A BIOGEOGRAPHIC STUDY OF THE
HERPETOFAUNA OF EASTERN TENNESSEE

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PREFACE

The only extensive survey that has been made of the total herpetofauna of the Great Smoky Mountains region is that of King (1939). This seems strange inasmuch as the Southern Appalachian Mountains have aroused the imagination of biogeographers as a possible refugium for northern biota during Pleistocene glaciation. I believe this lack of further study of the total herpetofauna may be attributed to at least two factors. First, the wealth of species of salamanders in eastern Tennessee has usurped the attention of most of the herpetologists working in this region. Second, I believe that herpetologists generally accept the work of King as definitive and tend to infer from his data the composition of the herpetofaunas of contiguous areas.

Since King's work, numerous intensive investigations have been conducted on various elements of the herpetofauna of the Great Smoky Mountains area. As mentioned above, most of these have been concerned with the salamanders, especially those occurring at the higher elevations. Little attention has been given to the herpetofauna of the mountain ranges to the north and south of the Great Smokies or to the herpetofaunas of the Valley of East Tennessee and the Cumberland Plateau to the west. Further, many of the existing distribution maps show the northern periphery of the ranges of "southern" amphibians and reptiles as coincident with the topographically defined physiographic province boundaries in eastern Tennessee and northern Georgia. This

lack of information on the total herpetofauna outside the limits of the Great Smoky Mountains area, and my lack of confidence in the validity of available definitions of the northern limits of ranges of southern amphibians and reptiles, have suggested the need for a study such as the present one.

This study has been an attempt to define and show the geographical distribution of distinctive assemblages of amphibian and reptile species in a physiographically diversified area. Specifically, I have endeavored (1) to determine insofar as practicable the specific and sub-specific identity of the various elements of the herpetofauna, (2) to determine if these various taxa exist in distinct assemblages which can be correlated with the macroenvironmental factors of climate, forest types, soil types, topographic features, and human activities, and (3) to test and propose biogeographic hypotheses concerning the herpetofauna of eastern Tennessee. This study cannot be considered as definitive. In fact, it has proposed more problems than it has solved. Many of these additional problems will not be answered until more is known of the ecology of the various animals involved and until paleontological information concerning the herpetofauna of eastern Tennessee during the Pleistocene Epoch becomes available.

I wish to express my gratitude to Dr. Archie Carr and Dr. H. K. Wallace, co-chairmen of my Supervisory Committee, and Dr. Arnold B. Grobman, Dr. William J. Riemer, and Dr. Richard A. Edwards, members of this committee. I am appreciative of their assistance, encouragement, and patience during this study and during the preparation of this paper.

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Last, but not least, I wish to thank Dr. LeRoy A. Martin, President, Tennessee Wesleyan College, for the encouragement and help that made it possible for me to carry out this study.

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I. INTRODUCTION

The herpetological material upon which this study is based is that which I have collected. Terrestrial forms were taken by the usual methods of turning logs, rocks, boards, and brush as well as by searching out those foraging in the open. Aquatic forms were collected with seine, hook-and-line, traps, and by swimming with a face mask. The last method was possible only in the mountain rivers and streams where clear water is found. Practically all of the specimens collected and examined during the course of this study have been deposited in the University of Florida Collections.

This study was not primarily taxonomic in nature, and relatively few comparative series of specimens were examined. Such series as were utilized were obtained from the University of Florida Collections. If the procedure had been followed of comparing all my specimens with topotypic material of the same species, the revisionary work involved would have diverted unreasonable amounts of time from the main objective of this study. The majority of my specimens have been identified by the use of existing literature and references. The origins of names are given in the text. In those instances where I was dissatisfied with a literature identification, I utilized comparative series. Even so, I was occasionally unable to arrive at a satisfactory identification. Instead of attempting to find new characters or to refine the existing characters--which procedure would have taken me too far afield

for the scope of this work--I have indicated the status of such series as questionable. These specimens have not been utilized in the biogeographic analysis, or have been used with qualifying statements appended.

Specimens of three genera of salamanders and one species of snake were collected by me but referred to others for identification. All specimens of the genus Plethodon (Woodland Salamanders) which I collected were given to Richard Highton and the species and subspecies of this genus which are reported as occurring in eastern Tennessee are included on the basis of his monographic study of this genus (Highton, MS). The genera Desmognathus (Dusky Salamanders) and Leurognathus (Shovel-nosed Salamanders) were omitted from this study. A brief statement is given concerning which species of these two genera are reported as occurring in eastern Tennessee (vide page 39). All of my specimens of the genus Haldea (Earth Snakes) were given to Miss Louise D. Zillig, who is engaged in a review of this genus.

The general taxonomic arrangement is that of Schmidt (1953). The common names used in the text are taken from Conant, et al. (1956).

Localities and elevations at which the specimens were collected were determined from topographic maps available from the Tennessee Valley Authority. The maps used were the following: Tennessee-North Carolina Quadrangle, 15 Minute Series; Tennessee-North Carolina Knob Quadrangle; Johnson City, Sheet MJ 17-10, Series V501; Knoxville, NI 17-1, AMS Series V501; Chattanooga, NI 16-3, AMS Series V501; Rome, NI 16-6, AMS Series V501; Great Smoky Mountains National Park and Vicinity, Edition of 1950, N3515-W 8300/35,5X67.5

The distribution maps indicate localities from which I have personally collected specimens and localities reported in the literature. On these maps the localities from which I have taken specimens are indicated by solid symbols; literature records are indicated by hollow symbols.

Thorntwaite (1948) presented a complicated system for classifying climate based upon mean annual, monthly and seasonal temperature, rainfall, and calculated runoff and evaporation. Shanks (1954) found good agreement between climate calculated by this method and the distribution of the spruce-fir forests of the high altitudes in the Great Smoky Mountains. Daubenmire (1956), on the other hand, was unable to find distinctness of climate among the belts of natural vegetation in eastern Washington and northern Idaho when the climate of these regions was calculated by the Thorntwaite 1948 system. Early in this study I used the Thorntwaite system to analyse the climatic data of eastern Tennessee. This system was abandoned when I was unable to obtain correlation between the resulting climatic areas and the distributions of the forest regions and soils groups. For example, climatic designation of the Cumberland Mountains region, where mixed mesophytic forest is climax, was the same as the climatic designation of the southern and of Valley where oak and hickory forests are climax. Daubenmire (loc. cit.) did find climatic distinctness among belts of natural vegetation in his study area by plotting climographs of mean monthly temperature and the median monthly rainfall. Although somewhat modified, I have used Daubenmire's method in presenting climatic data for my study area (Figs. 4 and 5).

The data utilized in an appraisal of the climate were furnished by the Tennessee Valley Authority. The weather stations selected are shown in Figure 1. Crossville, elevation 1,862 feet, represents the Cumberland Plateau; Knoxville, elevation 950 feet, Newport, elevation 1,096 feet, and Rogersville, elevation 1,375 feet, represent the northern segment of the Valley Province; Decatur, elevation 800 feet, and Chattanooga, elevation 670 feet, represent the southern segment of the Valley Province; Gatlinburg, elevation 1,460 feet, represents the lower slopes of the Unaka Mountains Province. The data for the northern segment of the Valley are mean values of the combined data from Knoxville, Newport, and Rogersville. The data for the southern segment of the Valley are mean values of the combined data from Decatur and Chattanooga.

Fig. 1.--Locations of weather stations from which data were obtained to construct Figures 4 and 5.

II. THE STUDY AREA

A. Physiography

The area called eastern Tennessee is not identical with the political subdivision "East Tennessee." The latter is only that portion of the state east of the western boundaries of Scott, Marion, and intervening counties (Rodgers, 1953: 3). As used in this study, eastern Tennessee is the area from the western escarpment of the Cumberland Plateau eastward to the summits of the Unaka Mountains (Fig. 2). The total area involved is approximately 14,700 square miles (Luebke, et al., 1939: 6-8).

There are three physiographic provinces in eastern Tennessee. Except as noted, the following descriptions of these provinces are summarized from Luebke, et al. (loc.cit.) and Rodgers (op. cit.).

The Cumberland Plateau Province comprises approximately 4,500 square miles of the study area. At the northern boundary, the Plateau is about 70 miles wide; the width of the southern boundary is about 50 miles. For the most part, the surface of the Plateau is undulating and submaturely dissected, with the steepness and depth of the valleys increasing toward the edges (Fenneman, 1938: 377). A characteristic feature of much of the Plateau is the entrenchment of many of the major streams to depths of as much as 200 to 300 feet below the surface of the Plateau. The resultant gorges have nearly vertical walls and may be a quarter of a mile in width. These features have resulted in the naming of this area the Cliff Section of the Plateau (Breun, 1950:97-98).

Fig. 2.--The physiographic provinces, political subdivisions, and principal rivers and streams of eastern Tennessee (modified from Luebke, et al., 1939).

From the Emery River northeastward to the Virginia line, the eastern front of the Plateau is separated from the main body of the tableland by a valley or line of valleys. This is the Cumberland Mountain Section of the Plateau (Fenneman, 1938: 329). This area is strongly dissected and contains some of the most rugged mountains of eastern Tennessee. Here, too, are the highest elevations of the Plateau. Some of the mountain summits and watershed divides are more than 3,000 feet in elevation. Most of the surface of the main body of the Plateau is at an elevation of 2,000 feet. The southern end of the Plateau, like the Cumberland Mountain Section, is in a more advanced stage of dissection than is the central portion. No flat upland occurs in the southernmost 30 or 40 miles (Fenneman, 1938: 338). The western front of the Plateau is quite ragged, with long spurs jutting out into the Highland Rim Province. Between these spurs are deep coves and valleys locally termed "gulfs." In contrast is the relatively smooth, straight edge of the eastern front, which for much of its length is a sheer cliff rising 1,000 feet above the Valley of East Tennessee. The entire eastern front, from the Tennessee River on the south to Cove Creek valley in Campbell County on the north, is known as Walden Ridge.

In the middle of the southern half of the Plateau is the Sequatchie Valley, an anticline approximately six miles wide and 60 miles long. It is entrenched 1,000 feet below the surface of the Plateau.

The surface of the Plateau is underlain by the Walden and Look-out sandstones of Pennsylvanian age. Beneath these is Bangor limestone of Mississippian age, which forms the floor of the larger valleys such

as Sequatchie Valley. The steepness of the cliffs in the Cliff Section and of the eastern and western escarpments is due to the sapping of these sandstones and limestone.

To the east of the Cumberland Plateau is that portion of the Ridge and Valley Province of Fenneman (1938: 195) locally known as the Valley of East Tennessee. It is the largest of the physiographic provinces in eastern Tennessee. It varies from 45 to 70 miles wide, with the greatest width occurring in the northern part, and is approximately 8,000 square miles in area. Ridges constitute less of the total area than do valleys (Fenneman, 1938: 265). However, there is little flat surface, most of it being dissected into valleys between ridges and knobs of varying elevations. The most level surfaces of the Valley floor occur in narrow strips five to six miles wide along the Tennessee and Hiwassee rivers (Fenneman, 1938: 271-272). This flat surface is about 800 feet in elevation and represents northern extensions of the Coosa penplain more extensively developed in Alabama and Georgia. Safford described five types of ridges in the Valley (quoted in Rodgers, 1953: 14-16). The differences among these types of ridges is the result of differences in lithology, which also has resulted in differences of natural fertility of the soil. These differences in natural soil fertility are reflected in differences of prevailing vegetation on the ridges. Thus, ridges with soils derived from sandstones have (had) forests composed principally of oaks and chestnut.

The valleys between the ridges do not lend themselves to generalized characterizations. Some are narrow and overlooked by mountains.

Others are sandwiched between a mountain and a conby ridge and have consistently barren acid soils derived from noncalcareous shales. Still others, often on the opposite side of a mountain from the above type, are fertile and rich.

Inliers of the Valley occur in the western portion of the mountain province, especially in the Smoky Mountains range. These are relatively flat-floored limestone valleys ranging from five to ten square miles in area and from 1,200 to 1,800 feet in elevation (Fenneman, 1938: 175). Surrounding them are mountains several thousands of feet higher. The surfaces of the coves (inliers) are presumed to represent Harrisburg peneplain surfaces. Among the better known of these coves are Wear, Cades, and Tuckaleechee.

Bordering the eastern margin of the Valley is the Unaka Mountains Province of eastern Tennessee. (Terminology is that of Keith, "Message from the President . . .," 1902: 114). The mountains of this province are the western front, in part, of the Southern Section of the Blue Ridge Province of Fenneman (1938: 173-174). This Unaka Province ranges from two to 20 miles in width and embraces an area of approximately 2,200 square miles. The mountains are a series of from two to five parallel ridges. The main axis is the most easterly one and for much of its length this straddles the Tennessee-North Carolina state line. Several names are applied to various segments of the main axis. Beginning in the southwest and proceeding northeastward these segments are: (1) the Unaka (Frog) Mountains, from Georgia to the Little Tennessee River, (2) the Great Smoky Mountains, from the Little

Tennessee River to the French Broad River, (3) the Bald Mountains, from the French Broad River to the Nolichucky River, (4) the Unaka Mountains, from the Nolichucky River to the Watauga River, (5) the Iron Mountains, from the Watauga River into Virginia (Keith, in "Message from the President . . .," 1902: Pl. IV). The maximum elevations of the Unaka Province, including some of the highest peaks in Eastern United States, are to be found in the Great Smoky Mountains. From these maximum elevations (in excess of 6,000 feet) in the Smoky Mountains, the Unakas have progressively lower summits in all directions. The westernmost edge of this province south of the French Broad River is prominently delimited by a series of outlying isolated mountains arranged in a linear series. These include (from southwest to northeast) Starr, Chilhowee, and English mountains. The lowest of these is Starr Mountain with an elevation of about 2,500 feet. The highest is English Mountain with a maximum elevation near 3,600 feet. The entire series is named the Chilhowee Range, after Chilhowee Mountain which is the longest of the group (Safford and Killebrew, 1900: 14-15). None of the various ranges included in the Unaka Province is continuous. There are seven rivers, all tributaries to the Tennessee River, which cut the Unakas into segments (Safford and Killebrew, 1900: 16). These rivers frequently have steep cliffs along their courses through the mountains, and, according to Safford and Killebrew, were untraversable to travelers until about the turn of the century (loc. cit.: 15).

Fenneman (1938: 174) describes these mountains as subdued, with summits commonly rounded and domes abundant. Crags, bare cliffs, and

talus slopes are rare. "The slopes of the Unakas, . . . are fairly steep on both sides, ranging generally from 20 to 50 degrees. About the interior ridges there is still greater variation. Some of the rocky faces are precipitous, while elsewhere the slopes are very gentle, ranging from 5 to 20 degrees. But taking the mountains and the valleys together, the land surface with a slope of less than 10 degrees is not more than 10 per cent of the whole" ("Message from the President . . .," 1902: 21). "The mountainous relief of this Appalachian region is due entirely to erosion in late Cenozoic time, after upwarping of the Schooley peneplain" (Moore, 1949: 411). Ashley (1930: 700) stated that the uplift of the Schooley peneplain occurred some 9,000,000 years ago, at least not before Miocene time. Fenneman (1938: 256) concurs in postulating a late or post-Miocene uplift of the Schooley surface.

Remnants of the Schooley surface persist in the southern end of the Unaka Province on summits at elevations of about 3,100 feet; to the north it is represented by summits from 3,800 to 4,000 feet high (Fenneman, 1938: 186-187). Braun (1950: 494) considered the uplift of the Schooley peneplain an important factor in the interpretation of the history of the Deciduous Forest Formation. Aside from the possible effects upon the biota of the upwarping per se is the fact that in the region of the Southern Appalachian Mountains numerous monadnocks and mountains hundreds of feet high surmounted the Schooley peneplain (vide Fenneman, 1938: 172). Thus, such high mountain peaks as Mt. Collins (6,400 feet), Mt. Guyot (6,636 feet), and Mt. LeConte (6,660 feet) must have been present in pre-Miocene time, possibly since early Cenozoic.

Although numerous post-Schooley cycles have been postulated, most of them were only of local significance (Fenneman, 1938: 188), and Braun (1950: 494) does not consider these postulated minor cycles as of general significance to the history of the Deciduous Forest Formation. The post-Schooley erosion cycle, termed the Harrisburg, is accepted by Braun as occupying the interval from the upwarp of the Schooley until the second major uplift at the close of the Pliocene. This second major uplift was the uplift of the Harrisburg surface.

B. Soils

Three types of mantle are recognized in eastern Tennessee (Rodgers, 1953: 115-119). The most widespread of these is residuum, which ranges in thickness from ten to hundreds of feet. A second type, locally transported material, accumulates in swales, sinkholes, small hollows, larger creek valleys, and areas adjacent to steeply rising slopes. The third type of mantle is river alluvium. Along the major rivers this has accumulated to depths as great as 40 feet and consists in large part, especially near the surface, of silty sand or silty loam. Similar alluvial deposits occur on terraces as high as 400 feet above the present course of the entrenched river. This terrace alluvium differs most from that of the present flood plain in being strongly leached and oxidized. The alluvium along present flood plains is presumed to have been deposited in historic times (Rodgers, loc. cit.). Terrace alluvium is considered to be of Pleistocene age, as are the large aprons of rock and talus mentioned above.

The soils of eastern Tennessee may be grouped into five associations (Fig. 3). The Hartsells-Muskingum and Muskingum-Lehew associations are azonal lithosols. These are immature soils developed over sandstones and shales. They are stony soils with frequent outcrops of sandstone and shale, medium to strongly acid in reaction, and low in mineral nutrients and organic matter. The Hagerstown-Frederick and Porters-Ash associations are mature zonal soils of the Gray-Brown Podzolic group. Parent materials of the Hagerstown-Frederick association are limestones and dolomitic limestones with some shales. Parent materials of the Porters-Ash association are granites, gneisses, and schists, with some dark-colored basic rocks. The soils of each of these associations have fair amounts of mineral nutrients and organic matter and are medium to strongly acid in reaction. The Decatur-Dewey-Clarksville association is a group of mature zonal Red and Yellow Podzolic soils. The parent materials are limestones, and dolomitic and cherty limestones. These soils are generally strongly leached, low in mineral nutrients and organic matter, and acid in reaction. For more detailed accounts of these soil associations, the reader is referred to the "Yearbook of Agriculture" (1938).

C. Drainage

The following account of the rivers and streams of the mountain province are from "Message from the President . . ." (1902: 28-30).

Probably no region in the United States is better watered or better drained than this Southern Appalachian Region; nor is there any region which can boast of being the source of so many streams. . . .

.....

Fig. 3.--General soils types of eastern Tennessee (from "Yearbook of Agriculture: 1938").

In the mountains themselves these streams have their sources at elevations from 3,000 to 6,000 feet, and before reaching a level of 2,000 feet many of them have reached considerable proportions. They subsequently flow across the mountain region for distances of from 20 to 50 miles before breaking through the border ranges onto the surrounding lowlands at elevations ranging from 1,000 to 1,200 feet. Along their courses stretches of smooth water are never long, and the descent is often accomplished by numerous rapids, cascades, and falls. . . . Such cascades, with descent in short distances of from 10 to 50 feet, are abundant, while in some of the smaller tributaries beautiful falls of from 100 to 300 feet are to be found.

.
No gorges in eastern America can equal in depth and wildness those carved across the Blue Ridge and the Unakes by these streams in making their way through the marginal ranges of the Southern Appalachians. . . .

But notwithstanding the steepness of the slopes of these gorges, even where descent is almost precipitous, they are forest-covered except where the trees and shrubs have been destroyed by fire and the soil has been removed by the storms.

Except where dams have resulted in the impoundment of some of the rivers and streams and where deforestation has been increased, these descriptions hold for present-day conditions.

In contrast to these mountain water courses are those of these same rivers and streams in the Valley. The major rivers, e.g., Hiwassee, Little Tennessee, and the Big Pigeon, leave the mountain province at elevations around 1,000 feet and enter the Tennessee River at elevations ranging from 700 to 900 feet. Except where knobs and ridges have been breached, relatively level flood plains up to several miles in width have developed. The courses of these rivers through the Valley are winding and in some places resemble entrenched meanders. The banks are steep and eroding as a result of being cut into the deep residual soils. Shoals and bars are of frequent occurrence. At all

times the water is slightly turbid and the current moderate to strong. As a result of the system of the Tennessee Valley Authority dams, the mouths of many of these tributaries to the Tennessee River are now drowned.

These impounded areas, including the backwater immediately behind the dams, are known locally as lakes and resemble lakes in physical appearance. A lakelike appearance is enhanced by cattails and bulrushes in the shallows; by turtles basking on logs and protruding stumps and snags; by shorebirds and ducks working in the shallows and along the shorelines.

Before impoundment, the width and depth of the channel of the Tennessee River were extremely variable along its course and at different seasons of the year. It is recorded that DeSoto and his army forded this river in the vicinity of Chattanooga. At Knoxville a flood flow of nearly 100 times its normal flow has been recorded. The gorge of the Tennessee River through Walden Ridge was a 30-mile stretch of narrow rapids variously termed the Narrows, the Suck, the Boiling Pot, and the Frying Pan. From the western end of the gorge to Muscle (or Mussel) Shoals was a 38-mile stretch of wide, shallow water with numerous eddying pools. Muscle Shoals had a fall of three and one-half feet per mile and is described as having been a series of rapids dotted with islands and segmented by reefs and bars.

The above accounts have been summarized from Davidson (1946: 12-16) and Williams (1937: 31-32).

In conversation with residents who remember the Tennessee River before the advent of the Tennessee Valley Authority, I have been told

of times when it was possible to walk across the river without getting your feet wet, and in many places it was possible to wade across.

Three major river systems drain eastern Tennessee (Fig. 1). Approximately four-fifths of the area is within the Tennessee River Basin. The extreme northwestern part of the study area is within the Cumberland River Basin. The extreme southeastern corner of the study area is within the Coosa River Basin in Gulf Coast drainage.

Much has been written concerning the zoogeographically important phenomenon of stream capture in the Southern Appalachian Mountains. Fenneman (1938: 187) does not believe that the direction of drainage was affected by post-Miocene uplift of the Schooley surface. The Tennessee River is assumed to have been following its present course prior to this uplift; at least that portion of its course through the gorge of Walden Ridge. There is the possibility that this uplift resulted in the capture of such transversely flowing streams as the Hiwassee and Little Tennessee. If so, these rivers, until their capture, must have been flowing northwestward across the Plateau to the Cumberland and/or the western portion of the Tennessee River. There is insufficient geological evidence to support the hypothesis of an outlet for the Tennessee River to the southward through the Coosa Valley (Fenneman, 1938: 277; White, 1904). Rather, as suggested by these authors, it is possible that the Conasauga River in Miocene time may have flowed northwestward through the Walden Ridge gorge. Consequent upon the post-Miocene uplift of the Schooley peneplain this river was captured by the headwater streams of the Coosa River. At present the Conasauga River

originates in the mountains of northeastern Georgia and flows northwestward through the southwestern corner of Polk County, Tennessee. Then it turns abruptly south and flows into Georgia. Near Calhoun it joins with the Coosawatee River to form the Oostanaula River.

D. Climate

Any discussion of the climate of a faunal area is complicated by discrepancies between zonal meteorology and local conditions in the constituent ecological niches of the area. The macroclimatic data obtained from standard meteorological stations may be quite different from microclimatic data obtained in the same region (Allée, et al., 1949: 211; Wolfe, 1951). However, such macroclimatic data are frequently all that are available to the biogeographer. There may be some validity in using such data to infer the general effect of climate on the distribution of the elements of the herpetofauna. Shanks (1956) reports a mean difference of only 0.25° C. between the temperature of the soil at a depth of six inches and the temperature of the air as recorded by standard meteorological procedures in a closed forest in the Great Smoky Mountains National Park.

Even a general appraisal of the climate of eastern Tennessee is not easy to make. That the climate varies considerably both horizontally and vertically may be inferred from the presence of a variety of climax associations in the region (vide pages 23-29). The moisture regime, as interpreted from the data presented in Figures 4 and 5, is one with two peaks of maximum precipitation and two periods of reduced precipitation. The two maxima are due to different causes. The late-

fall-to-early-winter maximum results from steady rainfall which may be of several days duration, and at times of several weeks duration. The summer maximum is characterized by thundershowers which produce several inches of rainfall within a few hours. While there is a decrease in the amount of precipitation in late spring and early summer, this decrease is not as severe as that which occurs in late summer and early fall. The areas represented by the selected stations differ by only one-half inch precipitation in late summer but by as much as one inch in the spring. In terms of annual average precipitation, the Valley north of Knoxville is the driest part, 44.7 inches. The Cumberland Plateau (at least around Crossville), the Knoxville-Chattanooga Segment, and the Gatlinburg areas are more nearly alike; 54.3, 53.8, and 53.8 inches respectively. The wettest areas in eastern Tennessee are the mountain summits, with a five year average of 90.0 inches recorded at Clingman's Dome in the Great Smoky Mountains (Shanks, 1954: 355).

Differences in mean monthly temperatures among the four areas are not as marked as moisture differences. The coldest temperatures are recorded from the Cumberland Plateau (Fig. 5). The lowest temperatures recorded in eastern Tennessee, but not evident from the data presented here, occur on the high summits of the mountains. Curiously, the coldest mean temperature at high elevations occurs in March (Shanks, loc. cit.: 356), while the coldest month at lower elevations is January ("Yearbook of Agriculture," 1941: 1119-1121). Conversely, both high and low elevations experience the hottest mean temperatures in July. Shanks (op. cit.: 357) presents data showing that the temperature de-

Fig. 4.--Warming curves and precipitation from January through July. Read up.

Fig. 5.--Cooling curves and precipitation from July through January. Read down.

creases 2.23° F. for every 1,000 feet increase in altitude in the Great Smoky Mountains.

For a more detailed summary of climatic data for eastern Tennessee, the reader is referred to the "Yearbook of Agriculture" (op. cit.: 1119-1128).

F. Vegetation

The vegetation of eastern Tennessee is varied and complex.

Among the factors responsible for this condition are the varied topography and the great age of the area. With few exceptions, the dominant vegetation is deciduous forest. Among the exceptions are the secondary forests, the spruce-fir forests of high mountain summits, and forests on poorer and drier sites. In the secondary forests and in those on poorer and drier terrain, pines frequently are the dominant trees.

Zonation is evident in the Unaka Mountains (sensu lato) and in the Cumberland Mountains. Frequently it is necessary to look for evidence of zonation in remnant trees or remnant patches of original forest. Elsewhere, the distribution of the various forest associations seems more related to edaphic conditions. Intensive lumbering operations have destroyed most of the original forest and the forests are generally secondary in nature.

The Tennessee Valley Authority (1941) characterizes the forests of eastern Tennessee within the Tennessee River Basin as hardwood (five types), coniferous (four types), and mixed-forest (four types). Each of these 13 principal forest types is subdivided into one or more cover types, totaling 31 associations, as defined by the Society of American

Foresters (1954). Some of the various cover types occur in more than one of the principal forest types. The forest regions shown in Figure 6 are from Braun (1950).

These forest regions of Braun are not to be construed as synonymous with climax associations. Although each of the regions is characterized by a specific climax association, these climaxes may occur in other forest regions under suitable conditions of habitat. Neither is the area of the forest region coextensive with the area occupied by the characteristic climax association. Secondary forests may have an areal extent much greater than that occupied by climax forest. For details of the various types of forest communities occurring in each of the various forest regions, the reader is referred to Braun (1950). For the purposes of this study the following general comments are included (summarized from Braun, unless otherwise noted).

The Mixed Mesophytic Forest Region is characterized by several mixed mesophytic climax associations, which are best developed in the Cumberland Mountains. The mixed mesophytic forest is the most complex and the oldest association of the Deciduous Forest Formation. From it or its progenitor have come all other climaxes of the Deciduous Forest Formation. During Miocene time this mixed mesophytic forest extended all the way to the Arctic. Harshberger (quoted by Braun, 1950: 40) delimited (in part) the northern boundary of this forest during Pleistocene glaciation along a line from the confluence of the Ohio and Mississippi rivers east to the Cumberland Mountains, thence northward along the Alleghany Mountains to the west branch of the Susquehanna River in Pennsylvania. The mixed mesophytic communities indicate "climatic

Fig. 6.--Forest regions of eastern Tennessee (from Braun, 1950).

equilibrium." Oak-hickory and oak-chestnut communities on the dry ridges and slopes in the Mixed Mesophytic Region are edaphic climaxes which have segregated from the mixed forest. Locally, prairie vegetation, northern vegetation, and coastal plain plants are to be found. These are interpreted as relics surviving changes in climatic and physiographic conditions. The occurrence of mixed mesophytic communities outside of this region is correlated with peculiarities of local environments. Without known exception, the local habitats occupied by these extraregional communities are mesic slopes. In the Smoky Mountains such communities are known as cove forests. In the Ridge and Valley Section of the Oak-Chestnut Forest Region, mixed mesophytic communities are limited to valley slopes of the present erosional cycle.

The forest communities of the surface of the Cumberland Plateau are quite distinct in appearance from those of the Cumberland Mountains and from the coves and stream valleys which incise the plateau margin. Depending upon site, the moist slope and valley forests are beech and white oak, hemlock and white oak, or beech, hemlock, white oak, and tuliptree. In contrast with these communities are the oak and the oak and hickory forests of the plateau surface. Among the prevalent tree species are Quercus alba, Q. montana, Q. falcata, Q. stellata, Carya glabra, C. tomentosa, Cornus floridana, Pinus echinata, and P. virginiana. Along cliff margins are pine-heath communities. In swampy places red maple prevails. A further point of contrast between the plateau surface communities and the mixed mesophytic communities involves canopy closure.

The mixed mesophytic forests typically exhibit a dense, closed canopy when the trees are in full foliage. According to Braun (1950: 113), the large showy summer-blooming herbaceous plants in the plateau surface communities suggest that there have always been open sunny spots. These herbaceous plants are not characteristically found in the mixed mesophytic forest community.

The Oak-Chestnut Forest Region is characterized by the former dominance of oak-chestnut forests on most slopes and the dominance of white oak forests on the Valley floor and extensive flats. Two sections of this region occur in eastern Tennessee: (1) the Southern Appalachian Section, (2) the Ridge and Valley Section.

In the Southern Appalachian Forest Section three principal forest groups are recognized: (1) northern forest, mostly at elevations in excess of 3,500 feet on northern slopes, (2) moist slope and cove forest, (3) dry slope and ridge forest. The last groups occur at moderate to low elevations. The northern forests are divided into northern hardwoods forest--with sugar maple, yellow birch, beech, and buckeye as the important tree species--and spruce-fir forest. As will be discussed later, the spruce-fir forest is not interpreted as an outlier of the northern coniferous forest. At elevations around 6,000 feet the trees become dwarfed. The stands are open and are referred to locally as "orchards." The moist slope forests are characterized by oak--Quercus alba, Q. borealis, Q. montana--and, formerly, chestnut. These forests occupy elevations between 1,300 and 4,500 feet or higher on the southern slopes and almost without exception have an ericaceous understory.

The cove (mixed mesophytic) forests occupy the deep ravines of the mountain slopes. The transition between moist slope oak forests and cove forests is gradual. On the drier ridges and south slopes the forests are oak--Q. falcata, Q. marilandica, Q. stellata--or oak-pine communities. The principal pines are Pinus echinata, P. pungens, and P. rigida. Ericaceous shrubs are abundant. These dry slope forests are rather sharply set off from the oak forests of northern, mesic slopes.

The Ridge and Valley Section of the Oak-Chestnut Forest Region is (or was) characterized by white oak forests. These oak communities differ from those of the mountain slopes in having an herbaceous rather than an ericaceous understory. On low shaly ridges black oak and hickory become prominent. Southern pines also become more important, especially in young secondary stands. As mentioned previously, mixed mesophytic communities occupy ravine slopes in this section.

The Gulf Slope Section of the Oak-Pine Forest Region is characterized by oak-hickory climaxes. There is almost a universal dominance of pine in the forest communities. The pines are most prevalent in successional and subclimax stands. This region is transitional between the central deciduous forest and southeastern evergreen forest. Moreover, the transition between the oak-chestnut region and the oak-pine region is so gradual that the boundary lines are necessarily arbitrary.

On some of the mountain summits of 5,000 feet and more in the Unaka Province, particularly in the Great Smoky Mountains, spruce-fir (Picea rubens-Abies fraseri) forest is climax. In physiognomy this forest appears to be an outlier of the northern coniferous forests.

The fir is endemic to the Southern Appalachian Mountains and a number of the understory species do not occur in the northern coniferous forest. Shanks (1954: 360) has shown that these spruce-fir forests exist in a climate much wetter than that of the northern coniferous forests. From these data presented by Braun and Shanks, I conclude that these spruce-fir forests are not disjunct communities of the northern coniferous forest.

Another feature of the summits of some of the higher peaks is the occurrence of treeless areas clothed with grasses or heaths, referred to respectively as grass or heath balds. Whittaker (1956: 56) states that in some instances they may represent primary seral stages; while in other instances they may be secondary, and a result of the destruction of forest. He concludes by regarding them as topographic climaxes, or, as parts of a complex climax pattern. Wells (1956) states that these balds are "artifacts or archeological disclimaxes" representing "camp sites of early hunter Indians who preceded the lowland Cherokee farmer of Bartram's day." Billings and Mark (1957) discuss the persistence of treeless areas regardless of their geographical location. Among the factors discussed as responsible for the persistence of balds are (1) inability of most tree seedlings to withstand the severity of the environment of bald areas, (2) occupancy by the balds of ecotonal areas at the margin of or beyond the tolerance ranges of the important regional tree species, and (3) extremes of climatic cycles which may eliminate certain tree species or reduce the population so that the variety of available biotypes is small. Regardless of their origin, evidence suggests that these areas may become forested (Brown, 1953).

III. THE HERPETOFAUNA

Twenty-seven forms of salamanders, 16 of frogs and toads, 14 of turtles, 9 of lizards, and 30 of snakes are discussed in the following accounts. If the forms in the subfamily Desmognathinae were included, the numbers of salamanders would total at least 37. One conspicuous feature in the following accounts is the large number of intergrading subspecies. A parallel situation among mammals of eastern Tennessee may be inferred from data presented by Hamilton (1943). Among 60 forms of mammals reported as occurring in eastern Tennessee, 12 of them represent 6 species.

A. Class Amphibia

1. Order Caudata

This order is represented in eastern Tennessee by 6 families, including 2 subfamilies, 13 genera, and a minimum of 19 species, excluding the species of the genus Desmognathus, the Dusky Salamanders, and of the genus Leurognathus, the Shovel-nosed Salamanders.

Family Cryptobranchidae

Genus Cryptobranchus, Hellbenders. Bishop (1943: 59-60) includes portions of eastern Tennessee in the range of the Hellbender, Cryptobranchus alleganiensis (Daudin). Schmidt (1953: 11-12) makes the Ozark Hellbender, Cryptobranchus bishopi Grobman, conspecific with C. alleganiensis and includes eastern Tennessee in the range of C. a.

alleganiensis. However, six specimens of C. alleganiensis--four females, two males--collected during the course of this study seem intermediate in a number of respects between C. a. alleganiensis and C. a. bishopi. As Grobman (1943: 6-9) did not distinguish between the sexes in his description of C. bishopi, the data from these six specimens are not separated as to sex.

C. a. alleganiensis may be distinguished from C. a. bishopi by the ratio between the diameter of the spiracle and internarial distance, the ratio between interorbital distance and internarial distance, the number of prevomerine teeth, and color. Meristic data obtained from the six specimens are as follows: ratio between internarial distance and diameter of spiracle, range 1.2 to 3.6, mean 2.4; ratio between interorbital distance and internarial distance, range 2.1 to 2.6, mean 2.4. The number of prevomerine teeth ranges from 33 to 55, mean 42.3. Grobman (1943: 6) reports only a single value of 3.8 for the ratio between interorbital distance and the diameter of the spiracle in C. bishopi; a value of 2.0 for this ratio in C. alleganiensis. None of these six specimens has this ratio as great as that reported for C. bishopi, and only one has a ratio as small as 2.0. The mean value for the ratio between interorbital distance and internarial distance and the maximum and mean numbers of prevomerine teeth of this series are larger than the corresponding values of these characters reported for either C. bishopi or C. alleganiensis (Grobman, 1943: 8). If the count of 55 prevomerine teeth is deleted from the counts of the six specimens, the range is then 33 to 47, mean 39.8, which agrees more closely with these same values for C. alleganiensis.

C. bishopi and C. alleganiensis are apparently more different from each other in matters of coloration than in body ratios. It is this character particularly which makes the six eastern Tennessee specimens more like C. bishopi than like C. alleganiensis. Three of the six specimens have black spots on the chin, and a fourth specimen has these spots plus a few large brown blotches on the lateral surfaces of the lower labial region. This is the type of chin coloration ascribed to C. bishopi (Grobman, 1943: 8). The remaining two specimens lack the spotting on the chin. These six specimens have a ground color more like a topotypic specimen of C. bishopi than like that of a C. alleganiensis from New York. Further, all of the specimens but one have large brown or black blotches on the posterior one-half to two-thirds of the body and on the lateral surfaces of the tail. Each of the specimens has black punctations on the ground color of the dorsum.

All of the specimens are from localities within the Tennessee River Basin (Fig. 7). The localities are at elevations ranging from 800 to about 1,500 feet. King (1939: 548) reports a specimen from the Little River at an elevation of 2,200 feet. Gentry (1955: 169) reports that C. alleganiensis is common in the Cumberland River watershed.

Family Proteidae

Genus Necturus, Waterdogs. Field work during this study has produced only a single specimen of this genus. This is a female with a snout-vent length of 167 mm. and a total length of 244 mm. It is from the Conasauga Creek, Monroe County (Fig. 7). This creek is a tributary to the Hiwassee River. King (1939: 546-548) discusses specimens from

Fig. 7.--Localities for the Hellbender, Cryptobranchus alleganiensis, the Waterdog, Necturus maculosus, and the Red-spotted Newt, Diemictylus v. viridescens.

the Clinch River below Norris Dam and from Abrams Creek in the Great Smoky Mountains National Park. Interrogation of local sport and commercial fishermen about encounters with Necturus has resulted in negative replies. Conversely, most of these persons are familiar with Cryptobranchus.

It is impractical to speculate upon the systematic status of a population on the basis of one specimen. However, this specimen is similar in appearance to a female N. m. maculosus figured by Viosca (1937: 129). King (1939: 546) figures a female designated as N. maculosus x alabamensis from the Clinch River. It appears to differ from the specimen reported here in possessing large irregular shaped dark spots and in having more extensive light areas on the venter. There is essentially no difference between the meristic data available for this specimen and those reported for females from the Clinch River by King.

Family Sirenidae

Genus Siren, Sirens. Although I have not encountered members of this genus in eastern Tennessee, it is included on the basis of a verbal communication from Mr. Ernest Liner of Lafayette, Louisiana.

Mr. Liner informs me that he collected a specimen of the Greater Siren, Siren lacertina Linnaeus, from a stream or roadside ditch in Knox County. This specimen may represent a weak population or an escape. I would suspect the latter; in the past few years the newspapers have carried several accounts of boa constrictors having been killed in eastern Tennessee.

Family Ambystomidae

Genus Ambystoma, Mole Salamanders. I have personally encountered only three species of this genus in eastern Tennessee. These are the Spotted Salamander, Ambystoma maculatum (Shaw), the Marbled Salamander, Ambystoma Opacum (Gravenhorst), as eggs and larvae only, and a single male Tiger Salamander, Ambystoma t. tigrinum (Green). There is an early literature record of the Jefferson Salamander, Ambystoma jeffersonianum (Green), from Roan Mountain at elevations from 4,000 to 5,200 feet (Rhoads, 1895: 382). Schmidt (1953: 19) in referring to the range of A. jeffersonianum reports it is of "isolated occurrence in . . . Tennessee," with Tennessee not qualified as to East, Middle, or West. Judging from the distribution of this form as given in Bishop (1947: 133), I infer that this isolated occurrence must be in West Tennessee. Schmidt (page 21) also includes Tennessee without qualification in the range of the Small-mouthed Salamander, Ambystoma texanum (Matthes). Bishop (page 157) shows only the northwestern corner of the state as being inhabited by this salamander. Bishop (page 160) does not include eastern Tennessee in the range of A. t. tigrinum.

A. maculatum is represented by a series of seven females and three males plus numerous egg clusters from widely scattered localities (Fig. 8). Meristic data from these specimens are as follows: snout-vent lengths, range 86 mm. to 116 mm., mean 106.3 mm.; tail lengths, range 67 mm. to 91 mm., mean 79.2 mm.; costal grooves, range 12 to 13, mean 12.5; number of dorsal spots, range 17 to 45, mean 28.5. As regards these meristic characters and color, these specimens agree with

Fig. 8.--Localities for the Spotted Salamander, Ambystoma maculatum, the Marbled Salamander, A. opacum, and the Eastern Tiger Salamander, A. t. tigrinum.

the description of this species as given by Bishop (1947: 144-145). This species, while widespread in eastern Tennessee, seems to be confined more to the heavily forested areas, especially in the Unaka Province. The highest elevation from which it has been collected is approximately 2,000 feet.

While the ambystomids are characterized as pond-breeding salamanders, the paucity of ponds in the mountains does not seem to hinder A. maculatum. Numerous egg masses and several spent adults were collected in a roadside ditch carrying rainfall runoff in the mountains. In a spring seep area not far distant from this ditch there were no indications of breeding by the Spotted Salamander. There is a locality in Polk County where this salamander regularly breeds in a spring-fed stream of moderate current and with a depth of 8 to 12 inches. The absence of breeding of the Spotted Salamander in the above mentioned seepage area would seem to be due to lack of sufficient depth to the water. It was at that time only about four or five inches deep.

As mentioned above, A. opacum is known by me only from eggs and larvae. Hence, the distribution of this salamander in eastern Tennessee is based upon collection sites of these stages of the life cycle and upon literature reports (Fig. 8). It is interesting to note that it seems to be most abundant in the Valley Province. Although infrequently collected in the same pool where A. maculatum breeds, these salamanders seem to breed in mutually exclusive areas most of the time. This difference in habitat preference is so noticeable, in my experience, that I am inclined to characterize A. opacum as a glade or forest-edge inhabitant.

The highest elevation from which A. opacum has been collected is around 1,800 feet.

The single male A. t. tigrinum is not different from published descriptions of this salamander. That it represents a population in eastern Tennessee may be questioned. It was collected on a porch during a hard spring rain. Following its capture, it was placed on display in a store window in the business section of Athens. During that time, no one was able to report ever having seen such a "lizard." The place where it was captured is adjacent to a lumber yard, and it is possible the animal was brought in with a shipment of cedar logs from West Tennessee. Gentry (1955: 170) reports this salamander as common in West and Middle Tennessee and as having been collected in Knox County (Fig. 8).

Family Salamandridae

Genus Diemictylus, Eastern Newts. The newts of eastern Tennessee are referable to the subspecies Diemictylus v. viridescens (Rafinesque). The series of 18 females and 41 males and 2 of undetermined sex, one of which is in the red eft stage, do not differ from the description of this form as given by Bishop (1947: 100-102). The largest female and male in total length (snout-vent length in parentheses) are 108 mm. (52 mm.) and 114 mm. (51 mm.) respectively.

This salamander is characteristic of woodland pools and coves of the T. V. A. impoundments, and not infrequently is found in the headwater spring pools of smaller streams and branches. There seems to be no special predilection for any of the physiographic or forest regions.

Family Plethodontidae, Subfamily Desmognathinae

Genus Desmognathus, Dusky Salamanders. Excluded from this study.

Genus Leurognathus, Shovel-nosed Salamanders. Excluded from this study.

A brief statement as to which species of these two genera are reported as occurring in eastern Tennessee is appropriate. These species will be left out of my analysis of the herpetofauna because of the confused taxonomic state of the genus Desmognathus and of lack of information on the distribution of the genus Leurognathus in eastern Tennessee.

Schmidt (1953: 29-32) includes eastern Tennessee in the ranges of five species of Desmognathus: the Northern Dusky Salamander, Desmognathus f. fuscus (Rafinesque); the Central Dusky Salamander, Desmognathus f. brimleyorum (Stejneger); the Allegheny Salamander, Desmognathus ochrophaeus carolinensis Dunn; the Ocoee Salamander, Desmognathus ocoee Nicholls; (?) the Appalachian Seal Salamander, Desmognathus m. monticola Dunn; the Black-bellied Salamander, Desmognathus quadramaculatus (Holbrook); the Pigmy Salamander, Desmognathus wrighti King. Mr. Barry Valantine (personal communication) informs me that some of my specimens of Desmognathus are the Cherokee Salamander, Desmognathus aeneus Brown and Bishop.

Bishop (1947: 220) reports the occurrence of the Northern Shovel-nosed Salamander, Leurognathus m. marmorata Moore, from Roan Mountain, Carter County. King (1939) reports specimens of the Southern Shovel-nosed Salamander, Leurognathus m. intermedia (Pope), from the Cades Cove area of the Great Smoky Mountains National Park.

Family Plethodontidae, Subfamily Plethodontinae

Genus Plethodon, Woodland Salamanders. The basis for the following remarks is the monograph of this genus by Highton (MS), unless otherwise qualified.

Three species of the Eastern Small Plethodons and three species of the Eastern Large Plethodons are reported as occurring in eastern Tennessee. The Eastern Small Plethodons are as follows: Weller's Salamander, Plethodon welleri Walker; Zigzag Salamander, Plethodon d. dorsalis Cope; Red-backed Salamander, Plethodon c. cinereus. On the basis of Highton's distribution map for the subspecies of Plethodon richmondi, it is possible that a fourth member of this group, Pope's Ravine Salamander, Plethodon r. popei Highton and Grobman, may be discovered in the northeastern part of Tennessee. The Eastern Large Plethodons in eastern Tennessee are as follows: Yonahlossee Salamander, Plethodon yonahlossee Dunn; Red-cheeked Salamander, Plethodon j. jordani Bletcherley; Unicoi Salamander, Plethodon j. unicolor Highton; Metcalf's Salamander, Plethodon j. metcalfei Brimley; Slimy Salamander, Plethodon g. glutinosus (Green). None of the localities shown for P. g. glutinosus is from Highton (MS) as he does not present a detailed distribution map for this subspecies. P. c. cinereus and P. d. dorsalis are shown as occurring in the same locality (Fig. 10). This locality is based upon data given to me by Dr. Highton, and, according to him, are "King's identifications." Both are from White Oak Sink, Great Smoky Mountains National Park.

Each of the above salamanders is a forest inhabitant. In my experience, P. c. cinereus and P. g. glutinosus have the greatest ecologi-

cal tolerance of all the plethodons in eastern Tennessee. Each may be encountered in a variety of situations ranging from edificarian habitats to dense forests. One factor which seems common to all localities where I have encountered plethodons is a mull or mor type of surface layer of the soil. That this is not just a consequence of their inhabiting forests is inferred from the relative absence of these salamanders in the grazed forests where the top soil has been compacted. This is the case in the mountains as well as in the valleys. Leaf litter and a canopy of trees alone do not seem sufficient to support them.

Five of the eight plethodons in eastern Tennessee have known distributions confined to the mountains of eastern Tennessee, western North Carolina, and southwestern Virginia (Fig. 9). The elevation at which they are known to occur are as follows: P. i. jordani, P. welleri, P. yonahlossee from 2,500 feet to above 5,000 feet; P. i. petcalfe from 3,000 to 5,800 feet; P. i. unicoi not below 4,000 feet. The remaining three plethodons are of widespread occurrence in eastern Tennessee (Fig. 10). Elevations at which they are known to occur are as follows: P. c. cinereus, P. g. glutinosus up to 5,000 feet; P. d. dorsalis up to 2,200 feet.

Genus Hemidactylium, Four-toed Salamander. King (1939) reports this Salamander from the Great Smoky Mountains National Park (Fig. 11). It is known from only two localities in the Park; Cades Cove and the head of Meadow Branch at an elevation of 1,800 feet. The site in Cades Cove is a small gum swamp with a ground cover of leaf litter and sphagnum moss. The head of the Meadow Branch is a sphagnum bog. I have

Fig. 9.--Localities for the subspecies of Jordan's Salamander, Plethodon jordani, Weller's Salamander, P. welleri, and the area in which the Yonahlossee Salamander, P. yonahlossee, is reported to occur.

Fig. 10.--Localities for the Red-backed Salamander, Plethodon c. cinereus, the Zigzag Salamander, P. d. dorsalis, and the Slimy Salamander, P. g. glutinosus.

Fig. 11.--Localities for the Four-toed Salamander, Hemidactylium scutatum, the Spring Salamander, Gyrinophilus porphyriticus, the Mountain Spring Salamander, G. danielsi, and the Tennessee Cave Salamander, G. pallaeus.

searched in sphagnum communities in the mountains and in the Valley without encountering this salamander.

Genus Gyrinophilus, Spring Salamander. Schmidt (1953: 45-47) includes eastern Tennessee in the range of the Northern Spring Salamander, Gyrinophilus p. porphyriticus (Green), and the Blue Ridge Salamander, Gyrinophilus d. danielsi Bishop (Fig. 11). Bishop (1947: 362) indicates intergradation between G. d. danielsi and the Carolina Spring Salamander, Gyrinophilus dunni Mittleman and Jopson, in the mountainous central portion of extreme eastern Tennessee. Gentry (1955: 172) reports G. p. porphyriticus as common on the Cumberland Plateau and as occurring in northeastern Tennessee.

All but two of the specimens of this genus which I have collected are in the possession of Mr. Barry Valentine, Mississippi Southern College. Consequently, except for the two available specimens of G. danielsi, taxonomic designation of the other specimens are those entered in the collection catalogue and may be suspect. Two of these are recorded as G. p. porphyriticus and one as G. danielsi. The two G. p. porphyriticus are from the twilight zone of a cave in Meigs County in the Valley Province, elevation 900 feet. The G. danielsi is from a spring seep at Whigg Meadow, Monroe County, elevation 5,000 feet. The two specimens of G. danielsi discussed below are also from Monroe County. One is from an elevation 1,800 feet, the other from 4,000 feet.

Meristic data from these last two specimens are within the range of both G. d. danielsi and G. d. dunni. As regards the combination of tooth counts, costal grooves, and color, these specimens seem to be intermediate between the two subspecies. The high-elevation specimen has

the reticulate brown pattern, the knife-edged distal part of the tail, and the seven vomerine teeth preceding the band as reported for G. d. danielsi. It resembles G. d. dunni in possessing 18 costal grooves, dorsal spotting, and having the legs marked like the dorsum. The low-elevation specimen resembles G. d. danielsi as follows: sides of the head converge toward the gular fold; knife-edged keel on the distal part of the tail; 18 costal grooves. It resembles G. d. dunni as follows: 15 vomerine teeth preceding the bend; acute band in the vomerine series of teeth; suggestion of a herring-bone dorsal pattern.

McCrady (1954) described the neotenic Tennesse Cave Salamander, Cyrinophilus pallaucus, from a cave near Sewanee, Franklin County (Fig. 11). This locality is in the southern end of the Cumberland Plateau. I have collected several individuals of an unidentified "giant" Cyrinophilus larva at Athens, McMinn County, in the Valley. The collection site is a roadside ditch which becomes flooded by the Oostanaula (Eastnalle) Creek. These specimens were collected at a time when the ditch was filled with flood water. They were near an opening to a hole in the ground about the size of a woodchuck burrow. Examination of the hole after the water receded failed to disclose its extent. Presumably it communicates with underground solution channels which abound in the area. Seining and trapping in the adjacent creek produced no additional specimens. These three are also in possession of Mr. Valentine.

Genus Pseudotriton, Red Salamanders. Schmidt (1953: 48, 49) records the Midland Salamander, Pseudotriton montanus diastictus Bishop, the Northern Red Salamander, Pseudotriton r. ruber (Sonnini), and the

Black-chinned Salamander, Pseudotriton r. schencki (Brimley), as occurring in eastern Tennessee (Fig. 12). Bishop (1947: 390) shows extreme northeastern Tennessee within the range of the Blue Ridge Salamander, Pseudotriton r. nitidus Dunn. The exact locality given is Roan Mountain, Carter County. King (1939: 557) records the Eastern Mud Salamander, Pseudotriton m. montanus Baird, from the Sinks on Little River and Mt. Sterling in the Great Smoky Mountains National Park. As King's paper antedates the description of P. m. diastictus, it is probable that these specimens are referable to this subspecies. My collecting has produced only one species, P. ruber.

Forty-three specimens (14 females, 27 males, and two of undetermined sex) of P. ruber were collected and examined. In assigning these specimens to P. ruber rather than to P. montanus, I used the key characters of Bishop (1947: 376) and Brimley (1944: 11). Special emphasis was placed upon spotting, configuration of vomerine teeth, and the presence or absence of a dark line through the eye to the nostril.

These specimens range in total length (snout-vent lengths in parentheses) from 69 mm. (43 mm.) to 156 mm. (98 mm.). Costal groove counts are as follows: 16, 36 specimens; 17, 5 specimens; 16 - 17, 2 specimens. The number of costal folds between appressed limbs is not considered because Grobman (1943) has demonstrated that this is an ontogenetically variable character. None of these data per se is sufficient for separating the races of P. ruber as they are presently defined. However, 19 of the specimens exceed the maximum total length recorded by Bishop for P. r. nitidus; 14 of them exceed the maximum length recorded for P. r. schencki; one exceeds the maximum length recorded for

Fig. 12.--Localities for the Midland Salamander, Pseudotriton m. diastictus, and the subspecies of the Red Salamander, P. r. ruber. The localities for P. m. diastictus are those for P. m. montanus in Dunn (1926).

P. r. vioscai. The taxonomic allocation of these specimens is based primarily upon coloration. Also, these specimens were compared with identified material in the University of Florida Collections.

On the basis of dorsal coloration, it is possible to arrange all specimens into a continuous series. At one extreme are those having a pattern of distinct spots on a coral pink background with no secondary spotting of smaller brownish or black spots and stellate markings. At the other extreme are those specimens having the primary and secondary spotting nearly obscured by a purplish-brown color. Thirty-one of the specimens possess large irregular shaped black spots, many of which coalesce, with smaller, brownish to black punctations and stellate markings in the spaces between the primary spots.

The upper surfaces of the legs, the sides, and at least the proximal one-half of the tail have black spots smaller in size than those of the dorsum. Generally, the spotting on the sides stops at the level of the insertion of the legs. With some specimens, fine spotting continues down the sides and onto the venter. With few exceptions the undersurfaces of the legs and tail are immaculate. There is apparent correlation between degree of darkness and spotting of the dorsum and the degree of spotting of the venter. All specimens in this series have what I consider black chins, black-tipped toes, and whitish spots around the snout. These three characters are presumably characteristic of P. r. schenckii. Thirty-one specimens have been designated as P. r. ruber on the basis of the following criteria: ground color purplish-brown; spots fused and of irregular sizes; secondary spotting on dorsum prominent; venter spotted; chin with black spots; in preservative, the

dorsal color darker than that of venter. Five specimens have been designated as P. r. schencki on the basis of the following criteria: total length less than 130 mm.; ground color not purplish-brown; spots distinct, not fused; no secondary spotting on dorsum; venter unspotted; chin solid black; dorsal color not distinct from ventral color in preservative. Five specimens have been designated as P. r. ruber x schencki intergrades by possessing various combinations of the characters of each of the subspecies.

Bishop (1947: 390) implies in his map of the distribution of the subspecies of P. ruber that P. r. schencki occupies the high mountains along the southeastern border of Tennessee. Examination of the respective distributions of the specimens I have assigned to P. r. ruber and P. r. schencki shows an interesting pattern (Fig. 12). The P. r. schencki assignees are from elevations of 900 feet in the Valley and from 2,100 feet in the Unakas. Geographically and altitudinally these specimens are surrounded by P. r. ruber. The P. r. ruber x schencki intergrades are from elevations of 900 feet in the Valley and from 1,500 and 2,500 feet in the Unakas. One inference is that P. r. schencki is a lowland form which can occur at high altitudes where suitable habitats exist. Dunn (1926: 284) states that P. r. schencki "Reaches 3,500 feet in the Balsam Mts." I infer he means it ascends to 3,500 feet. King (1939: 557) records this salamander from 5,000 feet in the Great Smoky Mountains National Park. He also states that it is most abundant at elevations below 3,000 feet. Another inference is that the P. ruber population on the western slope of the Unakas is an intergradient one between P. r. ruber and P. r. schencki. Also, it may be that specimens

I have designated as P. r. schencki and P. r. ruber x schencki intergrades may be individuals exhibiting various stages in the ontogenetic development of adult P. r. ruber coloration. I feel that distinguishing between these forms is highly subjective and indicative of the need for a thorough revision of the P. ruber complex.

None of these specimens is referable to P. r. nitidus.

Two specimens remain to be discussed. These are two females; one from Rhee County and one from Monroe County. The dorsum of the head, body, and tail to its tip is covered with large black spots and blotches, which suggest a herring-bone pattern. The entire ventral surfaces, except those of the legs in the Monroe County specimen and of the tail in the Rhee County specimen, are profusely covered with small black spots. The spots on the chin and gular regions are the largest. The margin of the upper jaw is barred with black. The margin of the lower jaw is black. Whitish spots are present around the snout.

Comparison of these two specimens with a series of P. r. vioscai from Tuscaloosa, Alabama, in the University of Florida Collections discloses differences between these specimens and the Tennessee specimens. First, the Tennessee specimens lack the midventral concentration of spots suggesting a linear series. Second, the spots on these specimens are more profuse and more clearly defined than those of the Alabama specimens. These two individuals are considered as P. r. ruber x vioscai intergrades. The collection of one of these in Rhee County tends to negate the suggestion of Mittleman (1946: 2) that this river is a barrier to the distribution of P. r. vioscai.

Situations in which Pseudotriton have been encountered range from beneath logs in relatively xerophytic second-growth oak and oak-pine forest, to edification situations in woodland, to spring-boil pools. They are most frequently found in spring seepage areas in woodland. The highest elevation at which both P. r. ruber and P. r. schencki have been encountered is 5,000 feet. The two designated as P. r. ruber x vioscai intergrades are from 1,900 feet in Rhea County and 2,000 feet in Monroe County.

Genus Aniades, Climbing Salamanders. Aside from one additional locality record (Fig. 13), I can add nothing to the knowledge of the Green Salamander, Aniades aeneus (Cope and Packard), that has not been reported by Gordon (1952). The two specimens, both males, do not differ from the description of this species as given by Bishop (1947: 328-332).

Genus Eurycea, Brook Salamanders. This genus is represented in eastern Tennessee by three species: Two-lined Salamanders, Eurycea bislineata; Long-tailed Salamanders, Eurycea longicauda; Cave Salamanders, Eurycea lucifuga (Figs. 13 and 14).

Six specimens (4 females, 2 males) are identified as the Southern Two-lined Salamander, Eurycea b. cirrigera (Green). These range in total length (snout-vent length measured to the anterior border of the vent in parentheses) from 75 mm. (36 mm.) to 101 mm. (47 mm.). The largest female is 101 mm. (47 mm.); the largest snout-vent length among males is 47 mm. The tail of this specimen is incomplete.

These specimens agree with description of E. b. cirrigera as given by Mittleman (1949: 90-91) as follows: 14 costal grooves; dark

Fig. 13.--Localities for the Green Salamander, Aneides seneus, and the subspecies of the Two-lined Salamander, Eurycea bislineata.

Fig. 14.--Localities for the subspecies of the Long-tailed Salamander, Eurycea longicauda, and the Cave Salamander, E. lucifuga.

brown dorsolateral lines extending to the tip of the tail; a row of white spots on the sides above the level of the legs; males with prominent cirri. The females have three costal folds between the appressed limbs. One of the males, snout-vent length 40 mm., has the toes of the appressed limbs meeting. The other male, snout-vent length 36 mm., has one costal fold between appressed limbs. These specimens are quite distinct from a series of the Midwest Two-lined Salamander, Eurycea b. rivicola Mittleman, from Ohio. They do not appear different from a series of E. b. cirrigera from Florida.

All of these six specimens are from the Unaka Province in extreme southeastern Tennessee but from elevations of 900 to 1000 feet (Fig. 13).

Sixty-three specimens of E. bislineata are identified as the Blue Ridge Salamander, Eurycea b. wildereri Dunn. They are like this subspecies as defined by Mittleman (1949: 91): distinct black dorsolateral lines not tending to blend with lateral pigmentation; dorsolateral lines do not extend uninterruptedly beyond the basal one-third of the tail; males possess cirri. Among 11 females, the frequency of number of costal folds between appressed limbs is as follows: two on five specimens; three on five specimens; four on one specimen. Among 15 males, the frequency of number of costal folds between appressed limbs is as follows: One in ten specimens; two in four specimens; three in one specimen. These data suggest a greater number of costal folds between appressed limbs in females than in males.

Among these 63 specimens, altitudinal variation is evident in the number of costal grooves. Twenty specimens have counts of 14

grooves on each side; 36 specimens have 15 grooves on each side; two specimens have 16 grooves on each side. Five specimens have counts of 14/15, 15/16, or are not countable. These last five specimens are from sites ranging in elevation from 2,100 to 5,400 feet. The vertical distribution of the 58 specimens with equal numbers of costal grooves on each side are as follows:

Elevation	Costal Grooves		
	14	15	16
Below 2,100 feet	19	3	0
Above 2,100 feet	1	33	2

Highton has informed me that the relationship of the number of costal groove to the number of vertebra appears to be the same in Eurycea as in Plethodon. Thus, specimens with 14 costal grooves have 15 trunk vertebra, those with 15 grooves have 16 trunk vertebra, and those with 16 grooves have 17 vertebrae. Until it is determined whether or not these variations in numbers of costal grooves are genetically or environmentally controlled, it is deemed desirable not to give nominal recognition to the lowland population of E. b. wilderae.

Among the males in this series of 63 specimens, some are more orange and have more profuse spotting of the middorsal band than others. Males of this kind are more frequent from elevations above 2,000 feet.

Included among localities for the subspecies of E. bislineata in Figure 13 are two for E. b. cirrigera x wilderae intergrades. These records are from King (1939: 557).

Eighteen salamanders (10 females, 8 males) are identified as the Long-tailed Salamander, Eurycea l. longicauda (Green). These range

in total lengths (snout-vent lengths in parentheses) from 100 mm. (50 mm.) to 163 mm. (65 mm.). The number of costal grooves ranges from 14 (12 specimens) to 15 (two specimens) on each side. Two specimens have counts of 13/14, two have counts of 14/15. Although the value of tooth counts is suspect, they are included here for completeness. Vomerine teeth vary from 16 (10/6) to 36 (18/18), mean 21 (12.6/11.3). Data for the parasphenoid teeth are as follows: parallel in 11 specimens, divergent posteriorly in seven specimens; separated from each other by the width of the choanae in eight specimens, by greater than the width of the choanae in three specimens, by less than the choanal width in six specimens; separated from the vomerine teeth in terms of width of the choanae from 1.5 to 6.0 times, mean is 2.8 times choanal width. The proportion of the total length attributable to the tail ranges from 50 per cent to 61.8 per cent, mean 57.7 per cent in the males and from 55.4 per cent to 64.9 per cent, mean 59.9 per cent in the females. Ratios of head dimensions into snout-vent lengths are as follows: females, snout-vent length/head width from 6.3 to 8.9, mean 6.4, snout-vent length/head length from 4.5 to 6.2, mean 4.6; males, snout-vent length/head width from 6.4 to 7.7, mean 7.7, snout-vent length/head length from 4.5 to 5.3, mean 4.9. These meristic characters are apparently intermediate between E. l. longicauda and the Midland Long-tailed Salamander, Eurycea longicauda pernix Mittleman, and in coloration these 18 specimens are not different from E. l. longicauda.

This salamander is infrequently encountered (Fig. 14). Collection sites range from the twilight zones of caves to beneath boards

near spring seeps in pastures. It seems to be confined to deciduous or dominantly deciduous forest. The highest elevation from which it is known is 2,500 feet.

Two male specimens of the Three-lined Salamander, Eurycea l. guttolineata (Nolbrook), do not differ from the description of this subspecies as given by Bishop (1947: 425-427). One specimen is 160 mm. in total length, 54 mm. in snout-vent length. The other has an incomplete tail. Its snout-vent length is 62 mm. Both have 14 costal grooves and a series of 20 vomerine teeth. The parasphenoid teeth rows are parallel and separated from the vomerine series by four times and by 2.8 times the diameter of the choanae. The parasphenoid teeth rows are separated from each other by one-half and one times the diameter of the choanae.

These two specimens are from Paint Creek, Green County. The collection site is one and three-quarter air miles northeast of the confluence of Paint Creek with the French Broad River (Fig. 14). The elevation is 1,400 feet. Both specimens were collected at night as they were prowling about the edge of the creek. This is the northernmost known locality for this salamander on the west side of the Appalachian Mountains.

The Cave Salamander, Eurycea lucifuga (Rafinesque), is represented by five female specimens. These range in total length (snout-vent length in parentheses) from 135 mm. (59 mm.) to 149 mm. (64 mm.). The longest snout-vent length is 67 mm., but this individual has an incomplete tail. Each has 14 costal grooves. In color these are not different from the description of E. lucifuga as given by Bishop (1947: 434-435).

All save one of these were taken in the twilight zone of caves. The exception is one which was taken on the highway late on a rainy night in the vicinity of second growth oak-pine forest. No known cave exists in this area. The highest known elevation for the occurrence of this salamander is 1,000 feet. The distribution of these specimens is shown in Figure 14.

2. Order Salientia

This order is represented in eastern Tennessee by 5 families, 7 genera, and a minimum of 15 species.

Family Palobatidae

Genus Scaphiopus, Spadefoot Toads. Wright and Wright (1949: 124) do not include eastern Tennessee within the range of the Eastern Spadefoot Toad, Scaphiopus h. holbrooki (Harlan). Gentry (1955: 174) does not record this toad from counties of eastern Tennessee. I have collected this toad from several localities in the Valley Province (Fig. 15). As is true in other parts of its range, this toad is infrequently encountered. Except for occasional individuals exposed during earth moving projects, it is seldom seen or heard at times other than during the heavy rains of early spring or summer. Its distribution in eastern Tennessee seems to be exclusive of the Unaka Province. I presume that it will be found in the Cumberland Plateau region. The highest known elevation of occurrence is 1,000 feet.

The Valley population is represented by nine female and nine male specimens. The range of body lengths respectively is 38 mm. to

Fig. 15.--Localities for the Eastern Spadefoot Toad, Scaphiopus h. holbrooki, the American Toad, Bufo t. americanus, and Fowler's Toad, B. w. fowleri.

66 mm. and 35 mm. to 70 mm. In other meristic characters, structure, and color these specimens are not different from the description of this toad as given by Walker (1946: 25) and Wright and Wright (1949: 124-126).

Family Bufonidae

Genus Bufo, Toads. Two forms of this genus occur in eastern Tennessee. They are the American Toad, Bufo terrestris americanus (Holbrook), and Fowler's Toad, Bufo woodhousei fowleri (Hinckley) (Fig. 15).

B. t. americanus is represented by a series of 12 females and 27 males. The largest body lengths for females and males respectively are 93 mm. and 79 mm. In their descriptions of this toad, Walker (1946: 28-29) and Wright and Wright (1949: 141-142) report horny excrescences on the backs of the first and second fingers of males. Wright and Wright (loc. cit.: 201) record these excrescences on the third finger as well as the first and second fingers of male Southern Toads, Bufo t. terrestris (Bonnaterre). Sixteen of the 27 male B. t. americanus possess this horny excrescence on the third as well as the first and second fingers. None of the 12 females or 27 males has the knob-like extensions on the cephalic crests nor the tuberculate parotoids found on B. t. terrestris. Eleven females and males (including two of the 16 males mentioned above) possess a dark line extending obliquely from above the shoulder to or close to the groin. This line is continuous in some specimens. In others it becomes broken into dark spots and/or mottled in an oblique linear arrangement to the groin. A similar oblique stripe

is mentioned for B. t. terrestris by Wright and Wright (*ibid.*). These terrestris-like characters may be within the normal range of variation of B. t. americanus. In other respects, these 39 specimens agree with the description of B. t. americanus as given by Walker and Wright and Wright.

B. w. fowleri is represented by a series of 15 females and 22 males. The largest body length for females and males respectively is 71 mm. and 68 mm. Except for several specimens, this series of toads agrees with the description of B. w. fowleri as given by Carr and Goin (1955), Walker (1946: 34-35), and Wright and Wright (1949: 211-212). The exceptions are construed as possible B. t. americanus x B. w. fowleri hybrids.

There are two such specimens, both females. Each has several warts on the tibiae much larger than those on the tarsi. Each also has intensively speckled abdomens. These two criteria are used to distinguish B. t. americanus. Further, they each have fewer spots with only one wart than other specimens in the series of B. w. fowleri. Neither has cranial crests save for faint suggestions of the supraorbital crests. The lack of these crests, plus the occurrence of spots with as many as four warts each, is considered as B. w. fowleri characters. Of the 39 specimens of B. t. americanus, only two possess this many warts per spot, while 28 of the 37 specimens assigned to B. w. fowleri possess this many warts per spot.

Walker and Wright and Wright give the following criteria to distinguish B. t. americanus from B. w. fowleri. As is evident from the

data, the differences are more of a quantitative than of a qualitative nature.

B. t. terrestris

Postorbital crest extending in short spur to anterior edge of parotoid.

Parotoids distinctly separated from postorbital crests.

Large dorsal warts; one or two warts in each dark spot.

Some warts of tibia much larger than warts on tarsus and foot.

Ventral surface usually mottled with black or dark brown.

Tibial length in adults 35 to 42 per cent of body length.

B. w. fowleri

Postorbital crest without short spurlike projection.

Parotoids frequently in contact with postorbital crests.

Small uniform dorsal warts; usually several warts per spot.

Warts on the tibia little larger than those of tarsus and foot.

Ventral surface usually unmottled or with a central dark spot.

Tibial length in adults 38 to 48 per cent of body length.

Comparing the above criteria with the descriptions of the two specimens speculated as being hybrid individuals emphasizes their intermediate nature. Further, the tibial length is 38 per cent and 40 per cent of the body length in these two specimens. It is quite possible that each of these two specimens is merely an extreme variant within the range of variation of either of the subspecies. Sufficient data are unavailable at present for further speculation.

Both B. t. americanus and B. w. fowleri are widespread in eastern Tennessee (Fig. 15). But the former is not known by me to occur in

the Valley and occurs at higher elevations than the latter. Known maximum elevations of occurrence for B. t. americanus and B. w. fowleri respectively are 6,000 feet and 2,500 feet. The two specimens discussed as possible hybrids are from an elevation of 3,500 feet and were taken in association with B. t. americanus. It is of interest to note that while specimens of B. t. americanus were collected at elevations as low as 1,000 feet (Kinzel Spring, Blount County), none was taken in the physiographically defined Valley Province. Conversely, B. w. fowleri seems to be confined to elevations of 2,500 feet or less, even in the physiographically defined Unaka and Cumberland Plateau provinces. King (1939: 565) reports a specimen of B. w. fowleri from 4,000 feet in the Great Smoky Mountains National Park, but speaks of its occurrence above 3,000 feet as sporadic. Thus, B. t. americanus in eastern Tennessee seems to be an upland form and B. w. fowleri seems to be a lowland form.

Family Hylidae

Genus Acris, Cricket Frogs. Although represented by only 19 specimens of undetermined sex, the Cricket Frog, Acris gryllus, is quite abundant along the shorelines of ponds, Tennessee Valley Authority impoundments, and low banks of and marshy areas adjacent to streams in the Valley and Cumberland provinces (Fig. 16). This frog is seldom encountered in woodlands. The highest elevation from which this frog is known is 1,800 feet atop the western escarpment of the Unaka Province. The site is an artificial lake with outlet streams descending into the Valley.

The range of body lengths of this series is within that given for the Northern Cricket Frog, Acris gryllus crepitans (Baird), by

Fig. 16.--Localities for the Northern Cricker Frog, Acris g. crepitans, the Northern Spring Peeper, Hyla c. crucifer, and the Eastern Gray Treefrog, H. v. versicolor.

Wright and Wright (1949: 223). The body lengths range from 22 mm. to 26 mm. In using the character "extent of webbing" I have used the distal termination of the web on the phalanx. As regards Dunn's characters (Wright and Wright, 1949: 223) for distinguishing A. g. crepitans from the Southern Cricket Frog, Acris g. gryllus (LeConte), these 19 specimens agree in amount of webbing with A. g. crepitans. However, in a few specimens, the termination of the web on the first toe is short of the distal tip by one-half the length of the terminal phalanx, suggesting the condition in A. g. gryllus. The width of the head across the base of the lower jaw is one to two millimeters greater than the distance from that point to the tip of the snout. This is an A. g. crepitans character. Further structural characters of A. g. crepitans possessed by these specimens are as follows: all but three have two subanal warts conspicuous because of color and structure; the heel of the extended leg of all but one does not reach the snout. Thus, on the basis of structure, these specimens may be assigned to the subspecies A. g. crepitans. This is also true as regards the color pattern of the posterior surface of the thigh.

The 19 specimens were compared with a series of A. g. gryllus from Aiken County, South Carolina. These latter specimens have at least two definite brown stripes separated by a white stripe. Occasional specimens may have a third dark stripe on the dorsal surface of the thigh separated from the median posterior brown stripe by a white stripe. The lowermost brown femoral stripe is separated from the mottled venter of the thigh by a white stripe. The lowermost brown femoral

stripe is separated from the mottled venter of the thigh by a white stripe. Thus, in rear view, the posterior surface of the thigh from top to bottom presents alternating white-brown-white-brown-white stripes; sometimes brown-white-brown-white-brown-white. The 19 Tennessee specimens have the following patterns: white-brown-white, the brown stripes are not always distinct and sometimes blending into the lowermost white stripe. Occasional specimens may have a pattern of white-brown-white-brown stripes. The lowermost brown stripe being a concentration of pigment of the ventral surface of the thigh.

Genus Hyla, Tree Frogs. This genus of frogs is represented in eastern Tennessee by two forms: the Northern Spring Peeper, Hyla c. crucifer (Wied), and the Eastern Gray Tree Frog, Hyla v. versicolor (LeConte). Neither of these frogs is represented by numerous collected specimens. But, these specimens plus call-note identifications indicate these frogs are of rather widespread occurrence in at least the Valley Province (Fig. 16). H. c. crucifer is found as high as 4,000 feet (King, 1939: 567). It is characteristic of marshy meadows and floodplain pools where forests are not dense. This is quite in contrast to the habitat of H. v. versicolor. This frog seems not attracted to ponds or pools which are not associated with forest. The highest elevation from which H. v. versicolor is known is 2,500 feet.

H. c. crucifer is represented by a series of 3 females and 12 males. These range from 28 mm. to 37 mm. in body length. The largest specimen is a female. The largest male has a body length of 31 mm. These specimens are not different from the description of H. c. crucifer as given by Walker (1946: 57-58) and Wright and Wright (1949: 311-313).

H. v. versicolor is represented by a series of one female and 13 males. These range in body lengths from 36 mm. to 45 mm. among the males. The female has a body length of 54 mm. The range of ratios between body length and third finger length is 5.1 to 7.1, mean 6.1. This range is greater than that given for this frog by Wright and Wright (loc. cit.: 91). There is a tendency among about half of the specimens to have a sub-circular spot enclosed by the dark reticulations on the posterior surface of the thigh. Such a color pattern is mentioned for the Southern Gray Tree Frog, Hyla v. chrysoscelis (Cope). However, this may be within the normal range of color variation of H. v. versicolor.

Genus Pseudacris, Chorus Frogs. Two species of chorus frogs are present in eastern Tennessee. They are the Mountain Chorus Frog, Pseudacris brachyphona (Cope), and the Chorus Frog, Pseudacris nigrata. As will be shown subsequently, the latter is interpreted as an intergrade population between the subspecies Pseudacris n. feriarum (Baird), the Upland Chorus Frog, and Pseudacris n. triseriata (Wied), the Western Chorus Frog.

P. brachyphona is represented by a series of 3 females, 20 males, and 22 of undetermined sex. The males range in body length from 25 mm. to 34 mm. The females range in body length from 31 mm. to 37 mm. The largest male and female are larger by three and four millimeters respectively than the largest from Ohio (Walker, 1946: 47). Among these specimens, 35.5 per cent (16) possess a cross-shaped dorsal pattern. Walker (loc. cit.: 46) reports a 20 per cent occurrence of this pattern in the Ohio specimens. Martoff and Humphreys (1955: 247) report a

50 per cent occurrence of this pattern in Georgia specimens. These data suggest a geographical gradient of this character. Among the remainder of my specimens, 42.3 per cent (19) possess a dorsal pattern of unconnected crescent-shaped marks, and 22.2 per cent (10) possess a dorsal pattern of spots and bars.

Ratios obtained from the sexed individuals are as follows: tibia length/body length, 0.46 to 0.58, mean 0.53; head width/body length 0.32 to 0.37, mean 0.35. These differ from ratios reported by Walker for Ohio specimens as follows: minimum tibial length/body length ratio of Tennessee specimens is 0.03 less than that for Ohio specimens; minimum head width/body length ratio for Tennessee specimens is 0.01 less than that for Ohio specimens. The maxima of these ratios for Tennessee specimens are, respectively, the same as and 0.02 less than the maxima for Ohio specimens. Presentation of these data in terms of the ratios of Wright and Wright (1949: 230) is as follows: body length/tibia length, 1.72 to 2.19, mean 2.06; body length/head width, 2.66 to 3.01, mean 2.98. These specimens possess larger body length/tibia length ratios than the extremes reported by Wright and Wright. The minimum body length/head width ratio of these specimens is larger, the maximum smaller, than the extremes of this ratio reported by Wright and Wright. These data also suggest geographic variation among populations of P. brachyphona.

P. nigrita is represented by a series of 5 female, 31 male, and 29 unsexed specimens. Smith and Smith (1952) designate the eastern Tennessee population of this frog as P. n. feriarum. Critical examination of the 36 sexed individuals indicates that the eastern Tennessee population is intermediate between P. n. feriarum and P. n. triseriata.

Smith and Smith (1952: 167, 173) give the following ratio values to distinguish P. n. feriarum from P. n. triseriata.

	<u>P. n. feriarum</u>	<u>P. n. triseriata</u>
Tibia length/ body length		
range =	?	41-47%
mean =	50.6%	42.6 ± .101%
Head length/ body length		
range =	29-40%	25-35%
mean =	33.7%	30%
Head width/ body length		
range =	26-36%	25-34%
mean =	31.8%	29%

The values of these ratios obtained from the 36 eastern Tennessee specimens are as follows: tibia length/body length, 0.43 to 0.51, mean 0.47; head length/body length, 0.28 to 0.35, mean 0.31; head width/body length, 0.30 to 0.35, mean 0.33. I conclude that, on the basis of these data, the eastern Tennessee population is intermediate between the two subspecies in regard to these characters. Similarly, the color pattern of the eastern Tennessee population is intermediate between that of P. n. feriarum and P. n. triseriata. This conclusion is based upon a comparison of these specimens with a series of P. n. triseriata from Harper County, Kansas, and with a series of P. n. feriarum from Tuscaloosa, Alabama, in the University of Florida Collections.

Difference in color pattern between the Tennessee specimens and the Tuscaloosa specimens are as follows: Tennessee specimens much darker, dorsal stripes less conspicuous; dorsal stripes narrower, more

interrupted, and with more irregular border in Tennessee specimens; white lip stripe bordered below by much more conspicuous brown stripe in Tennessee specimens; none of the Tennessee specimens lacks a median dorsal stripe that does not also lack the two lateral stripes. Comparison with the Kansas series is as follows: the dorsal stripes are of about the same relative widths in the two series; Tennessee specimens darker than the Kansas series; dark line beneath the white lip stripe is more conspicuous in the Tennessee series. Thus, fewer color differences exist between the eastern Tennessee frogs and the Kansas frogs than between the Tennessee frogs and the Alabama frogs.

The range of elevations of collecting sites where P. brachyphona is known to occur in eastern Tennessee is from 900 feet to 1,850 feet. It is apparently restricted in its distribution to the Unaka Province and to the Cumberland Plateau Province, where it is reported as common by Gentry (1955: 175). Martoff and Humphreys (1955: 247) record this frog from an elevation 2,500 feet on the Cumberland Plateau of Georgia. P. brachyphona is apparently absent from the Valley Province. The range of elevations of collecting sites for P. nigrata is from 800 feet to 2,500 feet in the Great Smoky Mountains National Park (King, 1939: 566). The distributions of the collecting sites of P. brachyphona and P. nigrata are suggestive of ecological differences affecting the distributions of these frogs (Fig. 17).

Although P. nigrata may be encountered in the Unaka Province, it is not abundant at low elevations along stream valleys. Two exceptions are known; King's record for this frog at 2,500 feet at Fighting Creek Gap, and a locality on Starr Mountain in Monroe County at an

Fig. 17.--Localities for the Chorus Frog, Pseudacris nigrita, the Mountain Chorus Frog, P. brachyphona, and the Eastern Narrow-mouthed Toad, Microhyla c. carolinensis.

elevation of 1,700 feet. Fighting Creek Gap is accessible from the park headquarters area without having to traverse heavily wooded land. The Monroe County site is an outlier of the Unaka Province which is separated from the mountains proper by a valley three to five miles wide. Moreover, this valley is rather intensively farmed. There are no records of P. brachyphona from Starr Mountain although it does occur on the mountain slopes on the east side of the interposed valley. These two frogs have been taken together only in pools of stream floodplains within the Unaka Province. Thus, while P. brachyphona may be taken at low elevations, it is always in areas contiguous with the mountains proper. Conversely, while P. nigrita may be collected in the Unaka Province, it is only along stream valleys or on mountain outliers surrounded by valleys. P. brachyphona seems to be restricted to forested land, especially deciduous forest. Conversely, P. nigrita seems to be an inhabitant of open grassy or glade-type habitats.

Smith and Smith (1952: 178) discuss a hiatus between the ranges of P. n. feriorum and P. n. triseriata from New England southwestward to the Nashville Basin of Tennessee. They attribute this hiatus to the occurrence of P. brachyphona in this region. The implication is that there is interspecific competition which prevents these two frogs from occurring in the same area. On the basis of the information presented above, this explanation seems untenable.

Family Microhylidae.

Genus Microhyla, Narrow-mouthed Toads. The Eastern Narrow-mouthed Toad, Microhyla c. carolinensis (Holbrook), is represented by

a series of four females and eight males. These range in body lengths, respectively, from 19 mm. to 31mm. and from 25 mm. to 30 mm. As regards structure and coloration, they are not different from the description as given by Wright and Wright (1949: 571-572).

This secretive toad is apparently restricted to elevations below 1,200 feet, although it may be found in the physiographically defined Unaka and Cumberland Plateau provinces (Fig. 17). It is not found in dense forest, but may be encountered in the edge between forest and field or in cut-over, open timber. Frequently males can be heard calling or individuals may be found at considerable distance from water. Next to the bufonids, it is apparently the most tolerant of the selientians in eastern Tennessee of xeric conditions.

Family Ranidae.

Genus Rana, True Frogs. Five species of this genus occur in eastern Tennessee. Considered as a whole, these frogs are rivaled only by Bufo in the variety of end range of elevation of habitats occupied.

The Bullfrog, Rana catesbiana Shaw, is represented by six females and 12 males. These agree in all particulars with the description of this frog as given by Walker (1946: 68-69) and by Wright and Wright (1949: 445-446). The females range in body length from 43 mm. to 149 mm., the males from 47 mm. to 132 mm.

In areas where ponds are a common feature of the landscape, this frog is a characteristic inhabitant of the ponds. In eastern Tennessee, where ponds are of infrequent occurrence, the Bullfrog is encountered along the banks of streams and rivers and along the shorelines of the

Tennessee Valley Authority impoundments. This frog is one of the most commonly encountered ranids in the streams of the Unaka Province up to an elevation of 1,800 feet. Locality records indicate it is of widespread occurrence in eastern Tennessee (Fig. 18).

The Green Frog, Rana clamitans melanota Latrille, is represented by 6 females, 22 males, and 4 specimens of undetermined sex. These range in body length from 27 mm. to 92 mm. The largest male and female have body lengths of 92 mm. Meristic data and color variation are within the range of variation as reported by Mecham (MS).

This frog may be encountered in ponds, along shorelines of impoundments, in marshy meadows, and along the banks of streams and rivers. With the Bullfrog, the Green Frog is one of the most frequently encountered ranids in the streams of the Unaka Province. Judging from locality records, it is of widespread occurrence in eastern Tennessee (Fig. 18). The highest known elevation from which this frog has been collected is 3,900 feet (King, 1939: 567).

The Wood Frog, Rana sylvatica, is represented by seven male specimens. Meristic data from these frogs are as follows: body length, 50 mm. to 57 mm.; ratio between tibia length and body length, 0.51 to 0.59, mean 0.57; ratio between head width and body length, 0.33 to 0.35, mean 0.34. The mean value of the ratio between tibia length and body length of these specimens is the same as reported by Walker (1946: 93) for Ohio specimens of the Northern Wood Frog, Rana sylvatica sylvatica (LeConte). The ratio between head width and body length are within the range of this ratio for Ohio wood frogs. Witschi (1953) does not present comparable data in his description of the Cherokee Wood Frog, Rana

Fig. 18.--Localities for the Bullfrog, Rana catesbiana, and the Green Frog, R. c. melanota.

sylvatica cherokiensis. The primary distinction between these two frogs seems to be difference in color.

These seven frogs are (and six in life were) much darker than Ohio wood frogs which I have seen. These frogs are a dark olive green on the dorsum. One frog in life was a bright reddish tan. Except for this specimen, the masks of these specimens are nearly obscured by the dark dorsal color.

Mr. Robert Humphreys informs me that the color differences among populations of the wood frog in eastern United States are clinal, making the validity of the subspecies R. s. cherokiensis suspect. Because of the inadequate type of description of the subspecies and of the few available specimens from eastern Tennessee, I am designating the wood frog population of eastern Tennessee as Rana sylvaticae subspecies.

These seven specimens are from scattered localities (Fig. 19). Additional localities indicated by question marks are shown on the basis of call-note identifications. Although specimens have not been collected in the Valley Province except near the edge of the Unaka Province, breeding choruses have been heard in the middle of the Valley Province (McMinn County). Invariably these Valley breeding sites have been marshy meadows flooded by late winter rains. In the forested mountain province egg masses presumably of this frog have been encountered in roadside ditches and floodplain pools. Gentry (1955: 176) reports the Wood Frog from Middle Tennessee 200 miles to the west of the Smoky Mountains. He makes no mention as to habitat. Available data indicate that this frog is restricted to elevations below about 2,500 feet, and that it is confined to areas in or near woodland.

Fig. 19.--Localities for the Wood Frog, *Rana sylvatica*, the Leopard Frog, *R. pipiens*, and the Pickerel Frog, *R. palustris*. The question marks indicate localities based upon call-note identifications.

The Leopard Frog, Rana pipiens, is represented by 3 females, 5 males, and 5 specimens of undetermined sex. Seven of the 13 specimens possess a white tympanic spot characteristic of the Southern Leopard Frog, Rana p. sphenocephala (Cope). Six of these lack the rostral spot ascribed to the Northern Leopard Frog, Rana p. pipiens Schreber (Welker, 1946: 87). Of the six frogs lacking the tympanic spot, only two have the rostral spot. Three of the specimens with the light tympanic spot possess light-bordered dorsal spots as in R. p. pipiens. R. p. pipiens is described as having distinctly spotted sides below the dorsoleateral line; R. p. sphenocephala is described as having this area mottled and/or vermiculate. Four of the specimens with tympanic spots have distinctly spotted sides as do three of the six specimens lacking the tympanic spot. The remainder have mottled and/or vermiculate patterns on the sides.

Metric data from these specimens without regard to sex are as follows: body lengths, 22 mm. to 82 mm. (the largest female 76 mm., the largest male 82 mm.); ratio between body length and tibia length, 1.62 to 1.96, mean 1.78; ratio between body length and snout length, 5.85 to 8.60, mean 7.17; ratio between body length and upper eyelid length, 11.4 to 18.6, mean 13.0. The ratios between body length and tibia length of these specimens are within the range given for R. p. pipiens and R. p. sphenocephala; the maximum body length/snout length ratio is much greater than the maximum reported for either subspecies, as is the mean ratio of this series; the maximum body length/upper eyelid length ratio is much greater than the maximum reported for either

subspecies, but the mean is within the range for R. p. pipiens (Wright and Wright, 1949: 102-103). On the basis of these meristic data, and especially on the basis of the intermediacy of coloration, the eastern Tennessee population of leopard frogs is designated as R. p. pipiens x sphenocephala intergrades.

The few specimens of this frog is indicative of the infrequency with which this frog is encountered. It is especially uncommon in the Unaka Province (Fig. 19). In the Valley, where it is more abundant, it is encountered along stream margins, shorelines of Tennessee Valley Authority impoundments, and in marshy meadows. As summer approaches, it is not unusual to find this frog in pastures at considerable distance from water. It seems to be characteristic of grassy communities if sufficient moisture is present. It is rarely encountered in forest land. The maximum elevation from which it is known is 3,200 feet.

The Pickerel Frog, Rana palustris La Conte, is not encountered much more frequently than the Leopard Frog or the Wood Frog. Only four males and one female are available as a result of this study. These range in body lengths from 55 mm. to 60 mm. (males). The female has a body length of 67 mm. Other data from these specimens are as follows: ratio between tibia length and body length, 0.59 to 0.62, mean 0.60; ratio between head width and body length, 0.33 to 0.35, mean 0.34. The head width/body length ratios are within the range reported for Ohio specimens by Walker (1946: 80). The minimum tibia length/body length ratio is larger than the maximum for Ohio specimens. As regards other structural features, these five specimens agree with Ohio material.

Generally, these specimens have color patterns and coloration as given for this frog by Walker (1946: 80) and Wright and Wright (1949: 478-479). However, certain differences are rather conspicuous. One male has a very small rostral spot, two have no rostral spot. These latter two frogs have scattered dorsal spots of irregular outline. The sides and upper surfaces of the legs are profusely mottled with brown. The dark crossbands of the upper surfaces of the limbs are absent on one of these two males; on the other specimen they are present only on the upper surfaces of the rear limbs. I do not know whether these color differences are within the range of variation of R. palustris.

R. palustris is apparently most abundant in wooded areas. All of the above specimens are from within or near the Unaka Province (Fig. 19). King (1939: 568) reports this frog as occurring by the thousands in a three acre pond on Chatahoochee Creek, Great Smoky Mountains National Park, Haywood County, North Carolina. I have not encountered an aggregation of this frog in excess of about a dozen individuals. Data indicate that the maximum elevation attained by the Pickerel Frog is around 2,000 feet.

B. Class Reptilia

1. Order Chelonis

This order is represented by 3 families, 7 genera and a minimum of 11 species.

Family Chelydridae

Genus Chelydra, Snapping Turtles. Fifteen females, five males, and two individuals of undetermined sex of the Snapping Turtle, Chelydra

serpentina, are the basis for designating the eastern Tennessee population as the Common Snapping Turtle, Chelydra s. serpentina (Linnaeus). All of them agree with the descriptions of this turtle as given by Carr (1952: 63-64).

The snapping turtle is found throughout eastern Tennessee (Fig. 20). Individuals may be encountered in nearly every conceivable aquatic situation: mud holes resulting from the accumulation of rainwater; major rivers; mountain branches; marshy meadows. The highest elevation recorded for this turtle in eastern Tennessee is 2,200 feet in the Great Smoky Mountains National Park (King, 1939: 578). Pope (1946: 74) states that this turtle occurs at altitudes in excess of 3,000 feet in eastern United States. To my knowledge it is exceeded in altitudinal distribution only by the box turtle. The apparent deterrent to the altitudinal distribution of the snapping turtle is the extremely rocky nature of the streams at high elevations.

Family Kinosternidae

Genus Sternotherus, Musk Turtles. Two species of this genus occur in eastern Tennessee: Sternotherus odoratus and S. minor. In using the specific name minor, I am following the terminology of Tinkle and Webb (1955).

The Stinkpot, Sternotherus odoratus (Latrielle), is represented by 11 females and 6 males. In all respects except two, and these are minor differences, these specimens agree with the description of this turtle as given by Carr (1952: 82-84). The differences are as follows: 14 of these specimens have a black edging on the posterior and postero-

Fig. 20.--Localities for the Common Snapping Turtle, Chelydra s. serpentina, the Stinkpot, Sternotherus odoratus, the Stripe-necked Turtle, S. m. peltifer, and the Eastern Mud Turtle, Kinosternon s. subrubrum.

dorsal margins of the lateral laminae and on the lateral and posterior margins of the central laminae; eight of the specimens have radiating yellowish lines on the first lateral laminae and at least on the ventral portion of the remaining laterals. Carr (loc. cit.: 3) states that this turtle has usually an unmarked carapace.

This turtle is encountered in stock tanks, rivers, backwaters of coves, and the lower reaches of the mountain streams. It is most common in situations where the bottom is muddy. Although its distribution is apparently limited, I suspect it is more widespread than the available information indicates (Fig. 20). The highest elevation at which this turtle has been encountered is 1,100 feet.

The Strip-necked Musk Turtle, Sternotherus m. peltifer (Smith and Glass), is represented by 4 females, 6 males, and the shells of 2 individuals. I could find no apparent discrepancies between these specimens and the type description (Smith and Glass, 1947). Tinkle (in litt.) informs me that he believes that the eastern Tennessee population differs from topotypic material. The eastern Tennessee specimens are "much flatter and [they have] more intense stripes on the head." Certain meristic data obtained from these specimens are as follows: females, carapace length, 46 mm. to 111 mm.; carapace width, 38 mm. to 88 mm.; plastron length, 29 mm. to 85 mm.; and ratio between carapace width and carapace length, 0.70 to 0.83, mean 0.747; ratio between bridge width and plastron length, 0.22 to 0.24, mean 0.233; males, carapace length, 41 mm. to 100 mm.; carapace width, 36 mm. to 69 mm.; plastron length, 26 mm. to 70 mm.; ratio between carapace width and carapace

length, 0.66 to 0.73, mean 0.706; ratio between bridge width and plas-tron length, 0.16 to 0.20, mean 0.186. The gular laminae are obviously paired in only two specimens; those of the two smallest specimens are unpaired. There are suggestions of dark radiating lines on the ventral margins of the first and second costal laminae of four specimens, including the two smallest. The remaining specimens have costal laminae with dark punctations, occasionally elongated into dashes and/or short lines. These punctations tend to be arranged into rows running longitudinally. The black and the yellow stripes on the dorsal half of the neck are of about equal widths. Those on the ventral half of the neck are of different widths; the yellow stripes are up to twice as wide as the black stripes. The temporal and parietal regions are marbled and/or reticulated with black and yellow.

It is of interest to note that S. odoratus and S. m. peltifer have not been collected together although they inhabit the same drainage systems (Fig. 20). Trapping in the Tennessee River has resulted in the capture of Pseudemys, Graptemys, and S. m. peltifer at one locality, but no S. odoratus. Trapping in Sweetwater Creek, Monroe County, has resulted in the capture of Chelydra, Chrysemys, and S. odoratus, but no S. m. peltifer. The explanation which seems most acceptable at present, aside from competition for food involves differences in habitat preference.

Nine of the S. m. peltifer specimens are from clear, moderate to swift, rock and sand bottom streams. Conversely, all but one of the S. odoratus are from turbid, mud and sand bottom streams or ponds. None of the S. m. peltifer is from a pond habitat. It is possible that the

impoundment of the major streams by the Tennessee Valley Authority has decreased the availability of habitats in those streams suitable for S. m. peltifer and increased the availability and extent of habitats suitable for S. odoratus. The highest elevation from which S. m. peltifer is known is 1,500 feet.

Genus Kinosternon, Mud Turtles. Carr (1952: 101) indicates the occurrence of the Eastern Mud Turtle, Kinosternon s. subrubrum (Lacépède), in eastern Tennessee. Only one specimen, an adult male, is available as a result of this study. This specimen is from a marshy pasture, elevation 1,000 feet, in McMinn County (Fig. 20). Meristic data from this specimen are as follows: carapace length, 92 mm.; carapace width, 67 mm.; plastron length, 84 mm.; width of anterior plastral lobe, 45 mm.; width of posterior plastral lobe, 39 mm.; length of anterior plastral lobe, 32 mm.; depth of shell, 38 mm.; width of bridge, 15 mm.

The upper borders of the marginals are even except for that of the last marginal, which is roughly triangular and higher by one-third than the highest marginal anterior to it. The carapace is rugose (growth rings) and not depressed along the middorsal region. Additionally, two broad lateral ridges cross the dorsal portions of the lateral laminae one through three. These ridges originate in the region of the birth plate of lateral lamina one and terminate in the region of the birth plate of lateral lamina three. The lack of a middorsal depressed region and the presence of two lateral keels may indicate this is a subadult specimen. Except for the above conditions, this specimen agrees with the description of K. s. subrubrum as given by Carr.

Family Emydidae

Genus Terrapene, Box Turtles. Thirty-five females, 29 males, and 5 specimens of undetermined sex of the Box Turtle, Terrapene carolina, are available. Shell dimensions of these specimens are as follows: carapaca length, 37 mm. to 140 mm.; carapaca width, 34 mm. to 119 mm.; plastron length, 34 mm. to 135 mm.; depth of shell, 28 mm. to 73 mm. The box turtle population of eastern Tennessee is designated in the literature as the Eastern Box Turtle, Terrapene c. carolina (Linnaeus). However, the range of variation in color and shell configuration among my specimens is such as to include almost all the combinations of characters used to distinguish the four subspecies of this turtle in eastern United States. The variability of these 69 specimens is so great as to almost preclude group description.

Comparison of these specimens with selected examples of the Gulf Coast Box Turtle, Terrapene c. major (Agassiz), the Three-toed Box turtle, Terrapene c. triunguis (Agassiz), and with T. c. carolina x triunguis and T. c. carolina x major intergrades in the University of Florida Collections does little to clarify the situation. The head, limb, carapaca, plastron color patterns, and the shell configurations of these selected examples can be duplicated in the 69 specimens from eastern Tennessee. Fully one-third to one-half of these 69 specimens possessed one or more of the diagnostic characters of each of the subspecies other than T. c. carolina. Even the color pattern characteristic of the carapaca of the Florida Box Turtle, Terrapene c. bauri Taylor, is present. The only subspecific character not exhibited by any of these specimens is the three-toed condition of T. c. triunguis and T. c. bauri.

Most of the 69 specimens have varying degrees of the characters attributed to T. c. carolina. A number of the specimens possess a combination of an elongate carapace with a distinctly flared posterior margin and a dark horn-colored to black carapace and plastron as described for T. c. major. Several specimens have the head and neck marbled and/or reticulated with orange or yellow and the anterior surface of the forelimbs with numerous small orange or yellow spots as described for T. c. triunguis. Most of these specimens are from the southeastern corner (Polk County) of the study area. These data suggest the possibility that the range of variation in T. b. carolina may be such as to include various combinations of the characters used to diagnose the subspecies T. c. major and T. c. triunguis.

The box turtle is one of the most ubiquitous reptiles in eastern Tennessee. It is widespread and may be encountered in all kinds of situations (Fig. 21). Aside from saying that it is most abundant in forested situations, little can be said about habitat preference. It may be found in residential areas in towns, plowed fields, along stream margins, and in dense forest. The highest elevation at which it is known to occur is 4,000 feet. This turtle and the snapping turtle are the only two which are known among the Copper Basin inhabitants (Ash, 1945: 265).

Genus Graptemys, Map Turtles. Two species of this genus occur in eastern Tennessee. The Map Turtle, Graptemys geographica (LeSueur), is reported by Carr (1952: 192), Gentry (1955: 331), and Rhoads (1895). I have not encountered this turtle during this study. The other is the

Fig. 21.--Localities for the Eastern Box Turtle, Terrapene c. carolina, and the Eastern Spiny Softshell, Trionyx f. spinifera.

Ouachita Map Turtle, Graptemys pseudogeographica ouachitensis Cagle.

Two specimens, both juveniles, of G. p. ouachitensis are available from the Tennessee River in Meigs County (Fig. 22). These agree in all particulars with the description of juveniles as given by Cagle (1953: 11-12). Cagle tentatively identified specimens from Humphreys County in Middle Tennessee as intergrades between G. p. ouachitensis and the False Map Turtle, Graptemys p. pseudogeographica (Gray). No indication of G. p. pseudogeographica influence is present in these specimens. These specimens extend the known range of G. p. ouachitensis nearly 400 miles upstream in the Tennessee River.

Genus Chrysemys, Painted Turtles. As previously reported (Johnson, 1954), the painted turtle population of eastern Tennessee is intermediate between the Eastern Painted Turtle, Chrysemys p. picta (Schneider), and the Midland Painted Turtle, Chrysemys p. marginata (Agassiz). Since publication of the above report, 54 additional specimens are available. These additional specimens are also intergrades and make it evident that the entire Tennessee River Valley from Chattanooga to as far north as the Nolichucky River is in the area of intergradation (Fig. 22).

This turtle inhabits all permanent types of aquatic situations except the swift, rocky streams of the mountains and small, shallow streams and branches of mountain and lowland. The one requisite for a suitable habitat seems to be a minimum depth of three or more feet of water. This is the turtle of stock tanks and flooded quarries to which reference is made as "hard-shelled water terrapins." Although the

Fig. 22.--Localities for the Map Turtle, Graptemys geographica, the Ouachita Map Turtle, G. p. ouachitensis, and the Painted Turtle, Chrysemys picta.

genus Chrysemys is generally considered a pond-type turtle, it is adept at survival in stream environs. The highest known elevation of occurrence is 1,750 feet.

Genus Pseudemys, Cooters and Sliders. This group of turtles is represented by two species: Cootar, Pseudemys floridana; Pond Slider, Pseudemys scripta. Available data indicate that each of these species is represented by two subspecies which intergrade in eastern Tennessee.

Six specimens of the Cootar, Pseudemys floridana, are the basis for the following remarks. These are from the Conasauga River, elevation 1,000 feet, in extreme southeastern Tennessee (Fig. 23). These specimens are four females and two males. Meristic data from the females are as follows: carapace lengths, 242 mm. to 303 mm.; carapace widths, 173 mm. to 187 mm.; plastron lengths, 218 mm. to 286 mm.; depth of shells, 78 mm. to 103 mm.; ratio between carapace length and carapace width, 1.39 to 1.46, mean 1.26; ratio between carapace length and shell depth, 2.75 to 3.10, mean 2.91. Meristic data from the males are as follows: carapace lengths, 197 and 230 mm.; carapace widths, 145 mm. and 160 mm.; plastron lengths, 176 mm. and 207 mm.; depths of shells, 63 mm. and 70 mm.; ratio between carapace length and carapace width, 1.36 and 3.20; ratio between carapace length and shell depth, 3.12 and 3.29. These data are equally applicable to the River Cootar, Pseudemys f. concinna (LeConte), and the Slider, Pseudemys f. heiroglyphica (Holbrook) (vide Carr, 1952: 287, 306).

Key characters separating these two subspecies are alveolar surfaces of the lower jaw, color of hind feet and upper surface of tail

Fig. 23.--Localities for the Cooter, Pseudemys floridana, and the subspecies of the Pond Slider, P. scripta.

(Garr, 1952: 237). On the basis of these key characters, the six specimens can be identified as P. f. heiroglyphica: broad alveolar surfaces with high, isolated, conical teeth; tail with a pair of dorso-lateral yellow stripes; leg stripes continued onto the toes. Each also possesses a C-shaped mark on the second lateral lamina as described for P. f. concinna by Granshaw (MS). In other respects, the color of the carapace is intermediate between that of P. f. concinna and P. f. heiroglyphica.

There is no extensive dark central plastral figure. What dark color there is on the yellow plastron is confined to the region of the seams of the various pairs of laminae. These dark areas are best described as smudges. There are light-centered black spots on the submarginal seams from seam 1-2 through seam 8-9. Posterior to seam 8-9, the light center persists merely as a lighter edge of each of the adjacent laminae or it is absent. On four specimens the blotches at the level of the bridge, or one or two spots anterior to the bridge, are as concentric black rings separated from each other by light-colored rings. The remaining spots on these and on other specimens are solid (except where there may be light central spots as mentioned above).

All of the specimens have dark bridge markings, in general, as elongate dark blotches on the lateral edges of the pectoral and abdominal laminae. In four of the specimens, the bridge markings are in contact with the submarginal marks. In one specimen there is a large dark paranthetical mark (open end directed posteriorly) on the posterior edge of the abdominal and the anterior edge of the inguinal laminae. The result is two pairs of rather doughnut-shaped marks on the bridge.

Each upper marginal lamina is split by a wide vertical bar, T-, or Y-shaped mark. Each intermarginal seam is streddled by a group of concentric light rings elternating with dark rings, the latter generally the broeder.

The paramedian head stripes are distinct on all but one of the specimens. On this exceptional specimen, the paramedian stripes join with the supratemporel stripes at the level of the orbit.

Because these specimens exhibit morphological and color characters intermediate between P. f. concinna and P. f. hairoglyphica, I am designating them as P. f. concinna x hairoglyphica intergrades. This places P. f. hairoglyphica in the Coose River system of Georgia.

The Cumberland Turtle, Pseudemys s. troosti (Holbrook), is reported from the Greet Smoky Mountains National Park (King, 1939) and from the upper reaches of the Tennessee River in eastern Tannasee by Carr (1952: 258) and by Burger (1952: 77). I have found no literature records of the occurrence of the Red-eared Turtle, Pseudemys s. elegans (Wied), in eastern Tennessee Waters. Eleven specimens (10 females, 1 male) from the Tennessee River, Meigs County, are available and indicate that P. s. elegans does occur et least this far north in the Tennessee River (Fig. 23).

Meristic data from the females are es follows; carapace length, 85 mm. to 182 mm.; carepace width, 73 mm. to 145 mm.; plastron length, 78 mm. to 179 mm.; depth of shell, 38 mm. to 76 mm.; ratio between cerepace length and carepece width, 1.17 to 1.28, mean 1.23; retio between carapace length and shell depth, 2.27 to 2.71, mean 2.47. These data

for the male are as follows: carapace length, 152 mm.; carapace width, 118 mm.; plastron length, 141 mm.; shell depth, 53 mm.; ratio between carapace length and carapace width, 1.29; ratio between carapace length and shell depth, 2.86.

Each specimen possesses a reddish or orange spot or wash superimposed upon a yellow supratemporal stripe. The supratemporal spot is an average of 3.1 times, range 2.3 to 4.2 times, wider than the continuation of the supratemporal stripe on the neck. These values are intermediate between the condition found in P. s. troosti and P. s. elegans, but more like that of the latter (Burger, 1952: 77-79). The supratemporal spot averages 1.3 times, range 0.8 to 1.8 times, wider than the subocular stripe, which condition is again intermediate between the two subspecies. The suborbital stripe is intercepted by the mandibular stripe posterior to the angle of the jaws, a condition reported for P. s. elegans (Carr, 1952: 252).

The bridge of these specimens is predominantly light colored. But, a circular or elongate black mark is present on the seam between adjacent lateral edges of the abdominal and pectoral laminae in all but one specimen. This exception has only one bridge spot on the left inguinal lamina. This is a troosti-like character (Carr, 1952: 260). The submarginal blotches of six of the specimens have a single C-shaped yellow mark on the anterior half, at least, of the blotch. The submarginal spots average 1.3 times, range 0.9 to 2.1 times, wider than the yellow interspaces, a P. s. elegans character (Burger, 1952: 77). The plastral color ranges from nearly immaculate yellow, as in P. s. troosti,

to yellow with bold black smudges on each of the laminae, as in P. s. elegans. Yellow predominates on the front legs, the undersurfaces of the hindlegs, and on the tail as in P. s. troosti. There is a single yellow stripe on the beak, which is more like the condition in P. s. troosti than in P. s. elegans.

While it is obvious that troosti-like characters predominate among these 11 specimens, it is also apparent that elegans-like characters are shared among these specimens. The presence of P. s. elegans this far up the Tennessee River may be further evidence of range extension of this turtle in recent times as suggested by Stejneger (Carr, 1952: 250-251). Perhaps the construction of dams across the Tennessee River has increased the suitability of this river as a habitat for this turtle and reduced its suitability for P. s. troosti. These 11 specimens were taken in a funnel trap in company with G. p. ouachitensis and S. m. peltifer.

Genus Trionyx, Softshell Turtles. Only one species of this genus is encountered in eastern Tennessee, vis., the Spiny Softshell, Trionyx ferox. Four specimens, 3 females and 1 juvenile of undetermined sex, are available. These agree essentially with the description of the Eastern Spiny Softshell, Trionyx f. spinifera (LeSueur), as given by Carr (1952: 427-428).

While this turtle is represented by only a few specimens, it is not to be assumed uncommon in eastern Tennessee. It is the one most complained about by fishermen as a bait robber. Individuals have been collected and/or seen in both the slower, turbid rivers of the Valley

and the more swift, clear, and rocky bottom streams of the Unaka Province up to elevations of 1,100 feet (Fig. 21). Field workers of the Tennessee Fish and Game Commission fish survey crew tell me it is rather abundant in such streams as the latter. These workers probably see more of them in these streams because of better visibility.

The absence of the Smooth Softshell, Trionyx mutica (LeSueur), is probably correlated with the relative absence of natural ponds in eastern Tennessee. It is conceivable that this turtle may eventually become established here as a result of the Tennessee Valley Authority impoundments, which simulate habitats suitable for T. mutica.

2. Order Squamata

This order is represented by four families, six genera, and at least eight species.

Family Iguanidae

Genus Anolis, Anoles. The Carolina Anole, Anolis c. carolinensis (Voigt), is represented by four female specimens. These are from 42 mm. to 55 mm. in snout-vent length. They agree with the description of this lizard as given by Carr and Goin (1955: 254) and by Smith (1946: 95-96).

This lizard occurs in each of the physiographic provinces contained in the study area (Fig. 24). Habitats in which they have been taken range from the dry oak-pine-heath community of cliff edges on the Plateau to mesic floodplain community at low elevations in the Unaka Province. On the basis of sight records and collection sites, the more

Fig. 24.--Localities for the Carolina Anole, Anolis c. carolinensis, and the Northern Fence Lizard, Sceloporus u. hyacinthinus.

open oak-pine community seems to be the more favorable habitat. The highest elevation of known occurrence is 1,600 feet.

Genus Sceloporus, Spiny Lizards. Forty-nine specimens (21 females, 27 males, 1 of undetermined sex) of this genus have the following meristic data: snout-vent length, 25 mm. to 78 mm.; dorsal scale rows, 35 to 46, modal frequency 39 (27 per cent of the specimens), 85 per cent of the series with 39 or more; scales around midbody, 38 to 48, modal frequency 44 (8 specimens); femoral pores, modal frequency 14 (17 specimens), 75 per cent of the specimens with 15 or fewer. As regards these characters and coloration, the series agrees with the description of the Northern Fence Lizard, Sceloporus undulatus hyacinthinus (Green), as given by Smith (1946: 222-224).

This lizard is abundant in eastern Tennessee and occurs in each of the physiographic provinces (Fig. 24). The most characteristic habitat is open, second growth oak-pine communities. It is very infrequently encountered in dense mesic forest, and then usually near clearings of less mesic areas. The highest elevation of known occurrence of this lizard is 4,000 feet.

Family Anguillidae

Genus Ophisaurus, Glass Snake. McConkey (1954: 148) includes eastern Tennessee in the range of the Eastern Slender Glass Lizard, Ophisaurus attenuatus longicaudus McConkey. O. a. longicaudus is differentiated from the Western Slender Glass Lizard, Ophisaurus a. attenuatus Baird, by the ratio between length of unregenerated tail and the snout-vent length. The two specimens of O. attenuatus available for

examination do not have complete tails, hence this character cannot be employed for these specimens. Several other differences exist between these specimens and the descriptions of the O. attenuatus subspecies given by McConkey.

One specimen has only 16 rows of scales around the base of the tail, which is two rows less than reported for either of the subspecies. This same specimen has 15 dorsal scale rows rather than the 14 or fewer reported for the species O. attenuatus. This specimen is from the Cumberland Plateau.

As regards coloration, each of these specimens differs from the type description of O. a. longicaudus in several respects. The Cumberland Plateau specimen exhibits the following differences: (1) the dorsal crossbands are from 1.5 to 2.0 scales wide, but are separated from each other by only 2.0 to 2.5 scales rather than by five scales, (2) laterally the crossbands extend to the upper half of scale row four rather than to scale row three. The Unaka Province specimen exhibits the following differences: (1) the dorsal body crossbands are only one scale wide rather than two and are separated by only four scales, (2) the median halves of the two dorsalmost scale rows have definite dark brown spots resulting in a distinct rather than a vague middorsal stripe, (3) the crossbands extend laterally to the upper half of scale row four, (4) the sides of the base of the tail possess only four dark brown stripes separated by three white ones rather than five and four respectively. Whether or not these color differences, as well as the differences in scutellation mentioned above, are within the range of variation of O. a. longicaudus is not known to me.

These two specimens, and a specimen found dead on the road, are assigned to the subspecies O. a. longicaudus primarily on the basis of geographic location (Fig. 25). All of them are from areas of second growth oak-pine-heath communities. The highest elevation of known occurrence is 2,200 feet.

Family Teiidae

Genus Cnemidophorus, Racerunners. Three females, 10 males, and 1 individual of undetermined sex comprise the series of this genus available for study. The greatest snout-vent length among these specimens is that of a female and is 81 mm. The tail is incomplete. The largest snout-vent length of a male is 77 mm. The tail of this specimen is incomplete. These specimens do not differ from the description of the Six-lined Racerunner, Cnemidophorus sexlineatus (Linnaeus), as given by Burt (1931: 81-82) and by Smith (1946:412-413).

I have no record of this lizard from the Cumberland Plateau, but I have no doubt that it occurs there. It is abundant in the Valley Province and in the Unaka Province up to elevations of about 2,000 feet (Fig. 25). Although it may be found in forested areas, it is not a deep-forest inhabitant. Rather, its distribution in the forests seems restricted to clearings, rock ledges, roadways, and the like. It is not uncommon in open oak or oak-pine communities, as well as in fields.

Family Scincidae

Genus Lygosoma. The Ground Skink, Lygosoma laterale (Say), is represented by a series of 17 females and 9 males. Snout-vent lengths

Fig. 25.--Localities for the Eastern Slender Glass Lizard, Ophisaurus a. longicaudus, and the Six-lined Racerunner, Cnemidophorus sexlineatus.

of females range from 26 mm. to 47 mm.; those of the males range from 24 mm. to 44 mm. While these specimens agree with the description of this species as given by Smith (1946: 337-338), none of them exhibits the intense dark streaking on the throat and abdomen as seen in specimens from Louisiana (Johnson, 1953: 14). The smallest individuals exhibit the three to four small keels on the scales as do specimens of comparable size from Louisiana. Comparison of the mean number of dorsal scales of the Tennessee material with that of Louisiana material suggests possible geographic variation of this character.

The number of dorsal scales for the Tennessee material are as follows: males, range 59 to 67, mean 62.7; females, range 66 to 75, mean 67.9. The mean value for these males is four rows less than the mean for Louisiana males. The mean number of scales for Tennessee females is 3.2 less than the mean for Louisiana females.

This lizard is widely distributed in eastern Tennessee (Fig. 26). It is most abundant in deciduous forest, although it is also encountered in open oak or oak-pine communities. It is not found in fields unless these are adjacent to woodland. The highest elevation of known occurrence is 2,500 feet.

Genus Eumeces, Striped Skinks. Four species of this genus occur in eastern Tennessee. These are the Five-lined Skink, Eumeces fasciatus (Linnaeus), the Broad-headed Skink, Eumeces laticeps (Schneider), the Southeastern Five-line Skink, Eumeces inexpectatus Taylor, and the Coal Skink, Eumeces anthracinus (Baird).

Fig. 26.--Localities for the Ground Skink, Lygosoma laterale, and the Coal Skink, Eumeces anthracinus.

E. fasciatus is represented by a series of 17 females, 9 males, and 2 juveniles of undetermined sex. The largest female has a snout-vent length of 72 mm. The largest male has snout-vent length of 73 mm. These 28 specimens are designated as E. fasciatus on the basis of the following combination of characters: (1) dorsolateral light lines on scale rows three and four at midbody, (2) scales around midbody ranging from 26 to 31, (3) two enlarged postlabial scales, (4) termination of the intercalary row of scales on the fourth toe at or on the second phalanx. Only 7 of the 28 specimens do not possess all 4 of these characters, and none of these 7 possesses more than one character which is usually associated with E. laticeps. Variations encountered are discussed under E. laticeps.

This skink is of widespread distribution (Fig. 27). While predominantly a woodland inhabitant, it is not infrequently encountered in clearings in and around woods and home sites. As with the other three species of Eumeces, it is seldom encountered in habitats as xeric as those in which Gnemidophorus and Sceloporus occur. The highest elevation of known occurrence for this lizard is 3,700 feet.

E. laticeps is represented by a series of 5 females and 3 males. Snout-vent lengths of the largest female and male are, respectively, 100 mm. and 85 mm. These 8 specimens are assigned to the species E. laticeps on the basis of the following combination of characters: (1) dorsolateral light lines on scale rows four and five or only row four, (2) scales around midbody 31 to 32, (3) one postlabial scale or two small ones, (4) termination of the intercalary row of scales on the

Fig. 27.--Localities for the Five-lined Skink, *Eumeces fasciatus*, the Broad-headed Skink, *E. laticeps*, and the Southeastern Five-lined Skink, *E. inexpectatus*.

fourth toe at or on phalanx three, (5) tertiary temporal scale in contact with the last supralabial scale. Only two specimens possess character number 5. Six of the 8 specimens possess all 5 of the characters. Of the remaining 2 specimens, one has the dorsolateral light lines on scale rows three and four, the other has the intercalary row of scales terminating on phalanx two.

Among the seven E. fasciatus mentioned above as exhibiting E. laticeps character, the variations are as follows: three specimens have the intercalary row of scales terminating on phalanx three of both feet; one specimen has this row of scales terminating on phalanx three on the left foot only; two specimens have the dorsolateral light lines on row four at midbody, one has them on rows four and five at midbody. Whether these variations in the specimens of E. fasciatus and E. laticeps are "normal" for the two species is not known by me. Conant (1951: 210, 212) reports that Ohio specimens of E. fasciatus do not have complete combinations of E. laticeps characters, and that E. laticeps specimens do not have more than one E. fasciatus character.

The criterion of enlarged or reduced postlabial scales is very subjective as employed in the literature. In order to make it a more objective criterion, I am basing the relative sizes on the height of postlabials/height of ear opening. The combined height of the postlabial scales and the height of the ear opening are measured with an ocular micrometer. The ratio between postlabial height and ear opening height from the two series of specimens are as follows: E. fasciatus, range 0.89 to 1.46, mean 1.24; E. laticeps, range 0.47 to 1.10, mean 0.70.

Only one of the 28 specimens of E. fasciatus has a ratio (0.89) of less than 1.00. Of the eight specimens of E. laticeps, six have this ratio less than 1.00, one has a ratio equal to 1.00, and one has a ratio of 1.10. Neither of these last two specimens has any of the other criteria assigned to E. fasciatus. Of the six E. laticeps with ratios of less than 1.00, two have only one postlabial on each side and two (including the specimen with the ratio of 1.00) have the tertiary temporal in contact with posterior supralabial. This criterion, postlabial height/ear opening height, is of questionable diagnostic value, but it is highly suggestive and presents a possible means of determining objectively whether or not the postlabials are enlarged. This ratio has been calculated for the specimens of E. inexpectatus and is reported in the discussion of that species.

The variation in numbers of scale rows is as follows: E. fasciatus, 26 (1 specimen), 28 (5 specimens), 29 (6 specimens) 30 (11 specimens), 31 (3 specimens), 32 (2 specimens); E. laticeps, 30 (5 specimens), 31 (2 specimens), 32 (1 specimen).

E. laticeps is restricted to woodland habitats, although it need not be dense woods. King (1939: 510) implies that this is a lizard of xeric habitats. I, too, have encountered it in oak-pine forest, but always in the vicinity of water. The frequent occurrence of this lizard in stream valleys makes it a characteristic inhabitant of floodplain communities. I have no record of the occurrence of this lizard on the Cumberland Plateau (Fig. 27). No doubt it will be found there, at least in the entrenched stream valleys of the edge of the plateau. The highest elevation of known occurrence is 3,000 feet.

E. inexpectatus is represented by a series of 8 females and 11 males. Snout-vent lengths of the largest female and male are, respectively, 72 mm. and 73 mm. These 19 specimens are allocated to this species on the basis of the following combination of characters: (1) dorsolateral light lines on scale row four or rows four and five; (2) scales around midbody 29 to 31, (3) termination of the intercalary row of scales on the fourth toe of the foot at or on phalanx two. As regards the ratio between height of postlabials and height of ear openings, 12 have this ratio less than 1.00, 6 have it equal to 1.00, and 1 has a ratio greater than 1.00; range 0.75 to 1.22, mean 0.96.

Two specimens have 29 scale rows around midbody, 16 have 30 rows, and 1 has 31 rows. Sixteen specimens have the intercalary row of scales on the fourth toe terminating at or on the second phalanx, 3 specimen have this row of scales terminating on the second phalanx of one foot, the third phalanx of the other foot. Nine specimens have the dorsolateral light lines on scale row four, ten specimens have these lines on rows four and five.

In E. inexpectatus the width of the median subcaudal scales is little if any greater than the length of these scales on unregenerated parts of the tail; the width of these scales is much wider than the length in both E. fasciatus and E. laticeps (Smith, 1946: 352). The results of ocular micrometer measurements of these dimensions on 22 E. fasciatus, 8 E. laticeps, and 13 E. inexpectatus are as follows (reported as ratios of length/width): E. fasciatus, range 0.31 to 0.55, mean 0.350; E. laticeps, range 0.31 to 0.51, mean 0.436; E. inexpectatus,

range 0.45 to 0.53, mean 0.507. These suggest that this character is of relative value rather than of absolute value. Further, I infer from all of the data presented above that these three species of Eumeces are in need of critical systematic review.

By far the greater number of specimens of E. inexpectatus are from the Unaka Province (Fig. 27). Here it is most frequently encountered in clearings, either natural or artificial, in the deciduous forest habitats. The highest elevation of known occurrence is 4,000 feet.

E. anthracinus is represented by two specimens, both juveniles. One is a male, the other presumably a female. Both are 31 mm. in snout-vent length. Each has 26 scale rows around the midbody and 7/7 upper-labials. Each of them is so darkened from preservation that color descriptions are questionable. It is deemed best merely to designate these as E. anthracinus subspecies.

These two specimens came from a grassy clearing in beech-hemlock forest at an elevation of 3,700 feet (Fig. 26). This collection site in the Unaka Province is in the area of intergradation between the Northern Coal Skink, Eumeces a. anthracinus (Beird), and the Southern Coal Skink, Eumeces a. pluvialis (Cope), as shown by Smith and Smith (1952: 681).

3. Order Serpentes

The snakes of eastern Tennessee consist of 2 families, 17 genera, and a minimum of 22 species. In the following accounts the numbers of ventrals and ventrals plus caudals are recorded according to the method of Schmidt and Davis (1941: 26) and Dowling (1951). The counts per Dowling's method are enclosed in parentheses.

Family Colubridae

Genus Natrix, Water Snakes. Two species of this genus are present in eastern Tennessee. These are the Queen Snake, Natrix septemvittata (Say), and the Common Water Snake, Natrix sipedon (Linnaeus).

N. septemvittata is represented by a series of five females and four males. Data obtained from these specimens are as follows: females, snout-vent length, 140 mm. to 524 mm.; tail length, 52 mm. to 161 mm.; ventrals, range 132 (131) to 141 (138), mean 137.6 (135.8); caudals, range, 72 to 78, mean 75; males, snout-vent length, 316 mm. to 436 mm.; tail length, 149 mm. to 175 mm.; ventrals, range 135 (135) to 140 (138), mean 137.5 (136.3); caudals, range, 79 to 89, mean 84. Data from both sexes considered together are as follows: upper labials, 7/7 (8 specimens), lower labials, 10/10 (7 specimens), 8/8 and 11/10 (1 specimen); pre- and postoculars, 2/2 (9 specimens); scale rows, 19-17 (9 specimens).

Scutellation data from these specimens differ from Ohio specimens (Conant, 1939: 77) and from Florida specimens (Carr and Goin, 1955: 288) in the following particulars: the minimum, maximum, and mean numbers of ventral scutes of these females are, respectively, 6, 12, and 8.1 scales less than these values for Ohio specimens, and 3, 7, and 4.4 less than these values for Florida females; the minimum, maximum, and mean numbers of caudals of these females are, respectively, 8, 6, and 7 more than these values for Ohio females, and 11, 6, and 7 more than these values for Florida females; the minimum, maximum, and mean numbers of ventrals of these males are, respectively, 3, 14, and 6.9 less than

these values for Florida males; the minimum, maximum, and mean numbers of caudals of these males are, respectively, 7, 10, and 8.6 more than these values for Ohio males, and 15, 5, and 6 more than for Florida males. Whether these differences are real or only apparent as a result of the small sample size is not known at present.

The color of five of the specimens (3 females, 2 males) agrees essentially with the descriptions as given by Conant and by Carr and Goin. The remaining four specimens (3 females, 1 male) have venters quite different from the above five specimens. Only the chin, gular region, and a maximum of 14 anteriormost ventrals can be considered as being yellow, where not occupied by paramedian series of gray or brown spots which unite in the gular region into a single median line. Posteriorly from ventral 14, these series of spots become lighter on three specimens and obsolete on the fourth specimen. The ground color between and on either side of the paramedian series of spots is whitish anteriorly, becoming dark slate gray, sometimes mottled with brown, posteriorly. On each of these four specimens the extreme lateral edges of the ventral scutes and the bottom half of the first scale row are clouded with brown and contrast distinctly with the color of the dorsum and the venter. The lateral light stripe is obsolete on the anterior half of the body of each of these four specimens.

The Queen Snake is probably more abundant than collected specimens indicate (Fig. 28). It is encountered most frequently along the minor streams of the Valley, but may also be found in the cooler, clearer, and more swift streams of the mountains. It does not, apparently,

Fig. 28.--Localities for the Queen Snake, Natrix septemvittata, and the Common Water Snake, N. sipedon. N. s. sipedon indicates specimens resembling this subspecies. N. s. pleuralis indicates specimens resembling this subspecies.

inhabit ponds or temporary aquatic situations. The highest elevation at which it is known to occur is 1,700 feet.

Fifty-three specimens (31 females, 22 males) of N. sipedon are available for study. Casual observation of these specimens suggests that some exhibit characteristics of the Northern Water Snake, Natrix s. sipedon (Linnaeus), and that others exhibit characteristics of the Midland Water Snake, Natrix s. pleuralis (Cope). Published data indicate that only the former is present in eastern Tennessee (Clay, 1938; Schmidt and Davis, 1941: 221; Wright and Wright, 1957: 512). However, Ash (1945: 264) reports that some of the specimens which he examined are very much like N. s. pleuralis.

Analysis of these specimens is based upon some of the criteria employed by Clay (1938) to distinguish the two subspecies. These criteria are as follows: relative widths of lateral bars and lateral interspaces--bars equal to or greater in width than interspaces in N. s. sipedon, narrower than interspaces in N. s. pleuralis; total number of dorsal body crossbands and blotches counting from the nape to a point above the cloacal aperture--31 or more in N. s. sipedon, 30 or fewer in N. s. pleuralis; general coloration--grayish to blackish in N. s. sipedon, brownish to reddish in N. s. pleuralis. Clay also employed the number of anterior crossbands and the number of ventral scutes in separating these two subspecies. I have found these two characters of little value. Conant (*in litt.*) also informs me that he finds these characters of little value in separating the two forms.

The total number of dorsal crossbands and blotches ranges from 26 to 39, mean 30.8. This mean value is approximately the upper limit

for M. s. pleuralis and the approximate lower limit for M. s. sipedon. Thus the average for the entire series is intermediate between the two subspecies. These data are based on 50 specimens; the other 3 have patterns too obsolete for accurate counts. Of 24 specimens with 30 or fewer dorsal blotches, only 3 specimens are from elevations in excess of 1,000 feet. These are from 1,600 feet and 1,800 feet in the Unaka Province. Of these 24, only 5 are from localities north of approximately latitude $35^{\circ} 30'$ N., and all 5 are from elevations below 1,000 feet. Twenty-seven specimens have total counts of 31 or more dorsal blotches. Eleven of these are from localities south of latitude $35^{\circ} 30'$ N. Four of these 11 are from localities at elevations of 1,000 feet or less; 7 from elevations in excess of 1,000 feet. The remaining 16 specimens of this group are from localities north of latitude $35^{\circ} 30'$ N. In summary, 21 (88 per cent) of the specimens with 30 or fewer dorsal spots are from collection sites south of latitude $35^{\circ} 30'$ N. and/or below 1,000 feet in elevation; 23 (85 per cent) of the specimens with 31 or more dorsal blotches are from localities north of latitude $35^{\circ} 30'$ N. and/or above 1,000 feet in elevation. The known maximum elevation attained by M. sipedon in eastern Tennessee is 4,800 feet.

Lateral bar and lateral interspace widths are reported in terms of scale lengths. These are determined as follows: the number of scales in each bar and each interspace is counted to the nearest half scale on three consecutive bars and interspaces beginning at a point below the level of the sixth dorsal band or blotch; the six counts, three from each side, for the bars and interspaces are averaged. The counting is done on the third scale row.

The widths of the lateral bars ranges from 1.1 to 2.7, mean 1.8, scales wide. The lateral interspaces range from 1.9 to 4.3, mean 2.8, scales wide. Only three specimens possess lateral bars as wide as the lateral interspaces. One of these is from an elevation of 900 feet at latitude 35°30' N. The other two are from localities ranging from 1,200 feet at latitude 35° 45' N. to 1,400 feet at latitude 35° 30' N. Thus, except for one specimen, those specimens exhibiting the N. s. sipedon character of lateral bars equal to or wider than lateral interspaces are restricted to latitudes north of 35° 30' N., or, if from areas south of this latitude, then they are restricted to elevations in excess of 1,200 feet. This situation parallels that reported above for the distribution of specimens with 31 or more dorsal blotches.

Color is a most difficult character to evaluate objectively in N. sipedon. Generally, N. s. pleuralis is described as being redder than N. s. sipedon. Conant (1939: 81-82) describes N. s. sipedon from Ohio as being extremely variable: blotches range from gray to brown to reddish; ground color ranges from whitish to gray or brown. Similarly, these specimens range from dark greenish gray to brown and red. In some instances, the dorsal blotches are rendered nearly obsolete by darkness of the specimen. Without exception, these specimens are from the higher latitudes or elevations.

The ground color of the venter of these specimens ranges from white to greenish white to yellow or pinkish. Occasional specimens exhibit a longitudinal midventral yellowish or pinkish area. The markings on the venter may be crescents and/or flecks and marbling, varying in

color from black to red. The crescents may occur in irregularly aligned longitudinal rows or as two well-defined rows which converge posteriorly. On many individuals the crescents may become obscured posteriorly by an increase in the amount of flecking and/or marbling, which may or may not be of the same color as the crescents. All localities considered, the majority of the specimens exhibit pairing of the crescent-shaped marks, a N. s. pleuralis character.

There is no definite correlation between color and collection site. However, more brown or reddish specimens and more specimens with paired reddish ventral crescents are from the Valley Province or from low elevations in the mountains. Conversely, more of the light to dark gray specimens are from the higher elevations in the mountains or from farther north in the Valley Province.

From the above data it is evident that the N. sipedon population of eastern Tennessee is at least an intergradient one between N. s. sipedon and N. s. pleuralis. The influence of the former is greatest in Valley areas north of latitude 35° 30' N., which is the approximate latitude of the Little Tennessee River, in the Cumberland Mountains, and at elevations in excess of 1,200 feet in the mountains south of the Little Tennessee River. The influence of N. s. pleuralis is most apparent in Valley areas south of the Little Tennessee River, in the Cumberland Plateau south of the Cumberland Mountains, and in the Unaka Province at elevations below 1,200 feet. These distributions are shown in Figure 28.

The Common Water Snake ranges throughout eastern Tennessee and may be encountered in nearly every type of aquatic situation. It is

most characteristic of rivers and streams, but is not infrequently encountered in ponds and pools.

Genus Storeria, Brown Snakes. This genus is represented in eastern Tennessee by two species: the Brown Snake, Storeria dekayi (Holbrook); the Red-bellied Snake, Storeria occipitomaculata (Storer).

Four female and three male specimens of S. dekayi are available. Data from the sexes considered separately are as follows: females--snout-vent length, 188 mm. to 325 mm.; tail length, 49 mm. to 68 mm.; ventrals, range, 123 (121) to 129 (128), mean 126 (125); caudals, range, 42 to 44, mean 42.8; ventrals plus caudals, range, 167 (165) to 171 (170), mean 168.8 (167.8); males--snout-vent length, 170 mm. to 225 mm.; tail length, 59 mm. to 76 mm.; ventrals, range 122 (120) to 124 (122), mean 123 (120.7); caudals, range 52 to 56, mean 54; ventrals plus caudals, range, 175 (174) to 178 (176), mean 177 (174.7). Data from the sexes considered together, and in part employing the methods of Conant (1951: 238-239), are as follows: scale rows, 17 (6 specimens), 17-16 (1 specimen); upper labials, 7/7 (all specimens); lower labials, 7/7 (6 specimens), 8/7 (1 specimen); pre- and postoculars, 1/1 (all specimens) and 2/2 (all specimens); temporals, 1+1/1+1 (2 specimens), 1+2/1+1 (2 specimens), 1+2/1+2 (3 specimens); number of dorsal crossbands, 0, 7+, 8+, and 13 (1 specimen each), and 18, 24+, and 33+ (1 specimen each).

Considering single specimens, two possess 175 or fewer ventrals plus caudals and 10 or fewer crossbands characteristic of the Northern Brown Snake, Storeria d. dekayi (Holbrook). One specimen possessed more than 175 ventrals plus caudals and more than 10 crossbands characteristic

of the Midland Brown Snake, Storeria d. wrightorum (Trapido). One specimen possesses more than 175 ventrals plus caudals and fewer than 10 crossbands. The remaining three specimens possess 175 or fewer ventrals plus caudals and more than 10 crossbands. Thus, 72 per cent of the specimens are intermediate between S. d. dekayi and S. d. wrightorum.

Admittedly these are scant data upon which to base conclusions regarding the S. dekayi population of eastern Tennessee. But I infer from these data that the S. dekayi population of this area is intermediate between S. d. dekayi and S. d. wrightorum.

The Brown Snake appears to be equally common under edificarian and forest conditions. Its greater frequency in grassy clearings in forested regions suggests that its occurrence in forested areas is abated by silvicultural and agricultural activity. The highest elevation from which this snake is known in eastern Tennessee is 4,000 feet (Fig. 29). It is interesting to note that the specimen from this elevation is the one possessing the high ventral plus caudal count and the high number of crossbands characteristic of S. d. wrightorum. Of the two specimens possessing the low ventral plus caudal count and the fewer than 10 crossbands characteristic of S. d. dekayi, one is from 1,000 feet in the Valley Province and one is from 1,500 feet on the Cumberland Plateau.

Two specimens, both males, of the Red-bellied Snake are available. These are 99 mm. and 145 mm. in snout-vent length and 32 mm. and 45 mm. in tail length. Other data are as follows: ventrals, 111 (109) and 122 (120); caudals, 46 and 48; dorsal scale rows, 15 each; upper

Fig. 29.--Localities for the Brown Snake, Storeria dekayi, and the Northern Red-bellied Snake, S. o. occipitomaculata.

labials, 6/6; lower labials, 7/7; pre- and postoculars, 2+2/2+2; temporals, 1+2/1+2 and 1+1+2/1+1+2. Each specimen has three occipital spots. The specimens are too darkened from preservation to discern longitudinal striping on the dorsum.

The ventral and caudal counts are lower than those given by Conant (1939: 92) for Ohio specimens of the Northern Red-bellied Snake, Storeria o. occipitomaculata (Storer). The number of ventrals of one of the males and the number of caudals of both are within the ranges of these counts as given for the Florida Red-bellied snake, Storeria o. obscura Trapido, by Carr and Goin (1955: 291). Because there are but two specimens, no conclusions are reached as to the exact systematic status of the eastern population of the S. occipitomaculata.

Available information indicates that this snake is restricted to deciduous forest areas. The distribution of the two specimens suggests that this snake may occur over most of eastern Tennessee where conditions are suitable (Fig. 29). The highest elevation of occurrence of this snake is 4,950 feet (King, 1939: 576). Highton (personal communication) informs me that he has encountered this snake at elevations in excess of 5,000 feet.

Genus Thamnophis, Garter Snakes. Two species of this genus are reported as occurring in eastern Tennessee. These are the Common Garter Snake, Thamnophis sirtalis (Linnaeus), and the Ribbon Snake, Thamnophis sauritus (Linnaeus). Ruthven (1908: 114), although including eastern Tennessee within the range of T. sauritus, does not give any locality records in this or immediately adjacent areas. Rhoads (1895),

King (1939), and Ash (1945) report no specimens of this snake. I have not encountered any during the course of this study.

Twenty-two female and 20 male specimens of T. sirtalis are identified as the Eastern Garter Snake, Thamnophis s. sirtalis (Linnaeus). The females have snout-vent lengths ranging from 174 mm. to 691 mm. and tail lengths from 49 mm. to 192 mm. The males have snout-vent lengths ranging from 161 mm. to 480 mm. and tail lengths from 50 mm. to 149 mm. As regards scutellation, these specimens are not different from the data reported for this subspecies by Ruthven (1903: 176). Two distinct color phases may be recognized.

These two color phases are apparently correlated with elevation. The majority of the specimens from elevations of 3,000 and more feet are a dull brown ground color with pale yellow stripes. Specimens from lower elevations are generally of the "typical" dark green ground color with bright yellow stripes. (These color differences become less distinct in preserved material.) Highton (personal communication) has remarked about this high-elevation brown form. He recalls encounters with them on the summits of mountains during his work on Plethodon. King (1939: 576) reports melanistic individuals from elevations in excess of 3,000 feet in the Great Smoky Mountains National Park. I have not encountered melanistic individuals at equally high elevations in the mountains to the north or the south of the Great Smokies.

King reports that the average and the maximum numbers of ventrals decrease slightly with a decrease in altitude, but he questions the significance of this trend. Data from my specimens indicate a reverse

trend, the more so when the sexes are considered separately. Presumably King utilized combined data from both sexes. Further, not only do the data suggest a decrease in the average and maximum numbers of ventrals with an increase in elevation, but there is a parallel decrease in the maximum and average numbers of caudals and ratios between tail length and total length.

The specimens are grouped for analysis according to sex and to elevation of the collecting site. The specimens are divided into low elevation series, 2,000 feet or less, and high elevation series, 3,000 feet or more. There are no specimens from elevations between 2,000 and 3,000 feet. Further, this rather arbitrary division also effectively segregates the green and brown phases. Data from the females are as follows:

	<u>Low-elevation</u> <u>Series</u>	<u>High-elevation</u> <u>Series</u>
Ventrals		
range	140(138) to 153(151)	143(141) to 147(144)
mean	146.9(144.8)	145.4(142.6)
number	9	5
Caudals		
range	66 to 73	62 to 67
mean	70.2	64.5
number	5	2
Tail length/ total length		
range	0.208 to 0.237	0.212 to 0.218
mean	0.225	0.215
number	5	2

These data from the male specimens are as follows:

	<u>Low-elevation Series</u>	<u>High-elevation Series</u>
Ventrals		
range	147(144) to 156(154)	145(143) to 154(152)
mean	152(149.5)	150.4(148)
number	7	12
Caudals		
range	77 to 91	71 to 81
mean	82	76.5
Number	5	11
Tail length/ total length		
range	0.242 to 0.259	0.206 to 0.244
mean	0.248	0.234
number	5	11

The inference from these data is that the above characters exhibit a vertical gradient. Because of the small number of specimens available, statistical analysis was not performed. Whether or not the gradient, if it really exists, is genetically or environmentally controlled remains to be discovered.

The Common Garter Snake is widespread throughout eastern Tennessee. It is apparently more abundant in deciduous forest than in agricultural areas, and more abundant in the mountains than in the Valley or on the Cumberland Plateau (Fig. 30). In the mountains it is particularly characteristic of the ecotone between forest and clearing. This snake may be encountered at elevations above 5,000 feet. The garter snake, the red-bellied snake, and the rattlesnake are probably the most high-ranging of eastern Tennessee serpents.

Fig. 30.--Localities for the Eastern Garter Snake, Thamnophis s. sirtalis, the Eastern Earth Snake, Haldea v. valeriae, and the Eastern Hognose Snake, Heterodon p. platyrhinos.

Genus Haldea, Earth Snakes. Fourteen specimens of the Eastern Earth Snake, Haldea v. valeriae (Baird and Girard), are available as a result of this study. All of these specimens are on loan to Miss Louise Zillig, Wesleyan College, Macon, Georgia, who is engaged in a study of the genus. Miss Zillig kindly furnished me information regarding these specimens, and I quote, in part, from her letter of August 19, 1957:

All of the specimens of Haldea which you sent on loan were good Haldea valeriae valeriae. The only Tennessee H. v. elegans known to me are from the western portion of the state. Elegans has also been reported from Davidson Co. (Sinclair 1951, Herpetologica VII, p. 145.)

There is no discernible altitudinal or physiographic variation indicated by this material, nor any significant variation from the typical form. There is definite infraspecific geographical variation in all forms of Haldea, which can only be defined in terms of frequency distribution of certain characters.

This snake is not often encountered, but is distributed from the Unaka to the Cumberland Plateau provinces (Fig. 30). All of the specimens are from open, grassy or "old field" situations near woodland. The known maximum elevation of occurrence for H. v. valeriae is 2,500 feet.

Genus Heterodon, Hognose Snakes. Four females and three males of the Eastern Hognose Snake, Heterodon p. platyrhinos (Latrielle), are available. The females range in snout-vent length from 235 mm. to 695 mm., in tail length from 40 mm. to 131 mm. The males range in snout-vent length from 435 mm. to 552 mm., in tail length from 100 mm. to 145 mm. Scale rows at midbody are 23 (3 specimens) and 24 (4 specimens). The terminal number of scale rows is 17 (2 specimens) and 19 (5 specimens). Other data are as follows: females--dorsal blotches, range, 20

to 25, mean 24.3; tail blotches, range, 7 to 9, mean 8.3; light body bands, range, 21 to 25, mean 23.5; ventral scutes, range, 139 (137) to 147 (145), mean 142.7 (140.7); caudal scutes, range, 44 to 45, mean 44.7; males--dorsal body blotches, range, 17 to 22, mean 19.3; tail blotches, range, 9 to 10.5, mean 9.8; light body bands, range, 18 to 22, mean 20; ventral scutes, range, 129 (127) to 135 (134), mean 131 (129.3); caudal scutes, range, 50 to 58, mean 54. In color these specimens are basically a reddish ground with black or dark brown dorsal blotches. The venter is yellowish green laterally, tending toward greenish black medially. The undersurface of the tail is distinctly lighter than the venter. In these respects, the specimens are in essential agreement with the description of H. p. platyrhinos as given in Carr and Goin (1955: 269-270) and in Wright and Wright (1957: 306-308).

The few specimens collected are not considered as representing a meager population. Rather, their most characteristic habitat of old fields, cultivated areas, etc., were not extensively collected. Most of the specimens encountered dead on the road are adjacent to such areas. The hognose snake is not a characteristic inhabitant of woodland, although occasional specimens may be encountered in second-growth oak and oak-pine communities. It is most prevalent in the Valley (Fig. 30). The known maximum elevation of occurrence is 2,500 feet.

Genus Diadophis, Ringneck Snakes. Eighty-four specimens (45 females, 39 males) of Eastern Ringneck Snake, Diadophis punctatus (Linnaeus), are the basis of the following remarks. These specimens are examined on the basis of criteria employed by Blanchard (1942) and Conant (1946).

On the basis of scutellation these specimens are closest to the Northern Ringneck Snake, Diadophis p. edwardsi (Merrem). All of the specimens have 15 dorsal scale rows. The frequency of occurrence of various numbers of upper labials is as follows: 7/6 (1 specimen); 7/7 (8 specimens); 7/8 or 8/7 (11 specimens); 8/8 (44 specimens). The remaining specimens are untabulated for this character. Other data from these specimens are as follows: females--ventrals, range, 153 (151) to 178 (177), mean 162.8 (161.6); caudal scutes, range, 42 to 63, mean 52.8; ventrals plus caudals, range, 198 (197) to 236 (235), mean 215.4 (214.3); width of neck ring in terms of scale lengths, range, 1 to 2, mean 1.39; ratio between tail length and total length, range, 0.184 to 0.285, mean 0.206; males--ventrals, range, 140 (139) to 166 (166), mean 153.9 (152.7); caudal scutes, range, 53 to 66, mean 54.2; ventrals plus caudals, range, 199 (197) to 224 (222), mean 213.1 (211.8); width of neck ring in terms of scale lengths, range, 1 to 2, mean 1.5; ratio between tail length and total length, range, 0.176 to 0.250, mean 0.226. There is no apparent geographic variation in these characters. Females range in snout-vent length from 113 mm. to 396 mm.; in tail length from 27 mm. to 100 mm. Males range in snout-vent length from 107 mm. to 400 mm., in tail length from 32 mm. to 102 mm. In both females and males, the longest snout-vent length is not correlated with the longest tail length. But, the smallest snout-vent length does correspond to the smallest tail length.

Three aspects of coloration are employed to distinguish D. p. edwardsi from the Southern Ringneck Snake, Diadophis p. punctatus (Linnaeus). Only 12 specimens, 5 females and 7 males, have all three of the

characteristics of D. p. edwardsi: uninterrupted neck ring, unspotted chin, and immaculate belly. The remaining 74 specimens possess one or more of these characters plus characters assigned to D. p. punctatus: interrupted neck ring, spotted chin and gular region, spotted belly (these spots usually in an uninterrupted median series and larger than the spots which are sometimes present in D. p. edwardsi). In employing these criteria to evaluate the specimens, I followed the plan used by Conant (1946). Additionally, my standards are based upon a series of D. p. punctatus from Aiken County, South Carolina.

Twenty-six specimens possess an incompletely or completely interrupted neck ring. Twenty-five of these are from the Unaka Province, one is from the Cumberland Plateau. Blanchard (1942: 119) reports an incidence of 15 out of 900 D. p. edwardsi with a broken neck ring, and 43 out of 91 D. p. punctatus with this condition. Conant (1946:477) reports an incidence of only one specimen out of 27 D. p. edwardsi from the Pocono Mountains, Pennsylvania, with an interrupted neck ring. The specimens are most like D. p. punctatus as regards incidence of interrupted neck ring.

Thirty-seven specimens possess a spotted chin, labials, and/or gular region. Of these, 32 are from the mountain sector, 1 is from the Valley Province, and 4 are from the Cumberland Plateau. Sixty-two specimens possess a venter which is heavily spotted with a median series of large, half-moon spots or are incompletely spotted on the venter with a median series of irregularly shaped spots. Fifty-two of these are from the Unaka Province, 3 are from the Valley Province, and 7 are from the

Cumberland Plateau. Of 21 specimens possessing an immaculate venter, 12 are from the Unaka Province, 1 is from the Valley, and 8 are from the Cumberland Plateau. Three specimens from the Unaka Province have belly patterns suggestive of that of the Mississippi Ringneck Snake, Diadophis p. stictogenys (Cope). The spots on the venter of one specimen are arranged in a paired median series and as if formed from the coalescence of paired paramedian spots in the other two specimens. Additionally, these latter two specimens have spots lateral to the median series.

From the above data on coloration, I conclude that intergradation occurs between D. p. edwardsi and D. p. punctatus in eastern Tennessee. The mountain population is most intermediate between these two subspecies. The populations of the Valley and the Cumberland Plateau are more nearly like the description of typical D. p. edwardsi. It may appear anomalous that a coastal plain snake may invade a physiographic mountainous region more readily than adjacent valley lands. I believe this is the reason Conant (in litt.) disagrees with my interpretation of the D. punctatus population in eastern Tennessee. For reasons to be presented later in the paper, I believe that it may be easier for mesic coastal plain reptiles to invade the mountainous region of southeastern United States than the drier Valley and Cumberland Plateau districts.

The ringneck snake is widespread in eastern Tennessee (Fig. 31). It is a snake characteristic of forest land, especially mesic deciduous forest. In the Valley and on the Plateau it seems to be confined to or near stream valleys or other moist areas. Individuals appearing to be typical D. p. edwardsi may be found in more xeric situations than the

Fig. 31.--Localities for the Eastern Ringneck Snake, Diadophis punctatus.

individuals appearing to be D. p. punctatus or D. p. edwardsi x D. p. punctatus intergrades. All three kinds of individuals may be encountered together in the mountains and at the same elevations. The known maximum elevation of occurrence for the ringneck snake is over 5,000 feet in the Unaka Province.

Genus Carphophis, Worm Snakes. Forty-eight females and 60 males of the Worm Snake, Carphophis amoenus (Say), are the basis for the following remarks. Females range in snout-vent length from 89 mm. to 216 mm., in tail length from 13 mm. to 37 mm. Males range in snout-vent length from 85 mm. to 204 mm., in tail length from 17 mm. to 50 mm. Twenty females and 27 males, selected to represent the Cumberland Plateau, the Valley, and Unaka provinces, are the source of the data recorded below.

Each of these specimens has 13 scale rows, 5 upper labials on each side and 6 lower labials on each side. There is slight variation in numbers of temporals as follows: 45 specimens have one temporal on each side; one specimen has one temporal on one side and two on the other; one specimen has the temporal fused to the last upper labial on each side. Among the 20 females, the number of ventral scutes ranges from 119 (116) to 128 (126), mean 124.7 (123). For these females, the number of caudals ranges from 25 to 36, mean 26.9. For 27 males, the number of ventrals ranges from 112 (110) to 122 (120), mean 117.2 (114.6), and the number of caudals ranges from 32 to 40, mean 36.

The minimal number of ventrals is lower than the minimum reported by Blanchard (1925) for either the Eastern Worm Snake, Carphophis

a. amoenus (Say), or for the Midwest Worm Snake, Carphophis a. helenae (Kennicott). The means are less than those given for either C. a. amoenus (mean 131) or C. a. helenae (mean 128).

Of these 47 specimens, 5 females and 6 males have fused internasal and prefrontal scutes on each side of the head. One female and 2 males have these scales fused on only one side. Of the total of 108 specimens, 18 have the internasals and prefrontals fused on each side and 5 have them fused on one side only. These data are interpreted as indicating intergradation in eastern Tennessee between C. a. amoenus and C. a. helenae. Of all specimens showing fusion of internasal and prefrontal scutes, 12 are from the Unaka Province, 8 are from the Cumberland Plateau, and 3 are from the Valley Province. On a percentage basis, 14.4 per cent of the Unaka specimens, 40 per cent of the Cumberland specimens, and 77.7 per cent of the Valley specimens exhibit fusion of these scutes. Thus the zone intergradation may be speculated as extending southward on the Cumberland Plateau and in the Valley from Middlesboro, Kentucky, (Smith, 1948) to the southern border of Tennessee.

The worm snake is characteristic of the deciduous forest, but it may be encountered in oak-pine communities if the soil is not too tight. It is most abundant in loose loam or sandy-loam soils and least abundant in the heavier clay soils. This snake is widespread throughout eastern Tennessee and is known to occur at elevations of 4,300 feet (Fig. 32).

Genus Coluber, Racers. Fourteen female and 14 male specimens of the Racer, Coluber constrictor (part) Linnaeus, are the basis for the following remarks. These are more specimens from eastern Tennessee than

Fig. 32.--Localities for the Worm Snake, *Carphophis amoenus*.

were available to Auffenberg (personal communication) for his reconsideration of this species in eastern United States (Auffenberg, 1955). These specimens range in snout-vent lengths as follows: females, 201 mm. to 982 mm.; males, 222 mm. to 1,122 mm. Tail lengths are as follows: females, 55 mm. to 326 mm.; males, 62 mm. to 337 mm. Other data from these specimens are as follows: Ventrals--females, range 175 (173) to 180 (178), mean 177.4 (175.5); males, range 173 (172) to 183 (182), mean 177.4 (175.1); caudals--females, range 80 to 99, mean 90.7; males, range 91 to 110, mean 97.5; supralabials, 7/6 (2 specimens), 7/7 (19 specimens), 7/8 and 8/7 (6 specimens), 8/8 (1 specimen); temporals 2·2·2/2·2·2 (20 specimens), remaining 8 specimens varying from 1·2·2 to 3·3·3; white anterior ventrals, 0 (2 specimens), 1 (1 specimen), 2 (9 specimens), 3 (6 specimens), 4 (3 specimens), 5 (1 specimen), 20 (2 specimens). Among the 11 adult males, 6 specimens have hemipenial basal hooks: 2 have one hook on each hemipenis; 4 have one hook on only one hemipenis. Among these 11 males, the ratio between length of basal spine and length of preceding spine ranges from 1.0 to 5.5, mean 3.2 Six (21.4 percent) of the 28 males and females have the first supralabial in contact with the loreal. As regards color, the dorsum ranges from a slaty black to black, 24 and 4 specimens respectively. The color of the venter ranges from greenish blue to black (1 specimen).

Auffenberg (1955: 93) utilizes two basic criteria in separating the various subspecies of C. constrictor. These are (1) color of dorsum and venter, (2) ratio of length of basal hemipenial spine/length of next preceding spine. The colors of the dorsum of these specimens are

within the range of variation of the Northern Black Snake, Coluber c. constrictor (Linnaeus), and the Southern Black Racer, Coluber c. priapus Dunn and Wood. The color of the venter is, in the majority of the specimens, more like that of the Yellow-bellied Racer, Coluber c. flaviventris (Say). Only one specimen has a black venter such as described for C. c. constrictor and C. c. priapus. The mean hemipenial spine ratio of 3.2 is the same as that reported for specimens from coastal North and South Carolina (Auffenberg, 1955: 111). Of the 6 specimens with basal hooks, the hemipenial spine ratio is from 4.0 to 5.5, mean 4.03. Each of these 6 males has a white chin. Three of these 6 males have the first supralabial in contact with loreal scute. On the basis of hemipenial spine ratios, the 11 males are intermediate between males of C. c. constrictor and C. c. priapus.

The mean number (3.9) of white ventrals among these specimens is close to the mean value for specimens from the area of intergradation between C. c. constrictor and C. c. priapus in coastal North Carolina, as are the mean number (94.1) of caudals and mean number of ventrals 177.9 (175.2) (Auffenberg, 1955: 91, 118, 119). The combination of white chin, basal hooks, and first supralabial in contact with the loreal favors C. c. priapus. These same three characters in combination with the greenish blue to bluish venter suggest the influence of C. c. flaviventris. Auffenberg, who has seen these specimens, concurs with this latter interpretation.

Of further interest, but of unknown significance, is the occurrence of black punctations on the venter of three of the specimens.

Each of these punctations is the site of attachment beneath the cuticle of a mite of undetermined identification. Auffenberg (1955: 144) does not record the occurrence of such mite-induced punctations above the Coastal Plain.

On the basis of all of the above data I conclude that the eastern Tennessee C. constrictor is one of three possible genetic complexes. These possibilities are: C. c. constrictor x flaviventris intergrades; C. c. prispus x flaviventris intergrades; C. c. constrictor x flaviventris x priapus intergrades. I believe that evidence presented above, plus the distributions of certain characters of C. constrictor as shown by Auffenberg (1955: 144), favors the first possibility.

The Racer is widespread in eastern Tennessee (Fig. 33). It does not seem to be characteristic of any particular habitat as it is encountered as frequently in edificarian and ruderal situations as in forest communities. The maximum elevation of known occurrence in eastern Tennessee is 4,000 feet.

Genus Opheodrys, Green Snakes. Two members of this genus are reported as occurring in eastern Tennessee; the Eastern Rough Green Snake, Opheodrys a. aestivus (Linnaeus), and the Eastern Smooth Green Snake, Opheodrys v. vernalis (Harlan). Neither King (1939) nor Ash (1945) report the capture of this latter snake. Grobman (1941:15) does not include Tennessee in the range of O. v. vernalis. I know of no specimens from eastern Tennessee.

Seven female and four male specimens of O. a. aestivus are available. Data from the females are as follows: snout-vent length from 293

Fig. 33.--Localities for the subspecies of the Racer, Coluber constrictor, and the Eastern Rough Green Snake, Opheodrys a. aestivus.

mm. to 502 mm.; tail length from 163 mm. to 265 mm.; ventrals, range, 154 (152) to 160 (159), mean 156.1 (155.1); caudals, range 124 to 141, mean 133.3; upper labials, 7/7; lower labials, 7-8/7-8; preoculars, 1/1; postoculars, 2/2 (6 specimens), 3/3 (1 specimen); temporals, 1·2·2/1·2·2 (2 specimens), 1·2/1·2 (5 specimens). Data from the males are as follows: snout-vent length, from 343 mm. to 455 mm.; tail length from 238 mm. to 293 mm.; ventrals, range, 150 (149) to 159) (156), mean 154.8 (153); caudals, range, 133 to 139, mean 136.3; upper labials, 7/7; lower labials, 7-8/7-8; preoculars, 1/1; postoculars, 2/2; temporals, 1·2/1·2. The number of scale rows for both males and females is 17-15. In life, this snake is lime green dorsally, greenish to yellowish white ventrally.

This snake is widespread in eastern Tennessee (Fig. 33). It may be encountered in a variety of habitats from open fields to forest. It seems to be most abundant in old fields and rarely occurs in dense mesic forest. The maximum elevation of known occurrence is 2,500 feet.

Genus Elaphe, Rat Snakes. Two species of Rat Snake occur in eastern Tennessee. These are the Corn Snake, Elaphe guttata (Linnaeus), and the Rat Snake, Elaphe obsoleta (Say). The former is represented by the subspecies Elaphe g. guttata (Linnaeus). The latter is an inter-gradient population between two subspecies, at least in the Valley Province and on the Cumberland Plateau.

Five females and 13 males of E. g. guttata are rather typical of this subspecies as defined by Dowling (MS). In general, however, this snake in eastern Tennessee is much darker than it is in the Coastal Plain. The ground color of adults is grayish brown or gray; the dorsal

blotches are usually a dark red or brownish. The venter presents the usual black and white checkerboard effect. One feature of the coloration, not mentioned for this snake by Dowling, but present on five of these specimens, is four brown dorsolateral and lateral lines. These lines are not conspicuous but are obvious. The ventrolateral lines occupy scale rows three to five or four to six. The dorsolateral lines occupy scale rows eight to eleven, nine to twelve, or nine to eleven.

Length measurements from these specimens are as follows: females--snout-vent, 609 mm. to 881 mm.; tail, 113 mm. to 158 mm.; males--snout-vent, 758 mm. to 1147 mm.; tail, 143 mm. to 212 mm. The ratio between tail length and total length as reported by Dowling for this snake is 19.5 per cent in males and 17 per cent in females. Among these specimens the mean ratios for males and females are 16 per cent and 15.7 per cent respectively. The numbers of ventral scutes for females ranges from 212 to 218, mean 216.2; for males they range from 208 to 220, mean 213.5. The mean values are intermediate between the means reported for New Jersey and South Carolina specimens. The mean number of caudal scales for females is 66 (range 65 to 69). This is closer to the mean value of Florida specimens than of females from north of Tennessee along the Atlantic Coastal Plain. The mean number of caudals for the males of this series is 67.4 (range 62 to 71). This is slightly less than the mean of males from southeastern United States. Dorsal body blotches of the females range from 28 to 36, mean 32.8, and for the males the range is 29 to 35, mean 32.1. These range and mean values are very similar to those reported for specimens from the Atlantic Coastal Plain at latitude 34°. Most of my specimens are from between 35°N. and 35° 30' N.

The Corn Snake is found throughout at least the southern two-thirds of eastern Tennessee up to elevations of 2,500 feet. It is most abundant in the Valley Province judging from specimens found dead on the road and otherwise collected (Fig. 34). It is most frequently encountered in nonforested habitats. It is not known to inhabit dense mesic forests, but may be encountered in open oak or oak-pine forest.

The Rat Snake, Elaphe obsoleta, is represented by 22 specimens; 5 females and 17 males. One specimen, a male, is designated as the Gray Rat Snake, Elaphe o. spiloides (Dumeril, Bibron, and Bibron); nine specimens, four females and five males, are designated as the Black Rat Snake, Elaphe o. obsoleta (Say); 12 specimens, 2 females and 10 males, are designated as E. o. obsoleta x spiloides intergrades.

The E. o. spiloides specimen, in addition to possessing distinct dark brown dorsal blotches on a yellowish-gray ground color, has a solid black postocular stripe and solid black prefrontal stripes. Other data from this specimen are as follows: snout-vent length 1,279 mm.; tail length 280 mm.; ventrals 231; caudals 86; dorsal body blotches 31; caudal blotches 14; temporals 2+3+4/2+3+3; scale rows one to three at mid-body smooth; scale rows 25-27-26-25-23-21-19-17. This specimen has one more dorsal body blotch than is reported by Dowling for E. o. spiloides.

The 9 E. o. obsoleta specimens (3 females, 6 males) have the following length measurements: females--snout-vent from 589 to 1,250 mm.; tail from 116 mm. to 283 mm.; males--snout-vent from 1,249 mm. to 1,294 mm.; the only tail which is complete is 250 mm. Other data from these specimens are as follows: females--ventrals, range 237 to 240, mean

Fig. 34.--Localities for the Corn Snake, Elaphe g. guttata, and the Rat Snake, E. obsoleta. "Black" indicates specimens identified as E. o. obsoleta; blotched indicates specimens identified as E. o. obsoleta x spiloides intergrades.

238.7; caudals, range 76 to 81, mean 78.5; dorsal body blotches (2 specimens) 27 and 32; total temporals, range 18 to 20, mean 19.3; males--ventrals, range 228 to 235, mean 231; caudals, one specimen with complete tail, 81; dorsal body blotches (1 specimen) 33; total temporals, range 14 to 18, mean 16.2. Two females and four males of this series of nine specimens are too dark to secure a dorsal body blotch count. None of these specimens possesses a discernible prefrontal or postocular stripe. On each of these specimens scale rows one and two at midbody are smooth.

The twelve specimens (2 females, 10 males) designated as E. o. obsoleta x spiloides intergrades have the following measurements: females--snout-vent, 829 mm. and 1,250 mm.; tail, not measured, incomplete; males--snout-vent, from 620 mm. to 1,421 mm.; tail, from 135 mm. to 271 mm. (I question the value of tail length measurements because of the frequency with which they are incomplete and the lack of ability to positively detect regenerated tails.) Other data from these specimens are as follows: females--ventrals, 232 and 234; caudals, not counted because of incomplete tails; dorsal blotches 30 on one, too indistinct on the others; total temporals 17; males--ventrals, range 230 to 239, mean 232.3; caudals, range 83 to 87, mean 85.1; dorsal blotches, range 28 to 34, mean 30.6; total temporals, range 13 to 26, mean 18.2. Each of these specimens possesses a blotched dorsal pattern, though it is too indistinct to count on one female and three of the males. The blotches range in color from purplish-brown to dark brown or black. The ground color varies from light gray through brownish-gray to dark brown. None of these possesses a discernible prefrontal stripe. Four of them possess a postocular stripe.

Of the 22 specimens, all but the E. o. spiloides and one of the intergrades possess 25 scale rows at midbody. The exceptional intergrade has 27 scale rows. Nine specimens (4 E. o. obsoleta, 5 E. o. obsoleta x spiloides) have a scale row formula of 25-27-25-23-21-19; 4 E. o. obsoleta and 5 E. o. obsoleta x spiloides have a scale row formula of 25-27-25-23-21-19-17; 2 E. o. obsoleta and 1 intergrade specimen have scale row formulae of 25-23-25-23-21-19-17. Conant (1939: 36) states that 17 is the normal minimal number of dorsal scale rows in E. o. obsoleta in Ohio.

Dowling (MS) does not discuss dark dorsolateral and lateral lines except in the Yellow Rat Snake, Elaphe o. quadrivittata (Holbrook). Neill (1949: 3-4) regards the presence of these lines on dark E. o. obsoleta-like specimens in Georgia as evidence of intergradation between this subspecies and E. o. quadrivittata. I cannot subscribe to this interpretation of these lines on such specimens as indicating intergradation between these two subspecies. I know of numerous specimens of "good" E. o. obsoleta from Ohio and West Virginia which have these lines. Further, these lines can be seen on 13 of the 22 specimens of E. obsoleta from eastern Tennessee.

On four of the E. o. obsoleta specimens the dorsolateral lines occupy rows nine to eleven (1 specimen), rows ten to twelve (2 specimens), and rows ten to thirteen (1 specimen); the lateral lines occupy rows one to five, rows one to six, rows two to six, and rows three to six on these specimens. On the E. o. spiloides specimen these lines occur on rows nine to eleven and rows three to five, respectively. Among

the intergrade specimens, the distributions of these lines are as follows: dorsolateral lines--rows nine to eleven (3 specimens), rows ten to twelve (9 specimens); lateral lines--rows two to five (1 specimen), rows two to six (2 specimens), rows three to six (6 specimens). According to Dowling, E. o. quadrivittata has the dorsolateral lines on rows ten to twelve and the lateral lines on rows three to five. Eleven of my specimens (2 E. o. obsolete and 9 intergrades) have the dorsolateral lines on rows ten to twelve as reported for E. o. quadrivittata. Only the E. o. spiloides specimen has the lateral line on rows three to five. Because of the presence of these lines on individuals of E. o. obsolete subspecies other than E. o. quadrivittata, and, as mentioned above, on E. g. guttata, I wonder if the lines par se may not be older than any of the subspecies of the obsolete complex. Instead of the presence or absence of the lines being of subspecific diagnostic value, the distribution of the lines may be a subspecific character.

All of the intergrade specimens and the E. o. spiloides are from the Valley Province south of the latitude of Knoxville, the Cumberland Plateau south of the Cumberland Mountains section, or from below an elevation of 1,200 feet in the Unaka Province (Fig. 34). Occasional specimens identifiable as E. o. obsolete may be encountered in the Valley, but the majority of such specimens seem to be confined to the higher elevations of the Unaka Mountains, to the Valley north of the latitude of Knoxville, and to the Cumberland Mountains section of the Cumberland Plateau Province. This distribution is similar to that of the subspecies of Natrix sipedon in eastern Tennessee.

The Rat Snake is essentially a woodland animal. All of the specimens which I have encountered in the Unaka Mountains have been in dense mesic deciduous forest. In the Valley and on the Plateau this snake is not uncommon in agrarian situations, perhaps because agriculture is much more intensive in these two areas than in the mountains. The maximum elevation of known occurrence of this snake in eastern Tennessee is 4,000 feet.

Genus Pituophis, Pine Snakes. The Northern Pine Snake, Pituophis m. melanoleucus (Daudin), is very infrequently encountered in eastern Tennessee. Ash (1945: 263) reports the collection of two individuals in the Copperhill area of Polk County. Highton (personal communication) informs me of a large specimen dead on the road which he saw near Chilhowee, Blount County. Stull (1940: 59-60) reports two from eastern Tennessee; one from Knox County, one from Blount County. This snake is also known from the Abrams Creek area of the Great Smoky Mountains National Park. I am informed by various persons that this snake is rather abundant on the Cumberland Plateau and as far west as Benton County, which lies partly in the Highland Rim and partly in the Mississippi embayment of the Gulf Coastal Plain.

Only two specimens are available for examination. One is a juvenile female from the Cumberland front in Rhea County. The other is a male from Polk County. The following data are from the female: snout-vent length 595 mm.; tail length 72 mm.; ventrals 212; caudals 51; scale rows 27-29-21; supralabials 7/8; infralabials 12/11; loreals 1/0; noazygous scale; dorsal body blotches 34; tail blotches 6. Data from the

male specimen are as follows: snout-vent length 1,300 mm.; tail length 190 mm.; ventrals 217; caudals 58; scale rows 27-29-21; supralabials 8/8; infralabials 12/12; loreals 1/1; azygous scale present; dorsal body blotchas 29; tail blotchas 6.

The female is a brown-spotted snake. The dorsal blotchas are rectangular with the long axis transverse to the body axis, rather than being quadrangular. The median series of lateral blotchas on the right side is replaced by a continuous line from the neck to the tail. On the left side this line is broken into elongate dashes on the posterior two-thirds of the body. There is a definite tendency for the dorsal spots to be in two series. One series, consisting of the large rectangular blotchas, has the anterior and posterior corners of these spots projecting forward and posteriorly to meet similar extensions from adjacent blotches. The result is an H-shaped pattern. Between the projecting arms of the larger spots is a smaller circular spot. This pattern occurs on the anterior and posterior thirds of the body. The color pattern of this snake is suggestive of the color pattern of the Louisiana Pine Snake, Pituophis m. ruthveni Stull, as given by Stull (1940: 74,76).

The male specimen has dark brown dorsal spots on an ivory ground rather than black spots on a white ground. The ground color of the dorsum is distinctly darker than that of the lower sides. Ash (1945: 263) reports that his specimens have brown spots on a yellowish ground color. These variations of coloration may be within the range of variation of P. m. melanoleucus. Present on this snake, but not recorded for any of the specimens examined by Stull, is an azygous scale.

In number of ventrals, caudals, and labials, these two specimens are closer to a Coastal Plain series than to a mountain series discussed by Stull (1940: 58).

Although not abundant, this snake is evidently widespread in eastern Tennessee (Fig. 35). Localities from which specimens are known vary from open pasture land to floodplain forest to mesic oak-hickory forest. The majority of my records indicate that this snake is an inhabitant of deciduous or deciduous-pine forest. I have no records of specimens from xeric oak or oak-pine-heath communities. Too few specimens are available for adequate habitat generalizations. The maximum elevation of known occurrence is 1,900 feet.

Genus Lampropeltis, Kingsnakes. Three species of kingsnakes occur in eastern Tennessee. These are the Prairie Kingsnake, Lampropeltis calligaster (Harlan), the Common Kingsnake, Lampropeltis getulus (Linnaeus), and the Milk Snake, Lampropeltis dolia (Linnaeus).

The Mole Snake, Lampropeltis c. rhombomaculata (Holbrook), is represented by four female and six male specimens. Data from these specimens are as follows: females--snout-vent length from 213 mm. to 700 mm.; tail length from 32 mm. to 93 mm.; ventrals, range 198 (197) to 209 (207), mean 203.3 (201); caudals, range 40 to 44, mean 42.5; dorsal body blotches (plus tail blotches in parentheses), range 40 (51) to 43 (57), mean 41.7 (53.3); males--snout-vent length from 214 mm. to 792 mm.; tail length from 31 mm. to 86 mm. (male with largest snout-vent measurement with incomplete tail); ventrals, range 197 (195) to 206 (204), mean 201.7 (199.8); caudals, range 44 to 48, mean 45.5;

Fig. 35.--Localities for the Northern Pine Snake, Pituophis m. melanoleucus, the Scarlet Snake, Cemophora coccinea, and the Crowned Snake, Tantilla coronata.

dorsal body blotches (plus tail blotches in parentheses), range 40 (50) to 43 (54), mean 41 (52.8); sexes combined--upper labials 7/7; lower labials, 9/9 (5 specimens), 9/8 (3 specimens), uncountable in 2 specimens; temporals, 2+3+4/2+3+4 (6 specimens), 2+3+3/2+3+4, 2+2+4/2+3+4, 2+3+4/2+3+5, 2+3+3/2+3+7 (1 specimen each); scale rows, 21-19 (5 specimens), 21-19-17 (2 specimens), 21-23-21-19, 19-21-19-17, 23-21-19 (1 specimen each). As regards dorsal blotch counts, only three females and four males have patterns distinct enough for accurate counts. As regards these characters and coloration, these specimens are not different from the description of L. c. rhombomaculata as given by Blanchard (1921: 128-134).

This snake is apparently confined to the Valley Province and the lower elevations in the Unaka Province (Fig. 36). It is characteristic of the cleared agricultural areas but may be encountered in open oak or oak-pine communities. The maximum elevation of known occurrence is about 2,000 feet.

The Common Kingsnake is represented by a series of five females and ten males. Data from these specimens are as follows: females--snout-vent length from 232 mm. to 372 mm.; tail lengths from 31 mm. to 119 mm.; ventrals, range 202 (201) to 212 (212), mean 206.4 (205); caudals, range 40 to 49, mean 45; crossbands on body (plus tail crossbands in parentheses), range 24 (33) to 36 (45), mean 30.3 (37.5); number of alternating light and dark spaces on side of the body on scale row I, range 30 to 45.5, mean 34.3; males--snout-vent length from 569 mm. to 1,045 mm.; tail length from 87 mm. to 156 mm.; ventrals, range

Fig. 36.--Localities for the Mole Snake, Lampropeltis c. rhombomaculata, subspecies of the Common Kingsnake, L. getulus, the Scarlet Kingsnake, L. d. dolia, and the Eastern Milk Snake, L. d. triangulum.

200 (198) to 212 (211), mean 206.6 (205.2); caudals, range 44 to 54, mean 44.2; crossbands on body (plus tail crossbands in parentheses), range 25 (34) to 52 (66), mean 35.8 (41.7); number of alternating light and dark spaces on scale row I, range 27 to 78, mean 46.2; sexes combined--upper labials, 7/7 (15 specimens); lower labials, 8/9 or 9/8, 10/10 (2 specimens each), 9/9 (10 specimens); temporals, 2+3+4/2+3+4 (11 specimens), 2+1+3/2+2+3, 2+1+4/2+2+4, 2+3+3/2+3+3, 2+3+4/2+3+2 (1 specimen each); preoculars 1/1 (15 specimens); postoculars 2/2 (15 specimens); scale rows, 19-21-19 (1 specimen), 21-19-17 (2 specimens), 21-19 (12 specimens).

When these data are compared with the descriptions in Blanchard (1921) of the Eastern Kingsnake, Lamproletis g. getulus (Linnaeus), and of the Black Kingsnake, Lampropeltis g. niger (Yarrow), the conclusion is reached that eastern Tennessee L. getulus are intermediate between these two subspecies. Only two specimens appear to be "typical" L. g. niger. One of these is from the Cumberland Mountains, the other is from Meigs County near the Tennessee River. The basis upon which 13 of these specimens are designated as L. g. getulus x niger intergrades is as follows (data for each of the subspecies are from Blanchard): number of crossbands on the back, range 29 to 51, mean 41.7 (L. g. getulus, range 23 to 48, mean 35.8; L. g. niger, range 50 to 86, mean 65); number of alternating light and dark areas on lower sides, range 27 to 50, mean 36.9 (L. g. getulus, with as few as 33); a majority of the specimens with scale rows 21-19 and the light dorsal crossbands as much as one scale wide (L. g. getulus characters). King (1939: 573) reports

evidence of intergradation of these subspecies in the Great Smoky Mountains National Park. Thus, the zone of intergradation between these two subspecies includes eastern Tennessee.

Although not of uncommon occurrence in the agricultural Valley Province, the Common Kingsnake is more frequently encountered in the Unaka Province (Fig. 36). This I believe is a result of its predilection for a woodland habitat. Even in the Valley, the majority of specimens are encountered in the vicinity of wooded stream valleys. The maximum elevation of known occurrence in eastern Tennessee is 2,500 feet.

Two subspecies of the Milk Snake are present in eastern Tennessee. These are the Scarlet Kingsnake, Lampropeltis d. doliata (Linnaeus), and the Eastern Milk Snake, Lampropeltis d. triangulum (Lacépède). King (1939: 573) reports a specimen of the Coastal Plain Milk Snake, Lampropeltis elapsoides virginie (= L. d. doliata), from the Great Smoky Mountains. Conant (1943: 20) regards this specimen as L. t. elapsoides (= L. d. doliata). Conant restricts L. d. doliata to the Coastal Plain and Piedmont and L. d. triangulum to the mountains. Subsequent to Conant's paper, Ash (1945) reports a single specimen from an elevation of 1,400 feet in Polk County. Blanchard (1921: 216) reports a specimen from Knoxville, Knox County. An additional specimen is available from Athens, McMinn County. Further, I am informed of the occurrence of L. d. doliata from the vicinity of Blue Ridge, Fannin County, Georgia, where it is known locally as "corel snake." The elevation of Blue Ridge is 1,800 feet.

The single L. d. doliata is a male with a snout-vent length of 392 mm. and a tail length of 67 mm. Other data from this specimen are as follows: ventrals 169; caudals 38; upper labials 7/7; lower labials 9/9; anterior temporals 2/1; loreals 0; 16 red bands on the body. In these characters and in coloration, this specimen agrees with the description of the subspecies L. d. doliata as given by Blanchard (1921: 207-209) and by Conant (1943: 7-8).

The subspecies L. d. triangulum is represented by four females and five males. Data from these specimens are as follows: females--snout-vent length 192 mm. to 638 mm.; tail length 30 mm. to 100 mm.; ventrals, range 202 (201) to 205 (204), mean 203.8 (203); caudals, range, 43 to 48, mean 46; dorsal body blotches, range 32 to 41, mean 35.5; males--snout-vent length 184 mm. to 730 mm.; tail length 30 mm. to 60 mm. (the tail of the largest male is incomplete); ventrals, range, 198 (197) to 207 (205), mean 203.2 (201.8); caudals, range 46 to 49, mean 47.7; dorsal body blotches, range 31 to 41, mean 36.4; sexes combined--scale rows 21-19 (4 specimens), 21-19-17 (5 specimens); upper labials 7/7 (9 specimens); lower labials 8/8, 9/10, 10/10 (1 specimen each), 9/9 (6 specimens); anterior temporals 1/1 (2 specimens), 2/2 (7 specimens); three series of dorsal spots on 7 specimens, five series of dorsal spots on two specimens. All of these characters are within the range of variation reported for L. d. triangulum by Blanchard (1921: 190-192, 197-202) and by Conant (1943: 6-7). In color and color pattern these specimens are also like the descriptions cited above.

Conant (1943: 20) states that L. d. triangulum and L. d. doliata are not known to occur in the same locality. The inference from this

discussion is that at least on the North Carolina side of the Smoky Mountains L. d. triangulum and L. d. doliata are altitudinally separated from each other. In eastern Tennessee locality records for these two subspecies show that the elevations of occurrence of these two snakes do overlap considerably. The maximum elevation for L. d. doliata is 1,800 feet; the minimum elevation for L. d. triangulum is 900 feet, and this in McMinn County from whence a specimen of L. d. doliata is known (Fig. 36). That these two snakes may occupy quite different ecological situations is possible. The known maximum elevation of occurrence of L. d. triangulum is 4,600 feet. This snake is definitely associated with deciduous forest communities. None of my records indicates that it is found in the more xeric oak or oak-pine communities, and none of the records is associated with cleared agricultural land.

Genus Cemophora, Scarlet Snake. Only two specimens of this snake are available. One is a mutilated specimen from Hamilton County, the other is from Monroe County (Fig. 35). King (1939: 574) records a single specimen from Cades Cove in the Great Smoky Mountains National Park.

Of my specimens, only the Monroe County specimen is in a condition permitting the collection of data. These data are as follows: snout-vent length 321 mm.; tail length 59 mm.; ventrals 157 (155); caudals 43; supralabials 6/6; lower labials 7/7; temporals 1+2/1+2; preoculars 1/1; postoculars 2/2; red saddles on body 17; red saddles on tail 4; light bands on body 16; light bands on tail 5; scale rows 19. In preservative, the scales of the light bands and the light lateral areas

ere grayish with centers stippled with brown. The venter is cream colored. In all respects this specimen does not appear different from the descriptions of the Scarlet Snake, Cemophora coccineae (Blumenbach).

Both of my specimens are from localities adjacent to hardwood-pine forest with an herbaceous understory. The inference is that this snake is an inhabitant of mesic forest. The maximum elevation of known occurrence is 2,000 feet.

Genus Tantilla, Black-headed Snakes. Five females and one male of the Crowned Snake, Tantilla coronata Beird and Girard, are available. Data from these specimens are as follows: females--snout-vent length 174 mm. to 242 mm.; tail length 33 mm. to 57 mm.; ventrals, range 142 (139) to 151 (148), mean 145.2 (142.6); caudals, range 42 to 46, mean 43.2; male--snout-vent length 207 mm.; tail length 41 mm.; ventrals 139 (136); caudals 41; both sexes--scale rows 15; upper labials 7/7; lower labials 6/6; postoculars 2/2; temporals 1+1/1+1; width of collar at midline in terms of scale lengths, range 2.5 to 4, mean 3.2; the light band crossing the posterior tips of the parietal scutes ranges from less than one scale wide in one specimen to two scales wide in one specimen.

Comparison of these data with data presented by Schwartz (1953) indicates that intergradation between the Southeastern Crowned Snake, Tantilla c. coronata Beird and Girard, and the Appalachian Crowned Snake, Tantilla c. mitrifer Schwartz, occurs on the western slope of the Southern Appalachian Mountains. It is of interest to note that the data presented above are from two specimens from the Cumberland Plateau, two

specimens from the Valley Province, and two specimens from the Unaka Province. The point of interest is that four of the specimens which possess characters intermediate between T. c. coronata and T. c. mitrifer are from well outside the limits of distribution of the latter subspecies as defined by Schwartz. I wonder if the characters used by Schwartz for diagnosing T. c. mitrifer might not be within the range of variation of T. c. coronata? Certainly the criterion of color differences in preservative is a questionable one.

Locality data for these specimens indicate that this snake is most abundant in the Unaka Province (Fig. 35). The known maximum elevation of occurrence in eastern Tennessee is 1,800 feet. This snake is apparently restricted to woodland, and most specimens are from oak-pine-heath communities with rather loose sandy to loamy soils. This latter condition is probably a requisite for their fossorial habits.

Family Crotalidae

Genus Ancistrodon, Copperheads and Cottonmouths. One species of this genus, the Copperhead, Ancistrodon contortrix (Linnaeus), is present in eastern Tennessee. The belief is prevalent among the people of this area that the Cottonmouth, Ancistrodon piscivorus (Lacépède), is found in eastern Tennessee. I have been unable to discover this snake, neither are there literature records of its occurrence here.

Thirteen females and seven males of A. contortrix are available for examination. Data from these specimens are as follows: females--snout-vent length 492 mm. to 699 mm.; tail length 74 mm. to 88 mm.; ventrals, range 149 (147) to 154 (153), mean 150.3 (148.6) caudals, range,

42 to 48, mean 45.3; body bands, range 14.5 to 18.5, mean 16.1; males--snout-vent length 537 mm. to 811 mm.; tail length 85 mm. to 124 mm.; ventrals, range 149 (147) to 153 (152), mean 151.1 (149); caudals, range 44 to 49, mean 46.9; body bands, range 16 to 18, mean 17.1; sexes combined--scale rows, 23-21-19 (4 specimens), 25-23-21 (2 specimens), 27-25-23-21-19 (3 specimens), 27-23-21 (1 specimen), 25-23-21-19 (10 specimens); upper labials, 7/7 (5 specimens), 7/8 or 8/7 (3 specimens), 8/8 (11 specimens), 9/8 (1 specimen); lower labials, 9/9 (5 specimens), 9/10 or 10/9 (7 specimens), 10/10 (8 specimens). All specimens, regardless of scale count formulae, have 23 scale rows at midbody. The ranges of the above characters are within the variation reported by Gloyd and Conant (1943: 168) for the Northern Copperhead, Ancistrodon c. mokeson (Daudin).

The color of these specimens agrees essentially with that given by Gloyd and Conant for A. c. mokeson. Each of these specimens has the dorsum and venter stippled with dark brown or grey. Dorsally, this stippling is most intense on the ground color between the bands. Ventrally, it is most intensive posteriorly and often along the lateral edges of the venter. The latter condition results in the appearance of a light midventral streak. Each specimen also possesses paramedian, irregularly shaped dark spots on the ground color between the dorsal crossbands. These paramedian pairs of spots are most frequent at midbody or posterior to the midbody region. These color patterns are within the range of variation for A. c. mokeson.

The copperhead is widespread in eastern Tennessee (Fig. 37). Collection sites vary from dry, rocky ledges to heavily timbered and

Fig. 37.--Localities for the Northern Copperhead, Ancistrodon c. mokeson, and the Timber Rattlesnake, Crotalus h. horridus.

deciduous floodplain communities. In each case, however, the collection site is in or near forest land. The maximum elevation of known occurrence is 3,000 feet.

Genus Crotalus, Rattlesnakes. Only the Timber Rattlesnake, Crotalus h. horridus Linnaeus, is present in eastern Tennessee. Some members of the populace, particularly in the Cumberland Mountain Section, refer to a "black diamond rattler." I can only infer that they have reference to the black phase of C. h. horridus. In a fishing supply store in Meigs County there is the skin of the Eastern Diamond-back Rattlesnake, Crotalus adamanteus Beauvois. The proprietor says the specimen is from the Cumberland Plateau in Marion County. Undoubtedly, this specimen is an escapee.

Only four females and two males of C. h. horridus are available. Data from these specimens are as follows: females--snout-vent length 695 mm. to 848 mm.; tail length 44 mm. to 55 mm.; ventrals, range 168 (164) to 176 (174), mean 170.5 (167.2); caudals, range 17 to 22, mean 20.8; body blotches and crossbands, range 22 to 25, mean 23.2; males--snout-vent length 827 mm. and 1,006 mm.; tail length 65 mm. and 80 mm.; ventrals 166 (163) and 167 (165); caudals 24 each; body blotches and crossbands 22 and 24; sexes combined--scale rows, 25-23-19 (5 specimens), 26-23-19 (1 specimen); upper labials, 13/14 or 14/13, 14/15 or 15/14 (2 specimens each), 14/14, 15/15 (1 specimen each); lower labials 14/14, 15/14, 14/16, 13/15 (1 specimen each), 16/15, 15/16 (1 specimen each).

One female is nearly black, although the dorsal pattern of the blotches and crossbands is clearly discernible. One male is sulfur

yellow between dark brown to black blotches and crossbands. The remaining specimens are grayish with dark brown to black blotches and crossbands. Each of the females has a median dorsal brown stripe which occupies the median and adjacent halves of the dorsal scale rows. This stripe is not discernible on the males.

In matters of scutellation and coloration, these specimens are within the range of variation for C. h. horridus as reported by Gloyd (1940: 180-183).

Although widespread in eastern Tennessee, I have not encountered the Timber Rattlesnake in the Valley Province (Fig. 37). I have been told of its occurrence on some of the more remote knobs in the Valley. Some of the knobs and ridges are named Rattlesnake Ridge or Knob. Undoubtedly the rattlesnake formerly occupied all suitable habitats in eastern Tennessee. I do not believe that it is lack of suitable habitat which now is responsible for its apparent absence from the Valley and restriction to the remote ridge and mountain tops. Rather, I am convinced it is so restricted as a result of the enmity of man. The rattlesnake is a forest inhabitant, though the types of forest inhabited range from northern hardwoods on the mountain tops to xeric oak and oak-pine-heath forests on the southern slopes. The maximum elevation of known occurrence is 5,500 feet.

IV. DISCUSSION

A. Herpetofaunal Assemblages

Cain (1944: 164) proposed the grouping of floristic elements of a territory into intraneous and extraneous species, "according as their occurrence in that territory is well within the area of the form or near the periphery of its area, respectively." I have employed these concepts in the analysis of the herpetofauna.

Eastern Tennessee is well within the known range of some of the amphibians and reptiles and near the periphery of the known range of others. Those amphibians and reptiles having known ranges extending far beyond the borders of eastern Tennessee are designated as intraneous forms. Those amphibians and reptiles in eastern Tennessee which are near the periphery of their respective known ranges are designated as extraneous forms. Among the extraneous forms, I am recognizing three different categories; western extraneous, northern extraneous, and southern extraneous. Western extraneous forms are those having the greater portion of their ranges extending westward across the Mississippi River and/or northwestward into Indiana, Illinois, and beyond. The eastern periphery of their respective ranges is in or immediately east of eastern Tennessee. Northern extraneous elements are those which have the greater part of their ranges extending northward into Indiana, Ohio, and the North Atlantic States. The southern periphery of the ranges of these forms is in or immediately south of eastern Tennessee.

The southern extraneous forms are those which have the greater part of their respective ranges to the south and southeast. The periphery of their respective ranges is in or immediately north of eastern Tennessee.

In addition to the above categories, I am recognizing a group termed endemic forms. These have their known ranges restricted to the immediate vicinity of, but not necessarily within, eastern Tennessee.

The amphibians and reptiles assigned to each of the above five categories are presented in Table 1. Excluded from the listings are Necturus, Siren, and Ambystoma tigrinum.

To determine the known ranges of the amphibians and reptiles, I have consulted the following sources: salamanders, exclusive of the genus Plethodon, Bishop (1947); the genus Plethodon, Highton (MS); anurans, exclusive of the species Rana clamitans, Wright and Wright (1949); species R. clamitans, Mechum (MS); turtles, Carr (1952) and Cagle (1953); lizards, exclusive of the genus Ophisaurus and the species Eumeces anthracinus, Smith (1946); genus Ophisaurus, McConkey (1954); species E. anthracinus, Smith and Smith (1952); snakes, exclusive of the genus Elaphe and the species Coluber constrictor and Tantilla coronata, Wright and Wright (1957); genus Elaphe, Dowling (MS); species C. constrictor, Auffenberg (1955); species T. coronata, Schwartz (1953).

The known ranges of some amphibians and reptiles have been extended as a result of this study. These are: Eurycea l. guttolineata; Scaphiopus h. holbrookii; Pseudacris n. triseriata; Rana p. sphenoccephala; Graptemys p. ouchitensis; Natrix s. pleuralis; Diadophis p. punctatus; Coluber c. flaviventris; Elaphe o. spiloides.

TABLE 1.--Intraneous, extraneous, and endemic elements of the herpetofauna

Extraneous			Intraneous	Endemic
Northern	Southern	Western		
Cryptobranchius al- leganiensis	Eurycea b. cirri- gera	Plethodon d. dor- salis	Ambystoma macula- tum	Plethodon j. jor- dani
Plethodon c. cine- reus	Eurycea l. gutto- lineata	Eurycea lucifuga	Ambystoma opacum	Plethodon j. mat- calfi
Hemidactylium acu- tatum	Scaphiopus h. hol- brooki	Pseudacris n. tri- sorata	Diemictylus v. vi- ridesceus	Plethodon j. uni- coi
Gyrinophilus p. porphyriticus	Pseudacris n. fe- riarum	Graptomys p. oua- chitensis	Plethodon g. glu- tinosus	Plethodon welleri
Pseudotriton m. diastictus	Microhyla c. caro- linensis	Chrysomys p. mar- ginata	Pseudotriton r. ruber	Plethodon yonah- lossee
Eurycea l. longi- cauda	Rana p. sphenom- cephala	Pseudomys f. heiro- glyphica	Aneides aeneus	Gyrinophilus dani- elsi
Bufo t. americanus	Sternotherus m. peltifer	Pseudomys s. ele- gans	Bufo v. fowleri	Gyrinophilus pal- leucus
Rana p. pipiens	Knostreron s. subbrum	Matrix s. pleural- is	Acris g. crepitans	Pseudotriton r. nitidus
Rana pelustris	Pseudomys f. con- cinna	Storeria d. wrightorum	Pseudacris brachy- phona	Pseudotriton r. schencki
Graptomys geogra- phica	Anolis c. caroli- nensis	Coluber c. flavi- ventris	Hyla c. crucifer	Eurycea b. wilderae
Chrysomys p. picta	Ophisaurus a. lon- gicaudus	Lampropeltis g. niger	Hyla v. versi- color	Rana s. charokiana
Trionyx f. spini- fera	Eumeces inexpecta- tus		Rana catesbiana	Pseudomys s. troos- ti
Matrix s. sipedon	Cnemidophorus sex- lineatus		Chelydra s. ser- pentina	Tantilla c. mitri- fer
Storeria d. dekayi	Diadophis p. punc- tatus		Sternotherus odor- atus	
Diadophis p. ed- wardsi			Terrapene c. caro- lina	
Carphophis a. amoe- nus			Sceloporus u. hya- cintinus	
Coluber c. con- strictor			Lygosoma laterale	

Elaphe o. obsoleta	Elaphe g. guttata	Eumeces fasciatus
Lampropeltis d. triangulum	Elaphe o. spiloides	Eumeces laticeps
	Lampropeltis c. rhombomaculata	Eumeces anthracinus
	Lampropeltis d. dolifata	Natrix septemvittata
	Lampropeltis g. getulus	Storeria o. occipitomaculata
	Cnemidophorus coccineus	Thamnophis s. sirtalis
	Tantilla c. coronata	Haidea v. valeriae
		Heterodon p. platyrhinos
		Opheodrys a. aestivus
		Pituophis m. melanoleucus
		Ancistronotus c. mokeson
		Crotalus h. horridus

Notes:

Subspecies of single species are based upon specimens intermediate between the two, except in the case of E. bislineata. C. danieli includes the subspecies C. d. danieli and C. d. dunni.

Omitted from this list are the subfamily Desmognathinae, the genera Necturus and Siren, and A. t. tigrinum.

A total of 95 species and subspecies is listed in Table 1. Of this number, 52 are designated as extraneous; 12 western, 19 northern, and 21 southern. Among the 13 forms considered endemic, 9 are salamanders. All except two of these nine salamanders are restricted in eastern Tennessee to the Unaka Mountains Province. The two exceptions are Gyrinophilus palleucus, restricted to the type locality in the Cumberland Plateau Province, and G. danielsi, which extends westward across the northern part of the Valley Province to the Cumberland Mountains (Bishop, 1947: 362). The endemic frog and snake are of questionable validity [Humphreys (in litt.) and Wright and Wright (1957: 732), respectively]. But, as presently recognized, both are restricted in eastern Tennessee to the Unaka Mountains Province. The turtle, P. s. troostii, is restricted to the upper reaches of the Cumberland and Tennessee rivers (Carr, 1952: 241). Thirty forms are designated as intraneous. Of these, eleven are monotypic species. Of 67 extraneous and endemic species, only 9 are monotypic.

The distributions of the various assemblages are of considerable interest (Tables 2 and 3). The blank spaces and omissions of names under the various physiographic sections may be interpreted as indicating the absence from these areas of the forms in question. However, this may be the result of insufficient knowledge of their distributions. I have more confidence in the implications of these omissions in regard to vertical distribution than I do in regard to horizontal distributions.

With few exceptions, the intraneous assemblage is rather uniformly distributed over eastern Tennessee to an elevation around 2,500

TABLE 2.--Distribution of the intraneous and endemic elements

Herpetofaunal Elements	Cumberland Plateau (Less Cumberland Mtn)	Cumberland Mountains	Valley, Knoxville- Chattanooga Segment	Valley, north of Knoxville	Unakas			
					Lower Slopes (to 2,500 feet)	2,500 to 3,500 feet	3,500 to 5,000 feet	5,000 to 6,600 feet
Intraneous								
<i>Ambystoma maculatum</i>	X	X	X	X	X			
<i>Ambystoma opacum</i>	X	X	X	X	X			
<i>Diemictylus v. viridescens</i>	X	X	X	X	X		X	
<i>Plethodon g. glutinosus</i>	X	X	X	X	X		X	
<i>Pseudotriton r. ruber</i>	X	X	X	X	X			
<i>Aneides aeneus</i>	X	X	X	X	X			
<i>Bufo w. fowleri</i>	X	X	X	X	X			
<i>Acris g. crepitans</i>	X	X	X	X	X			
<i>Pseudacris brachyphona</i>	X	X	X	X	X		X	
<i>Hyla c. crucifer</i>	X	X	X	X	X			
<i>Hyla v. versicolor</i>	X	X	X	X	X			
<i>Rana catesbiana</i>	X	X	X	X	X			
<i>Rana c. melanota</i>	X	X	X	X	X		X	
<i>Chelydra s. serpentina</i>	X	X	X	X	X			
<i>Terrapene c. carolina</i>	X	X	X	X	X		X	
<i>Sceloporus u. hyacinthinus</i>	X	X	X	X	X			
<i>Lygosoma laterale</i>	X	X	X	X	X			
<i>Rumeces fasciatus</i>	X	X	X	X	X			
<i>Rumeces laticaps</i>	X	X	X	X	X			
<i>Rumeces anthracinus</i>	X	X	X	X	X			

feet. Except for some of the peaks in the Cumberland Mountains and some of the outliers of the Unaka Mountains in the Valley, 2,500 feet is higher than the general level of the Cumberland Plateau and than the highest ridges in the Valley. The absence from the Valley of Aneides and Pseudacris brachyphona is probably due to the lack of suitable habitats.

Gordon (1952: 698) reports the absence of localities for Aneides from the Appalachian Valley and implies that this salamander is restricted in distribution to the mixed mesophytic forest and/or mixed mesophytic forest association segregates. According to Braun (1950: 232) there is some evidence of the presence of communities similar to mixed mesophytic association segregates in the ravines of the northern segment of the Valley. It is possible that diligent search in this section may result in the finding of isolated colonies, thus establishing links between the colonies of the Cumberland Mountains and the colonies of the Southern Appalachian Mountains. Pseudacris brachyphona seems to be restricted to areas where clear, shallow streams and/or woodland ponds furnish suitable breeding sites. I would anticipate isolated colonies of this frog in the northern part of the Valley Province. It is highly possible that both of these forest-dwelling amphibians ranged across the Valley Province prior to the extensive deforestation resulting from the advent of white settlers. Question marks after the various forms listed in Table 2 indicate implied occurrence on the basis of published accounts.

Of the 28 intraneous forms indicated as occurring on the lower slopes of the Unakas, 12 are not known to occur in excess of 2,500 feet.

This is a loss of 43 per cent of the elements. Amphibians account for 50 per cent of this loss. This is not too startling inasmuch as all these amphibians are generally considered as inhabitants of lentic situations. Such habitats are practically nonexistent above 2,500 feet. The absence of the two aquatic turtles may be explained on the basis of the streams of this elevation being much too swift, cold (?), and rocky. Even the ubiquitous Chelydra would find footing difficult in these upper-elevation streams. The same factors may be responsible for the absence of Natrix septemvittata. The dropping out of Haldea v. valeriae, Heterodon p. platyrhinos, and Pituophis m. melanoleucus may be associated with the change in soil type. At the higher elevations the soil becomes shallower and more moist, thus presenting an unfavorable fossorial habitat for these snakes.

A striking difference between the assemblage of the lower slopes and that of the zone between 2,500 and 3,500 feet is the greater number of endemic forms in the latter.

Between 3,500 and 5,000 feet there are 12 of the intraneous elements remaining from the assemblage of the preceding zone. The five forms which drop out are two salamanders, one toad, one lizard, and one snake. Lack of suitable habitat may explain the absence of Desmictylus and Aneides, although for the latter there are many apparently suitable rock-crevice habitats. The explanation for the absence of Bufo w. fowleri and Ancistronon c. mokeson is equally conjectural. It is possible that at this elevation minimal temperatures may be too low or of too long duration, or that optimal temperatures may be of too short duration,

for embryonic development. This is suggested because the toad (B. t. americanus) and the snakes that do enter this and the summit zones have ranges which go farther north than those of B. w. fowleri and A. c. mokeson. The snakes Crotalus h. horridus, Storeria o. occipitamaculata, and Thamnophis s. sirtalis are the only reptiles known by me to frequent the summits in excess of 5,000 feet. This may be the result of these snakes being able "to follow the sun" and thus maintain temperatures favorable for the development of embryos contained in the bodies of the females. If this assumption and the one concerning temperature and embryonic development of A. c. mokeson are true, then the above three snakes may be more tolerant of lower temperatures than is A. c. mokeson. The same speculation applies to the two toads.

In the summit zone, 5,000 to 6,000 feet, there is a depauperate herpetofauna. As mentioned above, only three snakes maintain themselves at these elevations. They are accompanied by the toad B. t. americanus, designated as a northern extraneous form (Table 3), and certain endemic plethodontid salamanders (Table 2).

Of the endemic forms presented in Table 2, only G. palleucus and G. danielsi are found outside the Unaka Province. G. palleucus is confined to the Cumberland Plateau Province. G. danielsi contains two subspecies. G. d. danielsi, apparently a lowland form, has a range extending from the Cumberland Mountains area eastward across the Valley to moderate elevations in the Unaka Province. G. d. dunni is implied (Bishop, 1947: 362) as occurring from moderate to high elevations in the Unaka Province. If such is the case, then these two forms are separated vertically. The remaining endemic forms are limited to the Unaka Province.

The subspecies Pseudotriton r. nitidus and P. r. schencki are apparently separated horizontally. According to Bishop (1947: 390), P. r. nitidus occupies the northern half of the Unaka Province in eastern Tennessee and P. r. schencki occupies the southern half. It would appear from Table 2 that P. r. ruber and P. r. schencki are sympatric. This is discussed in the systematic presentation of P. ruber. It may be added here that collection sites where P. r. ruber have been taken seem generally to be drier than sites where P. r. schencki have been taken. This suggests ecological separation rather than altitudinal separation.

The subspecies of Plethodon jordani are, according to the distribution maps of Highton (MS), horizontally separated. P. j. metcelfi is confined to that part of the Unaka Province in extreme northeastern Tennessee. P. j. jordani is restricted to the Great Smoky Mountains, and P. j. unicolor is restricted to the high summits of the Unaka Mountains south of the Little Tennessee River.

In summary, it may be said that there is a large intraregional herpetofaunal assemblage which is quite uniformly distributed horizontally over eastern Tennessee to an elevation of about 2,500 feet. Above this elevation the intraregional assemblage is divisible into three zonal sequences. The differentiation of these zones is based, in part, upon the loss of constituent members from one zone to the next. The most abrupt loss from the assemblage of the lower mountain slopes is amphibians characteristic of lentic habitats. Such habitats are absent above this elevation. In the 2,500 to 3,500 feet zone and the 3,500 to 5,000

feet zone there is loss of a large number of intraneous elements and there is an increase in the relative number of endemic forms in the total assemblages. The loss of the intraneous forms is rather difficult to explain. It may be due to (1) lack of suitable habitats, (2) interspecific competition, and/or (3) adverse effects of temperature upon embryonic development at the higher elevations. Above 5,000 feet the characteristic herpetofauna consists of 73 per cent endemic salamanders and 28 per cent intraneous elements. All of the intraneous elements are viviparous snakes. On the lower slopes are two forms of questionable validity which are endemic to the Southern Appalachian Mountains. One salamander and one turtle are endemic to the Cumberland Plateau Province.

The extraneous herpetofaunal elements can be grouped into three assemblages as the result of examination of distributions presented in this paper and examination of published distribution maps. Comparison of Table 3 with Table 2 shows a remarkable similarity of distributional pattern between intraneous and northern extraneous forms. There is, in general, a rather uniform horizontal distribution of the extraneous elements over the Cumberland Plateau (less the Cumberland Mountains), the Knoxville-Chattanooga Segment of the Valley (Fenneman, 1938: 271), and the lower slopes of the Unaka Province, north to about the latitude of the French Broad River. This applies to southern and western as well as northern extraneous forms. The Cumberland Mountains, the Valley north of Knoxville, and the Unakas north of the French Broad River are like the other areas as regards northern extraneous elements. They are

TABLE 3.--Distribution of the extraneous elements

Herpetofaunal Elements	Cumberland Plateau (less Cumberland Mtn)	Cumberland Mountains	Valley, Knoxville- Chattanooga Segment	Valley, North of Knoxville	Unakas			
					Lower Slopes (to 2,500 Feet)	2,500 to 3,500 feet	3,500 to 5,000 feet	5,000 to 6,000 feet
Northern								
<i>Cryptobranchus alleganiensis</i>	X	X	X	X	X			
<i>Plethodon c. cinereus</i>	X	X	X	X	X			
<i>Hemidactylum scutatum</i>		X	X	X				
<i>Gyrinophilus p. porphyriticus</i>	X	X	X	X				
<i>Pseudotriton m. diastictus</i>	X	X	X	X				
<i>Eurycea l. longicauda</i>	X	X	X	X	X			
<i>Bufo t. americanus</i>	X	X	X	X	X			
<i>Rana p. pipiens</i>	X	X	X	X	X			
<i>Rana palustris</i>	X	X	X	X	X			
<i>Matrix s. sipedon</i>	X	X	X	X	X			
<i>Storeria d. dekayi</i>	X	X	X	X	X			
<i>Diadophis p. edwardsi</i>	X	X	X	X	X			
<i>Carphophis a. amoenus</i>	X	X	X	X	X			
<i>Coluber c. constrictor</i>	X	X	X	X	X			
<i>Elaphe o. obsoleta</i>	X	X	X	X	X			
<i>Lampropeltis d. triangulum</i>	X	X	X	X	X			
Southern								
<i>Eurycea b. cirrigera</i>				X				
<i>Eurycea l. guttolineata</i>				X				
<i>Scaphiopus h. holbrookii</i>				X				
<i>Pseudacris n. feriarum</i>	X		X	X				

quite distinct in the apparent absence of southern and western extreme elements. This is negative evidence on both counts and is subject to amendment at any time.

What may seem peculiar is the large number of southern elements on the lower slopes of the Unaka Province (Table 3). Even more peculiar is the indication of two southern forms ascending as high as 3,500 to 5,000 feet on the mountains. In fact, one of these, Eumeces inexpectatus, is apparently absent from the Valley Province. As mentioned in the account of Diadophis, my designation of numerous specimens of ringneck snakes as intergrades (Diadophis p. punctatus x edwardsi) is not accepted by Conant. But I think there is a very plausible explanation for the occurrence of southern forms such as D. p. punctatus, in the mountain province.

The mountain province is the wettest province in eastern Tennessee. At the base of the mountains the annual precipitation averages 55 to 60 inches. The annual rainfall increases with altitude to a maximum of around 70 inches per year at about the 5,000 feet level. The southern forms which ascend to the higher elevations are animals occurring in mesic or wet habitats. The temperatures at high elevations are not exceedingly severe. During a five year study of the weather of the Great Smoky Mountains, the coldest month, November, did not average less than 35° F. at 5,000 feet (Shanks, 1954: 356). Further, Eurycea b. cirrigera and E. l. guttolineata, while not occurring at elevations in excess of 2,000 feet, are confined to the lower slopes of the Unaka Province. This, too, I think is explained on the basis of precipitation

and temperature. Each of these forms is characteristically associated with or found in the vicinity of mesic deciduous forest, or remnants thereof. Braun (1950), in discussing the communities of the Mixed Mesophytic Forest Region and the Oak-Chestnut Forest Region, repeatedly emphasizes the preponderance of southern plant species even at elevations in excess of 4,000 feet.

Specimens of Diadophis which in all respects are "typical" D. p. edwardsi may be taken in association with specimens which are "typical" D. p. punctatus save for the high ventral-plus-subcaudal count. This situation pertains only to the Unaka Province. I infer that D. p. edwardsi is able to survive in habitats as moist as those in which D. p. punctatus occurs. The paucity of specimens from the Valley and Cumberland Plateau provinces which may be designated as D. p. punctatus x edwardsi intergrades is inferred as indicating that D. p. punctatus cannot survive in habitats as xeric as those inhabited by D. p. edwardsi. The average annual precipitation in the Valley and on the Cumberland Plateau is around 50 inches. The average annual precipitation in the Unaka Mountains range from 53 inches along the western margin to 70 inches at high altitude stations where I have collected specimens considered as D. p. punctatus x edwardsi intergrades.

In many of the distribution maps I have examined, it seems that ranges of southern amphibians and reptiles have been drawn to coincide on their northern boundaries with the physiographically delimited Southern Appalachian Mountains. This I suppose is the result of the generally accepted belief that mountains act as barriers to lowland organisms. As

a result of this study, I believe that the Southern Appalachian Mountains serve as effectively as a northward dispersal route for southern amphibians and reptiles as they do as a southward dispersal route for northern forms. This hypothesis is substantiated by the equality of numbers of northern and southern forms on the lower slopes of the Unakas south of the French Broad River (Table 3). The occurrence of the southern forms in the mountains may be attributed to the moderate temperatures, even at higher elevations, and to the high summer precipitation. These data permit a further speculation. It is possible that southern forms are exhibiting postglacial expansion of their ranges while northern forms are exhibiting contraction of their ranges.

The occurrence of western forms on the lower slopes of the Unaka Mountains may seem contradictory to the above comments, especially as the annual precipitation of the Cumberland Plateau, where these western forms also occur, is as much as 15 inches less per year. Local conditions of soil, slope, and exposure result in more xeric conditions on ridges and slopes with southern exposures. This is reflected in local differences in physical factors such as insolation and temperature and in vegetation (Braun, 1950: 205; Shanks, 1954, 1956; Whittaker, 1956).

From the data presented in Table 3, I conclude that a line drawn at approximately the 2,500 foot level northward in the Unaka Province to the French Broad River and thence northwestward to the Cumberland Mountains would effectively separate two distinct herpetofaunal assemblages. Below this line the assemblages diverge because of admixture of southern, western, and northern extraneous elements. As stated in the systematic

accounts, this line also approximates the zone of intergradation between many of the conspecific forms occurring in eastern Tennessee (vide: accounts of Pseudemys scripta, Natrix sipedon, Coluber constrictor, Elaphe obsoleta). The herpetofaunas of the Cumberland Mountains and the Valley north of Knoxville are more like that for the 2,500- to 3,500-foot zone of the Unaka Province than the herpetofaunas of the contiguous areas to the south. Braun (1950: 201, 214, 215, 232) indicates vegetational similarity among the Cumberland Mountains, the Valley north of Knoxville, and the slopes of the Unakas between 2,500 and 3,500 feet.

In the Unaka Province above 2,500 feet, zonation is evident among the extraneous forms (Table 3). Explanation for this zonation would be similar to that given in the discussion of the zonal distribution of intraneous forms with similar habits and habitat preferences.

So far, only two turtles--C. s. serpentina, T. c. carolina--have been presented from the standpoints of geographical distribution and affinities (Table 2). Each of these turtles is considered as an intraneous form; the remaining turtles are considered as intraneous (1 form), extraneous (10 forms), or endemic (1 form) (vide Table 1). These 12 turtles have been purposely omitted from the previous discussions. None of them is known to occur at elevations in excess of 1,800 feet. Thus, while distribution maps may indicate these turtles occur within the confines of the Cumberland Plateau and Unaka Mountains Provinces, they are actually not "on the plateau or the mountains." For this reason I do not consider them as part of the herpetofaunas of the Plateau or the Unaka Mountains. Further basis for this point of view is the

ecologic relationships of these turtles to communities other than those of the major rivers and streams.

Except for C. picta, which may inhabit stock ponds and other artificial or natural lentic habitats, these 12 turtles are confined to the larger rivers and streams. As a consequence, they, unlike the ubiquitous C. s. serpentina and the terrestrial T. c. carolina, do not as a rule directly effect the economy of the communities of terrestrial habitats, small spring-fed branches, seepage areas, or temporary aquatic situations. For this reason, I have not included these turtles in the herpetofaunal assemblages in Tables 2 and 3 or the discussions relating to these tables.

The 10 extraneous turtles are designated as western (4 forms), southern (3 forms), and northern (3 forms) (Table 1). One of the northern forms, Graptemys geographica, might with equal validity be considered as a western form. The occurrence of so many extraneous forms is not difficult to understand when one considers the extent of the Tennessee River Basin. Western forms could migrate up the Tennessee River from its confluence with the Ohio River. Northern forms might enter via the large headwater rivers in the Ridge and Valley north of eastern Tennessee (Johnson, 1954). Southern forms could enter the Tennessee River from tributaries in Alabama and western Tennessee. One southern form, Pseudemys f. concinna, barely enters extreme southeastern Tennessee and perhaps should not even be considered as a part of the turtle fauna. So far as available data indicate, P. f. concinna does not occur in the Tennessee River drainage. Data are presented in the discussion on the

species P. floridana to indicate that P. f. hieroglyphica does enter Gulf Coast drainage (Conasauga River of southeastern Tennessee and northeastern Georgia). It is probable that the zone of intergradation between P. f. concinna and P. f. hieroglyphica should be altered to include all of eastern Tennessee (cf. Carr, 1952: 292).

For my evaluation of the present distribution of aquatic organisms in eastern Tennessee, a biological survey of the Tennessee River Basin made prior to the construction of dams by the Tennessee Valley Authority would have been helpful. It is probable that the raised water level and controlled flow of the major rivers have resulted in the expansion of the ranges of such forms as P. f. hieroglyphica, P. s. elegans, and G. p. ouachitensis. Conversely, these same factors may have resulted in the extirpation of some forms from the rivers below the dams.

These speculations are supported by data from a study by Dandy and Stroud (1949). They report that the Little Tennessee River below Fontana Dam has been changed from a warm-water river to a cold-water river. Calderwood Reservoir in August, 1938, had a surface temperature of 85° F. and a temperature at a depth of 20 feet of 80° F. While in August, 1949, these same levels had temperatures of 70° F. and 56.25° F., respectively. Calderwood Reservoir formerly supported bass (Micropterus dolomieu) and walleye (Stizostedion vitreum). These fish are now absent, and present temperature conditions suggest that rainbow trout (Salmo gairdnerii) and brook trout (Salvelinus fontinalis fontinalis) may be able to survive there. Such drastic changes must have some effect on distribution of the herpetofauna inhabiting these waters.

B. Environmental Factors and the Herpetofauna

Van Steenis (cited by Cain, 1944: 155) indicates three handicaps faced by the plant geographer in his appraisal of the past and present processes influencing the area occupied by plants. These are: "(1) the usual absence of any exact data regarding the age of species; (2) the usual absence of any proof regarding dispersal . . .; (3) an uncertainty whether an area is expanding or retracting." These same handicaps confront the animal geographer. Cain goes on to say that "any critical coordination between geographical data and paleoecology, geology, or paleoclimatology must be regarded as a piece of luck."

The attempt to discover causal relations, or even correlations, among the various herpetofaunal assemblages and sets of environmental factors is baffling. This is not entirely the result of the three handicaps mentioned above. Another serious limitation to an adequate interpretation is the lack of knowledge of the ecological requirements of the animals involved, and, where such knowledge may be available, the lack of information as to which processes of the life cycle are critically affected by the interaction of these factors. I have speculated at several points in the discussion of the various herpetofaunal assemblages as to why certain forms may be absent from adjacent assemblages. Assuming my conjectural appraisals to be correct, they by no means give a complete explanation of the presence of the form in question in its assemblage. The most that can be hoped for is that such speculation, and that which appears below, may suggest factors that interact to influence the distribution of the assemblages.

I am unable to detect any positive correlation among the various assemblages and the macroclimatic data from stations in their respective areas. However, speculation regarding the influence of certain climatic factors is possible. The greater number of southern forms on the lower slopes of the Unaka Mountains south of the French Broad River, as compared to contiguous areas to the north and to the west, may be attributed to the high summer precipitation in this area. The collective distributions of the southern and western forms suggest coincidence with (1) the isochronous lines of April 10 to 15 for the average dates of the latest killing frosts in the spring ("Yearbook of Agriculture," 1941: 1125) and/or (2) the 50 inch annual precipitation isohyet [in part] as shown on the map Tennessee River Basin Mean Annual Precipitation published by the Tennessee Valley Authority. If either or both of these last two possibilities are real rather than mere coincidence, then they prevail only in limiting the northern and eastern parts of the ranges of the southern and western forms respectively. Just how this limitation would be affected I do not know. I would speculate that the influence is exerted upon the reproductive processes. The absence of the southern and western forms from the Unaka Mountains north of the French Broad River, the northern part of the Valley, and the Cumberland Mountains may be the result of decreased precipitation and/or later average dates of latest killing frosts in the spring.

As regards the limits of horizontal and vertical distribution of the northern extraneous forms and the vertical distribution of the intraneous forms, I do not think climate is an important limiting factor.

A possible exception to this statement is discussed on pages 171-172. The northern extraneous and the intraneous forms range farther north where temperatures and precipitation are less than in eastern Tennessee. Conversely, the intraneous forms range farther south where at least the temperatures are greater. Many of the northern, southern, and western extraneous forms are subspecies of the same species. Consequently, the factors, other than climate, limiting their distributions may be those responsible for allopatry of subspecies.

Some of the high-altitude endemic salamanders have abrupt lower limits of distribution (Highton, personal communication). I do not consider present climatic conditions as a significant factor in limiting the descent of these forms. If such were the case, I would expect them to be confined to particular forest complexes such as the spruce-fir forests. This forest is coincident in distribution with a distinctive type of climate as determined by Shanks (1954). To my knowledge, the only endemic salamander that is apparently restricted to a particular forest association is P. j. unicoi. The forest association at the type locality is northern hardwoods.

Attention has been drawn to the coincident distribution of certain southern extraneous forms and the vegetational complexes characterized by a large number of southern plant species. Similarly, there is uniformity in the herpetofaunas of the Cumberland Mountains, the northern part of the Valley, and the slopes of moderate elevation (2,500 to 3,500 feet) of the Unakas and uniformity of the forest associations of these areas. Additional illustrations of parallel situations between

distributions of herpetofauna and vegetation are available. These apply to the separation of the assemblages into vertical groups. Whittaker (1956: 38) states that in the Great Smoky Mountains the "relative importance" of oak and pine stands in the climax forest pattern decreases with an increase in elevation, while the importance of mesophytic stands increases with an increase in altitude. These changes are evident at intervals of about 1,000 feet. Oak and pine stands are most prevalent between 2,500 and 3,500 feet. Mesophytic stands become increasingly prevalent from 3,500 to 4,500 feet. Above 4,500 feet, the summits are clothed in fir and spruce-fir forests. The decrease in number of northern extraneous and number of intraneous herpetofaunal elements with an increase in altitude parallels the situation of the oak and pine stands. The increase in number of endemic forms of salamanders with an increase in altitude parallels the situation obtaining with mesophytic stands.

These coincidences between herpetofaunal assemblages and vegetational associations do not explain why the assemblages exist where they do. It merely suggests that perhaps the same combination of factors may control the distribution of amphibians and reptiles, since all in a sense are endothermic organisms.

There is no correlation between the distribution of the various assemblages and the major soil types of eastern Tennessee. This is not to be construed as indicating that soil is of no importance to the distribution of amphibians and reptiles. Such soil factors as depth, texture, and moisture-retaining capacity undoubtedly influence the local distribution of fossorial forms.

Man is one of the most important environmental factors operating to influence the distribution of the herpetofaunal elements. Unfortunately, there are few data upon which to base an assessment of the effect of man's activities. Aside from direct extirpation, the greatest effects upon the distribution of the various assemblages would be that of causing the expansion of ranges of nonforest forms and the contraction of ranges of forest forms. The primary cause of these simultaneous expansions and contractions was, and is, deforestation consequent upon lumbering and clearing for agricultural activities. Ayres and Ashe (in "Message from the President," 1902: 45) report that in 1900 only 75 per cent of the Southern Appalachians was forest and of this only 7.4 per cent [5 per cent of the total] was primeval forest. This does not include the Cumberland Plateau nor the Valley, which, being more accessible, must have experienced even more extensive deforestation.

The effect of the impoundment of rivers by the Tennessee Valley Authority has been discussed previously (page 182).

To the discussion of the coincidence of the distribution of the herpetofaunal assemblages with climate and vegetation should be added an appraisal of the element of time. It is important to ask whether the various herpetofaunal assemblages are in equilibrium with their respective habitats or whether they are still undergoing postglacial readjustment. Braun (1950: 500 f.; 1951) states that the present pattern of deciduous forest distribution has changed little since the close of the Tertiary Period. Her supposition is based in part upon the occurrence of mixed mesophytic forest associations in the Great Smoky Mountains,

disjunct from the center of greatest development of mixed mesophytic forest in the Cumberland Mountains. Further, the occurrence of endemic species of plants in the Southern Appalachian Mountains is accepted as evidence that Pleistocene events did not seriously affect the vegetation of the Cumberland Plateau and Southern Appalachian Mountains. If the correlation between the distribution of the various vegetation complexes and the herpetofaunal assemblages is real, then the reasoning of Braun would apply to these assemblages. That is, the distributions of the various herpetofaunal assemblages are now essentially as they were at the close of the Tertiary, with minor fluctuation in Pleistocene time. To interpret the history of the distribution of the various herpetofaunal groups, the distribution of the intraneous elements is of negligible value. They would only indicate vertical movements. The effects of Pleistocene events upon vertical as well as horizontal movements of the assemblages might better be interpreted from the distributions of the extraneous and endemic forms.

A knowledge of the Pleistocene fossil herpetofauna of eastern Tennessee would of course be extremely helpful in this interpretation. The presence of fossil forms equivalent to those occurring in the area today would not be prima facie evidence that such forms have always existed in this area. But, it would indicate that they have at least returned to an area formerly inhabited. That some vertical shifting occurred during Pleistocene glaciation may be inferred from the evidence suggesting a timberline elevation of between 4,000 and 5,000 feet in the Great Smoky Mountains (King and Stupka, 1950). Latitudinal shifting of

herpetofaunal elements may be inferred from the work of Auffenberg (MS). He reports the findings of fossil (Pleistocene) Carphophis amoenus, Eumeces fasciatus, and Pseudemys scripta in peninsular Florida. These forms are not present in peninsular Florida today.

The peculiar distribution of the turtle Pseudemys s. troosti may perhaps be explained as the result of maximum Pleistocene glaciation. This turtle is considered endemic to the Cumberland Plateau area. Examination of its range (Carr, 1952: 241) shows that it is bounded on the north, west, and south by P. s. elegans. Part of this extensive distribution of P. s. elegans may be attributable to recent range expansion (vide page 72). P. s. troosti does not now inhabit waters which would have received melt-water from the glacier in southern Illinois, Indiana, and Ohio. Suppose a troosti-like ancestral form inhabited, prior to maximum glaciation, all of the area now occupied by P. s. elegans and P. s. troosti. During maximum glaciation, the ancestral form would have been driven from its range in southern Illinois, Indiana, and Ohio and some of the area west of the Mississippi River. Because of the cold melt-water flowing down the Ohio and Mississippi rivers, the ancestral form would have been forced to retreat southward, but some population could have survived in rivers not receiving melt-water. That population in the Cumberland River drainage would have been effectively isolated from populations farther south along the Mississippi Basin, and even in the Tennessee River Basin, by the cold water of the Mississippi and Ohio rivers. During this isolation, genetic differences could have arisen separating the isolated population in the Cumberland drainage and the populations farther south. That the Cumberland

population should have survived so near the glacial border is not a problem. Thomas (1951) discusses animal distributions in glaciated Ohio which are most plausibly explained on the basis of refugia in the Cumberland Plateau south of the ice margin. Similarly located refugia for plants are discussed by Braun (1951) and Wolfe (1951). That P. s. troostii is now confined to such a narrow range may be due to swamping out of troostii characters in the lower portions of the Cumberland drainage by the return of the perhaps more vigorous P. s. elegans. P. s. troostii is thus an epibiotic form (Ridley, 1925).

Possible influence of the postglacial xerothermic period upon the harpetofauna of eastern Tennessee is suggested by the distribution, or occurrence per se, of the western extraneous forms.

During the xerothermic period the western extraneous forms may have entered eastern Tennessee via the Cumberland Plateau and crossed the Valley to the lower slopes of the Unaka Mountains. Natural prairie post oak openings are at present on the Cumberland Plateau as relic communities (Shanks, personal communication). Braun (1950: 121, 155) discusses prairie communities in the Knobs Area of the Cumberland Plateau in Kentucky (Mixed Mesophytic Forest Region) and in the Western Mesophytic Forest Region of the Highland Rim area of Tennessee and Kentucky. If prairie conditions existed on the surface of the Plateau, 1,000 feet above the Valley, they must have occurred in the Valley and on the lower slopes of the Unaka Mountains. Whittaker (1956: 60) assumes the ascent of vegetational zones in the Great Smoky Mountains as a result of the xerothermic period to account for the present distribution of the

spruce-fir forests of that region. According to his hypothesis, this ascent must have been in the neighborhood of 2,000 feet. The occurrence of western herpetofaunal elements on the slopes of the Unakas is at present 500 to 1,000 feet above the general level of the Valley floor. The Cumberland Mountains and the Valley north of Knoxville apparently do not have these western extraneous forms among their respective herpetofauna assemblages. That these western forms may have ranged higher on the mountains and farther northward in the Valley is probable. Following the close of the xerothermic period, the western elements may have descended the mountains and retreated southward in the Valley.

Possible modes of formation of the endemic subspecies may be illustrated by discussing two groups of subspecies of salamanders. One mode of subspeciation has already been discussed in connection with the distribution of the turtle P. s. troostii. Further, this seems a propitious place to comment on the ages of the subspecies. I do not believe the subspecies discussed below, nor most of them for that matter, can be older than 1,000,000 years and are probably much younger. Deavey (1949: 1320-1321) expresses a similar opinion. Auffenberg (MS: 249) states that modern species of amphibians and reptiles became established in early Pleistocene time. Zeuner (1950: 373) presents data indicating that subspecific differentiation may occur in 5,000 to 7,500 years and states (loc. cit.: 382) that a species does not remain unaltered for more than 500,000 to 1,000,000 years.

Differentiation of the subspecies of Plethodon jordani as defined by Highton (MS) may be explained as the result of the effects of

the postglacial xerothermic period. Assume that an ancestral population was widespread throughout the Southern Appalachian Mountains prior to the advent of the xerothermic period, and, that there was a free exchange of genes in all directions except in the populations occurring at the higher elevations of the various mountain ranges; e. g., the Unakas north of the French Broad River, the Great Smokies, and the Unakas south of the Little Tennessee River. These populations would have experienced gene exchange only with contiguous populations on the lower slopes of their respective ranges. During this period of partial isolation of the high-elevation populations, minor genetic differences could have developed in response to vertical gradients of environmental factors. With unfavorable environmental differences in the lowlands as a result of the xerothermic climate, the lowland population would have been exterminated. The lowland segment of the ancestral population could not ascend the mountains because suitable habitats were already occupied. With the disappearance of the lowland population, the populations of the higher elevations became effectively isolated from each other. During this time of isolation, these populations became differentiated into the presently recognized subspecies of P. jordani.

Presumably, Clemson's Salamander, Plethodon j. clemsoni (Brimley), is the only lowland form. It may represent a remnant of the ancestral population which found refuge in gorge habitats during the xerothermic period.

Hairston and Pope (1948: 277) and Highton (op. cit.: 113-114) propose river entrenchment as the factor responsible for isolation of

populations differentiating into the subspecies of P. jordani. I presume Highton bases his acceptance of this hypothesis upon his failure to find intergradation among the subspecies in the major river valleys, which he states are presently ecologically unsuitable for occupancy. He does find intergradation among some of the subspecies on the mountains. This latter condition is not incompatible with the xerothermic hypothesis outlined above. Rather, it would be an anticipated situation. Amelioration of climate following the termination of the xerothermic period would have permitted the isolated populations to descend the mountains, with consequent expansion of their respective ranges. Wherever expanded ranges of adjacent populations come into contact, intergradation could occur. Absence of some of the subspecies from the major river valleys may be explained as the result of insufficient time to have reached the valleys, in addition to, or instead of, their being ecologically unfavorable.

I do not subscribe to the river entrenchment hypothesis for two reasons. First, the highest river terraces of Pleistocene age in eastern Tennessee are only 400 feet above the present river valleys (Rodgers, 1953: 119). I speculate that such entrenchment would have progressed so slowly that the salamander populations would have been able to become adjusted to any resultant changes in habitat. Second, as indicated previously in this paper, changes in zonal distribution of herpetofaunal assemblages and vegetation involve differences in elevation in the neighborhood of around 1,000 feet, not 400 feet. Moreover, the zonation in these associations is not evident below an elevation of

2,500 feet. The terraces of which Rodgers speaks do not exceed an elevation of about 1,500 feet.

Distribution of the subspecies of Pseudotriton ruber presents, to me at least, a more complicated situation than is the case with the P. jordani subspecies discussed above. The endemic subspecies P. r. nitidus and P. r. schencki are completely surrounded by the subspecies P. r. ruber. My data indicate the further possibility that the ranges of P. r. ruber and P. r. schencki may interdigitate at least in the Unakas south of the Little Tennessee River. Or, this may be an area of intergradation. If the first possibility is correct, then this must be a case of ecologic (microgeographic?) isolation. I shall not pursue this further because of my inadequate knowledge of the ecologic requirements of the various subspecies.

For purposes of this discussion, I shall assume that both P. r. nitidus and P. r. schencki are inhabitants of the higher elevations and that P. r. ruber is a lowland form capable of ascending to high elevations where conditions are suitable. Further, I should emphasize that I am not familiar with P. r. nitidus. I presume from descriptions and pictures that P. r. nitidus and P. r. schencki are more closely related to each other than either is to P. r. ruber or to P. r. vioscai, and, that the last two are more closely related than either is to the first two.

The distribution of the subspecies of P. ruber (Bishop, 1947: 390) suggests at least two interpretations. One of these involves an unfavorable climatic condition during the xerothermic period similar to

the discussion concerning the subspecies of P. jordani. With the advent of the xerothermic period, conditions became favorable for western biota. This western biota may have extended not only as far east as the lower slopes of the Southern Appalachian Mountains, but as far south as the "black belt" of Alabama. The presence of this western biota had a fourfold affect upon P. ruber (the ancestral population of the presently recognized subspecies). One population was isolated in the Gulf Coastal plain and differentiated into P. r. vioscai. Another population was displaced to the north and differentiated into P. r. ruber. Two other groups were displaced vertically into, or isolated in sites in, the Southern Appalachian Mountains. These two groups differentiated into P. r. nitidus north of the valley of the French Broad River and P. r. schencki south of the French Broad River. Xerothermic conditions prevailing in the wide and low valley of the French Broad effectively isolated these two mountain populations. With the waning of the xerothermic period and the return of more favorable conditions, each of the resultant subspecies began expansion of range. For some reason, P. r. ruber must possess an advantage enabling it to have expanded its range, vertically as well as horizontally, more rapidly than any of the other three.

A second possible interpretation of the distribution of these subspecies involves a taxonomic rather than a biological interpretation. The speculation is that the subspecies represent terminal populations of a species exhibiting clinal variations. Lowland forms, P. r. ruber and P. r. vioscai, may obtain some adaptive advantage from possession

of a greater amount of pigmentation than the lighter forms occurring at high elevations. Thus, P. r. vioscai would represent a terminal population exhibiting maximum expression of pigmentation. P. r. nitidus and P. r. schencki are vertically distributed populations exhibiting maximum expression of a different adaptive character--reduction of pigmentation. As each of these last two forms inhabits a different mountain range with different combinations of environmental factors, the manner of expression of the character differs between the two populations. This speculation is capable of being tested by intensive ecologic and taxonomic study of the species.

It is appropriate to conclude this section with a brief appraisal as to the relative importance of ecologic factors versus historic events as determinants of the distribution of the herpetofauna. In the discussion, ecologic factors refers to the environmental conditions existing now, including the affects of the activities of man; historic events refers to those changes associated with natural phenomena involving extensive periods of time.

The two categories of phenomena, ecologic factors and historic events, while interrelated, may be considered separately. The ecologic factors are responsible for the local distribution of the different amphibians and reptiles within their respective areas. The extraneous forms, because they are near the periphery of their ranges, and the endemic forms, because they occupy restricted areas, are apt to be more drastically affected by changes in ecologic conditions than the intraneous forms. Historic events, however, are responsible for distribution

patterns evident among the various herpetofaunal assemblages. The historic event interpreted as being of greatest significance relative to the distributional pattern is the xerothermic period. The effects of this period are discussed above in relation to the western extraneous forms and certain of the salamander subspecies. As with changes of ecologic factors, historic events are apt to have had more influence upon extraneous and endemic assemblages than intraneous assemblages. This situation may be attributable to greater vagility of intraneous organisms.

C. Biogeography

In a paper (unpublished) presented before the American Society of Ichthyologists and Herpetologists I discussed the question, "Where do the Mountains Begin?" This resulted from my collecting "in the mountains" amphibians and reptiles no different, or little different, from those occurring in the Valley.

It is widely known that mountain biota of higher altitudes is distinct from lowland biota (Hesse, et al., 1949: 588). The data presented in this paper and by others (Braun, 1950; Shanks, 1954; Whitaker, 1956) indicate that on the western slopes of the Southern Appalachian Mountains below 2,500 feet, the kinds of communities encountered are little if any different from those occurring in the Valley Province. Except in localized situations, biotic distinctness between Valley and Unaka provinces is not noticeable until an elevation of 2,500 to 3,000 feet is attained.

As implied earlier, the practice of defining ranges of amphibians and reptiles in terms of physiographic province boundaries may result in error. If the periphery of the range of a lowland form is shown as coincident with a mountainous physiographic unit, the implication is that distinct mountainous ecological factors (Hesse, et al., op. cit.) are operating at or near the edge of the area. The data presented in this paper, and the references cited, show that where the mountain front is not precipitous, this may not be the case. Since, to the biologist, the term mountain has specific ecologic connotations, care should be exercised in the use of this term for defining ranges of organisms. There should be some indication of how high or how low on the mountain the organism or community occurs.

The concept that the spruce-fir forests of the high summits of the Southern Appalachian Mountains represent relict communities of boreal forest is suspect. This idea must be based upon the assumption that during Pleistocene glaciation there was continuous boreal forest along the higher portions of the Appalachians. Following the retreat of the glacier, spruce-fir forests survived only on the highest summits of the Appalachian ranges. I believe that most biogeographers subscribing to this concept are influenced primarily by the physiognomic similarity between these Appalachian spruce-fir forest communities and those of boreal regions. The evidence is against genetic unity of these separate associations, hence, they are not identical biotic units.

Shanks (1954: 360) presents data indicating that the "taiga spruce-fir forests are, in general, both much colder and drier than the

spruce-fir of the Southern Appalechian Mounteins." The cool superhumid climate of the Southern Appalechien summits is approached near sea level only in northern New England, the adjacent Maritime Provinces of Canada, and coastal areas of Washington and Oregon. Braun (1950: Map of Forest Regions and Sections) does not include New England and the Maritime Provinces in the boreal spruce-fir forest. Further, the spruce (Picea rubens) and the fir (Abies fraseri) are considered as endemic to the Southern Appalachians (Braun, 1950: 209, Whittaker, 1956: 53). The characteristic shrub species of the spruce-fir forest are primarily Appalachian and Piedmont in distribution. That none of the herpeto-faunal elements occurring in the Appalechien spruce-fir zone is found in the boreal spruce-fir forest supports the idee of the distinctness of these two forests. The designation of the Appalechian spruce-fir forest as Canadian or boreal is in my opinion incorrect and obscures its singularity.

The above remarks lead to a considaration of the systems of classification of the biota of North America. I shall not attempt to review each of these systems. Kendaigh (1954) presents a history of and an evaluation of these concepts for North America. My own remarks will be concerned with certain of the criteria utilized by various authors in establishing biotic subdivisions.

Most of the attempts to divide North America into biotically distinct areas purportedly involve an analysis of soils, climates, floras, and faunas. Frequently, however, only one or two of these groups of factors are utilized, or at least are given primary emphasis, in

characterizing the areas. Although Merriam (1892) based his life zones primarily upon temperature, he quotes and endorses (loc. cit.: 397) a statement of Asa Gray: "'Plants,' says Dr. Gray, 'are the thermometers of the ages, by which climatic extremes and climate in general are best measured.'" Clements and Shelford (1939: 229-230) state that the best expression of land climates is the climax community with its characteristic life form. The life forms of most land communities are determined by the dominant plants. Dice (1943: 5) places great emphasis upon plant communities for defining his biotic provinces, districts, and belts because "the plants often indicate the characters of climate and soil upon which animals are dependent." According to Cain (1944: 14), the primary cause of vegetation is climate, with edaphic control secondary.

I believe that associations of amphibians and reptiles, or other kinds of poikilothermic animals, could be used as effectively as vegetation for interpreting affects of past and present climates upon biotic associations. To do this would require much more information of the ecologic requirements of these animals than is now available. However, data has been accumulated to indicate that physiological activities of "cold-blooded" animals are directly influenced by such factors as pH, moisture, and temperature of the atmosphere and substrate (Allee, et al., 1949; Hesse, et al., 1949). Among amphibians and reptiles, this is especially true of the reproductive processes. Conversely, the homoiothermic birds and mammals are less subject to the direct influence of these same factors. Thus, it seems incongruous to me that birds and

mammals should be given a status equal to plants in the defining of biotic regions. Rather, I think that poikilothermic animals should be key forms equal or secondary in importance to plants for defining biotically distinct regions. Perhaps permanently aquatic animals are best excluded because their habitats are generally less variable than terrestrial ones. Further, dispersal of permanently aquatic forms--excluding those with wind-born stages in the life cycle--is dependent upon contiguity of habitat.

Merriam (1892: 415) employs mammals to illustrate his life zones because "they answer the purpose better than any other single group." I question this for reasons given above. Allen (1892) considers mammals as key organisms because (1) their dispersal is less dependent upon fortuitous circumstances, (2) they are less dependent upon other groups of animals, (3) because of their "power of adaptation" they are able to exist over the whole globe, (4) their distribution and dispersal are dependent upon land areas and are modified by barriers such as mountains, forests, grassy or desert plateaus, (5) their geological history is better known, and (6) there is greater unanimity on their taxonomic affinities. It seems to me that each of these reasons, with the possible exception of numbers 5 and 6, could as well be cited to justify using amphibians and reptiles as key organisms for defining faunal regions. Admittedly our knowledge of reptiles and amphibians has increased greatly since the time of Merriam and Allen. But, I think they failed to understand the importance of the more direct relationship between the physiological activities of "cold-blooded" animals and the physical environment.

Rhoads (1895: 381-382) discusses the herpetofauna of Tennessee in terms of Allen's faunal regions. Accordingly, eastern Tennessee below an elevation of 3,000 feet is included in the Carolinian Fauna, characterized by the following: opossum, Didelphys marsupialis; pine mouse, Microtus pinetorum; least mole shrew, Blarina; typical forms of the eastern deer mouse, gray squirrel, wood rabbit, gray fox; Acadian flycatcher, Empidonax acadicus; yellow-breasted chat, Icteria virens; Kentucky warbler, Helminthophila pinus; Bewicks's wren, Thryothorus bewickii; pine-tree lizard, Sceloporus undulatus; nebulous toad, Engystoma carolinense; pilot snake, Coluber obsolatus; box tortoise, Terrapene carolina. (All names appearing in this and following lists are those employed by Rhoads.) Between elevations of 3,000 and 5,000 feet in both the Cumberland and Unaka mountains is the Alleghanian Fauna, characterized by the following: red squirrel, Sciurus hudsonius; mole shrew, Blarina talpoides; brown shrew, Sorex personatus; Canadian warbler, Sylvania canadensis; least flycatcher, Empidonax minimus; Wilson's thrush, Turdus fuscascens; dusky salamander, Amblystoma jeffersonianum; black salamander, Desmognathus nigra; northern spring frog, Rana clamitans melanota. In the spruce-fir zone above 5,000 feet is the Canadian Fauna, characterized by the following: mountain deer mouse, Peromyscus; great red-backed mole, Eutamias carolinensis; bog vole, Synaptomys; winter wren, Troglodytes hiemalis; golden-crowned kinglet, Regulus satrapa; common crossbill, Loxia c. minor. Though perhaps more clearly defined, these faunas are essentially the same in distribution as the life zones ascribed to this area by Merriam (1892). Merriam's equivalents of

Allen's faunas are as follows: Humid Upper Austrel Zone : Carolinian Fauna; Humid Austrel Transition Zone : Alleghanian Fauna; Canadian Zone : Canadian Fauna.

I consider these faunistic subdivisions of eastern Tennessee as inadequate. The inappropriateness of designating the high-summit areas as Canadian has already been discussed. In comparing Rhoad's lists of birds of the various faunas with those of Ganier (1933), a doubt is cast upon the efficacy of these birds as indicator organisms. In the first place, none of the birds listed by Rhoads is a permanent resident of eastern Tennessee. Moreover, the Canadian warbler, least flycatcher, Wilson's thrush, winter wren, and golden-crowned kinglet are "rare" high altitude summer residents. Also, the other birds are merely common summer residents. It seems to me that if an animal is to be thought of as characterizing a particular biotic region, it should be a permanent resident of the area in question.

The significance of the mammals listed as zone indicators is equally suspect. The opossum, for instance, has such a wide geographical distribution that the inclusion of it as a diagnostic species for a limited biotic unit is valueless. Other mammals are listed merely by generic name, hence evaluation of their significance is not possible. Finally, there are two species of rabbits inhabiting eastern Tennessee (Hamilton, 1943: 383, 388) and two subspecies of gray squirrels (loc. cit.: 228). It is not known to which rabbit and to which squirrel Rhoads referred.

In defining biotic units in a limited area, especially an area with as varied habitat conditions as eastern Tennessee, the distribution

of subspecies seems all-important. Deevey (1949: 1318) also expresses the opinion that distributions of infraspecific categories may be more helpful in biogeographic studies than distributions of species and species groups. My confidence in the validity of subspecies distribution as a biogeographic criterion is founded upon my concept of the subspecies. I subscribe to the belief that genetically controlled morphological and/or physiological differences between subspecies, developed during isolation of ancestral populations, are basically adaptive.

The inadequacy of the amphibian and reptile species cited by Rhoads is apparent from the systematic treatment of the same species as presented in this paper.

It is known that in some cases animals are associated more closely with particular life forms of vegetation than with particular kinds of plants (Kendeigh, 1954: 166). Nevertheless, if the communities of different kinds of plants of the same life form are found in different portions of a given region, then local habitat differences may be indicated. Likewise, the different combinations of species and subspecies of animals within a given region may indicate habitat differences even though the life form of the dominant plants in each of the associations is the same. This latter supposition is valid only if there are no physiographic barriers to the dispersal of the animals under consideration, and only if there has been sufficient time for them to have occupied all of the available habitats in the area. Usually, it is difficult to determine whether there has been sufficient time for the various animals to have occupied all available habitats. Conversely, uniformity of life

form of the climax communities of a region may be indicative of uniformity in major climatic features of the region.

Insofar as practicable, nomenclatorial recognition of ecological assemblages of organisms (in conformity with the *bios* concept) should indicate seral relationships. However, determination of the seral position of such assemblages is frequently difficult. In the present case the status of my knowledge of the ecological requirements of the reptiles and amphibians of eastern Tennessee does not permit me to evaluate the seral relationships of these animals. Accordingly, the noncommittal biotic-unit terminology of Dice (1943) is employed in designating the following herpetofaunal areas in eastern Tennessee. The primary purpose in proposing these areas is to call attention to the fact that the reptiles and amphibians are grouped into recognizably distinct assemblages (Fig. 38).

The Cumberland Plateau (exclusive of the Cumberland Mountains), the Knoxville-Chattanooga Segment of the Valley, the lower slopes of the Unakas (to 2,500 feet) south of the French Broad River, and all of the Unaka Province south of the Hiwassee River may be designated as the Transition Herpetofaunal District. This district penetrates the mountains along the valleys of the major rivers such as the Little Tennessee, the Little, and the Hiwassee. The term Transition is selected in recognition of the admixture in this region of southern, northern, and western extraneous forms. The northern boundary of southern forms and the eastern boundary of western forms nearly coincide with the northern and eastern boundaries of this district. The forests of this district are

Fig. 38.--Herpetofaunal areas of eastern Tennessee.

characterized by the preponderance of pines, oaks, and hickories. Pines may constitute 50 per cent or more of the dominant tree species. The temperature-moisture relationships of weather stations in this district are more nearly like each other than like those of stations in areas to the north or at higher elevations to the east.

The Cumberland Mountains, the Valley north of Knoxville, the Unaka Mountains north of the French Broad River to an elevation around 3,000 feet, and the slopes of the Unaka Mountains south of the French Broad River below elevations of 2,500 and 3,500 feet may be considered as the Alleghenian Herpetofaunal District. The term Alleghenian is selected because of the northern extraneous forms. These northern herpetofaunal elements are characteristic of the Allegheny plateaus and mountains to the north of eastern Tennessee. Negatively, the Alleghenian District is distinguished from the Transition District by having fewer southern forms and no western forms in the Unakas south of the French Broad River, no southern forms in the Cumberland Mountains area, and no southern or western forms north of the French Broad River. Characteristic forest communities are mixed mesophytic forest in the Cumberland Mountains and in the ravines and deeper stream valleys of the Valley and Unaka sections. On the ridges in the Valley, on the slopes of the Unakas, and in higher parts of the Cumberland Mountains, white oak, red oak, and (formerly) chestnut forests prevail. Pine is not a conspicuous tree except on poorer sites. Temperature-moisture regimes of the weather stations in this district are more nearly like each other than like those from the Transition District.

The Unaka Mountains between elevations of 3,000 to 4,500 feet in the north and between 3,500 and 5,000 feet in the south may be designated as the Jordanian Herpetofaunal Zone. The term Jordanian refers to the salamander Plethodon jordani, subspecies of which are prevalent in this zone. They may occur at the higher elevations of the preceding zone, but to my knowledge, this is the only area inhabited in common by all three subspecies in eastern Tennessee. It is also in this zone that the so-called "northern hardwoods" forest is encountered (Braun, 1950: 207). Climatically, this zone differs from the preceding zone in its lower mean monthly temperatures and increased precipitation.

The summits of the Unaka Mountains, in excess of 4,500 to 5,000 feet, may be termed the Summit Herpetofaunal Zone. The term Summit is chosen in preference to Boreal because the latter term has a definite association with the concept of the Boreal Forest. As discussed previously, the summit communities of the Unaka Mountains are not considered as outliers of the Boreal Forest. Herpetofaunally, this zone is depauperate (Tables 2 and 3). Only one extraneous form (B. t. americanus) and eight endemic salamanders are known by me to frequent these summit areas. Vegetationally, this zone is distinguished by spruce-fir, fir, and gray beech forests and by grassy or haath balds. Climatically, it is distinct in having the coldest temperatures and maximum precipitation.

The intraneous herpetofaunal elements are purposely omitted from the foregoing discussion of biotic districts and zones. These elements are of greater significance as "binding species" (Clements

and Shelford, 1939: 242). That each of the above districts and zones is but a part of a larger community is attested by several features. First, deciduous trees characterize the physiognomy of each of the climax communities, except for part of the summit zone. Moreover, the occurrence of the same dominant forms in different associations is accepted as indicating the common origin of the various associations (Clements and Shelford, loc. cit.). A possible exception to this concept may be the spruce-fir forests. Second, while differing qualitatively and quantitatively, in terms of extraneous and endemic herpetofaunal elements, the districts and zones are strikingly similar in terms of intraneous elements. Finally, the ranges of many of the intraneous forms nearly coincide with the extent of the Deciduous Forest Biome, within which is included eastern Tennessee and its highest mountain summits.

V. SUMMARY

The study area is eastern Tennessee from the western escarpment of the Cumberland Plateau eastward to the Tennessee-North Carolina state line along the summits of the Unaka Mountains, and from the Tennessee-Kentucky state line on the north to the Tennessee-Georgia state line on the south. The physiographic provinces, soil types, vegetation, climate, and drainage are discussed. Most of these discussions are summaries from published sources. This information is utilized in the interpretation of the regional distribution and ecologic associations of the amphibians and reptiles in eastern Tennessee.

Basic to the interpretation of the distribution and ecologic associations of the amphibians and reptiles was the task of compiling a list of the herpetofauna of the study area. This was accomplished by collecting in the field. However, to supplement field collections, I have drawn freely from published sources.

Nineteen species of salamanders (excluding the subfamily Desmognathinae), 15 species of anurans, 11 species of turtles, 8 species of lizards, and 22 species of snakes are reported as occurring in eastern Tennessee. Reporting the occurrence of these species in the study area is based upon critical examination of series of specimens collected during the study. The taxonomic allocation of each series is based upon a comparison of the material with descriptions in monographs and references. In several instances, the specimens are compared with series of identified material in the University of Florida Collections. When material from eastern Tennessee differs from taxonomic descriptions

and is difficult to identify taxonomically, this is emphasized in the account of the species to which the material is tentatively allocated. No attempt is made to redefine or to refine the existing taxonomic status of the species encountered. Reporting the occurrence of Scaphiopus h. holbrooki, Graptemys p. ouachitensis, Coluber c. flaviventris, Natrix s. pleuralis, Diadophis p. punctatus, and Elaphe o. spilioides in eastern Tennessee constitutes extension of the known ranges of these forms. Evidence is also presented to indicate that eastern Tennessee is in the zone of intergradation among subspecies of 3 salamanders, 2 anurans, 4 turtles, and 6 snakes. Included with the taxonomic discussion of each form are remarks concerning the known horizontal and vertical distribution of the various amphibians and reptiles in eastern Tennessee.

Intraneous, extraneous, and endemic forms are recognized among the elements of the herpetofauna. Extraneous forms are further characterized as of western, southern, or northern derivation. These five categories are based upon the spatial relationship between the occurrence of the various amphibians and reptiles in eastern Tennessee and the remainder of their respective ranges as presently defined. There are 52 extraneous forms; 19 with northern affinities, 21 with southern affinities, and 12 with western affinities. Intraneous forms total 30, and of endemic forms there are 13. Most of the western extraneous forms are confined to the Cumberland Plateau, the southern part of the Valley Province, and the lower slopes of the Unaka Mountains south of the French Broad River. Their occurrence in eastern Tennessee is

attributed to factors prevailing during the postglacial xerothermic period. Most of the southern extraneous forms are confined to the southern part of the Valley and to the lower slopes of the Unaka Mountains south of the French Broad River. Four "southern" forms (2 salamander, 1 lizard, 1 snake) are practically confined to these lower slopes of the mountains. The apparently anomalous restriction of southern amphibians and reptiles to the mountain province is attributed to the climatic conditions on the lower slopes, especially the high summer precipitation. The northern extraneous elements are most numerous in the Cumberland Mountains, the northern half of the Valley, and in the Unaka Mountains between elevations from 2,500 to 3,500 feet. Only one northern extraneous form occurs above an elevation of 5,000 feet. Intransaneous elements occur throughout eastern Tennessee except that only three (viviparous snakes) occur at the highest elevations around 6,000 feet. Of the endemic species, all but three are confined to the Unaka Mountains.

Differentiation of certain of the endemic salamanders is speculated as being the result of the isolation of ancestral populations at high elevations during the xerothermic period. The distribution of the endemic turtle P. g. troosti is explained as the result of separation of ancestral populations during the time of maximum Pleistocene glaciation.

As a result of this study, division of eastern Tennessee into four herpetofaunal areas is proposed. The basis for these proposed areas is the vertical and horizontal distribution of the amphibian and

reptile assemblages. Vegetation and climate are also employed in defining the areas. These areas are not coincident with physiographic boundaries.

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BIOGRAPHICAL SKETCH

The author was born in Carey, Ohio, on March 4, 1924. Following graduation from high school in 1942, he was inducted into the Army of the United States and served three years as a surgical technician in the Medical Department.

Upon separation from the service, he attended Ohio State University. He graduated from this institution in 1949 with the degree of Bachelor of Science in Wildlife Management. From February, 1950, until August, 1951, he was a graduate student in the Department of Zoology, Tulane University. Here he held a graduate assistantship and served as an assistant in the zoology laboratories, curator of the Research Collections, and curator of amphibians and reptiles in the Audubon Park Zoo. He was graduated from Tulane University in 1952 with the degree of Master of Science in Zoology.

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The author is a member of Gamma Sigma Delta, Phi Sigma, the Society of Sigma Xi, the American Society of Ichthyologists and Herpetologists, the Ecological Society of America, the Herpetologist's League, and the social fraternity Beta Theta Pi. He is married and with his wife has two daughters.

This dissertation was prepared under the direction of the co-chairmen of the candidate's supervisory committee and has been approved by all members of that committee. It was submitted to the Dean of the College of Arts and Sciences and to the Graduate Council, and was approved as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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