triassic, lands now included in Tennessee were part of a large continent called Pangaea. During the Triassic and Jurassic, the forces of continental drift separated Pangaea into a northern land mass called Laurasia and a southern land mass called Gondwanaland. These two newly formed continents were separated by the tropical Tethys Sea. The present-day lands of North America, Eurasia, and Greenland made up Laurasia. Gondwanaland included what is now South America, Africa, India, Australia, Antarctica, and New Zealand. By late Cretaceous both Laurasia and Gondwanaland had separated into several of the major land masses of today (Dietz and Holden, 1970).

According to Miller (1974), evidence indicates that at the beginning of the Mesozoic, lands now a part of Tennessee were primarily above sea level and subjected to the forces of landscape evolution. Miller stated that the early Mesozoic topography of east Tennessee included highlands and folded and tilted strata created by Permian orogeny. To the west of these, stretching from the present-day Sequatchie Valley to the Mississippi River, was a vast level coastal plain. Erosional cycles during the Mesozoic began the development of the modern physiographic features of Tennessee. Erosion of the eastern highland areas initiated the development of the Blue Ridge Mountains and the Appalachian Ridge and Valley. The wearing down of the extensive coastal plain began the formation of the Cumberland Plateau, Cumberland Mountains, and Eastern and Western Highland rims. Miller also postulates that headwater erosion of a river flowing westward across Tennessee's Mesozoic coastal plain eventually cut through what is now Walden Ridge, captured the drainage systems of east Tennessee, and began the development of a large gorge. During late Cretaceous, west Tennessee was inundated by a shallow sea called the Mississippi Embayment. This period of submergence lasted into Tertiary times.

Information on the Mesozoic environments of Tennessee is sketchy. Axelrod (1960) believed that a wide tropical belt covered most of Laurasia and Gondwanaland with temperate environments limited to their northern and southern tips, respectively. Savage (1973) illustrated the distribution of these environments in a series of figures that depicted the tropical belt narrowing in width as time passed during the Mesozoic. Thus, Tennessee, as part of Laurasia, probably possessed a tropical climate and vegetation during the Mesozoic with the possibility of temperate climates encroaching from the north during late Mesozoic times.

As stated earlier, the origin and early dispersal of most modern amphibian families can be traced back to the Mesozoic. Regarding the modern frog families currently present in Tennessee, Savage (1973) considers Microhylidae, Bufonidae, Hylidae, and Ranidae to be tropical Gondwanaland faunal elements and Pelobatidae a temperate Laurasian element. Savage contends that Laurasian frog elements have had a distributional history similar to salamanders. Cracraft (1974) lists all modern salamander families as originating from Laurasian faunas. Estes (1970) notes that fossil evidence for the families Ambystomatidae, Amphiumidae, Plethodontidae, and Sirenidae is only known from North America. He considered Eurasia as the dispersal center for Salamandridae and that members of this family did not occur in North America until the Teritary. Wake (1966) considers Plethodontidae to have originated during the Mesozoic in warm temperate climates of the southern Appalachians. In summary, environments of Tennessee during the Mesozoic were primarily tropical. Faunal elements possibly included ancestral forms of the families Pelobatidae, Ambystomatidae, Amphiumidae, Plethodontidae, Sirenidae, Necturidae, and Cryptobranchidae. Estes (1970) speculates that during the Mesozoic and early Tertiary, families presently associated with temperate environments, such as Pelobatidae, Plethodontidae, and Cryptobranchidae, may have been distributed north of Tennessee in the temperate climates of northern Laurasia.

B. Cenozoic, Tertiary Events

Continental drift continued during the Tertiary with western Eurasia and eastern North America separating sometime in early Tertiary (Dietz and Holden, 1970). Two other Tertiary land-related changes important in determining the amphibian fauna of North America were the formation of land bridges between western North America and eastern Asia and southern North America and northern South America.

In Tennessee, the Mississippi Embayment lasted until at least the end of the Eocene and covered all of west Tennessee and parts of western middle Tennessee (Miller, 1974). Luther (1977) described how the Mississippi River formed as this sea retreated to the south. He believed the Mississippi River formed on a flat area and began flood-plain development immediately. Elsewhere in Tennessee, the erosional forces begun during the Mesozoic continued to shape the physiographic and topographic features of the state (Miller, 1974).

During the Tertiary, Axelrod (1960) depicts North America as possessing an Arcto-Tertiary Geoflora in the north and a Neotropical-Tertiary Geoflora in the south. He also describes the development of an arid flora, the Madro-Tertiary Geoflora, in southwestern North America. Savage (1973) and Wake (1966) reviewed the concepts of Axelrod in terms of their importance in amphibian zoogeography and discussed several noteworthy worldwide climatic changes. Those involving North America included (1) a reduction of tropical environments and concurrent expansion of temperate environments to the south and (2) the expansion of semi-arid environments in southwestern North America.

New additions to the amphibian fauna of North America during the Tertiary were the families Microhylidae, Bufonidae, Hylidae, Ranidae, and Salamandridae. Savage (1973) believed that members of the tropical families Microhylidae, Bufonidae, and Hylidae entered North America from South America during the Paleocene. This faunal migration was accomplished by way of a Central American land bridge. Also, Savage proposed that the family Ranidae originated in Africa, spread into Asia, and adapted to temperate environments, and during the Eocene, migrated onto the North American continent across the Bering Land Bridge. Estes (1970) suggested that the salamander family Salamandridae also reached North America during the Oligocene by crossing the Bering Land Bridge.

Thus, in early Tertiary, at least by the Oligocene, all modern amphibian families now known in Tennessee were present in North America. A list of these families, their centers of origin, and dispersal routes are provided in Table 5. As noted for the Mesozoic fauna, amphibian families presently associated with temperate climates may have been distributed north of Tennessee during the early Tertiary. Later, as the Arcto-Tertiary Geoflora moved southward, these temperate forms may have migrated southward into areas now a part of Tennessee.

By the end of the Tertiary, most modern North American amphibian genera and species groups were established (Blair, 1965). Major species groups of the genus Bufo are thought to have resulted from late Tertiary or early Pleistocene speciation (Blair, 1972; Savage 1973). Savage (1973) believes the Bufo americanus group, three Hyla lineages, Acris, and Pseudacris became associated with the Arcto-Tertiary Forest in North America. Zweifel (1956) proposed that the differentiation of Scaphiopus occurred in late Tertiary; however, Blair (1965) considered the speciation of Scaphiopus a Pleistocene event. Sessions and Wiley (1985) speculated that Necturus maculosus is a relatively old species that dispersed southwestward from the southern Atlantic Coastal Plain. They speculate that its current distribution is the result of a recent rapid dispersal up the Mississippi River Drainage. Blair (1965) and

Table 5. Mesozoic and early Tertiary origins and dispersals of modern amphibian families of Tennessee.

Family	Geographic Source	North American Invasion Route	Time of Invasion
Bufonidae[a]	Tropical Gondwanaland (South America)	Central American Land Bridge	Paleocene
Hylidae[a]	Tropical Gondwanaland (South America)	Central American Land Bridge	Paleocene
Microhylidae[a]	Tropical Gondwanaland (South America)	Central American Land Bridge	Paleocene
Pelobatidae[a]	Temperate Laurasia (North America)		
Ranidae[a]	Tropical Gondwanaland (Africa)	Bering Land Bridge	Eocene
Ambystomatidae[b,c]	Laurasia (North America)		
Amphiumidae[b,c]	Laurasia (North America)		
Cryptobranchidae[b]	Laurasia		
Necturidae[b]	Laurasia		
Plethodontidae[b,c]	Temperate Laurasia (North America)		
Salamandridae[b,c]	Temperate Laurasia (Eurasia)	Bering Land Bridge	Oligocene
Sirenidae[b,c]	Laurasia (North America)		

[a]Savage (1973)

[b]Cracraft (1974)

[c]Estes (1970)

Wake (1966) reviewed how the invasion of an arid savannah-like geoflora into central North America divided the ranges of amphibian species groups adapted to the Arcto-Tertiary Geoflora. Wake (1966) believed that during the Miocene, this invasion led to the formation of present-day disjunct east-west species groups in the genera Plethodon and Aneides. Based on genetic and albumin immunological distances, Highton and Larson (1979) estimated the split between east and west Plethodon groups to have occurred in late Eocene. They concluded that all modern Plethodon species were present by the end of the Pliocene and that a late Pliocene speciation explosion resulted in the evolution of P. glutinosus, P. jordani, P. yonaholossee, P. cinereus, P. richmondi, and P. serratus in eastern North America. Wake (1966) expanded on the concepts of Dunn (1926) and described how the southern Appalachian Highlands served as the center of origin and dispersal for other modern plethodontid genera during the Tertiary. Several groups, such as Eurycea and Desmognathus, expanded their ranges into the Interior Highlands and other areas outside the Appalachian Highlands. Tihen (1958) proposed that ambystomatid ancestors once occupied a forested area across northern North America. He believed that during the Miocene this ancestral stock was split into eastern and western stocks. Although Tihen does not relate this to changing geofloras, his scheme parallels the early split described for the genera Plethodon and Aneides. Tihen places the center of dispersal for the eastern stock in the Great Lakes Region. From this area, migration has primarily been southward. Tihen suggests that A. opacum and A. talpoideum were derived from an A. maculatum stock in the southeastern United States, *A. texanum* from an *opacum-maculatum* precursor in the Gulf region of the southeastern United States, and *A. tigrinum* from ancestors in southwestern North America. The present occurrence of *A. tigrinum* in eastern North America was the result of northward migration. Tihen concludes that by early Pleistocene all *Ambystoma* species were developed and their distribution patterns established.

Due to the lack of fossil evidence from Tennessee, the following summary of Tertiary environments and amphibian faunas must be considered tentative. The geographic location of the state places it near the boundary between the expanding Arcto-Tertiary Geoflora and the receding Neotropical-Tertiary Geoflora. Elements of both probably occurred in Tennessee with temperate environments of the Arcto-Tertiary vegetation predominating in the eastern highlands and tropical environments in the lowlands near the Mississippi Embayment region. By the end of the Tertiary, major physiographic and topographic features of the state were becoming distinct. Most studies indicate that nearly all modern genera and species groups of amphibians were present in Tennessee by the end of the Tertiary. Their Tertiary distributions in Tennessee remain undocumented by fossil evidence; however, they possibly exhibited distribution patterns somewhat similar to modern forms.

C. Cenozoic, Quaternary Events

The relatively stable conditions during the Tertiary gave way to the dramatic climate fluctuations of the Pleistocene. The Pleistocene in North America was characterized by four extensive glacial periods with intervening interglacial periods (Flint, 1971). From oldest to youngest these included the Nebraskan glacial, Aftonian interglacial, Kansan glacial, Yarmouth interglacial, Illinoian glacial, Sangamon interglacial, and Wisconsinan glacial periods. Even in unglaciated areas, these warm-cold cycles and associated shifts in vegetation were the primary events that influenced distributions of amphibians during the Pleistocene (Blair, 1958, 1965; Wake, 1966; Porter, 1972). Post-Pleistocene climatic changes have also influenced the distributions of modern amphibian species (Smith, 1957).

In Tennessee, in addition to warm-cool climatic shifts, several other events modified the landscape. Miller (1974) and Corgan (1976) described how thick loess beds were deposited in west Tennessee. The presence of remnants of patterned ground indicates severe frost action in east Tennessee (Corgan, 1976). According to Miller (1974), modification of individual streams and entire drainage systems was common. Deep gorges buried under recently deposited alluvium indicate steeper stream gradients during periods of glaciation and lower sea levels. Corgan (1976) cited evidence of massive ice flows and jams on the Tennessee River. Miller (1974) stated that during full glacial periods, streams were subjected to high runoff, damming, and diversion.

Evidence from pollen studies from strata of Wisconsinan age indicates major vegetative changes occurred in response to the advance and retreat of glacial ice. Delcourt and Delcourt (1981) reviewed existing data on Pleistocene and Holocene fossil pollen sites and provided vegetation maps for eastern North America from early Wisconsinan times to 200 years B.P. Their series of maps clearly illustrate the north-south shifting of vegetation types associated with the advance and retreat of Wisconsinan glaciers. In a later study, Delcourt and Delcourt (1984) state that the patterns described for the Wisconsinan glacial age are probably typical of events during earlier Pleistocene times. Based on their 1981 series of maps, it is possible to summarize the major vegetation shifts that occurred during the late Pleistocene and Holocene in Tennessee. During early Wisconsinan times, approximately 40,000 years B.P., the northeastern half of Tennessee was covered by a Jack Pine-Spruce Forest that extended northward almost to the Great Lakes Region. The southwestern half of the state possessed an Oak-Hickory Southern Pine Forest that in total covered most of the southeastern United States. Between these two forests was a narrow belt of Mixed Conifer-Northern Hardwood Forest that extended from North Carolina, across Tennessee, and into western Kentucky. A Mixed Hardwood Forest occurred along the eastern bluffs of the Mississippi River and possibly entered extreme southwestern Tennessee. The vegetation of the Mississippi Alluvial Valley was probably a southern Cypress-Gum Forest. By 25,000 years B.P., a warming trend occurred that allowed a northward migration of the Mixed Conifer-Northern Hardwoods on the Atlantic Coast. However, the major vegetation change in the southeastern United States and Tennessee was the development of an Oak-Hickory Forest that displaced much of the Oak-Hickory Southern Pine Forest. The late Wisconsinan Glacial Maximum occurred approximately 18,000 years B.P. During this time, major forest types were shifted southward. Tennessee and most of the north-eastern United States were covered by a Jack Pine-Spruce Forest. Tundra vegetation occurred in a belt along the southern edge of the ice sheet, and evidence indicates tundra-like habitats may have occurred at high elevations as far south as the Great Smoky Mountains. Mixed Hardwood Forests occurred in a narrow north-south belt along the eastern bluffs of the Mississippi River, and an ecotype of white spruce extended along the Mississippi River floodplain. A warming trend was followed by a northward retreat of glacial ice. By 14,000 years B.P., major vegetation shifts included an eastward migration of Spruce-Jack Pine Forests into Kentucky and middle Tennessee and a northward extension of the Mixed Conifer-Northern Hardwood Forest into southern Tennessee. Delcourt and Delcourt (1981) place the end of the Pleistocene at approximately 12,500 years B.P.

The warming trend continued into the Holocene and by 10,000 years B.P., the Spruce Forest of the Mississippi River floodplain was replaced by Cypress-Gum Forest. The Mixed Hardwood Forest expanded eastward from the Mississippi River Blufflands to cover most of Tennessee and much of east-central North America. Spruce forests were shifted to the north of Tennessee with relict populations surviving at higher elevations in the Blue Ridge Mountains. Major changes occurred between 8,000 and 4,000 years B.P. This period, often called the Hypsithermal Interval, is characterized by an eastward extension of prairie and savannah environments and major vegetation changes in the southeastern United States. Approximately 5,000 years B.P., Spruce-Fir remained isolated at high elevations in the Blue Ridge Mountains. However, the Oak-Chestnut Forest became dominant in the southern Appalachian Mountains. The Mixed Hardwood Forest was greatly reduced and apparently restricted to the Appalachian Plateaus Region and the

Mississippi River Blufflands. An Oak-Hickory Forest covered most of Interior Low Plateaus area of Tennessee and extended in belt as far north as central Michigan. A Southern Pine Forest occupied most of the Atlantic and Gulf Coastal Plains and extended as far north as west Tennessee. A Cypress-Gum Forest continued to occupy the Mississippi River Floodplain. By presettlement times, about 200 years B.P., a slight cooling trend with increased precipitation occurred. Prairie environments retreated to the west, leaving pockets of hill prairie in Illinois and Ohio; however, the basic distribution patterns of forests in the southeast remained stable.

Relating events of the Quaternary to modern amphibian distributions is difficult. Species groups and many extant species were present at the beginning of the Quaternary and have survived at least four glacial-interglacial cycles. The history of the first three cycles is virtually unknown. However, the latest phenomena that dramatically influenced amphibian distributions occurred in the relatively well-documented Wisconsinan age and during the Holocene. For this reason, most studies of modern distribution patterns have relied heavily on the history of the late Pleistocene and Holocene.

Blair (1958, 1965) regarded most salamander groups as adapted to cool, mesic environments with their center of dispersal in the Arcto-Tertiary Forest. In contrast, he considered most frog groups to be warmth-adapted with a greater tolerance for xeric conditions. He concluded that, as a general rule, the cooler climates of Pleistocene glacial advances pushed the ranges of salamander groups southward and fragmented the ranges of southerly distributed frog groups into southeastern and southwestern refugia. Blair also proposed that migrations and fragmentation of ranges led to extensive Pleistocene speciation in North America. Three salamander families do not conform to Blair's generalizations. Several members of the family Ambystomatidae (Tihen, 1958) and all members of the families Sirenidae and Amphiumidae (Porter, 1972) probably had their most recent centers of dispersal in the warm environments of southern North America. Also, Blair's ideas regarding Pleistocene speciation have been questioned, especially for members of the family Plethodontidae (Wake, 1966; Highton and Larson, 1979). Regardless of these exceptions, Blair's work and Porter's (1972) similar discussion of the history of amphibians during the Pleistocene and Holocene appear valid and useful in a discussion of present-day distribution patterns. The following accounts are organized by family and briefly sketch the probable formation of present distribution patterns in Tennessee.

Bufonidae. Both Bufo americanus and B. woodhousei are considered as adapted to temperate climates. The modern distribution of B. americanus extends farther north than B. woodhousei (Conant, 1975) and B. americanus tends to breed at cooler temperatures (Blair, 1972). However, the ranges of both species were displaced southward during full glacial times, with B. woodhousei possibly being pushed farther south into a refugium in the lower southeastern United States (Blair, 1958, 1965; Porter, 1972). Although scant and inconclusive, the fossil evidence seems to indicate that while B. americanus probably survived in the Jack Pine-Spruce forests that covered much of Tennessee during the Wisconsinan glacial maximum (Delcourt and Delcourt, 1981), the range of *B. woodhousei* was pushed farther south. Fossils of *B. americanus* are reported from late Pleistocene deposits in Overton (Guilday, Hamilton, and McCrady, 1969) and Sullivan (Guilday, Hamilton, Anderson, and Parmalee, 1978) counties. Remains from the Sullivan County site were found at levels dating from about 19,000 years B.P. to historical times. Fossils of *B. woodhousei* were only found in Holocene deposits approximately 10,000 years old and younger. Thus, the modern statewide distribution of *B. woodhousei* is possibly the result of a northward migration that followed the northward advance of southern vegetation types during the Holocene.

Hylidae. The hylid fauna of Tennessee includes nine species. Although most have their Tertiary origins from southern tropical stocks, a few have become adapted to northern temperate forests (Savage, 1973). Blair (1958, 1965) and Porter (1972) considered *Acris crepitans, A. gryllus, Hyla avivoca, H. cinerea, H. gratiosa,* and *Pseudacris triseriata* to be southern forms whose present distributions are the result of Holocene northward dispersal from Wisconsinan glacial stage refugia in the southwestern and southeastern United States. According to Blair (1965) advance of Wisconsinan glaciers caused a southern shift and east-west split of *Acris* populations into refugia in the southwestern and extreme southeastern United States. Subsequent northward Holocene dispersal of *A. crepitans* from the southwestern refugium and *A. gryllus* from southeastern refugium resulted in their present distribution patterns. Presently, the range of *A. gryllus* is primarily restricted to the Atlantic and Gulf Coastal Plains and reaches its northern limit on the Gulf Coastal Plain in southwestern Tennessee.

Acris crepitans now occupies much of eastern North America, but is apparently absent from the central Appalachian Mountains, including a small section of northeastern Tennessee. Other southern hylids with a similar history include H. avivoca, H. gratiosa, and possibly H. cinerea. All three are thought to have reached their present distributional limits by northward dispersal from a southeastern Wisconsinan age refugium. In Tennessee, H. avivoca and H. cinerea are found on the Coastal Plain of west Tennessee. Hyla avivoca has extended its range up the Cumberland River Valley. The range of H. gratiosa in Tennessee includes the southern half of the Cumberland Plateau, the Coastal Plain of southwestern Tennessee and apparently disjunct populations in north-central Tennessee and south-central Kentucky. These disjunct populations of H. gratiosa and a similar disjunct population of H. cinerea in western Kentucky may be attributed to Holocene northward dispersals during a warm, Climatic Optimum period. A subsequent shift to drier climates caused an overall southerly retreat that left relictual populations in northern areas (Smith, 1957). Pseudacris triseriata appears to have dispersed northward from a southwestern glacial refugium and now occurs across most of central North America (Blair, 1965) and occurs statewide in Tennessee. Blair also believed the distribution of the cryptic species pair, H. chrysoscelis and H. versicolor, indicated Pleistocene speciation and east-west fragmentation of ranges. Ralin, Romano, and Kilpatrick (1983) determined that H. versicolor arose as an autoploid from H. chrysoscelis about 375,000 years B.P. near the close of the Illinoian glacial age. However, because the modern distributions of both species are poorly documented, including their ranges in Tennessee, it is difficult to speculate on their Quaternary center of origin and dispersal. *Hyla crucifer* is a widespread species that has undergone little or no differentiation during the Quaternary (Blair, 1965). Presently, the species ranges northward as far as east-central Canada and, with the exception of peninsular Florida, occurs throughout the eastern United States. Although Wisconsinan glacial advances resulted in a southward shift in its range, *H. crucifer* probably survived in Tennessee because its range was not shifted south of the state. Blair (1965) considered *Pseudacris brachyphona* as a member of the *P. triseriata* complex with its origin due to Pleistocene speciation in the Appalachian Highlands. The range of the species is centered on the Appalachian Plateau, including the Cumberland Plateau in Tennessee. Isolated populations are known from the Blue Ridge Mountains and Interior Low Plateaus of central Kentucky (Hoffman, 1980). These disjuncts probably indicate a late Quaternary range expansion and subsequent retreat. There are only two reported sites in Tennessee with Pleistocene and Holocene hylid fossils. Guilday, Hamilton, and McCrady (1969) reported *Hyla* sp. from Overton County and Guilday, Hamilton, Anderson, and Parmalee (1978) recorded *Hyla* sp. from Sullivan County.

Microhylidae. Like several other anurans of southern affinity, the range of *Gastrophryne carolinensis* was probably compressed southward into a southeastern refugium during glacial advances. Holocene warming trends allowed the species to disperse northward and occupy the southern half of North America (Blair, 1958, 1965).

Gastrophryne carolinensis has apparently not been able to invade the Blue Ridge Mountains.

Pelobatidae. Scaphiopus holbrooki is adapted to warm, xeric conditions (Blair, 1965). Blair lists S. holbrooki as another form that was forced southward and isolated into southwestern and southeastern refugia. Northward dispersal occurred during the Holocene. Except for a few isolated populations, the species has not successfully invaded the southern Blue Ridge Mountains and Piedmont. Guilday, Hamilton, and McCrady (1969) reported a fossil Scaphiopus sp. from late Pleistocene deposits in Overton County.

Ranidae. Six ranid species occur in Tennessee. Rana areolata was probably restricted to refugia in the southeastern and southwestern United States during maximum glacial advances. The northward advance of warm climates and southern vegetation types during the Holocene has allowed the species to disperse across the Coastal Plain in the southeastern United States and up the Mississippi Valley as far north as central Illinois (Blair, 1958, 1965). Information on the possible recent centers of dispersal for the presently wide ranging R. catesbeiana, R. clamitans, and R. palustris is scant. Blair (1958) thought all three species were probably continuously distributed across the Coastal Plain during periods of maximum glaciation. If this is true, ranges of these species during the Wisconsinan possibly included most of Tennessee or at least the Coastal Plain areas in the western third of the state. Whatever their distribution during the Wisconsinan, all three presently occur statewide in Tennessee. However, the range of R. palustris differs from the other two species in that it is absent from a large part of the southeastern Coastal Plain. Either the species never occurred in this area or there has been a northward range shift in the southeast during the Holocene. Blair (1958, 1965), Smith (1957), and Porter (1972) believe that the southern range boundaries of both R. palustris and R. sylvatica have retreated northward due to post-Pleistocene events. Rana sylvatica occurs further north than any other North American amphibian or reptile (Conant, 1975). Like Pseudacris brachyphona, it appears to be adapted to cool, temperate environments. It probably persisted in Tennessee during glacial maxima (Martof and Humphries, 1959; Blair, 1965), and is presently limited to eastern and north-central Tennessee. Pace (1974) tentatively described the eastern North American coast as the geographic origin of R. utricularia. Dispersal has been south and west, skirting the Piedmont and Blue Ridge Mountains. Guilday, Hamilton, Anderson, and Parmalee (1978) reported fossil remains of R. sylvatica from Wisconsinan to recent age deposits in Sullivan County. They also reported R. catesbeiana from deposits about 10,000 years old.

Ambystomatidae. As discussed previously, all modern species of Ambystoma are thought to have been present and their overall distribution patterns established by early Pleistocene (Tihen, 1958). The extent of southward range shifts during glacial advances is unknown. The presence in Sullivan County of fossil A. maculatum in deposits ranging in age from about 19,000 to 500 years B.P. (Guilday, Hamilton, Anderson, and Parmalee, 1978) indicates the range of the species was not shifted south of Tennessee during the Wisconsinan period. Guilday, Hamilton, Anderson, and Parmalee also reported A. opacum from approximately 10,000 years old and younger. Although inconclusive, these data may indicate the presence of _A_. _maculatum_ and absence of _A_. _opacum_ in east Tennessee during maximum Wisconsinan glacial conditions. This is consistent with the idea that _A_. _opacum_, _A_. _talpoideum_, _A_. _texanum_, and _A_. _tigrinum_ are of southern origin (Tihen, 1958) and were probably forced to retreat farther south during full glacial conditions. With the return of warmer conditions and the retreat of glacial ice, all _Ambystoma_ species dispersed northward. The modern distributions of _A_. _maculatum_ and _A_. _opacum_ are widespread across eastern North America and both occur statewide in Tennessee. The range of _A_. _talpoideum_ principally includes the southeastern Atlantic and Gulf Coastal Plains. Disjunct populations are known north of the main body of its range. Portions of two disjunct populations occur in Tennessee on the Cumberland Plateau and in the southeastern Blue Ridge Mountains. Smith (1957) considers these disjunct populations as Holocene relicts that were able to survive in northern refugia after the main species range was shifted southward during a xerothermic period. The modern ranges of _A_. _texanum_ and _A_. _tigrinum_ in Tennessee are probably the result of northward and eastward Holocene dispersal from southwestern North America. _Ambystoma texanum_ presently occupies the western half of the state, while _A_. _tigrinum_ occurs as far east as the Blue Ridge Mountains.

Amphiumidae. Blair (1958) considered the genus _Amphiuma_ another example of a southern adapted form that was forced into southern refugia during Pleistocene glacial advances. _Amphiuma tridactylium_ presently occurs in sluggish streams, swamps, and bayous in southern floodplain forests. Delcourt and Delcourt (1981) showed these habitats as occurring south of Tennessee during the Wisconsinan glacial maximum. Also, with the lowering of sea level during Wisconsinan times, stream gradients were increased, resulting in a decrease of sluggish aquatic habitats in the state. Thus, it is likely that the range of A. tridactylium was restricted to areas south of Tennessee during the last glacial episode and has subsequently expanded northward during the Holocene. In Tennessee, A. tridactylium is currently limited to the Coastal Plain.

Cryptobranchidae. Cryptobranchus alleganiensis is totally aquatic in habits and, like several other aquatic vertebrates during the Tertiary, its distribution was linked with the Mississippi River Drainage (Estes, 1970). Firschein (1951) speculated that during late Tertiary the cryptobranchids were widespread in North America. With the advance of Pleistocene glaciers, they were forced to retreat into the unglaciated Ozark and Appalachian Highlands. Firschein thinks the dispersal into the Appalachian Highlands occurred in relatively recent times with the Ohio River serving as the main corridor for dispersal. He considered headwater stream capture as the main means of dispersal into the upper Tennessee River Drainage and noted an absence of the species in the lower Tennessee River Drainage. Because he thought the species was absent from many Appalachian streams, Firschein did not consider the Appalachian Highlands as the center of dispersal for the genus. Recently reported fossil evidence and additional distribution data gathered during this study indicate that Firschein's Pleistocene account of the species in the Appalachian Highlands needs some modification. Newly acquired distribution data shows that C. alleganiensis is much more common in Appalachian streams than previously thought and is now known from several localities in the lower Tennessee River Drainage. Also, *Cryptobranchus* is an inhabitant of medium to large-sized streams; therefore, its distribution was less likely to be modified by headwater stream capture. Thus, Firschein's argument for stream capture as the primary method of dispersal into the Tennessee River Drainage appears invalid. Main channel dispersal seems to be a more plausible means of spread into both the Cumberland and Tennessee River drainages. Also, fossil evidence from Wisconsinan age deposits (Guilday, Hamilton, Anderson, and Parmalee, 1978) indicates the species was in the upper Tennessee River Drainage by at least 19,000 years B.P. Furthermore, it is logical to consider the Appalachian Highlands as the center of dispersal of the species. As previously mentioned, the species is not sparsely distributed, but is widely distributed in Appalachian streams. In addition, the presence of disjunct populations in a small area of the Ozark Highlands lends some credence to an eastern center of dispersal. This distribution pattern is also known for two genera of salamanders (Wake, 1966) and several species of fish (Starnes and Etnier, 1985). Wake (1966) described a Miocene Appalachian-Ozarkian corridor that allowed westward dispersal of *Plethodon* and *Eurycea* into the Ozark Highlands. Starnes and Etnier (1985) think that a pre-Wisconsinan corridor existed in the southern Illinois area that allowed east/west dispersal of ancestral members of the darter subgenera *Ozarka* and *Litocara.*

Necturidae. According to Sessions and Wiley (1985), the center of dispersal for the genus *Necturus* is the Atlantic Coastal Plain. Their karyological data supports the view that dispersal has been south and then north up the Mississippi River Drainage. They view the present-day distribution of N. maculosus as the result of a recent and explosive northward dispersal up the Mississippi River Drainage. Guilday, Hamilton, Anderson, and Parmalee (1978) reported fossil N. maculosus in Sullivan County from strata estimated to range in age from late Wisconsinan or early Holocene to recent historical times. Session and Wiley's (1985) proposed dispersal route and the presence of N. maculosus in the upper Tennessee River Drainage by late Wisconsinan times suggest a widespread distribution for the species in streams of Tennessee, at least by late Pleistocene. The effects on Necturus of glacial advances and associated changes in stream and drainage features in unglaciated regions is unknown. However, even if N. maculosus was forced to retreat to more southern or lowland waters during glacial maximia, it has subsequently successfully re-invaded northern and upland headwater areas during the Holocene.

Plethodontidae. Authorities agree that the Appalachian Highlands were the center of origin and dispersal for the plethodontid salamanders (Dunn, 1926; Hairston, 1949; Wake, 1966; Highton, 1971). The most primitative forms still occur in Appalachia and occupy the ancestral habitat, the mountain brook (Hairston, 1949; Wake, 1966). According to Hairston (1949), only those forms that were able to adapt to more terrestrial conditions were able to disperse great distances from the Appalachian Highlands. He considered it important to note that all highly aquatic species are still restricted to eastern North America. As previously discussed in regard to Tertiary events, Highton and Larson (1979) considered that most modern species of Plethodon were present by early Pleistocene and several species ranged widely across North America. Wake (1966) proposed a similar history for members of the genus Aneides. The dates of origin and past dispersal patterns of other plethodontid genera are not as well documented. However, regardless of the levels of taxonomic differentiation at the onset of the Pleistocene, it is evident that the majority of plethodontid species in Tennessee have remained primarily restricted to the ancestral Appalachian Highlands which in Tennessee includes the Cumberland Plateau, Cumberland Mountains, Sequatchie Valley, Appalachian Ridge and Valley, and Blue Ridge Mountains physiographic regions. Twenty-two species out of a total of 31 plethodontid species that occur in Tennessee are principally restricted to these physiographic regions. Of the remaining nine, three (Eurycea lucifuga, Hemidactylium scutatum, Pseudotriton montanus) occur in both the Appalachian Highlands and Interior Low Plateaus regions and six (Desmognathus fuscus, Eurycea bislineata, E. longicauda, Plethodon dorsalis, P. glutinosus, Pseudotriton ruber) have ranges that extend onto the Coastal Plain of western Tennessee. As indicated by the total number of species, the family Plethodontidae is the most diverse group of amphibians in the state. Like other modern amphibian groups, its Quaternary history is virtually unknown in the fossil record, and speculation as to origins and dispersal patterns are based on studies of current distribution patterns and ecological and taxonomic comparisons within various species groups. Many current distribution patterns in Tennessee indicate range expansions and subsequent restrictions during the Quaternary.

Two species and one subspecies have what appear to be disjunct populations on the Coastal Plain of west Tennessee. Desmognathus fuscus has been found on the Mississippi River Bluffs near Ripley, Tennessee, and Plethodon dorsalis and Eurycea l. longicauda on the Mississippi River Bluffs east of Reelfoot Lake. An additional population of P. dorsalis has been reported from along the Obion River in Henry County. Similar distributional patterns have been noted for fish and plant species. The presence of several non-coastal plain, upland fish species in streams draining the Mississippi River Bluffs east of Reelfoot Lake was noted by Starnes and Etnier (1985). They considered these disjunct populations as relicts from pre-Wisconsinan times when these species were more widely distributed in the Mississippi Embayment. Presumably pre-Wisconsinan drainages in the upper Mississippi Embayment were erosional and youthful in character. During post-Wisconsinan times, these streams matured and became more depositional in nature, thus eliminating suitable habitats for their upland adapted fish faunas. Further evidence that the bluffs along the eastern border of the Mississippi River Floodplain currently harbor relict populations of species now more northern or Appalachian in distribution was provided by Delcourt and Delcourt (1975). They termed this area the Blufflands and defined it as extending in a belt along the eastern border of the Mississippi River from near the mouth of the Ohio River to southern Louisiana. Delcourt and Delcourt proposed that during the Wisconsinan glacial maximum many northern plant species expanded their ranges into Coastal Plain areas. They envisioned the Blufflands as possessing a cool, moist climate and Mixed Mesophytic Forest that allowed the area to serve as a dispersal corridor for northern plant species. With the retreat of glacial ice and subsequent warming trends, several northern plant species were able to survive in the Coastal Plain in cool ravine refugia of the Blufflands. It is proposed here that the disjunct Coastal Plain populations in Tennessee of D. fuscus, P. dorsalis, and E. l. longicauda are also relictual and owe their origins to the same Quaternary events outlined by Starnes and Etnier (1985) and Delcourt and Delcourt (1975).

Species distributions in the Appalachian Highlands of Tennessee that indicate similar north-south late Quaternary range disruptions of previously wide ranging species include the presence of Plethodon serratus as an isolated population in southeastern Tennessee and adjacent areas of North Carolina (Highton and Webster, 1976) and the isolated occurrences of P. wehrlei in the Cumberland Mountains of Tennessee (Redmond and Jones, 1985) and Kentucky (Cupp and Towles, 1983).

Blair (1965) stated that even though salamander groups show evidence of north-south range disjunctions during the Quaternary, their current distributions mainly indicate east-west fragmentation. He supported this generalization by noting the distribution of related species in the Appalachian and Ozark Highlands. As previously mentioned, Wake (1966) and Highton and Larson (1979) have shown that the formation of Ozark and Appalachian plethodontid faunas was primarily a Tertiary event. A comparison of species distributions within the southern Appalachian Highlands of Tennessee and adjacent states also revealed east-west patterns. Of the 22 plethodontid species that are primarily restricted to the Appalachian Highlands in Tennessee, only two species, Desmognathus monticola and Gyrinophilus porphyriticus, occur continuously from west to east. Of the remaining 20, the distributions in Tennessee of 12 species are principally restricted to the Blue Ridge Mountains. These include Desmognathus aeneus, D. imitator, D. santeetlah, D. wrighti, Eurycea junaluska, Leurognathus marmoratus, Plethodon aureolus, P. cinereus, P. jordani, P. serratus, P. welleri, and P. yonahlossee. Of the remaining eight, D. welteri, P. kentucki, and P. wehrlei are restricted to the Cumberland Plateau and Cumberland Mountains. Again, if the conclusions of Highton and Larson (1979) are correct, the isolation and evolution of these two faunal groups, both of which share closely related species, probably occurred prior to the Pleistocene. How Quaternary events shaped the current distributions of these two groups is unknown. However, in situ development (Wake, 1966), north-south dispersals (Blair, 1958, 1965) along major mountain ranges, and altitudinal range shifts (Tilley and Harrison, 1969; Highton, 1970) probably played a role in shaping their current distributions in Tennessee. Only three Appalachian Highland plethodontid species possess distribution patterns that possibly suggest previously more widespread east-west distribution patterns during the Quaternary. The main body of the range of Aneides aeneus occupies the Appalachian Plateaus which includes the Cumberland Plateau and Cumberland Mountains in Tennessee. Disjunct populations occur on the Interior Low Plateaus, on two separate mountain ridges in the Appalachian Ridge and Valley, and in the Blue Ridge Mountains of North Carolina and possibly Tennessee. This fragmented distribution shows east-west tendencies and indicates a once widespread distribution for the species. Bruce (1968b) proposed that this fragmentation into the Appalachian Plateaus and Blue Ridge Mountains occurred during the Tertiary. He concluded that Pleistocene distributional shifts were limited by shifts in the Mixed Mesophytic Forests. Johnson (1958) anticipated that isolated populations of A. aeneus and P. brachyphona would eventually be found in the northern part of the Appalachian Ridge and Valley. He postulated that both species occurred continuously across the Ridge and Valley prior to deforestation by human settlers. Delcourt and Delcourt (1981) determined that during the early Holocene (10,000 years B.P.), a cool, moist climate favored the widespread distribution of a mixed hardwood forest from 34^{o} to 37^{o} north latitude in eastern North America. Although fragmentation of the range of A. aeneus may have occurred during the Tertiary, it is likely that the species was able to greatly expand its range during the early Holocene in this moist mixed hardwood forest. By 5,000 years B.P., the mixed hardwood forest was reduced to the Appalachian Plateaus (Delcourt and Delcourt, 1981). This breakup of the mixed hardwood forest can also be viewed as responsible for the presence of disjunct relictual populations of A. aeneus in areas outside the Appalachian Plateaus. The presence of disjunct populations of D. ochrophaeus and D. quadramaculatus in the Bays Mountains area in the Appalachian Ridge and Valley also are probably indicative of Holocene ranges that were more widespread than at present. These disjunct distributions may be the result of the same Holocene phenomena that resulted in the proposed expansion and fragmentation of the range of A. aeneus. The current distributions of *Gyrinophilus porphyriticus* and *G. palleucus* exhibit an east-west pattern and suggest past east-west range fragmentation, geographic isolation, and speciation. Brandon (1971) believed the origin of *G. palleucus* was the result of Pleistocene isolation and evolution at the western periphery of the current range of *G. porphyriticus.* Simmons (1975) proposed that during climatic irregularities of the Pleistocene, low elevation populations of *G. porphyriticus* took refuge in the stable environments of limestone caves. Subsequent environmental changes resulted in extirpation of surface dwellers at these low elevations and ultimately geographic isolation of the cave form from their surface dwelling progenitor, *G. porphyriticus.* Currently, the ranges of the two species overlap, but they have been found syntopically in only two cave systems in Knox County, Tennessee.

The Quaternary evolution and dispersal of plethodontid species now restricted to high elevations of the Blue Ridge Mountains is poorly documented. The presence of primitive forms, advanced forms, and many closely related forms that are only partially ecologically segregated seems to suggest the possibility of sympatric speciation (Hairston, 1949). However, Hairston concluded that ecological separation alone could not account for the amount of speciation that has occurred in the area. There is substantial evidence that elevational range migrations occurred during the Quaternary. Tilley and Harrison (1969) proposed that during cooler phases of the Pleistocene, the spruce-fir forest descended to lower elevations and developed a wider distribution than at present. As a result, they contend that the range of *D. wrighti* expanded in a similar fashion. The subsequent retreat of spruce-fir forests to higher elevations during warmer phases also resulted in constriction of the range of D. wrighti. Tilley and Harrison cite the current presence of isolated relictual populations of D. wrighti at low elevations in mesic hardwood forests as evidence of elevational shifts in distribution. Highton (1970) studied the distribution and variation of high elevation isolates of P. jordani. Based on the geographic closeness of some isolates and evidence of recent genetic exchange, he concluded that during Pleistocene cool phases when cool forests descended to lower elevations, P. jordani was more continuously distributed. Conversely, during warmer periods, populations were forced to retreat to higher elevations and formed geographic isolates. This trend of elevational range expansions and contractions and formation of geographic isolates during the Pleistocene may have played a major role in determining the current distributions of closely related species that replace each other altitudinally. Examples include P. jordani and P. aureolus (Highton, 1983), P. jordani and P. glutinosus (Highton, 1970), and D. fuscus and D. santeetlah (Tilley, 1981; Jones, 1982b). The role of rivers in the Blue Ridge Mountains as corridors and/or barriers of dispersal is also poorly understood. Hairston and Pope (1948) contend that rivers have served both functions in the southern Appalachians. Highton (1971) stated that rivers are seldom barriers to the dispersal of Plethodon species. Highton (1971) proposed that P. dorsalis was able to extend its range eastward into the Blue Ridge Mountains by way of low elevation habitats of the French Broad River Valley. The closely related species P. cinereus and

P. serratus occur at higher elevations immediately to the north and south, respectively, of the French Broad River Valley. Highton and Webster (1976) believed that P. dorsalis may exclude both P. cinereus and P. serratus from the lower elevations of the French Broad River Valley. Indication that rivers or their lowland habitats have served as barriers to dispersal in the Blue Ridge Mountains is evident in the distribution patterns of several other plethodontid species. The current distribution of P. yonahlossee is restricted to the east of the French Broad River (Pope, 1965). Highton (1971) noted no evidence of hybridization between P. jordani and P. glutinosus east of the French Broad River while several instances of hybridization were found west of the river. Hinderstein (1971) described color and biochemical differences between populations of D. quadramaculatus that occurred north of the French Broad River and those south of the river. The distribution of P. aureolus is bounded in the north by the Little Tennessee River and in the south by the Hiwassee River (Highton, 1983). In Tennessee, the northern distributional limit of D. aeneus is the Little Tennessee River. One population has recently been found north of the river in North Carolina (Tilley, pers. comm.).

Salamandridae. Notophthalmus is currently a widespread genus in eastern North America and a closely related genus, Taricha, occurs in western North America. Blair (1965) attributed this split to events during the Tertiary. Blair also noted the disjunct distribution pattern exhibited by N. viridescens and its western relative N. meridionalis. He attributed this pattern to Pleistocene east-west range fragmentation and subsequent speciation. Other evidence, such as a fossil *N. meridionalis* from late Miocene (Estes, 1981, cited in Clark, 1985) suggests an earlier split of these two species. Because *N. viridescens* can tolerate a wide variety of environments as indicated by its current widespread distribution and its apparently early origin, *N. viridescens* was probably present in Tennessee throughout the Pleistocene. Considering present day habitats occupied by the species, perhaps the only hostile Pleistocene environment was the tundra-like habitats thought to occur during glacial maxima at high elevations in the Appalachian Mountains (Delcourt and Delcourt, 1981).

Sirenidae. The Pleistocene history of *Siren intermedia* probably closely followed that of *Amphiuma tridactylium.* However, *S. intermedia* has dispersed farther eastward along the Gulf and Atlantic Coastal Plains and farther northward up the Mississippi Valley. Also, in addition to inhabiting the Coastal Plain of west Tennessee, the species has apparently invaded the lower Cumberland River Drainage.

CHAPTER V

ANALYSIS OF DISTRIBUTION PATTERNS

A. Dispersion Patterns

1. Methods

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 species (Figure 81), salamander species (Figure 82), and total amphibian species (Figure 83), clearly shows 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. To statistically test the type of dispersion pattern exhibited by North American mammals, Hagmeier and Stults determined a frequency distribution of indices of faunistic change (IFC) for selected geographic sample areas. They fitted these data to a Poisson distribution and used a chi square test. The IFC value is a measure of faunal change and is determined by the equation:

$$IFC=100\ L/n$$

where L is the number of range limits in a given sample area and n is the total number of species present in the sample area. Lee (1980) and Hammerson (1981) utilized a similar procedure but used the absolute

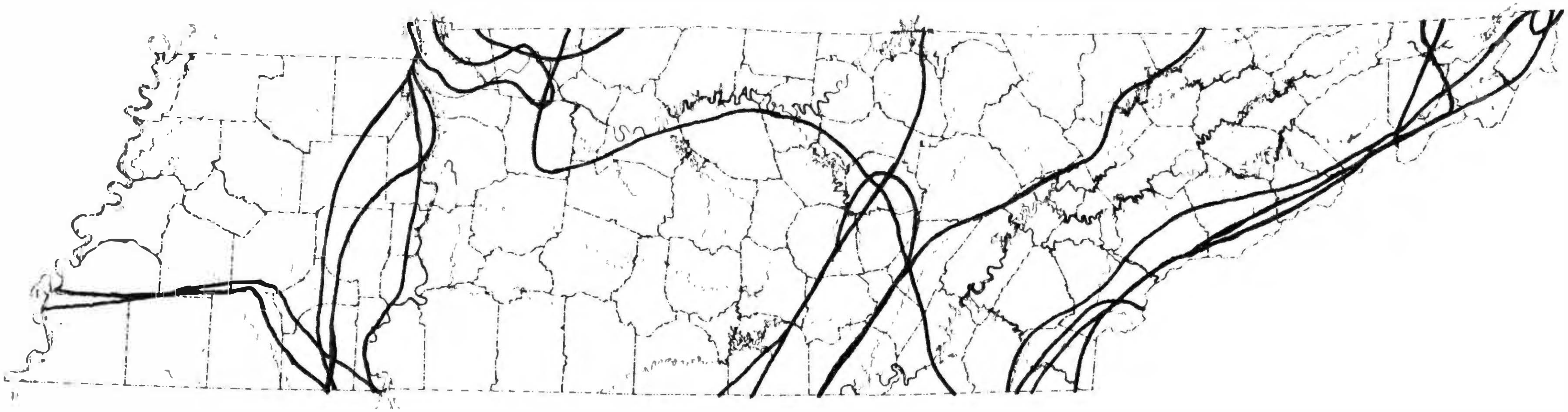

Figure 81. Geographic range limits of frog species in Tennessee. Each line depicts the range limit of a species.

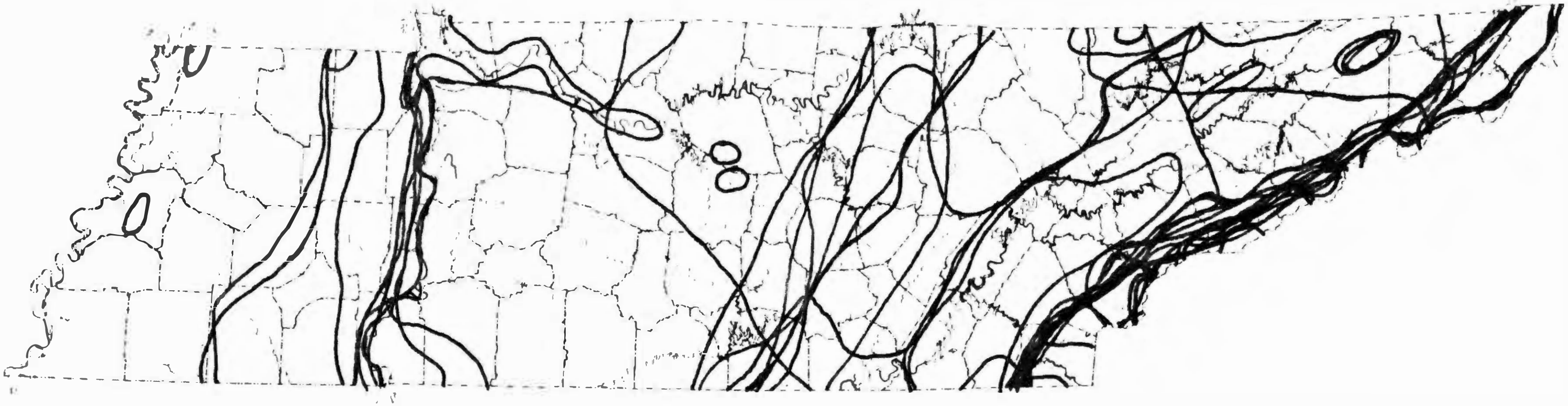

Figure 82. Geographic range limits of salamander species in Tennessee. Each line depicts the range limit of a species.

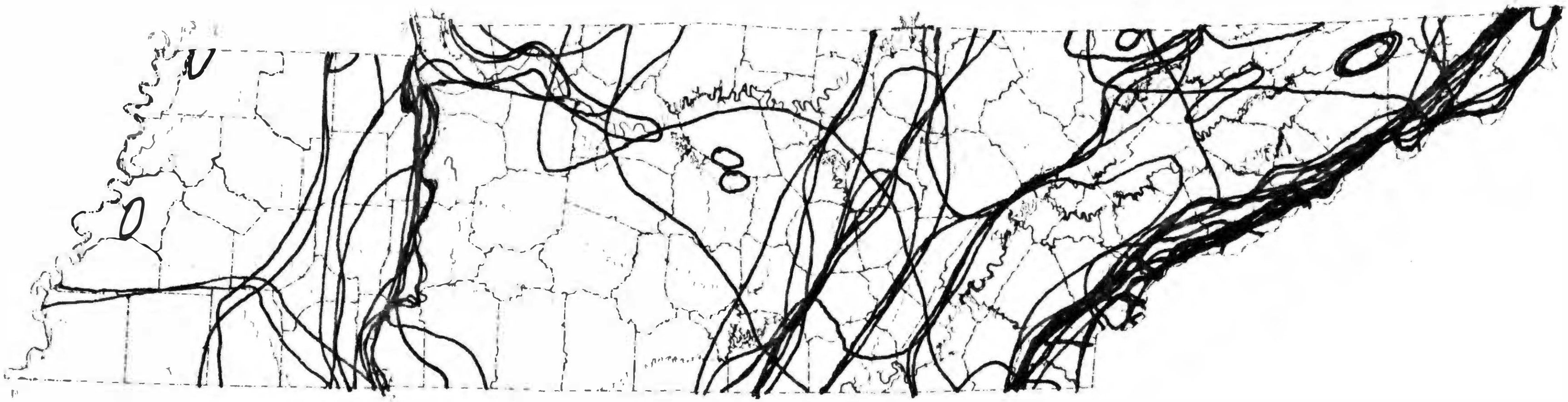

Figure 83. Geographic range limits of amphibian species in Tennessee. Each line depicts the range limit of a species.

number of range limits per sample area to construct frequency distributions. Indices of faunal change can be misleading (Hammerson, 1981) and represent continuous variables. Because the Poisson distribution is a discrete frequency distribution, the absolute number of range limits (discrete variables) are used to study dispersion patterns of amphibians in Tennessee. Sampling units were determined by dividing the state into 122 grid cells (Figure 84). Each grid cell is approximately 1024 km^2. The choice of grid cell size and shape will be discussed further in the following section dealing with areas of faunal homogeneity. The ranges of species were originally plotted on large state maps with a scale of approximately 1 cm = 10 km. At the same scale, the state boundary and grid cell pattern were drawn on a transparent mylar sheet. This grid overlay was superimposed on species range maps, and the distribution limits reached in each grid cell were tallied separately for frog (Figure 85), salamander (Figure 86), and then collectively for amphibian species (Figure 87). These data were arranged into three frequency distributions and each was compared to a Poisson distribution using an adjusted G-test (Gadj) (Sokal and Rohlf, 1981). These procedures allow a test of the independence of limits of distribution within each faunal group.

Throughout the remainder of this study, the fauna is organized into three major groups. These groups are frog species, salamander species, and all species grouped together as amphibians. This procedure is common among studies of this type (Kiester, 1971; Rogers, 1976; Lee, 1980; Bock, Bock, and Fritz, 1981; Hammerson, 1981; Lambert and Reid, 1981) and allows a comparison of results between faunal groupings.

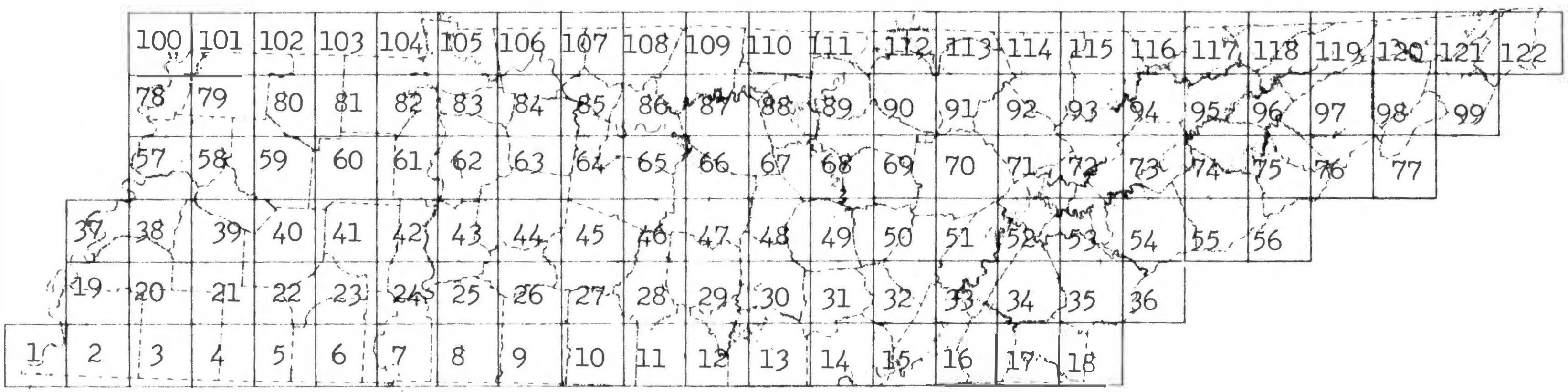

Figure 84. One hundred and twenty-two grid cells used in analysis of distribution patterns and species densities.

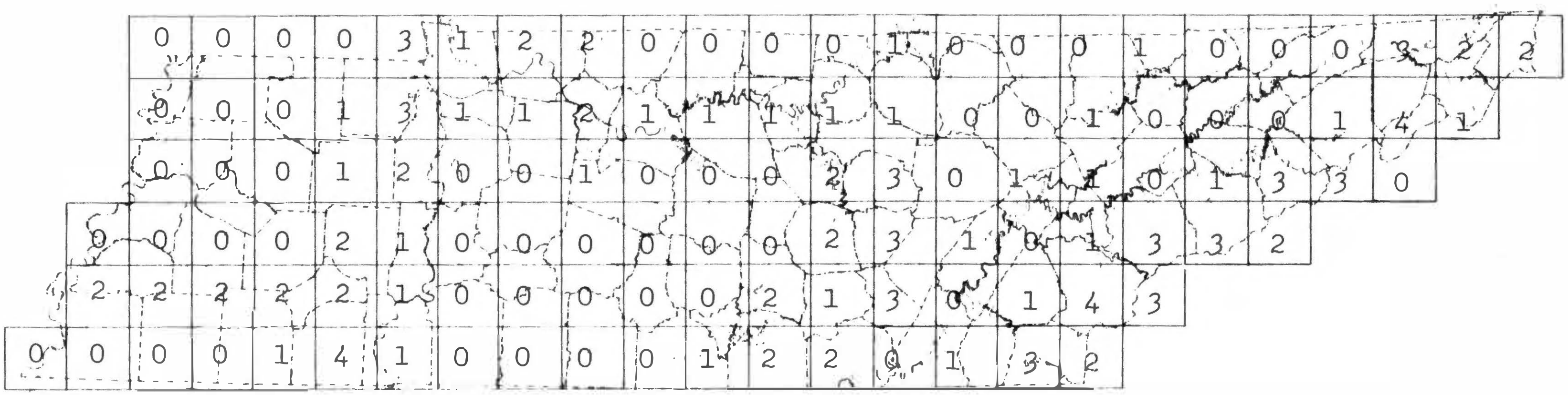

Figure 85. Number of frog distributional limits per grid cell.

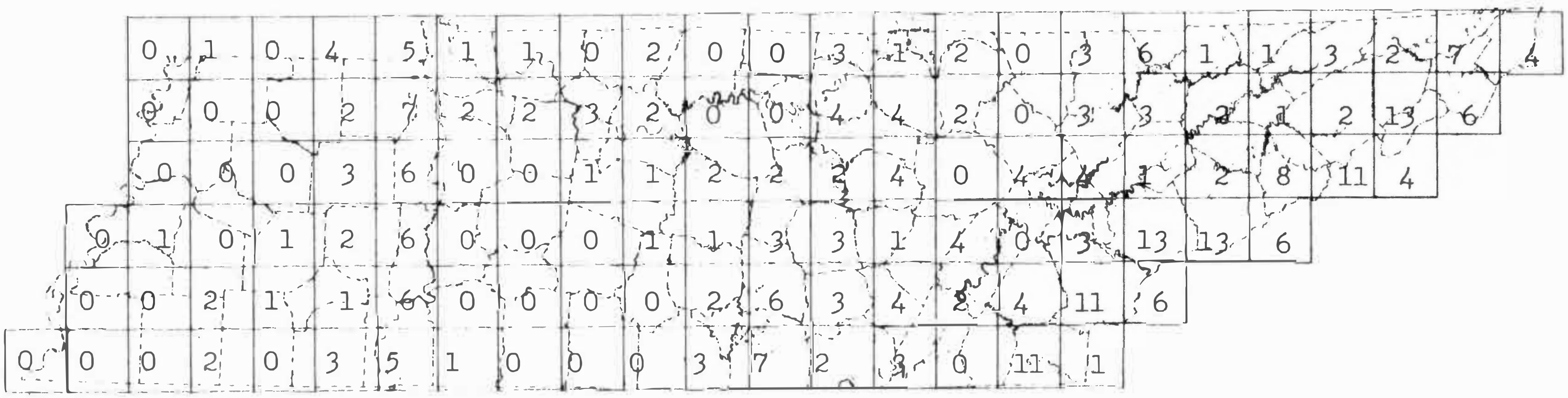

Figure 86. Number of salamander distributional limits per grid cell.

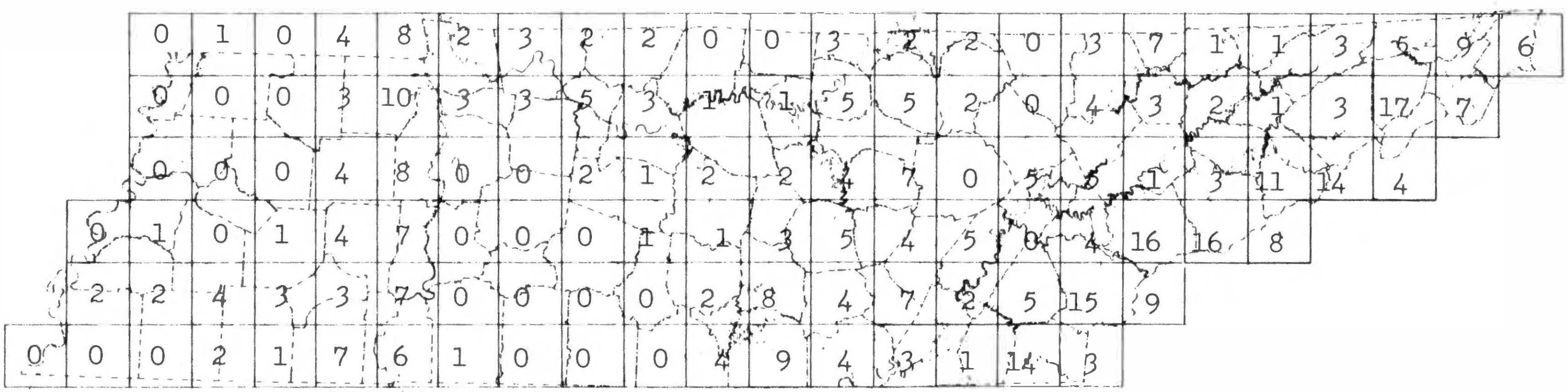

Figure 87. Number of amphibian distributional limits per grid cell.

2. Results

For all three faunal groups studied, the hypothesis that distributional limits within each group are random and occur independently of each other is rejected. Indicating a clumped or contagious dispersion for all three groups, the Gadj values exceed the expected chi square values at the 0.005 level of significance (Table 6). Also, all three Coefficients of Dispersion (CD) are greater than one and suggest clumped dispersion patterns.

3. Discussion

Considering the results summarized in Table 6, it is interesting to note that frog distributional limits 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 of frequency classes (a=4) for frog distributional limits, 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. On the Yucatan Peninsula, Lee (1980) found limits of distribution for all faunal groups to be clumped; however, his data indicated that frog distributional limits were more weakly clumped than the distributional limits of other groups.

In Tennessee, frog distribution limits are clumped near the western border of the Blue Ridge Mountains and along the eastern border of the Coastal Plain. Frog distributional limits in both these areas are

Table 6. Results of G-tests of frequency of geographic distribution limits per grid cell fitted to a Poisson distribution.[a]

Frogs

no. limits	observed	pooled observed	expected	pooled expected
0	59		47.5	
1	29		44.8	
2	19		21.1	
3	12	15	6.6	8.2
4	3		1.6	

$\bar{x}$=0.9426 s^2=1.25
CD=1.33 Gadj=14.35
X^2(.005)[2]=10.6

Salamanders

no. limits	observed	pooled observed	expected	pooled expected
0	38		10.1	
1	19		25.2	
2	20		31.4	
3	14		26.1	
4	11		16.2	
5	2		8.1	
6	8	18	3.4	5.1
7	3		1.2	
8	1		0.4	
9	0		0.1	
10	0		0.0	
11	3		0.0	
12	0		0.0	
13	3		0.0	

$\bar{x}$=2.4918 s^2=8.71
CD=3.50 Gadj=84.67
X^2(.005)[5]=16.7

Amphibians

no. limits	observed	pooled observed	expected	pooled expected
0	31	46	3.9	17.4
1	15		13.5	
2	15		23.2	
3	16		26.6	
4	12		22.8	
5	9		15.7	
6	2		9.0	
7	7	22	4.4	7.4
8	4		1.9	
9	3		0.7	
10	1		0.3	
11	1		0.1	
12	0		0.0	
13	0		0.0	
14	2		0.0	
15	1		0.0	
16	2		0.0	
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.

primarily the result of species reaching the eastern extent of their distributions in Tennessee. In comparison, salamander distributional limits show a similar pattern of clumping; however, two areas of concentration of salamander distributional limits are mainly representative of species reaching the western extents of their distributions in Tennessee. Exceptions to this general trend include several species in the genera *Ambystoma*, *Amphiuma*, and *Siren*. In addition to clumping of salamander distributional limits along the western border of the Blue Ridge Mountains and eastern border of the Coastal Plain, limits are concentrated along the eastern and western escarpments of the Cumberland Plateau. A quantitative examination of the relationships of these distribution patterns and the factors influencing them is the subject of the remaining analyses of this study.

B. Areas of Faunal Homogeneity

1. Methods

In the literature, 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. To delineate and compare areas of faunal homogeneity for frogs, salamanders, and amphibians in Tennessee, the sequential, agglomerative, hierarchic, nonoverlapping (SAHN) clustering techniques described by Sneath and Sokal (1973) were used. These techniques have been applied in several recent biogeographic studies (Hagmeier and Stults, 1964; Hagmeier, 1966; Fisher, 1968; Kaiser, Lefkovitch, and Howden, 1972; Bock, Mitton, and Lepthien, 1978; Lee, 1980; Lambert and Reid, 1981; Bock, Bock, and Fritz, 1981; Hammerson, 1981). Even though the interpretation of results obtained by these techniques must be based on subjective criteria, clustering methods allow the objective manipulation and organization of large numbers of variables (Bock, Bock, and Fritz, 1981).

Bock, Bock, and Fritz (1981) stated that species whose ranges are statewide do not yield biogeographic information, and they excluded these species from their study of distribution patterns. While this may be true for a given study area, their inclusion will not alter the results. Also, their inclusion will facilitate comparisons with the results of similar studies from adjacent states, where species that are ubiquitous in Tennessee may be restricted in their distributions. For the sake of completeness and to allow quantitative comparisons with the results of possible future studies in adjacent states, all species were utilized in the analysis.

To obtain meaningful results from a cluster analysis, the size and shape of sampling units is an important consideration. As summarized by Hammerson (1981), sampling units must be large enough to allow an accurate determination of faunal composition, yet small enough to detect subtle changes in faunal composition in the study area. Logistical considerations regarding sampling unit size include the ability to code data in a reasonable amount of time and the limitations of available computer software packages. In previous studies, sampling unit shape has been defined by county boundaries in Kansas (Fisher, 1968), Colorado (Lambert and Reid, 1981), and Illinois (Bock, Bock, and Fritz, 1981). Blocks or grid cell patterns were utilized by Hammerson (1981) for Colorado, Huheey (1965) for Illinois, and Lee (1980) for the Yucatan Peninsula. Because of the wide variation in the size of counties in Tennessee, county units were deemed inappropriate as sampling units. For the purposes of this study, a grid cell pattern with cells of equal dimensions was used. A grid cell size of 1024 km^2 was chosen. This choice was somewhat arbitrary but was made after careful review of the results of the aforementioned studies.

To perform the cluster analyses, the TAXON and related programs of the Numerical Taxonomy System of Multivariate Statistical Programs (NT-SYS) were used (Rohlf, Kishpaugh, and Kirk, 1974). Using the grid cell pattern (Figure 84) and following the procedures described in the preceding section for dispersion patterns, the presence or absence of each species was tabulated for each grid cell. A species presence was denoted by a one and its absence by a zero. The frog, salamander, and amphibian species composition of all pairwise combinations of grid cells was compared using the coefficient of Jaccard. The equation is:

$$J = C/N1+N2-C$$

where C is the number of species common to both grid cells, N1 is the number of species in the grid cell with the fewer number of species, and N2 is the number of species in the grid cell with the larger number of species (Long, 1963). The resultant matrices of 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. Another technique, suggested by Hammerson (1981), to evaluate faunal areas defined by clustering methods is to compare the geographic distribution of IFC values (see page 210) with areas of faunal homogeneity defined by the cluster analysis. Areas near the boundaries of faunal areas should have relatively high IFC values as compared to other areas. To make these comparisons for the fauna of Tennessee, IFC values were determined for frog, salamander, and amphibian species in each grid cell and were compared to areas of faunal homogeneity determined for each species group.

To quantitatively examine the relationships between the distribution of frog, salamander, and amphibian species and to compare these faunal patterns with the geographic distribution patterns exhibited by environmental variables, coefficients of correlation of similarity matrices (Rss) were calculated (Sneath and Sokal, 1973; Bock, Bock, and Fritz, 1981). The MXCOMP program of NT-SYS (Rohlf, Kishpaugh, and Kirk, 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). Similarity matrices of J values for climate (Figure 3), physiography (Figure 2), drainages (Figure 15), soils (Figure 16), vegetation (Figure 18), and ecoregions (Figure 19) were determined in the same manner as similarity matrices for frogs, salamanders, and amphibians. For example, data regarding the presence or absence of each major vegetation type was coded for every grid cell. Using J values, a similarity matrix was constructed that reflected the results of all pairwise comparisons of grid cells based on the distribution of vegetative types. The three Rss values determined by comparisons of the vegetation similarity matrix with the similarity matrices of faunal groups (frogs, salamanders, amphibians) are a measure of the congruence of the distribution pattern of vegetation types and the distribution patterns of frogs, salamanders, and amphibians.

In an effort to study the faunal composition of areas of faunal homogeneity in terms of the evolution and past dispersal patterns of their component species, all species were classified according to their proposed North American center of dispersal. For each frog, salamander, and amphibian area of faunal homogeneity, total species density was tabulated and the percent species composition from each major North American center of dispersal was calculated. The major centers of dispersal were determined from information provided in Chapter IV and are admittedly speculative. Also, the names of some centers (southern, northern) reflect the lack of detailed knowledge of past dispersal patterns. However, 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.

2. Results

To allow comparisons of results from cluster analyses for frogs, salamanders, and 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 frogs, salamanders, and amphibians. 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. In a study of the amphibians and reptiles of Colorado, Hammerson (1981) used a similarity value of 0.50 to define areas of faunal homogeneity and, in Illinois, Bock, Bock, and Fritz (1981) used a value of 0.60. For the herpetofauna on the Yucatan Peninsula, Lee (1980) used a value of 0.90 to recognize areas of faunal homogeneity for lizards and snakes and a value of 0.95 for frogs.

For the frog fauna of Tennessee, three areas of faunal homogeneity are recognized (Figure 88). The hierarchial relationships of these areas are illustrated in Figure 89. It is important to note that the phenogram in Figure 89 and the two subsequent phenograms presented in this study (for salamanders and amphibians) are condensed versions of the original phenograms and summarize groupings of grid cells at the 0.80 level of similarity. For the cluster analysis of frog distribution data, the cophenetic correlation coefficient was 0.892. Major areas of faunal homogeneity for frog species include: (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 89, the small area in northeastern Tennessee is the most distinctive of the three, while the other two are relatively more similar in terms of their frog faunas. The distribution of IFC values for frog species (Figure 90) tends to support the validity of these areas. Relatively high IFC values are found in grid cells along the eastern borders of frog areas one and two. Other parts of the state with high IFC values include grid cells along the eastern border of Tennessee south of frog area three, on the southern

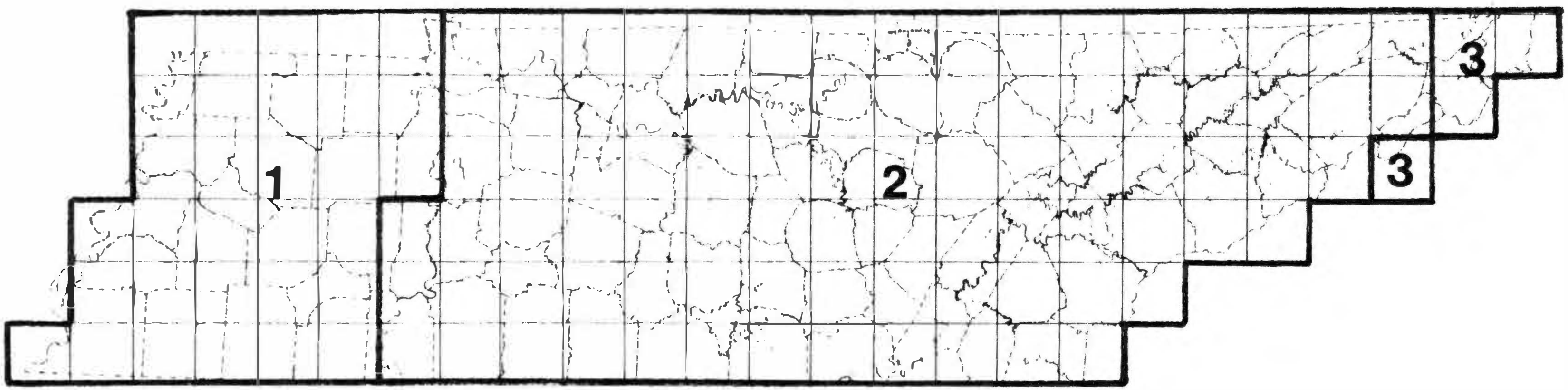

Figure 88. Major areas of faunal homogeneity based on cluster analysis of frog distributions. Areas were defined at the 0.80 level of similarity.

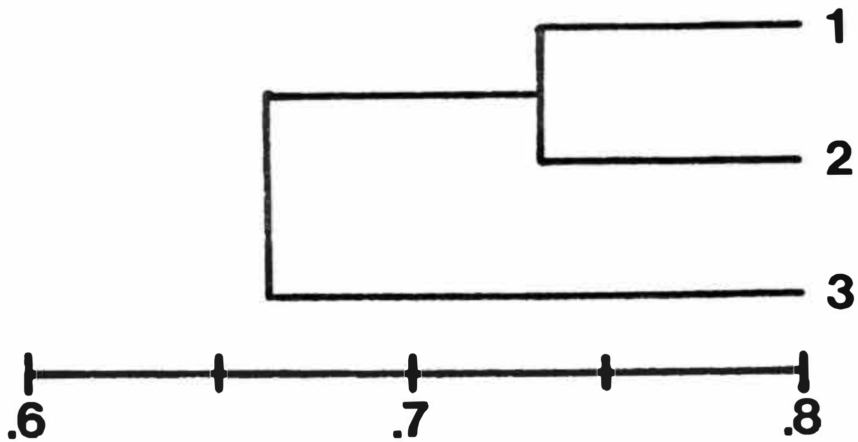

Figure 89. Phenogram showing hierarchial relationships of three major areas of faunal homogeneity based on frog distributions. Areas defined at the 0.80 level of similarity. The cophenetic correlation coefficient is 0.892.

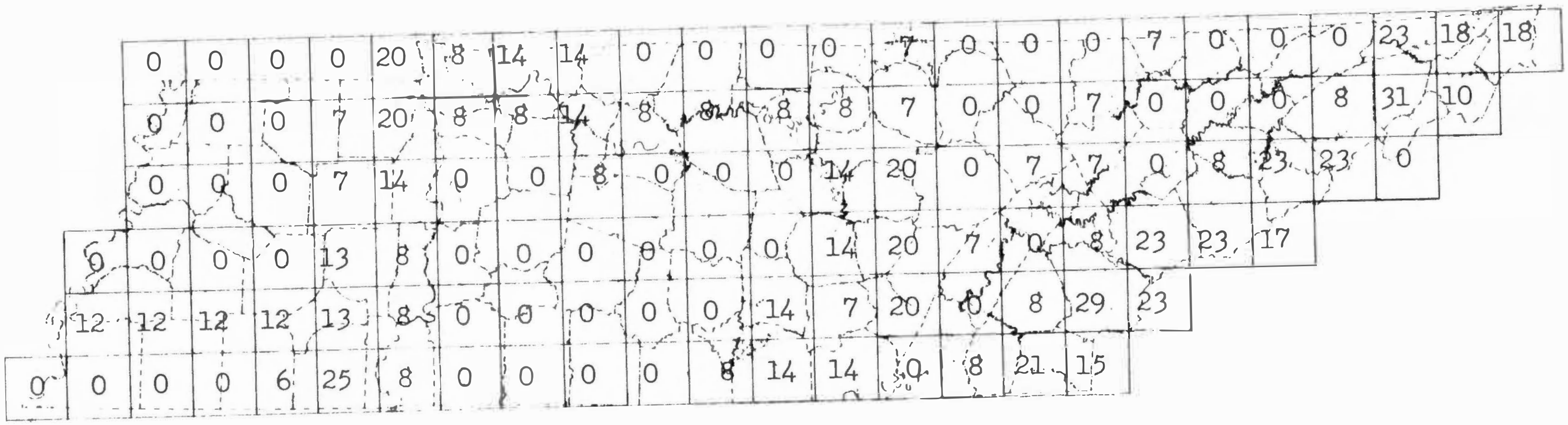

Figure 90. Indices of faunal change for frog species in 122 grid cells.

Cumberland Plateau, and near the border of the Cumberland Plateau and Western Highland Rim.

Nine areas of faunal homogeneity are recognized for the salamander fauna (Figure 91). Figure 92 depicts the hierarchial relationships of these areas. The cophenetic correlation coefficient was 0.889. Major areas of faunal homogeneity for salamander species include: (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 (Figure 92) 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. Figure 93 illustrates the distribution of IFC values for salamander species. As for frog species, IFC values for salamanders tend to be large near the boundaries of salamander areas of faunal homogeneity. However, IFC values for salamanders tend to be large in grid cells along both the eastern and western boundaries of faunal areas.

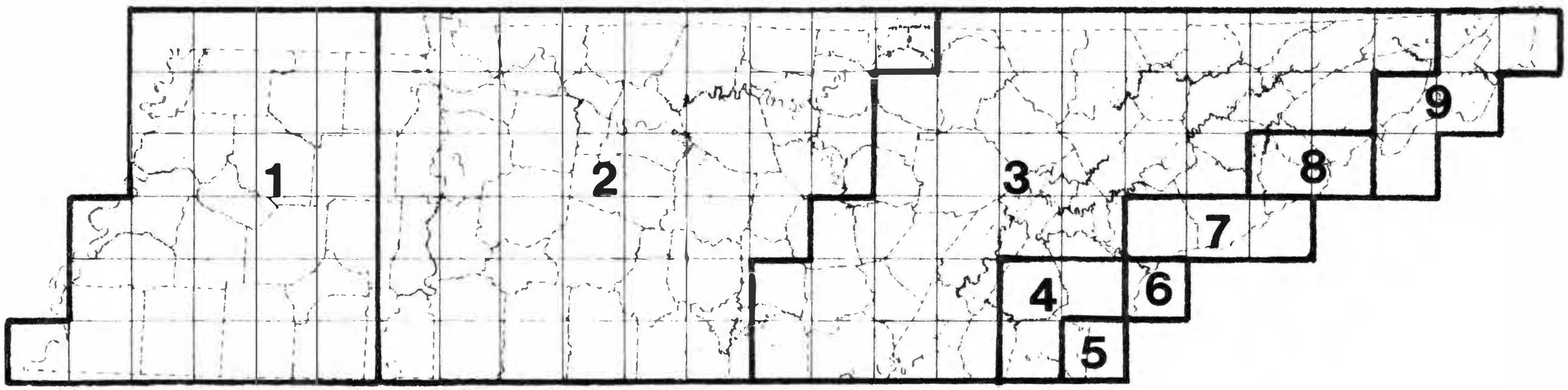

Figure 91. Major areas of faunal homogeneity based on cluster analysis of salamander distributions. Areas were defined at the 0.80 level of similarity.

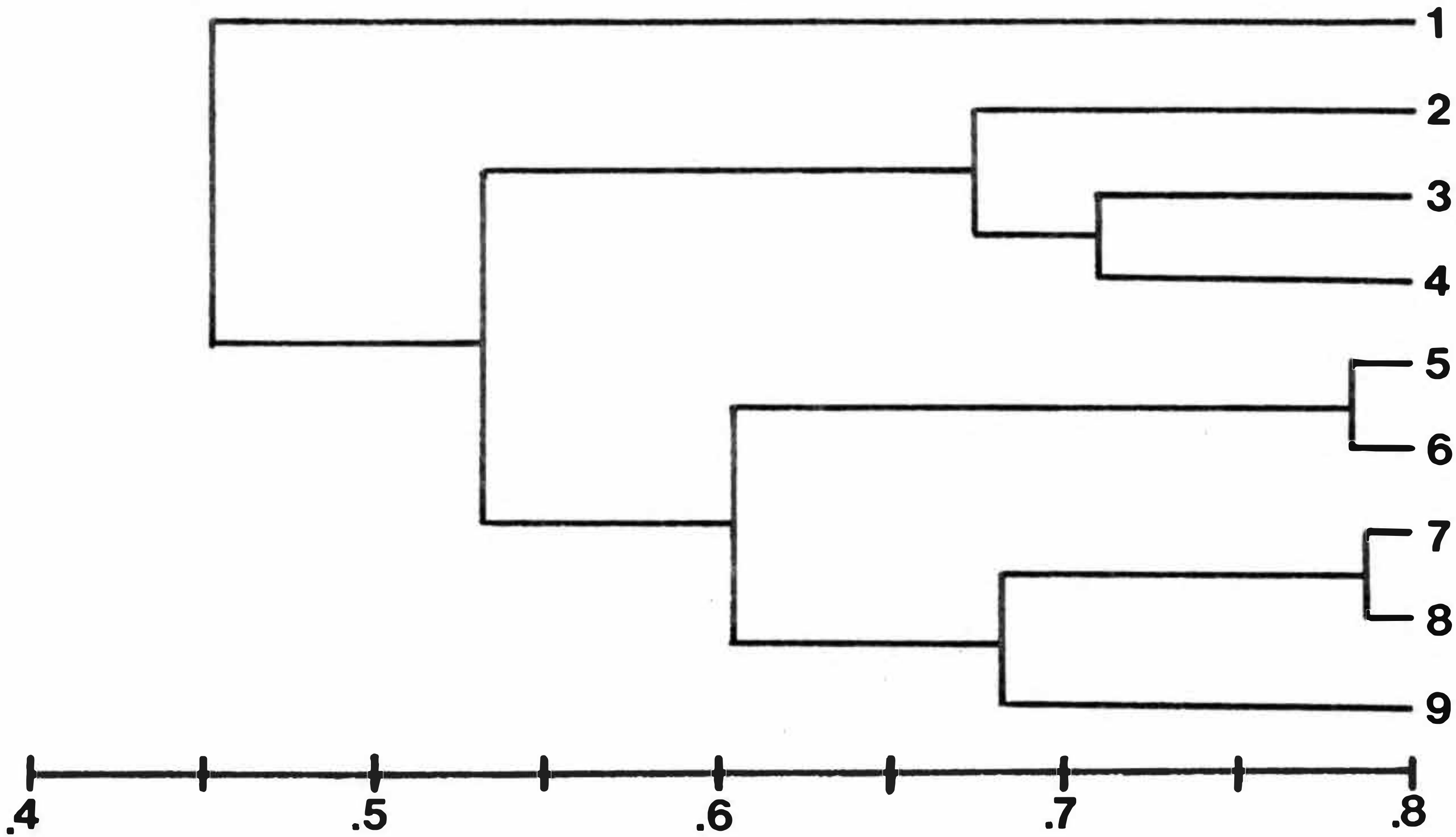

Figure 92. Phenogram showing hierarchial relationships of nine major areas of faunal homogeneity based on salamander distributions. Areas defined at the 0.80 level of similarity. The cophenetic correlation coefficient is 0.889.

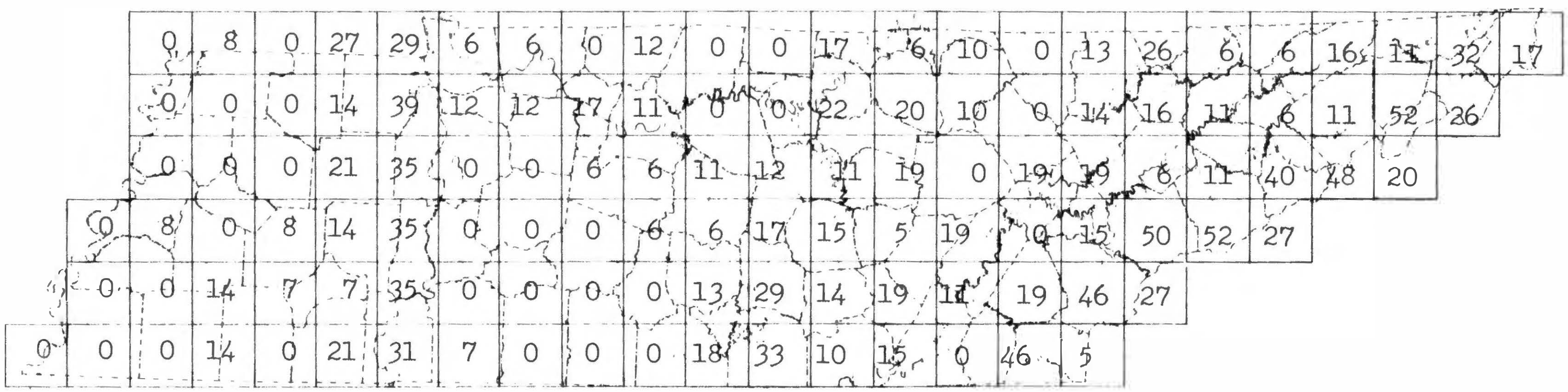

Figure 93. Indices of faunal change for salamander species in 122 grid cells.

For the total amphibian fauna of the state, six areas of faunal homogeneity are delineated (Figure 94), and their hierarchial relationships are shown in Figure 95. The cophenetic correlation coefficient was 0.873. Major areas of faunal homogeneity for amphibians include: (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. 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 95). Areas two, three, four, and five are grouped at the 0.68 level of similarity. Again, IFC values (Figure 96) are high near the boundaries of amphibian faunal areas and tend to be higher in grid cells along the western border of faunal areas.

The Rss values calculated for comparisons of frog, salamander, and amphibian similarity matrices are shown in Table 7. The Rss values determined for comparisons of the similarity matrices of all three faunal groups with those of six environmental variables are listed in Table 8. Based on the values in Table 7, the distribution of frogs is more closely correlated with the distribution of the total amphibians fauna than with the distribution of salamanders. Also, the distribution of salamanders is more closely correlated with the distribution of total

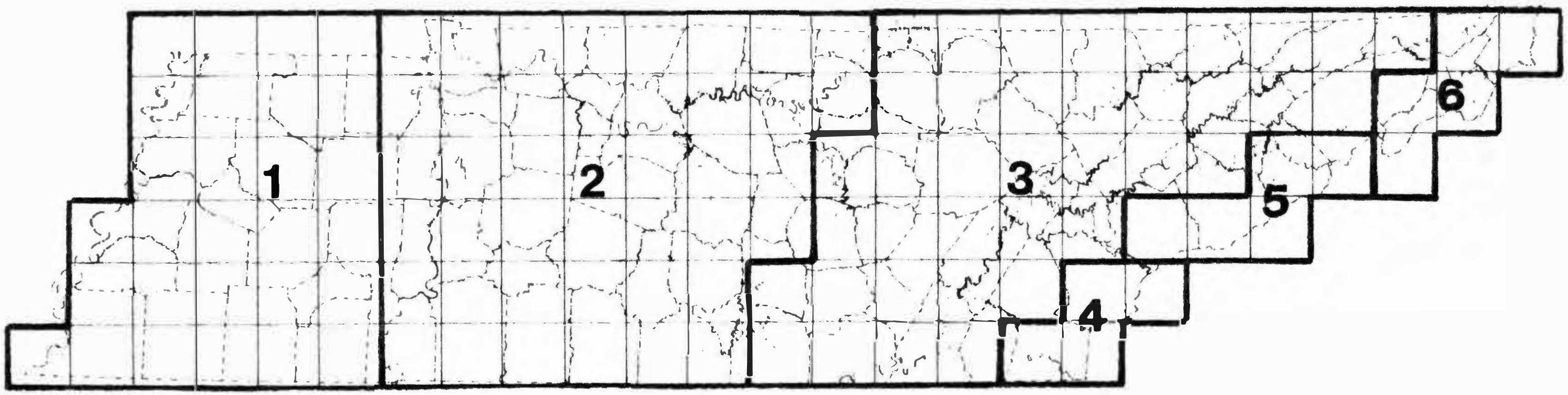

Figure 94. Major areas of faunal homogeneity based on cluster analysis of amphibian distributions. Areas were defined at the 0.80 level of similarity.

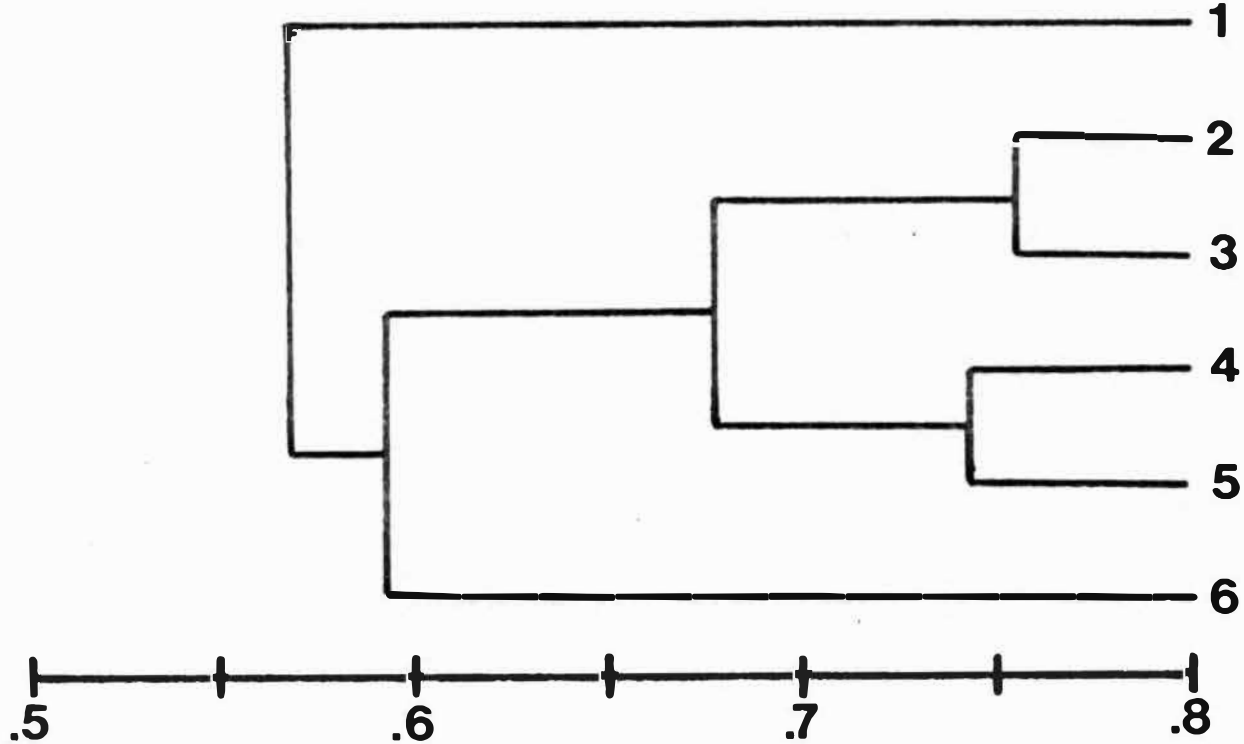

Figure 95. Phenogram showing hierarchial relationships of six major areas of faunal homogeneity based on amphibian distributions. Areas defined at the 0.80 level of similarity. The cophenetic correlation coefficient is 0.873.

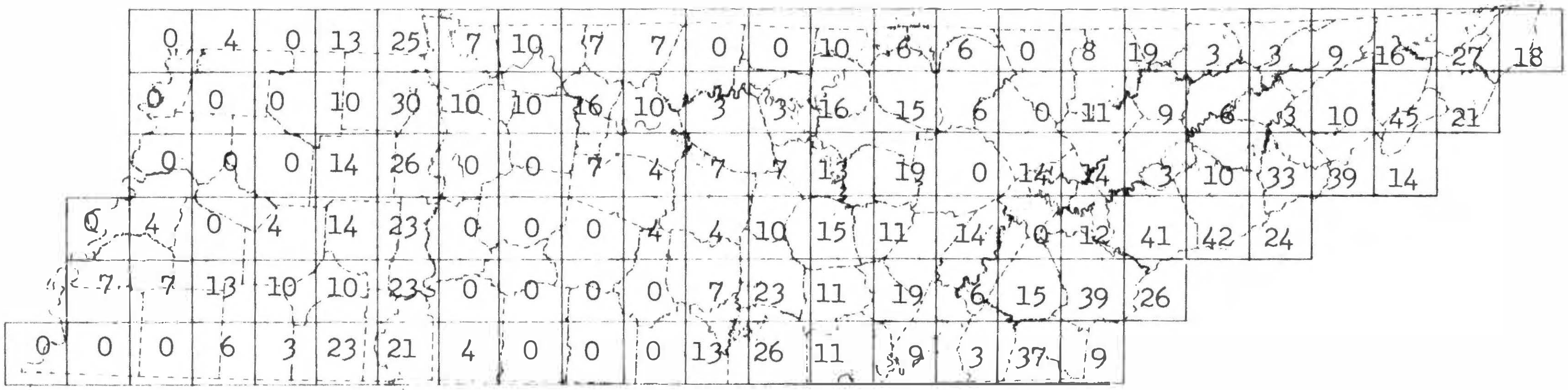

Figure 96. Indices of faunal change for amphibian species in 122 grid cells.

Table 7. Correlations (Rss values) of frog, salamander, and amphibian similarity matrices.[a]

	Frogs	Salamanders
Salamanders	0.757	
Amphibians	0.855	0.983

[a]Similarity matrices constructed using coefficients of Jaccard.

Table 8. Correlations (Rss values) of frog, salamander, and amphibian similarity matrices with those of six environmental variables.[a]

	Frogs	Salamanders	Amphibians
Climate	0.508	0.656	0.641
Physiography	0.403	0.556	0.535
Drainages	0.387	0.421	0.412
Soils	0.447	0.636	0.619
Vegetation	0.338	0.546	0.525
Ecoregions	0.396	0.532	0.516

[a]Similarity matrices constructed using coeficients of Jaccard.

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. This trend is also evident in the Rss values presented in Table 8. The Rss values comparing the distribution of amphibians with the distributions of six environmental variables are consistently closer to the Rss values for salamanders than to the values for frogs. Listing the environmental variables in order of importance, the distributions of frogs, salamanders, and all amphibians are most closely correlated with the geographic patterns of climate, soils, and physiography.

The six proposed North American centers of dispersal of amphibian species in Tennessee are given in Table 9. For several species, the source listed in Table 9 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. The percent composition of frog species from each North American center of dispersal for each area of frog faunal homogeneity is given in Figure 97. Figure 98 shows the percent composition for salamanders and Figure 99 for the total amphibian fauna.

Frog species with a southeastern center of dispersal dominate all three frog faunal areas. Species with a southeastern center make up 40 percent of area one, 31 percent of area two, and 33 percent of area three. Species associated with a southern center of origin rank second in order of dominance and make up 24 percent of area one, 25 percent of area two, and 33 percent of area three. Species with southwestern and eastern Atlantic Coast centers are minor faunal components of areas one

Table 9. Six proposed North American centers of dispersal for amphibian species in Tennessee.

Species	Proposed North American Center of Dispersal	Source
Scaphiopus holbrooki	Southeastern	Blair (1965)
Bufo woodhousei	Southeastern	Blair (1965)
Acris gryllus	Southeastern	Blair (1965)
Hyla avivoca	Southeastern	Blair (1965)
Hyla cinerea	Southeastern	Blair (1965)
Hyla gratiosa	Southeastern	Blair (1965)
Gastrophryne carolinensis	Southeastern	Blair (1965)
Ambystoma maculatum	Southeastern	Tihen (1958)
Ambystoma opacum	Southeastern	Tihen (1958)
Ambystoma talpoideum	Southeastern	Tihen (1958)
Ambystoma texanum	Southeastern	Tihen (1958)
Acris crepitans	Southwestern	Blair (1965)
Pseudacris triseriata	Southwestern	Blair (1965)
Rana areolata	Southwestern	Blair (1965)
Amphiuma tridactylium	Southwestern	Blair (1958)
Siren intermedia	Southwestern	Porter (1972)
Ambystoma tigrinum	Southwestern	Tihen (1958)
Hyla versicolor/ chrysoscelis	Southern	Blair (1965)
Rana catesbeiana	Southern	Blair (1958)
Rana clamitans	Southern	Blair (1958)
Rana palustris	Southern	Blair (1958)
Rana utricularia	Eastern Atlantic Coast	Pace (1974)
Necturus maculosus	Eastern Atlantic Coast	Sessions and Wiley (1985)
Bufo americanus	Northern	Blair (1965)
Hyla crucifer	Northern	Blair (1965)
Rana sylvatica	Northern	Porter (1972)
Notophthalmus viridescens	Northern	Estes (1970)
Pseudacris brachyphona	Appalachian Highlands	Blair (1965)
Cryptobranchus alleganiensis	Appalachian Highlands	this study
Plethodontidae (all 31 species)	Appalachian Highlands	Wake (1966)

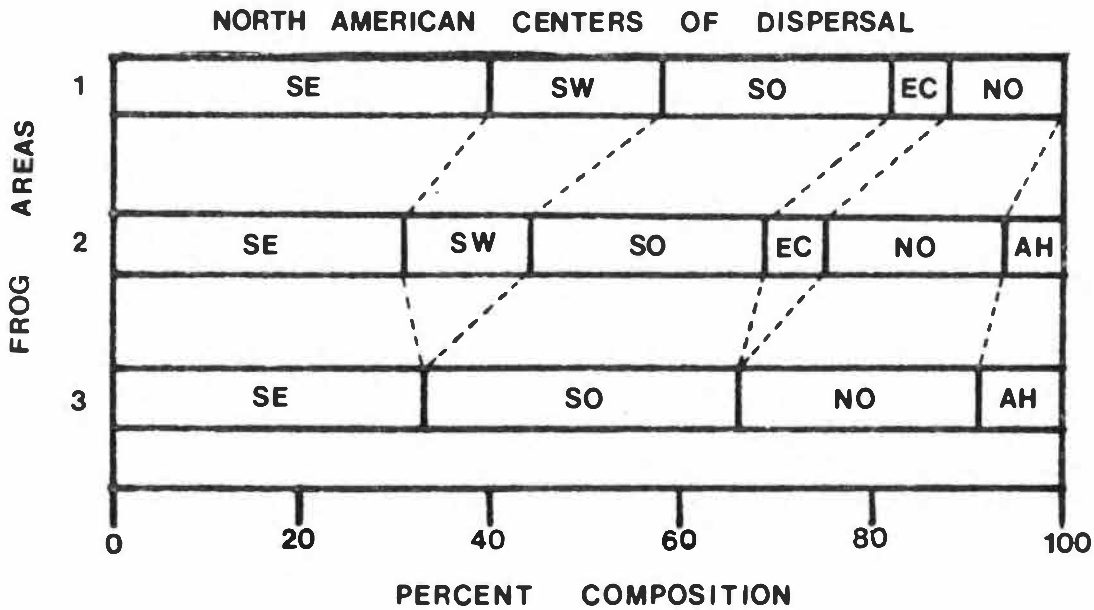

Figure 97. Percent composition of frog species grouped according to their North American centers of dispersal in the three areas of frog faunal homogeneity. SE denotes a southeastern center of dispersal, SW-southwestern, SO-southern, EC-eastern Atlantic Coast, NO-northern, and AH-Appalachian Highlands.

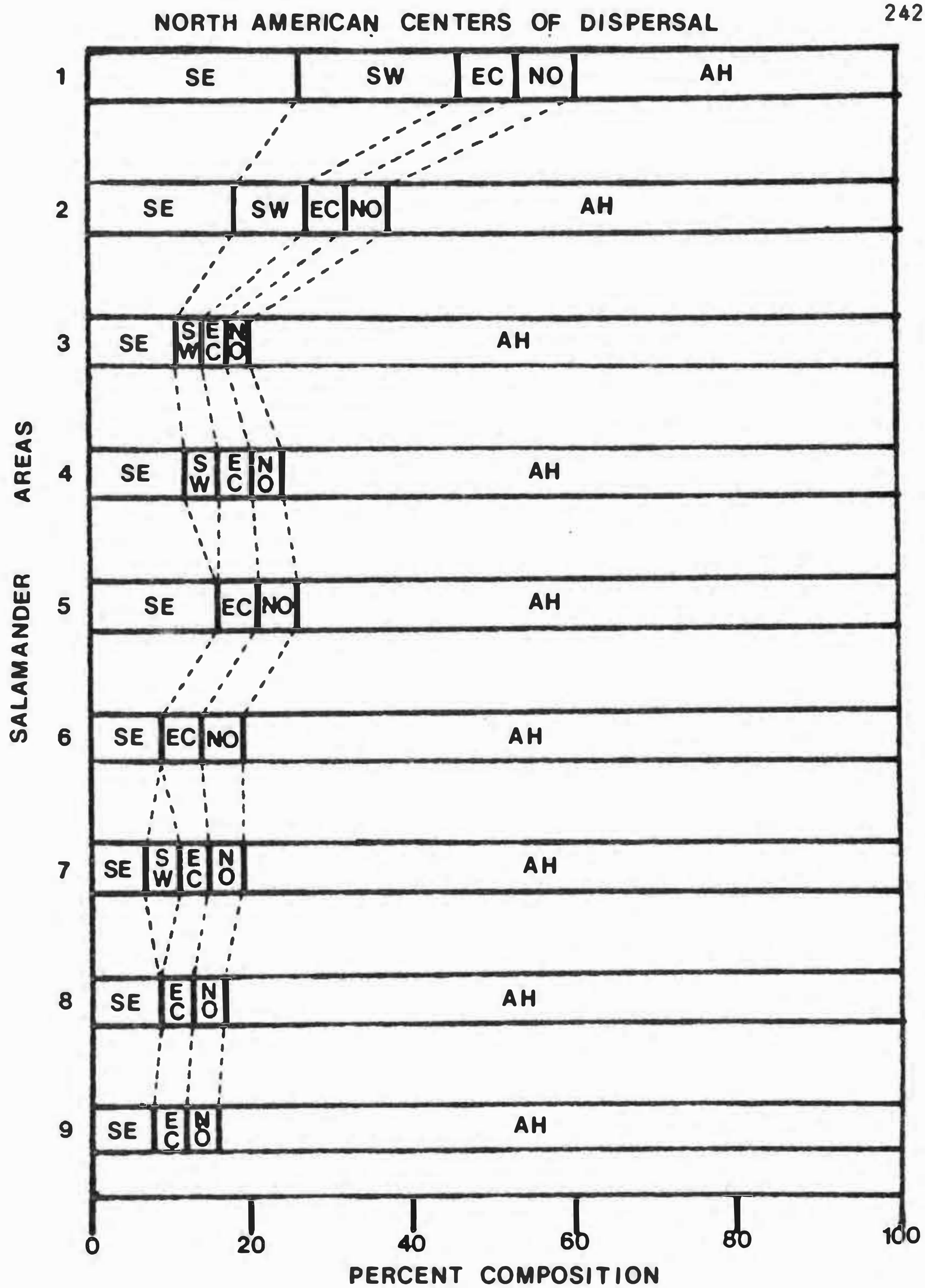

Figure 98. Percent composition of salamander species grouped according to their North American centers of dispersal in the nine areas of salamander faunal homogeneity. SE denotes a southeastern center of dispersal, SW-southwestern, SO-southern, EC-eastern Atlantic Coast, NO-northern, and AH-Appalachian Highlands.

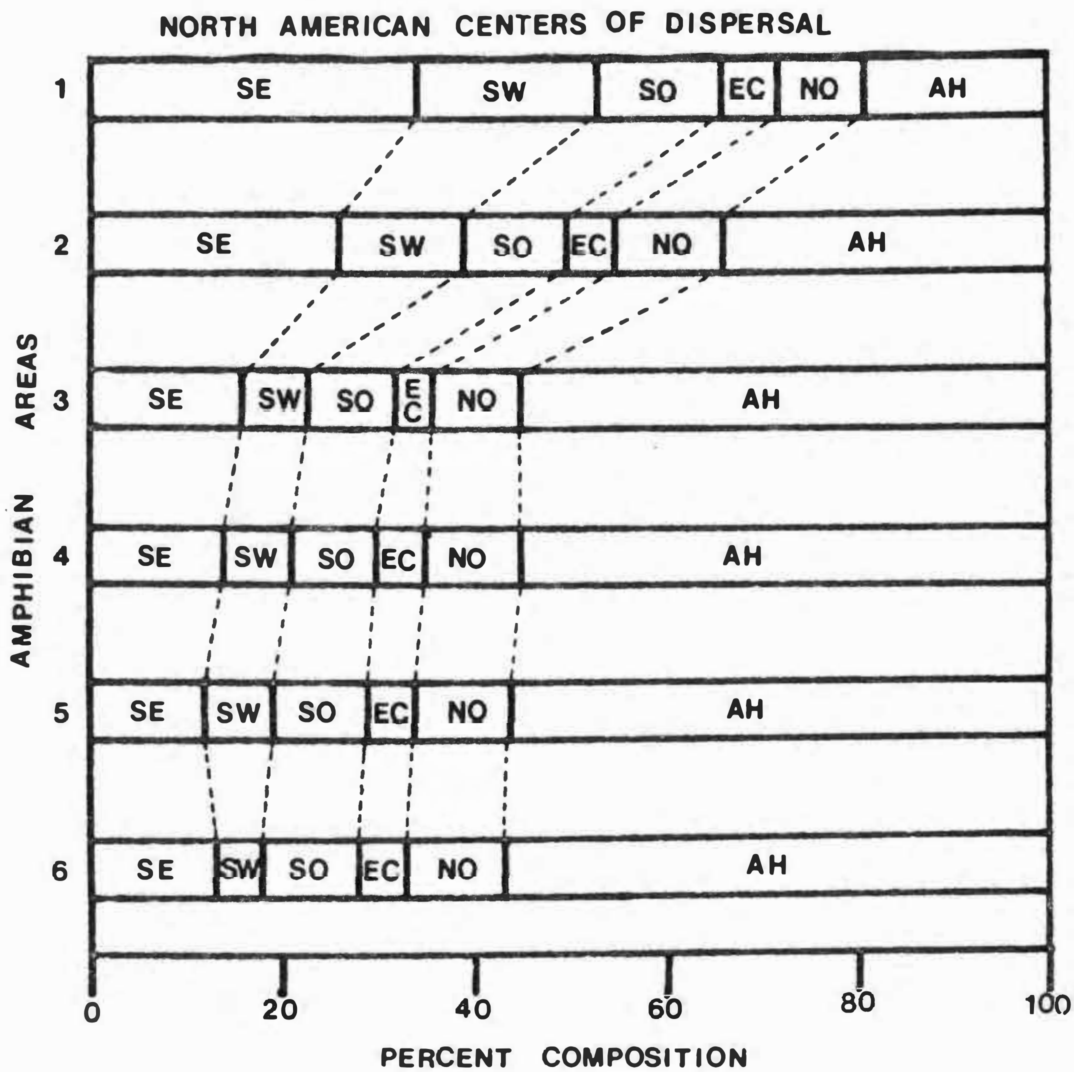

Figure 99. Percent composition of amphibian species grouped according to their North American centers of dispersal in the six areas of amphibian faunal homogeneity. SE denotes a southeastern center of dispersal, SW-southwestern, SO-southern, EC-eastern Atlantic Coast, NO-northern, and AH-Appalachian Highlands.

and two and are entirely absent from area three. Species with a northern center increase in importance from areas one through three and make up 25 percent of the total frog fauna in area three. Frog species with an Appalachian Highlands center are absent from area one and constitute nine percent of the fauna of area three. Except for area one, all areas of faunal homogeneity of salamander species are dominated by species with an Appalachian Highlands center of dispersal. Specific percentages include 40 percent in area one, 63 percent in area two, 80 percent in area three, 76 percent in area four, 74 percent in area five, 81 percent in area six, 81 percent in area seven, 83 percent in area eight, and 84 percent in area nine. Salamander species whose centers of dispersal are southeastern and southwestern North America are significant faunal components of areas one (46 percent) and two (27 percent), but are minor components of areas three through nine. No salamander species were determined to have a southern center of dispersal. The composition of areas of faunal homogeneity for all amphibians shows tendencies similar to those for salamander faunal areas. Amphibian species with an Appalachian Highlands center of dispersal constitute 19 percent of the total amphibian fauna in area one, 34 percent in area two, and over 50 percent in areas four, five, and six. Species associated with southeastern, southwestern, and southern centers of dispersal make up 66 percent of the total fauna in area one and 50 percent of area two, and approximately 30 percent of areas three, four, five, and six.

By comparing the results from Figure 97 with Figure 88, Figure 98 with 91, and 99 with 94, 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 in 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.

Lee (1980) and Hammerson (1981) refrained from formally naming areas of faunal homogeneity. For their study areas, they believed that delineation of faunal areas should not be the final goal, but should be considered as a starting point, from which it is possible to study the geographical and ecological relationships of these areas. In regards to a biogeographic study of amphibians in Tennessee, Lee's and Hammerson's conclusions are thought to be valid. Thus, areas of faunal homogeneity in Tennessee are not given names.

3. Discussion

The number of faunal areas determined for frogs were fewer than the number for salamanders or amphibians. The frequency distribution of the range limits of frog species has been 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. The occurrence of high IFC values along the eastern borders of areas one and two represent areas where several frog species reach the eastern limits of their distributions in Tennessee. Species primarily restricted to area one, the Coastal Plain in west Tennessee, include: Acris gryllus (Figure 24), Hyla avivoca (Figure 25), Hyla cinerea (Figure 26), and Rana areolata (Figure 34). Species that reach their eastern limits at the eastern border of area two include: Acris crepitans (Figure 23), Gastrophryne carolinensis (Figure 32), and Scaphiopus holbrooki (Figure 33). As evidenced by the high IFC values, there is significant faunal change occurring along the western border of the Blue Ridge Mountains in east Tennessee south of frog area three. In this area, frog species reaching the eastern limits of their distribution do so at the base of the mountains very near the state line. In most cases, these species were included as part of grid cells centered on the eastern boundary of the state. This negated the possibility of recognition of faunal areas. The use of smaller grid cells would probably result in recognition of more faunal areas or a southward extension of area three to include all of the mountainous area along the eastern border of the state.

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 species thought to have dispersed from a northern or Appalachian Highlands center, only Bufo americanus and Hyla crucifer occur in the Coastal Plain in west Tennessee.

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. Indices of faunal change are high on both sides of the boundary between areas one and two. A significant level of faunal turnover occurs here. 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 tridactylium (Figure 45) and Siren intermedia (Figure 80). Four species reach the western limits of their distribution in Tennessee near the western boundary of area two. These include Cryptobranchus alleganiensis (Figure 46), Eurycea lucifuga (Figure 61), Hemidactylium scutatum (Figure 64), and Plethodon dorsalis (Figure 68). Indicating relatively less faunal change between areas two and three, the IFC values along their common border are lower than IFC values along the borders of one and two. 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 are Aneides aeneus (Figure 48), Desmognathus monticola (Figure 52), D. ochrophaeus (Figure 53), and Gyrinophilus porphyriticus (Figure 63). However, one species, Ambystoma texanum (Figure 43), reaches the eastern extent of its range near the eastern boundary of area two. The greatest change in salamander faunas occurs in the transition from area three to the six salamander areas centered on the Blue Ridge Mountains of east Tennesse. Species that reach the eastern limits of their distributions near the eastern border of area three include: *Ambystoma tigrinum* (Figure 44), *Eurycea lucifuga* (Figure 61), *Gyrinophilus palleucus* (Figure 62), *Plethodon dorsalis* (Figure 68), and *Pseudotriton montanus* (Figure 77). Salamander species that reach western limits of distribution near the western borders of areas four, six, seven, eight, and nine include: *Desmognathus aeneus* (Figure 49), *D. imitator* (Figure 51), *D. ochrophaeus* (Figure 53), *D. quadramaculatus* (Figure 54), *D. santeetlah* (Figure 55), *D. wrighti* (Figure 57), *Eurycea junaluska* (Figure 59), *Leurognathus marmoratus* (Figure 65), *Plethodon aureolus* (Figure 66), *P. cinereus* (Figure 67), *P. jordani* (Figure 70), *P. serratus* (Figure 73), *P. welleri* (Figure 75), and *P. yonahlossee* (Figure 76). 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 in terms of north-south faunal changes is difficult. However, a few generalizations are possible. Two species, *Desmognathus aeneus* (Figure 49) and *Plethodon aureolus* (Figure 66), reach the northern limits of distribution in the northern Unicoi Mountains (area six), whereas the southern range limits of *D. santeetlah* (Figure 55) and *Plethodon jordani* (Figure 70) occur in the northern Unicois. Species whose ranges end near the southern terminus of the Great Smoky Mountains (area seven) include: *Desmognathus imitator* (Figure 51), *D. wrighti* (Figure 57), and *Leurognathus marmoratus* (Figure 65). *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 distribution of Plethodon serratus (Figure 73) occurs in area eight in mountains south of the French Broad River. The southern range limit of P. cinereus (Figure 67) also occurs in area eight, but in the mountains north of the French Broad River. Plethodon welleri (Figure 75) and Plethodon yonahlossee (Figure 76) are restricted to faunal area nine.

Seven salamander species, out of a total of 41, 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 fauna of all areas is 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).

Before a discussion of areas of homogeneity defined by all amphibian species and comparing these areas to those defined for frog and salamander species, it is important to review the Rss values given in Table 8. These values confirm what is self-evident in a comparison of

Figures 88, 91, and 94. That is, amphibian areas of faunal homogeneity more closely resemble salamander areas than they do frog areas. Stated differently, salamander distributions exerted a significantly larger influence on the determination of amphibian areas of homogeneity. 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, Bock, and Fritz (1981); and Lambert and Reid (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. Areas of faunal homogeneity for all amphibians are smaller in the Blue Ridge Mountains. This is primarily a result of 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 95, they represent the two most distinctive faunal areas. The total amphibian fauna in west Tennessee is dominated by species thought to have dispersed from southeastern, southwestern, and southern centers of dispersal. In the remainder of the state, amphibian faunal areas are predominately composed of species from an Appalachian Highlands center of dispersal. This is not unexpected because most of east Tennessee is considered part of the Appalachian Highlands.

Bock, Bock, and Fritz (1981) determined that Rss values are useful to contrast the association of environmental variables with different faunal groups, but it is inappropriate to use Rss values to rank the relative importance of environmental variables within faunal groups. In Tennessee, both faunal groups (frogs and salamanders) are most closely correlated with the same environmental variables (Table 8). These include climate, soils, and physiography. Because the geographic distributions of these environmental variables appear closely inter-related, interpretation of their relative importance to each faunal group is difficult. For example, except for soils of the major stream valleys, the boundaries of general soil areas are virtually identical to physiographic boundaries. Climatic division boundaries and physiographic boundaries are also very similar. Thus, contrasting the association of frog and salamander distributions with each environmental variable also seems inappropriate. However, one interesting comparison is that salamanders show a much stronger correlation to soils than do frogs. This is possibly due to the fact that 13 out of 41 salamander species in Tennessee are completely terrestrial in habits, while all frog species are dependent on aquatic habitats. In Illinois, Bock, Bock, and Fritz (1981) found reptilian distributions more closely correlated with climate and vegetation than were amphibian distributions. In Illinois, amphibian distributions were more strongly correlated with drainage patterns. The importance of climatic and topographic variables in Tennessee are studied in greater detail in the next subchapter dealing with species densities.

In conclusion, areas of faunal homogeneity determined during this study are compared to previously described faunal or biotic regions in Tennessee. 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 the frogs, salamanders, and amphibians of Tennessee. Hagmeier (1966) mapped three mammal provinces in Tennessee. The Louisianian Province (of southern affinity) includes a small strip of land along the entire southern border of Tennessee. Most of the rest of the state is included in the Carolinian Province. The Alleghenian Province (of northern affinity) includes a small area in the northeastern corner of Tennessee and corresponds closely to areas delineated during this study as distinct for frogs (area three), salamanders (area nine), and all amphibians (area six). Based on a subjective review of amphibian and reptilian distributions, Johnson (1958) determined two herpetofaunal districts and two zones for east 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 is characterized as possessing a northern hardwoods forest and the widespread occurrence of all color morphs of Plethodon jordani. The Summit Zone includes all peaks of the Blue Ridge Mountains above 1,368 and 1,520 m elevations. Johnson characterizes 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 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, thus, 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.

C. Species Densities

1. Methods

Another valid approach to study the distributions of amphibians in Tennessee is to analyze the relationships of environmental variables and species density. Species density is defined as the number of species per grid cell. Using the same procedures as described earlier, species densities for each grid cell were determined for frogs (FROGSD), salamanders (SALASD), and all amphibians (AMPHSD). These values are given in Figures 100, 101, and 102, respectively. Data for 17 environmental variables were tabulated for each grid cell. These environmental variables include: latitude (LAT), longitude (LONG), mean annual temperature (ANTEMP), mean maximum temperature for January (JANMAX), mean minimum temperature for January (JANMIN), mean maximum temperature for July (JULMAX), mean minimum temperature for July (JULMIN), mean annual number of days maximum temperature at or above 32^{o} C (WARMDAY), mean annual number of days minimum temperature at or below 0^{o} C (COLDDAY), average Julian date of first killing freeze in fall (FFREZ), average Julian date of last killing freeze in spring (LFREZ), mean length in days of freeze-free period (FFREE), mean annual precipitation (ANPREC), average soil temperature (STEMP), highest elevation (HELEV), lowest elevation (LELEV), and total relief (TOREL).

Using World Mapping System (WMS) software procedures of the Intergraph System, LAT and LONG were determined to the nearest tenth degree for the center point of each grid cell. Values for ANTEMP, JANMAX, JANMIN, JULMAX, JULMIN, WARMDAY, COLDDAY, FFREZ, LFREZ, FFREE, ANPREC, and STEMP were determined by overlaying a clear mylar sheet imprinted with an enlarged version of the grid cell pattern over the original maps (scale of 1cm = 10km) showing the statewide variation of each environmental variable. These original maps were reduced and appear in Chapter II as Figures 4 through 14, and Figure 17. In each

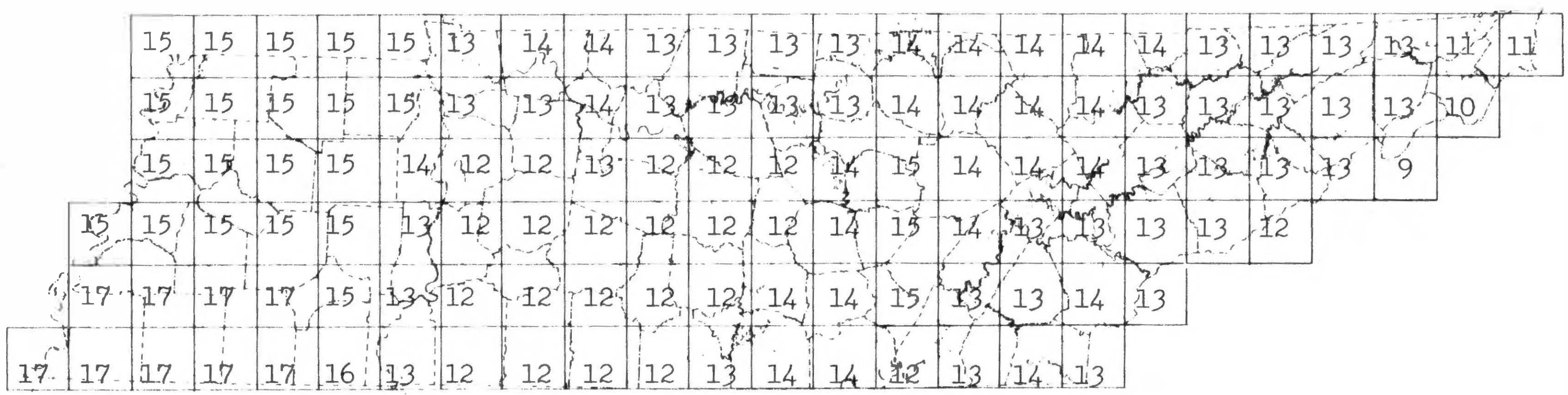

Figure 100. Density of frog species in 122 grid cells.

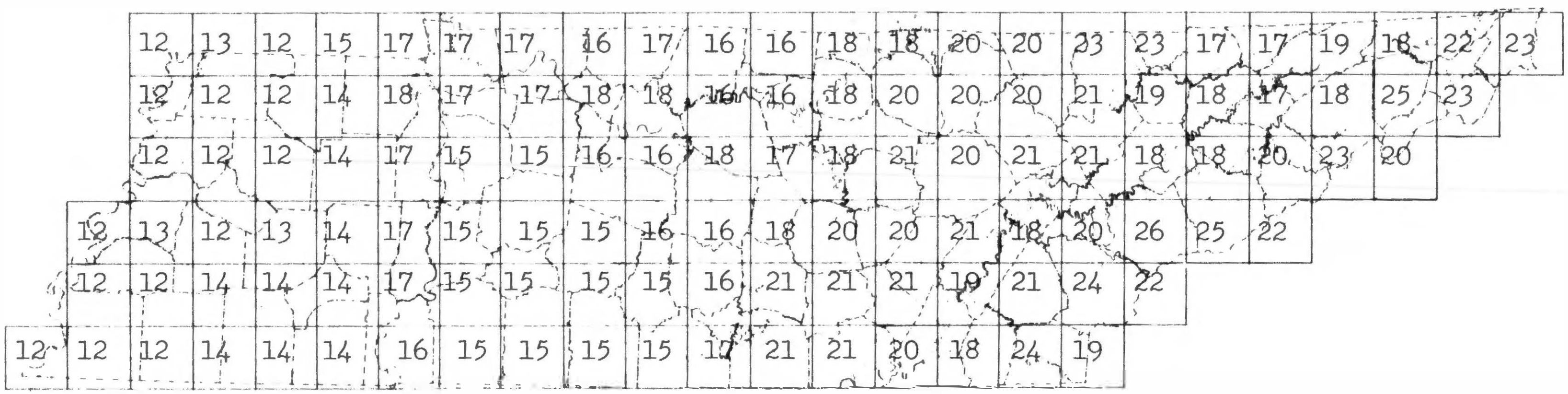

Figure 101. Density of salamander species in 122 grid cells.

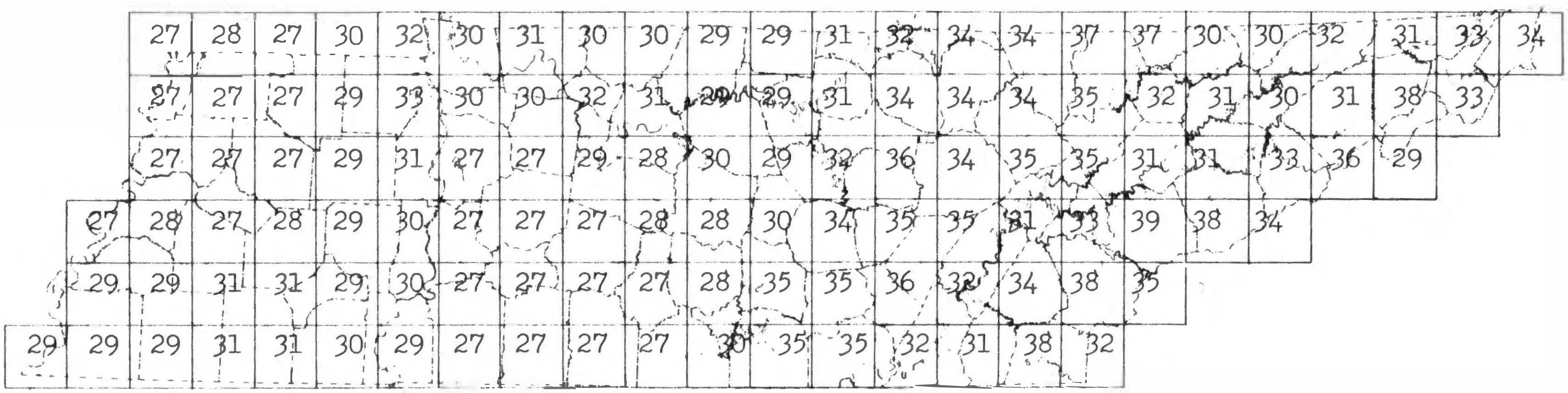

Figure 102. Density of amphibian species in 122 grid cells.

grid cell, the value for a given environmental variable was assigned the value of the isoline nearest to the center point of the grid cell. To estimate the highest elevation (HELEV) and lowest elevation (LELEV) present in each grid cell, the grid cell pattern was overlain on a topographic map of the state published by the U.S. Geological Survey (scale of 1:500,000). Elevations were converted from feet to meters. Total topographic relief (TOREL) was determined by subtracting LELEV from HELEV.

The selection and analysis of environmental variables were hampered by the limited availability of existing data in a format suitable for statistical analysis. For most of the environmental variables chosen, values in each grid cell are a rough estimation. However, broad patterns of variation for each variable are apparent and their analysis with regard to species densities should provide interpretable results.

To assess the degree of association of all pairwise combinations of variables, a bivariate correlation analysis was performed using the PEARSON CORR subprogram of SPSS (Nie, Hull, Jenkins, Steinbrenner, and Bent, 1975). Using frog (FROGSD), salamander (SALASD), and amphibian (AMPHSD) species densities as dependent variables and the 17 environmental variables as independent variables, a stepwise multiple regression was performed for each species group using the STEPWISE Regression procedure of SAS (SAS Institute, Inc., 1982). Stepwise multiple regression allowed an appraisal of the effects of the 17 environmental variables on the densities of frog, salamander, and amphibian species.

2. Results

The results of the bivariate correlation analysis of all pairwise combinations of variables are given in Table 10. Statistically significant positive correlations are denoted by a +; statistically significant negative correlations by a -; and no significant correlation by a 0. The presence of many significant correlations among the 17 environmental variables makes it difficult to interpret the significance of correlations of species densities and each of the environmental variables. With the exceptions of LAT, JANMAX, and ANPREC, FROGSD, and SALASD are significantly correlated with all environmental variables. Amphibian species density (AMPHSD) is significantly correlated with all environmental variables except LAT and JANMAX. A comparison of bivariate correlations of environmental variables with FROGSD and SALASD reveals the following general trends: (1) FROGSD increases as LONG increases while SALASD decreases as LONG increases, (2) FROGSD increases with increases in ANTEMP, JANMIN, JULMAX, JULMIN, WARMDAY, and STEMP while SALASD decreases with increases in these same variables, (3) FROGSD decreases with increases in COLDDAY while SALASD increases with increases in COLDDAY, (4) FROGSD increases as the length of the growing season (FFREE) increases while SALASD decreases with increases in FFREE, and (5) FROGSD decreases as HELEV, LELEV, and TOREL increases while SALASD increases with increases in these three variables.

A gradient representing an increase in FROGSD from east to west (increasing LONG) and a gradient representing an increase in SALASD from west to east (decreasing LONG) are visually apparent in Figures

Table 10. Summary of bivariate correlations between frog, salamander, and amphibian species densities and 17 environmental variables.[a]

	Variable (Numbers correspond to variables at left)																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
FROGSD(1)																				
SALASD(2)	-																			
AMPHSD(3)	0	+																		
LAT(4)	0	0	0																	
LONG(5)	+	-	-	-																
ANTEMP(6)	+	-	-	-	+															
JANMAX(7)	0	0	0	-	0	+														
JANMIN(8)	+	-	-	-	+	+	+													
JULMAX(9)	+	-	-	0	+	+	+	+												
JULMIN(10)	+	-	-	0	+	+	+	+	+											
WARMDAY(11)	+	-	-	-	+	+	0	+	+	+										
COLDDAY(12)	-	+	+	0	-	-	0	-	-	-	-									
FFREZ(13)	+	-	-	0	+	+	+	+	+	+	+	-								
LFREZ(14)	-	+	+	+	-	-	-	-	-	-	-	+	-							
FFREE(15)	+	-	-	0	+	+	+	+	+	+	+	-	+	-						
ANPREC(16)	0	0	+	-	0	0	0	0	0	-	0	0	-	0	0					
STEMP(17)	+	-	-	-	+	+	+	+	+	+	+	-	+	-	+	-				
HELEV(18)	-	+	+	0	-	-	0	-	-	-	-	+	-	+	-	0	-			
LELEV(19)	-	+	+	+	-	-	-	-	-	-	-	+	-	+	-	0	-	+		
TOREL(20)	-	+	+	0	-	-	0	-	-	-	-	+	-	+	-	+	-	+	+	

[a]The Pearson correlation coefficient was used. Significant positive correlation is denoted by a +; significant negative correlation by a -; and no significant correlation by a 0. Level of significance was 0.05.

100 and 101, respectively. That these two faunal gradients show opposing trends in direction is supported by the negative correlation between FROGSD and SALASD, the negative correlation between LONG and SALASD, and the positive correlation between LONG and FROGSD. A visual inspection of the figures provided in Chapter II and a comparison of the number of environmental variables that are significantly correlated with LONG (13) with the number significantly correlated with LAT (8), indicate that the predominant environmental gradients in Tennessee also occur in an east-west direction. A comparison of correlations of FROGSD and SALASD with each environmental variable indicates that frog and salamander faunas exhibit diametrically different responses to ANTEMP, JANMIN, JULMAX, JULMIN, WARMDAY, COLDDAY, FFREZ, LFREZ, FFREE, STEMP, HELEV, LELEV, and TOREL.

The results of stepwise multiple regression analysis are presented in Table 11. Of the 17 environmental variables considered, LONG was the best predictor of FROGSD and accounted for 33 percent of the variation in FROGSD. Listed in order of importance LONG, WARMDAY, LFREZ, ANTEMP, JULMIN, FFREE, COLDDAY, JANMIN, JANMAX, LELEV, AND ANPREC accounted for 60 percent of the variation in FROGSD. Longitude (LONG) was also the best predictor of SALASD and accounted for 71 percent of the variation in SALASD. In combination, LONG, TOREL, WARMDAY, LFREZ, JULMIN, ANTEMP, and STEMP accounted for 85 percent of the variation in SALASD. Forty-nine percent of the variation in AMPHSD was accounted for by TOREL. The combination of TOREL, ANTEMP, JULMIN, STEMP, JULMAX, LFREZ, and ANPREC accounted for 66 percent of the variation in AMPHSD.

Table 11. Results of stepwise multiple regression of environmental variables and frog, salamander, and amphibian species densities.

Frogs			Salamanders			Amphibians		
Step	Variable	R^2	Step	Variable	R^2	Step	Variable	R^2
1	LONG	0.33	1	LONG	0.71	1	TOREL	0.49
2	WARMDAY	0.38	2	TOREL	0.77	2	ANTEMP	0.55
3	LFREZ	0.42	3	WARMDAY	0.81	3	JULMIN	0.61
4	ANTEMP	0.48	4	LFREZ	0.82	4	STEMP	0.62
5	JULMIN	0.51	5	JULMIN	0.83	5	JULMAX	0.64
6	FFREE	0.53	6	ANTEMP	0.84	6	LFREZ	0.65
7	COLDDAY	0.54	7	STEMP	0.85	7	ANPREC	0.66
8	JANMIN	0.56						
9	JANMAX	0.57						
10	LELEV	0.59						
11	ANPREC	0.60						

3. Discussion

In terms of the 17 environmental variables studied and in view of the above generalizations, it is concluded that the major environmental and amphibian faunal gradients in Tennessee trend in an east-west direction and frog and salamander faunas have responded differently to the environmental gradients. Because gradients in FROGSD and SALASD appear to be the result of diametrically different responses to environmental gradients, the remaining discussions focus on these two groups. Where appropriate, existing theories regarding the formation of species density gradients are discussed and, where possible, comparisons with the results of similar studies are provided. Comparisons with the results of other studies were hampered because most previous authors studied species density gradients in terms of the total amphibian fauna.

In Tennessee, FROGSD is positively and SALASD is negatively correlated with LONG and according to the stepwise multiple regression analysis, LONG is the best predictor of both. Frog species density (FROGSD) and SALASD are significantly negatively correlated. This is contrary to the findings of Schall and Pianka (1978). They determined that in the United States, salamander and frog species densities are positively correlated. The geographic scale of their study and their use of large sampling units (10,500 km^2) probably precluded identification of relationships occurring in relatively smaller geographic areas. In many respects, this longitudinal relationship between FROGSD and SALASD parallels the longitudinal trends of North American reptile and mammal species densities noted by Kiester (1971) and discussed by

Schall and Pianka (1978). Kiester described the negative correlation between reptile and mammal species densities from west to east across North America as due to the fact that mammal diversity is higher and reptile diversity lower in the Sierra Nevada, Rocky, and Appalachian mountains, while reptile diversity is higher and mammal diversity is lower in the Great Basin, Mississippi Valley, and the Eastern Coastal Plain. Similarily, within the confines of Tennessee, FROGSD is higher and SALASD is lower in the lowlands of west Tennessee, while SALASD is higher and FROGSD is lower in the Appalachian Mountains of east Tennessee. To explain the complementarity between mammal and reptile densities, Kiester suggested that two questions regarding four distributional phenomena must be answered. Modified to fit the context of this study, Kiester's questions are: (1) why is FROGSD higher in the lowlands of west Tennessee and (2) lower in the Appalachian Mountains of east Tennessee, and (3) why is SALASD higher in the Appalachian Mountains of east Tennessee and (4) lower in the lowlands of west Tennessee. Although LONG is the best predictor of these effects, it is not clear what environmental or evolutionary factor or factors are underlying the observed correlations. There are numerous existing theories that attempt to explain gradients in species densities. These are summarized by Krebs (1972), Pianka (1983), and Schall and Pianka (1978).

Given the diametric nature of FROGSD and SALASD in Tennessee, the first theory that seems appropriate deals with competition (Kiester, 1971; Schall and Pianka, 1978). According to this theory, competition between salamanders and frogs may have contributed to the formation of their density gradients. With the exception of several species of plethodontids, both salamander and frog species in Tennessee are ecologically tied to aquatic or semiaquatic habitats. This is especially true of larval forms. Schall and Pianka (1978) noted the potential for intertaxa competition between larval forms in small ponds, but did not consider it a major influence in determining frog and salamander species gradients in the United States. Unfortunately, there is very little data regarding competitive interactions between frogs and salamanders, and none for Tennessee. Thus, the role of competition is unknown and cannot be evaluated.

According to the evolutionary time theory, older communities have been subjected to longer periods of evolution than younger communities and therefore the former possesses greater species diversity. This theory can be used to explain the gradient of high SALASD in the relatively old Appalachian Mountains of east Tennessee to low SALASD in the relatively younger Coastal Plain of west Tennessee. However, this only answers one of Kiester's two questions, and the evolutionary time theory must also account for the gradient of FROGSD. The gradient of FROGSD runs counter to the predictions of this theory. Attempts to explain FROGSD and SALASD gradients in Tennessee in terms of other theories of species diversity (ecological time, climatic stability, climate predictability, spatial heterogeneity, productivity, stability of primary production, rarefaction, and predation) suffered from the same shortcomings as attempts using competition and evolutionary time theories. Either existing data were not available and no evaluation was possible or predictions that were valid for SALASD were invalid for

FROGSD and vice versa. Schall and Pianka (1978) stated that most modern explanations of species gradients utilize portions as well as combinations of existing theories and that proposed explanations maybe modified by historical factors. This is the approach taken here. Because many important factors were not evaluated or were poorly portrayed by the chosen variables, the following discussions of FROGSD and SALASD must be considered tentative and limited in scope.

As previously discussed, the majority of frog species in Tennessee are thought to be of southern origin and are primarily adapted to warm climates (Blair, 1958, 1965). Their centers of dispersal and possibly centers of origin are extraneous to Tennessee and their dispersal into Tennessee is thought to have occurred via the Mississippi River Valley in west Tennessee. That most frog species in Tennessee are adapted to warm climates is supported by the positive correlations of FROGSD with variables (ANTEMP, JANMIN, JULMAX, WARMDAY, FFREZ, FFREE, STEMP) whose increase denotes warmer climates. Conversely, FROGSD is negatively correlated with variables (COLDDAY, LFREZ) whose increase denotes cooler climates. Ranking behind LONG, 10 climatic variables were the best predictors of FROGSD. Correlations between LONG and the environmental variables also reveal that climates tend to be warmer in west Tennessee and cooler in east Tennessee. Considering the historical aspects of the evolution and dispersal of frog species and the west to east gradients of FROGSD and environmental variables associated with climate, it is possible to interpret FROGSD changes in Tennessee in terms of the evolutionary and ecological time theories. Both theories propose that species diversity increases with the age of the community. In regard to the frog faunas, habitats in west Tennessee may be considered older than those in east Tennessee both in regard to evolutionary and ecological age. It is proposed that warming climatic conditions following the last major glacial retreat allowed many frog species to disperse northward into west Tennessee. Also, this warming trend allowed frog species, that during glacial maxima were restricted to west Tennessee, to disperse eastward. Thus, frog communities in west Tennessee can be considered older than those in east Tennessee.

In contrast to frog species, salamanders are principally northern in origin and are adapted to cool climates (Blair, 1958, 1965). The majority of species that occur in Tennessee had their center of origin and dispersal in the Appalachian Highlands, which includes most of east Tennessee. Correlations between SALASD, LONG, and those environmental variables dealing with climate support the contention that salamanders as a group are adapted to cool climates and their densities decrease from east to west across Tennessee. This trend in SALASD can also be explained in terms of the evolutionary and ecological time theories. Habitats in east Tennessee can be considered older than those in west Tennessee both geologically and in regard to historical aspects of the dispersal of salamander species. As indicated by the stepwise multiple regression, TOREL (topographic relief) was the second best predictor of SALASD. Topographic relief (TOREL) is considered to be a rough estimator of habitat diversity (Rogers, 1976; Hammerson, 1981) and, in Tennessee, it is positively correlated with SALASD and negatively correlated with LONG. According to the spatial heterogeneity theory, environments that are structurally complex have greater species diversity than less complex environments. When considering topographic relief, Lee (1980) suggests macrospatial heterogeneity as an appropriate term. As summarized by Lee, areas with greater topographic relief are likely to contain more habitats and possess more characteristics that promote speciation than areas with less relief.

CHAPTER VI

SUMMARY AND CONCLUSIONS

The environmental setting of Tennessee is described in terms of geology, physiography, climate, drainages, soils, vegetation, and ecoregions. Each environmental feature is described and mapped. Accounts for 20 species of frogs and 41 species of salamanders are provided. Accounts include descriptive, taxonomic, distribution, and habitat information. With the exceptions of *Hyla versicolor* and *H. chrysoscelis*, a range map is provided for each species. Previous reports of *Bufo terrestris, Hyla squirella, Necturus beyeri*, and *Ambystoma jeffersonianum* are considered erroneous.

Geologic, climatic, and evolutionary events of the past have played an important role in the development of the present-day distributions of amphibians in Tennessee. The amphibian fauna of Tennessee during the Mesozoic possibly included ancestral forms of the families Pelobatidae, Ambystomatidae, Amphiumidae, Plethodontidae, Sirenidae, Necturidae, and Cryptobranchidae. Early Tertiary additions to the fauna of Tennessee included Bufonidae, Hylidae, Microhylidae, Ranidae, and Salamandridae. Most modern genera and species groups were present at the beginning of the Pleistocene. Pleistocene and post-Pleistocene climatic and vegetation shifts were major factors shaping current distribution patterns. Modern amphibian species of Tennessee are tentatively grouped according to their proposed North American center of dispersal. Major centers of dispersal include the Appalachian Highlands; eastern Atlantic Coast; southeastern, southwestern, southern, and northern North America.

For the purposes of statistical analyses, the amphibian species of Tennessee are organized into three faunal groups. These groups include frog species, salamander species, and all species grouped together as amphibians. The dispersion pattern of all three faunal groups is determined to be clumped. At the 0.80 level of similarity, three areas of faunal homogeneity are determined for frog species, nine for salamander species, and six for total amphibian species. The distribution of indices of faunistic change (IFC values) for each faunal group supports the validity of these areas. Frog areas of faunal homogeneity are dominated by species that dispersed from southeastern, southwestern, and southern centers of dispersal. With the exception of area one (Coastal Plain), areas of faunal homogeneity for salamanders are dominated by species with an Appalachian Highlands center of dispersal. The six areas of faunal homogeneity for amphibian species are considered as a summary of the biogeographic patterns of frogs and salamanders. Of the geographic patterns exhibited by six environmental variables, climate, soils, and physiography are most closely correlated with both frog and salamander distribution patterns. Areas of faunal homogeneity determined for Tennessee bear little resemblance to biotic and faunal provinces proposed by previous authors for Tennessee or areas which include Tennessee.

The relationships of 17 environmental variables with frog, salamander, and total amphibian species densities are analyzed. Frog species density increases from west to east while salamander density increases from east to west. The predominant environmental gradients in Tennessee also occur in a west to east or an east to west direction. Frog and salamander faunas exhibit diametrically different responses to a majority of the environmental gradients studied. This complementarity between frog and salamander species densities made it difficult to interpret species densities in terms of existing theories of species diversity. Therefore, these discussions focused on each species group separately. Because many important factors could not be evaluated or were poorly portrayed by the chosen variables, interpretations are considered tentative and limited in scope. By accounting for historical factors and considering current environmental gradients, certain aspects of the evolutionary and ecological time theories can account for the observed gradients in frog and salamander species densities. For salamander species, factors associated with macrospatial homogeneity may have played a role in determining species densitites.

Frog and salamander faunas of Tennessee exhibit significantly different biogeographic patterns. This was evident in a delineation of areas of faunal homogeneity and an analysis of species densities. Interpretation of results from analyses of the total amphibian fauna would have obscured the unique characteristics of each faunal group.

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VITA

William H. Redmond, Jr., son of William Hal Redmond, Sr., and Sarah Nell (Poston) Redmond, was born in Jackson, Tennessee, on September 3, 1949. He attended grammar and high school in Maury City, Tennessee. From September, 1967, to June, 1968, he attended Freed-Hardeman College, Henderson, Tennessee. In September, 1968, he enrolled at Auburn University, Auburn, Alabama, and received a Bachelor of Science degree in June, 1971 and a Master of Sciences degree in June, 1975. After completion of the Army ROTC Program at Auburn University, he was awarded a reserve commission as a 2nd Lieutenant in the Transportation Corps, U.S. Army and he is currently a Captain in the U.S. Army Reserve. In September, 1975, he enrolled in the University of Tennessee Graduate Program in Ecology and also became a part-time employee for the Office of Natural Resources, Tennessee Valley Authority (TVA). In March, 1979, he became a full-time employee for TVA's Natural Heritage Project as a Biologist responsible for zoological research activities. In April, 1981, he was reclassified as an Environmental Scientist and became Data Base Coordinator for the Natural Heritage Project. Currently he serves as Project Manager for the Natural Heritage Project. He received a Ph.D. degree with a major in Ecology from the University of Tennessee in December, 1985.