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Geographic Variation in the Primary Burrowing Crayfish, Cambarus dubius Faxon and Cambarus carolinus (Erichson) (Decapoda: Astacidae) in Tennessee with Notes on Ecology and Life History

Joel P. Dewees
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To the Graduate Council:

I am submitting herewith a thesis written by Joel P. Dewees entitled "Geographic Variation in the Primary Burrowing Crayfish, Cambarus dubius Faxon and Cambarus carolinus (Erichson) (Decapoda: Astacidae) in Tennessee with Notes on Ecology and Life History." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Life Sciences.

David A. Etnier, Major Professor

We have read this thesis and recommend its acceptance:

William J. Davis, Charles D. Pless

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

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

November 27, 1972

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David A. Etnier
Major Professor

We have read this thesis
and recommend its acceptance:

William James Davis

Charles L. Pless

Accepted for the Council:

Hilton A. Smith
Vice Chancellor for
Graduate Studies and Research

GEOGRAPHIC VARIATION IN THE PRIMARY BURROWING CRAYFISH, *CAMBARUS DUBIUS* FAXON AND *CAMBARUS CAROLINUS* (ERICHSON) (DECAPODA: ASTACIDAE) IN TENNESSEE WITH NOTES ON ECOLOGY AND LIFE HISTORY

A Thesis

Presented to

the Graduate Council of

The University of Tennessee

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

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by

Joel P. Dewees

December 1972

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ABSTRACT

An investigation of Cambarus dubius and Cambarus carolinus was made in Tennessee to evaluate morphological variation found in populations of these species and to determine aspects of life history and ecology. Taxonomic position and history of C. carolinus and C. dubius was reviewed and discussed. Three clines or possible subspecies in C. dubius were indicated in Tennessee based on both qualitative and quantitative evidence including: width and length of areola, shape and size of chelae, rostrum, central projection, mesial process, and color.

C. dubius populations from northern West Virginia and southern Pennsylvania were significantly different from populations to the south. C. carolinus could not be separated by quantitative measurements from C. dubius, but could be distinguished on the basis of the central projection and other qualitative characters. Color phases were discussed for both C. dubius and C. carolinus. The range for both species in Tennessee was discussed and the range limits for C. dubius delineated. Life history and ecological data were reported for C. dubius and indicated for C. carolinus.

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INTRODUCTION

The crayfish Cambarus dubius Faxon and C. carolinus (Erichson) were among the earliest described species of the subgenus Jugicambarus, but to date relatively little is known about them. Most authors have commented only briefly on life history, behavior, and ecology. They are not readily observed or collected due in part to the borrowing habits of both species. Also confusing are the descriptions given by earlier investigators in separating these and closely allied relatives. This has resulted in uncertainty regarding the taxonomic status of C. dubius and C. carolinus for the past century. Moreover, substantial amounts of morphological and color variation have been found in C. dubius populations from different localities in Tennessee, suggesting possible specific or subspecific differences. However, a thorough study has never been made of this variation in Tennessee or elsewhere.

It was hoped that comparative ratios of morphological characters between different populations would help in the evaluation of these two problems. This, together with lack of knowledge of ecology and life history of both species formed the incentive for this investigation.

CHAPTER I

HISTORY AND TAXONOMIC STATUS

Early History

Cambarus carolinus was described by Erichson (1846:96) as *Astacus carolinus*, a red crayfish from western South Carolina in the vicinity of Greenville. Erichson noted the narrow areola and single cristiform row of tubercles on the inner margin of the palm. Unfortunately, the type specimen was lost, and neither photographs nor drawings were published although they were examined by Faxon (1914) and Hay (1902). Girard (1852) later elevated Erichson's subgenus *Cambarus* to generic rank. Faxon (1884:114) subsequently described another red crayfish, *Cambarus dubius*, from Terra Alta (formerly-called Cranberry Summit), Preston County, West Virginia. Faxon (1914) noted that *C. dubius* differed from *C. carolinus* in having only a single spine on the inner margin of the carpus, the internal median. He also noted that the outer margin of the palm of *C. carolinus*, as shown in the drawings, was rounded and lacked the subserrate edge characteristic of *C. dubius*. He noted that the rostrum of *C. carolinus* was narrower and had gently rounded anterior margins while that of *C. dubius* was subparallel and ended in sharper angles. Faxon's descriptions (1884,1914), and drawing (1885) of *C. dubius*, portrayed the central projection of form I males as recurved, pointed, and lacking a subapical notch, similar to that of *C. carolinus*. Thus, by the drawing and description of the pleopod given by Faxon, it would be very difficult or impossible to separate these two species.

In addition to the type locality, Faxon (1885,1914) reported C. dubius from southwestern West Virginia, northern West Virginia, Pennsylvania, Garret County, Maryland, Cumberland Gap, Tennessee and Pennington Gap, Lee County, Virginia. Specimens from one other locality, "a tributary of Stone River twenty miles from Columbia in central Tennessee" (Faxon, 1914) were formerly identified as C. dubius, but have recently been described as Cambarus gentryii Hobbs (Hobbs 1970a:161).

Hay (1902) and Harris (1903) did not recognize C. dubius as a distinct species, but placed it under the synonomy of C. carolinus. Ortmann (1905a,1906) likewise synonymized C. dubius and C. carolinus. Ortmann noted C. carolinus (plus C. dubius) was easily recognized by the color which he described as always "a vivid red." He also noted that C. carolinus appeared to be a true mountain species, being found generally at altitudes from 1,000 to 2,000 feet above sea level on the Allegheny Plateau in Pennsylvania with the Chestnut Ridge forming its boundry toward the northwest and the Allegheny Front in the northeast. In this same paper, Ortmann (1905a:395) recognized a new species, Cambarus monongalensis, which he destinguished from C. carolinus by the following:

> (1) narrower rostrum with margins more convergent, and lateral angle at base of acumen less well defined, (2) outer margin of hand not serrated, being swollen and evenly rounded, (3) carpus with more than 1 spine in the inner side, (4) color always blue with the distal part of the fingers of chela orange or reddish brown.

He described this crayfish as a more lowland form from elevations ranging from 800 to 1,200 feet above sea level and the range from the

Monongahela River drainage system, west of the Chestnut Ridge. Later Ortmann (1931), added an additional locality from Burnsville, Braxton County, West Virginia which extended the range to the Little Kanawha River system. In another paper (1906), Ortmann differentiated C. monongalensis from C. carolinus in addition, by the merus which in C. monongalensis, in most cases, has the outer lower margin formed by a smooth keel or one small spine on the outer row. He also noted differences in the epistome, telson and antennal scale.

Faxon (1914) later recognized Ortmann's synonomy of C. dubius and C. carolinus but still recognized C. dubius as a subspecies and separated it from C. carolinus on the basis of the single spine on the carpus, the broader rostrum with nearly parallel margins, and the subserrate outer margin of the chela. He felt that C. monongalensis was also a subspecies of C. carolinus and separated it on the basis of its blue color and the single spine on the lower, outer face of the merus. Ortmann (1931) continued to recognize C. monongalensis as a full species and C. dubius as a subspecies of C. carolinus. He summarized the distribution of C. carolinus which he noted was "extremely peculiar," from the

> High Mountains, formed by the southern extremity of the Blue Ridge, in N. C. (possibly as far south as northern Georgia), and the Piedmont Plateau. Just at the foot of the mountains, in South and North Carolina, the range swings over to the headwaters region of the Tennessee River, and across the Allegheny Mountains to the Cumberland-Allegheny Plateau in Southern W. Va. To the north exists a gap, probably due to defective knowledge, but in northern West Virginia, this species is again present on the Allegheny Plateau, on the part close to the Allegheny Front, and continues northward as far as Pennsylvania. Thus, generally speaking, C. carolinus is a mountain species, but is not found everywhere in the mountains.

Most investigators including Creaser (1934), Hobbs (1942, 1959,1968b,1969), Pennak (1953), Schwartz and Meredith (1962) and others, have continued to follow Hay's synonomy of C. dubius with C. carolinus until the present. W. L. Schmitt and C. L. Newcombe, (Newcombe 1929a, 1929b) considered both C. dubius and C. monongalensis as subspecies of C. carolinus, following Faxon's classification. Newcombe (1929b) recognized blue populations inhabiting elevations from 2400 to 4500 feet in the Allegheny Mountains of eastern West Virginia as a blue phase of C. carolinus dubius.

Present Status

In Northern Georgia, southeastern Tennessee, and western South Carolina, another population of crayfish exists which has been included within the synonomy of C. carolinus. Recent examination of these specimens has shown that they differ from C. carolinus in that they lack a single cristiform row of tubercles on the palm. There may be as many as five rows of tubercles on the dorsal surface of the palm. They also have a wide areola, Generally less than six times longer than broad, and, significantly, the form I males have a subapical notch on the central projection which is always lacking in C. carolinus. Specimens from Polk County, Tennessee were collected from shallow excavations in and at the edge of streams and are not primary burrowers (R. W. Bouchard, per. comm.). The color is typically a tan-olive common to fluvial species. None of these specimens had the coloration found in C. carolinus. For these reasons this population is regarded as distinct from C. carolinus Erichson (Hobbs and Bouchard, per. comm.).

Recent examination of topotypic form I males of both C. dubius and C. carolinus has revealed major differences between the two. In C. carolinus, the apex of the central projection is always long, and bladeshaped, lacking a subapical notch (Figure 1, a,b). All specimens of C. dubius, including those from the type locality, have a distinct subapical notch at the distal end of the central projection, including Faxon's type for C. dubius (M.C.Z. #3,631). Presently, C. carolinus (Erichson) is being redescribed (Hobbs and Bouchard, in press) to eliminate further confusion and reestablish C. dubius Faxon to specific rank.

The only localities for C. carolinus (sensu strictu) remaining, with the separation out of C. dubius and others, were the localities from the area around Greenville, Greenville County, South Carolina, and the following: one from among the Cherokees, Indian Territory (Faxon, 1890), a locality in Asheville, Buncombe County, North Carolina (Ortmann, 1931), a locality from Indian Gap in The Great Smoky Mountains National Park, and finally a locality above Tellico Plains, Monroe County, Tennessee.

Collections made in the Blue Ridge Province in east Tennessee and into western North Carolina from 1970 through 1972, included crayfish from several localities which were closely allied to typical C. carolinus but differed in the following respects: 1) carapace was not as vaulted and areola not as linear. The mean ratio of areola length to width was 7.54 on a sample comprised of 20 specimens, 2) the chela was not as flat and broad and was slightly more hirsute than C. carolinus from the type locality, 3) the rostrum was narrower and more elongate and, 4) the central projection of form I males was more

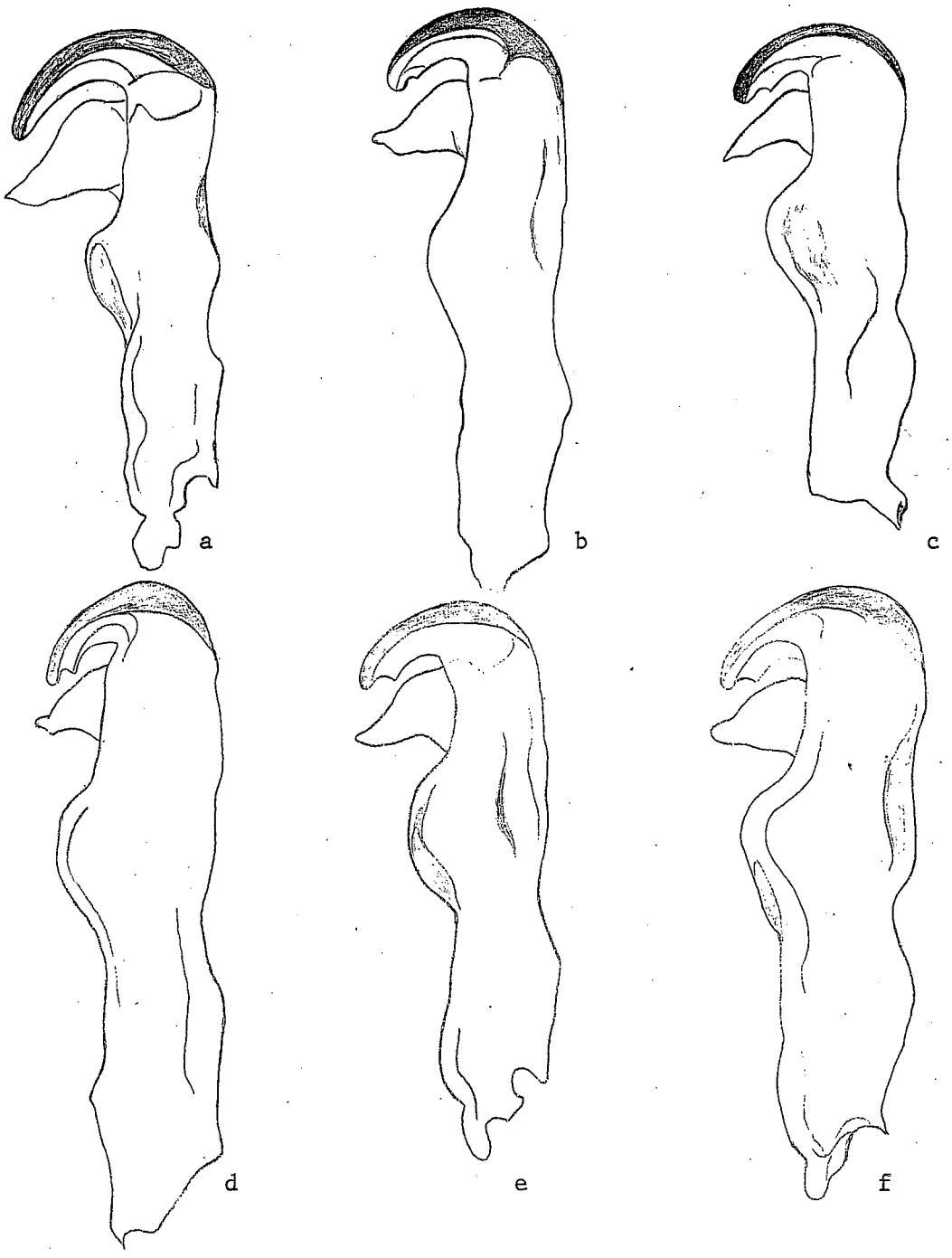

Figure 1. Lateral view of first pleopods of form I males of Cambarus carolinus and Cambarus dubius. a, C. carolinus, Elkmont, Sevier County, Tennessee; b, C. dubius, Terra Alta, Preston County, West Virginia; c, C. dubius, Mountain Lake, Giles County, Virginia; d, C. dubius, Baileysville, Wyoming County, West Virginia; e, C. dubius, Station Creek, Lee County, Virginia; f, C. dubius, Hickory Creek, Knox County, Tennessee.

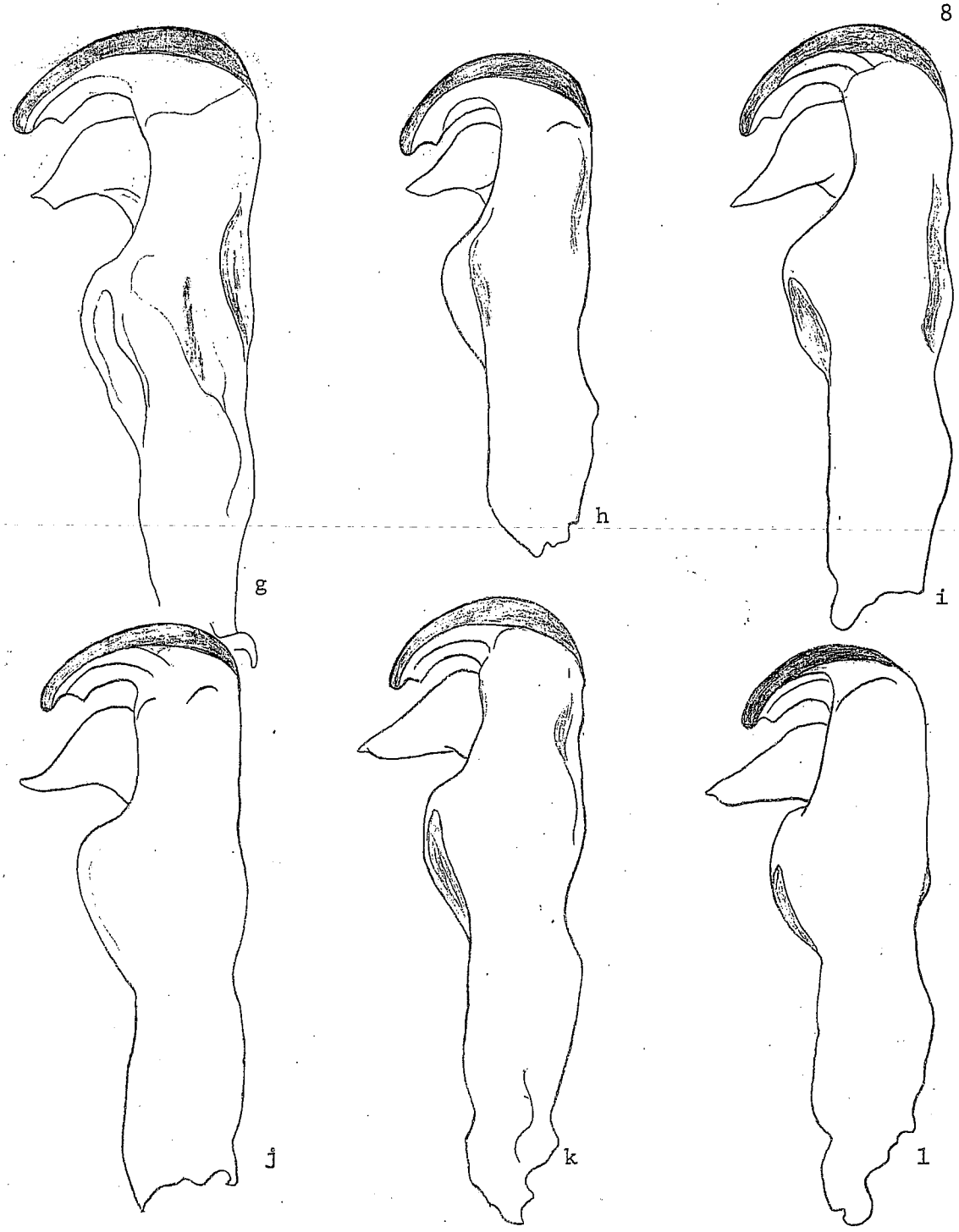

Figure 1 (continued). g, C. dubius, Strunk, McCreary County, Kentucky; h, C. dubius, Clear Creek, Anderson County, Tennessee; i, C. dubius, Bullrun Creek, Union County, Tennessee; j, C. dubius, Pressmans Home, Hawkins County, Tennessee; k, C. dubius, Roane Mountain, Carter County, Tennessee; l, C. dubius, Linville, Avery County, North Carolina.

recurved (angle = 185°). The characters of these populations, which were found at the higher elevations in the southern region of the Blue Ridge Province, appeared somewhat intermediate between typical C. carolinus and C. asperimanus Faxon (Faxon 1914:391). However, its closest affinities lie with C. carolinus and should probably be considered a mountain form of this species. More specimens from intermediate regions need to be examined before any definite conclusions may be drawn about this population.

CHAPTER II

MATERIALS AND METHODS

I. COLLECTING TECHNIQUES

Traps

Traps were experimented with initially, as a method of collecting specimens of Cambarus dubius and C. carolinus. The traps were designed and constructed from commercial cans measuring 17.5 cm. in height and 10.5 cm. in diameter. The bottom was removed and fitted with a wire screen funnel with a central opening measuring approximately 5 cm. in diameter. The funnel opening was placed at the mid-section of the can. The top of the can was removed and replaced with a plastic cover for easy baiting and removal of specimens and debris. Holes were made around both the top and bottom of the can to allow circulation of air and water into the trap. Bait was placed near the top of the trap and held in position with a piece of copper wire. The traps were placed in the entrance of the burrows after they had been slightly enlarged to allow the trap to be submerged about half way in water. Traps were checked at intervals of two or three days.

Trapping was later discontinued in this study for several reasons. Although trapping was a successful method of obtaining several species of burrowers, it proved the least successful with these two species. C. dubius specimens of all sizes and both sexes,

including three ovigerous females, were caught in traps but many settings yielded no results. No C. carolinus were captured in traps. Both species often succeeded in completely filling the interior of the trap with mud and gravel and then retired to the depths of their burrows. Another disadvantage was the time and expense envolved where long travel distances were required, since one trip was required just to set out the traps before they could be checked. Other disadvantages were: loss due to vandalism, time required for cleaning, repairing and baiting traps, and necessity to check traps frequently for specimens since the crayfish often succumbed if left in more than a day or two. Trapping might, however, prove to be one of the best capture methods for burrowers in studies gathering life history data under field conditions since the burrow and habitat is not destroyed or altered as it is by other methods.

Chemical

A second method of capture was the use of chemicals including sodium hydroxide (NaOH) pellets and a concentrated solution of ammonium hydroxide (NH_3OH). Under laboratory conditions, small amounts of these chemicals elicited an escape response. No after effects were observed and for this reason were chosen over more toxic materials. Neither of these chemicals proved satisfactory as a collecting tool. Either they became too diluted when placed in the burrow to have any effect, or the crayfish retreated to the bottom and remained there rather than come to the surface.

Other

The method most frequently employed, for collecting both C. dubius and C. carolinus, was the careful dissection of the burrow with a shovel. Although there are obvious disadvantages using this method including destruction of the burrows, it proved to be the most successful. Occasionally, specimens were caught which had come to the surface to investigate the disturbance created by digging, but this was rare. Neither C. dubius nor C. carolinus displayed the investigative behavior exhibited by some of the other burrowers such as Cambarus d. diogenes Girard which is often captured this way. On occasion, C. dubius was collected above ground completely out of the burrow. Both C. dubius and C. carolinus were sometimes found hiding under rocks in seep areas or at the edge of streams.

II. MEASUREMENTS

General

Specimens used in this study included collections from the University of Tennessee Museum (Aquatic Biology), the Museum of Comparative Zoology at Harvard University, and the United States National Museum, as well as collections conducted from May of 1971 through October of 1972. These collections, while primarily made in Tennessee, included the states of North Carolina, Virginia, and West Virginia as well. A total in excess of 300 specimens, excluding juveniles and young, were measured. Crayfish which were poorly preserved, damaged, or recently molted, were not included in the data. Regenerated chelae, because of their atypical proportions, were not measured.

Quantitative

The standard measurements of crayfish taxonomy were used with one exception. The standard length for all crayfish in this study was based on postorbital carapace length (Bouchard, in press) rather than total length carapace from the tip of the acumen to the posterior edge of the thorax used by other investigators (Fitzpatrick 1963, and 1967, Hobbs 1970b, Prins 1968 and others). This standard was chosen because the length and shape of the rostrum is very variable, even within a single population, and is frequently broken off or mishapen. However, the standard length is included for certain kinds of data. Normally the left chela was used in all measurements except when missing or regenerated in which case the right was used. Measurements were made with vernier micrometer calipers and standard millimeter rule. Width of areola and length and width of rostrum were both measured and read under a dissecting microscope. Other measurements were read under a dissecting microscope and all measurements recorded to the nearest 0.1 mm.

Measurements were made of the following:

1. Length of the cephalothorax (from tip to acumen as well as postorbitally).

2. Width of the cephalothorax.

3. Height of the cephalothorax.

4. Length of the rostrum.

5. Width of rostrum both at the anterior postorbital ridges and between the eyes.

6. Length of the areola.

7. Width of the areola.

8. Length of the outer margin of the chela.

9. Length of the inner margin of the palm.

10. Width of the palm.

11. Thickness of the palm.

12. Length of the dactyl.

13. Total body length from tip of the acumen to posterior edge of the telson.

Measurements include the combined data of both males and females as significant differences were not found between the sexes or sexual form (males) and because of the lack of large series of specimens from any one locality. Further, it was hoped that the study would show differences based on an entire population rather than those due to sexual dimorphism. Initially, crayfish of all sizes were measured but those below a postorbital length of 20.0 mm. were finally excluded when very high correlation coefficients were found in most of the characters used with increasing size. Much of this allometry was eliminated or reduced when only the larger crayfish were used. Ideally crayfish of one size should be used but this was not possible with these species since so few have ever been collected. Undoubtedly, this would eliminate many of the extremes in the ranges of the various characters.

Qualitative

Color notes were taken on all crayfish. Shape and number of spines and tubercles on the chela, carpus and merus were recorded as

well as the shape of the chela including thickness and curvature of the fingers, serrations and setation. The shape of the rostrum, epistome, postorbital ridges and suborbital angles were also noted. Differences in the shape of the first pair of pleopods in from I males were noted as were any variations in the annulus ventralis of females.

Statistical Procedures

Data are expressed after the method of Hubbs and Hubbs (1953) for presenting statistical analysis. Each sample mean ($\bar{X}$) is indicated by a vertical line with one standard error of the mean ($\sigma\bar{X}$) on either side of the mean, represented by the shaded portions of the bar. The unshaded portions of the bar represent one standard deviation (σ) on either side of the mean. The range for the sample is shown by the lower horizontal line. Populations of less than four specimens have only the mean and range shown. The number in each sample is included in parenthesis on the graph. Two examples from different localities in the same county are indicated by small letters.

Presentation of data in this manner allows for easy comparison of different samples and for easy evaluation of the dispersion and reliability about a mean. One standard deviation on either side of the mean includes about 84 percent of the population. Thus, when the open bars for two populations just meet, there is an 84 percent separation between the two populations for the character being considered. Eighty-four percent is considered adequate for subspecific separation by most investigators (Hubbs and Hubbs, 1953). Significance

of differences between populations was determined by the Student's t test. Statistical procedures were carried out on a Compucorp Model 145E Statistician calculator and on a SCM Merchant Cogito 240 SR calculator provided by the Departments of Zoology and Ecology at The University of Tennessee.

III. LIFE HISTORY AND ECOLOGICAL INVESTIGATION

Color and Morphological Changes

Specimens of all sizes, sexual form, and sex, both hatched in the laboratory and collected in the field, were maintained under uniform conditions for the length of the study in order to evaluate the effects of the environment on the variations in color and morphology evident in different populations. Both C. dubius and C. carolinus, representing different populations, were kept in transparent or opaque plastic cages measuring from 18 to 20 cm. wide and from 28.5 to 31 cm. long. Normal tap water was maintained in each cage at a depth of approximately 2.0 cm. depending on size. Temperatures of the water taken periodically throughout the year, varied from a low of 17.8°C to a high of 27.2°C with a mean of 22.6°C. A bivalve mollusk shell was provided in each cage to allow the crayfish access to the atmosphere. They were then checked one or more times each week and any changes were recorded.

Development and Rearing of Young

C. dubius females in berry were collected and maintained as described above. After the eggs hatched and the offspring were

independant, they were transferred to larger metal containers. Crushed rock was placed on the bottom, in addition to the shell, to provide additional escape cover. After approximately six months, these young crayfish were separated and raised individually as described above.

Growth and Sexual Maturity

Young C. dubius which were hatched in the laboratory as well as very small, spring hatched juveniles were raised in the laboratory and measurements taken during various stages of growth over a period of 18 months. Molts were recorded and sexual maturity of males recorded with the molt from form II to form I. Sexual maturity in females was indicated by the maturation of the cement or glair glands according to Stevens, 1952, and Yonge, 1937.

Ecology

Food preference in Cambarus dubius was studied by placing various types of food with the crayfish and recording the time required to consume the food. Uneaten material was removed after a period of a week. Burrow construction was observed primarily in the field since no satisfactory method of constructing a burrowing chamber could be found. Difficulties involved facilities for providing a constant supply of clear, fresh water and limitations of space and building materials. Laboratory observations were, therefore, limited to the manner in which construction of burrows was accomplished. Subjects were placed in an aerated aquarium filled with clean sand and behavior recorded.

CHAPTER III

RESULTS AND DISCUSSION

I. GEOGRAPHIC VARIATION

Morphological Characters

The geographic variation of Cambarus dubius populations ranging from western Pennsylvania and Maryland south through West Virginia, Kentucky and Virginia to Tennessee and North Carolina, presents a complex problem. Populations from different regions and even from different localities in an area may appear quite different from one another to varying degrees. However, there has never been any apparent way of separating these regional populations. Hobbs (1969) and Hobbs and Bouchard (in press) have indicated the possibility of one or more undescribed species in this group. One of the difficulties has been the lack of good series of specimens from any one locality together with the lack of collections from many areas so that it is difficult to determine whether populations represent local variants or a more distinct group. One of the principle objectives of this study was to determine if any of these different populations of C. dubius in Tennessee could be separated using measurements based on this morphological variation, together with qualitative differences. Originally, only populations from Tennessee were compared, but is was soon evident that with many of the headwaters of Tennessee rivers lying in Kentucky, Virginia and North Carolina, only a partial and biased picture might result from examining specimens only from Tennessee

since intergrades would not be taken into consideration if they existed. For this reason measurements were taken on as much material as possible in surrounding states. It was hoped that measurements might help determine whether morphologically different populations from different areas represented clines or microgeographic races of one species or two or more subspecies, or perhaps, species.

Because of the variability within even individuals from a single locality regarding shape of the epistome and number of spines on the ventral surface of the merus these characters were not evaluated quantitatively. However, it was noted that populations in the Allegheny Mountains in eastern West Virginia often possessed only two or three spines on the outer row of the merus which probably indicates a strong relationship with C. monongalensis. These populations should probably be considered in the synonomy of C. dubius, at present, for the purpose of taxonomic stability.

Another character which showed too much variability to be used was the number of spines and tubercles on the dorsal and medial side of the carpus. Most specimens measured has one to several tubercles in addition to two or more spines. The notable exception was the population from the region of the type locality, since they possessed only one internal median spine and lack tubercles on the carpus, with rare exception.

Variation also existed in the development of the suborbital angle, from practically obsolete to well developed. In general, populations in western portions of the range had a more pronounced suborbital angle than those in eastern portions. General carapace

shape varied from somewhat vaulted to ovate to slightly dorso-ventrally compressed. Although specimens from a particular locality possessed the same carapace shape, those from nearby localities were sometimes different. The shape of the carapace seldom could be correlated either with type of habitat or geographic region. As pointed out by Hobbs (1969), the primary burrowers found in clay substrates at lower elevations where water is usually more stagnant and oxygen supply low, have carapaces somewhat compressed or ovate, while crayfish found in headwaters of cool, swift streams at higher elevations possess carapaces slightly dorso-ventrally compressed with wider areolas. This was found to be generally true for C. dubius populations as well, but there were many exceptions in different regions.

The rostrum was quite variable from one locality to the next and varied somewhat within populations. The rostrum was short and broad with subparallel margins and strongly convergent angles in populations from Preston County, West Virginia northward and again in populations from Knox and Roane County, Tennessee (Figure 2, b,h). Very narrow rostrums were present in specimens from certain localities from Morgan County, Tennessee, Bell County, Kentucky, and Lee County, Virginia. Individuals from this last locality had the rostrum sharply pointed with little angle, similar to the rostrum of C. d. diogenes Girard (Girard 1852:88). Rostrums from populations in southwest West Virginia were often short and rounded with thick margins while populations from Carter County, Tennessee and Mitchell County, North Carolina (Figure 2 d) had wide, relatively long rostrums with gently converging margins and thin edges. Those from Cumberland County, Tennessee

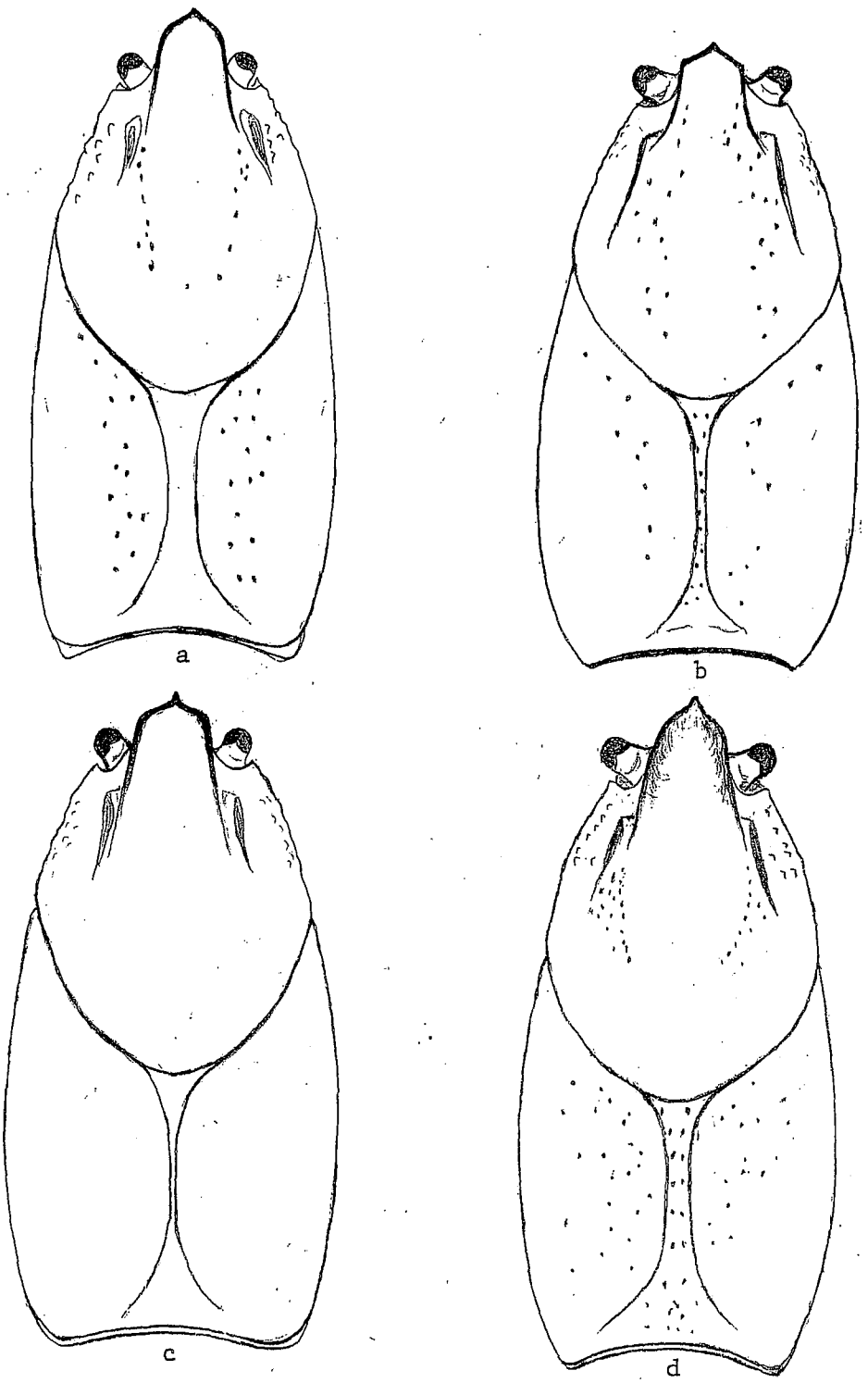

Figure 2. Dorsal aspects of carapaces of Cambarus carolinus and Cambarus dubius. a, C. carolinus, Elkmont, Sevier County, Tennessee; b, C. dubius, Terra Alta, Preston County, West Virginia; c, C. dubius, Pressmans Home, Hawkins County, Tennessee; d, C. dubius, Roane Mountain, Mitchell County, North Carolina.

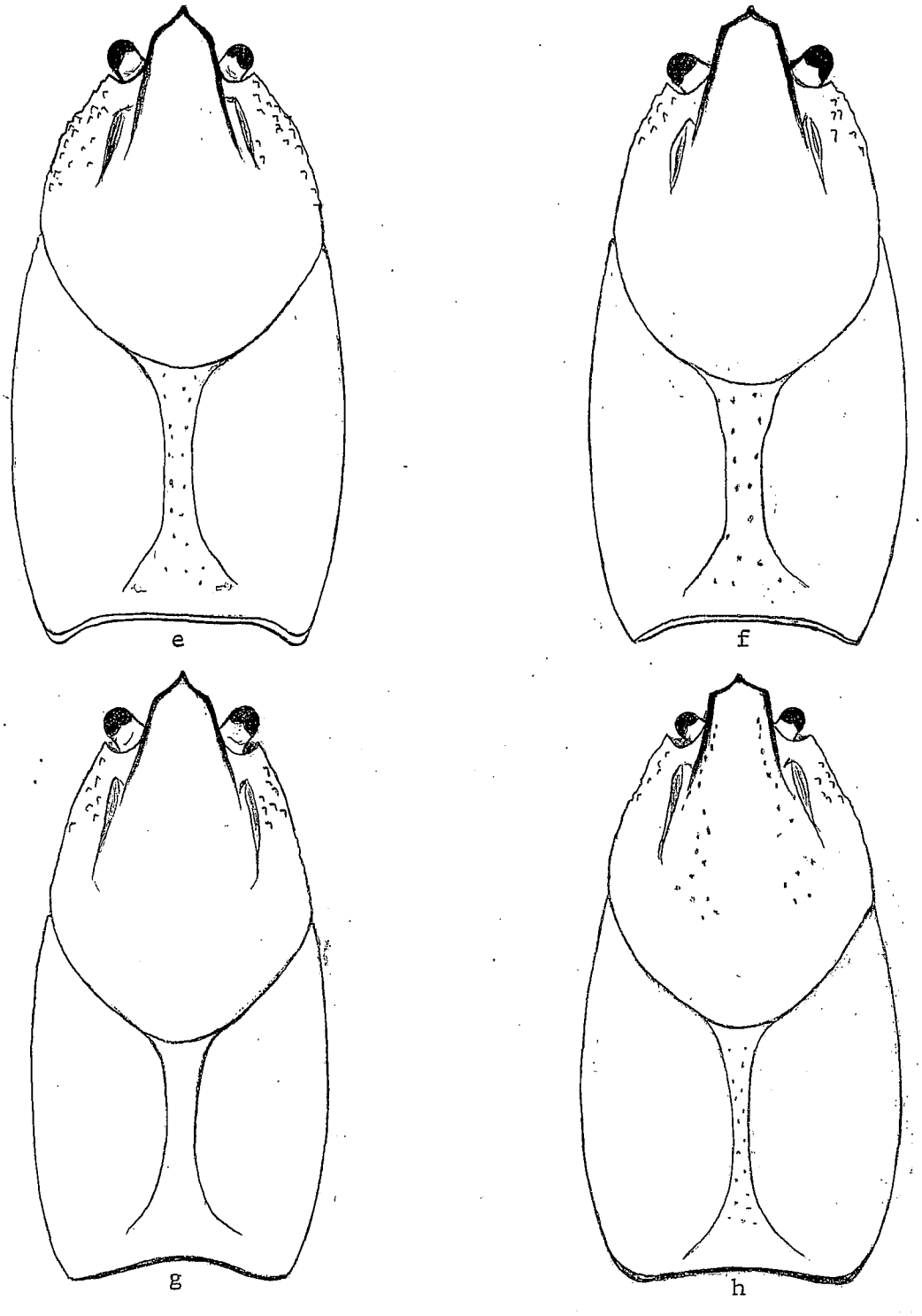

Figure 2 (continued). e, C. dubius, Strunk, McCreary County, Kentucky; f, C. dubius, Clear Creek, Anderson County, Tennessee; g, C. dubius, Pleasant Hill, Cumberland County, Tennessee; h, C. dubius, Hickory Creek, Knox County, Tennessee.

(Figure 2 g) and McCreary County, Kentucky (Figure 2 e) also had rostrums with gently converging margins, somewhat intermediate with those from the last three localities given. Again, there did not appear to be a strong correlation in Tennessee or elsewhere, with any particular habitat and rostrum shape or length, although it was usually shorter and broader in populations at lower elevations burrowing in clay or other fine substrate.

Some interesting variations existed between the pleopods of C. dubius populations in various regions. C. dubius from the type locality and north into Pennsylvania, had the central projection with a very reduced but distinct subapical notch. Careful examination of the pleopod is required or this notch may be overlooked (Figure 1 b, page 7). Populations of C. dubius from the region of Giles County, Virginia, had a more sharply downcurved mesial process and central projection (Figure 1 c). This sharp angle in the central projection was also found in specimens from southern West Virginia (Figure 1 d). A very large mesial process, at an angle of approximately 115° to the main axis of the pleopod, was found in form I males from Smyth County, Virginia, Carter County, Tennessee, and Avery County, North Carolina (Figure 1 k,l). Specimens from the Ridge and Valley Province in Tennessee, typically had the central projection recurved about 115° from the main axis and had a long tapering mesial process at right angles to the axis of the pleopod (Figure 1 j). Form I males from the Powell River and lower Clinch River systems and west, generally had the central projection and mesial process curved to varying degrees (Figure 1 e,h,i), as did form I males from southeastern Kentucky

(Figure 1 g, page 7). Although trends in pleopod shapes were evident in Tennessee, clear separation by this character was not possible since intermediate types were occasionally observed.

Areola width was one of the more variable characters between different populations. Populations of C. dubius in the Ridge and Valley Province of Tennessee and southern Virginia, east of the Clinch River where it joins the Powell, had uniformly narrower areolas with the exception of populations from Carter County, Tennessee (Figure 2 c,d,h, page 21). Populations from the lower Clinch River and to the west, had comparatively wide areolas (Figure 2 e,f,g). Examination of specimens from Kentucky, Virginia, North Carolina, and West Virginia, indicated that areola width was regionally and locally more variable than initially thought, and although there were definite trends, there was no way to separate the populations of these regions satisfactorily by areola width (Figure 3). Populations from the Ridge and Valley in Tennessee and Virginia, burrowing in clay substrates, generally had narrow areolas, while those from populations west of the lower Clinch River, burrowing in a variety of substrates ranging from clay and loam to chert and rocky gravel, had wider areolas. All C. dubius populations from the Cumberland Plateau in Tennessee had wide areolas regardless of altitude or substrate. The population from Clear Creek below Norris Dam (Clinch River) in Anderson County, Tennessee, at about 900 feet elevation (311 meters), had the widest areolas (mean ratio of 6.95) and most dorso-ventrally compressed carapaces of any population measured regardless of altitude or substrate (Figure 2 f, and Figure 3). Populations slightly to the north in Union

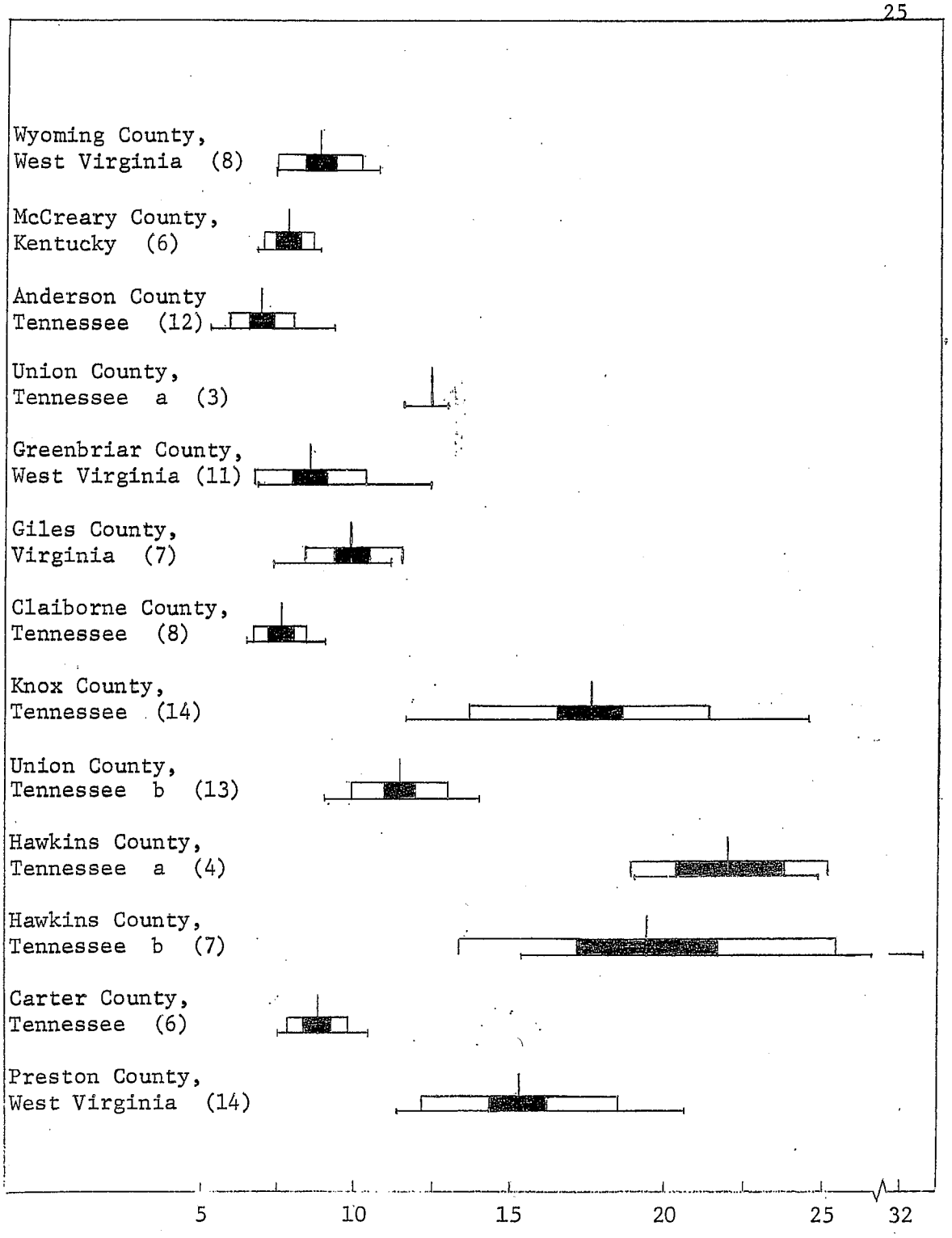

Figure 3. Areola length to width, expressed as percent of postorbital length in Cambarus dubius. (See text for explanation of symbols).

and Claiborne Counties, Tennessee, had narrower areolas (mean ratios of 11.48 and 7.67, respectively), although the altitude and substrate were similar at approximately 1,050 feet (334 meters) above sea level. Populations from the Blue Ridge Province, Carter County, Tennessee, and neighboring Mitchell County, North Carolina, had moderately wide areolas with a mean ratio of 8.85, although they were collected from both rocky gravel and clay substrates at elevations of 3,520 to 4,000 feet (1,154 to 1,311 meters). Specimens from Preston County, West Virginia (Figure 2 b, page 21) had narrow areolas (mean ratio of 15.36) although they also inhabited a clay substrate at moderately high altitudes of about 2,560 feet (840 meters). The population from Sullivan County, Tennessee, at an elevation of 1,740 feet (574 meters), had areola widths similar to populations in Knox County, Tennessee (Figure 2 h), at elevations of just over 800 feet (262 meters).

In order to evaluate the effects of environmental factors on this variation found, young were hatched and specimens of all age groups were maintained under uniform conditions. After 18 months, there was no measureable difference from the original populations. Therefore it is concluded that morphological variation, including areola width, is genetically controlled rather than directly induced by environmental factors. There is the possibility that the induction occurs early in the development of the egg. To ascertain this possibility, C. dubius specimens from various areas would have to be conceived, hatched, and raised under uniform conditions. The variation existing between different populations is best explained by the greater

adaptation of C. dubius in different regions, for a burrowing existence regardless of altitude, substrate or other factors.

Increase in the ratio of areola length to standard length, like a narrow areola is a measure of adaptation to a hypogean existence (Hobbs 1969). While no significant differences were found between the various populations of C. dubius, a slight correlation can be seen (Figure 4), between the ratio of areola length to width and the ratio of areola length to postorbital length. Populations of C. dubius, in the Ridge and Valley Province of Tennessee, east of the lower Clinch River (Figure 4), have both the highest ratio of areola length to width and ratio of areola length to postorbital carapace length. The population from Carter County, Tennessee and Mitchell County, North Carolina in the Blue Ridge Province, had the lowest mean of any of the samples, expressing agreement with the wider areola found in this population. Among populations outside Tennessee, little variation was found for this character, although the mean for the Preston County, West Virginia sample was higher. The ratio was similar to those of populations of C. dubius from the Ridge and Valley Province of Tennessee.

The subgenus Jugicambarus, to which C. carolinus and C. dubius are assigned, derives its name from the presence of a single crest-like ridge of tubercles along the mesial surface of the palm of the chela (Hobbs 1969). The chela presents one of the most perplexing problems among the various populations of C. dubius. A great deal of variability exists in the shape, size and ornamentation of the chela among different populations and for this reason the chela was selected

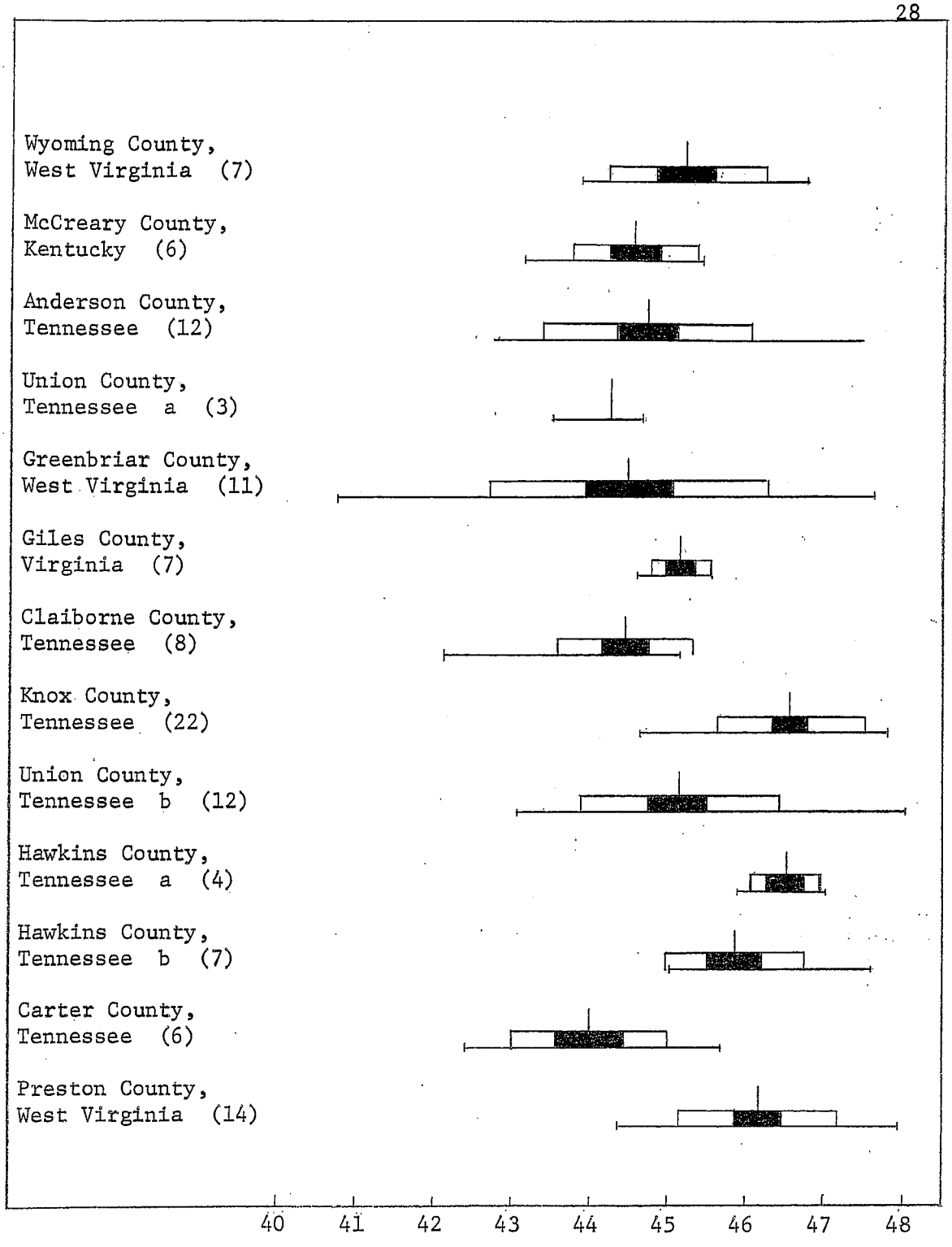

Figure 4. Areola length to postorbital carapace length, expressed as percent postorbital length in Cambarus dubius. (See text for explanation of symbols).

for use in separating various groups. The disadvantage in using chela measurements is the risk involved of including data from specimens with regenerated chela which are abnormal in size and shape. Much of the variation encountered within a sample can be attributed to size differences of the specimens, since the measurements involved were allometrically related to changes in body size. This was minimized by using specimens measuring 20.0 mm. or more in postorbital carapace length.

All of the C. carolinus examined displayed the typical subrectangular Jugicambarus chela (Figure 5 a). Although a similar type of chela was found in C. dubius specimens from Giles County, Virginia and Cumberland County, Tennessee (Figure 5 c), many variations were found. Often, a weak second row of two to four tubercles was found next to the mesial row (Figure 5 d). The mesial row itself varied from cristate (Figure 5 a,c,f), to strongly serrate with gaps between serrations (Figure 5 g). The chela of C. dubius from Carter County, Tennessee and Mitchell County, North Carolina, had a very low, reduced row of tubercles on the mesial surface (Figure 5 h). Overall shape of the chela varied from subrectangular to rounded with thick, curved fingers (Figure 5 e). The length of the inner margin of the palm also varied as did the width of the palm. Some of the similarities and differences between various populations of C. dubius and C. carolinus can be seen in Figure 5.

The graph in Figure 6, which expresses the ratio of the length of the inner margin of the palm to width of the palm, indicates the degree of rectangularity of the palm and overall chela. The higher

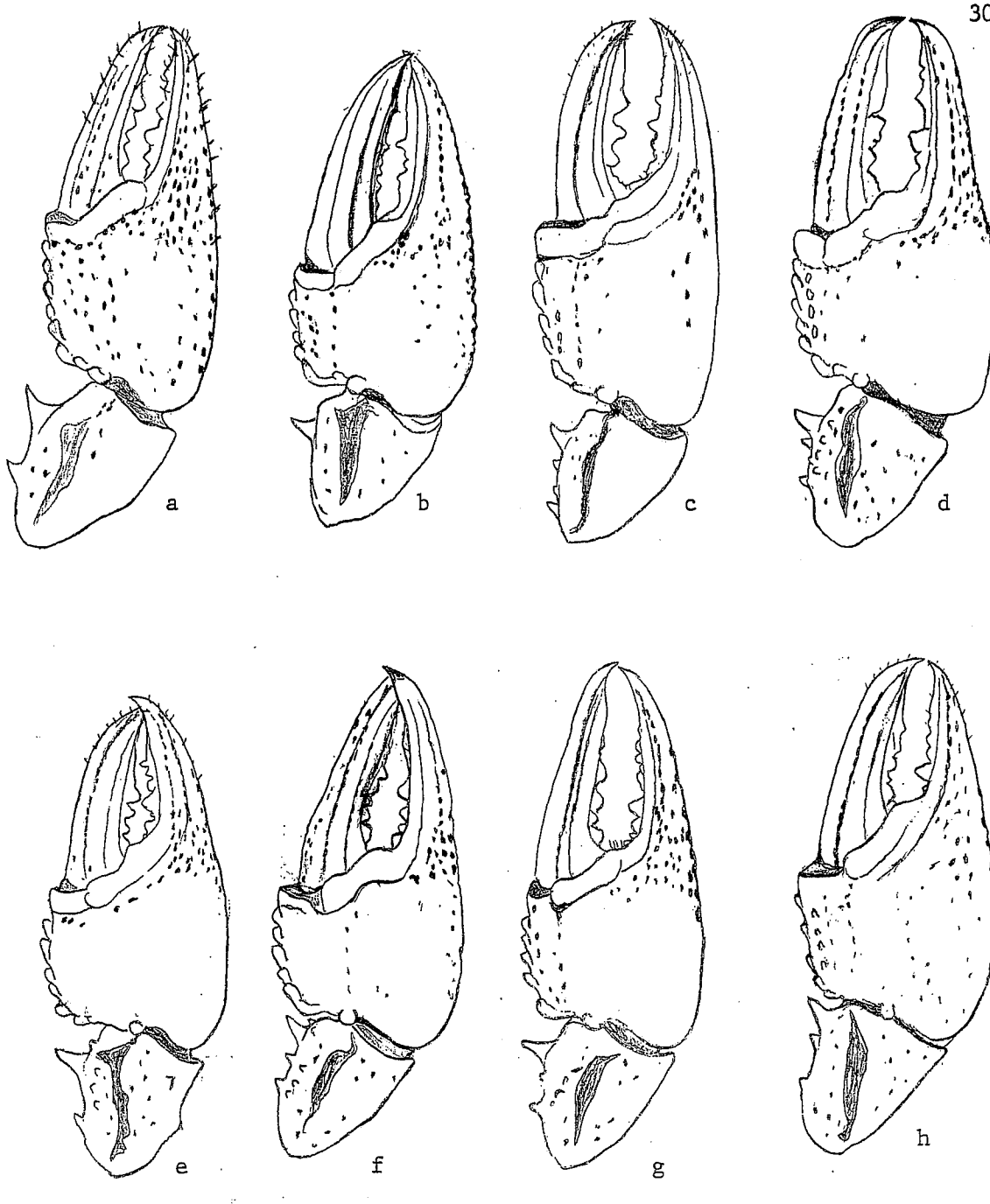

Figure 5. Dorsal view of the chelae of Cambarus carolinus and Cambarus dubius. a, C. carolinus, Elkmont, Sevier County, Tennessee; b, C. dubius, Terra Alta, Preston County, West Virginia; c, C. dubius, Pleasant Hill, Cumberland County, Tennessee; d, C. dubius, Strunk, McCreary County, Kentucky; e, C. dubius, Clear Creek, Anderson County, Tennessee; f, C. dubius, Bullrun Creek, Union County, Tennessee; g, C. dubius, Pressmans Home, Hawkins County, Tennessee; h, C. dubius, Roane Mountain, Mitchell County, North Carolina.

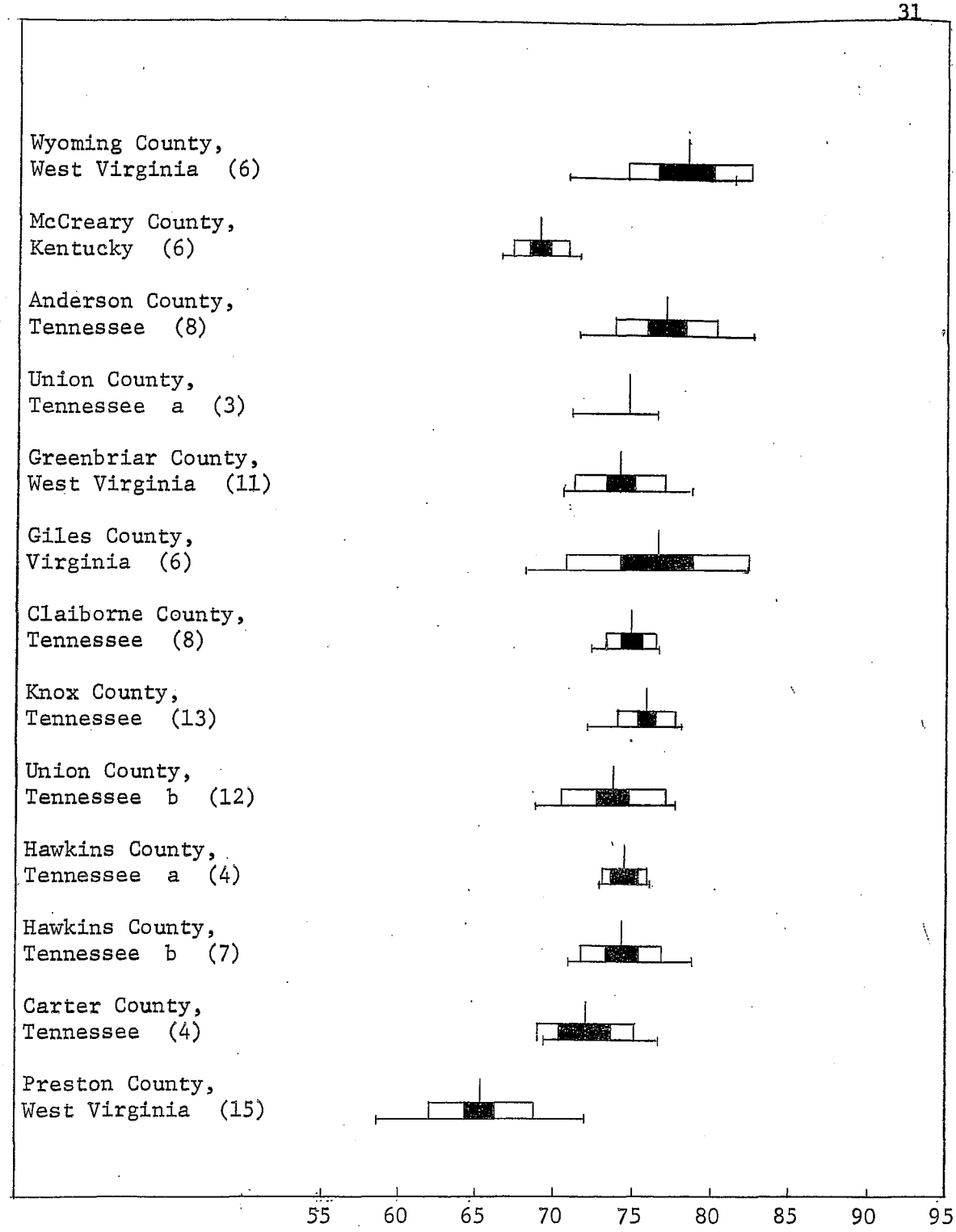

Figure 6. Length of the inner margin of the palm to width of the palm, expressed as percent postorbital length in Cambarus dubius. (See text for explanation of symbols).

this ratio the more rectangular the chela. Two populations of C. dubius deviated from the sample norm. The palm of specimens from Preston County, West Virginia, had the shortest inner margin in relation to chela width. Another population (McCreary County, Kentucky), also had a relatively short inner margin to palm width. No populations of C. dubius were found in geographically intermediate areas with intermediate ratios. However, occasional individuals were found both in Kentucky and south toward the Clinch River in Tennessee, which had ratios approaching those from McCreary County, Kentucky.

A fourth measurement involved the ratio of the width of the chela to postorbital carapace length. The graph in Figure 7, shows that the means of two C. dubius samples stand out again. The group which had the narrowest chela in relation to carapace length was the population from Preston County, West Virginia. Overlap occuring with two other samples is misleading since the region of overlap involves small individuals from very samll samples. The mean of the samples is a more reliable point of reference for this reason. Since the palm of the Preston County, West Virginia population of C. dubius was not very long (see Figure 6), this indicates overall small size of the palm. The population from near Strunk, McCreary County, Kentucky, had the widest chela of any group, most unlike the C. dubius population from Preston County, in contrast to the previous character. Although the Kentucky population from McCreary County was distinct, the sample was too small to determine if it merely represented a variant or a more distinct group. Individuals were found in Russell and Lee Counties in Virginia, Morgan County, Tennessee, and from several other counties

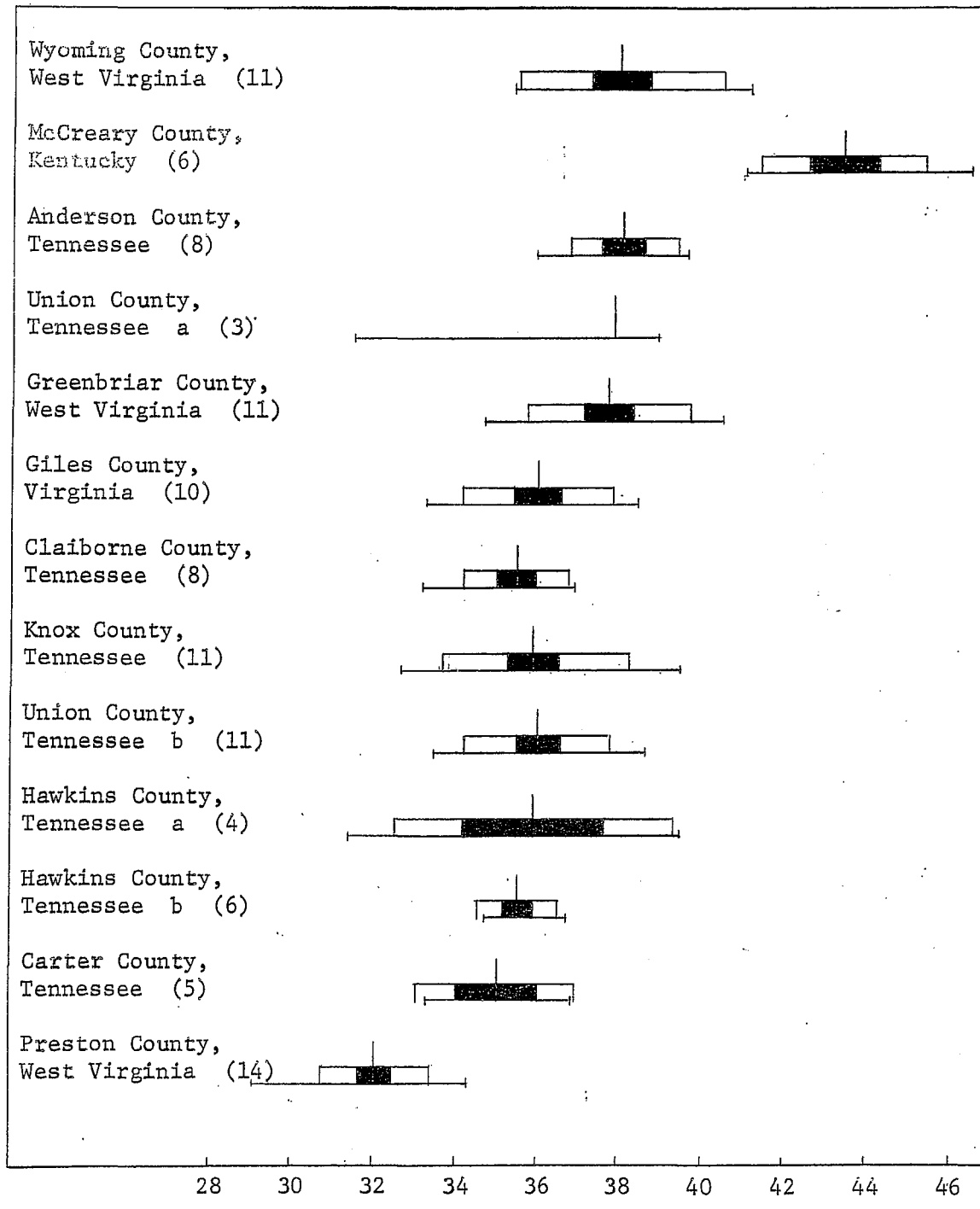

Figure 7. Width of the chela to postorbital carapace length, expressed as percent postorbital length in Cambarus dubius. (See text for explanation of symbols).

in southeastern Kentucky, which approached and occasionally overlapped with the McCreary County, Kentucky population, indicating clinal variation. One would expect these wide chela to be associated with populations of C. dubius with the greatest adaptations for burrowing but this was not found. The populations with the widest chela had the wider areolas with the exception of populations from Carter County, Tennessee, and Mitchell County, North Carolina.

Variations in length of the chela were measured by determining the ratio of the length of the outer margin of the chela to the postorbital carapace length. As seen in Figure 8, this character was variable within populations of C. dubius and overlap between samples was considerable. Again, allometry accounts for some of this overlap. The only sample with clear separation was that from Preston County, West Virginia, which had uniformly, short chela. The population of C. dubius from McCreary County, Kentucky, had the highest mean which, together with previous measurements, reflected the largest chela in both length and width.

As with the previous measurement, populations of C. dubius from on or near the Cumberland and Allegheny Plateaus had slightly higher ratios of length of the inner margin of the palm to postorbital carapace length. There was much overlap between the different samples but, again, the population of C. dubius from Preston County, West Virginia is clearly separate from the other groups. The population from McCreary County, Kentucky had the second highest mean of all the samples. Thus, this group had a relatively long inner margin (see Figure 9), but since the ratio of the inner margin to width of

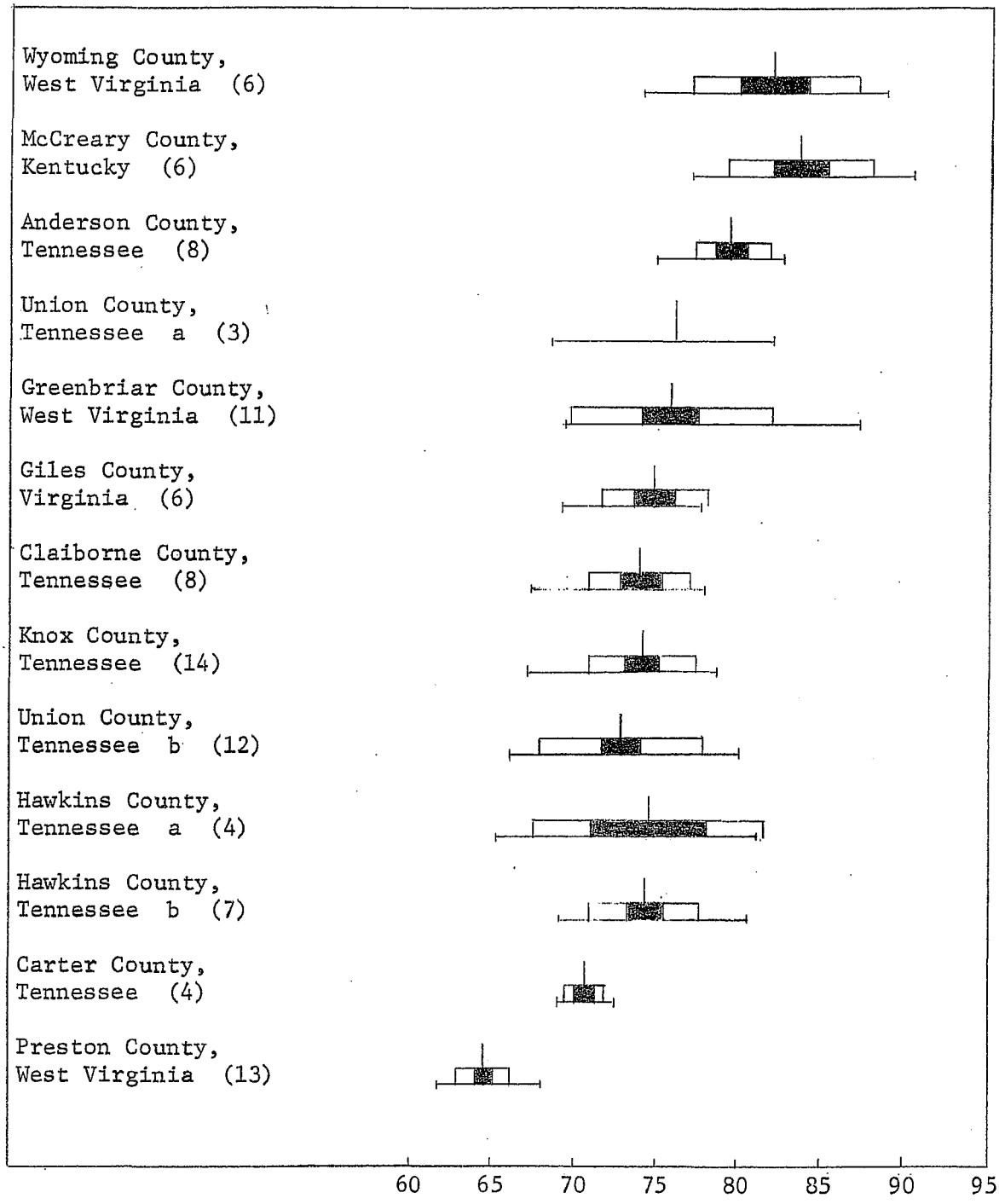

Figure 8. Length of the outer margin of the chela to post-orbital carapace length, expressed as percent postorbital length in Cambarus dubius. (See text for explanation of symbols).

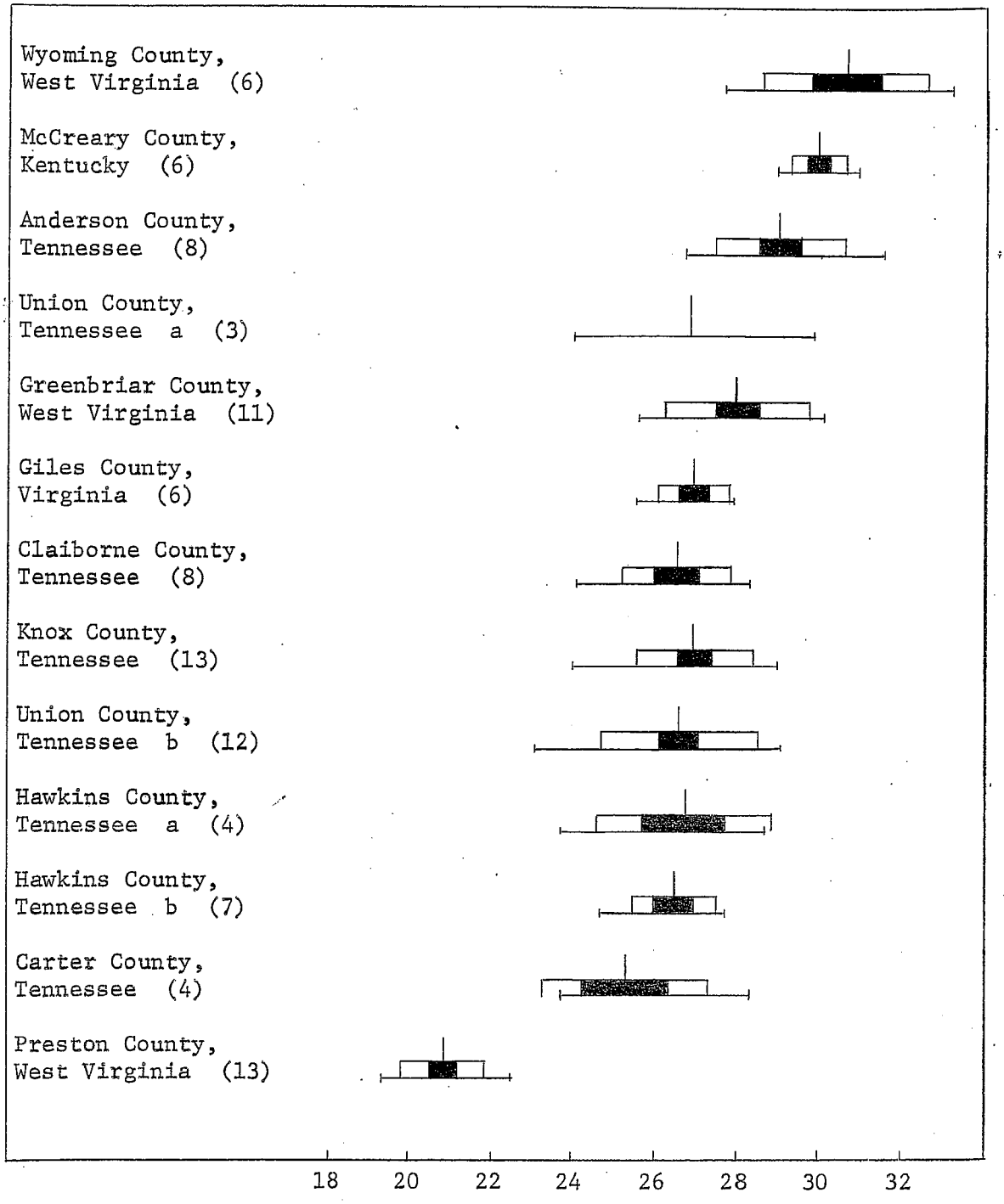

Figure 9. Length of the inner margin of the palm to postorbital carapace length, expressed as percent postorbital length in Cambarus dubius. (See text for explanation of symbols).

the palm of this population was among the lowest, the long inner margin to postorbital carapace length reflected a large rather than sub-rectangular chela.

Although there was not clear separation of any Tennessee populations of C. dubius based on the quantitative measurements of the chela and others previously discussed, three clines, or possibly subspecies were indicated; one in the Ridge and Valley Province, one to the west from the junction of the Powell and Clinch Rivers southward and west on the Cumberland Plateau, with a third in northern areas of the Blue Ridge Province. Further investigation should be conducted to properly evaluate these three populations. The population east of the Clinch River had slightly shorter chela and more slender fingers with less curvature than populations near and on the Cumberland Plateau, in addition to lower ratios of chela width to postorbital length already mentioned. C. dubius from the Blue Ridge Province had the smallest chela of any Tennessee populations as evidenced by the lowest means for all the chela measurements. The chela of this population were less flattened and had only a low subserrate row of tubercles on the mesial border of the palm. C. dubius from Preston County, West Virginia had chelae distinctly different from populations to the south. This group had evolved the most advanced chela with respect to burrowing habits, as indicated by the overall shortening and flattening of the chela, the shortness of the inner margin of the palm, the presence of but a single row of tubercles on the inner margin of the palm, and the loss of all spines and tubercles from the carpus, except the internal median.

Finally, a comparison was made to evaluate the differences in the characters between populations of C. dubius from the region of Preston County, West Virginia northward and C. dubius populations to the south of this region. The data on localities consisting of three or more specimens were combined for the southern group to obtain sufficient numbers for comparison. The purpose of comparing various populations from many different localities was first, to determine if the two populations of C. dubius still maintained the differences which were indicated earlier, over large areas. The second objective was to compare measurements of C. carolinus with those of C. dubius to determine if the two species could be separated on the basis of these measurements. Finally, it was hoped that a better understanding might be gained to the evolutionary adaptations for burrowing in the three populations.

C. dubius from Preston County, West Virginia and northward was clearly separate from C. carolinus in the five characters measured (Figures 10, 11, 12, 13, and 14). These characters included: a) ratio of length of inner margin to width palm, b) ratio of width of palm to postorbital length, c) ratio of the inner margin of the palm to postorbital length, d) ratio of the length of the chela to postorbital length, and e) ratio of areola length to postorbital length. The two populations of C. dubius overlap in length of areola (Figure 10), which is expected in two advanced burrowing groups. Nevertheless, the mean is higher for the northern population. There is clear separation between the two groups for the four remaining characters. Differences between northern and southern populations of C. dubius were tested with the Student's t test. A 99 percent confidence interval was

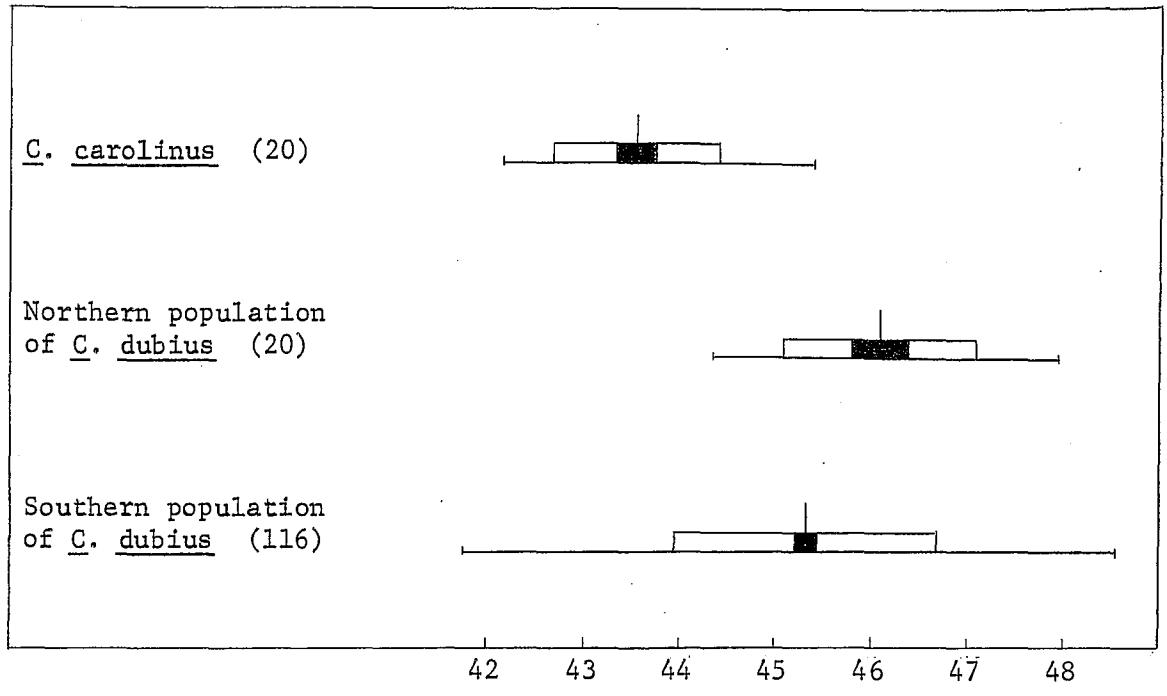

Figure 10. Length areola to postorbital carapace length, expressed as percent postorbital length for combined populations. (See text for explanation of symbols).

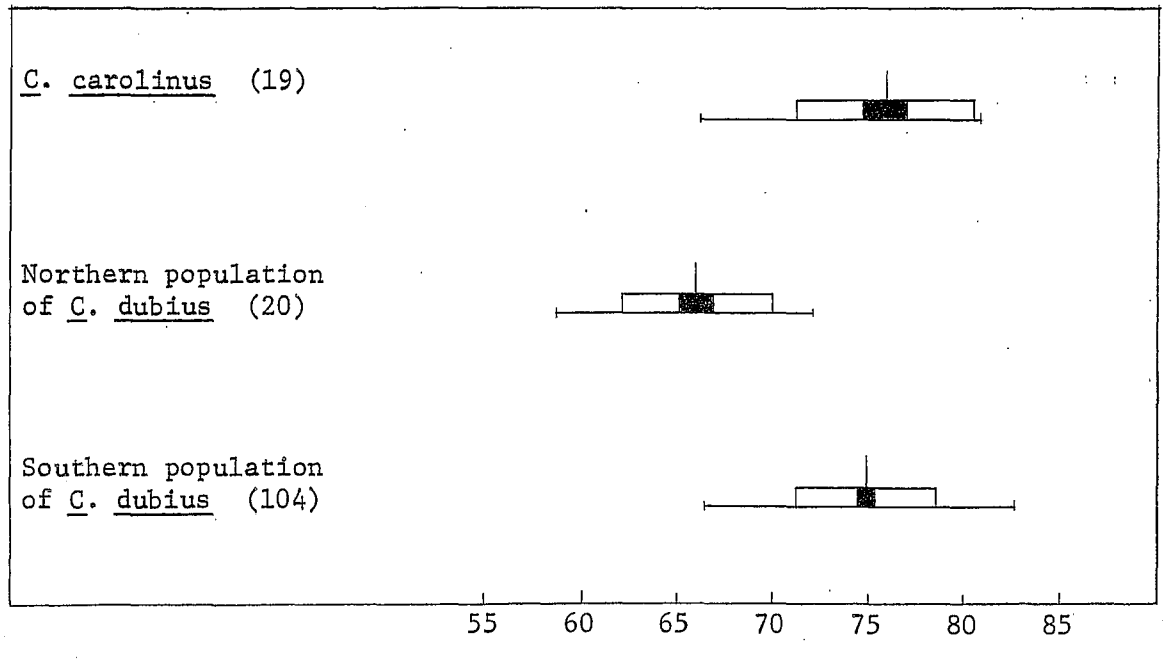

Figure 11. Length inner margin palm to width palm, expressed as percent postorbital length for combined population. (See text for explanation of symbols).

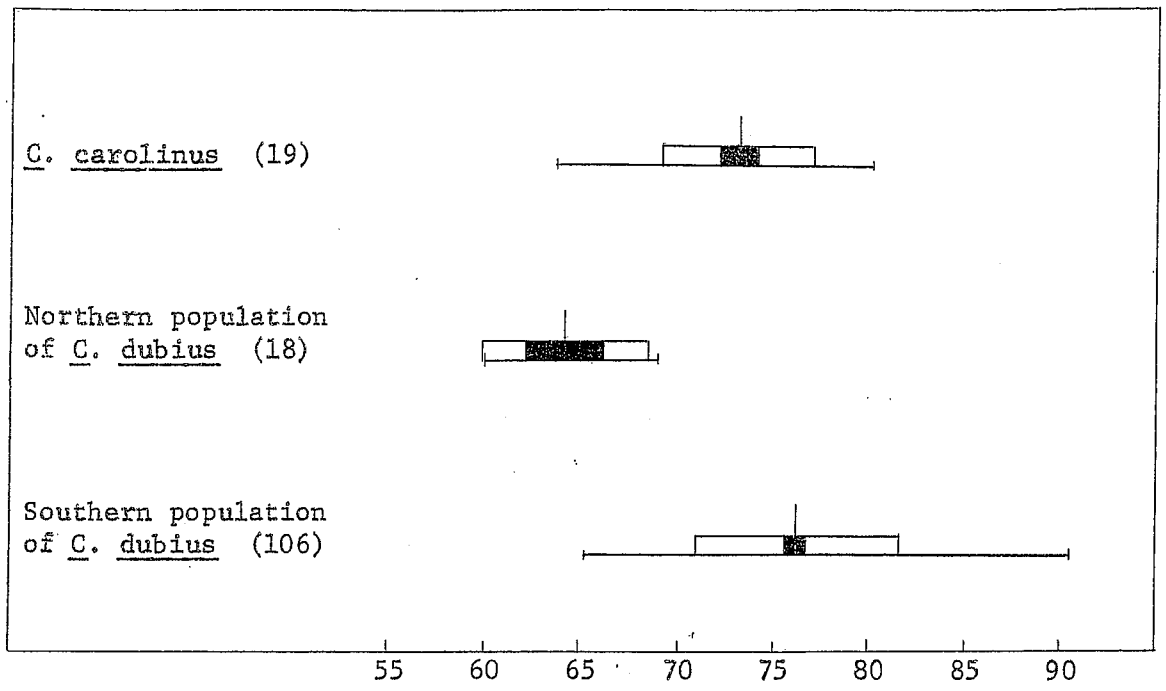

Figure 12. Length outer margin chela to postorbital carapace length, expressed as percent postorbital length, for combined populations. (See text for explanation of symbols).

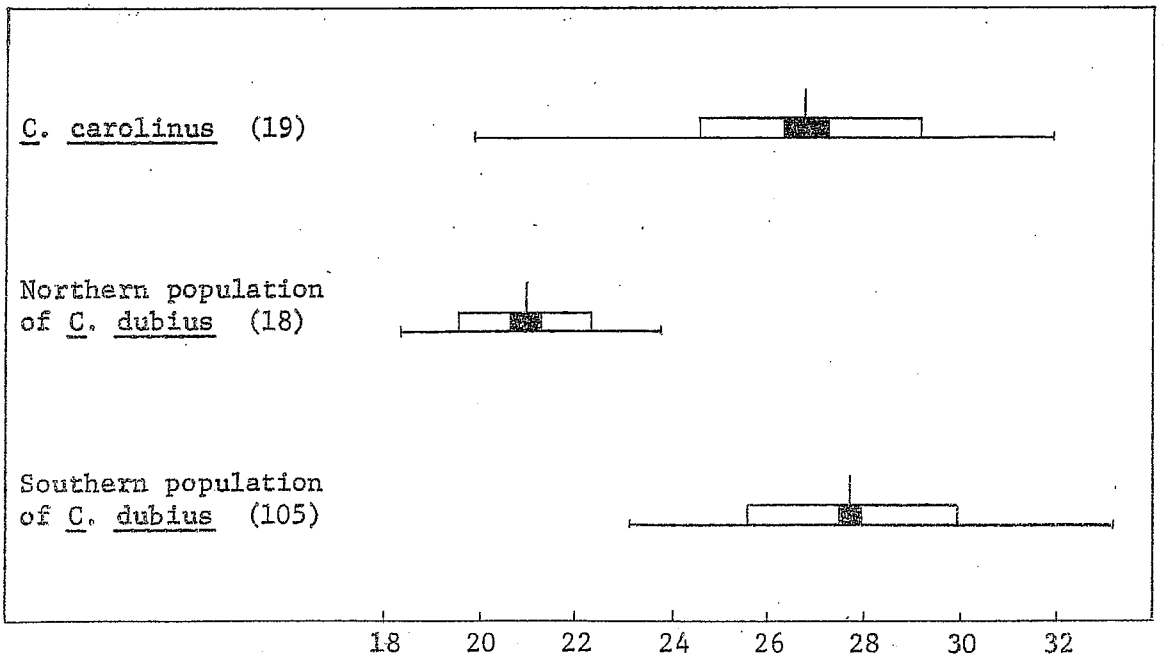

Figure 13. Length inner margin palm to postorbital carapace length, expressed as percent postorbital length, for combined populations. (See text for explanation of symbols).

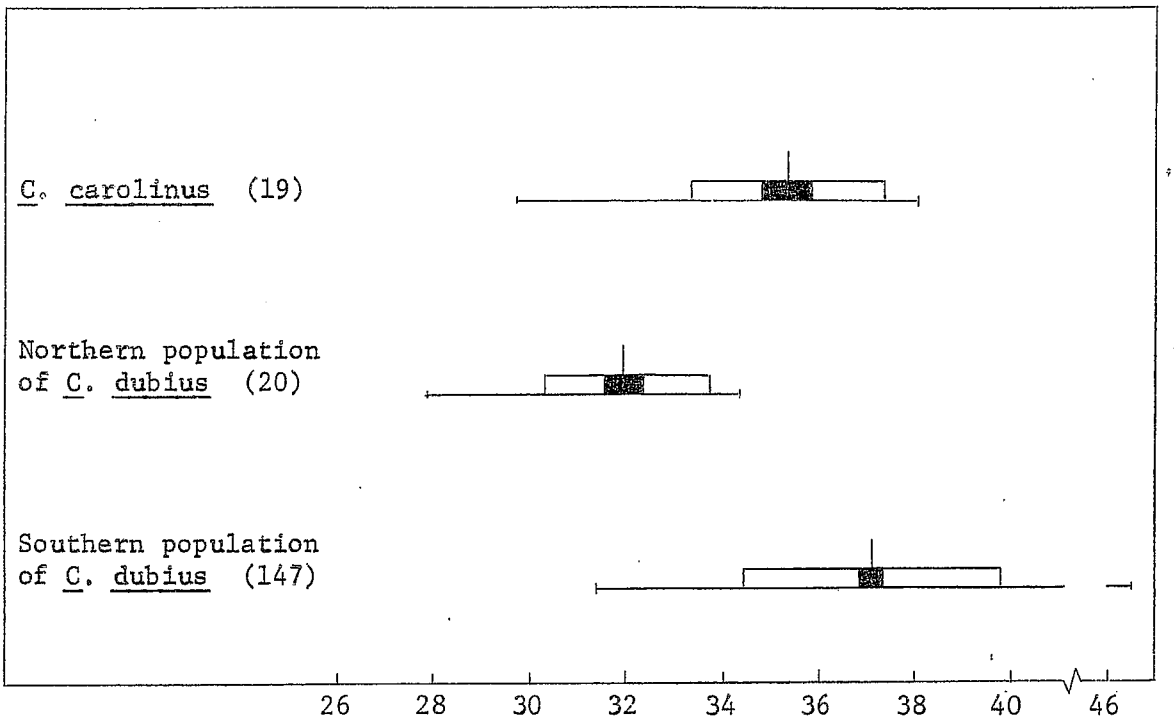

Figure 14. Width of the palm to postorbital carapace length, expressed as percent postorbital length, for combined populations. (See text for explanation of symbols).

calculated using the standard statistical formula

$$C.\ I. = \bar{X} \pm t_{0.01} (\sigma\bar{X})$$

with 2 degrees freedom (Dixon and Massey 1957). The t_{table} values ranged from 2.552 to 2.583 and $t_{calculated}$ values ranged from 3.3 to 24.71 indicating significant differences at the 0.01 level (effect of $\alpha \cong .05$) for all five characters.

The measurements of C. carolinus overlapped considerably with southern populations of C. dubius. The only character in which C. carolinus differed from both C. dubius populations was the lower ratio of areola length to postorbital carapace length, but even here there was overlap. Therefore, it would be difficult to separate these two species based on the measurements used in this study. C. carolinus is best separated by the pleopods of form I males.

A comparison of the three groups indicated that the northern populations of C. dubius are the most advanced burrowers. The chelae are the most shortened both in total length and in length of inner margin of the palm. Thus, the palm has lost the rectangularity typical of C. carolinus and of many of the southern populations of C. dubius. The northern populations of C. dubius also had the largest mean for areola length. While southern populations had relatively longer areolas and a slightly smaller ratio of length of inner margin palm to width palm, the length of both the outer margin of the chela and the length of the inner margin of the palm was larger than it was for C. carolinus. Thus C. carolinus appears to have made slightly

greater adaptations with the chela while southern populations of C. dubius have made greater burrowing adaptations with the carapace.

In conclusion, it should be stated that although there were significant differences between two regional populations of C. dubius, an intermediate area remains between the two which may have intergrades, although none have been found to date. Further collections from this region would clear up that possibility.

Color

Color patterns are quite variable among primary burrowers and this is especially true of populations of C. dubius and to a lesser extent in C. carolinus. Populations of these two species undoubtedly include the most brilliantly colored crayfish in the Southern Appalachians. No sexual dimorphism was found in either color pattern or brilliance.

C. carolinus in eastern Tennessee and adjacent western North Carolina, were a bright red-orange to orange shading to paler tones toward ventral areas. The abdominal terga were often a darker brick-red while the rostrum was bordered with dark brown or black pigmentation. Juveniles and young were usually entirely pale orange. Occasionally, specimens were collected which were a light brown shading to pale orange ventrally. One of these brown specimens, a form II male, molted into the typical red-orange coloration. Since this molt was into another from II, the red color did not seem to be associated with sexual maturity. Several other immature crayfish, although orange when collected, molted into a pale grey-blue and orange with orange ventrally.

However, most crayfish did not change color, even after several molts, under laboratory conditions. The pH of the water was lower in localities where C. carolinus was collected than in Knoxville. Therefore, an increase in various ion concentrations associated with increased pH, may have accounted for this color change in certain individuals.

Various populations of C. dubius have many different color patterns and, although generally uniform within a single population, there may be color phases. C. dubius from the type locality and north was always a red-orange to orange. Several females from Preston County, West Virginia were pale orange dorsally, shading to white laterally and ventrally. From this region northward, no other color has ever been reported for C. dubius. Populations, currently ascribed to this species, maintain this coloration as far south as the southern border of West Virginia, and into adjacent Virginia, in the southwest part of the state as far as the Clinch River in Russell County. In the Southwestern corner of Virginia, along the Kentucky border, blue coloration appears in both states. Only blue colors have been reported from Lee, Scott, Smyth, and Washington Counties, Virginia. From this region, south into North Carolina and Tennessee, the color is always blue. Red-brown and tan colors begin to appear at the Clinch River south and west of the region where it is joined by the Powell River.

This blue varied from a deep blue-black to purple and brilliant sky-blue with the distal tips of the chelae pigmented white or pale yellow to bright red-orange. The sides and ventral regions were generally white or pale blue. C. dubius from Carter County, Tennessee

and Mitchell County, North Carolina, was usually a slatey blue-grey with white or blue-grey on the tips of the chela and white on the ventral regions. Populations of C. dubius from Knox and Roane Counties, Tennessee, were medium blue to dark lavender dorsally with bright blue legs and chelae. Bright orange was found on the tips of the fingers as well as bordering the rostrum, spines, and tubercles. Ventral regions were white. A few individuals had pale yellow or white on the tips of the chela. Other populations from Scott County, Virginia and Union County, Tennessee were dark blue dorsally with pale orange or yellow over much of the chelipeds and ventral regions. Most of the spines and the tubercles were similarly colored. Populations of C. dubius from the Powell River system in Claiborne County, Tennessee and Lee County, Virginia, had very dark blue carapaces, abdomens, and legs, with bright orange-red fingers, spines, tubercles, and rostrum margins. Similarly colored blue specimens have been reported from the same locality with orange specimens in Virginia, but this orange phase was not found in any Tennessee populations of C. dubius.

In the lower Clinch River where it joins the Powell River and to the west on the Cumberland Plateau, the color changes from blue to predominantly red-brown or lavender-brown with light, bright blue legs. Light blue was also present on the chelipeds and rostrum. Tips of the fingers and edges of the rostrum were orange as were many of the spines and tubercles. Ventral regions were white. Populations of C. dubius to the south in Union, Morgan and Anderson Counties, Tennessee, were often a drab tan or brown dorsally, with the chelipeds and legs only faintly colored a pale blue. The tips

of the fingers, spines, and tubercles were also very pale in color. Specimens from localities near the Clinch River in Anderson and Union Counties, west to Fentress County, Tennessee and north to McCreary County, Kentucky, were typically a red to red-brown dorsally with light blue legs and chela, gradually changing to white ventrally. This red lacked any of the orange tones found in the populations of C. dubius from West Virginia and Virginia. Sometimes more than one color was observed within a single population. Completely blue specimens were collected from a locality near Strunk, McCreary County, Kentucky and from Clear Creek, Anderson County, Tennessee. Specimens from Clear Creek, while usually red-brown with blue legs as described above, occasionally, were pale lavender, pale blue, blue-green or predominately red. One lavender female had dark green pigmentation anterior to the cervical groove, blue legs and orange fingers, spines and tubercles.

A C. dubius female from the headwaters of the Caney Fork River, Cumberland County, Tennessee, was a drab, dark, blue-grey dorsally with grey-blue chela and legs. Ventral regions, tubercles and spines were pale orange, similar to colors often seen in stream-dwelling crayfish like Cambarus parvoculus Hobbs and Shoup (Hobbs and Shoup, 1947:142) and Cambarus bartonii (Fabricius) (Fabricius, 1798:407). This color pattern together with the more primitive burrowing characters possessed by this population, indicate that it may be the most similar in appearance to the ancestral stock of C. dubius and supports evidence for the Cumberland Plateau as the ancestral home of this species (Hobbs 1969).

One may only speculate why such varied color patterns have evolved in this species. Since primary burrowers such as C. dubius,

are nocturnal or are seldom, if ever, exposed to direct light, bright color patterns, which probably evolved randomly, would not be selected against, since there would be no disadvantage in possessing them. This, of course would not be true of stream inhabiting crayfish which would be more readily spotted by predators. Although C. dubius populations from most regions were uniformly colored, specimens from some areas, especially around the Clinch River system, may have a variety of color phases with all shades in between. This suggests, along with laboratory evidence, that the color is determined genetically and is not environmentally induced. Adults, as well as juveniles, maintained for as long as 18 months, retained the color patterns of the populations when they were originally collected, regardless of locality. It is concluded, therefore, that these color patterns have evolved in different burrowing stocks of C. dubius and the appearance of color phases indicates either a recombination of color genes from various gene pools, or incomplete separation of a genetic stock which possesses several color genes.

Colors are somewhat variable within all populations and this is noticeable throughout the molt cycle. Recently molted individuals are frequently very pale and not their brightest until the carapace is well hardened. Just before molting, the entire exoskeleton, in C. dubius specimens with some blue pigment, often becomes a deeper, more intense blue. Thus, freshly molted individuals, possessing both blue and red pigments, may gradually turn from red to almost blue again just before molting.

It is often difficult to determine what the color is with much accuracy in species such as C. dubius when they are first collected, as they are frequently encrusted with dirt particles so that they may appear black or brown like the substrate where they were collected.

II. DISTRIBUTION

Cambarus Dubius

C. dubius was described by Faxon (1884) as a mountain crayfish from the Appalachian Mountain region of Virginia and West Virginia, and Ortmann (1905 a, 1906), subsequently gave the range at elevations from 1,070 to 2,000 feet in swampy ground in and near cool springs on the top of hills with a substratus of stiff clay but not going above or below these elevations. C. dubius was referred to as an inhabitant beside cold mountain streams under rocks by Newcombe (1929 b). According to Ortmann (1906), C. dubius migrated from the south, postglacially, and this migration was halted, temporarily, by two different barriers. The first was the deep erosion of valley by the headwaters of the Conemaugh River in Pennsylvania, resulting in the lack of suitable burrowing habitat. The second barrier was formed by a cross divide of the longitudinal valley between the Chestnut and Laurel Hill Ridges. From this region of southern Pennsylvania, the range extends south through the Allegheny Mountains in West Virginia and onto the Allegheny Plateau in Southwestern West Virginia. In Kentucky, the range extends from the Allegheny Mountains in the east to the Cumberland Plateau south into Tennessee

(Figure 15). From here, the range extends east across the Ridge and Valley Province of Tennessee and southern Virginia to the Blue Ridge Province in east Tennessee and into western North Carolina as far south as McDowell County, at the edge of the Piedmont Plateau (Catawba River drainage).

One would expect the range of this species to extend further south in North Carolina and in Tennessee than has been found (Figure 16). Collections throughout eastern Tennessee to the mountains and into western North Carolina have not revealed populations in any areas to the south of the Nolichucky River in Tennessee. This seems peculiar since C. dubius is well established in the Allegheny Mountains north of Tennessee all the way to Pennsylvania. In Tennessee, C. dubius was found from Carter and Sullivan Counties in the northeast corner of the state, west across the Ridge and Valley Province south to the mouth of the Clinch River in Knox and Roane Counties. A few localities have been found in drainages of the Tennessee River Embayment (Fort Loudon Lake), in Knox County, but no localities further south of this river have ever been found. C. dubius was searched for in Loudon, Monroe, Meiggs, McMinn, Rhea, and Cumberland Counties west to Waldon's Ridge with no success, although favorable habitat was present.

C. dubius was fairly widespread on the Cumberland Plateau, in Tennessee from the northeast, south to the Emory River in Morgan County. The range extended west on the Plateau to the headwaters of western tributaries to the South Fork of the Cumberland River in Fentress County, and to the headwaters of the Caney Fork River on the western edge of the Plateau, in Cumberland County. No localities further south on the Cumberland Plateau have been reported which seems

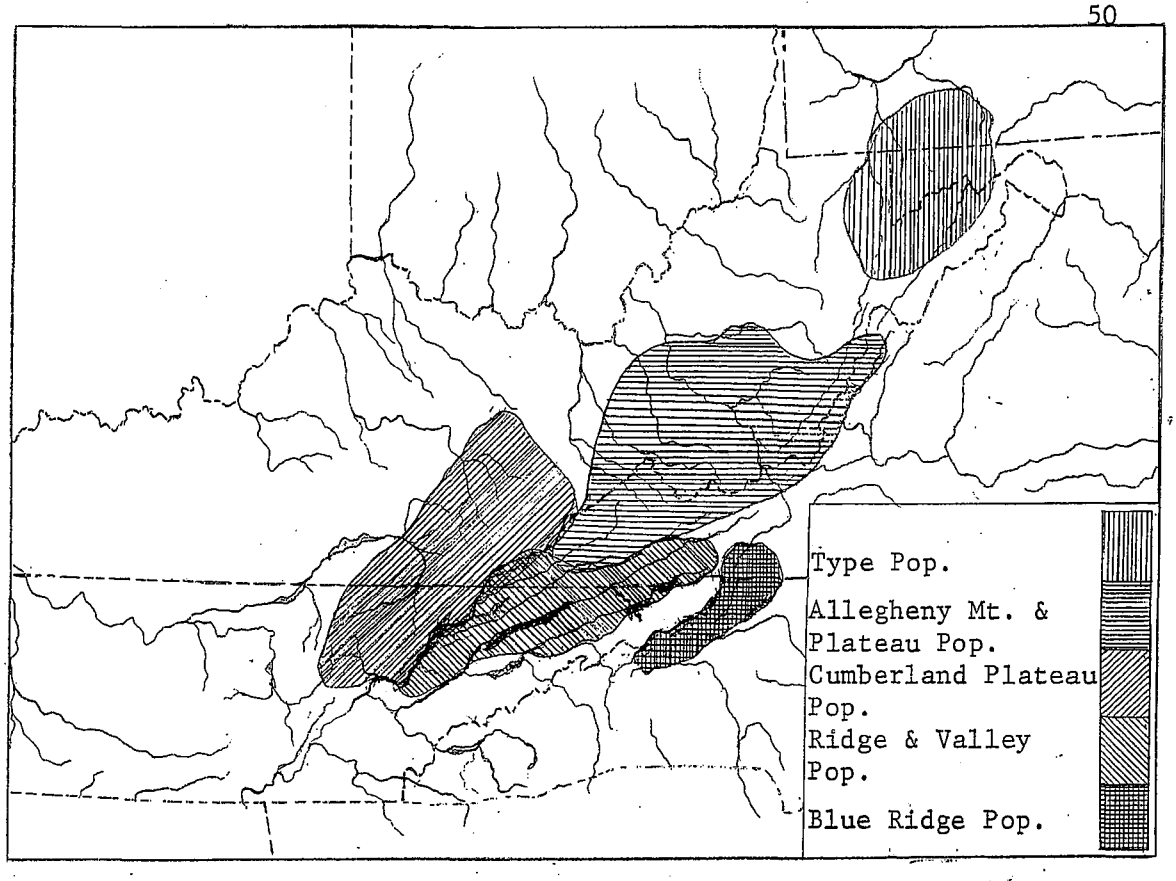

Figure 15. Distribution of Cambarus dubius.

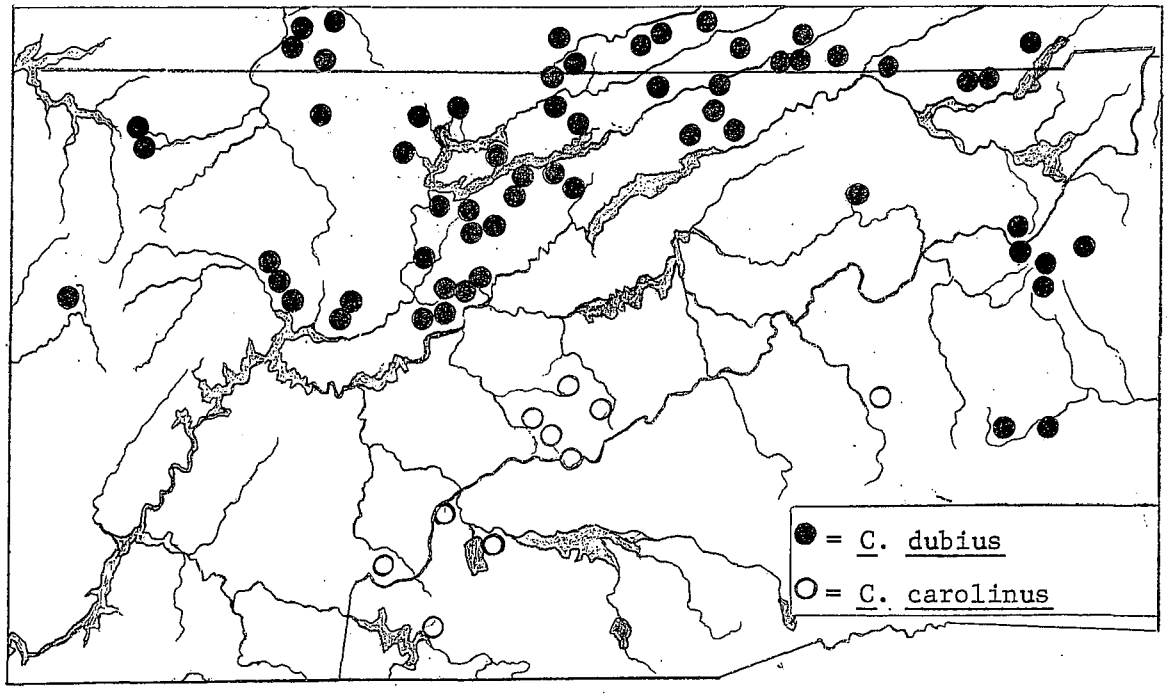

Figure 16. Localities for Cambarus carolinus and C. dubius in Tennessee and adjacent areas.

surprising since it is well known that C. dubius is capable of walking about over land on rainy or moist nights for extended periods (Ortmann 1913 and Hobbs, Hart and Walton 1967), and thus is not restricted to particular drainage systems as other species are apt to be. More thorough collecting of this area may extend the known range of C. dubius further south, perhaps as far as northern Alabama and northwestern Georgia.

High altitudes did not seem to be a major limiting factor to C. dubius, since it has been collected from altitudes of 4,500 feet (1,475 meters) in West Virginia, although localities were generally found at elevations ranging from 800 to 4,000 feet (262 to 1,311 meters) in Tennessee. C. dubius did not appear to be limited to any particular substrate, as it was collected in clay, loam, chert, gravel and rocks. Neither did the underlying bedrock in the range of C. dubius appear to be very important since these include several varieties including crystaline rocks with extensive areas of mica schists in the Blue Ridge Province, dating from the Precambrian in age (Hack 1969). Northwest of the Blue Ridge, the rocks are of sedimentary origin and are layered and folded or faulted. The less resistant rocks form valleys or lowlands, while the more resistant rocks form mountains and plateaus. Carbonate rocks and shales of Cambrian and Ordovician ages define the outlines of the Ridge and Valley Province, while the Cumberland Plateau and Allegheny Plateau are underlain with resistant sandstones.

Type of vegetation did not appear to restrict distribution, as localities included marsh vegetation, grass, pasture and forests

of various types including mixed mesophytic, northern hardwood, oak-hickory-pine and Appalachian oak.

One of the possibilities which exist to explain the limit to the distribution of C. dubius is that in many areas the substrate is porus and many of the streams dry up completely during the summer months to substantial depths below the surface, thus preventing successful migration into these areas. In addition to many of the headwater streams drying up, those remaining at lower elevations are often sluggish, warm and turbid (conditions unfavorable to this cool headwater inhabitant).

Biological barriers may also be responsible for limiting the range southward in east Tennessee. At lower elevations, around 800 feet in the Tennessee Valley, several primary burrowers are found which probably compete with C. dubius. C. d. diogenes has been collected from the same localities with C. dubius in Knox and Roane Counties and one or more undescribed members of the subgenus Depressicambarus are found in habitats which otherwise seem favorable to C. dubius. Although C. d. diogenes is generally found at lower elevations along streams or marshy groundwater habitats, it has also been taken from cold, spring seeps in Knox County, and from higher elevations (approximately 1,300 feet on Hatcher Mountain, Sevier County, Tennessee). Competition from these more advanced burrowers may prevent C. dubius from extending its range further southward and into some of the lower elevations. C. dubius has been collected with C. parvoculus and C. bartonii and although they are not primary burrowers and would not compete for living space, C. bartonii, for

instance, is well established throughout the streams in the Appalachian system and populations of this species may somehow interfere with the migration of C. dubius into the southern Appalachians. Another possibility is that evolutionarily, C. dubius has just begun to reach this area. Evidence indicates (Hobbs 1969) that the ancestors of C. dubius stocks arose somewhere in the headwaters of the Cumberland Plateau. From here, they may have migrated north into the Allegheny Mountains from the northeastern edge of the Cumberland Plateau and crossed the ridges in southern Virginia, by headwater stream migration across the Great Valley to the Blue Ridge where, in Virginia, the Valley consists of a single gap at its narrowest point (Ross 1969). From here, populations may have migrated into the mountains of western North Carolina and eastern Tennessee, with this migration still incomplete. Other populations may have extended their range eastward across the Ridge and Valley Province and may eventually reach the southern Appalachians in this manner. This would also explain some of the similarities found in populations from Virginia, western North Carolina and eastern Tennessee (Carter County), and differences between these populations and those from lower elevations of the Ridge and Valley Province. The Nolichucky and other river barriers may have prevented the successful migration of C. dubius further south into the Appalachian mountains (at least in Tennessee) as it has been searched for unsuccessfully.

Cambarus Carolinus

In Tennessee C. carolinus was restricted to cold and rocky,

gravel, sand, or loamy mica springs and seeps in the Blue Ridge Province south of the French Broad River. Vegetation of the habitat included northern hardwood and Appalachian oak forests. Hemlocks (Tsuga canadensis) were often present. The range probably extends through North Carolina into Georgia and South Carolina where habitat is favorable. C. carolinus was collected near the highest ridges in the Appalachian system. One locality was found on the Tennessee-North Carolina divide at Double Springs Gap just south of Clingman's Dome (5,500 feet elevation), in Sevier County, Tennessee. Although this species did not appear to be limited by high elevations, it was not found anywhere in Tennessee at the lower elevations at the edge of the mountains or in the larger valleys between the ridges, such as Cades and Tuckaleechee Coves, Blount County, or Wear and Emerts Coves, Sevier County, Tennessee. Northern migration was apparently prevented by the French Broad River which flows east to west through the mountains. The distribution of C. carolinus within these mountains was very spotty and it was absent from many favorable habitats. C. bartonii may likewise prevent C. carolinus from extending its range since it was often the only species collected in seeps where C. carolinus would be expected. C. bartonii was the only other crayfish associated in the same habitat with C. carolinus.

III. ECOLOGY

Habitat and Burrowing

Cambarus dubius, like other primary burrowers, completes the life cycle within the burrow system (Hobbs 1969). Occasionally,

specimens have been collected in streams or under rocks at the edge of streams or on dry land. Burrows constructed by this species varied from relatively simple excavations under rocks along streams to deep, complex burrows interconnected with those of other members of the colony, often some distance from open water. These burrows often extended vertically four feet or more beneath the surface well below the water table. Occasionally, the burrow consisted of only a single opening, but usually there were at least two which joined a short distance below the surface. One to several side branches, running parallel to the surface, were often found where the two vertical tunnels met. From these side branches, one to several burrows extended downward, and there were frequently blind side chambers, which were slightly enlarged. Usually, C. dubius specimens were captured here, since it was very difficult and time consuming to dissect out a crayfish which had descended to the deeper regions of its burrow. Frequently, some tunnels of the burrow were closed or sealed with clay or mud. The walls of the burrows are cylindrical and firmly packed so that they offered resistance even in soft clay and could be felt even after the tunnel had been sealed off with mud. C. dubius burrowing in rocky substrate, invariably positioned the burrow against and under large rocks and were, consequently, the most difficult to obtain. How extensive or interconnected the burrows between members of a colony are is not known. Several individuals were taken from different regions of the same burrow, including males and females, ovigerous females and males, and two or more females with young and juveniles

of all ages. Males probably visit and mate with females in the burrows but this has not been observed.

The depth of water in the burrows varied with the particular area and the season. In the spring or after periods of heavy rain, water was often observed flowing from the burrows into headwater streams. Water depth or pressure was apparently regulated to some degree by C. dubius since, when the burrow walls were broken into, water often gushed out of the burrow. They maintained the level of water in their burrows along creeks as well, often several feet above surface water during dry weather. When these burrows were broken into from the side, large amounts of water often rushed out. Unlike some of the Depressicambarus burrowers, C. dubius was found near cool, flowing water and not in marshy groundwater habitats which may become warm and stagnant. However, some of these small headwater seeps and streams did dry up completely at the surface during the driest parts of the summer.

Like other primary burrowers, C. dubius produced chimneys of various shapes and sizes depending on weather, substrate and other factors. Little evidence of chimney building was found in rocky or sandy substrates or after heavy rains. When conditions were favorable, chimneys were often elaborate cylindrical structures several inches high, but sometimes were merely random piles of mud heaped toward one side of the burrow entrance. When a burrow had two openings, one usually had a chimney and was used in discarding loose mud and other debris from the burrow. The other opening usually did not have a chimney. During certain periods one or both openings may be capped

or plugged with mud. If this mud seal was removed, it was usually replaced within a day or two, indicating some purpose for its presence. A C. dubius female with young of various sizes was found in a burrow which had a sealed chimney (Harris 1903), so perhaps the seal serves to prevent predators from detecting and entering the burrow. During cold weather, this seal might serve to protect the crayfish from low temperatures and help to conserve water or prevent temperatures from rising in hot weather. The design of the chimney, itself, would tend to prevent the flow of mud and other debris into the burrow during heavy winds or rain.

Burrowing behavior of C. dubius was not observed in the field or at the surface of the burrow either at night or during the day under a variety of weather conditions. In the laboratory, after investigating its surroundings, the crayfish soon selected a corner and attempted to dig a burrow, using the first three pairs of periopods and the third pair of maxillipeds. The third pair of periopods was used to investigate the substrate and if found satisfactory, the first two pairs were inserted. The chelipeds were brought together until they almost touched so that the chelipeds and first pair of walking legs held a clump of material pressed against the third pair of maxillipeds under the rostrum in a basket like fashion. With the remaining three pairs of legs the crayfish carried its "load" to the edge of the burrow and deposited it over the edge, then returned to repeat the process.

The presence of burrows was even less evident in C. carolinus colonies, due in part to the rocky seeps and steep slopes that this

species occupied in Tennessee. Where the ground was level and topsoil had accumulated, well constructed burrows were found which were similar in appearance to those of C. dubius.

Associates

Crayfish associates of C. dubius include only one primary burrower, C. d. diogenes, Girard, as far as is known. Crayfish found in burrows from the same locality with C. dubius included Cambarus sphenoides Hobbs (Hobbs, 1968 a:262), C. parvoculus, and C. bartonii. The only crayfish associated with C. carolinus was C. bartonii, as mentioned earlier. Salamanders and newts were often found at the burrow entrances of C. dubius in cool areas at higher elevations.

Associates found directly on C. dubius included the branchiobdellid worms; Bdellodrilus illuminatus (Moore), Cambarincola fallax (Hoffman) and Xironogiton instabilius, (Moore) plus the ostracods; Ascetocythere asceta, (Hobbs and Walton, Dactylocythere chalaza (Hobbs and Walton) and D. myura Hobbs and Walton (Hobbs, Holt and Walton 1967, and Hobbs and Walton 1970). A. asceta and D. chalaza have never been found on any other species of crayfish. The branchiobdellid worms are generally found at the posterior and lateral edges of the carapace, but are also found near the bases of the legs and anterior regions of the head. B. illuminatus inhabits the gills. Ostracods are usually concentrated among the setae of the gnathal appendages and setiferous portions of the abdomen. One mating pair was found attached to the eyestalk. The burrows of C. dubius may be important resevoirs for

aquatic organisms such as isopods, amphipods and other aquatic invertebrates which do not produce resting eggs during the driest periods of the summer when surface water is not present in certain types of microhabitats.

Food Habits

Little is known regarding food habits of C. dubius or C. carolinus. Limited food preference tests under laboratory conditions indicated C. dubius is an omniverous scavenger as similarly reported for other species, including C. bartonii (Chidester 1908, 1912). They ate a variety of aquatic and marsh plants as well as many types of grasses. In the month of November, a burrow in the mountains of southwest Virginia was found to contain a large number of leaves from various hardwoods, indicating that they may store food in the winter months, at least in colder regions. This species was reported by Ortmann (1905 a) to cause considerable damage in Pennsylvania by feeding on growing crops. C. dubius did not attack and kill healthy aquatic organisms including tadpoles, snails and newts. However, dead organisms were readily eaten. Live earthworms were by far the most preferred food and they were eagerly sought by most crayfish, which could detect their presence from a considerable distance in water.

The young and juveniles of C. dubius may be important in aquatic ecosystems as food for fish and other carnivores especially in cold, clear mountain streams where animal protein is limited.

IV. LIFE HISTORY OF CAMBARUS DUBIUS

Reproductive Cycle in the Male

Form I males were collected in Tennessee in the months of March, April, May, July and October with the greatest number captured in April and again in October. Throughout the entire range, form I males have been taken in all months except January and Feburary. Lack of collections during these two months is probably the main reason they have not been found. Under laboratory conditions, sexually immature males first molted into form I condition from the last two weeks of July to the last week in September. Most of these remained in form I until late spring or early summer (April to June) when they molted into form II. After three to four months, they again molted to form I. Although this could not be tested under field conditions, it is in agreement with field data and strongly suggests that C. dubius males undergo two molts annually, corresponding with the mating season.

Reproductive Cycle in the Female

Although it has never been observed in the field, mating in C. dubius, as with other members of the genus, is believed to occur in the fall and perhaps again in early spring. Ovigerous females have been collected in Tennessee only during May (May 2 to May 31), but have been collected in other states from April through July. However, young may occasionally be produced at other times of the year since young of various sizes were found from the same locality. For example, young from the type locality in the headwaters of the Youghiogheny River, from a single burrow complex containing two adult

females, contained one group which averaged seven mm. in total length while another averaged 24 mm.

The eggs of C. dubius varied from salmon or amber color in some populations to a brilliant orange-red in others. The eggs from three ovigerous females from Carter County, Tennessee and Mitchell County, North Carolina were a dark grey in color but these failed to develop so the color may have been due to some abnormality. Eggs from most localities measured about 2.0 mm. in diameter although some were as large as 2.6 mm.

The number of eggs carried per female ranged from 8 to 91 with a mean number of 34.2 eggs per female, based on a sample of 20. A slightly positive correlation coefficient (+.42) was found with increase in postorbital carapace length and number of eggs produced. The largest females sometimes had the fewest numbers of eggs, indicating that older C. dubius females may become less productive as they reach old age. The total number of eggs produced by C. dubius is low when compared with the figures for other species (Crocker and Barr 1968, Prins 1968, Tack 1941 and others) but, it is not unusual for broods to be smaller where protection of the offspring is provided by the parents after hatching so that survival of existing offspring is high.

The smallest C. dubius female found carrying eggs in Tennessee, had a postorbital length of 23.6 mm. (26.7 mm. standard length). The largest female had a postorbital length of 35.7 mm. (40.2 mm. standard length). Females generally underwent a molt after the young became independent. This usually occured within a month after the eggs hatched, but occasionally did not occur for as long as four months or

more. One female did not molt until 16 months after laying her eggs.

Development of Young

Early development of the eggs and instars of C. dubius was similar to descriptions for other species of Cambarus by other investigators including Andrews (1904), Prins (1968), Tack (1941), Van Deventer (1937), and others. Females constantly aerated the eggs with the abdomen extended but when disturbed, brought the abdomen forward protecting the eggs. The young crayfish remained closely attached to their mother for about one week at which point they began exploring their surroundings. When disturbed, they ran to their mother's pleopods for protection and if the mother was removed, the young would cling to each other forming a tight ball. This behavior ceased after about ten days when the young crayfish became independent. The period of dependence for C. dubius was shorter than described for other crayfish which may have been due in part to warmer temperatures under laboratory conditions (mean of 22.2° C).

It is not known how long young C. dubius normally stay with their mother in the burrows, but juveniles of all sizes have been collected with mature females indicating that they may remain until they have matured enough to fend for themselves and begin building their own burrows. Larger juveniles were sometimes found in small side burrows off the main burrows of the adults and this may explain the development of the complex network of interconnected burrows often found in this species. The young crayfish is already in an ideal habitat

and has simply to expand its burrow off that of its parent's, thus eliminating exposure to predators and the risk of not finding suitable habitat. However, many offspring do leave the protection of the burrow since they were found along stream banks with no burrows of adults in proximity.

Growth and Sexual Maturity

Five months after hatching, young C. dubius from eight females had a mean standard length of 13.7 mm. (ranges = 11.5 to 18.5 mm.). Males did not differ significnatly in size from females. Females from one group had a mean standard length of 12.9 mm. while males had a mean standard length of 13.5 mm. In another group, females had a mean standard length of 14.0 mm. and males, a mean standard length of 13.75 mm. The above figures are based on a sample of 59 specimens. Young C. dubius in the fall of their second year of growth, approximately 16 to 17 months old, had a mean postorbital length of 22.4 mm. (standard length = 24.5 mm.) based on a sample of 32. A range in postorbital length of 19.7 mm. to 28.3 mm. was found in the above group. Females were slightly larger than males, with a mean postorbital length of 22.6 mm. while that for males was 22.1 mm. Only one male from this group was sexually mature. This male molted into form I on July 27, 1972, with a postorbital length of 21.4 mm. (standard length = 24.1). This specimen was the smallest form I male observed in Tennessee. Three females from this group were judged to be sexually mature with the development of the cement glands. These females had postorbital lengths of 24.2, 26.7, and 28.3 mm. (standard lengths = 27.1, 30.0,

and 33.0 mm., respectively). Admittedly, figures for the above data are small and were not conducted under field conditions. Nevertheless, they do indicate that C. dubius probably does not reach sexual maturity until late in its second year of growth in Tennessee. The majority of both males and females of C. d. diogenes, of the same age and raised under identical conditions, had reached sexual maturity by mid-summer or about 14 to 15 months of age.

Longevity has never beed determined in C. dubius, but members of this species are probably longer lived than many epigean forms. The largest specimen observed was a female which had a postorbital length of 42.6 mm. (47.8 mm. standard length) and a total length of 89.5 mm. The largest male, a form I, measured 36.2 mm. in postorbital length (40.45 mm. = standard length) with a total length of 72.5 mm. Mean postorbital length for 147 adults over 20.0 mm. in length was 27.9 mm. This figure is probably somewhat lower than it should be due to the difficulty in obtaining the larger specimens, and therefore biased sampling.

V. LIFE HISTORY OF CAMBARUS CAROLINUS

Although the life history of C. carolinus is probably similar in most respects to that of C. dubius, very little can be stated with much accuracy since so few specimens have ever been collected. The only ovigerous female collected to date, was caught on June 7, 1927, and was carrying 32 eggs. This female had a postorbital length of 25.1 mm. (standard length = 27.7 mm.) with a total length of 59.5 mm.

Juveniles of various ages have been found during May, October and November. The largest female collected, which had numerous young in her burrow, had a postorbital length of 33.7 mm. (standard length = 37.5 mm.) and a total length of 71.5 mm. Form I males have been collected only during the month of October. The largest form I male had a postorbital length of 25.0 mm. (standard length = 28.0) with a total length of 53.0 mm. The smallest form I male had a postorbital length of 23.1 mm. (standard length = 25.0 mm.) and a total length of 51.5 mm. It should be kept in mind that the above figures apply only to the C. carolinus populations found in the Blue Ridge Province and do not apply to populations from the lower elevations near the type locality.

CHAPTER IV

SUMMARY

An investigation of the geographic variation in the primary burrowing crayfish, Cambarus dubius Faxon and C. carolinus (Erichson) was made throughout their ranges in Tennessee and neighboring areas. Field collections were made to obtain specimens for comparative purposes and to gain information regarding distribution, ecology and life history. This data was supplemented by the collection of several museums. Life history as well as the effect on color and morphological change due to environmental factors were studied under laboratory conditions.

Statistical and qualitative comparisons between various populations of C. dubius showed no significant differences between Tennessee populations, although three regional clines or possible subspecies were indicated. Both qualitative and quantitative evidence suggested the Tennessee population of C. dubius, as well as other populations south of the type locality, are significantly different from those near the type locality and to the north. C. dubius and C. carolinus could not be separated on the basis of the measurements used. The color phases of C. carolinus in Tennessee consisted of bright red-orange to red-brown, while color and color phases for C. dubius varied from concolorous tan, brown, tan-red, lavender, purple, blue and blue-grey of all shades to various combinations of these colors. Variation in color and morphology were not due to environmental

induction as far as could be determined in C. dubius. Color did appear to be influenced to some degree by environmental factors in C. carolinus.

The range of C. dubius in Tennessee extends from the Blue Ridge Province in the northeast corner of the state, south in the Ridge and Valley Province to the mouth of the Clinch River. From here, the range extends west over the Cumberland Plateau to the Caney Fork and South Fork of the Cumberland River system.

The habitat of C. dubius in Tennessee was associated with cool, clear, headwater streams, springs and marshy areas at altitudes ranging from 800 to 4,000 feet (262 to 1,311 meters). C. carolinus inhabited cold, clear mountain springs and seeps at altitudes ranging from 950 feet to over 5,500 feet (312 to 1,803 meters). C. carolinus was limited in Tennessee to the Blue Ridge Province from the French Broad River southward. Neither species appeared to be restricted to a particular type of soil or substratum.

Mature C. dubius males underwent two annual molts, one in late spring to early summer in to a sexually immature form (form II), and another in late summer to early fall into a sexual form (form I). Young were born primarily in the spring. Sexual maturity was reached not earlier than the fall of the second year. No significant differences were found in the growth rates for either sex. A minimum postorbital length of 21.4 mm. (24.1 mm. standard length) was found for sexually mature males, and a postorbital length of 24.2 mm. (27.1 mm. standard length) was found for sexually mature females. Ovigerous females had a mean postorbital length of 30.4 mm. (34.0 mm. standard length) with a mean of 34.2 eggs per female.

LITERATURE CITED

LITERATURE CITED

Andrews, E. A. 1904. Breeding habits of crayfish. Am. Nat. 38:165-206.

Bouchard, R. W. (in press). A new crayfish of the subgenus Jugicambarus from Tennessee with an emended definition of the subgenus (Astacidae, Decapoda). Amer. Midl. Nat.

Chidester, F. E. 1908. Notes on the daily life and food of Cambarus bartonius bartoni. Am. Nat. 42:710-716.

_____. 1912. The biology of the crayfish. Am. Nat. 46:279-293.

Creaser, E. P. 1934. Some notes on North American crayfish. Science 79(2051):364.

Crocker, D. W. and D. W. Barr. 1968. Handbook of the crayfishes of Ontario. Univ. of Toronto Press, Toronto. 158p.

Dixon, W. J. and F. J. Massey Jr. 1957. Introduction to statistical analysis. McGraw-Hill Book Co., Inc., New York. 488p.

Erichson, W. F. 1846. Uebersicht der Arten der Gattung Astacus. Arch. für Naturgeschichte, 12(1):86-103.

Fabricius, J. C. 1798. Supplementum Entomologiae. Systematicae Proft et Storch, Hafniae 572p.

Faxon, Walter. 1884. Descriptions of new species of Cambarus, to which is added a synonymical list of the known species of Cambarus and Astacus. Proc. Amer. Acad. Arts Sci. 20:107-158.

_____. 1885. A revision of the Astacidae. (Part I. The genera Cambarus and Astacus). Mem. Mus. Comp. Zool., Harvard Coll. 10(14):1-186, 10 pls.

_____. 1890. Notes on North American crayfishes, family Astaciae. Proc. U. S. Nat. Mus. 12(785):619-634.

_____. 1914. Notes on the crayfishes in the United States National Museum and the Museum of Comparative Zoology with descriptions of new species and subspecies to which is appended a catalogue of the known species and subspecies. Mem. Mus. Comp. Zool., Harvard Coll. 40(8):351-427, 13 pls.

Fitzpatrick, J. F. 1963. Geographic variation in the crawfish Faxonella clypeata (Hay) with the definition and defense of the genus Faxonella Creaser (Decapoda, Astacidae). Tulane Stud. Zool. 10(1):57-79.

_____. 1967. The Propinquus Group of the crawfish genus Orconectes (Decapoda: Astacidae). Ohio Journ. Sci. 67(3):129-172.

Girard, C. 1852. A revision of the North American Astaci, with observations on their habits and geographical distribution. Proc. Acad. Nat. Sci. Philad. 6:87-91.

Hack, J. T. 1969. The area, its geology: Cenozoic development of the Southern Appalachians. In Holt, Perry C., et al., The distributional history of the biota of the Southern Appalachians, Part I: Invertebrates. Virginia Polytechnic Institute, Research Division Monograph 1:1-17, 4 figs.

Harris, J. A. 1903. An ecological catalogue of the crayfishes belonging to the genus Cambarus. Kansas Univ. Sci. Bull. 2(3): 51-187, 5 pls.

Hay, W. P. 1902. On the proper application of the name Cambarus carolinus Erichson. Proc. Biol. Soc. Wash., 15:38.

Hobbs, H. H., Jr. 1942. A generic revision of the crayfishes of the subfamily Cambarinae (Decapoda, Astacidae) with the description of a new genus and species. Amer. Midl. Nat. 28(2):333-357, 23 figs.

_____. 1959. (In Edmonson, W. T.) Fresh-water Biology. John Wiley and Sons, Inc., New York. Pages 883-901, figs. 31.18-31.41.

_____. 1968a. Two new crayfish of the genus Cambarus from Georgia, Kentucky, and Tennessee (Decapoda, Astacidae). Proc. Biol. Soc. Wash. 81(31):261-274, 22 figs.

_____. 1968b. Crustacea:Malacostraca. In Parrish, F. K., Keys to water quality indicative organisms (Southern United States). Federal Water Pollution Control Administration, Department of the Interior. pp. K-1-K36.

_____. 1969. On the distribution and phylogeny of the crayfish genus Cambarus. In Holt, P. C., et al., The distributional history of the biota of the Southern Appalachians, Part I: Invertebrates. Virginia Polytechnic Institute, Research Division Monograph 1: 93-178, 20 figs.

_____. 1970a. A new crayfish from the Nashville Basin, Tennessee. Proc. Biol. Soc. Wash. 83(14):161-169, 1 fig.

_____. 1970b. New crayfishes of the genus Cambarus from Tennessee and Georgia (Decapoda, Astacidae). Proc. Biol. Soc. Wash. 83(23): 241-260.

_____ and R. W. Bouchard. (in press). A new crayfish from the Cumberland River System with notes on Cambarus carolinus (Erichson). Proc. Biol. Soc. Wash.

_____, P. C. Holt and M. Walton. 1967. The crayfishes and their epizootic ostracod and branchiobdellid associates of the Mountain Lake, Virginia, Region. Proc. U. S. Nat. Mus. 123(3602):1-84, 22 figs.

_____ and M. Walton. 1970. New entocytherid ostracods from Tennessee and Virginia. Proc. Biol. Soc. Wash. 82(68):851-863, 3 figs.

_____ and C. S. Shoup. 1947. Two new crayfishes (Decapoda, Astacidae) from the Obey River drainage in Tennessee. Journ. Tenn. Acad. Sci., 22(2):138-145, 22 figs.

Hubbs, C. L. and C. Hubbs. 1953. An improved graphical analysis and comparison of samples. Systematic Zool. 2:49-57.

Newcombe, C. L. 1929a. A new blue crayfish. Science 70:217.

_____. 1929b. The crayfish of West Virginia. Ohio Journ. Sci. 29(6):267-288, 2 figs.

Ortmann, A. E. 1905a. The crawfishes of western Pennsylvania. Ann. Carnegie Mus. 3(2):387-406.

_____. 1905b. The mutual affinities of the species of the genus Cambarus and their dispersal over the United States. Proc. Amer. Philos. Soc. 44(180):91-136, 1 pl.

_____. 1906. The crawfishes of the state of Pennsylvania. Mem. Carnegie Mus. 2(10):343-523, 7 pls.

_____. 1913. The Alleghenian Divide, and its influence upon the freshwater fauna. Proc. Amer. Philos. Soc. 52(210):287-390, 3 pls.

_____. 1931. Crawfishes of the southern Appalachians and the Cumberland Plateau. Ann. Carnegie Mus. 20(2):61-160.

Pennak, R. W. 1953. Freshwater invertebrates of the United States. The Ronald Press Co., New York. 769 pages, 470 figs.

Prins, R. 1968. Comparative ecology of the crayfishes Orconectes rusticus and Cambarus tenebrosus in Doe Run, Meade County, Kentucky. Int. Revue ges. Hydrobiol. 53(5):667-714.

Ross, R. D. 1969. Drainage evolution and fish distribution problems in the Southern Appalachians of Virginia. In Holt, Perry C., et al., The distributional history of the Southern Appalachians, Part I: Invertebrates. Virginia Polytechnic Institute, Research Division Monograph. 1:93-178, 20 figs.

Schwartz, F. J. and W. G. Meredith. 1962. Crayfishes of the Cheat River watershed in West Virginia and Pennsylvania. Part II: Observations upon ecological factors relating to distribution. Ohio Journ. Sci. 62(5):260-273, 9 figs.

Stevens, G. C. 1952. The control of cement gland development in the crayfish Cambarus. Biol. Bull. 103(1):242-258.

Tack, P. I. 1941. The life history and ecology of the crayfish Cambarus immunis Hagen. Amer. Midl. Nat. 25:420-446.

Van Deventer, W. C. 1937. Studies on the biology of the crayfish Cambarus propinquus Girard. Ill. Biol. Monogr. 15:1-67.

Yonge, C. M. 1937. The nature and significance of the membrane surrounding the developing eggs of Homarus vulgaris and other Decapoda. Proc. Zool. Soc. London. (A)107:449-515.

APPENDIX

APPENDIX

GLOSSARY

Acumen--median anterior tip of the rostrum.

Annulus ventralis--median sclerite located between the bases of the fourth and fifth pairs of periopods in females, which receives the sperm during copulation.

Areola--the area on the mid-dorsal surface of the thorax, bounded by the grooves which mark the dorsomedial limits of the gill chambers. Areola length is defined by the cervical groove cephalically and posteriorly by the caudal edge of the cephalothorax.

Carapace--the exoskeleton covering the cephalothorax.

Carpus--the third endopodite from the distal end of the first periopod.

Central projection--the corneous extension at the end of the first pleopod (in males), cephalic to the mesial process.

Cervical groove--the deep groove that delineates the head from the thorax region.

Chela--the pincer of distal two segments of the first pair of periopods composed of the dactyl and prododus.

Cheliped--the entire leg bearing the chela consisting of the protopodites and endopodites.

Dactyl--the first segment at the free tip of the first pair of periopods; the smaller movable finger of the chela.

Epistome--ventral sclerite anterior to the mouth.

Glair--the semitransparent secretion of the cement glands used to attach the eggs to the pleopods of the female.

Instar--the stage between molts in the early development of immature arthropods.

Merus--the fourth segment from the distal end of the first pair of periopods.

Mesial process--the terminal process of the first pleopod (in males) located caudally to the central projection.

Palm--propodite of the chela posterior to the dactyl and fixed finger.

Pleopod--a serially homologous, two-branched appendage of the abdomen.

Postorbital length--length of the carapace posterior to the eye to the posterior edge of the thorax.

Postorbital ridges--grooved ridges on the dorsal aspect of the head, posteriolateral to the margins of the rostrum.

Punctation--small pit or depression in the exoskeleton.

Rostrum--dorsomedial cephalic extension of the carapace between the eyes.

Suborbital angle--the angle formed by the extension of the exoskeleton ventrocephalad, forming a point below the eye.

Telson--median postsegmental body division at the posterior terminus of the body.

Tubercle--low rounded eminence of the exoskeleton.

VITA

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