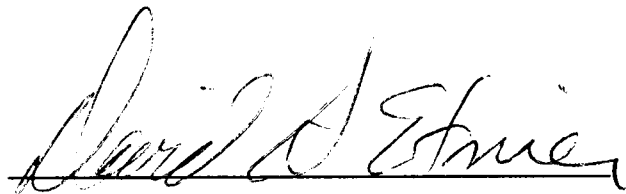


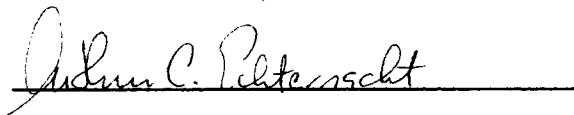
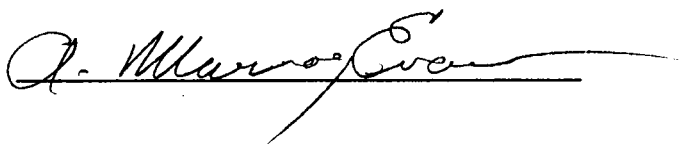
To the Graduate Council:

I am submitting herewith a dissertation written by Mary Jane Krotzer entitled "Variation and Systematics of Etheostoma nigrum Rafinesque, the Johnny Darter (Pisces: Percidae)." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Zoology.

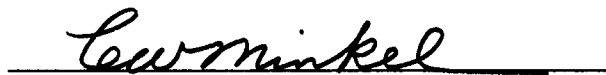


David A. Etnier, Major Professor

We have read this dissertation
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Vice Provost

and Dean of the Graduate School

VARIATION AND SYSTEMATICS OF
ETHEOSTOMA NIGRUM RAFINESQUE,
THE JOHNNY DARTER (PISCES: PERCIDAE)

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Mary Jane Krotzer

December 1990

DEDICATION

I would like to dedicate this work to my husband, R. Stephen Krotzer, without whom I might never have completed this project. Steve, I thank you for your help, advice, and constant emotional support during all the time that I have known you.

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Finally, I would like to thank my parents, Kathryn and David Larkin, for providing me with emotional and financial support both prior to and during my graduate studies.

ABSTRACT

Populations of Etheostoma nigrum, the johnny darter, were examined to determine the presence or absence of geographic variation in meristic, morphometric, and karyotypic characters. These populations were from primarily south of the Great Lakes and west of the Appalachian Mountains. Meaningful geographic variation was found in the following meristic characters: dorsal soft rays, pectoral rays, supratemporal canal pores, . infraorbital canal pores, preoperculomandibular canal pores, squamation, and branchiostegal rays. While morphometric analysis demonstrated that the sexes of E. nigrum are dimorphic, with the male having longer fins and the female having a deeper body, measurements were not very useful for the separation of E. nigrum populations. Karyotypic analysis of E. nigrum populations demonstrated geographic variation in the number of types of chromosomes present and in fundamental arm number. Southern populations of E. nigrum had a fundamental arm number of 90, while northern E. nigrum had a fundamental arm number of 86. Etheostoma olmstedi, the presumed sister species of E. nigrum, was karyotyped and also had a fundamental arm number of 86.

Two races of E. nigrum are recognized. One race is found in the Bayou Pierre, Homochitto, Big Black, Yazoo, and Obion river systems of Mississippi, Tennessee, and Kentucky. This race differs from other southern populations in having a higher number of dorsal soft rays (modally 13 compared with 12 in other southern populations), a more complete infraorbital canal system (modally 10, 11, or 12 pores compared with 8 or 9 pores

in other southern populations), and a more complete supratemporal canal system (with 89% complete compared with 0-64% complete in other southern populations). A second race of E. nigrum is recognized from the Ohio River drainage. This race has fewer branchiostegal rays (modally 10 or 11 compared with 12 elsewhere) and fewer pectoral rays (modally 11 rays compared with 12 elsewhere).

The variation possessed by E. nigrum populations provides important biogeographical evidence for several stream captures and past river associations. A hypothesis for the evolutionary history of E. nigrum and other members of the subgenus Boleosoma is presented.

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CHAPTER I.

INTRODUCTION

Etheostoma nigrum (Family Percidae), the johnny darter, has one of the largest distributions of any darter. As seen in Figure I-1, its range extends from the Hudson Bay drainage of Canada in the north to southern Alabama and Mississippi, and from the Tar River system of North Carolina in the east to the Rocky Mountains in the west (Bruner, 1980). Within this area, it is notably missing from below Cumberland Falls in the Cumberland River system of Tennessee; the Forked Deer, Hatchie, Loosahatchie, and Wolf river systems of west Tennessee; and the Coosa River system of Alabama.

Etheostoma nigrum is a member of the subgenus Boleosoma, which is presently considered to contain the following species: E. nigrum, E. olmstedii, E. longimanum, E. podostemone, and E. perlongum (Cole, 1971; Page, 1983; Bailey and Etnier, 1988).

Etheostoma nigrum was described by Rafinesque in 1820 in Ichthyologica Ohiensis, and since that time it has had a varied taxonomic history. For many years nigrum Rafinesque and olmstedii Storer were considered to be subspecies of E. nigrum (Hubbs and Lagler, 1941). However, research presented by Stone (1947) cast doubts on the subspecific status of these two forms, and instead suggested that at least in certain areas of their ranges they were acting as true species. Species status was

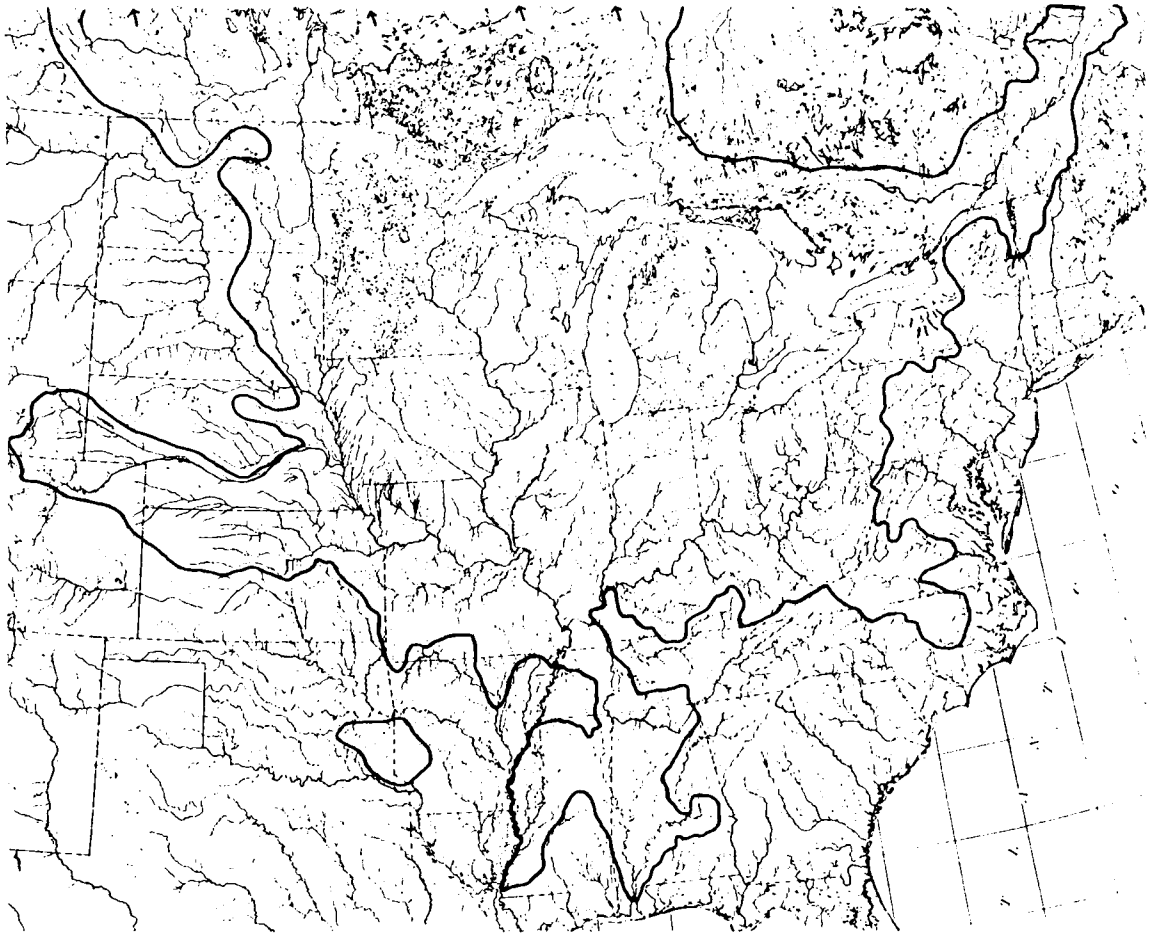


Figure I-1. Distribution of Etheostoma nigrum throughout the United States and part of Canada (modified from Bruner, 1980). As indicated by the arrows, the distribution of E. nigrum continues northward into Canada to the southern tributaries of the Hudson Bay drainage.

further substantiated by the investigation of the two along the east coast (Cole, 1957, 1965) and by demonstration of electrophoretic differences between the two forms in the James River drainage of Virginia (Falls, 1982).

Specimens of E. nigrum from east of the Appalachian divide, upper Ohio River, Kanawha River of West Virginia, and the eastern Great Lakes region of the United States and Canada have been investigated (Cole, 1957). After studying this portion of the range, Cole considered E. nigrum to have seven subspecies. They were: E. n. nigrum; E. n. eulepis, a glacial lake form from the Midwest; E. n. susanae, an upper Cumberland River form; E. n. jamesense, a James River form; E. n. roanoke, a Roanoke River form; E. n. digitale, a Tar and Neuse River form; and E. n. maculaticeps. However, by 1971 Cole had decreased the number of nigrum subspecies to three. The three were E. n. nigrum, E. n. eulepis, and E. n. susanae. The James, Roanoke, Tar, and Neuse River forms were redetermined to be racial distinctions of E. nigrum, while E. n. maculaticeps was reassigned to subspecific status under E. olmstedii.

Etheostoma nigrum eulepis was described by Hubbs and Greene (1935) as a glacial lake form from Minnesota and northern Iowa east to southern Ontario, northern Ohio, and northern Pennsylvania. It differs mainly from the nominate subspecies in the degree of squamation of the breast, opercles, cheek, and nape, with eulepis having a consistently higher degree of squamation than E. n. nigrum. In addition, E. n. eulepis is typically found in quiet or slow moving water with extensive vegetation and

bottoms of mud or silt, while E. n. nigrum is found in faster moving streams or areas of lakes with wave action and a firmer substrate (Lagler and Bailey, 1947). Because of these ecological differences, it was postulated that these were ecophenotypes and that the degree of squamation might not be genetically fixed. Breeding studies were performed where physical conditions were held constant, and degree of squamation in offspring of intrasubspecific and intersubspecific crosses was examined. It was found that degree of squamation was genetically determined and that offspring were nearly identical to respective parents while hybrids were intermediate in degree of squamation (Lagler and Bailey, 1947). Despite these findings, subspecific status of E. n. eulepis has generally been rejected due to insufficient morphological differences (the only difference is in degree of squamation), geographical evidence (eulepis exhibits a mosaic geographic distribution within the range of E. nigrum which is not consistent with subspecies rank), and ecological evidence (apparent habitat differences do not hold up) (Underhill, 1963).

The remaining subspecies, E. nigrum susanae, was originally described by Jordan and Swain (1883) as an endemic species from the Cumberland River system. Since the time of its description susanae has become rare, and lack of specimens to examine had caused some authors to doubt its validity (Jenkins et al., 1972). However, Starnes and Starnes (1979) obtained additional specimens and investigated its status. Etheostoma n. susanae was found to differ from E. n. nigrum by having the top of the head, opercles, and midbelly without any scales, the

preoperculomandibular canal always interrupted, and the preorbital stripe interrupted below the naris, thus appearing as a preorbital spot. In addition, an area of apparent intergradation between E. n. susanae and the nominate subspecies was found in the headwaters of the Kentucky River.

Etheostoma nigrum has also been investigated in the Canadian portion of its range. A morphological and allozymic study of E. nigrum and E. olmstedii from the Ottawa area revealed two distinct species and a group believed to be interspecific hybrids (McAllister et al., 1972). In addition, two populations of E. nigrum from Ontario were compared and variation in lateral-line scales, degree of squamation, and snout shape was reported (Kott and Humphreys, 1978).

During a preliminary analysis of E. nigrum for The Fishes of Tennessee (Etnier and Starnes, in progress), differences were found between specimens from the lower eastern Mississippi river tributaries of Kentucky, Tennessee, and Mississippi and those from the Mobile Bay and Tennessee River drainages. The lower eastern Mississippi River specimens were noted as attaining a larger maximum size, having a higher number of soft dorsal rays, and possessing a more complete supratemporal and infraorbital canal system than the Mobile Bay and Tennessee River forms. It was even suggested that E. nigrum from the Homochitto, Bayou Pierre, Big Black, Yazoo, and Obion River systems might be different enough to merit species status.

In summary, Etheostoma nigrum has been investigated throughout the northern and eastern United States and in

a portion of its Canadian range. When these areas are compared with the previously cited range of E. nigrum, it is obvious that a large portion of its range remains to be investigated. It is the purpose of this study to determine the relationships of populations of E. nigrum found primarily west of the Appalachian Mountains and south of the Great Lakes. The objectives are to examine geographic variation, analyze characters which exhibit variation, determine if any of the populations within this area merit species or subspecies status, and generate an evolutionary scenario to explain the distribution of characters and populations of Etheostoma nigrum.

Since past research in the study of geographic variation has shown that almost any character which has some inherent plasticity will exhibit geographic variation (Mayr, 1963), only those characters whose variation can be explained in a biogeographical context will be considered to be "meaningful". In other words, if a character varies as much within a population as it does between populations, or if the variation of a character has no geographic pattern or trend, the variation would be considered to be random and therefore would not be considered "meaningful".

During the course of this study the evolutionary species concept will be applied. This concept states that a species is "a single lineage of ancestor-descendent populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate" (Wiley, 1978; modified from Simpson, 1961). A subspecies will be considered to be a group of populations within a single species which

differ taxonomically from other populations of that same species and which are formally named in the form of a trinomen (Mayr, 1963). Where two subspecies meet, a zone of intergradation is usually formed and the characters that differ between the subspecies show some degree of intermediacy. A race is considered to be a group of populations within a single species which are differentiated to the extent that they are recognizable but are not distinctive enough to be considered a named subspecies (Mayr, 1963).

CHAPTER II.

MERISTICS

1. Introduction

Meristic characters are those structures which can be counted. They may be external, such as number of fin rays or number of pores in a cephalic canal system; or they may be internal, such as number of vertebrae. Meristic characters have long been used in ichthyology for the delineation of species, and the methodology for the counting of meristic characters is well standardized (Hubbs and Lagler, 1958). This standardization of methodology allows for the comparison of studies performed by different researchers and greatly enhances the comparative nature of systematic ichthyology.

As stated previously, meristic characters, as well as other characters, have been examined in various portions of the range of E. nigrum. This chapter will emphasize the meristic characters of populations of E. nigrum found primarily west of the Appalachian Mountains and south of the Great Lakes. In addition, these findings will be compared with the findings of previous investigations in an attempt to summarize the meristic variability of E. nigrum throughout its range.

2. Methods

Counts were made on a total of 1,340 individuals for 23 variables. The list of material examined is given in Appendix A. The following counts were made according to the methods outlined by Hubbs and Lagler (1958), except where noted: dorsal spines; dorsal soft rays; principal caudal rays; anal spines; anal soft rays; pectoral fin rays (counted only on left side of body); branchiostegal rays; pored lateral line scales; scales in lateral series; scales above the lateral line (the oblique scale row counting down and back from the first dorsal soft ray, not including the lateral line scale or any scale extending onto the midline); scales below the lateral line; and caudal peduncle scale rows.

The supratemporal, lateral, infraorbital, preoperculomandibular, and coronal pores of the cephalic canal system were counted as described by Page (1977), with the exception that the infraorbital and preoperculomandibular pores were counted on both sides of the head, and one pore was subtracted from the total count for each termination point that occurred in the interior portion of the canal. For example, in Figure II-1 the infraorbital canal is interrupted, with the posterior portion having two pores and the anterior portion having four pores. The total count from both sides of the head is twelve, but four pores are subtracted to give a final count of eight (in other words, the "pores" resulting from canal interruption were not counted). The supratemporal canal was noted as being

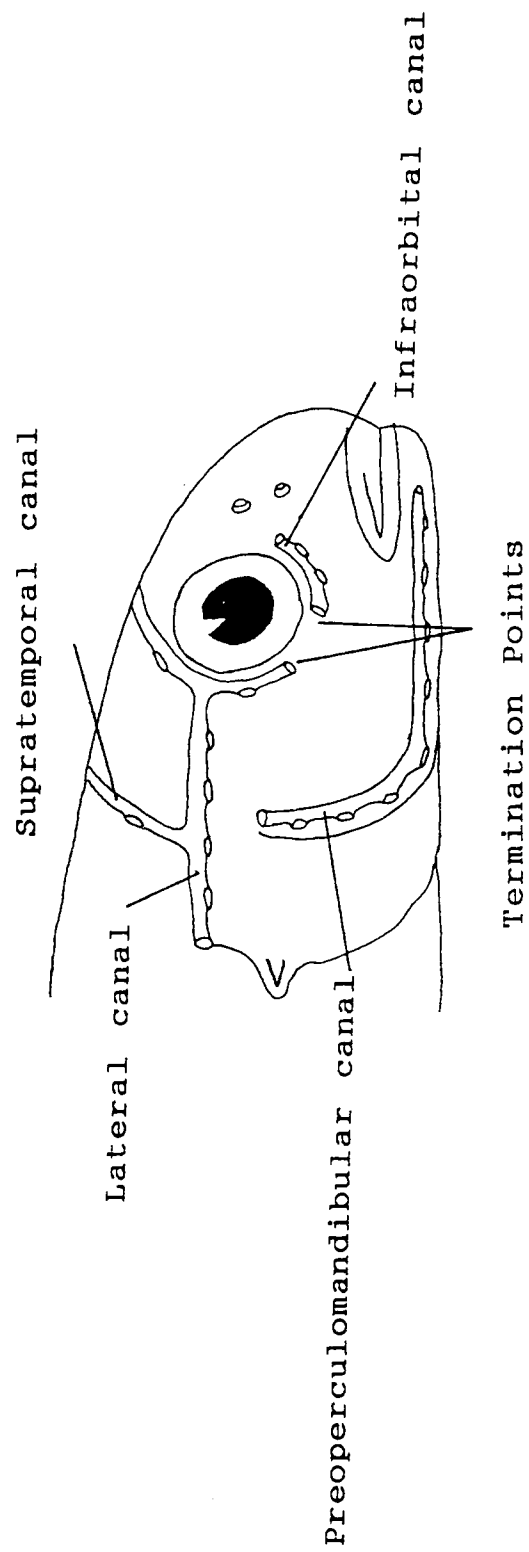


Figure II-1. Lateral view of the head of Etheostoma nigrum indicating the components of the cephalic lateralis canal system.

either complete or interrupted. A complete supratemporal canal had three pores, while an interrupted canal had four pores.

The number of scales located in the following areas was counted: opercle, cheek, nape, breast, prepectoral area, and belly. Vertebral counts were made on a total of 70 individuals, from seven different localities, as outlined by Bailey and Gosline (1955).

For each of the meristic variables the mode, mean, standard deviation, and standard error were calculated by river system. Frequency tables of these variables are presented in Appendix B. When collections within a river system exhibited no meaningful variation, as determined by examining Hubbs and Hubbs (1953) graphs, they were amalgamated. In the following discussion of results, each meristic variable will be considered, important variation will be indicated and, where possible, results from other studies will be included.

3. Results

The first meristic variable to be considered is the number of dorsal spines. The distribution of number of dorsal spines, mean, standard deviation, and standard error by river system are shown in Table B-1. With very few exceptions, the modal number of dorsal spines was 9. The exceptions occurred where sample sizes were low, and then there were usually an equal number of specimens with 8 or 9 dorsal spines. The number of dorsal spines ranged from 6 to 10, and the means ranged from 8.0 to 9.2. These numbers are similar to Cole's (1957) findings. In

his study he found the number of dorsal spines ranged from 6 to 10, and with only one exception (the modal number for the Genesee River was 8) the modal number of dorsal spines was 9. From these data it would seem that, although there is some variability in number of dorsal spines within and between populations, it is not meaningful throughout the range of E. nigrum.

The frequency table for dorsal soft rays is given in Table B-2. In the lower eastern Mississippi River tributaries-- the Homochitto, Bayou Pierre, Big Black, Yazoo, and Obion rivers, the modal number of dorsal rays was 13, 13, 14, 13, and 13, respectively. The number of dorsal rays ranged from 12 to 15 in these river systems, and the mean number of dorsal rays was 12.8, 13.0, 13.6, 12.9, and 13.4, respectively. In contrast, the river systems of the Mobile Bay drainage had a modal number of 12 dorsal rays, with the exception of the Tallapoosa River, which had a modal number of 13. All six of these river systems-- the Alabama, lower Tombigbee, upper Tombigbee, Cahaba, Black Warrior, and Tallapoosa, had means of 12.5 or fewer and a range of from 11 to 14 dorsal rays. The river systems of the Red River drainage of Arkansas and Oklahoma also had modes of 12 and means of 12.5 or fewer dorsal rays. The Tennessee, Cumberland, and upper Ohio river systems also had modal numbers of 12 dorsal rays and had means of 12.5 or fewer rays. However, when the lower Ohio river, upper Mississippi river, and Missouri river systems of the Midwest are included, the modal number of soft dorsal rays forms a mosaic pattern. For example, within the Missouri River drainage the Chariton River, a northern tributary, had a mean of 13.0 and a mode of 13 dorsal rays, while the

Osage River, a southern tributary, had a mean of 12.1 and a mode of 12. The river systems in the Midwest had modal dorsal ray numbers ranging from 12 to 14 and means ranging from 12.1 to 14.0. The reader is referred to Table B-2 for information on specific river systems. Cole (1957) studied northeastern E. nigrum and found the modal number of dorsal rays to be 11 with means ranging from 11.0 to 11.6. However, E. nigrum from the Tar River of North Carolina had a modal number of 13 dorsal rays and a mean of 12.9. Kott and Humphreys (1978) examined two populations of E. nigrum from the Great Lakes region of Ontario and found means of 11.0 and 11.1 for dorsal rays. Populations of E. nigrum from near Ottawa were found to have a modal number of either 11 or 12 and a mean of 11.5 dorsal rays (McAllister et al., 1972). From these data it can be seen that in certain peripheral areas of the range of E. nigrum the number of soft dorsal rays exhibits meaningful geographic variation. However, in the central portion of the range this meaningful variation breaks down, and a mosaic pattern for the distribution of dorsal soft rays predominates.

Etheostoma nigrum throughout its range was found to have a mode of one anal spine. Occasionally a specimen had two anal spines, but this occurred in less than 10% of the specimens examined and is not considered to be taxonomically important.

Table B-3 illustrates the frequency table for the number of anal soft rays. Throughout the majority of the range of E. nigrum, including the lower eastern Mississippi River tributaries, the Red River drainage, the Arkansas River drainage, the Mobile Bay drainage, the

Tennessee, Cumberland, and Ohio rivers, the Great Lakes drainage, and the Hudson Bay drainage of Canada, the modal number of anal soft rays was either 8 or 9. The range of anal rays was from 6 to 11 and the range of means was from 8.0 to 9.4. In the central portion of the range, predominantly the Missouri River drainage and the upper Mississippi River, the modal number of anal soft rays was usually 9 or 10. The mean number of soft rays for this area ranged from 8.2 to 10.0. The extreme western populations of E. nigrum in the Cache la Poudre River of Colorado and the Laramie River of Wyoming had modally 10 anal rays and means of 9.6 and 9.8, respectively. Populations of E. nigrum from the northeastern portion of the range had modal numbers of 8 anal rays, ranges of from 6 to 9 anal rays, and means of from 7.5 to 8.0 (Cole, 1957). Etheostoma nigrum from North and South Carolina river systems were reported as having a modal count of 7 anal rays and means ranging from 6.9 to 7.4 (Cole, 1957). Ontario populations of E. nigrum were found to have means of 8.2 and 9.0 anal rays (Kott and Humphreys, 1978). In summary, while there is overlap, E. nigrum from the southern, eastern, and northern parts of the range have lower anal ray counts (7-9), while E. nigrum from the western and central part of the range have higher anal ray counts (9-10).

The frequency table for the number of pectoral rays is given in Table B-4. Throughout most of the range of E. nigrum the modal number of pectoral rays was 12, the range was from 9 to 13, and the range of means was from 11.4 to 12.0. However, there were some exceptions to 12 as a mode for pectoral rays. In the Miami, Muskingum, Scioto, and Mahoning rivers and Kinniconick Creek of the

Ohio River drainage and in the Cumberland River drainage, a mode of 11 pectoral rays was found. The number of pectoral rays ranged from 10 to 12 and the range of means was from 11.0 to 11.6 from this area. The extreme western populations of Colorado and Wyoming had a mode of 11 pectoral rays, a range of 10 to 12 rays, and means of 11.4 and 11.2. In addition the Maumee River and the Grand River, both tributaries of Lake Erie, had a mode of 11 pectoral rays and means of 11.4 and 11.3, respectively. Populations of E. nigrum from the northeast were found to have modally 11 pectoral rays, with the exception of Lake Ontario and specimens from the river systems of North and South Carolina, which had modally 12 pectoral rays (Cole, 1957). Specimens from two populations in Ontario were found to have means of 12.0 and 11.5 and ranges of from 11 to 13 pectoral rays (Kott and Humphreys, 1978). Etheostoma nigrum from near Ottawa, Canada had a modal number of 12, a range of 11 to 14, and a mean of 11.8 pectoral rays (McAllister et al., 1972). Although there are some differences in the modal number of pectoral rays throughout the range of E. nigrum, the range of pectoral rays and the range of means are somewhat overlapping, so that separation of E. nigrum populations on the basis of pectoral ray counts alone is not possible.

Table B-5 gives the frequency table for the number of principal caudal rays. Throughout most of the range of E. nigrum the modal number of principal caudal rays was either 15 or 16. There was no geographic pattern in so far as which mode was found, although the mode of 16 was more common. The number of principal caudal rays

ranged from 11 to 18 and the means ranged from 12.7 to 16.3. There were three exceptions to the mode of 15 or 16 for principal caudal rays. The first was the Big River system of Missouri, which had modally 17 principal caudal rays, a range of 16 to 17 rays, and a mean of 16.9. The Maumee River of Ohio had a modal number of 13 or 14, a range of 13 to 17, and a mean of 14.3. The final exception was the Portage Creek system of Michigan, which had a modal number of 11 or 13, a range of 11 to 16, and a mean of 12.7 principal caudal rays. To summarize, there does not appear to be any meaningful geographic variation in the number of principal caudal rays within the range of E. nigrum.

The frequency table for number of scales in the lateral series is given in Table B-6. This table also includes the percentage of specimens within each river system that possessed a complete lateral line. Although there was some variation in the number of scales in the lateral series throughout the range of E. nigrum, with means ranging from 41.9 to 55.0, there was no consistent geographic pattern. As can be seen in Table B-6, the lateral line of E. nigrum ranges from complete to incomplete. Although there was no real pattern to degree of completeness of the lateral line, the lower eastern Mississippi River populations appeared to have consistently more complete lateral lines than any other area within the range of E. nigrum. Cole (1957) found that E. nigrum populations from the northeast had means of from 43.5 to 46.4 for scales in the lateral series, while populations from North and South Carolina and Virginia had lower means, ranging from 39.9 to 43.8. Specimens from Saskatchewan, Manitoba, and Ontario had

means ranging from 46.3 to 51.5 for number of scales in the lateral series (Kott and Humphreys, 1978). Neither of these studies presented data on completeness of the lateral line.

Table B-7 gives the frequency table for number of scales above the lateral line. The most common modal number of scales above the lateral line was 5; however, in the Mountain Fork River system of Oklahoma and in the Whitewater River and River aux Vases systems of Missouri the modal number of scales above the lateral line was 6. There were a few other instances, where sample size was low, that the mode was either 4, 5, or 6. The number of scales above the lateral line ranged from 4 to 7, and the means ranged from 4.4 to 6.0. Overall, there appears to be no significant variation in number of scales above the lateral line throughout the range of E. nigrum. As stated previously in the methods section of this chapter, the scales above the lateral line count was made from the oblique scale row counting down and back from the first dorsal soft ray. The reason for beginning at the base of the second dorsal fin is that in many populations the nape of E. nigrum is unscaled, so that a true count of scales above the lateral line cannot be made by beginning at the spinous dorsal fin. In all other reports of this character in E. nigrum, the oblique scale row beginning lateral to the spinous dorsal fin was counted, so that direct comparison of studies was not possible. For example, Cole (1957) found a mode of 4 scales above the lateral line for all of the populations he investigated. Kott and Humphreys (1978) examined two populations from Ontario and also reported a mode of 4, but the range of scales above the lateral line was from 4 to 6.

Populations of E. nigrum from near Ottawa were also reported as having a mode of 4 scales above the lateral line and a range of from 3 to 5 scales (McAllister et al., 1972). Regardless of the technique used, the number of scales above the lateral line does not vary throughout the range of E. nigrum to the extent that it is considered to be taxonomically important.

The frequency table for scales below the lateral line is given in Table B-8. The most common mode of scales below the lateral line was either 7 or 8, but modes of 6 and 9 were also found in some populations. The range of scales below the lateral line was from 5 to 10 and the means ranged from 6.2 to 8.7. Generally, there appear to be larger scales, and therefore, lower counts in the northern part of the range, but this is not completely reliable, since several populations in this area were found to have a mode of 8 scales below the lateral line. Cole (1957) reported modes of 5, 6, and 7 for the populations he investigated, but this count does not include smaller secondary scales, which were included in the present study. For this reason, direct comparison of these two studies is not possible for this variable. Kott and Humphreys (1978) reported a mode of 7 and a range of from 6 to 9 scales below the lateral line for Ontario populations. The number of scales below the lateral line does not appear to be a character which shows meaningful geographic variation.

Table B-9 gives the frequency table for the number of scale rows around the caudal peduncle. The most common mode of scales around the caudal peduncle throughout the range of E. nigrum was 15. However, modes

of 13, 14, 16, and 17 were also found in various populations. The number of scales around the caudal peduncle ranged from 12 to 19 and the means ranged from 13.3 to 17.0. Cole (1957) also found a high degree of variability in this character. For example, the modes ranged from 14 to 17 and the means from 14.9 to 17.7 for the populations investigated. Ontario populations were found to have a mode of either 16 or 17 and ranges of from 15 to 20 scales around the caudal peduncle (Kott and Humphreys, 1978). From this information it can be seen that the number of scales around the caudal peduncle forms a mosaic geographic pattern and therefore provides further evidence that recognition of subspecies throughout most of the range of E. nigrum is not warranted.

The next set of variables to be considered are portions of the cephalic lateralis canal system. The lateral canal of E. nigrum exhibited no variation throughout the range, with all specimens examined having 5 pores. The coronal pores also exhibited very little variation, with the modal number of coronal pores being 1 throughout the range, and with less than 1% of the specimens examined having two coronal pores. Therefore, neither the lateral canal nor the coronal pore exhibit geographic variation.

Table B-10 gives the condition of the supratemporal canal in E. nigrum throughout its range. In the lower eastern Mississippi River tributaries the supratemporal canal was most often complete, with three pores; however, a few specimens (less than 10%) had interrupted canals. In the Mobile Bay drainage populations all the river systems, except for the Black Warrior River, had modally

complete canals. However, the percentage of specimens with interrupted supratemporal canals (36%) was greater than that of the lower eastern Mississippi River tributaries. The river systems of the Arkansas and Red river drainages of Arkansas, Kansas, Missouri, and Oklahoma had consistently interrupted supratemporal canals. Throughout the remainder of the range, including the Tennessee, Cumberland, Ohio, upper Mississippi, and Missouri rivers, and the Great Lakes and Hudson Bay drainages the most common condition was for an interrupted supratemporal canal, with a few specimens (11% overall) having a complete supratemporal canal. In summary, the southern populations east of the Mississippi River have mostly complete supratemporal canals, the southern populations west of the Mississippi River have consistently interrupted supratemporal canals, and E. nigrum populations throughout the rest of the range have mostly interrupted but some complete supratemporal canals.

Table B-11 gives the frequency table for the number of pores in the infraorbital canal. There are two areas within the studied range of E. nigrum where infraorbital pore counts were high (10 or more). The first of these areas was in the lower eastern Mississippi River tributaries. The modal number of infraorbital pores for the Homochitto, Bayou Pierre, Big Black, Yazoo, and Obion River systems was 10, 12, 12, 11, and 12, respectively. The number of pores ranged from 9 to 18 and the means ranged from 11.1 to 13.0. These numbers translate into a canal which is incomplete and typically has four pores opening from the canal under the eye and 3 or 4 pores

opening from the posterior end of the canal. The second area with a high number of infraorbital pores was in the upper Midwest region near the Great Lakes. This area had modes ranging from 10 to 12, counts ranging from 8 to 18, and means ranging from 9.6 to 12.1. However, the same area also had populations with a low number of infraorbital pores, with modes of 8 or 9. Throughout the rest of the range of E. nigrum, the modal number of infraorbital pores was either 8 or 9. The number of infraorbital pores ranged from 5 to 12 and the means ranged from 7.3 to 9.2. These numbers translate into an infraorbital canal which is incomplete and typically has 4 pores opening from the anterior part of the canal and 2 or 3 pores opening from the posterior part of the canal. One exception to the mode of 8 or 9 was in the Spring River of Kansas and Missouri, which had a mode of 7 infraorbital pores. Cole (1957) reported a mode of 6 infraorbital pores for seven northeastern populations and for the Roanoke River. Cole's mode of 6 would convert to a mode of 8 under the current methodology and, therefore, is in agreement with the findings of the present study. However, a mode of 7 was reported for the James, Tar, and Neuse River populations, which would convert to a mode of 10. Therefore, a third area of high infraorbital pore counts is found along the Atlantic coast range of E. nigrum. To summarize, E. nigrum has an incomplete infraorbital canal, which throughout most of the range is very incomplete with modes of 8 or 9 pores; however, in the lower eastern Mississippi River tributaries, several rivers in the upper midwest, and the James, Tar, and Neuse rivers the canal is more complete, with modes of 10, 11, or 12 pores.

In Table B-12 the frequency table for number of preoperculomandibular pores is given. Throughout the range of E. nigrum the preoperculomandibular canal ranges from complete, with as many as 10 pores on each side of the head, to incomplete, with as few as 6 pores on each side of the head. In the eastern part of the range, including the lower eastern Mississippi River tributaries, the Mobile Bay drainage, and the Tennessee, Cumberland, and Ohio river systems, the canal was either complete or barely incomplete. The modes ranged from 17 to 19, the number of pores ranged from 10 to 21, and the means ranged from 15.5 to 19.0. In the western part of the range, including the Missouri River systems, upper Mississippi River systems, and western Hudson Bay tributaries, the canal was very incomplete. The modes from this area ranged from 10 to 12, the number of pores ranged from 9 to 10, and the means ranged from 9.7 to 12.6. In some populations the canal was so degenerate that the anterior portion of the canal was completely lacking, so that only 6 pores were found along the edge of the preopercle bone. Where these areas of high and low preoperculomandibular pore counts came together, an area of intermediate pore counts was found. This intermediate area was most apparent in the upper Midwest along the Great Lakes and in the southwestern populations of the Red River drainage. Here the modes ranged from 14 to 17, the pore numbers ranged from 9 to 19, and the means ranged from 13.5 to 16.0. One exception to this intermediate area in the southwest was the Spring River population of the Arkansas River drainage, which had a mode of 10 preoperculomandibular pores, a mean of 9.8,

and a range of from 7 to 11 pores. Converting Cole's (1957) data for northeastern populations resulted in modes of from 14 to 18 pores, with the exception of the Niagara River which had a mode of 10 pores. Populations along the Atlantic coast were found to have modes of 18 or 20 preoperculomandibular pores. Etheostoma nigrum from near Ottawa, Canada were reported as having a mode of 9 pores, counted on one side of the head only (McAllister et al., 1972). In summary, the number of pores in the preoperculomandibular canal shows meaningful geographic variation even though there is some overlap of number of pores and mean number of pores.

The frequency tables for number of scales on the opercle, cheek, prepectoral area, nape, breast, and belly are given in tables B-13 through B-18, respectively. In order to determine if there were any trends in degree of squamation in E. nigrum throughout its range, the mean numbers of scales per area of the body were added for each population, and the resulting numbers were examined for biogeographical trends. The southern populations, including those in the Red River drainage, the Arkansas River drainage, the lower eastern Mississippi River tributaries, the Mobile Bay drainage, the Tennessee River, and the Cumberland River, had a low degree of squamation. When the mean numbers of scales in the six areas were added, the numbers ranged from 4.5 to 32.0 for these populations. One notable exception to this trend was the Spring River population of the Arkansas River system, where the means added to a total of 160.9 scales. Specimens from this population were highly scaled in all six areas examined and were very much like the "eulepis" form of E. nigrum from the upper Midwest. Cross (1967)

also reported the presence of a highly scaled form of E. nigrum from the Spring River. Throughout the rest of the Midwest, except for a few specific populations, the trend was for a moderately scaled E. nigrum. The total mean number of scales ranged from 22.3 to 91.8 for this area. The following populations had a total mean number of scales of over 100: Moreau Creek, James River, and Little Sioux and Big Sioux rivers of the Missouri River drainage; the DuPage River of the Illinois River system; the Apple, Minnesota, and Prairie rivers of the upper Mississippi River drainage; and the Shiawassee River, a tributary of Lake Huron. Cole (1957) reported E. nigrum from the northeast as having the cheeks, nape, and breast usually naked, and the belly usually naked anteriorly. Populations of E. nigrum from near Ottawa were reported as most often having the cheek, nape, and breast naked; however, a few individuals were found which had these three areas partly scaled (McAllister et al., 1972). To summarize, there appears to be a trend for a higher degree of squamation in the northern part of the distribution than in the southern part. Secondly, there are some populations which exhibit a high degree of squamation but, as was found in earlier investigations (Underhill, 1963), these populations form a mosaic geographic pattern and therefore based on this character, subspecific status for these populations is not warranted.

Table B-19 gives the frequency table for the number of branchiostegal rays. As can be seen in this table, throughout most of the range of E. nigrum the modal number of branchiostegal rays was 12, the number of rays

ranged from 8 to 14, and the means ranged from 11.2 to 12.4. However, E. nigrum from the Ohio River drainage were a notable exception to having modally 12 branchiostegal rays. With the lone exception of the Wabash River population, the river systems of the Ohio drainage had modal numbers of either 10 or 11 branchiostegal rays. The range of rays was from 9 to 12 and the means ranged from 10.0 to 10.6 for this area. The Wabash River, a lower Ohio River tributary, had modally 12 branchiostegal rays, a range of from 11 to 12 rays, and a mean of 12.0. Specimens from the Grand River, a tributary of Lake Erie, had consistently 10 branchiostegal rays, suggesting a recent association between the Ohio River and Grand River. Etheostoma nigrum from the Cumberland River also had a mode of 10 branchiostegal rays. The range of rays was from 10 to 12 and the mean was 10.6 for the Cumberland River. While specimens from the Tennessee River had a mode of 12 branchiostegal rays, the mean was only 11.6, suggesting a slight influence of the Ohio River E. nigrum branchiostegal condition upon E. nigrum in the Tennessee River system. Two populations from Ontario were both reported as having consistently 12 branchiostegal rays (Kott and Humphreys, 1978). This information illustrates that the number of branchiostegal rays in E. nigrum exhibits meaningful geographic variation, with specimens from the upper Ohio River having consistently fewer branchiostegal rays than specimens from the rest of the range. It also illustrates that there has probably been a recent association between the upper Cumberland and Kentucky Rivers and the Grand River and Ohio River.

The frequency table for the number of vertebrae in E. nigrum is given in table B-20. The modal number of vertebrae throughout the range was 38, the number of vertebrae ranged from 37 to 40, and the means ranged from 37.9 to 38.2. Bailey and Gosline (1955) reported E. nigrum from Michigan as having a mode of 38 vertebrae, a range of from 37 to 39, and a mean of 38.1. Etheostoma n. eulepis from Wisconsin also had a mode of 38 vertebrae, a range of from 37 to 39 vertebrae, and a mean of 37.7. From this it is evident that no meaningful geographic variation in number of vertebrae exists throughout the range of E. nigrum.

4. Discussion

In examining the meristic data taken from populations of E. nigrum, the following characters were found to demonstrate meaningful geographic variation: dorsal soft rays, anal soft rays, pectoral rays, supratemporal canal pores, infraorbital canal pores, preoperculomandibular canal pores, squamation, and branchiostegal rays. However, very few of these characters show the same geographical pattern of variation. For example, if E. nigrum populations were grouped on the basis of anal ray counts, one cluster would contain the southern, eastern, and northern populations, and another cluster would contain the western and central populations; but if the infraorbital canal was used as the basis for grouping populations, one cluster would contain the lower eastern Mississippi River populations, the eastern populations, and some of the northern populations, whereas the second cluster would

contain the Mobile Bay populations, the western, central, and some of the northern populations. Therefore, the southern populations, those of the lower eastern Mississippi River tributaries and Mobile Bay, are clustered on the basis of one character and separated on the basis of a second character. This means that while there is geographic variation in several characters, the variation does not appear to be consistent enough nor extensive enough to merit species or subspecies status for any of the populations examined. Cole (1971) reached the same conclusion regarding eastern populations of E. nigrum, since there was no consistent pattern of meristic variation.

There are a few populations examined in the present investigation which demonstrate racial distinctions. The populations of E. nigrum in the lower eastern Mississippi River tributaries, that is the combined Bayou Pierre, Homochitto, Big Black, Yazoo, and Obion river populations, exhibit racial distinctions. These populations differ greatly from the adjacent southern populations in having a higher number of dorsal soft rays (with modes of 13 compared to 12 elsewhere), a more complete infraorbital canal (with modes of 10, 11, or 12 pores compared to 8 or 9 elsewhere), and a more complete supratemporal canal (with 89% complete compared to 0-64% complete elsewhere). However, when E. nigrum populations from the Midwest are also considered in this comparison the distinction blurs, and the differences do not appear extensive enough to warrant species or subspecies status.

A second area which is racially distinct is the Ohio River drainage. The populations within the Ohio River

drainage are distinctive in having modally 10 or 11 branchiostegal rays compared with the modal number of 12 rays found elsewhere in the range of E. nigrum. The only population within the Ohio River drainage that had modally 12 branchiostegal rays was that of the Wabash River. The Wabash is a lower Ohio River tributary whose populations may have been influenced by populations from the nearby Mississippi and Tennessee rivers, and from the Great Lakes, due to a recent connection by way of the Miami River/Lake Erie canal which connects the Maumee River to the Wabash River. A second character that is distinctive of the Ohio River populations, with exception of the Kentucky (mode of 12) and Wabash (bimodally 11 or 12) river populations, is the presence of modally 11 pectoral rays compared to modally 12 pectoral rays in most of the range of E. nigrum.

The Cumberland River population of E. n. susanae also had modally 10 branchiostegal rays and 11 pectoral rays. Starnes and Starnes (1979) list three characters useful in differentiating E. n. susanae from the nominate subspecies: 1) susanae lacks scales on the belly, opercles, and top of the head; 2) the preorbital stripe is interrupted below the naris, forming a preorbital spot; and 3) the preoperculomandibular canal is consistently interrupted. These characters were found in most of the Cumberland River specimens examined; however, two collections from the Poor Fork, in the upper Cumberland drainage, were examined in which intermediacy was found in all three characters. Specimens from the Poor Fork collections had scales on the opercles, complete preoperculomandibular canals, and no interruption in the preorbital stripe. In fact, the

specimens from these two collections were very similar to specimens from the Kentucky River, a middle Ohio River tributary. This information reinforces the hypothesis that there has been recent contact between the upper Cumberland and the middle Ohio River tributaries (Burr and Page, 1986; Starnes and Etnier, 1986). Starnes and Starnes (1979) also found evidence of intergrades between E. n. nigrum and E. n. susanae in the headwaters of the Kentucky River. More specimens are needed for examination before a final decision on the status of the Cumberland River population can be made, but of the three characters given, the pigmentation of the preorbital spot seems to be the most significant. This is based on the fact that squamation has proved to be a highly variable and very plastic character even within a population, and that incomplete preoperculomandibular canals have been found in numerous other populations throughout the Ohio River drainage and elsewhere in the range of E. nigrum.

Not only have the meristic data of E. nigrum revealed racial distinctions in populations, but these data also have biogeographical implications. The connection between the Ohio and Cumberland rivers has already been discussed, but there are other past river associations suggested by these data worthy of note. First, as noted in the previous results section, the population in the Grand River of Ohio, a tributary of Lake Erie, has a mode of 10 branchiostegal rays and 11 pectoral rays. The condition of these two characters are typical of the Ohio River race of E. nigrum. The specimens from Grand River were collected in a small tributary of the Grand River in Trumbull Co., Ohio. In

this area the tributaries of the Grand River and the Mahoning River, which is an upper tributary of the Ohio, are less than 2.5 km apart at one point and are separated only by a marsh area. This situation makes it possible, even probable, that in high water events movement of individual fish could occur in either direction. This could result in the presence of Ohio River race characters in a Lake Erie tributary population.

The Spring River population of E. nigrum in Kansas and Missouri is one whose characters suggest the possibility of a stream capture. This population is unique in having a very incomplete preoperculomandibular canal, with a mode of 10 and a mean of 9.8, and a high degree of squamation, with a total mean number of 160.9 scales for the six areas of squamation added. The Spring River is an upper tributary of the Arkansas River and is unique because other populations within the Arkansas River drainage are sparsely scaled and have a higher number of preoperculomandibular pores. The low number of preoperculomandibular pores in the Spring River population suggests a past connection between the Spring River and the Osage River, a southern tributary of the Missouri River, where E. nigrum also has a low number of preoperculomandibular pores. This connection between the Arkansas and Missouri river drainages has been hypothesized in the past based on geological data, proximity of the headwaters of the two systems, and faunal composition (Cross et al., 1986). Based on electrophoretic data, Buth and Mayden (1981) also found evidence of gene flow between Notropis zonatus, in tributaries of the Missouri River, and N. pilsbryi, in the upper reaches of the Arkansas River. Although the

number of preoperculomandibular pores can be explained by a recent connection with the Missouri River drainage, the extensive squamation of the Spring River population was probably not influenced by this connection, since the Osage populations are only moderately scaled. The highly scaled Spring River population of E. nigrum, which is now completely isolated from populations in the Missouri River and partially isolated from other Arkansas River populations, probably resulted from either random genetic drift leading to fixation or from fixation due to a founder effect.

The presence of a degenerate preoperculomandibular canal in the Hudson Bay populations of E. nigrum also has biogeographical implications. As discussed in the previous results section, the Missouri River drainage, upper Mississippi River, and western Hudson Bay drainage populations have a low number of preoperculomandibular pores. This suggests a connection of either the Missouri River or the upper Mississippi River to the Hudson Bay at some time in the past. This in fact has been hypothesized previously by several researchers (Crossman and McAllister, 1986; Robison, 1986). Prior to the glaciation of the Pleistocene era, the Missouri River is believed to have drained into Hudson Bay, rather than into the Mississippi River as it does presently (Robison, 1986). As the glaciers moved southward during the Pleistocene, the fish populations of the Hudson Bay drainage were forced southward into refugia in either the Missouri or Mississippi rivers. As the glaciers receded, new pathways for fish movement were opened and the fish populations could move back to the north. This northward

movement could have occurred either by way of glacial lakes connecting the Missouri River to the Hudson Bay tributaries or by way of Lake Agassiz, which connected the upper Mississippi River to the Hudson Bay tributaries (Crossman and McAllister, 1986). These past connections make several scenarios for the evolution of the degenerate preoperculomandibular canal system possible. First, this condition could have arisen in the Hudson Bay and then been transferred southward into the Missouri or Mississippi river refugia during the glaciation period. Secondly, the degenerate preoperculomandibular canal could have evolved in either the Missouri River or upper Mississippi River populations, then could have spread into the adjacent river system, and then finally may have been transferred to the Hudson Bay either prior to or after glaciation.

The state of the preoperculomandibular canal in the Illinois River drainage also has biogeographical implications. In Macoupin Creek, a lower tributary of the Illinois River, the population of E. nigrum has a degenerate preoperculomandibular canal system with a mode of 11 pores and a mean of 11.5 pores. In the Yellow River, an upper Illinois River tributary, the preoperculomandibular canal is more complete with a mode of 14 pores and a mean of 14.2 pores. Finally, in the Du Page River, another upper Illinois River tributary, the preoperculomandibular canal is even more complete with a mode of 16 pores and a mean of 15.6 pores. There are two possible explanations for this pattern of variation in the Illinois River. First, Macoupin Creek is near the connection of the Illinois River to the Mississippi River and may have been influenced by nearby upper Mississippi

River or Missouri River populations which also have a degenerate preoperculomandibular canal. Secondly, there has been a recent connection between the Du Page River and Lake Michigan via the Chicago sanitary canal (Burr and Mayden, 1980; Underhill, 1986). This connection may have allowed for an influx of Lake Michigan E. nigrum, which have a higher number of preoperculomandibular pores, into the upper Illinois River, and it may have influenced the state of the preoperculomandibular canal in this portion of the river.

In summary, the meristic characters of E. nigrum have illustrated the presence of geographical variability at the racial level. Two races of E. nigrum are recognized here: one in the lower eastern Mississippi River tributaries and one in the Ohio River drainage. The meristic characters of E. nigrum have also provided biogeographical evidence of several stream captures and recent river associations.

CHAPTER III.

MORPHOMETRICS

1. Introduction

The use of measurements in darter systematics has traditionally consisted of comparing the mean of each body measurement, expressed as thousandths of standard length. These comparisons were made by using either a student t-test, for two samples, or by analysis of variance (ANOVA), followed by pairwise multiple comparisons, for more than two populations. Recently, systematists have turned to multivariate techniques, which allow for the comparison of several characters at one time, rather than the traditional univariate analysis. One such technique is principal component analysis (PCA). The following discussion of PCA is summarized from Wiley, 1981; Page and Cordes, 1983; and Felley, 1984.

Principal component analysis is a technique that is designed to allow the systematist to find relationships among characters and/or specimens without an *a priori* decision as to which samples should be grouped. PCA works by partitioning the total variance of all characters considered into a limited number of uncorrelated new variables, which are termed principal components. These new variables are orthogonal to the original variables and are constructed in such a way that

the first explains the largest proportion of variability, the second explains the next largest amount of variability, and so on. The amount of variation explained by each PC axis is termed an eigenvalue. Once the total variation is broken down into these principal components, the relative contribution of the original variables to the new PC axis can be calculated. These relative contributions are termed character loadings. A character that has a large loading contributes relatively more to the PC axis than one that has a small loading. Therefore, if PCA is performed on a group of organisms that is believed to be heterogeneous, one can then examine those components that explain the largest amount of variation (those with large eigenvalues) and, by determining which characters load heavily, can determine which variables maximize the separation of individual specimens into similar groups. PCA can therefore be used as either a clustering technique or a data reduction technique.

2. Methods

Measurements were made to the nearest 0.1 mm on a total of 640 individuals for 25 characters, using needle-point dial calipers. The following measurements were made according to the methods outlined by Hubbs and Lagler (1958), except where noted: standard length (SL); minimum caudal peduncle depth (CPD); body depth at dorsal fin origin (BD); predorsal length (PREDL); length of spinous dorsal fin base (DOBASE1); length of soft dorsal fin base (DOBASE2); length of depressed spinous dorsal fin (D1L); length of depressed soft dorsal fin (D2L);

length of longest dorsal spine (DSPL); length of longest dorsal soft ray (DRL); length of caudal peduncle (CPL); length of anal fin base (ABASE); length of depressed anal fin (AL); length of anal spine (ASPL); length of longest anal soft ray (ARL); length of longest pectoral ray (P1L); length of pelvic fin (P2L); transpelvic width (TRANSP2W) = distance between outer bases of the pelvic spines (Bailey and Etnier, 1988); length of head (HL) = distance from the tip of the snout to the end of the opercular spine (Bailey and Etnier, 1988); depth of head at occiput (HD); width of head (HW); length of snout (SNL); length of orbit (ORL); length of upper jaw (UJL); and interorbital width (IOW).

An attempt was made to measure an equal number of males and females from each locality and, when possible, to measure specimens that were collected in or near the breeding season. However, since it was necessary to use museum samples to complete this study, it was virtually impossible to compare "like" samples due to differences in time of the year in which the samples were collected, ratio of males to females within a sample, overall size of specimens, method of preservation, and length of time since the samples were collected.

Statistical analysis of morphometric data was performed by principal component analysis. PCA was performed on the statistical program, SYSTAT, on a Macintosh SE personal computer. For the PCA a covariance matrix was used and the first three principal components were retained, all of which had eigenvalues of 0.5 or greater. PCA was used as a guideline to indicate shape differences between populations. When differences were indicated by the analysis, the fish were then reexamined

and indicated differences in shape were assessed visually. This was done to ensure that slight shape differences, which might be due to the previously mentioned problems of comparing "like" samples, were not interpreted as true taxonomic differences between populations.

3. Sexual Dimorphism

Males and females were found to be sexually dimorphic when their morphometrics were subjected to principal component analysis (Fig III-1). Character loadings for the first three principal components on the 25 measurements examined are shown in Table III-1. Principal component one is a general size vector since all the loadings are of the same sign and except for a few variables are equal in magnitude (Wiley, 1981). The first PC explains 91.8% of the total variance but is not useful in separating the sexes. As seen in Fig. III-1, the second principal component is useful in separating males from females. It accounts for 2.7% of the total variance. The characters which load heavily on this component are standard length, body depth, length of longest dorsal spine, length of second dorsal fin, length of anal base, length of anal fin, and pelvic fin length. This means that males have longer fins than females, and females have deeper bodies than males. These characters have traditionally proved useful in the separation of males from females in other sexually dimorphic percoid species (Winn, 1958; Page and Burr, 1976; Etnier and Bailey, 1989). The third principal component accounts for only 1.5% of the total variance and is not very useful in separating males from females (Fig. III-2).

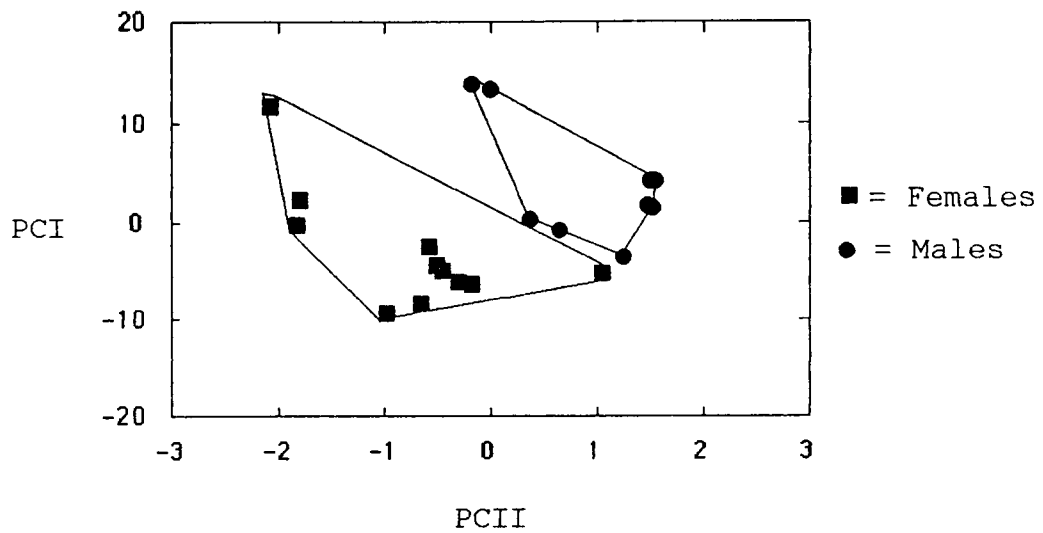


Figure III-1. Principal component analysis of 25 measurements on male vs. female Etheostoma nigrum from the Muskingum River showing PCI vs. PCII.

Table III-1. Character loadings for the principal components in the analysis of morphometric variables for male and female Etheostoma nigrum from Muskingum River.

Variable	PCI	PCII	PCIII
SL	4.695	-0.464	0.216
CPD	0.579	0.105	-0.017
BD	0.845	-0.370	-0.216
PREDL	1.474	-0.014	0.029
DOBASE1	1.358	-0.125	-0.468
DOBASE2	1.144	0.047	-0.276
D1L	1.473	0.039	-0.408
DSPL	0.647	0.225	0.044
D2L	1.806	0.476	-0.193
DRL	0.866	0.141	0.078
CPL	1.624	-0.174	0.255
ABASE	0.720	0.427	0.057
AL	1.271	0.567	0.050
ASPL	0.207	0.116	0.016
ARL	0.611	0.117	-0.049
P1L	1.142	0.126	0.039
P2L	0.697	0.227	0.146
TRANSP2W	0.488	-0.046	-0.004
HL	1.135	0.018	0.126
HD	0.764	0.117	0.027
HW	0.883	0.080	0.092
SNL	0.427	0.053	0.008
ORL	0.249	0.044	0.053
UJL	0.401	0.047	0.096
IOW	0.282	0.090	0.009

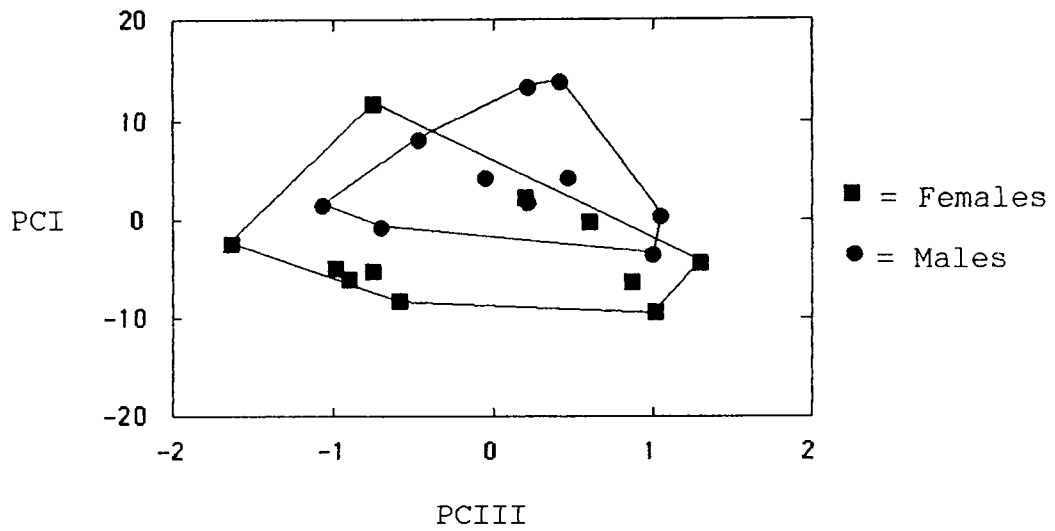


Figure III-2. Principal component analysis of 25 measurements on male vs female Etheostoma nigrum from the Muskingum River showing PCI vs PCIII.

PCA was performed on three other samples, also collected during the breeding season, and similar results were attained.

3. Interpopulation Analysis

To determine the usefulness of measurements in separating presumed taxa, a series of principal component analyses was performed on 25 measurements taken from specimens from various river systems. Figure III-3 illustrates the PCA performed on all the lower eastern Mississippi tributaries combined. There is considerable overlap of the five river systems, suggesting no differentiation in size or shape for these populations. These results agree with those taken from the meristic analysis. When the same analysis was performed on all the Mobile Bay specimens combined (Fig. III-4), similar results were attained, with the exception that specimens from the upper Tombigbee River separated somewhat from the other Mobile Bay river systems. Next, a PCA was performed on the lower eastern Mississippi tributaries and the Mobile Bay river systems combined (Fig. III-5). As seen in this figure, although there is some separation of specimens from these two geographic areas, there is enough overlap that based on morphometrics, specimens are not separable. This is in contrast to the results attained from the meristic data, where specimens were separable.

When a PCA was performed on specimens from the Mobile Bay river systems and from the Mountain Fork River system of Oklahoma (Fig. III-6), specimens were found to

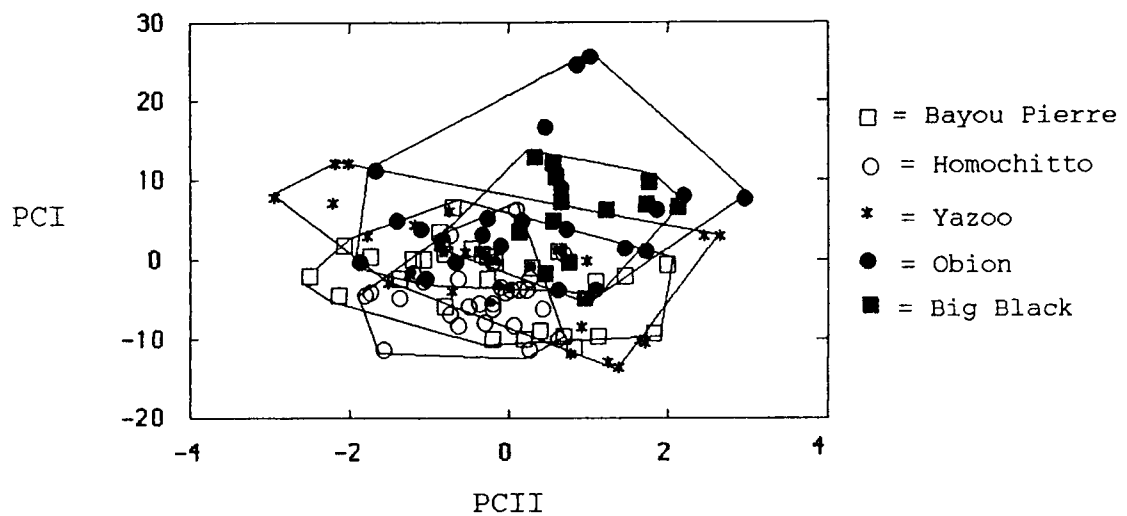


Figure III-3. Principal component analysis of 25 measurements on *Etheostoma nigrum* from lower eastern Mississippi tributaries.

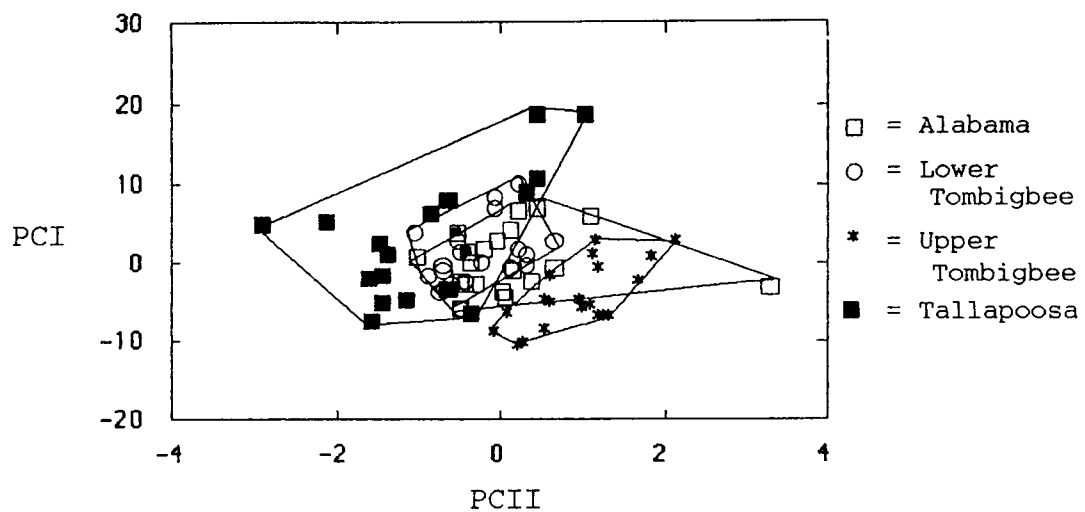


Figure III-4. Principal component analysis of 25 measurements on Etheostoma nigrum from Mobile Bay River systems.

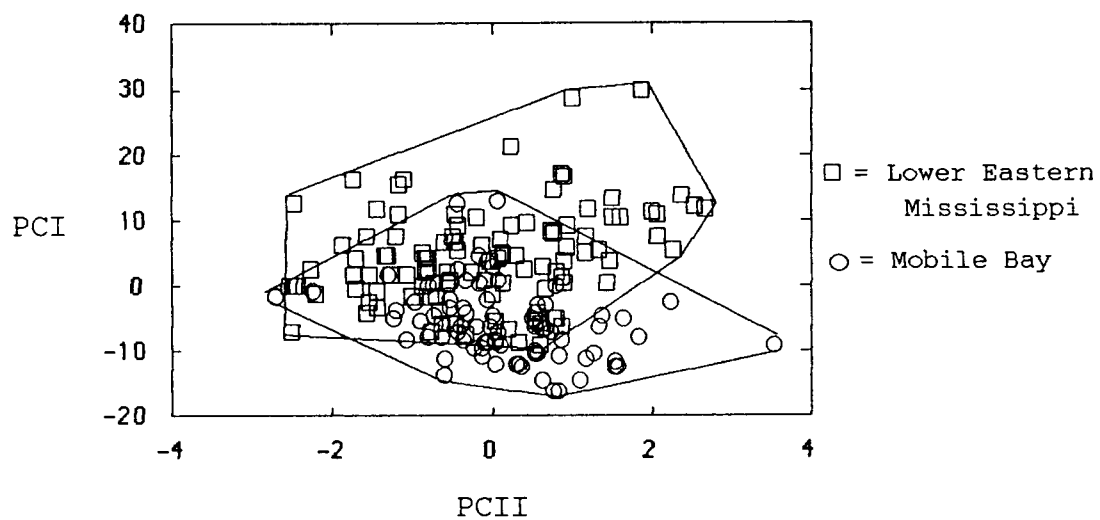


Figure III-5. Principal component analysis of 25 measurements on *Etheostoma nigrum* from eastern lower Mississippi vs. Mobile Bay.

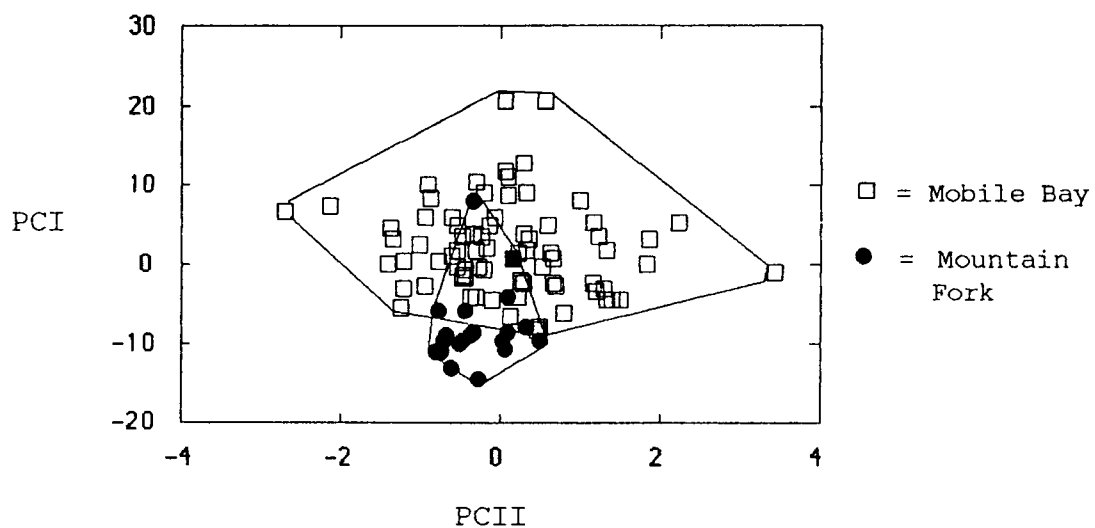


Figure III-6. Principal component analysis of 25 measurements on *Etheostoma nigrum* from Mobile Bay vs. Mountain Fork.

overlap considerably. Specimens from the Mountain Fork were also compared with specimens from the lower eastern Mississippi River tributaries (Fig. III-7). Although some separation along PCI is apparent, PCI is a general size vector and therefore should not be used to distinguish specimens among populations. In the meristic analysis of these populations, the Mississippi specimens were found to be different from the Mountain Fork River specimens, yet based on morphometrics they cluster together.

Specimens from the Tennessee River system were compared with specimens from the Mobile Bay drainage (Fig. III-8). There is almost complete overlap of these two geographic areas when measurements are considered. These results agree with those obtained from the meristic analysis. However, when measurements taken from specimens from the lower eastern Mississippi River tributaries were compared with those from the Tennessee River system (Fig. III-9), the results disagree with the meristic analysis. Figure III-9 illustrates that, based on measurements, specimens from the lower eastern Mississippi River tributaries and Tennessee River are not separable, while meristic data indicated differences between the two drainages.

PCA was performed on specimens from the Wabash River system of Ohio versus specimens from the Mobile Bay drainage (Fig. III-10). The only separation of individuals from these two geographic areas occurs along PCI, and as stated previously PCI is a general size vector and therefore is not important taxonomically. Separation of individuals from the Wabash River versus

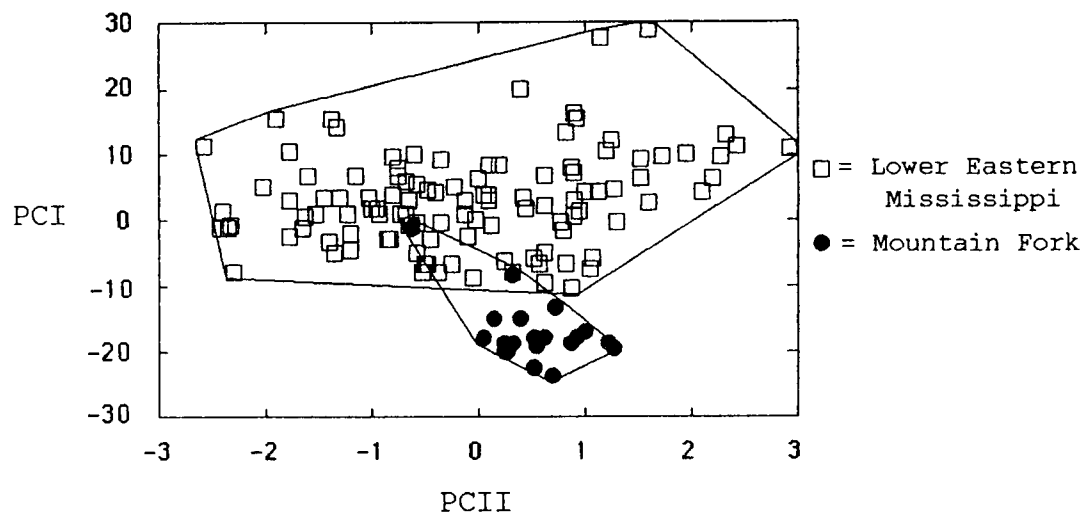


Figure III-7. Principal component analysis of 25 measurements on *Etheostoma nigrum* from lower eastern Mississippi vs. Mountain Fork.

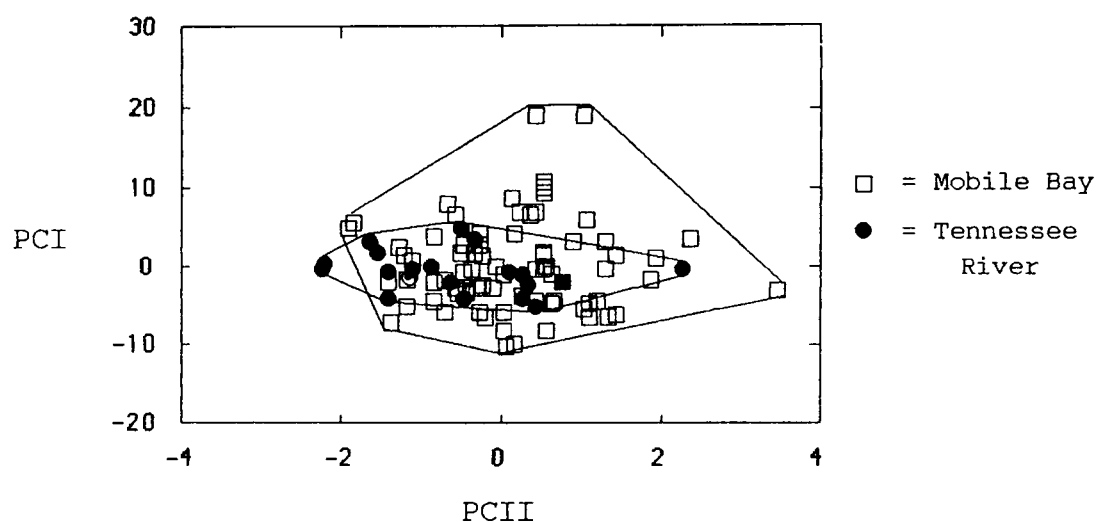


Figure III-8. Principal component analysis of 25 measurements on *Etheostoma nigrum* from Mobile Bay vs. Tennessee River.

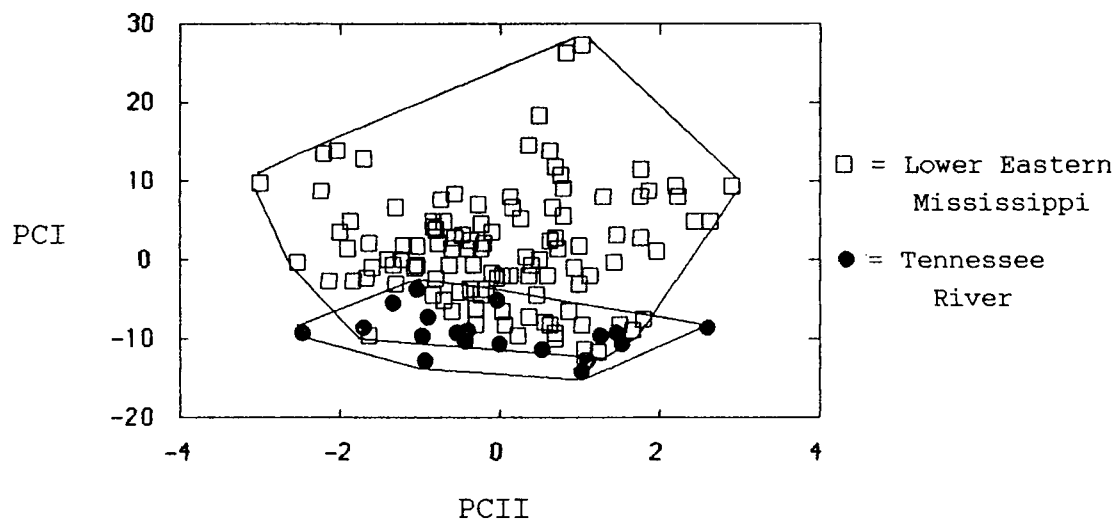


Figure III-9. Principal component analysis of 25 measurements on Etheostoma nigrum from lower eastern Mississippi vs. Tennessee River.

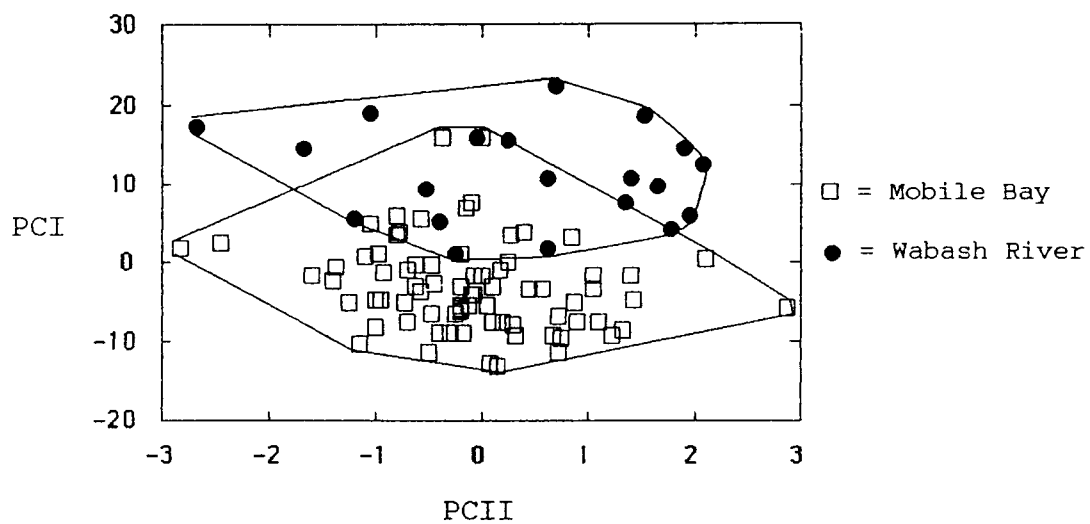


Figure III-10. Principal component analysis of 25 measurements on *Etheostoma nigrum* from Mobile Bay vs. Wabash River.

lower eastern Mississippi River tributaries was not possible either (Fig. III-11). This indicates that, based on size and shape, E. nigrum from the Wabash River are very similar to E. nigrum from the southern United States.

When specimens from the Osage River of Missouri were compared with specimens from the Mobile Bay drainage (Fig. III-12), considerable overlap was found, indicating no differentiation in size and or shape for these populations. Figure III-13 illustrates the results of a PCA performed on individuals of E. nigrum from the Osage River and the lower eastern Mississippi River tributaries combined. The only separation attained is along PCI, which is not important taxonomically. Therefore, based on morphometrics, specimens from the Osage River system are not separable from specimens from either the Mobile Bay drainage or the lower eastern Mississippi tributaries.

The next comparison made by PCA was between individuals from the Laramie River of Wyoming and those from the Mobile Bay (Fig. III-14). As seen in this figure, PCII, which explains 4.8% of the total variance, serves to separate individuals from these two areas. Table III-2 gives the character loadings for the first three principal components for the 25 measurements taken. The characters which load heavily on PC II are standard length, body depth, length of spinous dorsal fin base, length of depressed spinous dorsal fin, caudal peduncle length, anal fin length, length of anal fin base, and pelvic fin length. However, when these specimens were reexamined visually, these differences were too subtle to

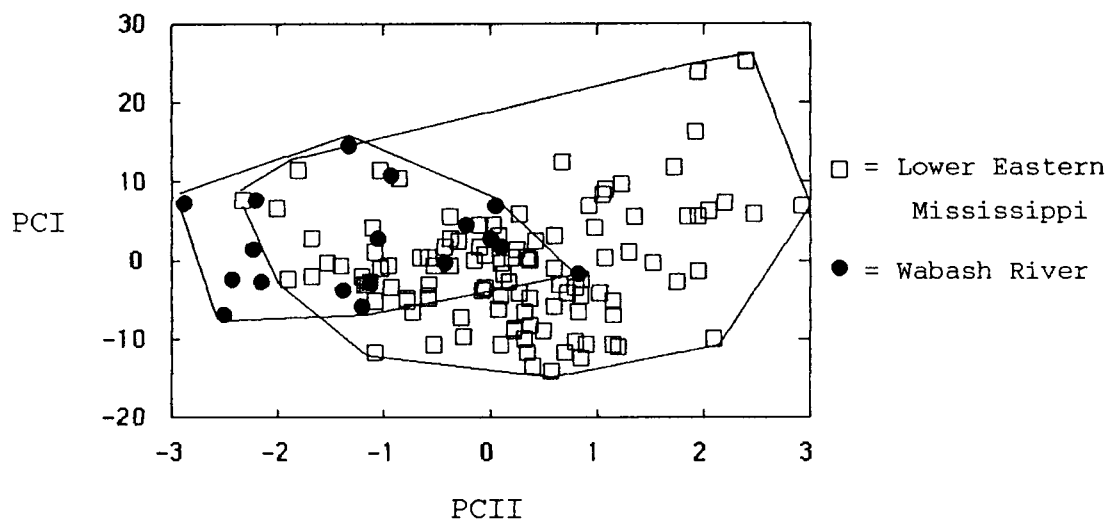


Figure III-11. Principal component analysis of 25 measurements on *Etheostoma nigrum* from lower eastern Mississippi vs. Wabash River.

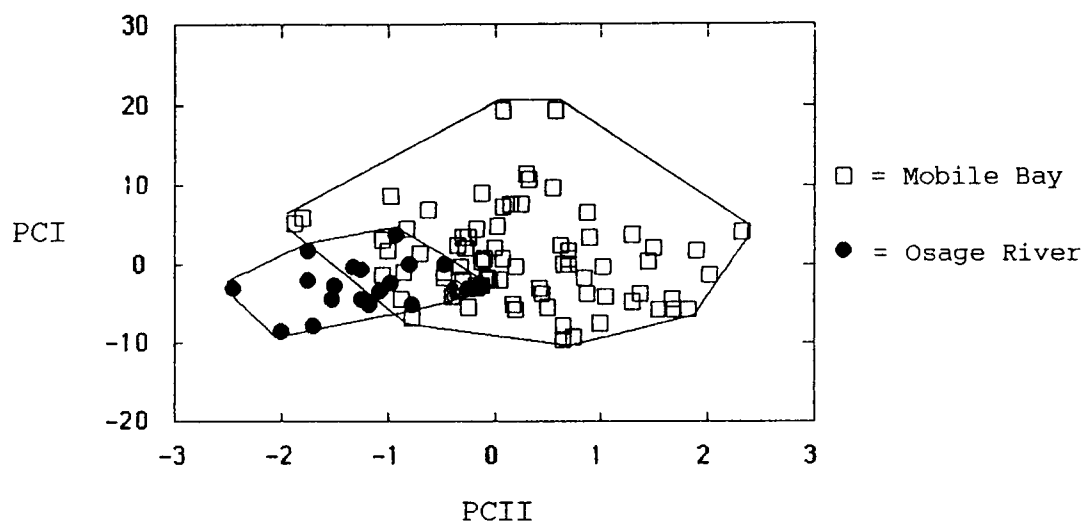


Figure III-12. Principal component analysis of 25 measurements on *Etheostoma nigrum* from Mobile Bay vs. Osage River.

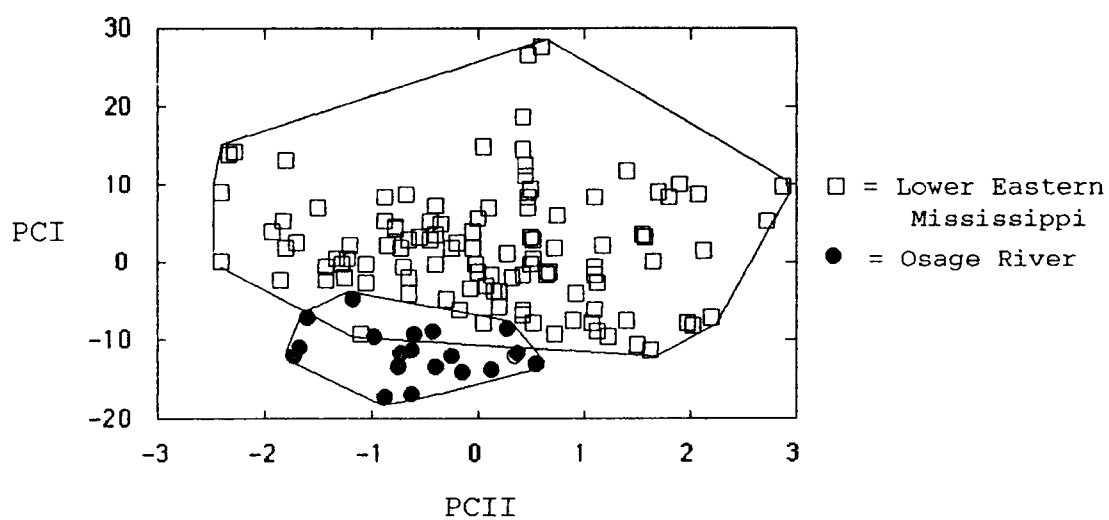


Figure III-13. Principal component analysis of 25 measurements on *Etheostoma nigrum* from lower eastern Mississippi vs. Osage River.

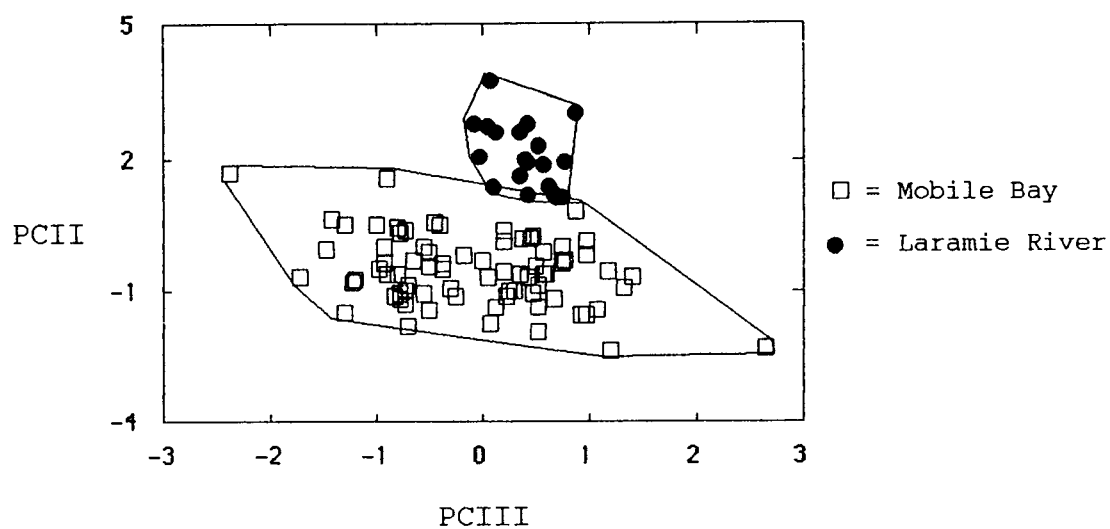


Figure III-14. Principal component analysis of 25 measurements on *Etheostoma nigrum* from Mobile Bay vs. Laramie River.

Table III-2. Character loadings for the principal components in the analysis of morphometric variables of Etheostoma nigrum from Mobile Bay versus Laramie River.

Variable	PCI	PCII	PCIII
SL	3.987	-0.359	0.041
CPD	0.429	0.039	-0.008
BD	0.672	0.253	-0.384
PREDL	1.181	0.128	-0.097
DOBASE1	1.161	-0.345	-0.202
DOBASE2	0.920	0.118	-0.121
D1L	1.230	-0.338	-0.131
DSPL	0.636	0.251	0.330
D2L	1.444	0.225	-0.228
DRL	0.649	0.245	0.080
CPL	1.278	-0.539	0.383
ABASE	0.603	0.379	0.070
AL	1.008	0.446	0.019
ASPL	0.124	0.235	0.096
ARL	0.480	0.243	0.093
P1L	0.998	0.258	-0.117
P2L	0.737	0.354	0.251
TRANSP2W	0.369	0.082	0.072
HL	0.931	0.212	0.079
HD	0.530	0.189	-0.012
HW	0.637	0.178	0.039
SNL	0.289	0.117	0.017
ORL	0.140	-0.065	-0.138
UJL	0.283	0.079	0.011
IOW	0.175	0.102	0.023

be detected. When specimens from the Laramie River were compared with specimens from the lower eastern Mississippi tributaries, no separation was possible (Fig. III-15).

When PCA was performed on specimens from the Apple River system of Wisconsin and those from the Mobile Bay drainage, separation occurred along PCII (Fig. III-16). PCII explains 1.7% of the total variance. Table III-3 gives the character loadings for the first three principal components. The characters which load heavily are body depth, length of spinous dorsal fin base, length of depressed spinous dorsal fin, caudal peduncle length, and anal fin length. While these characters may be slightly different between these samples, the differences were too subtle to be detected upon visual reexamination of specimens and are therefore interpreted as taxonomically insignificant. Specimens of E. nigrum from the lower eastern Mississippi tributaries were compared with those from the Apple River by way of PCA (Fig. III-17). Some separation of individuals is possible along PCIII, which explains 1.6% of the total variance. The character loadings for the first three principal components are given in Table III-4. The characters that load heavily are body depth, length of soft dorsal fin base, caudal peduncle length, and length of anal fin base. Specimens were reexamined visually and, while the Apple River specimens were slightly more robust, other differences were so subtle that they were interpreted as taxonomically insignificant.

A principal component analysis was performed on specimens from the Manistee River of Michigan and the

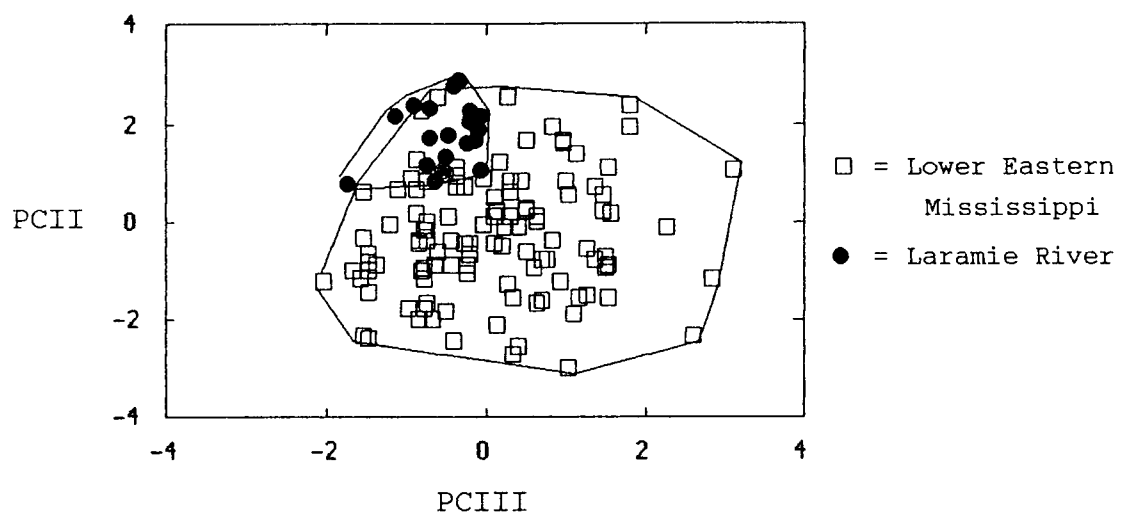


Figure III-15. Principal component analysis of 25 measurements on *Etheostoma nigrum* from lower eastern Mississippi vs. Laramie River.

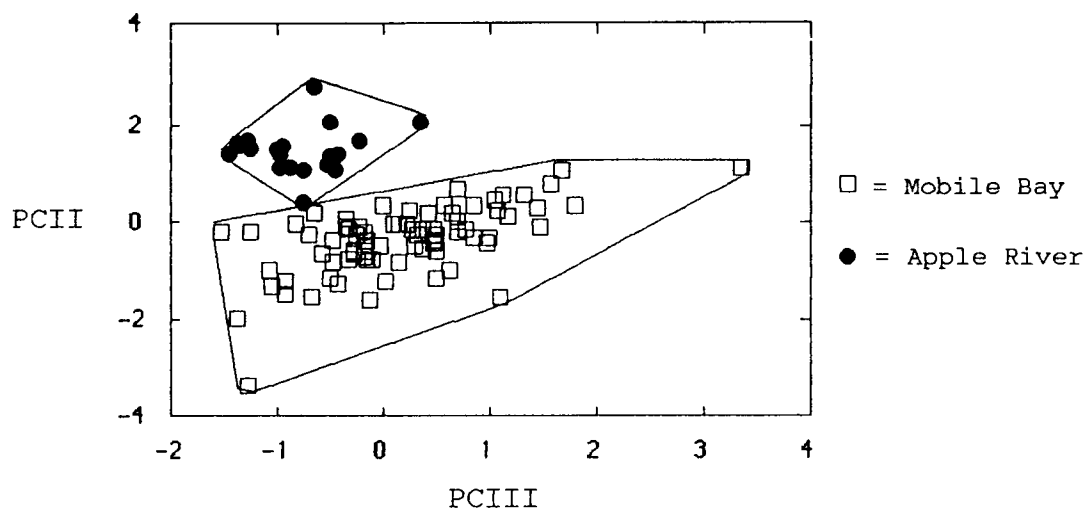


Figure III-16. Principal component analysis of 25 measurements on *Etheostoma nigrum* from Mobile Bay vs. Apple River.

Table III-3. Character loadings for the principal components in the analysis of morphometric variables of Etheostoma nigrum from Mobile Bay versus Apple River.

Variable	PCI	PCII	PCIII
SL	5.395	-0.108	-0.161
CPD	0.510	-0.002	0.022
BD	0.963	0.615	-0.003
PREDL	1.579	0.192	0.016
DOBASE1	1.504	-0.338	0.249
DOBASE2	1.276	-0.023	0.201
D1L	1.594	-0.350	0.208
DSPL	0.711	-0.054	-0.209
D2L	1.855	0.014	0.343
DRL	0.870	-0.024	0.074
CPL	1.705	-0.291	-0.506
ABASE	0.834	0.157	0.063
AL	1.401	0.230	0.166
ASPL	0.228	0.157	-0.065
ARL	0.716	0.202	-0.048
P1L	1.348	0.077	0.237
P2L	1.001	0.188	-0.208
TRANSP2W	0.476	0.020	-0.059
HL	1.197	0.171	-0.109
HD	0.705	0.172	-0.033
HW	0.854	0.035	-0.011
SNL	0.351	0.027	-0.004
ORL	0.220	-0.000	0.123
UJL	0.377	0.034	0.003
IOW	0.169	-0.008	0.001

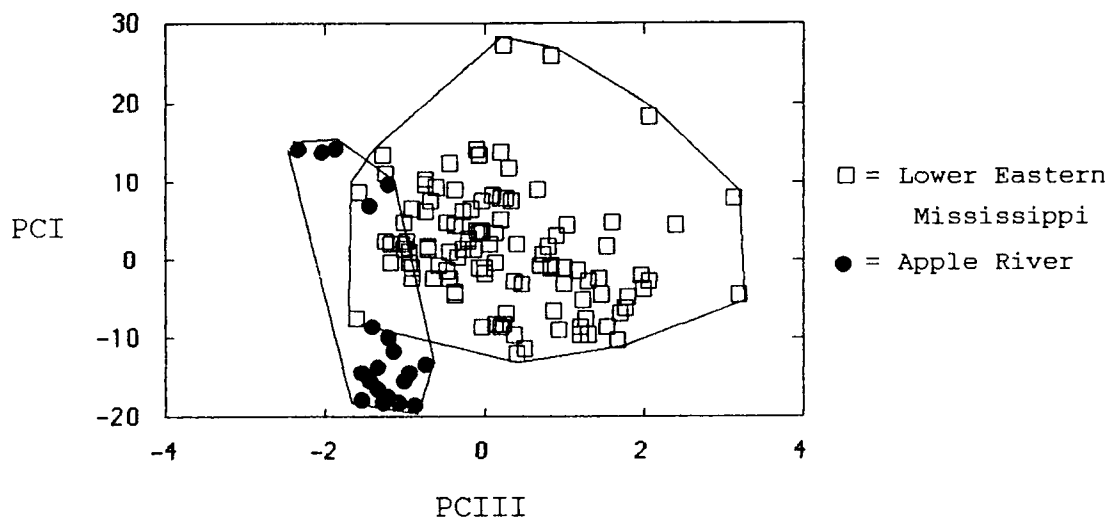


Figure III-17. Principal component analysis of 25 measurements on *Etheostoma nigrum* from lower eastern Mississippi vs. Apple River.

Table III-4. Character loadings for the principal components in the analysis of morphometric variables of Etheostoma nigrum from lower eastern Mississippi River tributaries versus Apple River.

Variable	PCI	PCII	PCIII
SL	6.302	-0.554	-0.206
CPD	0.577	0.061	0.085
BD	1.054	0.272	-0.402
PREDL	1.0710	-0.085	-0.214
DOBASE1	1.679	-0.007	-0.011
DOBASE2	1.768	0.262	0.306
D1L	1.950	0.142	-0.020
DSPL	0.925	0.183	0.081
D2L	2.605	0.560	0.225
DRL	1.146	0.198	0.086
CPL	1.717	-0.484	0.637
ABASE	1.065	0.250	0.360
AL	1.826	0.401	0.116
ASPL	0.365	0.035	0.092
ARL	0.861	0.103	-0.073
P1L	1.455	-0.014	-0.042
P2L	1.062	0.002	0.009
TRANSP2W	0.593	0.093	-0.055
HL	1.389	0.069	-0.233
HD	0.890	0.126	-0.278
HW	1.116	0.154	-0.249
SNL	0.390	0.034	0.066
ORL	0.267	0.016	0.076
UJL	0.465	0.055	0.008
IOW	0.143	0.023	0.107

Mobile Bay drainage (Fig. III-18). As seen in this figure, PCII, which explains 3.5% of the total variance, serves to separate the specimens. Character loadings for the first three principal components are shown in Table III-5. The characters which load heavily on PCII are length of soft dorsal fin base, length of soft dorsal fin, caudal peduncle length, anal fin length, and pectoral fin length. Principal component three explains 1.7% of the total variance and loads heavily for body depth, predorsal length, and caudal peduncle length. When these specimens and characters were reexamined visually, slight differences were detected in body depth, predorsal length, and pectoral fin length. However, these differences in shape were not extensive enough to be considered taxonomically important. Specimens from the Manistee River were also compared with those taken from the lower eastern Mississippi River tributaries (Fig. III-19). There is considerable overlap and neither PCII nor PCIII serves to adequately separate specimens.

4. Summary

Principal component analysis performed in this study has shown that, based on morphometrics, Etheostoma nigrum is a sexually dimorphic species. The male of the species has a higher spinous dorsal fin and longer soft dorsal, anal, and pelvic fins, while the female has a deeper body.

Principal component analysis performed here has also shown that there are slight differences in shape of E. nigrum among geographically distant populations.

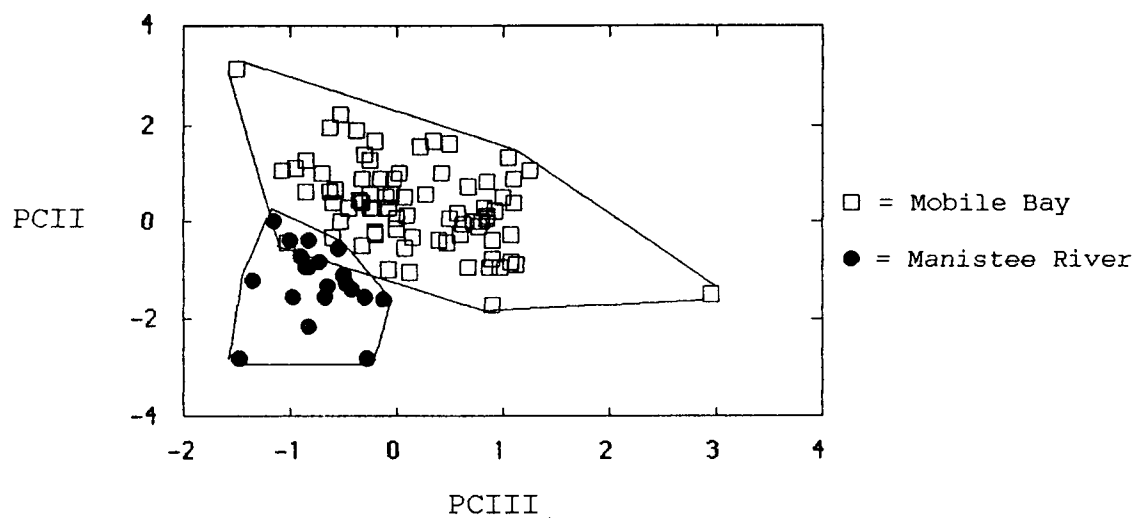


Figure III-18. Principal component analysis of 25 measurements on Etheostoma nigrum from Mobile Bay vs. Manistee River.

Table III-5. Character loadings for the principal components in the analysis of morphometric variables of Etheostoma nigrum from Mobile Bay versus Manistee River.

Variable	PCI	PCII	PCIII
SL	3.844	-0.323	-0.075
CPD	0.416	0.077	0.025
BD	0.579	0.095	-0.468
PREDL	1.094	-0.061	-0.228
DOBASE1	1.155	0.006	-0.056
DOBASE2	0.947	0.367	0.092
D1L	1.222	0.018	0.011
DSPL	0.582	-0.118	0.168
D2L	1.427	0.498	0.050
DRL	0.637	0.153	0.119
CPL	1.273	-0.464	0.368
ABASE	0.560	0.176	0.033
AL	0.961	0.351	0.049
ASPL	0.101	-0.027	-0.015
ARL	0.462	0.038	0.005
P1L	0.993	0.430	0.142
P2L	0.680	-0.006	0.137
TRANSP2W	0.345	-0.021	0.028
HL	0.876	-0.115	-0.123
HD	0.459	-0.118	-0.197
HW	0.578	-0.064	-0.069
SNL	0.267	0.005	-0.026
ORL	0.147	0.093	-0.075
UJL	0.267	0.014	-0.018
IOW	0.167	0.016	-0.006

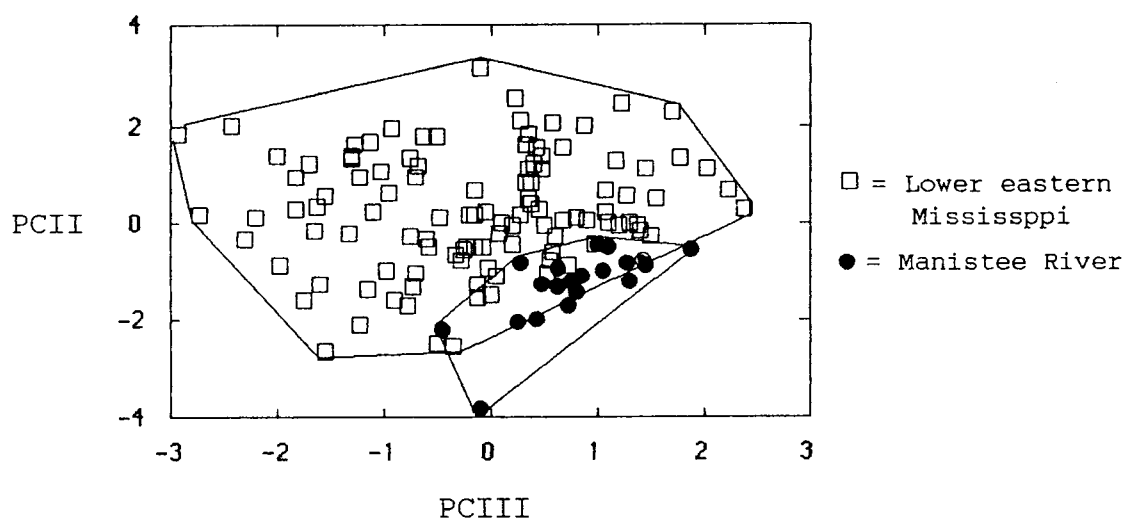


Figure III-19. Principal component analysis of 25 measurements on *Etheostoma nigrum* from lower eastern Mississippi vs. Manistee River.

Overall, populations at the extremes of the midwestern area are morphometrically more similar to E. nigrum from the lower eastern Mississippi River tributaries than to Mobile Bay populations (Figures III-14 through III-19). This may be due to the fact that most specimens from the Midwest and lower eastern Mississippi River tributaries were fairly large while the majority of Mobile Bay specimens were small. However, the small size of the Mobile Bay specimens appears to be a sampling artifact, since a few samples did contain specimens as large as those from the Midwest and Mississippi River. Therefore, if a higher percentage of the Mobile Bay specimens had been larger in size, the shape differences between them and the extreme Midwest populations might not have been as pronounced.

Although there is slight separation of several populations based on principal component analysis, no morphometric differences were visually observed that allowed complete separation of populations. Based on the findings of principal component analysis and visual examination it appears that morphometrics are not very useful in the separation of Etheostoma nigrum populations.

CHAPTER IV.

KARYOTYPES

1. Introduction

Speciation in plants and animals may often be accompanied by chromosomal rearrangements such as translocations, inversions, and centric fusions (White, 1978). Karyotypes may therefore be important to systematists making decisions about potential species or subspecies when morphological differences are not readily apparent. For example, Howell and Black (1981) found that Fundulus notatus and Fundulus olivaceus, two morphologically similar species of topminnows, had different chromosome numbers, with F. notatus having a diploid number of 40 and F. olivaceus having a diploid number of 48.

The study of chromosomes, known as karyology, may be broken down into three levels (Wiley, 1981): 1) alpha karyology, in which the chromosome number and size can be determined; 2) beta karyology, in which the chromosome number and centromeric location can be determined; and 3) gamma karyology, in which the chromosome number, centromeric location, and banding patterns can be determined. In the study of most fishes, beta karyology is the level attained; however, some attempts at examining banding patterns of chromosomes in cyprinid fishes have provided useful information. While the

karyotypes of some groups of fishes have been well documented, those of the family Percidae have been very poorly studied. Fewer than 10% of percid species and about 7% of described darter species have been karyotyped.

Etheostoma nigrum is a species for which the karyotype has been documented (Ross, 1973). The karyotype was made from specimens from the Ohio and Lake Erie drainages and was reported as having 4 metacentric and 44 acrocentric chromosomes. However, E. nigrum is a wide ranging species, and within that range it has been found to exhibit an array of geographic variation in both morphological characters (Lagler and Bailey, 1947; Underhill, 1963; Kott and Humphreys, 1978) and life history characters (Propst and Carlson, 1989). Since these characters exhibit variation, the possibility exists that genetic characters such as chromosome number and types might also be variable. For this reason, a karyotypic analysis of E. nigrum from southern and northern populations was performed. Etheostoma olmstedi, the presumed sister species of E. nigrum, was also karyotyped in order to make a comparison between the two possible.

2. Material and Methods

Specimens for karyotypic analysis were collected by seining the following locations: southern E. nigrum at Chilatchee Creek, 0.5 km N of Alberta at AL Hwy. 5, Dallas Co., AL, and Long Creek, 7.7 km SE of Dentville, Copiah Co., MS; northern E. nigrum at North Fork of the Zumbro River at Kenyon, Goodhue Co., MN; and E. olmstedi

at Killian Cr., Co. Rd. 1511, 1.6 km W of Lowesville, Lincoln Co., NC.

Freshly caught specimens were transported to the laboratory, caudal fin clips were made, and the fish were placed in aquaria and fed for four-days, thus allowing for regrowth of fin tissue. After the four day period the fish were placed in a beaker containing a 0.01% colchicine solution and held with aeration for three hours. The fish were then sacrificed, and the gills and regenerated caudal fin tissue were removed and placed in a 0.7% salt-colchicine solution for three hours. Tissues were washed, then allowed to swell in distilled water for 45 min, and fixed in two changes of 3:1 methanol:glacial acetic acid for 30 min each. Tissues were dabbed onto slides, air or flame dried, and stained in 6% Giemsa (Howell & Villa, 1976).

Measurements of long arm (L), short arm (S), and total length were made with dial calipers from photographs of 5 well spread mitotic cells from each of the three geographic areas. The L/S ratios were calculated and the chromosomes were classified by centromeric position according to Levan et al. (1964). The centromere is considered to be median (m) if the L/S ratio is between 1.00-1.70, submedian (sm) if the ratio is between 1.71-2.99, subterminal (st) if the ratio is between 3.00-6.99, and terminal (t) if the ratio is greater than 7.00. In addition, 129 other cells were scanned to determine modal diploid number. Next, the chromosome formula, a ratio of A chromosomes to B chromosomes, was calculated by grouping median and submedian chromosomes into a group designated A and

subterminal and terminal chromosomes into a group designated B (Bickham, 1975). Finally, the fundamental arm number, which is the total number of arms in the chromosome complement, was calculated by scoring A chromosomes as biarmed and B chromosomes as uniarmed.

3. Results

The karyotypes from the two southern populations were found to be identical and were therefore grouped. Etheostoma nigrum from the southern populations had a modal diploid number of 48 (Table IV-1 and Fig. IV-1). The southern populations had a fundamental arm number of 90 (Table IV-1) and had modally 8 median, 34 submedian, and 6 subterminal chromosomes (Table IV-2 and Fig. IV-1).

Etheostoma nigrum from the northern population also had a modal diploid number of 48 (Table IV-1 and Fig. IV-2). However, the northern population had a fundamental arm number of 86 (Table IV-1) and had modally 4 median, 34 submedian, and 10 subterminal chromosomes (Table IV-2 and Fig. IV-2).

Etheostoma olmstedii was also found to have a modal diploid number of 48 (Table IV-1 and Fig. IV-3). It was similar to the northern E. nigrum population in having a fundamental arm number of 86 (Table IV-1). However, it differed from both E. nigrum populations by having modally 6 median, 32 submedian, and 10 subterminal chromosomes (Table IV-2 and Fig. IV-3).

Table IV-1. Aspects of the karyotype of Etheostoma olmstedi and E. nigrum from two geographic areas.

Taxon	Number of		Modal	Chromosome		Fundamental
	Specimens	Cells Counted	Diploid Number	Formula	Arm Number	
<u>E. olmstedi</u>	4	41	48	38:10		86
<u>E. nigrum</u> (Northern)	4	30	48	38:10		86
<u>E. nigrum</u> (Southern)	7	58	48	42:6		90

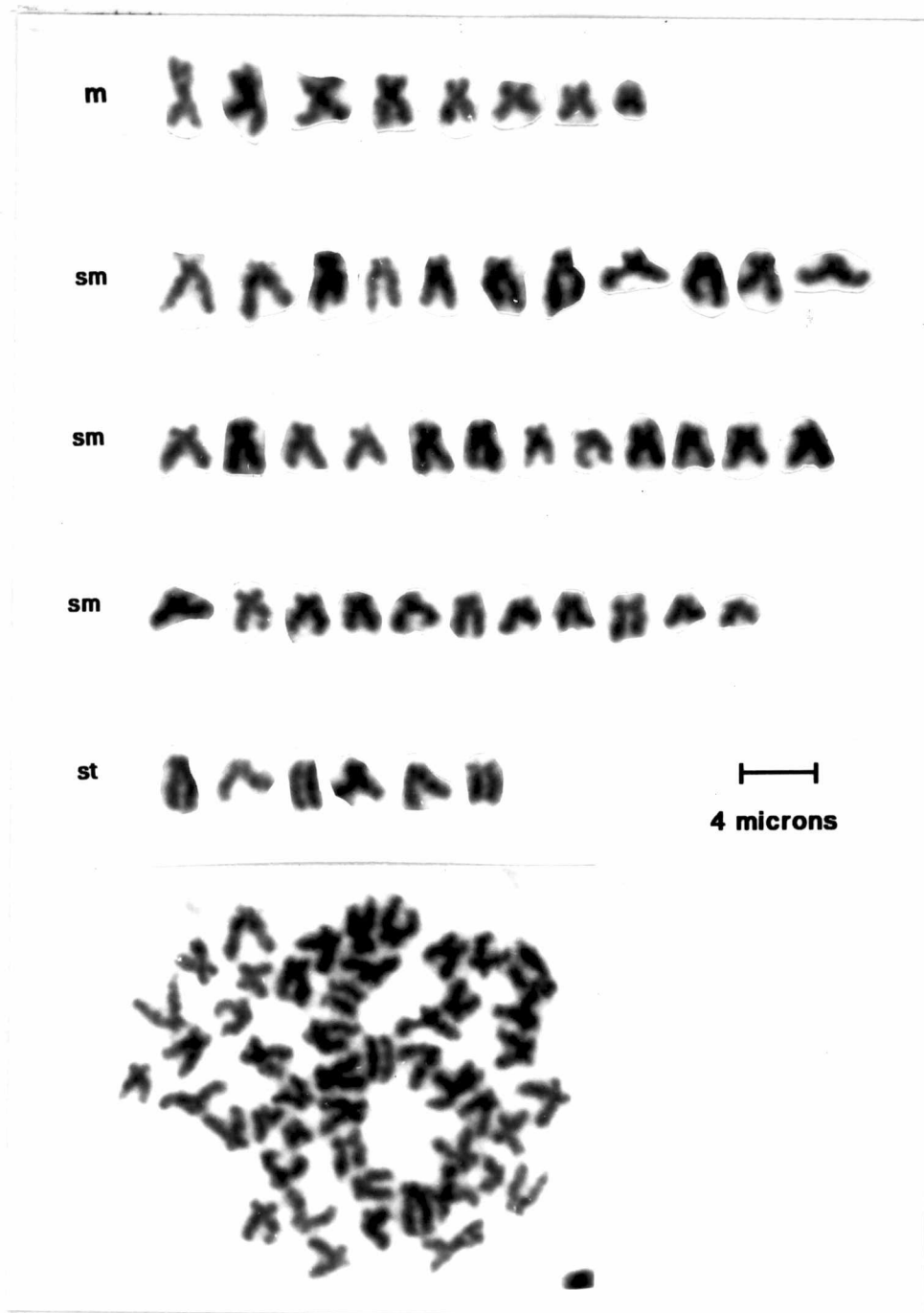


Fig. IV-1. Karyotype of *Etheostoma nigrum* from southern populations based on mitotic gill epithelium cells.

Table IV-2. Distribution of chromosome type for Etheostoma olmstedii and E. nigrum from two geographic areas.

Taxon	Chromosome Type									
	median			submedian			subterminal			
	Range	$\bar{x}$	Mode	Range	$\bar{x}$	Mode	Range	$\bar{x}$	Mode	
<u>E. olmstedii</u>	-	6	6	31-33	32	32	9-11	10	10	
<u>E. nigrum</u> (Northern)	-	4	4	32-34	34	34	10-11	10.2	10	
<u>E. nigrum</u> (Southern)	-	8	8	33-35	34	34	5-7	6	6	

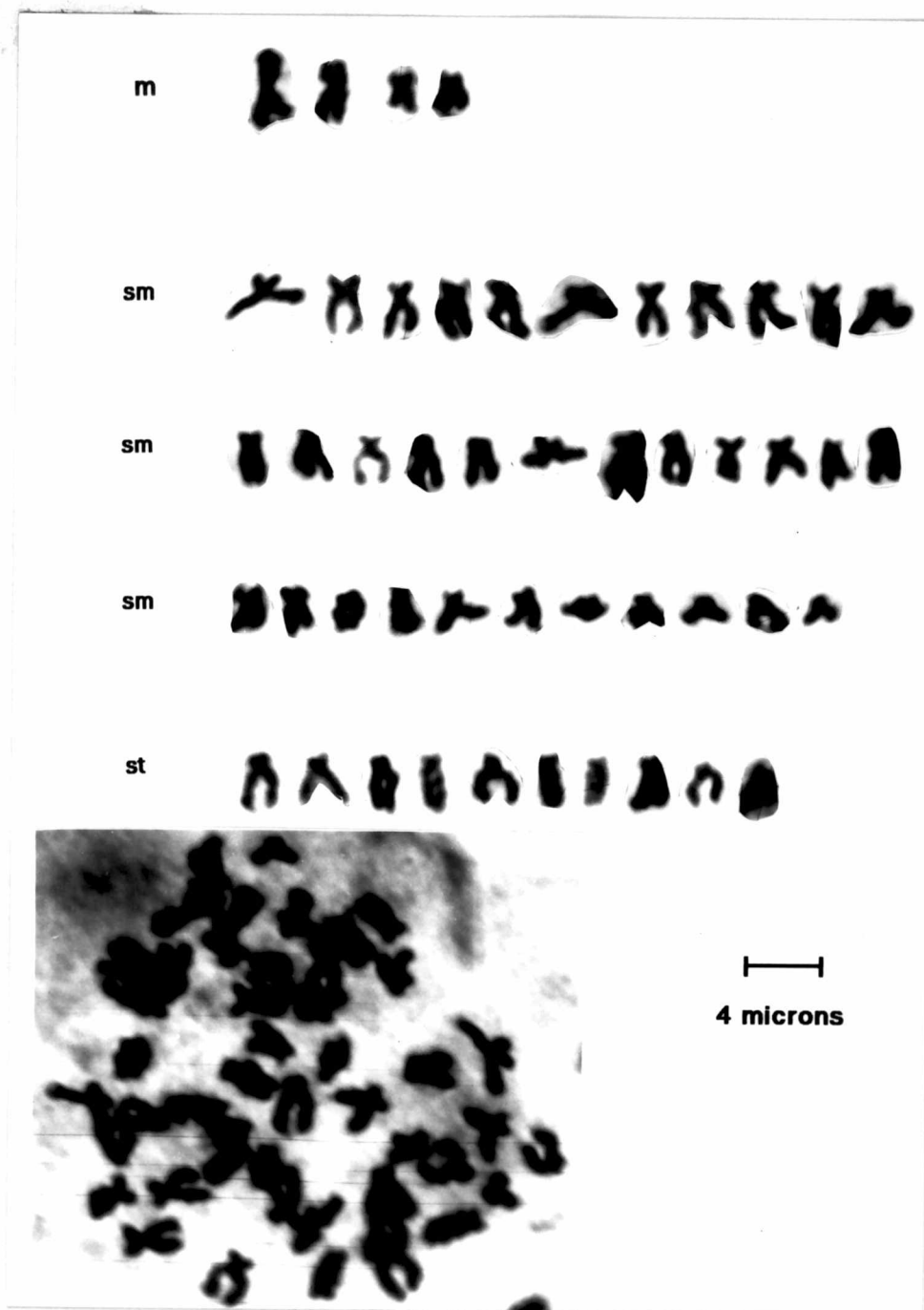


Fig. IV-2. Karyotype of *Etheostoma nigrum* from northern populations based on mitotic gill epithelium cells.

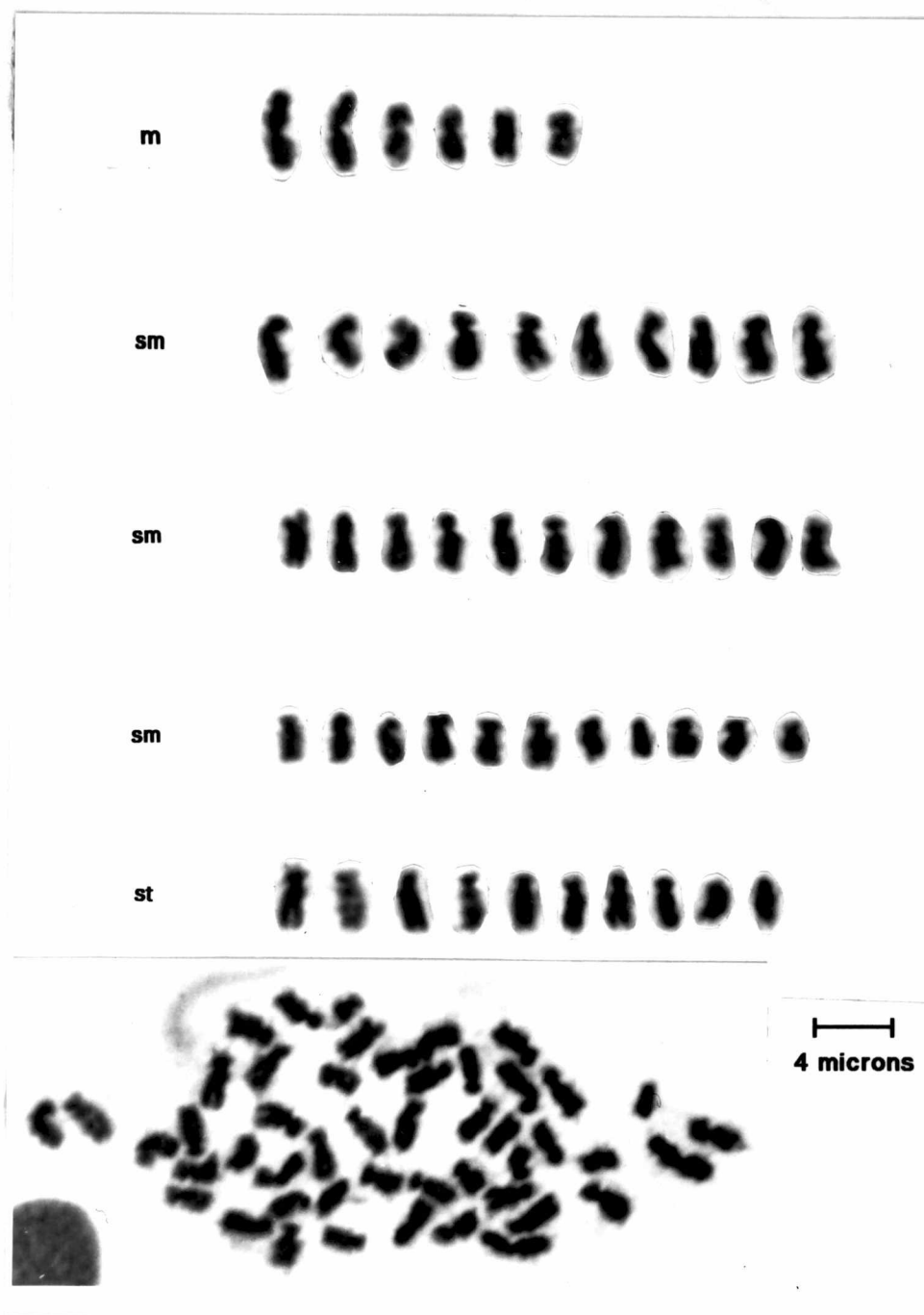


Fig. IV-3. Karyotype of *Etheostoma olmstedii* based on mitotic gill epithelium cells.

4. Discussion

The data reported here illustrate that Etheostoma nigrum exhibits geographic variation in the number of types of chromosomes present and, therefore, in fundamental arm number. In fact, based on fundamental arm number data, the populations of E. nigrum from the north would appear to be karyotypically more similar to E. olmstedii than to southern E. nigrum populations. However, as noted by Gold et al. (1979), the chromosomes of darters are small and asymmetrical, so the interpretation of fundamental arm number data should be conservative.

The earlier karyotype of E. nigrum (Ross, 1973) consisted of 4 metacentric and 44 acrocentric chromosomes. This karyotype would result in a fundamental arm number of 52 for northern E. nigrum populations rather than the fundamental arm number of 86 reported by the present study. However, upon enlarging the karyotype of E. nigrum in the earlier study, and then measuring and calculating the L/S ratios, several of the chromosomes scored as acrocentrics were found to have ratios that would place them as submedians in the Levan et al. classification scheme. Taking this into consideration the fundamental arm number would be somewhat higher than 52. Gold et al. (1979) also suggested the possibility that some of the chromosomes might be incorrectly scored as uniarmed. Regardless, it should be noted that the 4 metacentric chromosomes reported for these northern populations agrees with the 4

median chromosomes from the northern population of the present study.

The karyotype of primitive teleosts is generally believed to have been composed of 46 to 48 acrocentric, uniarmed chromosomes (Nayyar, 1966). By way of centric fusion, biarmed chromosomes such as submedian and median chromosomes were formed and a more derived karyotype evolved (Denton, 1973). The direction of evolution from uniarmed to biarmed chromosomes is thought to be more likely, since centric fusion requires only one step and centric fission is a two or more step process (Legrande and Fitzsimmons, 1976). Therefore, based on fundamental arm number data alone the southern karyotype with 8 median chromosomes would appear to be more advanced than the northern karyotype with 4 median chromosomes. Further discussion of the evolutionary aspects of E. nigrum and E. olmstedii karyotypes will be addressed in the following chapter.

CHAPTER V.

EVOLUTIONARY CONCEPTS

AND

SUMMARY

The subgenus Boleosoma is presently considered to contain five species: Etheostoma nigrum, E. olmstedii, E. longimanum, E. podostemone, and E. perlongum (Cole, 1971; Page, 1983; Bailey and Etnier, 1988). However, Shute (1984) found electrophoretic evidence that E. perlongum and E. olmstedii are conspecific, and in the future E. perlongum may be synonymized with E. olmstedii. Etheostoma longimanum, E. podostemone, and E. perlongum have very restricted ranges, in the James River of Virginia and West Virginia, the Roanoke River of Virginia, and in Lake Waccamaw of North Carolina, respectively (Cole, 1957). Etheostoma nigrum and E. olmstedii are more wide ranging. Etheostoma nigrum is found from the east coast to the Rocky Mountains and from Hudson Bay to the southern Gulf Coast, and E. olmstedii is distributed along the east coast from Georgia and Florida to Canada. Since four or five species of Boleosoma are located in the area of North Carolina and Virginia this area probably served as the center of origin for this group. This hypothesis is based on the evolutionary biogeographical tenet that states: "the area with the most species is probably the center of origin" (Wiley, 1981). Since the time of the speciation events,

E. nigrum and E. olmstedii have had more time for or more success at dispersal and therefore, have larger present ranges than the other three species.

Cole (1971) hypothesized that E. nigrum and E. olmstedii speciated from a common Boleosoma stock prior to Pleistocene glaciation, and I agree with this premise. Cole also stated that E. nigrum evolved west of the Appalachians in isolation from E. olmstedii and later moved eastward. Although this is certainly possible, I hypothesize that E. nigrum evolved from a Boleosoma stock east of the Appalachian Mountains in the area of North Carolina and Virginia. This scenario is supported by the center of origin theory already mentioned. I hypothesize that E. nigrum moved westward by way of stream capture into the pre-Pleistocene Teays River and then radiated southeast into the Tennessee River, north and south into the Mississippi River, and west into the Missouri River. Dispersing south in the Mississippi River, E. nigrum could then move west into the Arkansas and Red river drainages and east into the Obion, Yazoo, Big Black, Homochitto, and Bayou Pierre river systems. Etheostoma nigrum dispersing north in the Mississippi River could populate the rivers of the midwest, the Great Lakes, and the Hudson Bay drainage. Finally, E. nigrum could have dispersed into the Mobile Bay drainage either by way of a Tombigbee-Tennessee river connection or by moving eastward from the mouth of the Mississippi River, along the Gulf Coast, to the mouth of the Mobile Bay, and then north into the Alabama and Tombigbee rivers (Swift et al., 1986). All of this probably occurred prior to Pleistocene glaciation, so that the distribution of

E. nigrum at the beginning of the Pleistocene may have been very similar to its present distribution.

At the maximum extent of Pleistocene glaciation, populations of E. nigrum probably existed in the Tennessee River, Mobile Bay drainage, lower eastern Mississippi River tributaries, Red River, Arkansas River, and Missouri River drainages, and in the James, Roanoke, Tar, and Neuse rivers east of the Appalachians. In addition, populations of E. nigrum may have existed in the area presently drained by the Cumberland River and the southern tributaries to the Ohio River. During the period of glaciation, I believe that while the refugia populations of E. nigrum in the lower eastern Mississippi River tributaries retained ancestral characters such as a high number of dorsal rays and a more complete cephalic lateralis canal system, refugia populations in the Mobile Bay drainage and in the Arkansas, Red, Tennessee, and Missouri river drainages began to diverge from each other and also from the lower eastern Mississippi River tributary populations. This divergence resulted in a decrease in the number of dorsal rays and in a reduction of the cephalic lateralis canal system in these refugia populations. The polarity of these characters is based on the fact that a more complete cephalic lateralis canal system and a higher number of fin ray elements are believed to be primitive characters for darters as a whole (Bailey and Etnier, 1988), and are characters of E. olmstedii and other Boleosoma species (the immediate outgroups). As the glaciers receded, E. nigrum from the various refugia populations could move back into the previously glaciated area of the upper Midwest. As this

recolonization occurred, the characters from these various refugia populations could have mixed, resulting in the E. nigrum populations of the upper Midwest having the mosaic pattern of meristic characters seen today.

There are two alternative explanations for the mosaic pattern of variation present in the Midwest. First, there may have been a mosaic pattern of variation present in the populations of the Midwest prior to glaciation. During glaciation some populations could have been displaced to the south, become isolated, and later diverged; however, a continuous band of populations with the original pattern of mosaic variation might have persisted south of the glacial front, so that no variation was lost. Then as the glaciers receded these populations could reinvade the Midwest resulting in the mosaic pattern of variation present today. Secondly, after glaciation the Midwest could have been reinvaded by undifferentiated E. nigrum populations and since that time the mosaic pattern of variation has arisen *in situ* as a result of one or more factors such as, selective forces, genetic drift, mutation, etc.

The recolonization of the Ohio River appears to have been mainly from one or two E. nigrum stocks, probably from the Tennessee River or from the east coast rivers, so that the mosaic pattern of meristic characters is not present there. Later the Ohio River populations may have evolved into the current race, which has fewer branchiostegal rays and fewer pectoral rays. Alternatively, the Ohio River may have been stocked from now extinct populations which already possessed fewer branchiostegal and pectoral rays.

From examining populations of E. nigrum found primarily west of the Appalachian Mountains and south of the Great Lakes the following conclusions were reached:

- 1) The populations of E. nigrum in the Bayou Pierre, Homochitto, Big Black, Yazoo, and Obion river systems of Mississippi, Tennessee, and Kentucky exhibit racial distinctions. They have a higher number of dorsal soft rays (modally 13 compared with 12 in other southern populations), a more complete infraorbital canal system (modally 10, 11, or 12 pores compared with 8 or 9 pores in other southern populations), and a more complete supratemporal canal system (with 89% complete compared with 0-64% complete in other southern populations). These characters are similar to those of E. olmstedii populations and may have been retained from the ancestral condition or be independent responses to the coastal plain regime in which they both live. The populations of the Mobile Bay drainage are believed to be the most closely related to these populations based on similarity of meristic characters.
- 2) The populations of the Ohio River drainage (excluding the Wabash River) exhibit racial distinctions. They have fewer branchiostegal rays (modally 10 or 11 compared with 12 elsewhere) and fewer pectoral rays (modally 11 rays compared with 12 elsewhere).

The populations of E. nigrum in the upper Cumberland River, presently designated a subspecies, E. n. susanae, show similarities to the Ohio River race of E. nigrum. Further examination of specimens from this area is necessary before a final decision on the status of these populations can be made.

- 3) The following meristic characters have shown meaningful geographic variation: dorsal soft rays, pectoral rays, supratemporal canal pores, infraorbital canal pores, preoperculomandibular canal pores, squamation, and branchiostegal rays. The distribution of these characters in E. nigrum has important biogeographical implications and provides evidence for several stream captures and past river associations.
- 4) Morphometric analysis has shown that E. nigrum is sexually dimorphic, with males having longer spinous dorsal, soft dorsal, anal, and pelvic fins, and females having deeper bodies. Lack of any notable separation of E. nigrum populations based on morphometric analysis has also shown that measurements are not very useful in separating closely related populations of this species.
- 5) Populations of E. nigrum exhibit geographic variation in the number of types of chromosomes present and in the fundamental arm number. Southern populations from the Bayou Pierre River of Mississippi and Alabama River of Alabama had 8 median, 34 submedian, and 6 subterminal chromosomes, resulting in a fundamental arm

number of 90. A northern population from the Zumbro River of Minnesota had 4 median, 34 submedian, and 10 subterminal chromosomes, resulting in a fundamental arm number of 86. Although the fundamental arm number data indicate that the southern populations, which have more biarmed chromosomes, are more advanced than the northern populations, meristic data indicate that the southern populations are primitive and the northern populations are advanced. E. olmstedii had 6 median, 32 submedian, and 10 subterminal chromosomes and a fundamental arm number of 86.

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APPENDIXES

APPENDIX A

MATERIAL EXAMINED

MATERIAL EXAMINED

Following is a list of the specimens of E. nigrum examined in the course of this study. The material is first grouped by drainage basin; within each basin entries are grouped by river drainage or river system, beginning with the southernmost populations and then moving northward. Within a river drainage or system entries are arranged alphabetically according to the county in which they were collected. With the exception of the University of Alabama Ichthyological Collection (UAIC), the abbreviations for the institutions from which study collections were obtained follow Leviton et al. (1985), as follows: INHS = Illinois Natural History Survey; KU = University of Kansas; OSM = Ohio State University Museum; OSUS = Oklahoma State University; ROM = Royal Ontario Museum; SIUC = Southern Illinois University (Carbondale); TU = Tulane University; UF = University of Florida, Florida State Museum; UMMZ = University of Michigan Museum of Zoology; UT = University of Tennessee.

Mobile Bay Basin

Alabama River system, Alabama: UAIC
2341.19(2), Cane Creek, 4.8 km S of Lower Peach Tree, Clarke Co.; UAIC 526.10(1), Chilatchee Creek, Alberta, Dallas Co.; UAIC 2392.22(3), Bogue Chitto Creek on dirt road, 8.0 km N of Rives, Dallas Co.; UAIC 2394.07(3), Tatum Creek, 4.0 km N of Orrville, Dallas Co.; UT

91.3392(6), Chilatchee Creek at AL Highway 5 and 66, Dallas Co.; UT 91.3529(1), Soapstone Creek, 13.4 km SE of Selma, Dallas Co.; UT 91.3530(13), Chilatchee Creek at AL Highway 5, Dallas Co.; UAIC 542.01(1), Dry Cedar Creek, 6.4 km E of Braggs on AL Highway 11, Lowndes Co.; UAIC 2370.20(14), unnamed tributary of Limestone Creek on Co. Rd. 20, 3.2 km E of Monroeville, Monroe Co.; UAIC 2374.08(4), unnamed creek 2.4 km SE of Vredenburgh on Co. Rd. 56, Monroe Co.; UAIC 3511.10(2), Big Flat Creek, Monroe Co.; UT 91.3449(3), Lovetts Creek 15.4 km WNW of Megargel on Co. Rd. 1, Monroe Co.; UT 91.3531(16), Tallahatchee Creek 3.2 km SSW of Vredenburgh, Monroe Co.; UAIC 2405.21(2), Pintlalla Creek on U.S. 80, Montgomery Co.; UAIC 2123.09(1), Washington Creek on AL Highway 183, Perry Co.

Black Warrior River system, Alabama: UAIC 3836.08(6), Creek at Smith Lake at Cold Springs, Cullman Co.; UT 91.2195(17), Boxes Creek at AL Highway 13, 1.0 road km S of Fayette Co. Rd. 44, and 6.2 km S of Walker Co. line, Fayette Co.; UAIC 3831.07(5), Cane Creek outside Jasper on AL Highway 69, Walker Co.; UAIC 3848.08(2), Mill Creek, 4.0 km N of Carbon Hill, Walker Co.

Cahaba River system, Alabama: UAIC 4707.16(3), Sandy Creek, off AL Highway 82, 12.0 km E of Centreville, Bibb Co.; UAIC 964.10(3), Wells Creek, AL Highway 14, 4.5 km SE of Sprott, Perry Co.

Tallapoosa River system, Alabama: UAIC 1474.08(2), Moores Creek, 1.6 km S of Bullock-Macon Co.

line on AL Highway 29, Bullock Co.; UAIC 1484.11(7), Coleman Creek, .6 km W of Fitzpatrick, Bullock Co.; UAIC 1353.06(2), Wallahatchee Creek, 2.1 km S of Tallasee, Elmore Co.; UAIC 1369.08(2), Calabee Creek, 2.2 km N of AL Highway 80 at Calabee Presbyterian Church, Macon Co.; UAIC 1480.13(1), Opintlocco Creek, 7.0 km N of Creek Stand on dirt road, Macon Co.; UAIC 1482.12(5), Calfbee Creek, .8 km S of Davisvillle on AL Highway 29, Macon Co.; UAIC 1512.02(3), Cubahutchee Creek, NE of Hardaway on farm road, Macon Co.; UAIC 1238.06(1), Miller Creek, 3.2 km E of Mt. Miegs on I-85, Montgomery Co.

Tombigbee River system, Alabama: UAIC 7025.19(8), Shambley Creek, Greene Co.; UAIC 6032.18(16), Beaver Creek on AL Highway 43, Marengo Co.; UAIC 7440.16(83), Horse Creek, Marengo Co.; UT 91.2184(2), Sipseý River at U.S. Highway 82, W of Tuscaloosa, Tuscaloosa Co.; UAIC 7012.12(38), New River at Natural Bridge Park on U.S. Highway 82, Winston Co.

Tombigbee River system, Mississippi: UT 91.3532(12), Jim's Creek, 6.4 km S of Tremont and 1.3 km W of Cadamy, Itawamba Co.; UF 15091(1), Mattuby Creek, 7.5 km NW of Aberdeen of U.S. Highway 45, Monroe Co.; UAIC 7078.19(16), Little Noxubee River, Winston Co.

Mississippi River Basin

Red River Drainage- Mountain Fork River system, Oklahoma: OSUS 2322(6), Mountain Fork River at Smithville, McCurtain Co.; OSUS 7520(27), Mountain

Fork River at Highway 70 bridge, E of Broken Bow, McCurtain Co.; UT 91.1409(1), Little River at gravel road crossing, ca. 41.8 airkm ENE of Antlers, 8.8 km E of Cloudy, Pushmataha Co. **Kiamichi River system,**
Oklahoma: KU 12954(3), Kiamichi River, S of Whitesboro, Leflore Co.; OSUS 5628(11), Kiamichi River, 1.6 km S of Kiamichi, Pushmataha Co. **Ouachitae River system,**
Arkansas: UT 91.1383(2), Ouachitae River at Mc Guire access off Ark. Highway 88, Polk Co.

Homochitto River system, Mississippi: UF 46579(12), McGeehee Creek, Little Springs quadrangle, Franklin Co.; TU 66985(19), Homochitto River, 8.0 km E of Union Church on MS Highway 553, Lincoln Co.; TU 124242(4), Homochitto River, 7.2 km E of Union Church on MS Highway 550, Lincoln Co.

Bayou Pierre River system, Mississippi: UT 91.2946(18), Thompson Creek at MS Highway 28 bridge, 14.4 air km SW of Hazelhurst, Covich Co.; UT 91.2949(2), Bayou Pierre tributary 7.2 air km NW of I-50 S at Lincoln Co. line, Covich Co.; TU 103762(144), Mill Creek, tributary to Bayou Pierre, 2.7 km NW of Gallatin, Covich Co.; UF 46578(55), Bayou Pierre Creek, Midway quadrangle, Lincoln Co.; UF 46580(22), Bayou Pierre Creek, ca. 12.8 km NW of Brookhaven, Lincoln Co.

Big Black River system, Mississippi: UF 60795(2), Tributary of Bogue Falaya Creek, 5.1 km E of junction of Route 12 and 429 just N of Sallis, Attala Co.; TU 139421(41), Poplar Creek at MS Highway 413 in French

Camp, Choctaw Co.; UF 59177(5), Calabrella Creek, 11.7 miles E of Kilmichael on U.S. 82, Webster Co.

Yazoo River system, Mississippi: TU 83561(285), Pumpkin Creek, 1.0 km E of Yocona turn off, MS Highway 6, Lafayette Co.; TU 87667(9), Pumpkin Creek, 10.7 km SE of Oxford on MS Highway 334, Lafayette Co.; UT 91.2168(10), Chewalla Creek at State Section road crossing, ca. 8.0 air km E of Holly Springs, Marshall Co.; UF 60846(1), Tributary of Tillabota Creek, 11.8 km S of Oakland on U.S. 51, Yalobusha Co.

Arkansas River Drainage- Poteau River system, Oklahoma: OSUS 1231(1), Poteau River, LeFlore Co. **Poteau River system, Arkansas:** UMMZ 81132(1), Poteau River, .8 km N of Waldron, Scott Co. **Spring River system, Kansas:** KU 18455(6), Spring River at KS route 96, Cherokee Co. **Black River system, Missouri:** UT 91.986(1), Cane Creek at US 60, Butler Co. **Current River system, Missouri:** UT 91.1820(1), Current River at MO 21, ca. 1.6 air km NW of Doniphan, Ripley Co.

Obion River system, Kentucky: UT 91.1615(39), Terrapin Creek at Co. Rd. 1485 crossing, ca. 1.6 air km SW of Bell City, Graves Co. **Obion River system, Tennessee:** UT 91.459(11), South Fork of the Obion River at TN Highway 22, Carroll Co.; UT 91.460(61), North Fork of the Obion River at TN Highway 69, Henry Co.; UT 91.697(15), Birds Creek on road off 8021, about .8 km W of Whitlock, Henry Co.; UT 91.704(9), Clear Creek on gravel road about 2.4 km S of Co. Rd. 8172, SW of

Pureyear, Henry Co.; UT 91.967(26), Terrapin Creek, just S of Kentucky border on TN Highway 69, Henry Co.; UT 91.2230(100), Terrapin Creek, just below TN Highway 69 crossing, ca. 2.4 km N of Midway, Henry Co.; UT 91.2290(100), Terrapin Creek, below TN 69 bridge, Henry Co.; UT 91.2323(3), Clear Creek, 4.0 air km SW of Pureyear, Henry Co.; UT 91.145(5), stream 3.7 km E of Glass, on Glass-Obion road, Obion Co.

Tennessee River Drainage- Blood River system, Tennessee: UT 91.574(14), North Fork, Blood River at Co. 8160, Henry Co. **Birdsong Creek system, Tennessee:** UT 91.2279(3), Birdsong Creek, middle bridge on new TN 69, Benton Co.; UT 91.199(83), Sycamore Creek, .8 km E of Holladay on old TN 69, Benton Co.; UT 91.3514(28), Sycamore Creek, .8 km E of Holladay on old TN 69, Benton Co. **Duck River system, Tennessee:** UT 91.1569(1), Hurricane Creek, lower 185 m, above confluence with Duck River, Humphreys Co. **Indian Creek system, Tennessee:** UT 91.2787(44), Alexander Branch at bridge between TN 128 and Co. 8230, Hardin Co. **Robinson Creek system, Tennessee:** UT 91.834(36), Robinson Creek at TN 57, Hardin Co.; UT 91.2939(7), Robinson Creek an TN 57, Hardin Co. **Paint Rock River system, Alabama:** Paint Rock River, along Co. Rd. 9 at Bostwick Church, just S of Estillfork, Jackson Co.

Cumberland River Drainage, Kentucky: SIUC 9464(2), Bridge Fork directly above mouth, on KY Highway 478, McCreary Co.; SIUC 14544(4), Youngs Creek, 1.1 km above mouth, Whitley Co.; UT 91.3121(1), Bunch Creek just

above confluence with Cumberland River, Whitley Co.; SIUC 9371(2), Bunches Creek, 1.5 km above mouth, Whitley Co.; UT 91.2782(2), Poor Fork of Cumberland River, behind primitive Baptist Church, Letcher Co.; INHS 64300(13), mouth of Bad Branch on Hwy. 119, Poor Fork of Cumberland River, Letcher Co.

Ohio River Drainage- Wabash River system,
Illinois: UMMZ 169772(27), Creek near Middle Fork of Vermillion River, near Penfield, Champaign Co. **Wabash River system, Indiana:** UMMZ 66950(19), Wolf Creek, Bartholomew Co.; KU 17754(58), Indian Creek, 3.2 km SE of Octagon, Tippacanoe Co. **Green River system,**
Kentucky: UF 43788(2), Bylew Creek at Bylew Cave, Edmonson Co.; UT 91.1483(1), Falling Timber Creek at Hwy. 63 crossing, Barren Co. **Kentucky River system,**
Kentucky: UMMZ 154494(26), Big Creek at Big Creek, ca. 1.6 km above mouth in Redbird Creek, Clay Co. **Miami River system, Ohio:** UMMZ 107675(3), Miami River at Quincy, Miami Twp., Logan Co. **Ohio River, Ohio:** UT 91.3225(3), Ohio River, RM ca. 440, Clermont Co.
Kinniconick Creek system, Kentucky: UT 91.2599(29), Kinniconick Creek along Co.Rd. 2524 at ford 1.6 air km NE of Camp Dix, Lewis Co. **Scioto River system, Ohio:** KU 11348(16), Rocky Fork Creek, Franklin Co. **Muskingum River system, Ohio:** UT 91.3314(134), Clear Fork and Rocky Fork near Mansfield, Richland Co. **Ohio River, Ohio:** UMMZ 87678(7), Opossum Creek, tributary of Ohio River, eastern Salem Twp., Monroe Co.; UT 91.2904(5), Ohio River at Steubenville, RM 64.2, Jefferson Co.
Captina River system, Ohio: UMMZ 66890(5),

Stillwater Creek, 8 km N of Barnesville, Belmont Co. **Mahoning River system, Ohio:** UMMZ 107852(23), Mahoning River, southern Smith twp., Mahoning Co.

Whitewater River system, Missouri: UMMZ 139628(26), Little Whitewater River, tributary to Whitewater River, 4.8 km N of Bufordville, Cape Girardeau Co.

Little Muddy River system, Illinois: UMMZ 130279(26), Little Kinkaid Creek, 9.7 km S of Oraville, Jackson Co.

Kaskaskia River system, Illinois: INHS 020391(26), Hurricane Creek, 3.2 km W of Pittsburg, Fayette Co.; INHS 8298(15), Kaskaskia River, 4.0 km SE of Sullivan, Moultrie Co.

River Aux Vases system, Missouri: OSUS 44592(50), River Aux Vases at I-55, St. Genevieve Co.

Meramac River system, Missouri: UMMZ 142269(14), Big River at Cedar Hill, Jefferson Co.

Missouri River drainage- Gasconade River system, Missouri: KU 10283(2), Gasconade River, 6.4 km below Jerome, Phelps Co. **Osage River system, Missouri:** KU 5183(2), Loose Creek, Osage Co.; KU 7762(3), Niangua River on St. Rd. M, Dallas Co.; KU 7847(2), Niangua River on St. Rd. M, 2.4 km E of Charity, Dallas Co.; KU 11134(6), Little Clear Creek on Co.Rd. O, St.Clair Co.; OSM 43757(29), Bear Creek at St. Rd. P,

Cedar Co. **Moreau River system, Missouri:** KU
 11209(5), North Moreau Creek, 2.8 km E of Lohman, Cole
 Co. **Cedar Creek system, Missouri:** UT 91.1858(10),
 Rocky Fork Creek at US 63, 8.4 road km N of Columbia,
 Boone Co. **Moniteau Creek system, Missouri:** OSM
 39735(6), Moniteau Creek, 12.9 km E of Fayette, Howard
 Co. **Chariton River system, Missouri:** OSM 54852(81),
 South Fork Shoal Creek, Putnam Co.; UMMZ 148768(20),
 Blackbird Creek, 9.7 km E of Unionville on M4, Putnam Co.
Crooked River system, Missouri: KU 10463(23),
 Crooked River, 11.7 km W of Polo, Caldwell Co. **Kansas
 River system, Kansas:** UMMZ 156746(18), Rock Creek,
 tributary of Wakarusa River, 20 km S and 13.7 km E of
 Topeka, Douglas Co.; KU 21754(4), Deer Creek, tributary
 of Wakarusa River, S of Stull, Douglas Co.; KU 2971(26),
 Mill Creek, Wabaunsee Co.; KU 21959(6), West branch of
 Mill Creek, 12.2 km SW of Alma, Wabaunsee Co.; KU
 17467(43), French Creek, tributary of Vermillion River,
 Nemaha Co.; KU 21221(4), Pole Creek, tributary of Blue
 River, Marshall Co.; KU 4372(15), Coon Creek, tributary
 of Blue River, Washington Co.; KU 8224(6), Clarks Creek,
 tributary of Solomon River, 6.4 km S and 3.2 km W of
 Skiddy, Morris Co. **Platte River system, Nebraska:**
 UMMZ 213147(12), Norfolk Creek at Norfolk junction,
 Madison Co.; KU 7178(2), Elkhorn River, 1.6 km S of
 Atkinson on Hwy. 11, Holt Co.; UMMZ 106395(12), Lodgepole
 Creek, 3.2 km W of Chapell, Deuel Co. **Platte River
 system, Colorado:** KU 4787(102), Cache la Poudre River,
 3.2 km S and 6.4 km E of Ft. Collins, Larimer Co.; KU
 4803(18), tributary of Cache la Poudre River at
 Livermore, Larimer Co.; KU 5533(3), North Fork of Cache

la Poudre River, 3.2 km W of Livermore, Larimer Co.
Platte River system, Wyoming: KU 4814(31), North
Laramie River at Ura, Platte Co. **Little Sioux River
system, Iowa:** UMMZ 101528(9), Spirit Lake, Dickinson
Co. **James River system, South Dakota:** UMMZ
163822(6), James River, 14.5 km E of Woonsocket at
bridge, 3.2 km N of Forestburg, Sanborn Co.; UMMZ
189493(40), Pipestem Creek at Jamestown, Stutsman Co.
Big Sioux River system, South Dakota: UMMZ
166872(17), Springhole and outlet creek, tributary to
Six Mile Creek, 9.7 km NE of Brookings, Brookings Co.

Illinois River system, Illinois: UMMZ
105764(5), Macoupin Creek, Macoupin Co.; UMMZ 105802(5),
Dry Fork Creek, branch of Macoupin Creek, near Gillespie,
Macoupin Co.; KU 9485(20), tributary of Du Page River,
1.6 km S of 87th and Plainfield Naperville Road, Will Co.
Illinois River system, Indiana: UMMZ 81372(11),
Yellow River near Plymouth, Marshall Co.; UMMZ
213109(9), Yellow River at Plymouth, from the flouring
mill upstream to the dam, tributary of the Kankakee
River, Marshall Co.

Mississippi River, Missouri: KU 9719(2),
Mississippi River at Clarksville, Pike Co.

Skunk River system, Iowa: UMMZ 181099(18), Squaw
Creek at Ames, Story Co.

Iowa River system, Iowa: UMMZ 100989(30), ditch
tributary to Willow Creek, beside Clear Lake nursery

pond, Cerro Gordo Co.; UMMZ 212992(20), Iowa River at Belmond, below dam, Wright Co.

Rock River system, Wisconsin: UMMZ 76950(13), Thunder Branch of W Pecatonia River, ca. 11.3 km NW of Gratiot, Layfayette Co.; KU 7290(14), Mineral Point Branch, Iowa Co.

Big Platte River system, Wisconsin: UMMZ 76750(14), Big Platte River, W of Platteville, on STH 14, Grant Co.

Bad Axe River system, Wisconsin: UT 91.888(5), South from Bad Axe River, Vernon Co.

Wisconsin River system, Wisconsin: UT 91.889(5), Narrows Creek, Sauk Co.

Black River system, Wisconsin: UMMZ 75818(17), tributary of East Fork Black River, ca. 19.3 km NW of Pittsville, Wood Co.

Whitewater River system, Minnesota: OSUS 6970(7), south branch of Whitewater River, Olmstead Co.

Buffalo River system, Wisconsin: UT 91.891(5), unnamed tributary to Buffalo River, Buffalo Co.

St. Croix River system, Wisconsin: UMMZ 77779(30), Apple River, 3.2 km above Somerset, St. Croix Co.

Minnesota River system, Minnesota: UMMZ
72048(16), Minnesota River, above Cedar Avenue bridge,
ca. 12.9 km above mouth, Hennepin Co.

Minnesota River system, South Dakota: UMMZ
166905(29), Whetstone Creek, 1.6 km W of Big Stone City,
Grant Co.

Rum River system, Minnesota: OSUS 12615(28),
Cedar Creek E of Bethel, Anoka Co.

Elk River system, Minnesota: UT 91.2622(30),
Upper St. Francis River just S of junction of Minn. 95
and Co. 6, Benton Co.

Prairie River system, Minnesota: UMMZ
80096(15), Prairie River, near Grand Rapids, Itasca Co.

Great Lakes Basin

St. Lawrence River system, Quebec, Canada:
ROM 25459(30), Ruisseau l'est de la Baie St. Placide.

Lake Erie Drainage- Grand River system, Ohio:
UMMZ 107839(15), small tributary to Grand River, NC
Bristol Twp., Trumbull Co. **Maumee River system, Ohio:**
UMMZ 109190(11), Little Auglaize River, west-central
Washington Twp., Van Wert Co.; UMMZ 107448(9), Ottawa
Creek, tributary of Blanchard River, southern Union twp.,
Hancock Co. **Maumee River system, Michigan:** UMMZ

212096(22), West branch of St. Joseph River, N of territorial Rd., Hillsdale Co.

Lake Huron Drainage- Shiawassee River system, Michigan: UMMZ 137193(30), Swan Creek, ca. .8 km above mouth in Shiawassee River, Swan Creek Twp., Shiawassee Co. **Au Sable River system, Michigan:** UMMZ 194276(29), main stream of Au Sable River at McMaster's bridge, Crawford Co.

Lake Michigan Drainage- St. Joseph River system, Michigan: UT 91.3347(15), Portage Creek, Kalamazoo Co. **Muskegon River system, Michigan:** UMMZ 71766(30), Williams Creek, Garfield Twp., Newaygo Co. **Manistee River system, Michigan:** UMMZ 91564(41), Manistee Lake, Excebiar Twp., Kalkaska Co. **Oconto River, Wisconsin:** UMMZ 74597(7), Oconto River, ca. 8 km N of Mountain, Oconto Co.

Lake Superior Drainage- UT 91.2481(3), Lake Superior, Chequamegon Bay, Bayfield Co.

Hudson Bay Basin

James Bay Drainage- ROM 12323(28), Lake Attawapiskat, Ontario, Canada.

Hudson Bay Drainage- ROM 19382(53), Minnedosa River in Manitoba, Canada. ROM 17830(16), Echo Lake, Qu'Appelle Lakes, Saskatchewan, Canada.

APPENDIX B

FREQUENCY TABLES

Table B-1. Number of dorsal fin spines in Etheostoma nigrum.

Population	6	7	8	9	10	N	$\bar{X}$	SD	SE
Mobile Bay Basin									
Alabama R.			4	43	19	66	9.2	.55	.07
Black Warrior R.			4	9		13	8.3	.48	.13
Cahaba R.			1	4		5	8.8	.45	.20
Tallapoosa R.			1	28	4	33	9.1	.38	.07
Tombigbee R. (lower)			8	26	2	36	8.8	.51	.08
Tombigbee R. (upper)			12	29	3	44	8.8	.55	.08
Lower eastern									
Mississippi R.									
Homochitto R.			4	28	2	34	8.9	.42	.07
Bayou Pierre R.	2		20	39		61	8.6	.56	.07
Big Black R.			2	23		25	8.9	.28	.06
Yazoo R.			1	13	6	20	9.2	.55	.12
Obion R.			2	25	10	37	9.2	.53	.09
Red River Drng.									
Ouachitae R.			2			2	8.0	.00	.00
Mountain Fork R.			6	20		26	8.8	.43	.08
Kiamichi R.			2	11	1	14	8.9	.47	.13

Table B-1. (Continued)

Population	6	7	8	9	10	N	$\bar{x}$	SD	SE
Arkansas River Drng.									
Current R.				1		1	9.0	.00	.00
Poteau R.				2		2	9.0	.00	.00
Spring R.			1	4	1	6	9.0	.63	.26
Tennessee R. Drng.			10	15	1	26	8.6	.56	.11
Cumberland R. Drng.	1		2	13	2	18	8.9	.68	.16
Ohio R. Drng.									
Wabash R.			7	24	13	44	9.1	.67	.10
Green R.				2		2	9.0	.00	.00
Kentucky R.			4	6		10	8.6	.52	.16
Miami R.			2	1		3	8.3	.58	.33
Kinniconick Cr.			1	8	1	10	9.0	.47	.15
Scioto R.			5	5		10	8.5	.53	.17
Muskingum R.			8	11	1	20	8.6	.59	.13
Captina R.			1	3	1	5	9.0	.71	.32
Mahoning R.			5	5		10	8.5	.53	.17
Whitewater R. Syst.			1	13		14	8.9	.27	.07
Little Muddy R. Syst.			7	13		20	8.6	.49	.11
Kaskaskia R. Syst.			8	25	2	35	8.8	.51	.09
River Aux Vases Syst.			6	14		20	8.7	.47	.10
Big. R. Syst.				10		10	9.0	.00	.00

Table B-1. (Continued)

Population	6	7	8	9	10	N	$\bar{X}$	SD	SE
Missouri R. Drng.									
Gasconade R.				2		2	9.0	.00	.00
Osage R.			5	32	4	41	9.0	.47	.07
Moreau R.			1	4		5	8.8	.45	.20
Cedar Cr.			1	9		10	8.9	.32	.10
Moniteau Cr.				3		3	9.0	.00	.00
Chariton R.			3	15	2	20	8.9	.51	.11
Crooked R.			11	8	1	20	8.5	.61	.14
Wakarusa R.				6		6	9.0	.00	.00
Mill Cr.			5	15	2	22	8.9	.52	.12
Vermillion R.			4	14	2	20	8.9	.55	.12
Blue R.			6	8		14	8.6	.51	.14
Solomon R.				5		5	9.0	.00	.00
Elkhorn R.				12		12	9.0	.00	.00
Lodgepole R.			4			4	8.0	.00	.00
Cache la Poudre R.			6	6		12	8.5	.52	.15
Laramie R.		1	8	11		20	8.5	.61	.14
Little Sioux R.			4	4		8	8.5	.53	.19
James R.			6	10		16	8.6	.50	.12
Big Sioux R.			5	5		10	8.5	.53	.17

Table B-1. (Continued)

Population	6	7	8	9	10	N	$\bar{X}$	SD	SE
Upper Mississippi R.									
Drng.									
Macoupin Cr.	1		1	7	1	10	8.8	.79	.25
Yellow R.			5	9	2	16	8.8	.65	.16
Du Page R.			4	13	3	20	8.9	.61	.14
Mississippi R.			2			2	8.0	.00	.00
Skunk R.			1	16	1	18	9.0	.34	.08
Iowa R.			3	6	1	10	8.8	.63	.20
Pecatonia R.			6	16		22	8.7	.46	.10
Bad Axe R.				5		5	9.0	.00	.00
Wisconsin R.			1	4		5	8.8	.45	.20
Black R.			1	15	1	17	9.0	.35	.09
Whitewater R.			1	6		7	8.9	.38	.14
Buffalo R.			2	3		5	8.6	.55	.24
Apple R.			4	16		20	8.8	.41	.09
Minnesota R.			11	18	1	30	8.7	.55	.10
Rum R.			6	13	1	20	8.8	.55	.12
Elk R.			3	7		10	8.7	.48	.15
Prarie R.			4	6		10	8.6	.52	.16
Great Lakes Basin									
St. Lawrence R.	1	1		6		8	8.4	1.19	.42
Grand R.			4	6		10	8.6	.52	.16
Maumee R.			9	8	2	19	8.6	.68	.16
St. Joseph R.			1	4		5	8.8	.45	.20

Table B-1. (Continued)

Population	6	7	8	9	10	N	$\bar{x}$	SD	SE
Great Lakes Continued									
Shiawassee R.				14	6	20	9.3	.47	.10
Au Sable R.			6	14		20	8.7	.47	.10
Portage Cr.			3	4	3	10	9.0	.82	.26
Muskegon R.			7	13		20	8.6	.50	.11
Manistee R.				19	1	20	9.1	.22	.05
Oconto R.				5		5	9.0	.00	.00
Lake Superior				3		3	9.0	.00	.00
Hudson Bay Basin									
James Bay			1	6	3	10	9.2	.63	.20
Minnedosa R.			1	8	1	10	9.0	.47	.15
Qu'Appelle R.			4	4		8	8.5	.54	.19

Table B-2. Number of dorsal fin soft rays in Etheostoma nigrum.

Population	10	11	12	13	14	15	N	$\bar{X}$	SD	SE
Mobile Bay Basin										
Alabama R.	2		32	28	4		66	12.5	.66	.08
Black Warrior R.			9	4			13	12.3	.48	.13
Cahaba R.			3	2			5	12.4	.55	.24
Tallapoosa R.	1		15	16	1		33	12.5	.62	.11
Tombigbee R. (lower)	2		20	14			36	12.3	.59	.10
Tombigbee R. (upper)	2		30	12			44	12.2	.52	.08
Lower eastern										
Mississippi R.										
Homochitto R.			7	25	2		34	12.8	.50	.09
Bayou Pierre R.			6	49	4	2	61	13.0	.55	.07
Big Black R.				11	14		25	13.6	.51	.10
Yazoo R.			5	12	3		20	12.9	.64	.14
Obion R.			2	19	16		37	13.4	.59	.10
Red River Drng.										
Ouachitae R.			2				2	12.0	.00	.00
Mountain Fork R.			15	11			26	12.4	.50	.10
Kiamichi R.	2		10	2			14	12.0	.56	.15

Table B-2. (Continued)

Population	10	11	12	13	14	15	N	$\bar{X}$	SD	SE
Arkansas River Drng.										
Current R.			1				1	12.0	.00	.00
Poteau R.			1	1			2	12.5	.71	.50
Spring R.			1	5			6	12.8	.41	.17
Tennessee River Drng.	6		17	3			26	11.9	.59	.12
Cumberland River Drng.	9		9				18	11.5	.51	.12
Ohio River Drng.										
Wabash R.	2		14	27	1		44	12.6	.62	.09
Green R.				2			2	13.0	.00	.00
Kentucky R.			9	1			10	12.1	.32	.10
Miami R.			3				3	12.0	.00	.00
Kinniconick Cr.			5	5			10	12.5	.53	.17
Scioto R.	1		9				10	11.9	.32	.10
Muskingum R.	4		13	3			20	12.0	.60	.13
Captina R.	1		3				5	11.4	.89	.40
Mahoning R.	1		7	2			10	12.1	.57	.18
Whitewater R. Syst.			9	5			14	12.4	.50	.13
Little Muddy R. Syst.			4	14	2		20	12.9	.55	.12
Kaskaskia R. Syst.	1		13	20	1		35	12.6	.60	.10
River Aux Vases Syst.			3	11	6		20	13.2	.67	.15
Big R. Syst.			3	7			10	12.7	.48	.15

Table B-2 (Continued)

Population	10	11	12	13	14	15	N	$\bar{X}$	SD	SE
Missouri R. Drng.										
Gasconade R.			1	1			2	12.5	.71	.50
Osage R.	3	32	6				41	12.1	.47	.07
Moreau R.		1	3		1		5	13.0	.71	.32
Cedar Cr.		2	8				10	12.8	.42	.13
Moniteau Cr.		2	1				3	12.3	.58	.33
Chariton R.		2	16		2		20	13.0	.46	.10
Crooked R.		7	10		3		20	12.8	.70	.16
Wakarusa R.			4		2		6	13.3	.52	.21
Mill Cr.		3	9		8	2	22	13.4	.85	.18
Vermillion R.		3	14		3		20	13.0	.56	.13
Blue R.		5	7		2		14	12.8	.70	.19
Solomon R.					5		5	14.0	.00	.00
Elkhorn R.	1	8		2	1		12	12.2	.75	.22
Lodgepole R.				3	1		4	13.2	.50	.25
Cache la Poudre R.		2	7		3		12	13.1	.67	.19
Laramie R.			14		5	1	20	13.3	.59	.13
Little Sioux R.		1	5		2		8	13.1	.64	.23
James R.		2	11		3		16	13.1	.57	.14
Big Sioux R.		4	5		1		10	12.7	.67	.21

Table B-2. (Continued)

Population	10	11	12	13	14	15	N	$\bar{X}$	SD	SE
Upper Mississippi R.										
Drng.										
Macoupin Cr.			3	7			10	12.7	.48	.15
Yellow R.			9	7			16	12.4	.51	.13
Du Page R.			8	12			20	12.6	.50	.11
Mississippi R.				2			2	13.0	.00	.00
Skunk R.			8	10			18	12.6	.51	.12
Iowa R.			4	5	1		10	12.7	.67	.21
Pecatonia R.	1		12	9			20	12.4	.58	.12
Bad Axe R.			2	3			5	12.6	.55	.24
Wisconsin R.			2	3			5	12.6	.55	.24
Black R.			1	9	7		17	13.5	.61	.15
Whitewater R.	1		5	1			7	12.0	.58	.22
Buffalo R.			3	2			5	12.4	.55	.24
Apple R.			8	12			20	12.6	.50	.11
Minnesota R.			4	21	5		30	13.0	.56	.10
Rum R.			7	12			20	12.6	.60	.13
Elk R.	1		5	5			10	12.5	.53	.17
Prarie R.			2	8			10	12.8	.42	.13
Great Lakes Basin										
St. Lawrence R.	1		4	2	1		8	12.4	.92	.32
Grand R.			4	6			10	12.6	.52	.16
Maumee R.	2		7	10			19	12.4	.69	.16

Table B-2. (Continued)

Population	10	11	12	13	14	15	N	$\bar{x}$	SD	SE
Great Lakes Continued										
St. Joseph R.			2	3			5	12.6	.55	.24
Shiawassee R.			11	9			20	12.4	.51	.11
Au Sable R.	3		12	4	1		20	12.2	.74	.17
Portage Cr.			4	5		1	10	12.8	.92	.29
Muskegon R.	1		12	7			20	12.3	.57	.13
Manistee R.	2		14	4			20	12.1	.55	.12
Oconto R.			1	4			5	12.8	.45	.20
Lake Superior			1	1	1		3	13.0	1.00	.58
Hudson Bay Basin										
James Bay			1	7	2		10	13.1	.57	.18
Minnedosa R.			5	5			10	12.5	.53	.17
Qu'Appelle R.			5	3			8	12.4	.52	.18

Table B-3. Number of anal fin soft rays in Etheostoma nigrum.

Population	6	7	8	9	10	11	N	$\bar{X}$	SD	SE
Mobile Bay Basin										
Alabama R.		1	13	49	3		66	8.8	.52	.06
Black Warrior R.				11	2		13	9.2	.38	.10
Cahaba R.			4	1			5	8.2	.45	.20
Tallapoosa R.		1	12	19		1	33	8.6	.70	.12
Tombigbee R. (lower)			3	33			36	8.9	.28	.05
Tombigbee R. (upper)	1		16	26	1		44	8.6	.66	.10
Lower eastern										
Mississippi R.										
Homochitto R.			10	22	2		34	8.8	.55	.09
Bayou Plerre R.	1		24	34	2		61	8.6	.58	.07
Big Black R.			1	19	5		25	9.2	.47	.09
Yazoo R.		1	11	8			20	8.4	.59	.13
Obion R.		2	7	26	1		37	8.6	.75	.12
Red River Drng.										
Ouachitae R.			2				2	8.0	.00	.00
Mountain Fork R.			7	19			26	8.7	.45	.09
Kiamichi R.			9	5			14	8.4	.50	.13

Table B-3 (Continued)

Population	6	7	8	9	10	11	N	$\bar{X}$	SD	SE
Arkansas River Drng.										
Current R.			1				1	8.0	.00	.00
Poteau R.			1	1			2	8.5	.71	.50
Spring R.			3	3			6	8.5	.55	.22
Tennessee R. Drng.	2	4	11	9			26	8.0	.92	.18
Cumberland R. Drng.		1	5	12			18	8.6	.61	.14
Ohio R. Drng.										
Wabash R.			6	32	6		44	9.0	.53	.08
Green R.				2			2	9.0	.00	.00
Kentucky R.			2	8			10	8.8	.42	.13
Miami R.			2	1			3	8.3	.58	.33
Kinniconick Cr.			3	7			10	8.7	.48	.15
Scioto R.			7	3			10	8.3	.48	.15
Muskingum R.			11	9			20	8.4	.51	.11
Captina R.			3	2			5	8.4	.55	.24
Mahoning R.			4	4	2		10	8.8	.79	.25
Whitewater R. Syst.				14			14	9.0	.00	.00
Little Muddy R. Syst.			3	13	4		20	9.0	.60	.13
Kaskaskia R. Syst.			1	17	17		35	9.5	.56	.09
River Aux Vases Syst.				13	7		20	9.4	.49	.11
Big R. Syst.			3	7			10	8.7	.48	.15

Table B-3. (Continued)

Population	6	7	8	9	10	11	N	$\bar{X}$	SD	SE
Missouri R. Drng.										
Gasconade R.				2			2	9.0	.00	.00
Osage R.	1	2	27	11			41	8.2	.63	.10
Moreau R.				5			5	9.0	.00	.00
Cedar Cr.				9	1		10	9.1	.32	.10
Moniteau Cr.			1	2			3	8.7	.58	.33
Chariton R.				4	15	1	20	9.8	.52	.12
Crooked R.				6	14		20	9.7	.47	.10
Wakarusa R.				4	2		6	9.3	.52	.21
Mill Cr.			2	4	14	2	22	9.7	.77	.16
Vermillion R.			1	9	10		20	9.4	.60	.13
Blue R.			1	5	7	1	14	9.6	.76	.20
Solomon R.				3	2		5	9.4	.55	.24
Elkhorn R.			1	11			12	8.9	.29	.08
Lodgepole R.				1	2	1	4	10.0	.82	.41
Cache la Poudre R.				5	7		12	9.6	.51	.15
Laramie R.				4	16		20	9.8	.41	.09
Little Sioux R.					8		8	10.0	.00	.00
James R.				3	13		16	9.8	.40	.10
Big Sioux R.			1	6	3		10	9.2	.63	.20

Table B-3. (Continued)

Population	6	7	8	9	10	11	N	$\bar{x}$	SD	SE
Upper Mississippi R.										
Drng.										
Macoupin Cr.				9	1		10	9.1	.32	.10
Yellow R.			2	12	2		16	9.0	.52	.13
Du Page R.			1	16	3		20	9.1	.45	.10
Mississippi R.				1		1	2	10.0	1.41	1.00
Skunk R.				11	7		18	9.4	.50	.12
Iowa R.				7	3		10	9.3	.48	.15
Pecatonla R.			8	13	1		22	8.7	.57	.12
Bad Axe R.				2	3		5	9.6	.55	.24
Wisconsin R.				4	1		5	9.2	.45	.20
Black R.			2	5	10		17	9.5	.72	.17
Whitewater R.		1		6			7	8.7	.76	.29
Buffalo R.				3	2		5	9.4	.55	.24
Apple R.			1	8	11		20	9.5	.61	.14
Minnesota R.				10	19	1	30	9.7	.53	.10
Rum R.			1	14	5		20	9.2	.52	.12
Elk R.				8	2		10	9.2	.42	.13
Prarie R.				9	1		10	9.1	.32	.10
Great Lakes Basin										
St. Lawrence R.			2	4	2		8	9.0	.76	.27
Grand R.			1	8	1		10	9.0	.47	.15
Maumee R.			5	12	2		19	8.8	.60	.14

Table B-3. (Continued)

Population	6	7	8	9	10	11	N	$\bar{X}$	SD	SE
Great Lakes Continued										
St. Joseph R.		1	2	2			5	8.2	.84	.37
Shiawassee R.		1	5	11	3		20	8.8	.77	.17
Au Sable R.			2	7	1		10	9.0	.39	.09
Portage Cr.		1	3	4	2		10	8.7	.95	.30
Muskegon R.			4	14	2		20	8.9	.55	.12
Manistee R.			4	16			20	8.8	.41	.09
Oconto R.				3	2		5	9.4	.55	.24
Lake Superior					3		3	10.0	.00	.00
Hudson Bay Basin										
James Bay				7	3		10	9.3	.48	.15
Minnedosa R.	1		2	7			10	8.5	.97	.31
Qu'Appelle R.			1	4	3		8	9.2	.71	.25

Table B-4. Number of left pectoral fin rays in Etheostoma nigrum.

Population	9	10	11	12	13	N	$\bar{X}$	SD	SE
Mobile Bay Basin									
Alabama R.			5	55	6	66	12.0	.41	.05
Black Warrior R.			5	8		13	11.6	.51	.14
Cahaba R.			1	4		5	11.8	.45	.20
Tallapoosa R.			10	22	1	33	11.7	.52	.09
Tombigbee R. (lower)			2	32	2	36	12.0	.34	.06
Tombigbee R. (upper)			9	33	2	44	11.8	.48	.07
Lower eastern									
Mississippi R.									
Homochitto R.			4	28	2	34	11.9	.42	.07
Bayou Pierre R.			9	48	4	61	11.9	.46	.06
Big Black R.			1	22	2	25	12.0	.35	.07
Yazoo R.			3	17		20	11.8	.37	.08
Obion R.			9	27	1	37	11.8	.48	.08
Red River Drng.									
Ouachitae R.				2		2	12.0	.00	.00
Mountain Fork R.				26		26	12.0	.00	.00
Kiamichi R.			4	10		14	11.7	.47	.12

Table B-4. (Continued)

Population	9	10	11	12	13	N	$\bar{X}$	SD	SE
Arkansas R. Drng.									
Current R.				1		1	12.0	.00	.00
Poteau R.			1	1		2	11.5	.71	.50
Spring R.			1	5		6	11.8	.41	.17
Tennessee R. Drng.			12	13	1	26	11.6	.58	.11
Cumberland R. Drng.			14	4		18	11.2	.43	.10
Ohio R. Drng.									
Wabash R.		22	22	22		44	11.5	.51	.08
Green R.		1	1	1		2	11.5	.71	.50
Kentucky R.		4	4	6		10	11.6	.52	.16
Miami R.		3	3			3	11.0	.00	.00
Kinniconick Cr.		7	7	3		10	11.3	.48	.15
Scioto R.		6	6	4		10	11.4	.52	.16
Muskingum R.		16	16	4		20	11.2	.41	.09
Captina R.	1	1	1	3		5	11.4	.89	.40
Mahoning R.	1	6	6	3		10	11.2	.63	.20
Whitewater R. Syst.			1	13		14	11.9	.27	.07
Little Muddy R. Syst.			5	15		20	11.8	.44	.10
Kaskaskia R. Syst.			15	19	1	35	11.6	.55	.09
River Aux Vases Syst.			6	13	1	20	11.7	.55	.12
Big R. Syst.		2	2	8		10	11.8	.42	.13

Table B-4. (Continued)

Population	9	10	11	12	13	N	$\bar{x}$	SD	SE
Missouri R. Drng.									
Gasconade R.				2		2	12.0	.00	.00
Osage R.			9	29	3	41	11.8	.53	.08
Moreau R.			2	3		5	11.6	.55	.24
Cedar Cr.			6	4		10	11.4	.52	.16
Moniteau Cr.			1	2		3	11.7	.58	.33
Chariton R.			8	12		20	11.6	.50	.11
Crooked R.	1		7	12		20	11.5	.76	.17
Wakarusa R.				6		6	12.0	.00	.00
Mill Cr.			6	14	2	22	11.8	.59	.12
Vermillion R.			7	13		20	11.6	.49	.11
Blue R.			5	8	1	14	11.7	.61	.16
Solomon R.			1	3	1	5	12.0	.71	.32
Elkhorn R.			4	7	1	12	11.8	.62	.18
Lodgepole R.		1	3			4	10.8	.50	.25
Cache la Poudre R.			7	5		12	11.4	.51	.15
Laramie R.	1		13	6		20	11.2	.55	.12
Little Sioux R.			1	6	1	8	12.0	.53	.19
James R.			4	12		16	11.8	.45	.11
Big Sioux R.			3	7		10	11.7	.48	.15

Table B-4. (Continued)

Population	9	10	11	12	13	N	$\bar{x}$	SD	SE
Upper Mississippi R.									
Drng.									
Macoupin Cr.			3	6	1	10	11.8	.63	.20
Yellow R.		1	5	10		16	11.6	.63	.16
Du Page R.			6	14		20	11.7	.47	.10
Mississippi R.			1	1		2	11.5	.71	.50
Skunk R.			3	15		18	11.8	.38	.09
Iowa R.			4	6		10	11.6	.52	.16
Pecatonia R.			10	12		22	11.5	.51	.11
Bad Axe R.				5		5	12.0	.00	.00
Wisconsin R.			1	4		5	11.8	.45	.20
Black R.			6	11		17	11.6	.49	.12
Whitewater R.			2	5		7	11.7	.49	.18
Buffalo R.			2	3		5	11.6	.55	.24
Apple R.			1	19		20	12.0	.22	.05
Minnesota R.			10	20		30	11.7	.48	.09
Rum R.	1		2	14	3	20	11.9	.85	.19
Elk R.			2	6	2	10	12.0	.67	.21
Prarie R.			2	8		10	11.8	.42	.13
Great Lakes Basin									
St. Lawrence R.			3	2	3	8	12.0	.93	.33
Grand R.			7	3		10	11.3	.48	.15
Maumee R.			11	8		19	11.4	.51	.12

Table B-4. (Continued)

Population	9	10	11	12	13	N	$\bar{X}$	SD	SE
Great Lakes Continued									
St. Joseph R.	2		3			5	11.6	.55	.24
Shiawassee R.	6		14			20	11.7	.47	.11
Au Sable R.	2		7		1	10	11.9	.39	.09
Portage Cr.	5		5			10	11.5	.53	.17
Muskegon R.	3		13		4	20	12.0	.60	.13
Manistee R.	1		18		1	20	12.0	.32	.07
Oconto R.	2		3			5	11.6	.55	.24
Lake Superior			3			3	12.0	.00	.00
Hudson Bay Basin									
James Bay	1		9			10	11.9	.32	.10
Minnedosa R.	4		6			10	11.6	.52	.16
Qu'Appelle R.			8			8	12.0	.00	.00

Table B-5. Number of principal caudal fin rays in Etheostoma nigrum.

Population	11	12	13	14	15	16	17	18	N	$\bar{X}$	SD	SE
Mobile Bay Basin												
Alabama R.				2	17	47			66	15.7	.53	.07
Black Warrior R.				2	4	7			13	15.4	.77	.21
Cahaba R.				1	1	3			5	15.4	.89	.40
Tallapoosa R.				1	8	24			33	15.7	.53	.09
Tombigbee R. (lower)					32	4			36	15.9	.32	.05
Tombigbee R. (upper)			1	4	20	19			44	15.3	.73	.11
Lower eastern												
Mississippi R.												
Homochitto R.				1	8	24	1		34	15.7	.57	.10
Bayou Pierre R.			1	4	22	34			61	15.5	.70	.09
Big Black R.					3	22			25	15.9	.33	.07
Yazoo R.					1	18	1		20	16.0	.32	.07
Obion R.				1	9	24	3		37	15.8	.63	.10
Red River Drng.												
Ouachitae R.					2				2	15.0	.00	.00
Mountain Fork R.				1	10	15			26	15.5	.58	.11
Kiamichi R.					3	11			14	15.8	.43	.11

Table B-5. (Continued)

Population	11	12	13	14	15	16	17	18	N	$\bar{X}$	SD	SE
Arkansas R. Drng.												
Current R.						1			1	16.0	.00	.00
Poteau R.						2			2	16.0	.00	.00
Spring R.					3	3			6	15.5	.55	.22
Tennessee R. Drng.				1	2	23			26	15.8	.46	.09
Cumberland R. Drng.	1			1	8	8			18	15.3	1.02	.24
Ohio R. Drng.												
Wabash R.			1	1	10	30		2	44	15.7	.70	.11
Green R.					2				2	15.0	.00	.00
Kentucky R.					7	3			10	15.3	.48	.15
Miami R.					1	1		1	3	16.0	1.00	.58
Kinniconick Cr.					3	7			10	15.7	.48	.15
Scioto R.					3	7			10	15.7	.48	.15
Muskingum R.			1	2	11	6			20	15.1	.79	.18
Captina R.				1	3	1			5	15.0	.71	.32
Mahoning R.				3	2	5			10	15.2	.92	.29
Whitewater R. Syst.				1	4	9			14	15.6	.65	.17
Little Muddy R. Syst.						20			20	16.0	.00	.00
Kaskaskia R. Syst.			2	17	15	15	1		35	15.4	.65	.11
River Aux Vases Syst.				2	2	18			20	15.9	.31	.07
Big R. Syst.						1	9		10	16.9	.32	.10

Table B-5. (Continued)

Population	11	12	13	14	15	16	17	18	N	$\bar{x}$	SD	SE
Missouri R. Drng.												
Gasconade R.						2			2	16.0	.00	.00
Osage R.				2	5	34			41	15.8	.52	.08
Moreau R.					1	4			5	15.8	.45	.20
Cedar Cr.					1	9			10	15.9	.32	.10
Moniteau Cr.						3			3	16.0	.00	.00
Chariton R.					3	17			20	15.8	.37	.08
Crooked R.						20			20	16.0	.00	.00
Wakarusa R.					1	5			6	15.8	.41	.17
Mill Cr.					2	18		2	22	16.0	.44	.09
Vermillion R.					1	18		1	20	16.0	.32	.07
Blue R.				1		12		1	14	15.9	.62	.16
Solomon R.						4		1	5	16.2	.45	.20
Elkhorn R.					4	8			12	15.7	.49	.14
Lodgepole R.					1	3			4	15.8	.50	.25
Cache la Poudre R.			1	3	5	3			12	14.8	.94	.27
Laramie R.						19		1	20	16.0	.22	.05
Little Sioux R.				3	1	4			8	15.1	.99	.35
James R.					2	14			16	15.9	.34	.08
Big Sioux R.						10			10	16.0	.00	.00

Table B-5. (Continued)

Population	11	12	13	14	15	16	17	18	N	$\bar{X}$	SD	SE
Upper Mississippi R.												
Drng.												
Macoupin Cr.					5	5			10	15.5	.53	.17
Yellow R.	1	2	1	2	6	4			16	14.4	1.59	.40
Du Page R.					6	14			20	15.7	.47	.10
Mississippi R.						2			2	16.0	.00	.00
Skunk R.				1	4	13			18	15.7	.59	.14
Iowa R.				1	5	4			10	15.3	.67	.21
Pecatonia R.				4	8	9	1		22	15.3	.84	.18
Bad Axe R.						5			5	16.0	.00	.00
Wisconsin R.			1			4			5	15.4	1.34	.60
Black R.			1	1	6	9			17	15.4	.86	.21
Whitewater R.				1	1	5			7	15.6	.79	.30
Buffalo R.					3	2			5	15.4	.55	.24
Apple R.				3	9	8			20	15.2	.72	.16
Minnesota R.				1	8	21			30	15.7	.55	.10
Rum R.					6	14			20	15.7	.47	.10
Elk R.					2	8			10	15.8	.42	.13
Prarie R.			1	1	2	6			10	15.3	1.06	.33
Great Lakes Basin												
St. Lawrence R.				1	5	2			8	15.1	.64	.23
Grand R.				1	6	3			10	15.2	.63	.20
Maumee R.			6	6	4	2	1		19	14.3	1.19	.27

Table B-5. (Continued)

Population	11	12	13	14	15	16	17	18	N	$\bar{X}$	SD	SE
Great Lakes Continued												
St. Joseph R.				1	3	1			5	15.0	.71	.32
Shiawassee R.			1			17	1	1	20	16.0	.86	.19
Au Sable R.				2	5	13			20	15.6	.69	.15
Portage Cr.	3	2	3		1	1			10	12.7	1.70	.54
Muskegon R.				2	5	13			20	15.6	.69	.15
Manistee R.			2	2	15	1			20	14.8	.72	.16
Oconto R.					3	2			5	15.4	.55	.24
Lake Superior						3			3	16.0	.00	.00
Hudson Bay Basin												
James Bay					1	9			10	15.9	.32	.10
Minnedosa R.						9	1		10	16.1	.32	.10
Qu'Appelle R.					5	3			8	15.4	.52	.18

Table B-6. Number of scales in the lateral series of Etheostoma nigrum, and percentage of specimens with complete lateral line.

Population	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	N	$\bar{x}$	SD	SE	%Comp	
Mobile Bay Basin																											
Alabama R.				1				2	2	6	9	5	12	7	7	5	3	3	4			66	49.3	2.99	.37	60	
Black Warrior R.					1	1	2	1	1	2	2	1	3	1	2							13	47.8	2.23	.62	8	
Cahaba R.												1		1		3						5	50.8	1.79	.80	80	
Tallapoosa R.										1	4	4	4	9	3	3	4		1			33	49.9	2.15	.37	100	
Tombigbee R. (lower)							1	1	3	2	5	3	3	7	5	1	3			2		36	49.1	3.08	.51	100	
Tombigbee R. (upper)					1	1	1	1	1	4	9	12	7		5	2	1					44	48.0	2.26	.34	43	
Lower eastern																											
Mississippi R.																											
Homochitto R.								1		2	7	3	8	5	4	1	2	1				34	49.0	2.21	.38	100	
Bayou Pierre R.							3	5	9	5	10	9	10	5	2	2	1	1				61	48.3	2.38	.30	95	
Big Black R.								1	1	2	11	4	1	1	2	1			1			25	48.9	2.22	.45	100	
Yazoo R.								1	2		4	3	3	3	1	4		2				20	49.6	2.54	.57	100	
Obion R.							1	2	5	10	7	5	2	1	1	1	1			1		37	47.2	2.70	.44	100	
Red River Drng.																											
Ouachitae R.													1	1								2	49.5	.71	.50	0	
Mountain Fork R.									1	1			3	4	3	6	1	4	1	1	1	26	51.6	2.61	.51	8	
Kiamichi R.									1	2	2	3	2	2	2	1	1					14	49.3	2.02	.54	14	
Arkansas River Drng.																											
Current R.														1								1	50.0	.00	.00	0	
Poteau R.												1						1				2	51.0	4.24	3.00	0	
Spring R.													2	1	3							6	50.2	.98	.40	0	

Table B-6. (Continued)

Population	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	N	$\bar{x}$	SD	SE	%Comp
Tennessee R. Drng.			1	1			1	1	1		2	4	2	2	4	3		2	1	1		26	49.0	4.24	.83	46
Cumberland R. Drng.							1	3	1	3	5	4		1							18	46.4	1.82	.43	17	
Ohio R. Drng.																										
Wabash R.					1	1	5	7	6	4	8	4	3	2	3							44	46.1	2.53	.38	75
Green R.					1						1											2	44.5	3.54	2.50	0
Kentucky R.								1			2	1	4	1			1					10	48.5	2.32	.73	0
Miami R.								1	1		1											3	45.3	1.53	.88	0
Kinniconick Cr.				1	2		2	1	1	1		2										10	43.9	2.85	.90	0
Scioto R.						3	1	4	2													10	43.5	1.18	.37	30
Muskingum R.		1		2	2	3	7	2	2		1											20	42.6	2.01	.45	10
Captina R.				2			1	1		1												5	43.0	2.12	.95	0
Mahoning R.					2		3	1	2		2											10	44.1	1.85	.59	20
Whitewater R. Syst.									2	2	1	4		3	3		1					14	49.1	2.09	.56	36
Little Muddy R. Syst.								1	2	3	4	3	2	4			1					20	47.8	2.20	.49	55
Kaskaskia R. Syst.									3	2	2	7	4	5	5	2	4	1				35	49.4	2.47	.42	60
Big R. Syst.													2	2	3	1	1			1		10	51.2	2.10	.66	0
Missouri R. Drng.																										
Gasconade R.													1			1						2	50.5	2.12	1.50	50
Osage R.					1			3	3	2	8	6	5	5	5	2	1					41	48.1	2.52	.39	12
Moreau R.												2	1		1		1					5	49.8	2.17	.97	0
Cedar Cr.						1			2	1	2		1	1		1		1				10	47.7	3.59	1.14	10
Moniteau Cr.										1	2											3	46.7	.58	.33	67
Chariton R.							1	2	2	4	5	3	2	1								20	46.8	2.07	.46	5
Crooked R.									1	2	2	5	5	2	3	1	1					20	49.2	1.78	.40	30
Wakarusa R.										2	2	2										6	47.0	.89	.37	0

Table B-6. (Continued)

Population	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	N	$\bar{x}$	SD	SE	%Comp	
Missouri R. Drng. Continued																											
Mill Cr.					1	2	4	4	4	3	3	2		1	2							22	50.0	2.50	.53	14	
Vermillion R.			1		2	2	4	4	4	3	3	1										20	44.6	2.01	.45	40	
Blue R.				1		3	3	2	2	3	1		1									14	44.7	2.02	.54	29	
Solomon R.					1					2	2											5	45.8	1.64	.73	0	
Elkhorn R.										2	2	1	1	2	2	2						12	49.1	2.23	.64	42	
Lodgepole R.										1	2	1										4	47.0	.82	.41	25	
Cache la Poudre R.									1	2	2	1	1	1	1	3						12	48.8	2.60	.75	33	
Laramie R.								1		1	2	3	3	2	5	3						20	49.3	2.20	.49	95	
Little Sioux R.										1	1	2		3	1							8	48.8	1.75	.62	12	
James R.								1	1	3	2	3	5			1						16	47.6	1.96	.49	25	
Big Sioux R.									1	2		2	3	2								10	48.0	1.76	.56	100	
Upper Mississippi R. Drng.																											
Macoupin Cr.									1	1	2	2	1	1	1			1				10	48.5	2.63	.83	40	
Yellow R.								1	1	3	1	5	2	1		1				1		16	48.2	3.06	.76	50	
Du Page R.					2	2	2	2	2	3	2	3	1	1	1	1						20	46.3	2.89	.64	75	
Mississippi R.									1									1				2	49.5	6.36	4.50	0	
Skunk R.										2	3	2	3	4	2	1						18	48.5	2.23	.52	94	
Iowa R.										3	2		4		1							10	47.9	1.73	.55	30	
Pecatonia R.					1	3	2	6	4	2	3				1							22	45.5	2.09	.44	68	
Bad Axe R.						1		1	1	1	1	1										5	45.8	1.92	.86	20	
Wisconsin R.									1	2				1			1					5	48.0	3.39	1.52	20	
Black R.				1		2	2	4	5	1	1	1	1									17	45.2	1.92	.47	6	
Whitewater R.				1		1	1	1		1	3											7	45.0	2.38	.90	43	

Table B-6. (Continued)

Population	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	N	$\bar{x}$	SD	SE	%Comp	
Upper Miss. R. Continued																											
Buffalo R.									1			1	2	1								5	48.2	1.92	.86	40	
Apple R.										1	1	2	5		3	4		1	3			20	50.7	2.70	.60	35	
Minnesota R.								2	4	2	7	2	8	2	2		1					30	47.7	2.20	.40	30	
Rum R.							1	1	6	2	2	2	3	3	2	1						20	48.0	2.19	.49	60	
Elk R.									2	4	2	2										10	46.4	1.07	.34	10	
Prarie R.							1	3		2	1		1	2								10	46.3	2.63	.83	10	
Great Lakes Basin																											
St. Lawrence R.		1	1	1	1	3	1															8	41.9	1.73	.61	63	
Grand R.					1	1	1	4	1	1	1	1										10	45.0	1.76	.56	20	
Maumee R.						1	1		4	3	2	4	3	1								19	47.6	2.14	.49	21	
St. Joseph R.										1	1	3										5	48.4	.89	.40	40	
Shiawassee R.				1	2	1			2	2	2	2	4	2	2							20	46.8	3.45	.77	90	
Au Sable R.					5	4			5	2	1	1		2								20	44.7	2.56	.57	40	
Portage Cr.								2	3	3		1					1					10	46.2	2.66	.84	70	
Muskegon R.				1		1	4		1	1	4		2									20	44.4	2.91	.65	100	
Manistee R.						1	3	2	2	2	3	1	1		2	5						20	47.8	3.25	.73	0	
Oconto R.									1	1	1	2										5	46.8	1.30	.58	0	
Lake Superior																1					1	3	55.0	2.65	1.53	100	
Hudson Bay Basin																											
James Bay																				1		10	49.5	2.59	.82	0	
Minnedosa R.						2	1					1	2	2	2							10	47.8	3.22	1.02	80	
Qu'Appelle R.						1					1	1	1	3				1				8	48.9	3.14	1.11	12	

Table B-7. Number of scales above the lateral line in Etheostoma nigrum.

Population	4	5	6	7	N	$\bar{x}$	SD	SE
Mobile Bay Basin								
Alabama R.	37	29			66	5.4	.53	.06
Black Warrior R.	13				13	5.0	.00	.00
Cahaba R.	5				5	5.0	.00	.00
Tallapoosa R.	21	12			33	5.4	.49	.08
Tombigbee R. (lower)	1	27	8		36	5.2	.47	.08
Tombigbee R. (upper)	15	26	3		44	4.7	.59	.09
Lower eastern								
Mississippi R.								
Homochitto R.	24	10			34	5.3	.46	.08
Bayou Pierre R.	41	20			61	5.3	.47	.06
Big Black R.	21	4			25	5.2	.37	.07
Yazoo R.	5	10	5		20	5.0	.72	.16
Obion R.	35	2			37	5.0	.23	.04
Red River Drng.								
Ouachitae R.		2			2	6.0	.00	.00
Mountain Fork R.	7	18	1		26	5.8	.51	.10
Kiamichi R.	10	4			14	5.3	.47	.12

Table B-7. (Continued)

Population	4	5	6	7	N	$\bar{X}$	SD	SE
Arkansas R. Drng.								
Current R.		1			1	5.0	.00	.00
Poteau R.		1	1		2	5.5	.71	.50
Spring R.		6			6	5.0	.00	.00
Tennessee R. Drng.	1	25			26	5.0	.20	.04
Cumberland R. Drng.		14	4		18	5.2	.43	.10
Ohio R. Drng.								
Wabash R.	2	31	11		44	5.2	.51	.08
Green R.		2			2	5.0	.00	.00
Kentucky R.		5	5		10	5.5	.53	.17
Miami R.		2	1		3	5.3	.58	.33
Kinniconick Cr.	1	9			10	4.9	.32	.10
Scioto R.		10			10	5.0	.00	.00
Muskingum R.	3	17			20	4.8	.37	.08
Captina R.	3	2			5	4.4	.55	.24
Mahoning R.		10			10	5.0	.00	.00
Whitewater R. Syst.	2	1	11		14	4.9	.47	.13
Little Muddy R. Syst.	1	17	2		20	5.0	.39	.09
Kaskaskia R. Syst.	2	32	1		35	5.0	.29	.05
River Aux Vases Syst.		5	15		20	5.8	.44	.10
Big R. Syst.	2	4	4		10	5.2	.79	.25

Table B-7. (Continued)

Population	4	5	6	7	N	$\bar{x}$	SD	SE
Missouri R. Drng.								
Gasconade R.		1	1		2	5.5	.71	.50
Osage R.	1	35	5		41	5.1	.37	.06
Moreau R.		3	2		5	5.4	.55	.24
Cedar Cr.		6	4		10	5.4	.52	.16
Moniteau Cr.	1	2			3	4.7	.58	.33
Chariton R.	3	17			20	4.8	.37	.08
Crooked R.		16	4		20	5.2	.41	.09
Wakarusa R.	1	3	2		6	5.2	.75	.31
Mill Cr.	3	17	2		22	5.0	.49	.10
Vermillion R.	2	18			20	4.9	.31	.07
Blue R.		13	1		14	5.1	.27	.07
Solomon R.	1	4			5	4.8	.45	.20
Elkhorn R.		11	1		12	5.1	.29	.08
Lodgepole R.		4			4	5.0	.00	.00
Cache la Poudre R.	5	7			12	4.6	.51	.15
Laramie R.		18	2		20	5.1	.31	.07
Little Sioux R.		8			8	5.0	.00	.00
James R.		16			16	5.0	.00	.00
Big Sioux R.	1	9			10	4.9	.32	.10

Table B-7. (Continued)

Population	4	5	6	7	N	$\bar{x}$	SD	SE
Upper Mississippi R.								
Drng.								
Macoupin Cr.		5	5		10	5.5	.53	.17
Yellow R.		11	5		16	5.3	.48	.12
Du Page R.	5	14	1		20	4.8	.52	.12
Mississippi R.		2			2	5.0	.00	.00
Skunk R.	1	14	3		18	5.1	.47	.11
Iowa R.	3	7			10	4.7	.48	.15
Pecatonia R.		19	3		22	5.1	.35	.07
Bad Axe R.	1	4			5	4.8	.45	.20
Wisconsin R.	1	4			5	4.8	.45	.20
Black R.	5	12			17	4.7	.47	.11
Whitewater R.	2	5			7	4.7	.49	.18
Buffalo R.	1	4			5	4.8	.45	.20
Apple R.		18	2		20	5.1	.31	.07
Minnesota R.		25	5		30	5.2	.38	.07
Rum R.	1	18	1		20	5.0	.32	.07
Elk R.	5	5			10	4.5	.53	.17
Prarie R.	1	9			10	4.9	.32	.10
Great Lakes Basin								
St. Lawrence R.	2	6			8	4.8	.46	.16
Grand R.		8	2		10	5.2	.42	.13
Maumee R.	3	15	1		19	4.9	.46	.10

Table B-7. (Continued)

Population	4	5	6	7	N	$\bar{X}$	SD	SE
Great Lakes Continued								
St. Joseph R.		3	2		5	5.4	.55	.24
Shiawassee R.		15	5		20	5.2	.44	.10
Au Sable R.	3	17			20	4.8	.37	.08
Portage Cr.		10			10	5.0	.00	.00
Muskegon R.		11	9		20	5.4	.51	.11
Manistee R.	6	14			20	4.7	.47	.10
Oconto R.		5			5	5.0	.00	.00
Lake Superior		3			3	5.0	.00	.00
Hudson Bay Basin								
James Bay	4	6			10	4.6	.52	.16
Minnedosa R.	1	8	1		10	5.0	.47	.15
Qu'Appelle R.	1	7			8	4.9	.35	.12

Table B-8. Number of scales below the lateral line in Etheostoma nigrum.

Population	5	6	7	8	9	10	N	$\bar{X}$	SD	SE
Mobile Bay Basin										
Alabama R.			9	29	26	2	66	8.3	.75	.09
Black Warrior R.			4	6	3		13	7.9	.76	.21
Cahaba R.			3	2			5	7.4	.55	.24
Tallapoosa R.			5	15	12	1	33	8.3	.76	.13
Tombigbee R. (lower)	1	2	11	15	7		36	7.7	.95	.16
Tombigbee R. (upper)		15	21	7	1		44	6.9	.76	.11
Lower eastern										
Mississippi R.										
Homochitto R.			1	19	10	4	34	8.5	.75	.13
Bayou Pierre R.			4	24	24	9	61	8.6	.82	.11
Big Black R.			4	7	13	1	25	8.4	.82	.16
Yazoo R.			7	7	6		20	8.0	.83	.18
Obion R.			4	13	20		37	8.4	.69	.11
Red River Drng.										
Ouachitae R.			1	1			2	7.5	.71	.50
Mountain Fork R.			4	14	8		26	8.2	.67	.13
Kiamichi R.		1	7	5	1		14	7.4	.76	.20

Table B-8. (Continued)

Population	5	6	7	8	9	10	N	$\bar{x}$	SD	SE
Arkansas R. Drng.										
Current R.				1			1	8.0	.00	.00
Poteau R.			1		1		2	8.0	1.41	1.00
Spring R.				3	2	1	6	8.7	.82	.33
Tennessee R. Drng.		5	8	10	3		26	7.4	.94	.18
Cumberland R. Drng.		3	2	9	4		18	7.8	1.00	.24
Ohio R. Drng.										
Wabash R.	1	8	21	11		3	44	8.2	.89	.13
Green R.			2				2	7.0	.00	.00
Kentucky R.			5	5			10	7.5	.53	.17
Miami R.	1	1			1		3	7.3	1.53	.88
Kinniconick Cr.			7	2	1		10	7.4	.70	.22
Scioto R.			3	6	1		10	7.8	.63	.20
Muskingum R.		2	14	3	1		20	7.2	.67	.15
Captina R.	1		3	1			5	6.8	1.09	.49
Mahoning R.		1	7	1	1		10	7.2	.79	.25
Whitewater R. Syst.			5	5	4		14	7.9	.83	.22
Little Muddy R. Syst.	2	10		6	2		20	7.4	.82	.18
Kaskaskia R. Syst.			2	17	15	1	35	8.4	.65	.11
River Aux Vases Syst.			3	4	12	1	20	8.6	.83	.19
Big R. Syst.			2	3	5		10	8.3	.82	.26

Table B-8. (Continued)

Population	5	6	7	8	9	10	N	$\bar{X}$	SD	SE
Missouri R. Drng.										
Gasconade R.			1		1		2	8.5	1.41	1.00
Osage R.			4	18	16	3	41	8.4	.78	.12
Moreau R.				4	1		5	8.2	.45	.20
Cedar Cr.				7	3		10	8.3	.48	.15
Moniteau Cr.				3			3	8.0	.00	.00
Chariton R.	1		8	9	2		20	7.6	.75	.17
Crooked R.			3	13	3	1	20	8.1	.72	.16
Wakarusa R.			1	1	4		6	8.5	.84	.34
Mill Cr.	1		6	12	3		22	7.8	.75	.16
Vermillion R.			6	11	3		20	7.8	.67	.15
Blue R.			8	5	1		14	8.5	.65	.17
Solomon R.			2	2	1		5	7.8	.84	.37
Elkhorn R.			6	5	1		12	7.6	.67	.19
Lodgepole R.			2	1	1		4	7.5	.50	.25
Cache la Poudre R.	4		5	3			12	6.9	.79	.23
Laramie R.	1		12	7			20	7.3	.57	.13
Little Sioux R.			6	2			8	7.2	.46	.16
James R.	2		11	2	1		16	8.1	.72	.18
Big Sioux R.	8		2				10	6.2	.43	.13

Table B-8. (Continued)

Population	5	6	7	8	9	10	N	$\bar{X}$	SD	SE
Upper Mississippi R.										
Drng.										
Macoupin Cr.	1		2	3	4		10	8.0	1.05	.33
Yellow R.			4	8	3	1	16	8.0	.85	.21
Du Page R.	2		10	8			20	7.3	.66	.15
Mississippi R.			1		1		2	8.0	1.41	1.00
Skunk R.	1		4	10	3		18	7.8	.79	.19
Iowa R.	2		8				10	6.8	.42	.13
Pecatonia R.			8	13	1		22	7.7	.57	.12
Bad Axe R.			3	2			5	7.4	.55	.24
Wisconsin R.			3	2			5	7.4	.55	.24
Black R.	1	8	6	2			17	6.5	.80	.19
Whitewater R.		1	5	1			7	7.0	.58	.22
Buffalo R.			5				5	7.0	.00	.00
Apple R.		4	10	6			20	7.1	.72	.16
Minnesota R.		3	16	11			30	7.3	.64	.12
Rum R.		6	9	5			20	7.0	.76	.17
Elk R.		3	5	2			10	6.9	.74	.23
Prarie R.	1	5	4				10	6.3	.67	.21
Great Lakes Basin										
St. Lawrence R.	3		1	4			8	7.1	.99	.35
Grand R.	2		3	5			10	7.3	.82	.26
Maumee R.	1		7	8	3		19	7.7	.82	.19

Table B-8. (Continued)

Population	5	6	7	8	9	10	N	$\bar{x}$	SD	SE
Great Lakes Continued										
St. Joseph R.			2	2	1		5	7.8	.84	.37
Shiawassee R.			3	9	8		20	8.2	.72	.16
Au Sable R.	6	10	4				20	6.9	.72	.16
Portage Cr.		1	6	3			10	8.2	.63	.20
Muskegon R.		3	14	3			20	8.0	.56	.13
Manistee R.	6	11	3				20	6.8	.67	.15
Oconto R.	3	1	1				5	6.6	.89	.40
Lake Superior		2	1				3	7.3	.58	.33
Hudson Bay Basin										
James Bay	8	2					10	6.2	.42	.13
Minnedosa R.	2	6	1	1			10	7.1	.88	.28
Qu'Appelle R.	1	5	2				8	7.1	.64	.23

Table B-9. Number of caudal peduncle scales rows in Etheostoma nigrum.

Population	12	13	14	15	16	17	18	19	N	$\bar{x}$	SD	SE
Mobile Bay Basin												
Alabama R.	1	8	12	20	10	11	4		66	15.2	1.47	.18
Black Warrior R.		2	7	4					13	14.2	.69	.19
Cahaba R				2	2	1			5	15.8	.84	.37
Tallapoosa R		1	7	14	7	3	1		33	15.2	1.08	.19
Tombigbee R. (lower)	1	3	8	11	9	3			36	15.0	1.21	.20
Tombigbee R. (upper)		7	14	14	7	1	1		44	14.6	1.14	.17
Lower eastern												
Mississippi R.												
Homochitto R.			6	5	6	11	6		34	16.2	1.38	.24
Bayou Pierre R.		2	13	21	14	9	1	1	61	15.4	1.21	.15
Big Black R.			2	3	9	10	1		25	16.2	1.00	.20
Yazoo R.			1	3	5	6	5		20	16.5	1.19	.27
Obion R.		2	5	12	14	4			37	15.3	1.03	.17
Red River Drng.												
Ouachitae R.				1		1			2	16.0	1.41	1.00
Mountain Fork R.	1	3	4	8	7	3			26	15.0	1.33	.26
Klamichi R.			2	5	6	1			14	15.4	.85	.23

Table B-9. (Continued)

Population	12	13	14	15	16	17	18	19	N	$\bar{X}$	SD	SE
Arkansas R. Drng.												
Current R.					1				1	16.0	.00	.00
Poteau R.			1	1					2	14.5	.71	.50
Spring R.				2	2	2			6	16.0	.89	.36
Tennessee R. Drng.		2	3	9	5	6	1		26	15.5	1.30	.26
Cumberland R. Drng.		2	4	9	3				18	14.2	2.45	.58
Ohio R. Drng.												
Wabash R.	1	4	5	26	6	2			44	14.9	1.00	.15
Green R.		1	1						2	13.5	.71	.50
Kentucky R.	1	3	2	4					10	13.9	1.10	.35
Miami R.	1		2						3	13.3	1.15	.67
Kinniconick Cr.		3	5	1	1				10	14.0	.94	.30
Scioto R.		6	3	1					10	13.5	.71	.22
Muskingum R.		5	9	6					20	14.0	.76	.17
Captina R.	1	2	1	1					5	13.4	1.14	.51
Mahoning R.		4	4	2					10	13.8	.79	.25
Whitewater R. Syst.			7	7					14	14.5	.52	.14
Little Muddy R. Syst.		2	9	5	3	1			20	14.6	1.05	.23
Kaskaskia R. Syst.			5	10	14	6			35	15.6	.95	.16
River Aux Vases Syst.			1	10	5	4			20	15.8	.81	.18
Big R. Syst.		2	1	5	2				10	14.7	1.06	.33

Table B-9. (Continued)

Population	12	13	14	15	16	17	18	19	N	$\bar{x}$	SD	SE
Missouri R. Drng.												
Gasconade R.						2			2	17.0	.00	.00
Osage R.		4	9	19	8	1			41	14.8	.95	.15
Moreau R.				1	2	2			5	16.2	.84	.37
Cedar Cr.	1	3	2	3	1				10	14.0	1.25	.39
Moniteau Cr.		1	2						3	13.7	.58	.33
Chariton R.		2	9	9					20	14.4	.67	.15
Crooked R.		2	7	8	3				20	14.6	.88	.20
Wakarusa R.			2	2	2				6	15.0	.89	.37
Mill Cr.		1	1	8	5	6	1		22	15.8	1.19	.25
Vermillion R.			4	10	6				20	15.2	.70	.16
Blue R.				10	3	1			14	15.4	.63	.17
Solomon R.					4	1			5	16.2	.45	.20
Elkhorn R.			2	4	5	1			12	15.4	.90	.26
Lodgepole R.				1	3				4	15.8	.50	.25
Cache la Poudre R.			3	5	2	2			12	15.2	1.05	.30
Laramie R.				3	10	7			20	16.2	.70	.16
Little Sioux R.			4	2	2				8	14.8	.89	.31
James R.		1	4	9	2				16	14.8	.77	.19
Big Sioux R.			2	7	1				10	14.9	.57	.18

Table B-9. (Continued)

Population	12	13	14	15	16	17	18	19	N	$\bar{X}$	SD	SE
Upper Mississippi R.												
Drng.												
Macoupin Cr.			1	5	4				10	15.3	.67	.21
Yellow R.	1	3	9	3					16	14.9	.81	.20
Du Page R.	5	11	4						20	14.0	.69	.15
Mississippi R.				1	1				2	15.5	.71	.50
Skunk R.			4	11	3				18	14.9	.64	.15
Iowa R.			2	8					10	14.8	.42	.13
Pecatonica R.	1		9	10	2				22	14.5	.86	.18
Bad Axe R.		1	2	2					5	14.2	.84	.37
Wisconsin R.		1	2	1	1				5	14.4	1.14	.51
Black R.	2		7	8					17	14.2	.97	.23
Whitewater R.		1	3	2	1				7	14.4	.98	.37
Buffalo R.	2		3						5	13.6	.55	.24
Apple R.			1	6	8	5			20	15.8	.87	.20
Minnesota R.			6	10	9	5			30	15.4	1.01	.18
Rum R.			7	12	1				20	14.7	.57	.13
Elk R.	1	2	3	2	2				10	14.2	1.32	.42
Prarie R.		1	3	6					10	14.5	.71	.22
Great Lakes Basin												
St. Lawrence R.			4	4					8	14.5	.53	.19
Grand R.		1	6	2	1				10	14.3	.82	.26
Maumee R.	1	1	5	9	3				19	14.6	1.01	.23

Table B-9. (Continued)

Population	12	13	14	15	16	17	18	19	N	$\bar{x}$	SD	SE
Great Lakes Continued												
St. Joseph R.		1			4				5	15.4	1.34	.60
Shiawassee R.			5	12	3				20	14.9	.64	.14
Au Sable R.	2	7	9	2					20	13.6	.83	.18
Portage Cr.		1	2	3	4				10	15.0	1.05	.33
Muskegon R.		3	5	9	3				20	14.6	.94	.21
Manistee R.		7	11	2					20	13.8	.64	.14
Oconto R.		2	2	1					5	13.8	.84	.37
Lake Superior			1	2	3				6	15.3	.82	.33
Hudson Bay Basin												
James Bay		1	2	7					10	14.6	.70	.22
Minnedosa R.		1	3	3	2	1			10	14.9	1.20	.38
Qu'Appelle R.		1	3	3	1				8	14.5	.93	.33

Table B-10. Condition of the supratemporal canal in
Etheostoma nigrum.

Population	Interrupted	Complete	N
Mobile Bay Basin			
Alabama R.	12	54	66
Black Warrior R.	12	1	13
Cahaba R.	1	4	5
Tallapoosa R.	12	21	33
Tombigbee R. (lower)	14	22	36
Tombigbee R. (upper)	21	23	44
Lower eastern			
Mississippi R.			
Hommochitto R.	0	34	34
Bayou Pierre R.	4	57	61
Big Black R.	3	22	25
Yazoo R.	0	20	20
Obion R.	3	34	37
Red River Drng.			
Ouachitae R.	2	0	2
Mountain Fork R.	26	0	26
Kiamichi R.	14	0	14
Arkansas River Drng.			
Current R.	1	0	1
Poteau R.	2	0	2
Spring R.	6	0	6
Tennessee R. Drng.	22	4	26
Cumberland R. Drng.	21	0	21
Ohio R. Drng.			
Wabash R.	25	19	44
Green R.	2	0	2
Kentucky R.	6	4	10
Miami R.	3	0	3
Kinniconick Cr.	6	4	10
Scioto R.	9	1	10
Muskingum R.	20	0	20
Captina R.	5	0	5
Mahoning R.	10	0	10

Table B-10. (Continued)

Population	Interrupted	Complete	N
Whitewater R. Syst.	14	0	14
Little Muddy R. Syst.	15	5	20
Kaskaskia R. Syst.	29	6	35
River Aux Vases Syst.	20	0	20
Big R. Syst.	10	0	10
Missouri R. Drng.			
Gasconade R.	2	0	2
Osage R.	41	0	41
Moreau R.	5	0	5
Cedar Cr.	8	2	10
Moniteau Cr.	3	0	3
Chariton R.	20	0	20
Crooked R.	20	0	20
Wakarusa R.	6	0	6
Mill Cr.	22	0	22
Vermillion R.	20	0	20
Blue R.	14	0	14
Solomon R.	5	0	5
Elkhorn R.	12	0	12
Lodgepole R.	2	2	4
Cache la Poudre R.	12	0	12
Laramie R.	20	0	20
Little Sioux R.	8	0	8
James R.	16	0	16
Big Sioux R.	9	1	10
Upper Mississippi R.			
Drng.			
Macoupin Cr.	8	2	10
Yellow R.	13	3	16
Du Page R.	15	5	20
Mississippi R.	2	0	2
Skunk R.	6	12	18
Iowa R.	10	0	10
Pecatonica R.	22	0	22
Bad Axe R.	5	0	5
Wisconsin R.	4	1	5

Table B-10. (Continued)

<u>Population</u>	<u>Interrupted</u>	<u>Complete</u>	<u>N</u>
Upper Miss. R. Continued			
Black R.	16	1	17
Whitewater R.	7	0	7
Buffalo R.	5	0	5
Apple R.	20	0	20
Minnesota R.	29	1	30
Rum R.	20	0	20
Elk R.	9	1	10
Prarie R.	10	0	10
Great Lakes Basin			
St. Lawrence R.	6	2	8
Grand R.	8	2	10
Maumee R.	19	0	19
St. Joseph R.	1	4	5
Shiawassee R.	15	5	20
Au Sable R.	13	7	20
Portage Cr.	10	0	10
Muskegon R.	20	0	20
Manistee R.	20	0	20
Oconto R.	5	0	5
Lake Superior	3	0	3
Hudson Bay Basin			
James Bay	9	1	10
Minnedosa R.	7	3	10
Qu'Appelle R.	8	0	8

Table B-11. Number of pores in the infraorbital canal in Etheostoma nigrum.

Population	5	6	7	8	9	10	11	12	13	14	15	16	17	18	N	$\bar{X}$	SD	SE
Mobile Bay Basin																		
Alabama R.	1	8	44	8	5										66	8.1	.77	.09
Black Warrior R.		5	8												13	7.6	.51	.14
Cahaba R.				4	1										5	8.2	.45	.20
Tallapoosa R.			1	27	3	2									33	8.2	.58	.10
Tombigbee R. (lower)			3	33											36	7.9	.28	.05
Tombigbee R. (upper)	1	5	30	7	1										44	8.0	.68	.10
Lower eastern																		
Mississippi R.																		
Homochitto R.					3	13	4	8	4	2					34	11.1	1.42	.24
Bayou Pierre R.						19	12	25	3	2					61	11.3	1.07	.14
Big Black R.					1	5	8	9	2						25	11.2	1.01	.20
Yazoo R.						3	6	4	4	2	1				20	12.0	1.43	.32
Obion R.					1	5	3	10	4	3	5	4	1	1	37	13.0	2.25	.37
Red River Drng.																		
Ouachitae R.				1	1										2	8.5	.71	.50
Mountain Fork R.	1	4	4	15	2										26	7.5	.99	.19
Kiamichi R.		3	5	5	1										14	7.3	.91	.24
Arkansas River Drng.																		
Current R.														1	1	11.0	.00	.00
Poteau R.	1				1										2	7.5	2.12	1.50
Spring R.			3	2	1										6	7.7	.82	.33

Table B-11. (Continued)

Population	5	6	7	8	9	10	11	12	13	14	15	16	17	18	N	$\bar{x}$	SD	SE
Tennessee R. Drng.	1			20	5										26	8.1	.59	.11
Cumberland R. Drng.	1			17	3										21	8.0	.59	.13
Ohio R. Drng.																		
Wabash R.				9	11	18	2	3	1						44	9.6	1.21	.18
Green R.					2										2	9.0	.00	.00
Kentucky R.				10											10	8.0	.00	.00
Miami R.				3											3	8.0	.00	.00
Kinniconick Cr.	1		1	8											10	7.7	.67	.21
Scioto R.			2	8											10	7.8	.42	.13
Muskingum R.			3	16	1										20	7.9	.45	.10
Captina R.				5											5	8.0	.00	.00
Mahoning R.			1	8	1										10	8.0	.47	.15
Whitewater R. Syst.			1	11	2										14	8.1	.48	.13
Little Muddy R. Syst.			1	10	5	4									20	8.6	.88	.20
Kaskaskia R. Syst.			1	15	4	11	1	2	1						35	9.2	1.40	.24
River Aux Vases Syst.			1	9	8	3									20	8.7	.73	.16
Big R. Syst.				9	1										10	8.1	.32	.10
Missouri R. Drng.																		
Gasconade R.				2											2	8.0	.00	.00
Osage R.	4	11	23	1	2										41	7.7	.88	.14
Moreau R.				4		1									5	8.4	.89	.40
Cedar Cr.				7	2	1									10	8.4	.70	.22
Moniteau Cr.				1	2										3	8.7	.58	.33
Chariton R.			1	19											20	8.0	.22	.05

Table B-11. (Continued)

Population	5	6	7	8	9	10	11	12	13	14	15	16	17	18	N	$\bar{x}$	SD	SE
Missouri R. Drng. Continued																		
Crooked R.			17	1	2										20	8.2	.64	.14
Wakarusa R.			5	1											6	8.2	.41	.17
Mill Cr.			13	7	2										22	8.5	.67	.14
Vermillion R.			11	6	3										20	8.6	.75	.17
Blue R.	2	8	3	1											14	8.2	.80	.21
Solomon R.			1	1	3										5	9.4	.89	.40
Elkhorn R.			7	3	2										12	8.5	.67	.19
Lodgepole R.			2	1	1										4	8.8	.96	.48
Cache la Poudre R.			10		1	1									12	8.5	1.00	.29
Laramie R.			12	7	1										20	8.4	.60	.13
Little Sioux R.			4	2	1	1									8	8.9	1.13	.40
James R.			9	4	3										16	8.6	.81	.20
Big Sioux R.			7	3											10	8.3	.48	.15
Upper Mississippi R. Drng.																		
Macoupin Cr.			2	6	2										10	9.0	.67	.21
Yellow R.			2	1	13										16	9.7	.70	.18
Du Page R.			3	2	3	5	4	3							20	10.7	1.66	.37
Mississippi R.			2												2	8.0	.00	.00
Skunk R.			4	7	6		1								18	9.2	1.02	.24
Iowa R.	1	2	1	5	1										10	9.3	1.25	.40
Pecatonica R.			7	3	7	4	1								22	9.5	1.26	.27
Bad Axe R.			3	2											5	8.4	.55	.24

Table B-11. (Continued)

Population	5	6	7	8	9	10	11	12	13	14	15	16	17	18	N	$\bar{x}$	SD	SE
Upper Mississippi R. Continued																		
Wisconsin R.				3	1	1									5	8.6	.89	.40
Black R.			1	13	3										17	8.1	.48	.12
Whitewater R.				6	1										7	8.1	.38	.14
Buffalo R.				2	2	1									5	8.8	.84	.37
Apple R.				4	4	9	3								20	9.6	1.00	.22
Minnesota R.	1	1	12	7	9										30	8.8	.99	.18
Rum R.				8	3	9									20	9.0	.95	.21
Elk R.				2	4	4									10	9.2	.79	.25
Prarie R.				3	7										10	8.7	.48	.15
Great Lakes Basin																		
St. Lawrence R.				3	3	2									8	8.9	.83	.29
Grand R.			1	7	2										10	8.1	.57	.18
Maumee R.				8	7	2		2							19	9.0	1.25	.29
St. Joseph R.				1	2	2									5	9.2	.84	.37
Shlawassee R.				2	1	11		3		3					20	10.7	1.78	.40
Au Sable R.					2	10	5	3							20	10.4	.89	.20
Portage Cr.				1	1	4	2	2							10	10.3	1.25	.40
Muskegon R.					2	3	3	6	3		1	1			20	12.1	2.29	.51
Manistee R.															20	7.9	.60	.13
Oconto R.	1	1	16	2											5	8.8	.84	.37
Lake Superior				2	1										3	8.3	.58	.33

Table B-11. (Continued)

Population	5	6	7	8	9	10	11	12	13	14	15	16	17	18	N	$\bar{x}$	SD	SE
Hudson Bay Basin																		
James Bay		1		8	1										10	7.9	.74	.23
Minnedosa R.				4	6										10	8.6	.52	.16
Qu'Appelle R.				7	1										8	8.1	.35	.12

Table B-12. Number of pores in the preoperculomandibular canal in Etheostoma nigrum.

Population	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	N	$\bar{X}$	SD	SE	
Mobile Bay Basin																				
Alabama R.							1			7	10	42	6			66	17.6	.97	.12	
Black Warrior R.						1		2	1	3	5	1				13	16.8	1.68	.46	
Cahaba R.							1		1		3					5	16.8	1.79	.80	
Tallapoosa R.							3	1	6	6	8	7	2			33	17.3	1.65	.29	
Tombigbee R. (lower)							1		5	6	21	3				36	17.5	1.03	.17	
Tombigbee R. (upper)						2	7	7	8	9	9	2				44	16.1	1.64	.25	
Lower eastern																				
Mississippi R.																				
Homochitto R.									1	8	25					34	17.7	.52	.09	
Bayou Pierre R.								2	3	38	13	5				61	18.3	.81	.10	
Big Black R.									5	11	4	5				25	18.4	1.04	.21	
Yazoo R.									1	6	6	6	1			20	19.0	1.02	.22	
Obion R.									6	26	3	2				37	18.0	.69	.11	
Red River Drng.																				
Ouachitae R.									2							2	16.0	.00	.00	
Mountain Fork R.				1	4	5	15	1								26	13.5	1.03	.20	
Kiamichi R.						3	8	3								14	14.0	.68	.18	
Arkansas River Drng.																				
Current R.								1								1	14.0	.00	.00	
Poteau R.									2							2	15.0	.00	.00	
Spring R.															1	6	9.8	1.47	.60	

Table B-12. (Continued)

Population	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	N	$\bar{x}$	SD	SE
Tennessee R. Drng.						1	1	2	2	5	2	7	1	5		26	17.0	2.26	.44
Cumberland R. Drng.						3	1	1	2	2	2	9	1			21	16.2	2.34	.51
Ohio R. Drng.																			
Wabash R.			2			1	3	3	7	3	7	16	2			44	16.2	2.27	.34
Green R.									1	1						2	15.5	.71	.50
Kentucky R.							1	2	1	1	1	3	1			10	16.2	2.10	.66
Miami R.										1	1	1				3	17.0	1.00	.58
Kinniconick Cr.										2	3	5				10	17.3	.82	.26
Scioto R.									1	1	8					10	17.5	1.08	.34
Muskingum R.				1	2	2	2	2	1	2	3	7				20	15.6	2.43	.54
Captina R.						1			1	1		2				5	16.0	2.12	.95
Mahoning R.								1	1	1		6	1			10	17.2	1.62	.51
Whitewater R. Syst.				9	1	4										14	10.6	.93	.25
Little Muddy R. Syst.			1	9	4	3	1	2								20	11.0	1.41	.32
Kaskaskia R. Syst.			1	17	5	6	3			2	1					35	11.3	1.90	.32
River Aux Vases Syst.				13	1	3	2		1							20	11.1	1.71	.38
Big R. Syst.				8	1			1								10	10.5	1.27	.40
Missouri R. Drng.																			
Gasconade R.					2											2	11.0	.00	.00
Osage R.				32	1	3	2	1	2							41	10.7	1.41	.22
Moreau R.					2	2	1									5	11.8	.84	.37
Cedar Cr.				5	1	1	3									10	11.2	1.40	.44
Moniteau Cr.			1	2												3	9.7	.58	.33

Table B-12. (Continued)

Population	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	N	$\bar{X}$	SD	SE	
Missouri R. Drng. Continued																				
Chariton R.	1	16	2	1												20	10.2	.59	.13	
Crooked R.		12	3	3		2										20	10.8	1.31	.29	
Wakarusa R.		5		1												6	10.3	.82	.33	
Mill Cr.		13	2	3	2	2										22	11.0	1.41	.30	
Vermillion R.		8	6	5	1											20	11.0	.94	.21	
Blue R.		11	2					1								14	10.5	1.34	.36	
Solomon R.		3	2													5	10.4	.55	.24	
Elkhorn R.		11	1													12	10.2	.58	.17	
Lodgepole R.			3	1												4	11.2	.50	.25	
Cache la Poudre R.		5	4	3												12	10.8	.83	.24	
Laramie R.			2	9	5	4										20	12.6	.94	.21	
Little Sioux R.		5	2	1												8	10.6	1.06	.37	
James R.		9	5	1	1											16	10.8	1.18	.30	
Big Sioux R.		3	3	2	1	1										12	11.4	1.35	.43	
Upper Mississippi R.																				
Drng.																				
Macoupin Cr.	1	2	3	2	1					1						10	11.5	1.96	.62	
Yellow R.	1	2	1	1	1	3	1	1	2	1	2	1	2			16	14.2	3.26	.81	
Du Page R.					1		1	4	11	3						20	15.6	1.14	.25	
Mississippi R.		2														2	10.0	.00	.00	
Skunk R.		13	1	2	1	1										18	10.9	1.64	.39	
Iowa R.		3	1	1	2	1	1	1	1	1	1					10	12.6	2.50	.79	
Pecatonica R.		1	1	1	3	3	3	3	3	3	4	1				22	14.4	2.22	.47	

Table B-12. (Continued)

Population	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	N	$\bar{x}$	SD	SE	
Upper Miss. R. Continued																				
Bad Axe R.			2			2	1									5	12.0	1.87	.84	
Wisconsin R.			4				1									5	10.8	1.79	.80	
Black R.			12		5											17	10.6	.94	.23	
Whitewater R.			2	3	2											7	11.0	.82	.31	
Buffalo R.			1	1	2			1								5	11.8	1.48	.66	
Apple R.			3	3	8	3			3							20	12.2	1.53	.34	
Minnesota R.			24	3	3											30	10.3	.65	.12	
Rum R.				1		2	6	6	4			1				20	14.6	1.46	.33	
Elk R.			7	2		1										10	10.5	.97	.31	
Prarie R.			6	3	1											10	10.5	.71	.22	
Great Lakes Basin																				
St. Lawrence R.								1	2	2	3					8	16.9	1.13	.40	
Grand R.								1		1	7	1				20	17.7	1.06	.34	
Maumee R.	1	7	2	4	1	3	1									19	11.5	1.77	.41	
St. Joseph R.									1	1	3					5	17.4	.89	.40	
Shiawassee R.						1		1	3	3	10	1	1			20	17.3	1.52	.34	
Au Sable R.						1	2	4	10	1	1	1				20	15.8	1.33	.30	
Portage Cr.	1	5	2	1					1							10	10.9	1.97	.62	
Muskegon R.						1	1	3	11	1	1	3				20	16.0	1.23	.28	
Manistee R.	1	5	5	3	2	4										20	11.6	1.60	.36	
Oconto R.				2				2	1							5	13.6	1.67	.75	
Lake Superior								1	1	1						3	15.0	1.00	.58	

Table B-12. (Continued)

Population	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	N	$\bar{X}$	SD	SE
Hudson Bay Basin																			
James Bay			1	8	1											10	10.0	.47	.15
Minnedosa R.				3	2	4	1									10	11.0	.94	.30
Qu'Appelle R.				6	1	1										8	10.4	.74	.26

Table B-13. Number of scales on the opercle in
Etheostoma nigrum.

Population	Range	N	$\bar{x}$	SD	SE
Mobile Bay Basin					
Alabama R.	8-26	66	14.9	3.81	.47
Black Warrior R.	11-20	13	15.2	3.22	.89
Cahaba R.	13-16	5	14.4	1.14	.51
Tallapoosa R.	8-20	33	13.6	2.79	.49
Tombigbee R. (lower)	8-24	36	17.7	3.65	.61
Tombigbee R. (upper)	0-23	44	9.6	7.05	1.06
Lower eastern					
Mississippi R.					
Homochitto R.	13-21	34	17.7	2.13	.36
Bayou Pierre R.	12-23	61	17.5	2.50	.32
Big Black R.	12-23	25	17.6	3.57	.71
Yazoo R.	14-24	20	20.0	2.76	.62
Obion R.	10-28	37	21.2	3.47	.57
Red River Drng.					
Ouachitae R.	5-6	2	5.5	.71	.50
Mountain Fork R.	0-14	26	4.9	2.92	.57
Kiamichi R.	6-16	14	10.9	2.87	.77
Arkansas River Drng.					
Current R.	22	1	22.0	.00	.00
Poteau R.	3-6	2	4.5	2.12	1.50
Spring R.	10-20	6	14.3	3.45	1.41
Tennessee R. Drng.	0-11	26	6.0	2.31	.45
Cumberland R. Drng.	0-13	21	5.9	4.67	1.02
Ohio R. Drng.					
Wabash R.	9-25	44	18.5	3.70	.56
Green R.	10	2	10.0	.00	.00
Kentucky R.	5-13	10	8.4	2.87	.91
Miami R.	2-15	3	7.0	7.00	4.04
Kinniconick Cr.	5-12	10	8.4	2.27	.72
Scioto R.	12-24	10	15.6	3.53	1.12
Muskingum R.	6-17	20	12.2	3.20	.72
Captina R.	11-20	5	15.2	3.27	1.46
Mahoning R.	11-17	10	13.3	1.89	.60

Table B-13. (Continued)

Population	Range	N	$\bar{X}$	SD	SE
Whitewater R. Syst.	1-15	14	7.2	4.12	1.10
Little Muddy Syst.	10-25	20	15.8	3.53	.79
Kaskaskia R. Syst.	3-22	35	15.0	4.24	.72
R. Aux Vases Syst.	15-26	20	19.7	3.08	.69
Big R. Syst.	5-10	10	7.1	1.66	.53
Missouri R. Drng.					
Gasconade R.	8-15	2	11.5	4.95	3.50
Osage R.	6-23	41	13.0	3.75	.59
Moreau R.	16-26	5	19.8	3.90	1.74
Cedar Cr.	6-13	10	9.5	2.27	.72
Moniteau Cr.	14-16	3	15.0	1.00	.58
Chariton R.	5-13	20	8.5	2.50	.56
Crooked R.	3-19	20	11.4	3.38	.75
Wakarusa R.	7-23	6	14.3	6.19	2.52
Mill Cr.	5-22	22	11.5	3.51	.75
Vermillion R.	10-21	20	14.9	2.84	.64
Blue R.	10-22	14	16.6	3.78	1.01
Solomon R.	9-17	5	12.4	2.97	1.33
Elkhorn R.	4-10	12	7.5	2.07	.60
Lodgepole R.	5-13	4	9.5	3.70	1.85
Cache la Poudre R.	2-12	12	7.4	3.23	.93
Laramie R.	7-16	20	11.7	2.00	.45
Little Sioux R.	17-36	8	27.3	5.57	1.97
James R.	9-19	16	13.7	2.91	.73
Big Sioux R.	5-24	10	16.7	7.42	2.35
Upper Mississippi R.					
Drng.					
Macoupin Cr.	9-28	10	18.5	5.99	1.89
Yellow R.	4-19	16	12.2	4.02	1.01
Du Page R.	9-24	20	17.3	3.91	.87
Mississippi R.	18-21	2	19.5	2.12	1.50
Skunk R.	8-22	18	15.1	3.51	.83
Iowa R.	4-13	10	9.2	2.53	.80
Pecatonia R.	8-26	22	18.2	4.16	.89
Bad Axe R.	13-16	5	14.2	1.30	.58
Wisconsin R.	1-13	5	9.2	4.97	2.22

Table B-13. (Continued)

Population	Range	N	$\bar{x}$	SD	SE
Upper Miss. R. Continued					
Black R.	4-18	17	8.9	3.15	.76
Whitewater R.	4-11	7	8.1	2.41	.91
Buffalo R.	11-17	5	13.4	2.30	1.03
Apple R.	17-30	20	22.8	3.57	.80
Minnesota R.	1-35	30	13.9	7.32	1.34
Rum R.	3-12	20	8.5	2.16	.48
Elk R.	4-9	10	6.8	1.87	.59
Prarie R.	5-26	10	14.4	5.52	1.75
Great Lakes Basin					
St. Lawrence R.	9-16	8	13.2	2.76	.98
Grand R.	6-12	10	8.8	1.99	.63
Maumee R.	0-21	19	11.7	5.34	1.23
St. Joseph R.	11-16	5	12.8	2.17	.97
Shiawassee R.	14-28	20	21.6	3.75	.84
Au Sable R.	11-21	20	16.8	2.62	.59
Portage Cr.	9-17	10	13.2	2.78	.88
Muskegon R.	13-25	20	19.6	2.98	.67
Manistee R.	9-17	20	12.7	2.43	.54
Oconto R.	4-8	5	6.0	1.58	.71
Lake Superior	2-15	3	10.0	7.00	4.04
Hudson Bay Basin					
James Bay	1-5	10	2.8	1.62	.51
Minnedosa R.	9-23	10	15.2	4.39	1.39
Qu'Appelle R.	6-20	8	12.2	5.99	2.12

Table B-14. Number of scales on the cheek in
Etheostoma nigrum.

Population	Range	N	$\bar{x}$	SD	SE
Mobile Bay Basin					
Alabama R.	0	66	0.0	.00	.00
Black Warrior R.	0	13	0.0	.00	.00
Cahaba R.	0	5	0.0	.00	.00
Tallapoosa R.	0	33	0.0	.00	.00
Tombigbee R. (lower)	0	36	0.0	.00	.00
Tombigbee R. (upper)	0-2	44	0.1	.30	.05
Lower eastern					
Mississippi R.					
Homochitto R.	0-2	34	0.4	.73	.13
Bayou Pierre R.	0-5	61	0.3	.88	.11
Big Black R.	0	25	0.0	.00	.00
Yazoo R.	0-8	20	2.6	2.26	.51
Obion R.	0-9	37	2.3	1.94	.32
Red River Drng.					
Ouachitae R.	0	2	0.0	.00	.00
Mountain Fork R.	0-14	26	4.9	2.92	.57
Kiamichi R.	6-16	14	10.9	2.87	.77
Arkansas River Drng.					
Current R.	14	1	14.0	.00	.00
Poteau R.	0	2	0.0	.00	.00
Spring R.	0-12	6	5.3	4.46	1.82
Tennessee R. Drng.					
	0	26	0.0	.00	.00
Cumberland R. Drng.					
	0	21	0.0	.00	.00
Ohio R. Drng.					
Wabash R.	0-19	44	2.2	3.39	.51
Green R.	0	2	0.0	.00	.00
Kentucky R.	0	10	0.0	.00	.00
Miami R.	0	3	0.0	.00	.00
Kinniconick Cr.	0	10	0.0	.00	.00
Scioto R.	0-1	10	0.2	.42	.13
Muskingum R.	0-7	20	0.8	1.76	.39
Captina R.	0	5	0.0	.00	.00
Mahoning R.	0	10	0.0	.00	.00

Table B-14. (Continued)

Population	Range	N	$\bar{x}$	SD	SE
Whitewater R. Syst.	0	14	0.0	.00	.00
Little Muddy R. Syst.	0	20	0.0	.00	.00
Kaskaskia R. Syst.	0-5	35	0.3	1.00	.17
River Aux Vases Syst.	0-2	20	0.2	.52	.12
Big R. Syst.	0	10	0.0	.00	.00
Missouri R. Drng.					
Gasconade R.	0-2	2	1.0	1.41	1.00
Osage R.	0-4	41	0.8	1.24	.19
Moreau R.	0-3	5	1.4	1.34	.60
Cedar Cr.	0	10	0.0	.00	.00
Moniteau Cr.	0	3	0.0	.00	.00
Chariton R.	0	20	0.0	.00	.00
Crooked R.	0	20	0.0	.00	.00
Wakarusa R.	0-1	6	0.2	.41	.17
Mill Cr.	0	22	0.0	.00	.00
Vermillion R.	0-3	20	0.7	1.02	.23
Blue R.	0-1	14	0.1	.36	.10
Solomon R.	0-2	5	0.6	.89	.40
Elkhorn R.	0	12	0.0	.00	.00
Lodgepole R.	0	4	0.0	.00	.00
Cache la Poudre R.	0	12	0.0	.00	.00
Laramie R.	0	20	0.0	.00	.00
Little Sioux R.	32-49	8	40.8	6.04	2.14
James R.	0-4	16	0.9	1.48	.37
Big Sioux R.	0-20	10	9.3	7.65	2.42
Upper Mississippi R.					
Drng.					
Macoupin Cr.	0-9	10	1.8	3.05	.96
Yellow R.	0	16	0.0	.00	.00
Du Page R.	0-15	20	2.4	3.44	.77
Mississippi R.	0	2	0.0	.00	.00
Skunk R.	0	18	0.0	.00	.00
Iowa R.	0-1	10	0.1	.32	.10
Pecatonia R.	0-3	22	0.9	.99	.21
Bad Axe R.	0	5	0.0	.00	.00
Wisconsin R.	0	5	0.0	.00	.00

Table B-14. (Continued)

Population	Range	N	$\bar{x}$	SD	SE
Upper Miss. R. Continued					
Black R.	0	17	0.0	.00	.00
Whitewater R.	0	7	0.0	.00	.00
Buffalo R.	0	5	0.0	.00	.00
Apple R.	4-51	20	27.8	13.78	3.08
Minnesota R.	0-39	30	8.1	10.57	1.93
Rum R.	0	20	0.0	.00	.00
Elk R.	0	10	0.0	.00	.00
Prarie R.	0-32	10	12.0	13.22	4.18
Great Lakes Basin					
St. Lawrence R.	0-9	8	2.8	2.96	1.05
Grand R.	0	10	0.0	.00	.00
Maumee R.	0-5	19	0.7	1.45	.33
St. Joseph R.	0-1	5	0.2	.45	.20
Shiawassee R.	0-26	20	10.2	7.35	1.64
Au Sable R.	0-14	20	2.8	3.42	.76
Portage Cr.	0-2	10	0.2	.63	.20
Muskegon R.	0-7	20	0.6	1.60	.36
Manistee R.	0	20	0.0	.00	.00
Oconto R.	0	5	0.0	.00	.00
Lake Superior	0	3	0.0	.00	.00
Hudson Bay Basin					
James Bay	0	10	0.0	.00	.00
Minnedosa R.	0	10	0.0	.00	.00
Qu'Appelle R.	0-13	8	4.1	5.87	2.07

Table B-15. Number of scales on the prepectoral area in
Etheostoma nigrum.

Population	Range	N	$\bar{X}$	SD	SE
Mobile Bay Basin					
Alabama R.	0-1	66	0.1	.17	.02
Black Warrior R.	0	13	0.0	.00	.00
Cahaba R.	0	5	0.0	.00	.00
Tallapoosa R.	0	33	0.0	.00	.00
Tombigbee R. (lower)	0	36	0.0	.00	.00
Tombigbee R. (upper)	0	44	0.0	.00	.00
Lower eastern					
Mississippi R.					
Homochitto R.	0	34	0.0	.00	.00
Bayou Pierre R.	0-1	61	0.2	.18	.02
Big Black R.	0-1	25	0.1	.20	.04
Yazoo R.	0	20	0.0	.00	.00
Obion R.	0-5	37	0.3	.91	.15
Red River Drng.					
Ouachitae R.	0	2	0.0	.00	.00
Mountain Fork R.	0	26	0.0	.00	.00
Kiamichi R.	0	14	0.0	.00	.00
Arkansas River Drng.					
Current R.	7	1	7.0	.00	.00
Poteau R.	0	2	0.0	.00	.00
Spring R.	6-7	6	6.3	.52	.21
Tennessee R. Drng.					
Cumberland R. Drng.	0	21	0.0	.00	.00
Ohio R. Drng.					
Wabash R.	0-8	44	2.4	2.32	.35
Green R.	0	2	0.0	.00	.00
Kentucky R.	0	10	0.0	.00	.00
Miami R.	0	3	0.0	.00	.00
Kinniconick Cr.	0	10	0.0	.00	.00
Scioto R.	0	10	0.0	.00	.00
Muskingum R.	0	20	0.0	.00	.00
Captina R.	0	5	0.0	.00	.00
Mahoning R.	0	10	0.0	.00	.00

Table B-15. (Continued)

Population	Range	N	$\bar{x}$	SD	SE
Whitewater R. Syst.	0	14	0.0	.00	.00
Little Muddy R. Syst.	0-1	20	0.2	.44	.10
Kaskaskia R. Syst.	0-2	35	0.3	.63	.11
River Aux Vases Syst.	0-1	20	0.3	.47	.10
Big R. Syst.	0	10	0.0	.00	.00
Missouri R. Drng.					
Gasconade R.	8-10	2	9.0	1.41	1.00
Osage R.	0-8	41	2.8	1.79	.28
Moreau R.	2-6	5	4.6	1.95	.87
Cedar Cr.	0-2	10	0.5	.85	.27
Moniteau Cr.	0-2	3	1.0	1.00	.58
Chariton R.	0-2	20	0.4	.68	.15
Crooked R.	0-4	20	0.8	1.10	.25
Wakarusa R.	2-7	6	3.3	1.97	.80
Mill Cr.	0-2	22	0.1	.47	.10
Vermillion R.	0-2	20	0.6	.75	.17
Blue R.	0-6	14	1.6	1.95	.52
Solomon R.	0-3	5	1.4	1.14	.51
Elkhorn R.	0-1	12	0.2	.39	.11
Lodgepole R.	0	4	0.0	.00	.00
Cache la Poudre R.	0	12	0.0	.00	.00
Laramie R.	0-1	20	0.1	.22	.05
Little Sioux R.	10-15	8	12.1	1.96	.69
James R.	0-6	16	3.6	1.54	.39
Big Sioux R.	0-9	10	4.3	3.50	1.11
Upper Mississippi R.					
Drng.					
Macoupin Cr.	0-5	10	1.3	1.83	.58
Yellow R.	0	16	0.0	.00	.00
Du Page R.	3-13	20	6.6	2.66	.60
Mississippi R.	0-3	2	1.5	2.12	1.50
Skunk R.	0-2	18	0.4	.61	.14
Iowa R.	0-7	10	2.9	2.51	.79
Pecatonia R.	0-6	22	1.7	1.93	.41
Bad Axe R.	0-7	5	1.4	3.13	1.40
Wisconsin R.	0-1	5	0.2	.45	.20

Table B-15. (Continued)

Population	Range	N	$\bar{x}$	SD	SE
Upper Miss. R. Continued					
Black R.	0	17	0.0	.00	.00
Whitewater R.	0-1	7	0.3	.49	.18
Buffalo R.	0-1	5	0.4	.55	.24
Apple R.	4-17	20	11.2	4.52	1.01
Minnesota R.	0-11	30	4.5	3.99	.73
Rum R.	0-3	20	0.7	.92	.21
Elk R.	0-4	10	0.7	1.25	.40
Prarie R.	0-16	10	6.5	5.36	1.70
Great Lakes Basin					
St. Lawrence R.	0-5	8	1.6	1.77	.62
Grand R.	0	10	0.0	.00	.00
Maumee R.	0-2	19	0.2	.50	.11
St. Joseph R.	0	5	0.0	.00	.00
Shiawassee R.	2-10	20	6.2	2.28	.51
Au Sable R.	0-6	20	1.9	1.89	.42
Portage Cr.	0-2	10	0.5	.85	.27
Muskegon R.	0-6	20	0.8	1.64	.37
Manistee R.	0	20	0.0	.00	.00
Oconto R.	0	5	0.0	.00	.00
Lake Superior	0-3	3	1.3	1.53	.88
Hudson Bay Basin					
James Bay	0-2	10	0.5	.85	.27
Minnedosa R.	0	10	0.0	.00	.00
Qu'Appelle R.	0-4	8	1.0	1.41	.50

Table B-16. Number of scales on the nape in Etheostoma nigrum.

Population	Range	N	$\bar{x}$	SD	SE
Mobile Bay Basin					
Alabama R.	0	66	0.0	.00	.00
Black Warrior R.	0	13	0.0	.00	.00
Cahaba R.	0	5	0.0	.00	.00
Tallapoosa R.	0	33	0.0	.00	.00
Tombigbee R. (lower)	0	36	0.0	.00	.00
Tombigbee R. (upper)	0	44	0.0	.00	.00
Lower eastern					
Mississippi R.					
Homochitto R.	0	34	0.0	.00	.00
Bayou Pierre R.	0-3	61	0.2	.57	.07
Big Black R.	0-2	25	0.1	.40	.08
Yazoo R.	0-2	20	0.2	.55	.12
Obion R.	0-3	37	0.2	.60	.10
Red River Drng.					
Ouachitae R.	0	2	0.0	.00	.00
Mountain Fork R.	0	26	0.0	.00	.00
Kiamichi R.	0	14	0.0	.00	.00
Arkansas River Drng.					
Current R.	31	1	31.0	.00	.00
Poteau R.	0	2	0.0	.00	.00
Spring R.	27-35	6	30.2	2.86	1.17
Tennessee R. Drng.	0-15	26	0.8	3.12	.61
Cumberland R. Drng.	0	21	0.0	.00	.00
Ohio R. Drng.					
Wabash R.	0-34	44	13.3	10.66	1.61
Green R.	0	2	0.0	.00	.00
Kentucky R.	0	10	0.0	.00	.00
Miami R.	0	3	0.0	.00	.00
Kinniconick Cr.	0	10	0.0	.00	.00
Scioto R.	0-5	10	0.9	1.73	.55
Muskingum R.	0-4	20	0.5	1.23	.28
Captina R.	0	5	0.0	.00	.00
Mahoning R.	0	10	0.0	.00	.00

Table B-16. (Continued)

Population	Range	N	$\bar{X}$	SD	SE
Whitewater R. Syst.	0	14	0.0	.00	.00
Little Muddy R. Syst.	0-5	20	0.4	1.39	.31
Kaskaskia R. Syst.	0-8	35	1.0	1.89	.32
River Aux Vases Syst.	0-9	20	2.7	2.94	.66
Big R. Syst.	0	10	0.0	.00	.00
Missouri R. Drng.					
Gasconade R.	0-6	2	3.0	4.24	3.00
Osage R.	0-8	41	1.6	2.39	.37
Moreau R.	4-28	5	14.6	10.90	4.87
Cedar Cr.	0-1	10	0.1	.32	.10
Moniteau Cr.	1-10	3	4.3	4.93	2.85
Chariton R.	0	20	0.0	.00	.00
Crooked R.	0-7	20	1.5	2.19	.49
Wakarusa R.	2-17	6	7.8	5.42	2.21
Mill Cr.	0-2	22	0.2	.59	.12
Vermillion R.	0-8	20	2.5	2.26	.50
Blue R.	0-7	14	4.0	2.11	.56
Solomon R.	0-5	5	2.2	1.92	.86
Elkhorn R.	0	12	0.0	.00	.00
Lodgepole R.	0	4	0.0	.00	.00
Cache la Poudre R.	0	12	0.0	.00	.00
Laramie R.	0	20	0.0	.00	.00
Little Sioux R.	24-36	8	31.1	3.64	1.29
James R.	0-17	16	7.7	4.74	1.19
Big Sioux R.	0-28	10	9.9	9.40	2.97
Upper Mississippi R.					
Drng.					
Macoupin Cr.	0-11	10	4.8	3.19	1.01
Yellow R.	0-4	16	0.4	1.09	.27
Du Page R.	5-31	20	23.0	7.80	1.74
Mississippi R.	0-12	2	6.0	8.48	6.00
Skunk R.	0	18	0.0	.00	.00
Iowa R.	9-17	10	12.7	2.79	.88
Pecatonia R.	2-23	22	7.7	5.37	1.14
Bad Axe R.	2-4	5	3.0	1.00	.45
Wisconsin R.	0-4	5	1.0	1.73	.78

Table B-16. (Continued)

<u>Population</u>	<u>Range</u>	<u>N</u>	<u>$\bar{x}$</u>	<u>SD</u>	<u>SE</u>
Upper Miss. R. Continued					
Black R.	0-5	17	0.3	1.21	.29
Whitewater R.	0-10	7	4.1	4.49	1.70
Buffalo R.	0-6	5	2.4	3.29	1.47
Apple R.	16-45	20	37.0	6.72	1.50
Minnesota R.	0-31	30	10.4	10.56	1.93
Rum R.	0-8	20	1.8	2.55	.57
Elk R.	0-5	10	1.6	2.01	.64
Prarie R.	0-36	10	23.3	12.94	4.09
Great Lakes Basin					
St. Lawrence R.	0-20	8	8.1	6.96	2.46
Grand R.	0	10	0.0	.00	.00
Maumee R.	0-15	19	2.7	4.63	1.06
St. Joseph R.	0-11	5	4.4	6.02	2.69
Shiawassee R.	9-33	20	26.4	6.60	1.47
Au Sable R.	2-30	20	7.9	7.14	1.60
Portage Cr.	3-13	10	7.9	3.98	1.26
Muskegon R.	0-27	20	7.7	7.61	1.70
Manistee R.	0	20	0.0	.00	.00
Oconto R.	0	5	0.0	.00	.00
Lake Superior	0	3	0.0	.00	.00
Hudson Bay Basin					
James Bay	0	10	0.0	.00	.00
Minnedosa R.	0-3	10	1.0	1.25	.39
Qu'Appelle R.	0-12	8	3.5	4.96	1.75

Table B-17. Number of scales on the breast in
Etheostoma nigrum.

Population	Range	N	$\bar{x}$	SD	SE
Mobile Bay Basin					
Alabama R.	0	66	0.0	.00	.00
Black Warrior R.	0	13	0.0	.00	.00
Cahaba R.	0	5	0.0	.00	.00
Tallapoosa R.	0	33	0.0	.00	.00
Tombigbee R. (lower)	0	36	0.0	.00	.00
Tombigbee R. (upper)	0	44	0.0	.00	.00
Lower eastern					
Mississippi R.					
Homochitto R.	0	34	0.0	.00	.00
Bayou Pierre R.	0	61	0.0	.00	.00
Big Black R.	0	25	0.0	.00	.00
Yazoo R.	0	20	0.0	.00	.00
Obion R.	0	37	0.0	.00	.00
Red River Drng.					
Ouachitae R.	0	2	0.0	.00	.00
Mountain Fork R.	0	26	0.0	.00	.00
Kiamichi R.	0	14	0.0	.00	.00
Arkansas River Drng.					
Current R.	44	1	44.0	.00	.00
Poteau R.	0	2	0.0	.00	.00
Spring R.	43-62	6	55.2	7.11	2.90
Tennessee R. Drng.					
	0	26	0.0	.00	.00
Cumberland R. Drng.					
	0	21	0.0	.00	.00
Ohio R. Drng.					
Wabash R.	0-48	44	7.5	15.51	2.34
Green R.	0	2	0.0	.00	.00
Kentucky R.	0	10	0.0	.00	.00
Miami R.	0	3	0.0	.00	.00
Kinniconick Cr.	0	10	0.0	.00	.00
Scioto R.	0	10	0.0	.00	.00
Muskingum R.	0	20	0.0	.00	.00
Captina R.	0	5	0.0	.00	.00
Mahoning R.	0	10	0.0	.00	.00

Table B-17. (Continued)

Population	Range	N	$\bar{x}$	SD	SE
Whitewater R. Syst.	0	14	0.0	.00	.00
Little Muddy R. Syst.	0	20	0.0	.00	.00
Kaskaskia R. Syst.	0	35	0.0	.00	.00
River Aux Vases Syst.	0	20	0.0	.00	.00
Big R. Syst.	0	10	0.0	.00	.00
Missouri R. Drng.					
Gasconade R.	0-3	2	1.5	2.12	1.50
Osage R.	0-10	41	0.7	1.87	.29
Moreau R.	0-22	5	8.8	9.31	4.16
Cedar Cr.	0	10	0.0	.00	.00
Moniteau Cr.	0	3	0.0	.00	.00
Chariton R.	0	20	0.0	.00	.00
Crooked R.	0	20	0.0	.00	.00
Wakarusa R.	0-6	6	1.8	2.86	1.17
Mill Cr.	0	22	0.0	.00	.00
Vermillion R.	0	20	0.0	.00	.00
Blue R.	0-3	14	0.2	.80	.21
Solomon R.	0	5	0.0	.00	.00
Elkhorn R.	0	12	0.0	.00	.00
Lodgepole R.	0	4	0.0	.00	.00
Cache la Poudre R.	0	12	0.0	.00	.00
Laramie R.	0	20	0.0	.00	.00
Little Sioux R.	88-100	8	93.2	3.95	1.40
James R.	11-27	16	18.9	4.86	1.22
Big Sioux R.	23-90	10	57.5	29.11	9.21
Upper Mississippi R.					
Drng.					
Macoupin Cr.	0	10	0.0	.00	.00
Yellow R.	0	16	0.0	.00	.00
Du Page R.	0-53	20	20.6	12.75	2.85
Mississippi R.	0	2	0.0	.00	.00
Skunk R.	0	18	0.0	.00	.00
Iowa R.	0-25	10	9.9	8.06	2.55
Pecatonia R.	0-4	22	0.6	1.22	.26
Bad Axe R.	0	5	0.0	.00	.00
Wisconsin R.	0	5	0.0	.00	.00

Table B-17. (Continued)

Population	Range	N	$\bar{X}$	SD	SE
Upper Miss. R. Continued					
Black R.	0	17	0.0	.00	.00
Whitewater R.	0	7	0.0	.00	.00
Buffalo R.	0	5	0.0	.00	.00
Apple R.	72-97	20	85.8	6.76	1.51
Minnesota R.	0-78	30	24.9	25.46	4.65
Rum R.	0-13	20	2.2	3.86	.86
Elk R.	0-9	10	1.3	2.83	.89
Prarie R.	0-94	10	52.5	34.85	11.02
Great Lakes Basin					
St. Lawrence R.	0	8	0.0	.00	.00
Grand R.	0	10	0.0	.00	.00
Maumee R.	0	19	0.0	.00	.00
St. Joseph R.	0	5	0.0	.00	.00
Shiawassee R.	0-70	20	22.4	17.89	4.00
Au Sable R.	0-12	20	2.6	3.54	.79
Portage Cr.	0	10	0.0	.00	.00
Muskegon R.	0-2	20	0.1	.45	.10
Manistee R.	0	20	0.0	.00	.00
Oconto R.	0	5	0.0	.00	.00
Lake Superior	0-7	3	4.0	3.61	2.08
Hudson Bay Basin					
James Bay	0	10	0.0	.00	.00
Minnedosa R.	0	10	0.0	.00	.00
Qu'Appelle R.	0-50	8	17.5	24.25	8.57

Table B-18. Number of scales on the belly in Etheostoma nigrum.

Population	Range	N	$\bar{x}$	SD	SE
Mobile Bay Basin					
Alabama R.	0-28	66	5.1	8.77	1.09
Black Warrior R.	0	13	0.0	.00	.00
Cahaba R.	0	5	0.0	.00	.00
Tallapoosa R.	0	33	0.0	.00	.00
Tombigbee R. (lower)	0	36	0.0	.00	.00
Tombigbee R. (upper)	0-26	44	1.4	4.33	.65
Lower eastern					
Mississippi R.					
Homochitto R.	0-5	34	0.5	1.31	.22
Bayou Pierre R.	0-15	61	0.6	2.47	.32
Big Black R.	0-3	25	0.2	.71	.14
Yazoo R.	0-5	20	1.2	1.87	.42
Obion R.	0-35	37	8.0	7.37	1.21
Red River Drng.					
Ouachitae R.	0	2	0.0	.00	.00
Mountain Fork R.	0	26	0.0	.00	.00
Kiamichi R.	0	14	0.0	.00	.00
Arkansas River Drng.					
Current R.	57	1	57.0	.00	.00
Poteau R.	0	2	0.0	.00	.00
Spring R.	47-54	6	49.7	2.42	.99
Tennessee R. Drng.	0-30	26	3.6	7.91	1.55
Cumberland R. Drng.	0	21	0.0	.00	.00
Ohio R. Drng.					
Wabash R.	17-62	44	39.5	12.30	1.85
Green R.	0	2	0.0	.00	.00
Kentucky R.	0	10	0.0	.00	.00
Miami R.	26-32	3	28.0	3.46	2.00
Kinniconick Cr.	12-26	10	20.9	3.93	1.24
Scioto R.	17-30	10	25.0	4.55	1.44
Muskingum R.	26-51	20	41.2	7.81	1.75
Captina R.	7-27	5	20.4	7.92	3.54
Mahoning R.	19-48	10	31.0	8.96	2.83

Table B-18. (Continued)

Population	Range	N	$\bar{x}$	SD	SE
Whitewater R. Syst.	0-25	14	12.5	7.33	1.96
Little Muddy R. Syst.	7-50	20	28.0	11.36	2.54
Kaskaskia R. Syst.	0-41	35	18.9	11.69	1.98
R. Aux Vases Syst.	6-40	20	25.8	8.41	1.88
Big R. Syst.	0-27	10	12.9	7.65	2.42
Missouri R. Drng.					
Gasconade R.	50	2	50.0	.00	.00
Osage R.	29-79	41	52.6	8.72	1.36
Moreau R.	53-68	5	62.8	5.72	2.56
Cedar Cr.	20-50	10	30.4	9.89	3.13
Moniteau Cr.	37-41	3	38.7	2.08	1.20
Chariton R.	15-66	20	32.0	11.48	2.57
Crooked R.	37-72	20	55.6	9.62	2.15
Wakarusa R.	44-60	6	55.8	6.11	2.50
Mill Cr.	6-30	22	13.7	6.12	1.30
Vermillion R.	16-41	20	25.4	7.81	1.75
Blue R.	13-54	14	35.8	12.93	3.46
Solomon R.	30-60	5	48.2	12.13	5.43
Elkhorn R.	41-62	12	54.8	6.16	1.78
Lodgepole R.	12-22	4	17.5	4.20	2.10
Cache la Poudre R.	6-40	12	21.6	10.52	3.04
Laramie R.	16-60	20	39.4	12.09	2.70
Little Sioux R.	49-62	8	56.5	4.57	1.62
James R.	52-68	16	59.7	4.42	1.11
Big Sioux R.	40-57	10	51.0	5.94	1.88
Upper Mississippi R.					
Drng.					
Macoupin Cr.	21-48	10	34.0	9.16	2.90
Yellow R.	0-27	16	15.4	8.09	2.02
Du Page R.	39-62	20	51.4	5.87	1.31
Mississippi R.	58-60	2	59.0	1.41	1.00
Skunk R.	33-63	18	46.2	9.26	2.18
Iowa R.	50-63	10	57.0	4.40	1.39
Pecatonia R.	27-53	22	38.4	6.92	1.47
Bad Axe R.	23-60	5	46.4	15.08	6.74
Wisconsin R.	26-50	5	42.6	9.74	4.35

Table B-18. (Continued)

Population	Range	N	$\bar{x}$	SD	SE
Upper Miss. R. Continued					
Black R.	6-34	17	19.9	8.59	2.08
Whitewater R.	34-56	7	42.0	8.58	3.24
Buffalo R.	35-55	5	49.8	8.41	3.76
Apple R.	55-67	20	59.0	3.21	.72
Minnesota R.	16-61	30	49.0	11.15	2.04
Rum R.	35-62	20	50.2	9.16	2.05
Elk R.	36-62	10	52.3	8.64	2.73
Prarie R.	45-60	10	53.4	6.20	1.96
Great Lakes Basin					
St. Lawrence R.	26-49	8	40.4	8.31	2.94
Grand R.	6-30	10	19.1	7.69	2.43
Maumee R.	0-37	19	13.8	15.13	3.47
St. Joseph R.	26-40	5	33.4	5.90	2.64
Shiawassee R.	24-61	20	51.6	9.31	2.08
Au Sable R.	28-55	20	43.6	7.30	1.63
Portage Cr.	22-40	10	31.3	6.06	1.91
Muskegon R.	26-56	20	43.2	7.21	1.61
Manistee R.	6-25	20	9.6	5.58	1.25
Oconto R.	30-53	5	47.2	9.83	4.40
Lake Superior	55-59	3	56.7	2.08	1.20
Hudson Bay Basin					
James Bay	14-50	10	40.5	10.96	3.46
Minnedosa R.	29-40	10	33.4	4.17	1.32
Qu'Appelle R.	48-60	8	53.1	4.32	1.53

Table B-19. Number of branchiostegal rays in Etheostoma nigrum.

Population	8	9	10	11	12	13	14	N	$\bar{x}$	SD	SE
Mobile Bay Basin											
Alabama R.		1			64	1		66	12.0	.39	.05
Black Warrior R.			1		12			13	11.8	.56	.15
Cahaba R.					5			5	12.0	.00	.00
Tallapoosa R.					33			33	12.0	.00	.00
Tombigbee R. (lower)					36			36	12.0	.00	.00
Tombigbee R. (upper)			1		43			44	12.0	.30	.04
Lower eastern											
Mississippi R.											
Homochitto R.			2	8	24			34	11.6	.60	.10
Bayou Pierre R.			1	1	59			61	11.9	.28	.04
Big Black R.					25			25	12.0	.00	.00
Yazoo R.				2	18			20	11.9	.22	.05
Obion R.				1	36			37	12.0	.16	.03
Red River Drng.											
Ouachitae R.					2			2	12.0	.00	.00
Mountain Fork R.				1	25			26	11.9	.27	.05
Kiamichi R.					14			14	12.0	.00	.00

Table B-19. (Continued)

Population	8	9	10	11	12	13	14	N	$\bar{x}$	SD	SE
Arkansas River Drng.											
Current R.					1			1	12.0	.00	.00
Poteau R.					2			2	12.0	.00	.00
Spring R.					6			6	12.0	.00	.00
Tennessee R. Drng.											
	4	2	20					26	11.6	.75	.15
Cumberland R. Drng.											
	12	2	4					18	10.6	.86	.20
Ohio R. Drng.											
Wabash R.					42			44	12.0	.21	.03
Green R.	1	1						2	10.5	.71	.50
Kentucky R.	10							10	10.0	.00	.00
Miami R.	3							3	10.0	.00	.00
Kinniconick Cr.	1	2	1					10	10.3	.82	.26
Scioto R.	8				2			10	10.4	.84	.27
Muskingum R.	14	3	3					20	10.4	.76	.17
Captina R.	2	3						5	10.6	.55	.24
Mahoning R.	10							10	10.0	.00	.00
Whitewater R. Syst.	1	1			12			14	11.8	.58	.15
Little Muddy R. Syst.					20			20	12.0	.00	.00
Kaskaskia R. Syst.					35			35	12.0	.00	.00
River Aux Vases Syst.					20			20	12.0	.00	.00
Big R. Syst.					10			10	12.0	.00	.00

Table B-19. (Continued)

Population	8	9	10	11	12	13	14	N	$\bar{x}$	SD	SE
Missouri R. Drng.											
Gasconade R.					2			2	12.0	.00	.00
Osage R.					40	1		41	12.0	.16	.02
Moreau R.					5			5	12.0	.00	.00
Cedar Cr.					10			10	12.0	.00	.00
Moniteau Cr.					3			3	12.0	.00	.00
Chariton R.					20			20	12.0	.00	.00
Crooked R.					20			20	12.0	.00	.00
Wakarusa R.					6			6	12.0	.00	.00
Mill Cr.					22			22	12.0	.00	.00
Vermillion R.					20			20	12.0	.00	.00
Blue R.					14			14	12.0	.00	.00
Solomon R.					5			5	12.0	.00	.00
Elkhorn R.					12			12	12.0	.00	.00
Lodgepole R.					4			4	12.0	.00	.00
Cache la Poudre R.					12			12	12.0	.00	.00
Laramie R.					20			20	12.0	.00	.00
Little Sioux R.					8			8	12.0	.00	.00
James R.					15	1		16	12.1	.25	.06
Big Sioux R.					10			10	12.0	.00	.00

Table B-19. (Continued)

Population	8	9	10	11	12	13	14	N	$\bar{x}$	SD	SE
Upper Mississippi R.											
Drng.											
Macoupin Cr.					10			10	12.0	.00	.00
Yellow R.					16			16	12.0	.00	.00
Du Page R.					20			20	12.0	.00	.00
Mississippi R.					2			2	12.0	.00	.00
Skunk R.					18			18	12.0	.00	.00
Iowa R.					10			10	12.0	.00	.00
Pecatonia R.					22			22	12.0	.00	.00
Bad Axe R.					5			5	12.0	.00	.00
Wisconsin R.	1				4			5	11.2	1.79	.80
Black R.					17			17	12.0	.00	.00
Whitewater R.					7			7	12.0	.00	.00
Buffalo R.					5			5	12.0	.00	.00
Apple R.					20			20	12.0	.00	.00
Minnesota R.					28	1	1	30	12.1	.43	.08
Rum R.					15	3	2	20	12.4	.67	.15
Elk R.					10			10	12.0	.00	.00
Prarie R.					10			10	12.0	.00	.00
Great Lakes Basin											
St. Lawrence R.					8			8	12.0	.00	.00
Grand R.		10						10	10.0	.00	.00
Maumee R.					19			19	12.0	.00	.00

Table B-19. (Continued)

Population	8	9	10	11	12	13	14	N	$\bar{X}$	SD	SE
Great Lakes Continued											
St. Joseph R.					5			5	12.0	.00	.00
Shiawassee R.					20			20	12.0	.00	.00
Au Sable R.					20			20	12.0	.00	.00
Portage Cr.					10			10	12.0	.00	.00
Muskegon R.					20			20	12.0	.00	.00
Manistee R.					20			20	12.0	.00	.00
Oconto R.					5			5	12.0	.00	.00
Lake Superior					3			3	12.0	.00	.00
Hudson Bay Basin											
James Bay					10			10	12.0	.00	.00
Minnedosa R.					10			10	12.0	.00	.00
Qu'Appelle R.					8			8	12.0	.00	.00

Table B-20. Number of vertebrae in Etheostoma nigrum.

Population	37	38	39	40	N	$\bar{X}$	SD	SE
Mobile Bay Basin								
Tombigbee R.		8	2		10	38.2	.42	.13
Lower eastern								
Mississippi R.								
Homochitto R.	2	6	1	1	10	38.1	.88	.28
Obion R.	1	6	3		10	38.2	.63	.20
Tennessee R. Drng.	1	8	1		10	38.0	.47	.15
Ohio R. Drng.								
Mahoning R.	1	7	2		10	38.1	.57	.18
Missouri R. Drng.								
Cedar Cr.		8	2		10	38.2	.42	.13
Laramie R.	1	9			10	37.9	.32	.10

VITA

Mary Jane Larkin Krotzer, daughter of C. David and Kathryn Larkin, was born in Meridian, Mississippi on March 8, 1962. She attended elementary school in Sumter County, Alabama and was graduated from high school at Sumter Academy in 1980. She entered Samford University in Birmingham, Alabama the following September and in May of 1984 received a Bachelor of Science degree in Biology. In the fall of 1984 she received a teaching assistantship at Samford University and began study toward a Master's degree in Biology. She received this degree in August of 1986. The following fall she accepted a teaching assistantship at University of Tennessee, Knoxville and became a candidate for a Ph.D. degree in Zoology (Ichthyology). This degree was awarded in December 1990.

Mrs. Krotzer was married to R. Stephen Krotzer in June 1989 and will live in Birmingham after graduation. She is a member of American Society of Ichthyologists and Herpetologists, Association of Southeastern Biologists, and Southeastern Fishes Council.