To the Graduate Council:

I am submitting herewith a dissertation written by John Lowrey Harris entitled "Systematics, Distribution, and Biology of Fishes Currently Allocated to Erimystax (Jordan), a Subgenus of Hybopsis (Cyprinidae)." 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. Ethier, Major Professor

We have read this dissertation
and recommend its acceptance:

Accepted for the Council:

Vice Provost
and Dean of The Graduate School

SYSTEMATICS, DISTRIBUTION, AND BIOLOGY OF FISHES CURRENTLY ALLOCATED TO *Erimystax* (JORDAN), A SUBGENUS OF *Hybopsis* (CYPRINIDAE)

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

John Lowrey Harris

August 1986

ACKNOWLEDGMENTS

I would like to extend thanks to the many curators and colleagues who provided specimens, locality information, and/or life history data during the course of this study. Countless other individuals assisted with the field work for this project. Individual acknowledgments will accompany the published portions of this dissertation. I must specifically thank the special group of friends and colleagues who shared the good and bad, the academic and social, at the University of Tennessee. This legion includes B. H. Bauer, J. P. Beets, A. E. Bogan, R. T. Bryant, N. M. Burkhead, W. Dickinson, B. B. Dinkins, C. Eason-Louton, D. A. Etnier, J. A. Louton, D. L. Nieland, M. G. Ryon, L. B. Starnes, and W. C. Starnes.

R. A. Pimentel graciously provided the multivariate statistical program DISANAL. The computer analysis was patiently and unerringly performed by D. Broach, University of Tennessee Computer Center. Many thanks are due E. Sullivan and W. Welch for drafting the figures.

My sincere appreciation is extended to my major professor, Dr. D. A. Etnier, for his guidance, patience, and most of all, administrative dexterity. Dr. Etnier was the reason I came to Tennessee, and the reason I stayed. Were it not for him, I would have given up many years ago. Dr. A. C. Echternacht meticulously reviewed the dissertation manuscript which led to an immeasurably improved final product. Other members of my graduate committee, Drs. D. L. Bunting, P. W. Parmalee, and H. W. Robison, provided guidance and editorial assistance, often on very short notice. To them I offer sincere thanks.

Appreciation is expressed to my mentors, Drs. H. W. Robison and N. H. Douglas, for pointing me in the right direction.

The late Dr. C. L. Hubbs graciously granted permission for me to take over this project, which he had begun years earlier. My warmest and most heartfelt thanks are reserved for my wife, W. K. Welch, who provided editorial assistance, endured my tirades, listened to my whining, and gave me the support, emotional and otherwise, which brought this project to completion.

ABSTRACT

Intra- and interspecific variation of species of the subgenus Erimystax, genus Hybopsis, are analyzed using multivariate statistical techniques. Diagnoses, descriptions, figures, supporting tables, and distribution maps are provided to facilitate identification of the subgenus and component species. Results of multivariate analyses support the elevation of the Ozark subspecies of Hybopsis dissimilis to specific standing as Hybopsis harryi. Two subspecies of Hybopsis insignis are recognized with Hybopsis i. insignis distributed in the lower Tennessee and Cumberland river drainages and H. insignis eristigma found in eastern tributaries of the upper Tennessee River drainage. Populations interpreted as intergrades occur in the Clinch, Powell, and Holston rivers. Two subspecies of Hybopsis x-punctata are recognized with H. x. x-punctata occurring in the upper Mississippi, Missouri, Neosho, and Ouachita river drainages and H. x-punctata trautmani inhabiting the Ohio, Thames, and White (Arkansas and Missouri) river drainages. Missouri River drainage populations are possible intergrades, pending further analysis. Two species groups are recognized within Erimystax. These are the dissimilis species group, composed of Hybopsis dissimilis, H. harryi, and H. insignis, and the x-punctata species group, composed of H. x-punctata and H. cahni.

Phylogenetic comparisons among the subgenus Erimystax, Hybopsis monacha, and subgenus Cyprinella of Notropis reveal H. monacha is an enigmatic species sharing characters with both subgenera. The exact

phylogenetic placement of Hybopsis monacha is not known, but it is not considered a member of Erimystax.

Life history studies of Hybopsis x-punctata, H. harryi, H. dissimilis, and H. insignis were conducted and the findings are presented. Dietary analyses show H. harryi feeds primarily on periphytic detrital aggregate (PDA) and algae, whereas, the other species are more omnivorous and feed on relatively equal amounts of benthic invertebrates and PDA. Hybopsis harryi is the only Erimystax with a coiled gut configuration. The remaining species have a simple s-shape gut.

All species spawn over clean, gravel substrate during a three to four week period in April or May. Spawning may be initiated by a combination of rising water temperature and increased stream discharge. Males grow faster during the first 12 months of life but females are larger by the end of the second year. Females reach a larger maximum size and generally have higher survival rates than males. Maximum age recorded for each species is: Hybopsis harryi--42 months; H. x-punctata--32 months; H. insignis--30 months; and H. dissimilis--approximately 30 months.

TABLE OF CONTENTS

CHAPTER PAGE

LIST OF TABLES

TABLE PAGE

TABLE PAGE

TABLE PAGE

LIST OF FIGURES

FIGURE PAGE

FIGURE PAGE

CHAPTER I

INTRODUCTION

The taxonomic history of the North American cyprinid genus Hybopsis has been complex and confusing (Jenkins and Lachner, 1971; Reno, 1969a) due, in part, to the lack of critical intra- and interspecific analyses of variation. Prior to 1960, taxonomic treatment of Hybopsis was restricted to original descriptions of species and superficial keys for their identification. Olund and Cross (1961) performed the first intraspecific variation study in Hybopsis when they analyzed Hybopsis gracilis throughout its range. Jenkins and Lachner (1971) laid the framework for definition of the genus Hybopsis and its subgenera. Clemmer (1971) defined and summarized variation in the subgenus Hybopsis, which led to a clearer understanding of the polyphyletic nature of genus Hybopsis as currently recognized.

Hubbs and Crowe (1956) redefined the subgenus Erimystax of Hybopsis and described three new species and six new subspecies in a scant eight-page paper. These descriptions appeared without synonomies, figures of species, distribution maps, or analyses of intraspecific variation. The purpose of this study is to define characteristics of and species within the subgenus Erimystax, analyze intra- and interspecific variation, redescribe the component taxa, and present a complete taxonomic treatment for each species with synonomy, figure, and distribution map.

Definitive life history studies have not been performed on species of Hybopsis with the exception (Kinney, 1954) of Hybopsis storeriana. Jenkins and Burkhead (1984) summarized the data on biology of Hybopsis monacha based on the relatively few specimens available. Likewise, Jenkins (1975) and Burkhead and Jenkins (1982) provided information on the biology of Hybopsis cahni based on a relatively small sample of the endangered species. Information on the remaining species of Hybopsis is generally limited to field observations and examination a few specimens from single collections.

It has become increasingly apparent that behavioral or biological characteristics of species or genera can be important in deciphering phylogenetic relationships. Jenkins and Lachner (1971) utilized behavioral characters in their assessment of Hybopsis and elevation of Nocomis to generic standing. Page (1981, 1983) and others used breeding behavior as a primary character for definition of the subgenus Catonotus of Etheostoma (Percidae). With this in mind, life history analyses were performed for four species of Erimystax. The purpose was 1) to provide basic life history information on the poorly known biology of these species and 2) to attempt to uncover life history variables which might provide phylogenetic information for deciphering relationships.

Detailed accounts of objectives and methods are given in each of Chapters II-V. These chapters are intended as individual papers to be published at a later date. Chapter VI is a brief summary of the major findings of this study.

CHAPTER II

SYSTEMATICS AND DISTRIBUTION OF FISHES CURRENTLY ALLOCATED TO *Erimystax* (JORDAN), A SUBGENUS OF *Hybopsis* (CYPRINIDAE)

1. INTRODUCTION

Jordan (1882) described the taxon *Erimystax* as a monotypic genus with *E. dissimilis* (Kirtland) as the type. Since the original description, *Erimystax* has been realigned and redefined numerous times with the most recent whole taxon treatment that of Hubbs and Crowe (1956). In their preliminary analysis of *Erimystax*, Hubbs and Crowe described three species and six subspecies as new, all in a scant eight pages, without synonomies, tables, figures, or distribution maps. The subgenus *Erimystax* of Hubbs and Crowe contained *Hybopsis cahni* Hubbs and Crowe, *H. dissimilis* (Kirtland), *H. harperi* (Fowler), *H. insignis* Hubbs and Crowe, *H. monacha* (Cope), and *H. x-punctata* Hubbs and Crowe. Hubbs and Crowe left intact Bailey's (1956) relegation of *Erimystax* to subgeneric status intact, but stated that this interpretation "rests on an unsteady basis."

One change in the component species of *Erimystax* is pertinent to the scope of this study. Gilbert and Bailey (1972) reassigned *Hybopsis harperi* (Fowler) to the genus *Notropis*. This has been accepted by the majority of ichthyologists (Robins et al., 1980; Gilbert, 1980c).

Hybopsis monacha has been the subject of intense and prolonged investigation by R. E. Jenkins and N. M. Burkhead which culminated in a recent publication covering description, biology, and distribution of this distinctive species (Jenkins and Burkhead, 1984). At the inception of this research, evidence indicated that H. monacha was more closely aligned with the subgenus Cyprinella of Notropis and consequently, H. monacha was omitted from further consideration. Subsequently, the work of Jenkins and Burkhead (1984) and Mayden (1985b) has again, at least partially, aligned H. monacha with Erimystax. Phylogenetic relationships will be discussed later in this chapter.

The purpose of this study was threefold: 1) redescribe Erimystax and component taxa (species and subspecies); 2) describe interspecific geographic variation and present hypothetical causal relationships, and 3) map the distribution of each taxon.

2. METHODS

Investigations pertaining to inter- and intraspecific morphological variation in North American freshwater fishes are abundant in the recent ichthyological literature. Since 1970, a plethora of variation studies at the generic, subgeneric, and/or species group level have appeared. These include treatments of Ammocrypta (Williams, 1975); Fundulus (Wiley, 1977); Hybopsis (Clemmer, 1971); Hydrophlox (Swift, 1970); Hypentelium, Lagochila, and Moxostoma (Jenkins, 1970); Lythrurus (Snelson, 1972); Lythrurus (Snelson, 1970), Microperca (Burr, 1978); Nocomis (Lachner and Jenkins, 1971); and Nothonotus (Zorach, 1972). The systematic methodology common to these works

generally consisted of measurements (morphometrics) and counts (meristics) of characters from individuals of a population subsample which represents the range of character variation for the population. The characters of population samples from different geographic locales were then compared qualitatively and/or quantitatively to determine if inter-populational variation was significant. If significant, a decision concerning level of taxonomic recognition was made.

Variables

For systematic analysis of the subgenus Erimystax, 14 meristic and 20 morphometric variables were analyzed (Table II-1). Measurements were made to the nearest 0.05 mm using needle point Helios dial calipers. Methods of variable counts and measurements follow Hubbs and Lagler (1964) with the following clarifications and/or modifications. Post dorsal length was the distance from the point of the origin of the dorsal fin to the base of the caudal fin. Orbit width was measured across the fleshy orbital rim but interorbital width was determined by measuring the least distance across the frontal bones. Isthmus width was the distance between the ventral connections of the opercular membranes to the breast. Upper lip width was measured at the widest anterior expansion of the lip. Body width was measured across the ventral surface at the anterior pectoral fin insertions. The left pelvic and left pectoral fins were measured to obtain paired fin lengths. Per cent ventral scalation was estimated using the morphological reference points as illustrated in Figure II-1. Embedded scales were revealed with a probe and are included in ventral

Table II-1. Morphometric and Meristic Variables.

	Variables	Abbreviation
	Morphometrics	
1)	Standard length	STL
2)	Predorsal length	PRL
3)	Postdorsal length	PDL
4)	Caudal peduncle length	CPL
5)	Caudal peduncle depth	CPD
6)	Body depth	BDD
7)	Body width	BWP
8)	Head length	HDL
9)	Snout length	SNL
10)	Upper lip length	ULL
11)	Upper lip width	ULW
12)	Gape width	GPW
13)	Interorbital width	IOW
14)	Orbital width	ORW
15)	Isthmus width	ISW
16)	Post orbital length	POL
17)	Dorsal fin length	DFL
18)	Anal fin length	AFL
19)	Pectoral fin length	P1L
20)	Pelvic fin length	P2L
	Meristics	
1)	Lateral-line scales	LLS
2)	Scales above lateral-line	ALL
3)	Scales below lateral-line	BLL
4)	Circumbody scales	CRS
5)	Circumpeduncle scales	CPS
6)	Predorsal scales	PDS
7)	Per cent ventral scalation	PBS
8)	Left pectoral rays	LP1
9)	Right pectoral rays	RP1
10)	Left pelvic rays	LP2
11)	Right pelvic rays	RP2
12)	Anal rays	ANR
13)	Lateral Blotches	LTB
14)	Dorsal Blotches	DBL

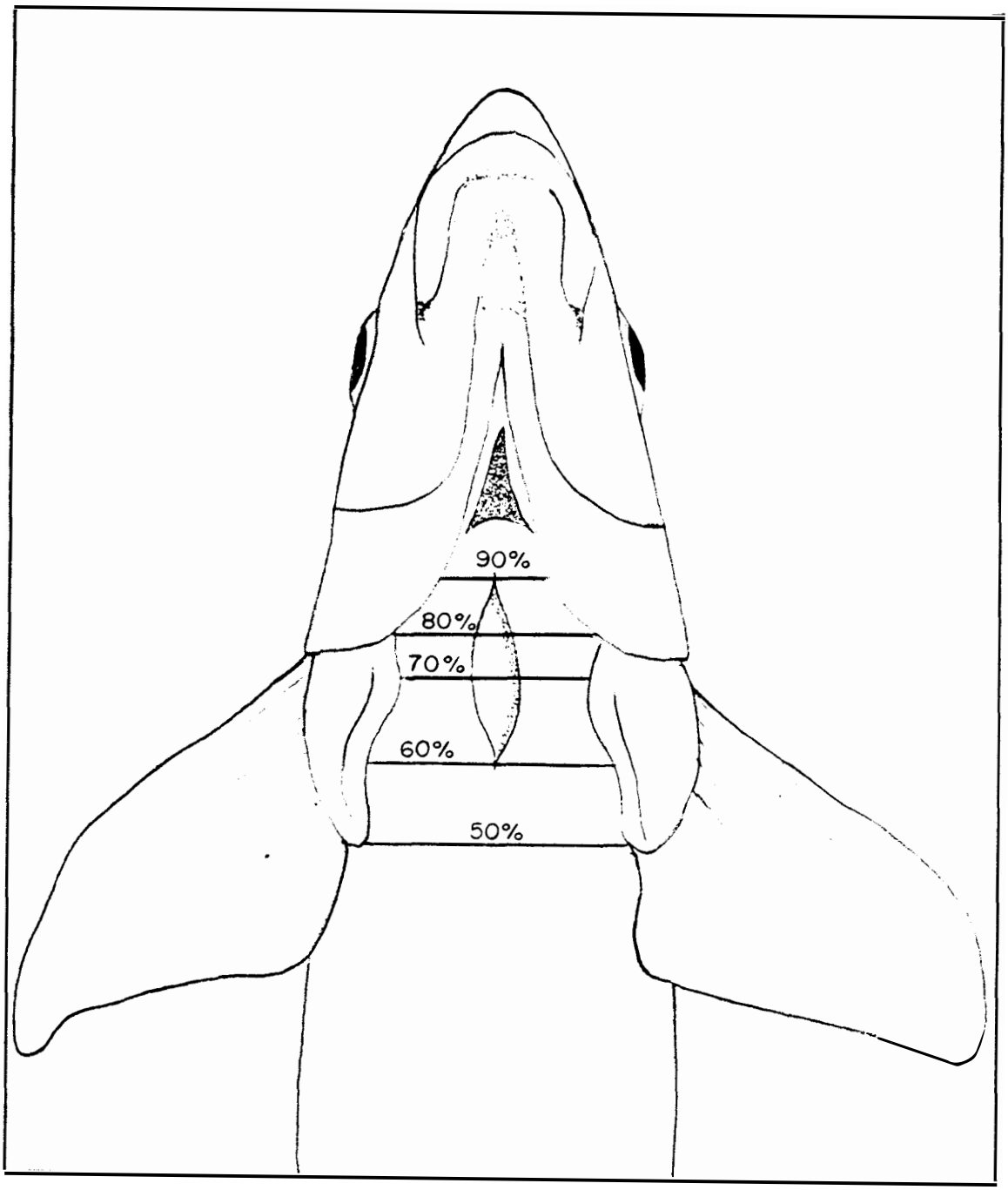


Figure II-1. Morphological coordinates used to assign per cent ventral scalation (PBS) values for Erimystax species.

scalation estimates. Gill raker counts were made on the outer portion of the first right arch and include even the most rudimentary rakers. Vertebral counts were made from x-rays following the method of Jenkins and Lachner (1971) with Weberian vertebrae counted as four. Gut length was determined by the method of Snelson (1971).

Counts and measurements were taken only from adult specimens (i.e. reproductively mature individuals as determined by gross examination of gonads) in an attempt to reduce allometric and ontogenetic variances. Life history studies (Harris, msB, msC, msD) revealed that Hybopsis cahni, H. insignis, and H. x-punctata were sexually mature at greater than 45 mm standard length (= SL), while H. dissimilis was generally mature at greater than 55 mm. No smaller individuals were utilized unless gonadal development or secondary sexual characters indicated they were reproductively mature.

Populations

When available, at least 25 specimens were analyzed for each population of each species. Populations were defined by major drainage systems, hence each individual river population and several large creek populations (e.g., Shoal Creek, AL) were analyzed separately at the outset. If no significant inter- or intra-drainage variation between smaller tributaries and the next larger system was evident, then these were pooled. Statistical analyses were conducted for two populations of Hybopsis cahni, 33 populations of H. dissimilis, 23 populations of H. insignis, and 27 populations of H.

x-punctata. The boundaries of all Erimystax populations analyzed in this study are defined in Table II-2 and outlined in Figure II-2.

Statistics

Common practice for data manipulation in taxonomic studies has been the transformation of morphometric measurements to ratios in an attempt to eliminate the body size component of variation (Atchley, et al., 1976; Corrucini, 1975; Hubbs and Lagler, 1964; Mayr, et al., 1953). Most recent descriptive works and/or variation studies (geographic and sexual) utilized this scaling of ratios in their analyses (Burr, 1978; Clemmer, 1971; Lachner and Jenkins, 1971; Snelson, 1972; and Swift, 1970 to name but a few).

Recent controversy has surfaced regarding bivariate ratios and proportions, especially when used as the raw variables in multivariate statistical analyses (Albrecht, 1978; Atchley, 1978, Atchley and Anderson, 1978; Atchley, et al., 1976; Corrucini, 1977). Atchley, et al. (1976) advised against the use of ratios as raw data in multivariate analyses because most proportional data are strongly skewed to the right and leptokurtic and, when used in a covariance or correlation matrix, produce spurious results.

In this study ratios of morphometric variables were expressed as thousandths of standard length (= TSL). They were used for descriptive purposes and in comparison of inter-population variation of individual variables that were significant contributors to multivariate analyses. Procedure PROC MEAN in SAS (1985) was used to calculate mean ($\bar{x}$), standard deviation (SD) and range for each

Table II-2. Populations of Erimystax Analyzed.

Population (Abbreviation)		Definition
Allegheny River	(ALG)	Allegheny R. and tributaries, PA and NY
Elk River	(EWV)	Kanawha, Elk Rs. and tribs., WV
Muskingum River	(MUS)	Muskingum, Walhonding, Tuscarawas, Mohican Rs. and tribs., OH
Scioto River	(SCO)	Scioto R. and tribs., OH
Miami River	(MIA)	Great Miami, Little Miami, Whitewater Rs. and tribs., OH and IN
White River	(WRI)	White R. and tribs., IN
Wabash River	(WAB)	Wabash, Tippecanoe, Eel, Vermillion, Embarras, Little Wabash Rs. and tribs., OH and IL
Green River	(GRK)	Green, Pond, Nolin, Barren Rs. and tribs., KY and TN
Rolling Fork River	(SRK)	Salt, Rolling Fork Rs. and tribs., KY
Kentucky River	(KRK)	Kentucky, Dix Rs. and tribs., KY
Big Sandy River	(BSR)	Big Sandy R. and tribs., KY, WV, and VA
Rock River	(RCK)	Rock, Sugar Rs. and tribs., IL and WI
Root River	(ROT)	Root R. and tribs., MN
Upper Iowa River	(UIO)	Upper Iowa R. and tribs., IO and MN
Turkey River	(TUR)	Turkey, Volga Rs. and tribs., IO
Wapsipinicon River	(WAP)	Wapsipinicon R. and tribs., IO
Cedar River	(CED)	Iowa, Cedar Rs. and tribs., IO and MN
Des Moines River	(DES)	Des Moines, Racoon Rs. and tribs., IO and MN
Salt River	(SRM)	Salt R. and tribs., MO

Table II-1. (Continued)

Population (Abbreviation)		Definition
Osage River	(OSG)	Osage, Maries, Niangua, Pomme de Terre, Sac, Marais des Cygnes, South Grand Rs. and tribs., MO and KA
Gasconade River	(GAS)	Gasconade, Big Piney Rs. and tribs., MO
Meramec River	(MER)	Meramec, Bourbeuse Rs. and tribs., MO
Neosho River	(NEO)	Neosho, Cottonwood, Spring Rs. and tribs., OK, KA, and MO
Illinois River	(ILO)	Illinois R. and tribs., OK and AR
White River	(WRA)	White, James, Kings Rs. and tribs., AR and MO
Buffalo River	(BRA)	Buffalo R. and tribs., AR
Little Red River	(LRR)	Little Red R. and tribs., AR
Strawberry River	(STR)	Strawberry R. and tribs., AR
Spring River	(SPR)	Spring R. and tribs., AR and MO
Eleven Point River	(ELP)	Eleven Point R. and tribs., AR and MO
Current River	(CUR)	Current R. and tribs., AR and MO
Black River	(BLK)	Black R. and tribs., MO
St. Francis River	(STF)	St. Francis R. and tribs., MO
Ouachita River	(OUA)	Ouachita R. and tribs., AR
Caddo River	(CAD)	Caddo R. and tribs., AR
Little Missouri River	(LMR)	Little Missouri R. and tribs., AR
Saline River	(SAL)	Saline R. and tribs., AR
Red River	(RRK)	Red R. and tribs., KY and TN
Harpeth River	(HAR)	Harpeth R. and tribs., TN

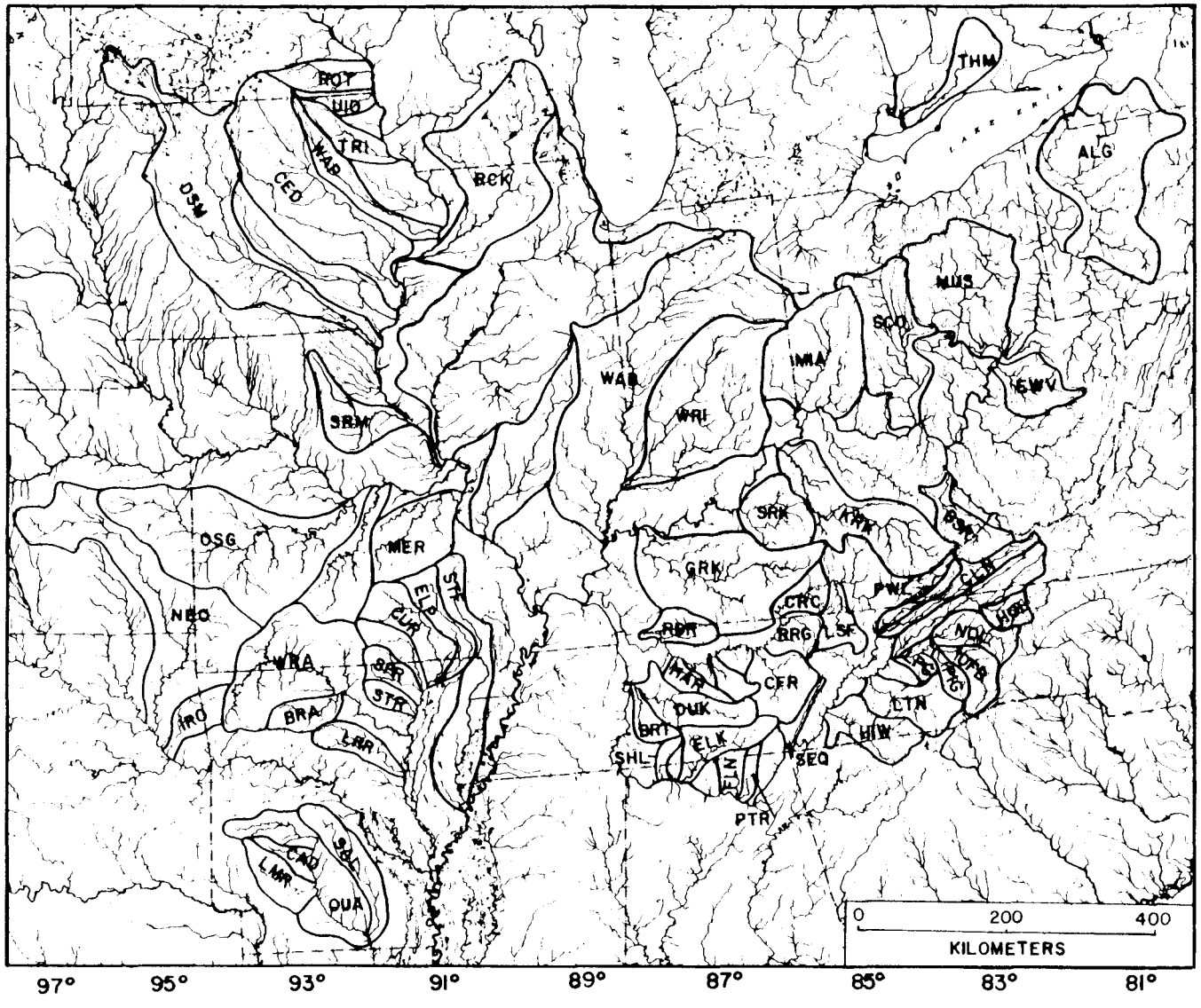
Table II-2. (Continued)

Population (Abbreviation)		Definition
Stones River	(STN)	Stones R. and tribs., TN
Caney Fork River	(CFR)	Caney Fork R. and tribs., TN
Roaring River	(RRG)	Roaring, Wolf, Obey Rs. and tribs., TN and KY
Cumberland River	(CRC)	Cumberland R. at Crocus Creek and tribs., KY
Little South Fork Cumberland River	(LSF)	Little South Fork Cumberland R. and tribs., KY and TN
Duck River	(DUK)	Duck, Piney Rs. and tribs., TN
Buffalo River	(BRT)	Buffalo R. and tribs., TN
Shoal Creek	(SHL)	Shoal Cr. and tribs., TN and AL
Elk River	(ELK)	Elk R. and tribs., TN and AL
Flint River	(FLN)	Flint R. and tribs., TN and AL
Paint Rock River	(PTR)	Paint Rock R. and tribs., TN and AL
Sequatchie River	(SEQ)	Sequatchie and Little Sequatchie Rs. and tribs., TN
Hiwassee River	(HIW)	Hiwassee, Toccoa, Nottely, Ocoee Rs. and tribs., TN, GA, and NC
Little Tennessee	(LTN)	Little Tennessee, Tellico Rs. and tribs., TN and NC
Little River	(LIT)	Little R. and tribs., TN
Little Pigeon River	(LPG)	Little Pigeon R. and tribs., TN
Pigeon River	(PIG)	Pigeon R. and tribs., TN and NC
Upper French Broad River	(UFB)	French Broad (above confluence with Pigeon), Mills, Davidson, Little Rs. and tribs., TN and NC

Table II-2. (Continued)

Population (Abbreviation)		Definition
Nolichucky River	(NOL)	Nolichucky R. and tribs., TN and NC
Holston River	(HOL)	Holston, Watauga, Doe Rs. and tribs., TN, NC, and VA
Clinch River	(CLN)	Clinch R. and tribs., TN and VA
Powell River	(PWL)	Powell R. and tribs., TN and VA

Figure II-2. Populations of Erimystax examined.


ROT
WIS
TRI
WAP
CED
BCK
OSW
THM
ALG
MUS
SCO
IMA
WAB
WRI
EWV
SRM
OSG
MER
ELD
STF
CUR
NEO
WRA
SAR
STR
IRO
BRA
LAR
GRK
SRK
CRC
RDR
BRG
LSF
CFR
DUK
BRT
ELK
SHL
SEQ
LTN
HIW
PTR
CAD
LMR
OUA
SBR
0
200
400
KILOMETERS
43°
41°
39
37°
35°
33
97°
95°
93°
91°
89°
87°
85°
83°
81°

meristic and morphometric variable. Tests of significant difference among population means for individual variables were performed using the Gabriel multiple-comparison procedure (SAS, 1985; Sokal and Rohlf, 1981). Attempts to quantify intra- and inter-population variation were made using two multivariate statistical techniques.

Multigroup discriminant function analysis (MDA) was performed using program DISANAL developed by R. A. Pimentel (1979). As employed in this study, MDA was composed of four statistical procedures which include multivariate analysis of variance (MANOVA), Geisser classification analysis, generalized distance analysis, and canonical analysis of discriminance. MANOVA provided the basic statistics for each population and tested the equality of population centroids using the multivariate F-test. Results of the MANOVA and contrasts among group centroids must be considered approximate because the equality of group dispersions and multivariate normality of the data were not tested. However, these multivariate techniques may be relatively insensitive to violation of these assumptions when large samples are used (Sullivan, 1985; Pimentel, 1979; Neff and Marcus, 1980).

Geisser classification probabilities classify individuals into the a priori poulations which they most resemble. Geisser classification was used to evaluate the relationships (i.e., similarity) of population group members to other population group members. Generalized distances between group centroids quantified differences between populations in discriminant space. Canonical analysis of discriminance (= canonical variates analysis) was used for ordination. Canonical analysis maximized within-group variation by rotation of the

data, rescaled the data to standardize the within-group variation, and then maximized between-group variation by rotation (Albrecht, 1980). Pimentel (1979) stated that canonical analysis provides the best reduced dimension model to simply but effectively indicate measured differences among groups. Canonical graphs were utilized to viusalize the relationships among populations in canonical space.

MDA was applied because 1) the design of MDA utilizes subsamples from defined populations which coincides with the goals of this study, definition of intra- and interspecific variation, and 2) the design of discriminant analysis leads to more comprehensive results (Pimentel, 1979). Conclusions were reached concerning taxonomic status of each population by melding statistical results with geographic distributions and biological species concepts.

The second multivariate technique employed was principal component analysis (PCA) using SAS procedure PRINCOMP. Humphries, et al. (1981) criticized discriminant functions because: 1) the method requires a priori assignment of individuals to groups, and 2) information is lost about correlations among variables because eigenvalues are derived by maximizing a function of the ratio of the among-group to within-group covariance matrices. PCA does not presume multiple groups which allows for their discovery and PCA coefficients are more easily interpretable (Humphries, et al., 1981). For these reasons, both MDA and PCA were employed and results of the two methodologies compared and contrasted. Initial runs of MDA and PCA were performed to analyze intraspecific variation in the four species of Erimystax. MDA analysis was performed on untransformed variables for 19

morphometric and 10 meristic variables. Standard length, dorsal and lateral blotches, right pectoral rays, and right pelvic rays were excluded from multivariate analyses. Initial PCA runs were performed on log transformed variables in a correlation matrix using morphometric variables, meristic variables, and morphometric + meristic variables. If two or more clusters were apparent from preliminary PCA analysis (Humphries, et al., 1981:300), "sheared PCA" was employed (on morphometric variables only, using the covariance matrix) to reduce the size effect and gain a clear view of size-free variation. Humphries, et al. (1981), Strauss and Bookstein (1982), Bookstein, et al. (1985), and Strauss (1985) warned of the problems associated with allometric variation, especially in fishes. They recommend use of the "sheared PCA" technique that produces a size component and a shape component which has size regressed from its scores so that it bears all the discriminatory information of the first two principal components (Humphries, et al., 1981). Sheared PCA analysis was attempted for the entire data set (i.e., all putative species combined) and the data set composed of putative Hybopsis dissimilis populations.

Results of statistical analyses are presented for each species and for the subgenus Erimystax. An account is presented for each species which includes discussion of geographic variation, illustration, synonomy, redescription, and map of distribution. Materials examined are presented for each species at the end of the chapter.

3. RESULTS

A. Subgenus Erimystax Jordan, 1882.

Description

Diagnosis. Combination of the following characters serves to differentiate members of Erimystax from congeners currently recognized as Hybopsis. Pharyngeal teeth are 4-4 and anal rays number seven. A single small to large, terminal labial barbel is present on each side of the mouth, often with enlarged sensory papillae. The mouth is inferior and subterminal and the upper lip is expanded anteriad. The relatively large dorsolateral eyes are directed slightly posteriad. Lateral-line scales number 36-53. The lachrymal groove is well developed. Dark pigment is present on the snout posterior to the lachrymal groove and anterior to the eye. The pectoral fin has sensory papillae between the first two rays. A maxillary flap is present, often bearing sensory papillae. Nuptial males develop a nuptial pad and the sexes are without nuptial coloration.

Species within Erimystax are Hybopsis cahni, H. dissimilis, H. harryi, H. insignis, and H. x-punctata. Phylogenetic relationships are discussed more fully later in this chapter.

Etymology. Erimystax, eri = intensifying prefix, mustax = moustache, referring to the barbel (Jordan, 1882).

B. *Hybopsis dissimilis* (Kirtland, 1841)

Spotted chub

Analysis

Thirty one populations referrable to *Hybopsis dissimilis*, sensu Hubbs and Crowe (1956), were examined. Twenty three of the populations were located east of the Mississippi River, and thus represent the nominal form *H. d. dissimilis*, while the remaining eight populations examined reside in the Arkansas and Missouri Ozarks west of the Mississippi and represent *H. dissimilis harryi* (Hubbs and Crowe, 1956). Data were obtained from a total of 615 specimens.

Tests of overall discrimination (= equality of group centroids) using MDA MANOVA for meristic + morphometric variables revealed group centroids were significantly different ($F = 5.56$; $P<0.001$).

Canonical variate (CV) 1 described 54.5% of the total variation and the first three canonical variates combined accounted for 69% of the variation among the *H. dissimilis* populations. Correlations between meristic and morphometric variables and the first three canonical variates are presented in Table II-3. CV1 loaded strongly for per cent ventral scalation with considerably smaller loadings for the variables upper lip width and isthmus width. CV2 had relatively high correlations with caudal peduncle length and anal fin length and somewhat lower correlations with predorsal length and pelvic fin length. Significant correlations of individual variables with CV3 were not readily discernible.

Table II-3. Correlations between Canonical Variates and Morphometric + Meristic Variables of Hybopsis dissimilis.

Variable	Canonical Variate 1	Canonical Variate 2	Canonical Variate 3
PRL	0.041	-0.149	-0.474
PDL	0.060	-0.322*	-0.418
CPL	0.045	-0.458*	-0.416
HDL	-0.004	-0.161	-0.501
SNL	0.027	-0.223	-0.463
ULL	-0.053	-0.180	-0.410
GPW	-0.074	-0.135	-0.363
IOW	-0.016	-0.144	-0.333
ORW	-0.022	-0.280	-0.387
BDD	0.054	-0.128	-0.261
CPD	0.132	-0.142	-0.469
ISW	0.219* [a]	-0.074	-0.393
DFL	0.031	-0.289	-0.369
AFL	0.028	-0.456*	-0.358
P1L	0.051	-0.275	-0.369
P2L	0.084	-0.332*	-0.355
POL	0.006	-0.074	-0.494
ULW	0.221*	-0.086	-0.293
BWP	0.042	-0.131	-0.333
LLS	0.137	-0.262	0.047
ALL	0.003	0.104	0.020
BLL	0.003	0.079	-0.017
CRS	-0.003	0.110	0.018
CPS	0.019	0.072	0.046
PDS	0.043	0.126	-0.229
PBS	0.534*	-0.086	0.284
LP1	-0.092	0.001	0.053
LP2	0.008	-0.051	0.093
ANR	0.014	-0.047	-0.063

[a] The * indicates highly correlated variables.

MDA MANOVA using only morphological variables indicated population centroids were significantly different ($F = 6.76$; $P<0.001$). The first three canonical variates described 49%, 11%, and 8% of total variation, respectively. Variable correlations with these three canonical variates (Table II-4) indicated CV1 described variation in isthmus and upper lip width while CV2 reflected the contribution of caudal peduncle length and anal fin length to total discrimination.

Twenty eight populations were visually compared by plotting group centroids on canonical axes. Centroids obtained from the all variables data set were plotted on canonical axes 1 versus 2, 2 versus 3, and 1 versus 3. The plot of group centroids on canonical axes 1 versus 2 gave the best discrimination in canonical space (Figure II-3). Vectors of the seven variables PDL, CPL, AFL, P2L, ISW, ULW, and PBS were drawn from the grand centroid and show relative contributions for both raw and z-score variables. Figure II-4 illustrates the group centroids with 95% confidence circles supplied showing complete discrimination between populations east of the Mississippi River and the Ozarkian populations.

Plots of the population group centroids in canonical space (Figures II-5 and II-6) based on morphological variables only, showed a similar alignment. However, the Little Red River population centroid appeared intermediate between the two large groups. This indicates morphological intermediacy of this population between the eastern and Ozarkian phenotypes.

PCA analysis of morphological variables described >90% of total variation on the first three principal components with PC1, PC2, and

Table II-4. Correlations between Canonical Variates and Morphological Variables of Hybopsis dissimilis.

Variable	Canonical Variate 1	Canonical Variate 2	Canonical Variate 3
PRL	0.076	0.206	-0.308
PDL	0.097	0.377	-0.319
CPL	0.075	0.522*	-0.334
HDL	0.022	0.222	-0.427
SNL	0.059	0.281	-0.354
ULL	-0.046	0.227	-0.346
GPW	-0.075	0.177	-0.257
IOW	0.000	0.182	-0.231
ORW	-0.005	0.328	-0.282
BDD	0.088	0.155	-0.153
CPD	0.309*[a]	0.122	-0.132
DFL	0.058	0.377	-0.272
AFL	0.056	0.502*	-0.180
P1L	0.092	0.314	-0.156
P2L	0.127	0.374	-0.192
POL	0.035	0.133	-0.448
ULW	0.305*	0.112	-0.039
BWP	0.077	0.173	-0.202

[a]The * indicates highly correlated variables.

Figure II-3. Population centroids and variable vectors of Hybopsis dissimilis in canonical space determined from the meristic and morphometric data set.

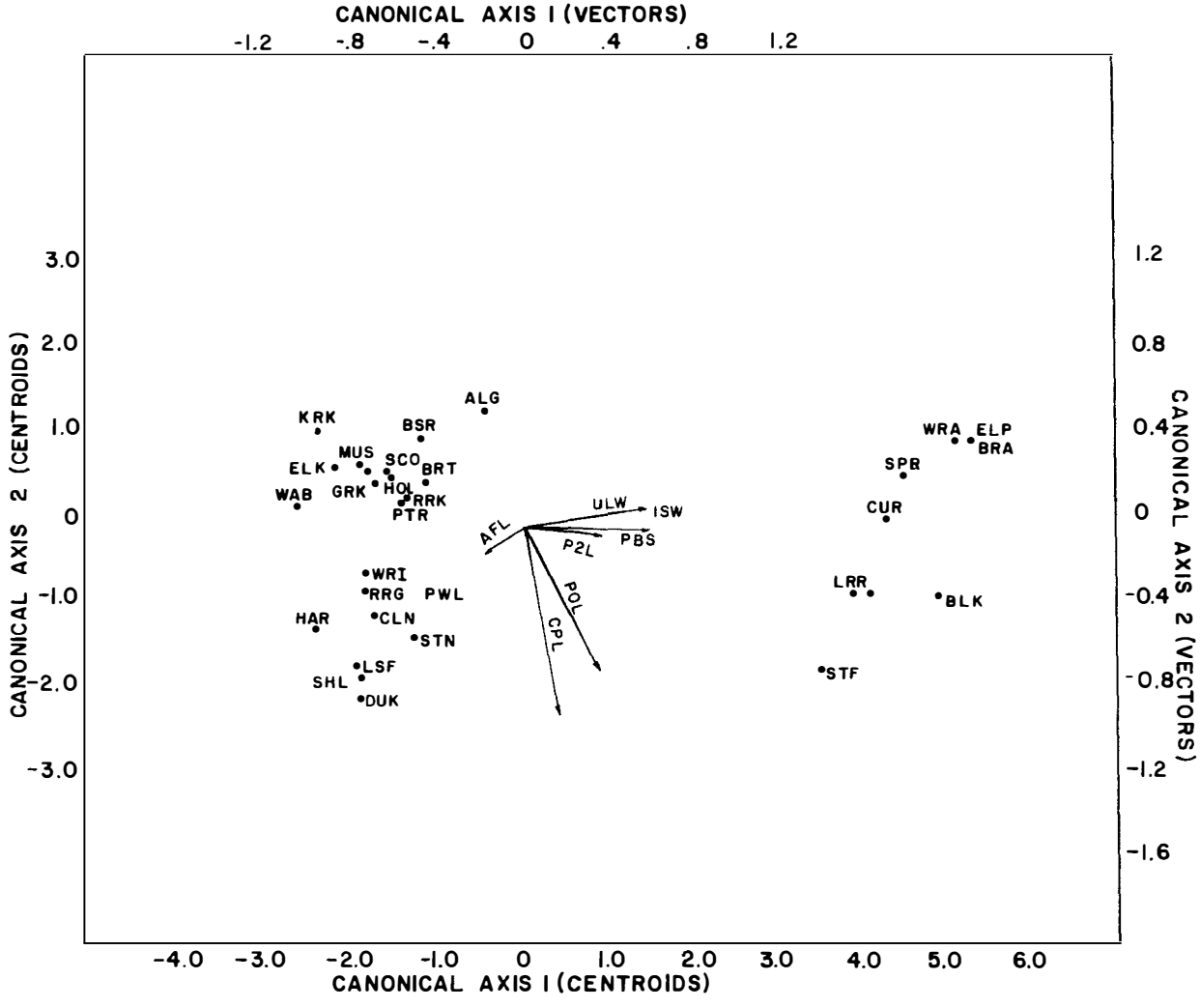

CANONICAL AXIS I (VECTORS)
-1.2
-.8
-.4
0
.4
.8
1.2
CANONICAL AXIS 2 (CENTROIDS)
3.0
2.0
1.0
0
-1.0
-2.0
-3.0
CANONICAL AXIS 2 (VECTORS)
1.2
0.8
0.4
0
-0.4
-0.8
-1.2
-1.6
-4.0
-3.0
-2.0
-1.0
0
1.0
2.0
3.0
4.0
5.0
6.0
CANONICAL AXIS I (CENTROIDS)
ALG
KRK
BSR
MUS
SCO
ELK
BRT
WAB
GRK
HOL
RRK
PTR
WRI
RRG
PWL
HAR
CLN
STN
LSF
SHL
DUK
WRA
ELP
BRA
SPR
CUR
LRR
BLK
STF
ULW
ISW
AFL
P2L
PBS
POL
CPL

Figure II-4. Population centroids with 95% confidence circles for Hybopsis dissimilis in canonical space determined from the meristic and morphometric data set.

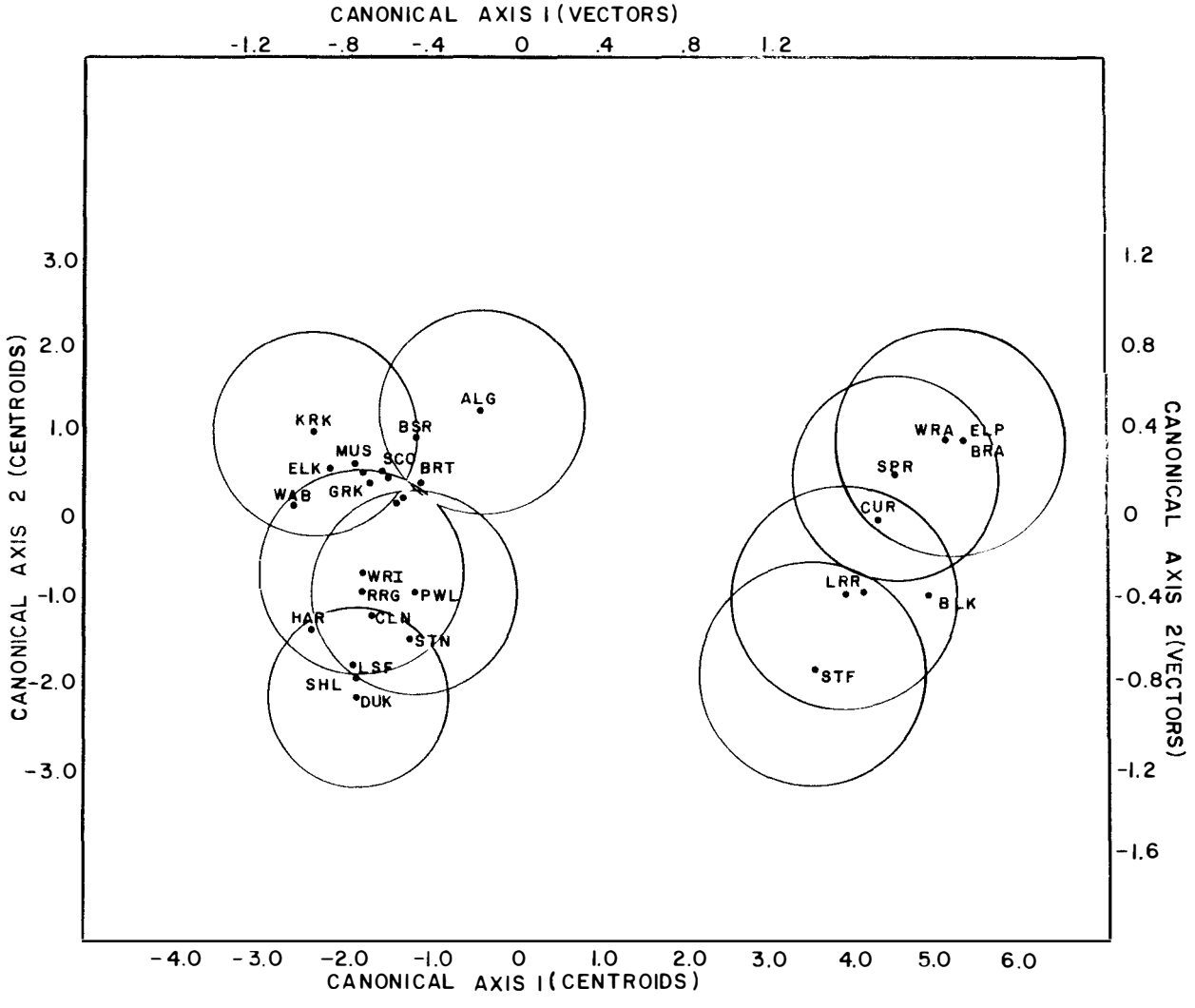

CANONICAL AXIS I (VECTORS)
-1.2 -.8 -.4 0 .4 .8 1.2
CANONICAL AXIS 2 (CENTROIDS)
3.0 2.0 1.0 0 -1.0 -2.0 -3.0
CANONICAL AXIS 2(VECTORS)
1.2 0.8 0.4 0 -0.4 -0.8 -1.2 -1.6
-4.0 -3.0 -2.0 -1.0 0 1.0 2.0 3.0 4.0 5.0 6.0
CANONICAL AXIS I (CENTROIDS)
ALG
KRK
BSR
MUS
SCO
ELK
BRT
WAB
GRK
WRI
RRG
PWL
HAR
CLN
STN
LSF
SHL
DUK
WRA
ELP
BRA
SPR
CUR
LRR
BLK
STF

Figure II-5. Population centroids and variable vectors of Hybopsis dissimilis in canonical space determined from the morphometric data set.

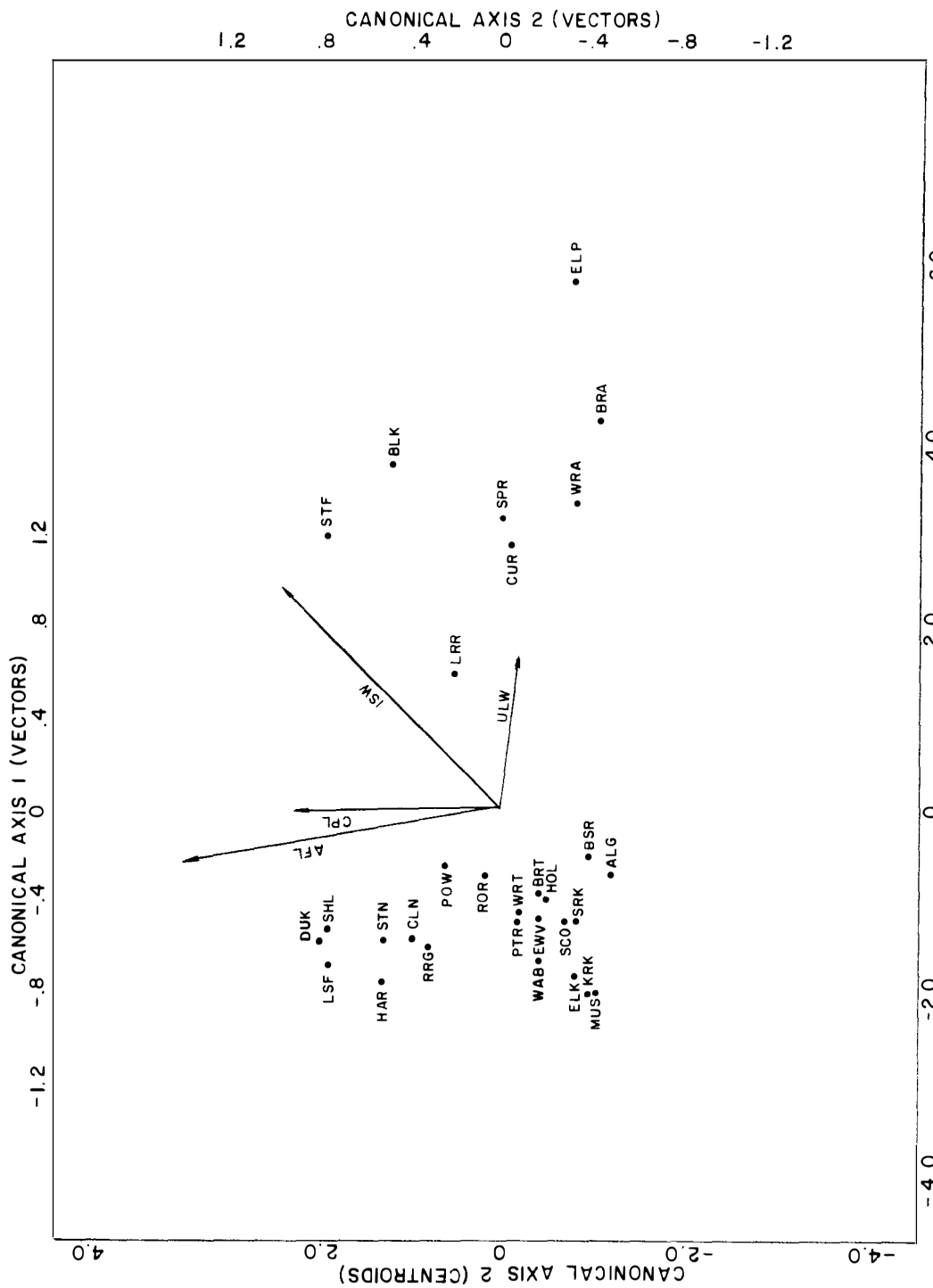
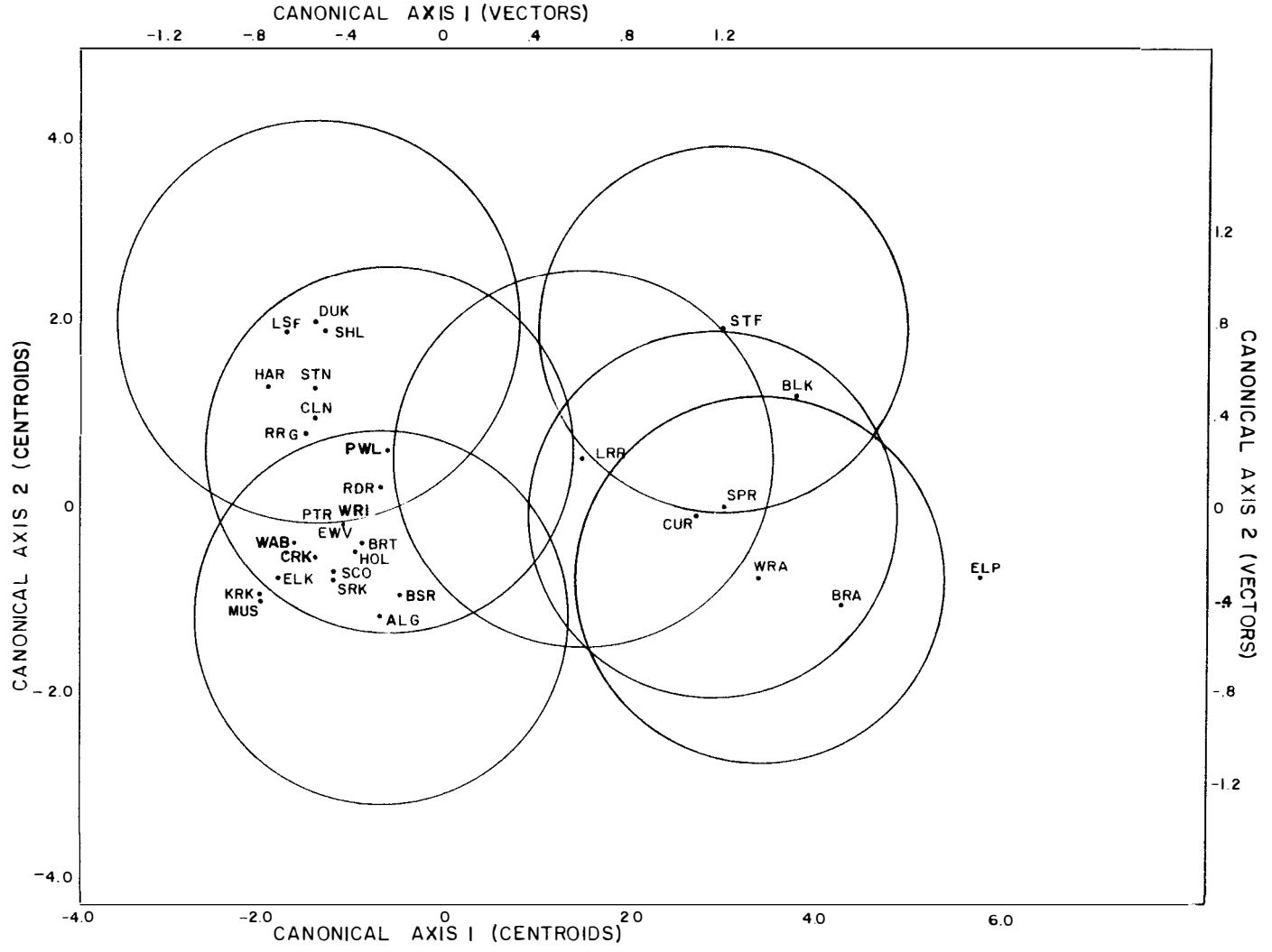

CANONICAL AXIS 2 (VECTORS)
1.2
.8
.4
0
-.4
-.8
-1.2
CANONICAL AXIS 1 (VECTORS)
-1.2
-.8
-.4
0
.4
.8
1.2
CANONICAL AXIS 1 (CENTROIDS)
-4.0
-2.0
0
2.0
4.0
6.0
CANONICAL AXIS 2 (CENTROIDS)
4.0
2.0
0
-2.0
-4.0
ISW
ULW
CPL
AFL
ELP
BRA
BLK
WRA
STF
SPR
CUR
LRR
BSR
ALG
BRT
HOL
WRT
PTR
SRK
SCO
EWV
WAB
KRK
MUS
ELK
ROR
POW
CLN
STN
RRG
HAR
SHL
LSF
DUK

Figure II-6. Population centroids and 95% confidence circles of Hybopsis dissimilis in canonical space determined from the morphometric data set.


CANONICAL AXIS I (VECTORS)
-1.2
-.8
-.4
0
.4
.8
1.2
4.0
2.0
0
-2.0
-4.0
CANONICAL AXIS 2 (CENTROIDS)
1.2
.8
.4
0
-.4
-.8
-1.2
CANONICAL AXIS 2 (VECTORS)
-4.0
-2.0
0
2.0
4.0
6.0
CANONICAL AXIS I (CENTROIDS)
DUK
LSF
SHL
HAR
STN
CLN
RRG
PWL
RDR
PTR
WRI
EWV
WAB
CRK
BRT
HOL
ELK
SCO
SRK
KRK
MUS
BSR
ALG
STF
BLK
LRR
SPR
CUR
WRA
BRA
ELP

PC3 contributing 84%, 4%, and 3%, respectively. PC1 was a general size component while PC2 loaded heavily on the variables isthmus width and upper lip width (Table II-5). PC3 contrasted a high positive loading for gape width with negative loadings for fin lengths and caudal peduncle lengths. Figure II-7 depicts individuals plotted on PC axes with lines joining population members. The Ozarkian and eastern groups were discriminated but with considerable overlap, particularly by the Allegheny, St. Francis, and Little Red River populations. Sheared PCA and PCA of meristic variables offered little additional discrimination and, therefore, are not discussed.

Mean values are presented for the seven variables judged significant contributors to the multivariate analyses (Table II-6). The Gabriel multiple-comparison procedure was performed on variable means to determine populations which are significantly different from each other. Results for the variables per cent ventral scalation, isthmus width, gape width, and upper lip width are presented in Table II-7.

Geisser classification probabilities based on all variables correctly classified 72% of the specimens (440 of 608) to their a priori designated populations. The distinctiveness of eastern and Ozarkian populations was indicated by the classification of 98% of (168 of 171) Ozarkian specimens to west of the Mississippi populations and 99.5% (435 of 437) of eastern specimens to east of the Mississippi populations. Similar results were obtained from Geisser classification based on morphological variables with 98.8% (169 of 171) of Ozarkian specimens classified to Ozark populations and 98.9% (432 of

Table II-5. Loadings of Morphological Variables on Principal Components of *Hybopsis dissimilis*.

Variable	Principal Component 1	Principal Component 2	Principal Component 3
PRL	0.244	-0.040	0.106
PDL	0.243	-0.036	-0.126
CPL	0.226	-0.112	-0.286
HDL	0.243	-0.145	0.145
SNL	0.244	-0.037	0.095
ULL	0.227	-0.213	0.246
GPW	0.222	-0.212	0.342*
IOW	0.223	-0.141	0.236
ORW	0.228	-0.193	-0.055
BDD	0.235	0.061	0.082
CPD	0.237	0.158	0.030
ISW	0.197	0.538*[a]	0.005
DFL	0.239	-0.077	-0.250
AFL	0.230	-0.038	-0.423*
P1L	0.229	0.059	-0.320
P2L	0.233	0.093	-0.365
POL	0.232	-0.124	0.254
ULW	0.171	0.679*	0.256
BWP	0.242	0.025	0.100

[a]The * indicates highly correlated variables.

Figure II-7. Population polygons of Hybopsis dissimilis on principal component axes determined from the morphometric data set. Only outlier populations are plotted and dashed lines represent Ozark populations, solid lines represent eastern populations.

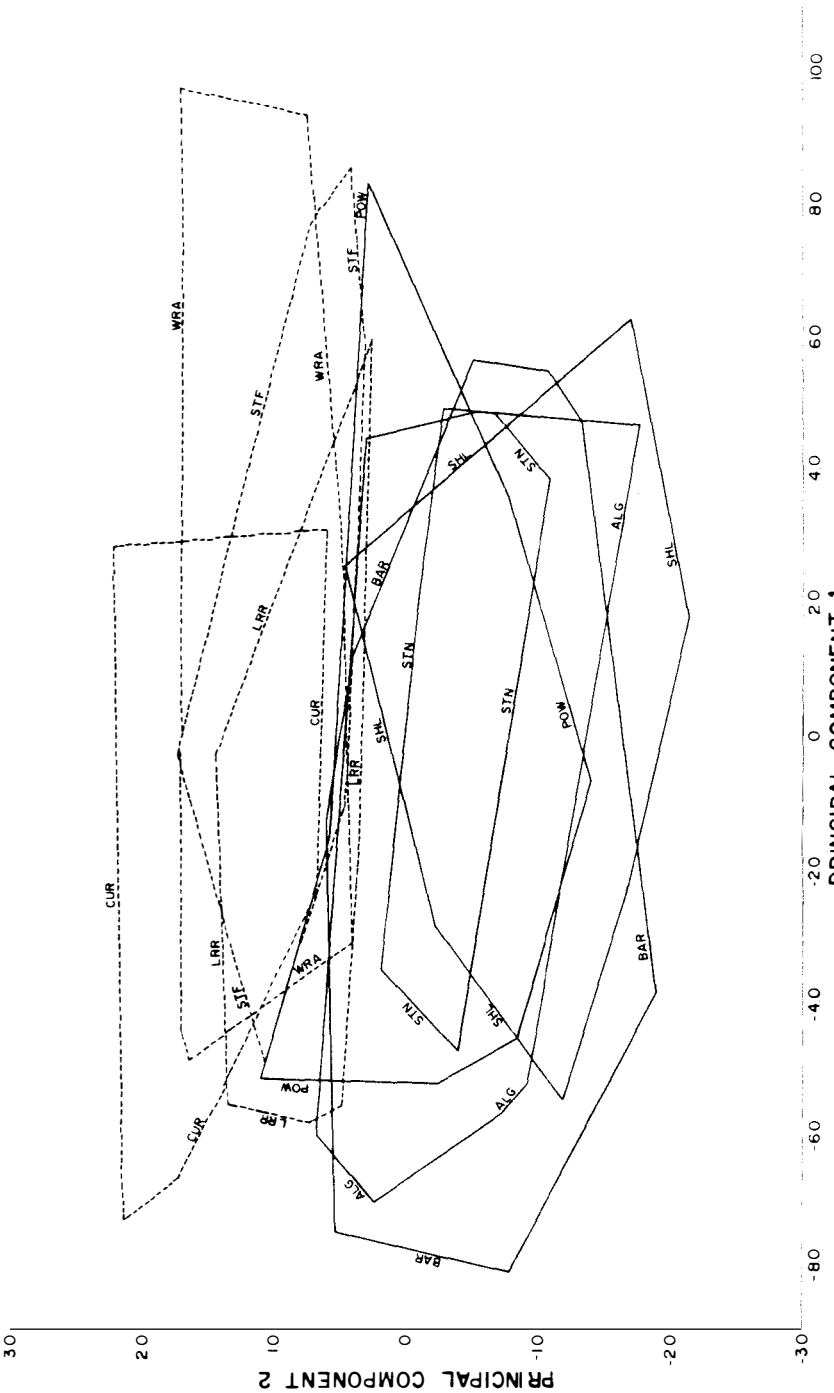

PRINCIPAL COMPONENT 2
30
20
10
0
-10
-20
-30
PRINCIPAL COMPONENT 1
-80
-60
-40
-20
0
20
40
60
80
100
WRA
STF
LRR
CUR
POW
BAR
STN
SHL
ALG

Table II-6. Population Means[a] for Variables of Hybopsis dissimilis Highly Correlated with Canonical Variates or Principal Components.

	Variable							
Population	ISW	ULW	PBS	PDL	CPL	AFL	P2L	GPW
ALG	54	10	63	497	218	149	130	52
MUS	49	11	56	492	212	159	140	55
SCO	55	10	53	494	215	166	141	49
EWV	44	9	52	488	225	145	124	50
BSR	53	10	50	489	221	156	134	50
KRK	48	10	52	509	210	146	124	52
BAR	50	11	51	494	215	150	128	55
WRI	55	13	49	501	207	158	136	52
WAB	46	11	49	493	209	153	135	53
RDR	51	10	53	488	226	156	129	52
HAR	44	9	52	484	231	157	132	52
STN	51	11	57	490	227	159	134	55
RRG	51	11	53	497	219	156	132	57
LSF	54	10	53	487	225	160	135	55
DUK	50	10	50	489	228	146	124	52
BRT	57	11	55	499	216	151	132	55
SHL	50	9	50	478	232	159	132	48
ELK	58	11	50	502	219	159	131	58
FLN	43	10	55	486	232	155	133	51
PTR	49	11	52	501	217	162	140	53
HOL	55	10	53	506	206	151	133	54
CLN	57	10	56	492	229	157	134	55
PWL	54	11	52	487	225	160	136	50
SRK	54	14	51	491	209	165	136	57
STF*[b]	58	13	71	479	229	156	134	46
LRR*	55	12	85	550	230	159	139	45
SPR*	62	13	77	503	210	153	137	45
ELP*	78	14	66	490	207	152	137	47
CUR*	65	13	79	497	219	159	143	46
BLK*	63	12	84	483	227	154	138	47
BRA*	66	14	75	496	217	144	132	45
WRA*	66	12	71	495	214	141	129	48

[a]Means in thousandths of standard length.

[b]The * indicates Ozark populations.

Table II-7. Gabriel Multiple-Comparison of Population Means[a].

Variable	PBS	ISW	GPW	ULW
F-value	49.5	16.4	14.7	13.1
Low Value	WAB[c]	HAR	*SPR	HAR
	WRI	EWV	*BRA	SHL
	SHL	WAB	*STF	EWV
	ELK	KRK	*CUR	KRK
	BSR	MUS	*LRR	RDR
	DUK	PTR	*BLK	ALG
	BAR	DUK	*ELP	DUK
↑	SRK	SHL	*WRA	SCO
	KRK	BAR	SHL	BSR
P	EWV	RDR	SCO	HOL
O	PTR	STN	EWV	LSF
P	HAR	RRG	POW	CLN
U	POW	BSR	BSR	BRT
L	SCO	POW	HAR	POW
A	RRG	ALG	ALG	BAR
T	LSF	LSF	WRI	ELK
I	HOL	SRK	RDR	STN
O	RDR	SCO	DUK	WAB
N	BRT	WRI	KRK	PTR
S	CLN	*LRR	PTR	RRG
↓	MUS	HOL	WAB	MUS
	STN	CLN	HOL	*BLK
	ALG	BRT	MUS	*LRR
	[b]*ELP	ELK	BRT	*WRA
	*STF	*STF	CLN	WRI
	*WRA	*SPR	BAR	*CUR
	*BRA	*BLK	STN	*STF
	*SPR	*CUR	LSF	*SPR
	*CUR	*WRA	RRG	SRK
	*BLK	*BRA	SRM	*ELP
High value	*LRR	*ELP	ELK	*BRA

[a]Means in thousandths of standard length.

[b]The * indicates Ozark populations.

[c]Lines connect homogenous subsets.

437) of eastern specimens relegated to east of the Mississippi populations.

Clinal variation appeared insignificant among the populations examined. General distribution of the Hybopsis dissimilis populations was from southwest to northeast. Populations were arranged in east to west, north to south, and soutwest to northeast allignments and variable means compared for clinal tendencies. Lateral line scales showed a weak clinal tendency for increase in size (i.e., reduction in counts) from southwest to northeast. Head and snout length also showed tendencies for increase in a southwest to northeast direction. Other variables did not reveal clinal tendencies.

Discussion

Hubbs and Crowe (1956) distinguished their subspecies of Hybopsis dissimilis on the basis of lip width, lateral blotches, head length, snout length, and caudal peduncle depth. They found the Ozark form, H. dissimilis harryi, to possess a shield shaped upper lip expanded near the mid-line; small, intense lateral blotches usually numbering more than 10; head length 4.0-4.5 in SL; snout length 2.5-2.7 in SL; and caudal peduncle depth 2.7-3.2 in SL. The eastern subspecies, H. d. dissimilis, was described as having a horseshoe-shaped upper lip that was narrow throughout; lateral blotches usually larger, less intense, and less numerous (<10); head length 3.8-4.2 in SL; snout length 2.8-3.0 into SL; and caudal peduncle depth 3.0-3.6 in SL.

Ozarkian population samples (= Hybopsis harryi) were combined as were all eastern population samples (= H. dissimilis) and the range,

mean, and standard deviation for all variables presented in Table II-8. Distributions of meristic variables for H. harryi and H. dissimilis are presented in Table II-9. Based on t-test results, Hybopsis dissimilis is significantly larger ($P<0.001$) than H. harryi in head length, gape width, and orbit width. On the other hand, H. harryi possesses a significantly wider isthmus and upper lip, as well as more breast scalation and lateral blotches. Vertebral counts are presented for all Erimystax species in Table II-10. There is considerable differentiation in vertebral numbers between dissimilis and harryi.

As stated by Hubbs and Crowe (1956), there are notable pigmentation differences in the lateral band and lateral blotches between the Ozarkian and eastern forms. Ozarkian populations usually have 9-15 lateral blotches that are more intensely pigmented and small, with diameter generally less than pupil of the eye. Eastern populations have 6-12 blotches that are more diffusely pigmented and with diameter greater than or equal to the pupil of the eye. Some populations tend toward loss of lateral spots. It is not unusual for more than half the specimens from Clinch River samples to lack lateral spotting while the Little Red River population from the Ozarks has lost lateral spotting completely. However, all populations have maintained mid-dorsal spotting to some degree.

Historical distribution of the two forms is shown in Figure II-8. They are broadly disjunct with a distance of some 250 linear kilometers between nearest populations, and considerably longer distance in stream kilometers. The Mississippi River lowlands seem to present

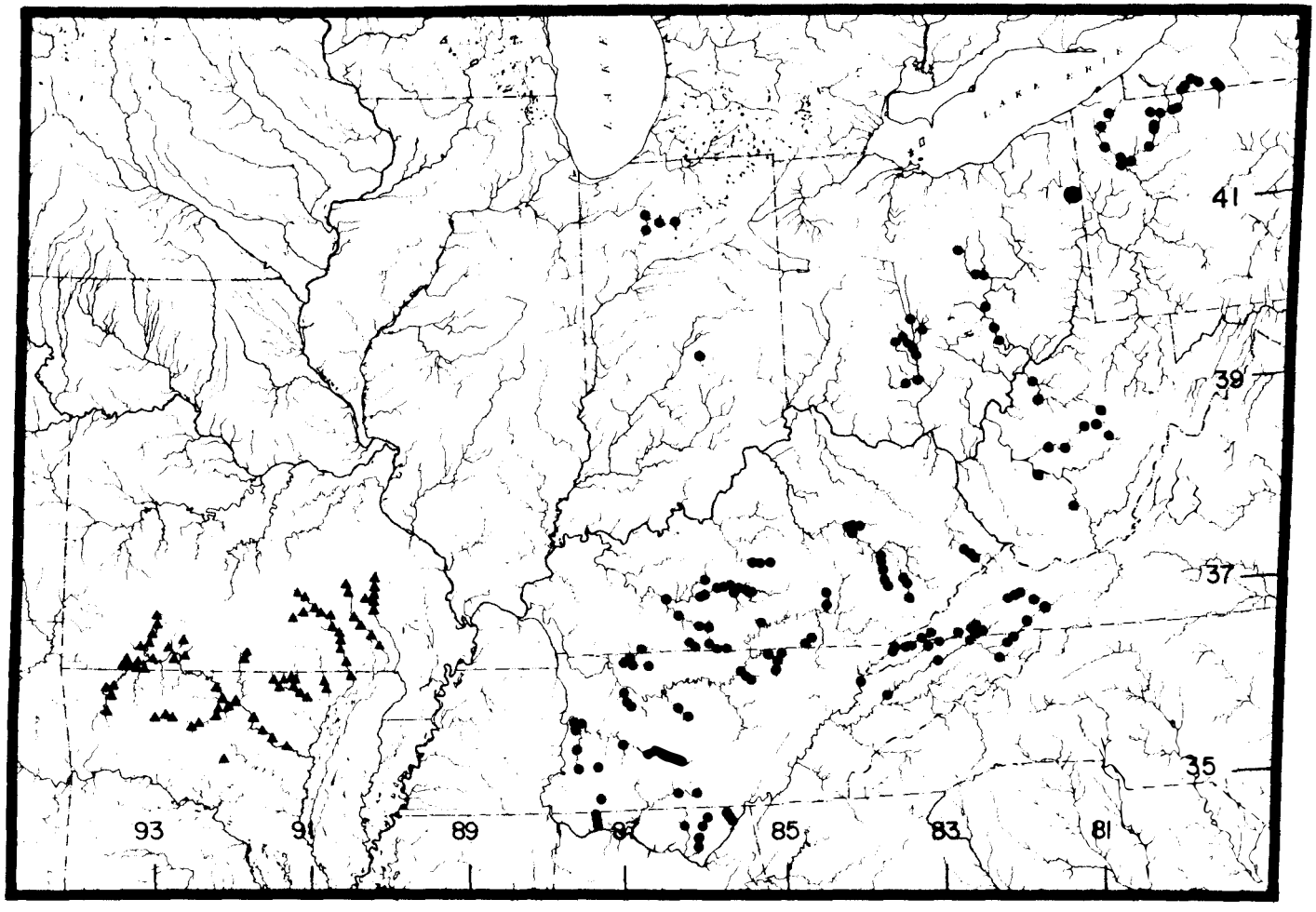


Figure II-8. Distribution of Hybopsis dissimilis (circles) and H. harryi (triangles).

Table II-8. Range, Mean, and Standard Deviation of Morphometric[a] and Meristic Variables of *Hybopsis dissimilis* and *H. harryi*.

Variable	*Hybopsis dissimilis* Range	*Hybopsis dissimilis* Mean (SD)	*Hybopsis harryi* Range	*Hybopsis harryi* Mean (SD)
		Morphometrics		
PRL	428-533	494 (16)	461-531	490 (15)
PDL	428-584	527 (15)	499-577	534 (14)
CPL	172-324	219 (15)	182-248	220 (13)
HDL	217-272	245 (9)	212-306	233 (9)
SNL	73-115	92 (5)	75-104	90 (5)
ULL	24-75	58 (4)	45-62	53 (3)
GPW	42-73	53 (5)	36-60	47 (4)
IOW	33-57	45 (3)	31-67	43 (7)
ORW	58-88	71 (4)	44-85	67 (5)
BDD	138-220	179 (13)	153-203	180 (11)
CPD	62-85	74 (4)	71-88	79 (3)
ISW	20-122	52 (8)	40-87	63 (9)
DFL	160-238	194 (11)	166-217	191 (11)
AFL	119-191	154 (12)	119-178	151 (11)
P1L	135-229	182 (15)	150-221	182 (16)
P2L	87-196	132 (10)	109-159	135 (9)
POL	75-112	94 (6)	75-140	90 (6)
ULW	5-19	10 (2)	7-21	13 (2)
BWP	105-164	137 (10)	118-156	136 (8)
		Meristics		
LLS	38-53	46.3 (1.8)	43-52	47.7 (1.7)
ALL	6-9	7.2 (0.4)	6-8	7.2 (0.5)
BLL	5-8	6.4 (0.5)	5-8	6.4 (0.5)
CRS	28-38	32.0 (1.4)	28-36	31.9 (1.5)
CPS	12-20	15.9 (0.5)	14-18	15.9 (0.4)
PDS	13-24	20.0 (1.3)	18-24	20.3 (1.3)
PBS	10-80	53.0 (6.8)	50-95	75.9(11.1)
LP1	14-21	17.4 (0.9)	13-19	16.9 (0.9)
LP2	7-9	8.1 (0.4)	7-9	8.1 (0.3)
ANR	6-7	7.0 (0.1)	6-7	7.0 (0.1)
LTB	1-14	8.7 (1.8)	8-17	11.9 (2.1)
DBL	3-12	7.9 (1.2)	2-11	7.4 (1.6)

[a]Range, mean, and standard deviation of morphometric variables are in thousandths of standard length.

Table II-9. Frequency Distribution of Meristic Variables of Hybopsis dissimilis and H. harryi.

Species	Frequency Distribution															
	Lateral Line Scales															
	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53
dissimilis	1	1	0	2	4	10	40	100	118	102	61	22	13	5	0	1
harryi						2	1	16	32	35	41	38	15	8		
	Circumbody Scales															
	28	29	30	31	32	33	34	35	36	37	38					
dissimilis	2	6	55	111	144	94	42	18	6	0	1					
harryi	1	5	33	37	53	38	13	6	3							
	Circumpeduncle Scales															
	12	13	14	15	16	17	18	19	20							
dissimilis	4	2	1	31	432	8	1	0	1							
harryi			1	15	168	3	2									
	Predorsal Scales															
	13	14	15	16	17	18	19	20	21	22	23	24				
dissimilis	1	0	2	1	7	29	128	163	96	38	11	3				
harryi						12	47	56	38	28	7	1				
	Per Cent Ventral Scalation															
	40	45	50	55	60	65	70	75	80	85	90	95				
dissimilis	3	13	310	36	82	4	10	3	8							
harryi			3	5	23	12	29	21	43	7	42	2				

Table II-9. (Continued)

Species	Frequency Distribution													
	Left Pectoral Fin Rays													
	13		14		15	16	17	18	19	20	21			
dissimilis			1		5	47	202	185	37	2	1			
harryi	1		0		8	50	83	42	5					
	Lateral Blothches													
	4	5	6	7	8	9	10	11	12	13	14	15	16	17
dissimilis	4	5	19	55	84	96	55	32	15	5	2			
harryi					2	11	13	15	20	10	6	12	3	1

Table II-10. Frequency Distribution of Vertebrae of Species of Erimystax.

Species	Frequency Distribution							
	Total Vertebrae							
	36	37	38	39	40	41	42	43
cahni				9	4			
dissimilis					16	15		
harryi						8	15	5
i. insignis			11	36	5			
i. eristigma		2	14	11				
x. x-punctata		1	12	25	1			
x. trautmani		4	24	2				

	Precaudal Vertebrae				
	19	20	21	22	23
cahni	1	10	2		
dissimilis		1	21	9	
harryi			6	20	2
i. insignis	19	32	1		
i. eristigma	22	6			
x. x-punctata	8	27	4		
x. trautmani	12	18			

	Caudal Vertebrae				
	17	18	19	20	21
cahni		1	8	4	
dissimilis		2	20	9	
harryi			5	16	7
i. insignis		4	32	16	
i. eristigma		3	17	7	
x. x-punctata	1	10	26	2	
x. trautmani	2	16	12		

a formidable barrier to dispersal between the Ozark and eastern populations.

During life history investigations of Ozarkian and eastern Hybopsis dissimilis populations (Harris, msC), significant variation was encountered in gut configuration and length. Seven populations, three Ozarkian and four eastern, were analyzed for gut length with means and ranges presented as portion of SL: Ozarkian populations; Buffalo River x = 2.25 (1.49-2.73, n = 54), Little Red River x = 2.16 (1.74-2.67, n = 10), St. Francis River x = 1.70 (1.44-2.01, n = 10) and eastern populations; Allegheny River x = 1.05 (0.86-1.19, n = 20), Holston River x = 0.84 (0.79-0.86, n = 10), Duck-Buffalo River x = 0.94 (0.77-1.11, n = 38), Green River x = 0.91 (0.75-1.02, n = 10).

The St. Francis River population was somewhat intermediate between other populations of the Ozarkian and eastern forms. Intermediacy was expressed in gut length and body pigmentation. Other Ozark population had average gut length two times standard length. Gut length mean for the St. Francis population was 1.7 times standard length, but still considerably longer than eastern population gut length means or upper extremes. Some St. Francis specimens had lateral pigmentation that was more similar to eastern populations in that the spots were diffuse and as wide as pupil diameter. The Little Red River population was closer to eastern populations in isthmus width and overall morphology as indicated in Figure II-5 (p. 28).

Jenkins and Lachner (1971) suggested that the differences between subspecies of Hybopsis dissimilis appeared substantial enough to warrant specific recognition. Based on canonical variates analysis,

differences in gut morphology, differences in life history parameters, and disjunct distribution, Hybopsis d. dissimilis and H. dissimilis harryi should be elevated to species standing as Hybopsis dissimilis and Hybopsis harryi.

Common Name and Types

Kirtland (1841) described and figured the spotted chub as Luxilus dissimilis from two specimens, apparently caught in the Mahoning River, OH and supplied by "an experienced fisherman". Additionally, Kirtland stated, "I have since found several dead specimens upon the shore of Lake Erie near Cleveland". Kirtland (1850) later realized that he was mistaken concerning the Lake Erie occurrence and revised the distribution of the species by stating only that "it inhabits the Mahoning River, near Youngstown" (Trautman, 1957, 1981). The types are apparently not extant but, based on Kirtland (1841, 1850), the type locality is hereby restricted to the Mahoning River near Youngstown, Mahoning County, OH.

Kirtland (1841) gave Luxilus dissimilis the common name spotted shiner in the original description. Publications following Henshall (1888), Fowler (1919), and Hubbs (1926), referred to Hybopsis dissimilis and its congeners as chubs and this species was called the spotted chub. Without explanation, Hubbs and Crowe (1956) changed the common name to streamline chub and this designation was followed in the inaugural edition of Common and Scientific Names of Fishes (Bailey, et al., 1960). I suggest the original common name "spotted" chub be retained in honor of Kirtland's original description and

because it describes the distinctive mid-lateral and mid-dorsal spotting of the species.

Synonomy

Luxilus dissimilis Kirtland, 1841:341-342; Plate IV Figure 2 [original description, type locality as Mahoning R., OH and Lake Erie. Trautman (1957 and 1981) states Lake Erie locality in error based on Kirtland (1850) and lack of specimens or historic records from Lake Erie drainage.]; DeKay, 1842:214 (description; extralimital to NY); Jordan, 1920:419 (type of Erimystax).

Leuciscus dissimilis Kirtland, 1850:189 (description; line drawing; habitat; Mahoning R., OH).

Ceratichthys dissimilis. Cope, 1868:226 (comparison with C. hyalinus); Gunther, 1868:177 (description; distribution); Cope, 1869:367-368, Plate XII Figure 1 (description; distribution; pharyngeal arch figured; specimen figured); Jordan, 1875:23, 37 (key to genera in IN); Jordan and Gilbert, 1883:215-216 (description; distribution; synonomy); Cope, 1883:143 (description; distribution).

Nocomis dissimilis. Jordan, 1876:377 (in part, White R., IN); Jordan, 1877:45 (White R., IN); Cope, 1881:98 (description; distribution).

Erimystax dissimilis. Jordan, 1882:858-859 (description; habitat; synonomy); Jordan, 1929:75 (description; distribution); Jordan, et al., 1930:138 (distribution); Blatchley, 1938:53-54 (description; distribution IN); Fowler, 1940:14 (distribution PA); Eddy and Surber, 1943: 151 (description; distribution); Gerking, 1945:50 (distribution

IN); Driver, 1942:279 (in key); Patriarche and Campbell, 1958:256 (Black R. and Clearwater L., MO).

Hybopsis watauga. Jordan, 1889:355-356 (original description by Jordan and Evermann; comparison with H. dissimilis; distribution); Woolman, 1892:258, 269 (Barren R. and Drake Cr., KY; Powell R., TN; scale counts to separate dissimilis and watauga); Kirsch, 1893: 264 (Obey R., TN); Eigenmann and Beeson, 1894:91 (distribution IN); Kirsch, 1895:37 (Eel R., IN); Jordan and Evermann, 1896:315, 319 (in key; description; distribution); Jordan and Evermann, 1900:137 Plate LIII (figure); Large, 1903:19 (in key; brief description); Smith, 1907:102 (extralimital NC); Meek, 1908:151 (distribution); Evermann, 1918:318-319, 321, 322, 324, 326, 329, 345, 365, 367 (literature summary and list for KY and TN; distribution); Jordan 1929:75 (description; distribution); Jordan, Evermann and Clark, 1930:138 (distribution); Blatchley, 1938:54 (description; distribution); Kuhne, 1939:49 (listed TN).

Hybopsis dissimilis. Henshall, 1888:79 (Little Miami R. and O'Bannon Cr., OH); Meek, 1891:248 (distribution); Eigenmann and Beeson, 1894:90 (White R., IN); Osburn, 1901:62 (in key; description; distribution OH); Smith, 1907:102-103 (in key; description; distribution; partial synonomy NC); Meek, 1908:151 (distribution); Evermann and Hildebrand, 1916:445 (distribution E TN); Fowler, 1919:62 (Monongahela and Youghiogheny R., PA); Fowler, 1922:24 (Paint Rock R., AL); Gerking, 1955:69 (in key, IN); Hubbs and Crowe, 1956:4, 6 (in key; description; distribution); Moore, 1957:68, 69-70 (in key; distribution); Becker, 1961:247 (status); Ross and Carico, 1963:16, 21 (N

and Middle Forks Holston R., VA); Reno, 1969b (description, figures and discussion of cephalic lateral-line system); Smith-Vaniz, 1968:41, Figure 64 (distribution AL; figure); TVA, 1970:Tables 5-7 (Powell R., TN; frequency occurrence; relative abundance); Comiskey and Etnier, 1972:141, 144 (listed Little S. Fork Cumberland R., KY; zoogeography; habitat); TVA, 1973:Tables 5-7 (Buffalo R., TN; frequency occurrence; relative abundance); Menhinnick, et al., 1974:30 (extralimital NC); Branson and Batch, 1974:20 (Red R., KY); Clay, 1975: 138, 141-142 (in key; description; distribution KY; habitat; fish associates); Denoncourt, et al., 1975:118 (WVA checklist); TVA, 1975:Tables 5-7 (Duck R., TN; frequency occurrence; relative abundance); Hendricks, et al., 1979:Table 2 (checklist Youghiogheny R., PA); Hocutt, et al., 1979:65 (expected occurrence Gauley R., WVA); Burr, 1980:64 (distribution KY); Harris, 1980a:184 (distribution; habitat; biology); Werner, 1980:17, 101 (in key; distribution by drainage, NY); Branson and Schuster, 1982:63, 64 (distribution and relative abundance Little S. Fork Cumberland R., KY); Branson and Batch, 1983:9 (distribution S. Fork KY R., KY); Cooper, 1983:91,92 (in key; figure; distribution PA); Dixon, et al., 1983:113 (stream order correlation Kentucky and Cumberland Rivers, KY); Hendricks, et al, 1983:148, 150, 157 (Youghiogheny River, PA, WV, MD).

Erimystax (Hybopsis) dissimilis. Osburn, et al., 1930:172 (listed OH).

Erimystax dissimilis dissimilis. Fowler, 1945:110 (synonomy).

Hybopsis dissimilis dissimilis. Hubbs and Crowe, 1956:4, 6 (in key; distribution); Ross, 1959:12, 25 (in key; checklist New R., VA);

Jenkins, et al., 1972:49, 93 (distribution and zoogeography Southern Appalachians); Trautman, 1981:93, 282-284 (in key; description; distribution OH; habitat; biology; history in OH); Stauffer, et al., 1982:30-31 (checklist Central and Northern Appalachian drainages).

Hybopsis (Erimystax) dissimilis. Davis and Miller, 1967:5 (brain morphology; habitat; distribution; feeding habits).

Hybopsis (Erimystax) dissimilis dissimilis. Jenkins and Lachner, 1971:4, 6-7 (scale lepidology; vertebral counts).

Diagnosis

A member of the subgenus Erimystax which differs from Hybopsis x-punctata and H. cahni by possessing well defined mid-lateral spots and/or mid-dorsal spots. It differs from H. insignis by having round mid-lateral spots and smaller scales, usually 43-50 in the lateral-line, whereas H. insignis has quadrate mid-lateral blotches and usually 37-46 lateral-line scales. Hybopsis dissimilis is differentiated from H. harryi by the simple s-shaped gut, longer head length ($\bar{x}$ = 245 TSL), narrowly conjoined opercular membranes at the breast ($\bar{x}$ = 52 TSL), a lower percentage of ventral scalation ($\bar{x}$ = 53%), less numerous (6-12) mid-lateral spots with diameter usually larger than pupil of the eye, and fewer total vertebrae (40-41). Hybopsis harryi possesses a double looped gut, shorter head ($\bar{x}$ = 233 TSL), more broadly conjoined opercular membranes ($\bar{x}$ = 63 TSL), more ventral scalation ($\bar{x}$ = 76%), 9-15 mid-lateral spots smaller than pupil diameter, and more total vertebrae (41-43).

Description

The body is elongate, anteriorly cylindrical, tapers gradually from the pelvics posteriad to the caudal, and is slightly compressed laterally posterior to the dorsal. The snout is bluntly rounded and slightly overhangs the subterminal, ventral mouth. The eyes are medium size, located dorsolaterally and directed somewhat posteriad. A terminal labial barbel, minute to well developed, is present and the upper lip is not noticeably expanded anteriad. The lower jaw is slightly included. Pharyngeal teeth are 4-4. Scales are moderate in size with 44-50 in the lateral-line. The mid-lateral band has 4-15 distinctive, oval to slightly oblong, spots (occasionally absent) that are larger than the diameter of the pupil. The mid-dorsal line has 3-10 darkened dashes. Dorsolateral spots appear as x- or comma-shaped melanophores on the scale periphery. No interradial fin pigment is present. The dorsal profile from the dorsal fin insert to the snout is straight to slightly curved.

External morphology. Morphometry: Fin shape and placement as well as general body physiognomy are illustrated in Figure II-9. Proportional data for measured characters are given in Table II-8 (p. 41) and characters showing significant sexual dimorphism are presented in Table II-11.

Meristics: Table II-8 (p. 41) summarizes data on countable characters giving range, mean, and standard deviation for each. Table II-9 (p. 42) gives the distribution of meristic variables. No sexual dimorphism was evident for meristic characters.

Figure II-9. Photographs of Hybopsis dissimilis and H. harryi.

Figure II-9 A. Hybopsis dissimilis - Spotted chub. AL, Jackson Co. Paint Rock River. 66mm SL.

Figure II-9 B. Hybopsis harryi - Ozark chub. MO, Ripley Co. Current River. 58.2mm SL. (Lateral aspect)

Figure II-9 C. Hybopsis harryi - Ozark chub. MO, Ripley Co. Current River. 58.2mm SL. (Dorsal aspect)

Figure II-9 D. Hybopsis harryi - Ozark chub. AR, Van Buren Co. Little Red River. 75.9mm SL female.

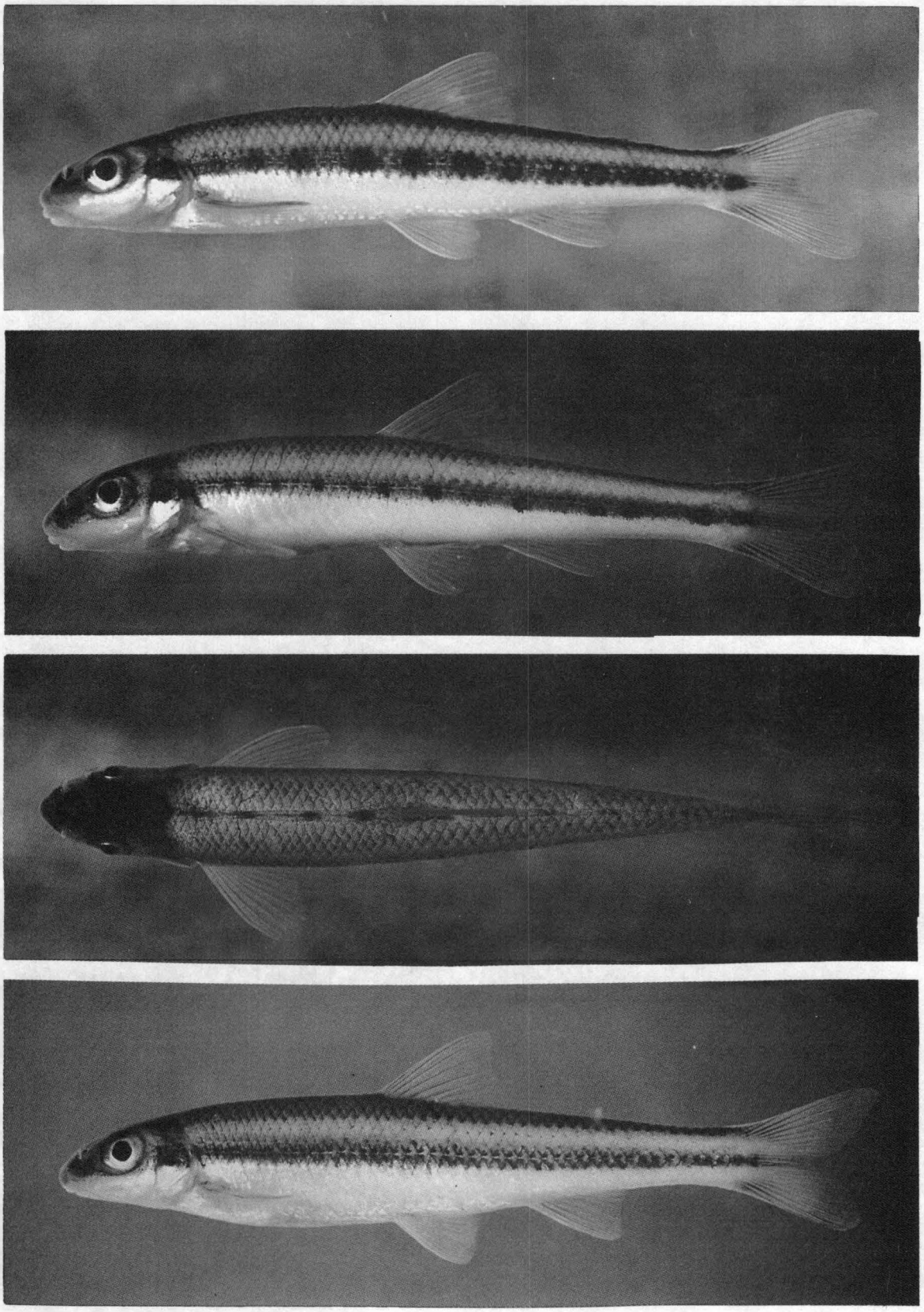


Table II-11. Sexually Dimorphic Variables of Hybopsis dissimilis.

Variable	Sex(N)	Range	Mean	SD	t-value	P
CPL	M(221)	181-324	222.1	14.39	2.1460	<.05
	F(200)	189-250	219.2	13.09		
ORW	M(221)	58-88	71.6	4.13	3.1187	<.005
	F(200)	58-82	70.3	4.04		
CPD	M(221)	62-85	74.4	3.74	2.2105	<.05
	F(200)	63-83	73.6	3.78		
DFL	M(221)	167-238	196.7	10.61	4.3035	<.001
	F(200)	160-223	192.1	11.08		
AFL	M(220)	125-186	156.0	11.48	3.3223	<.001
	F(200)	119-191	152.2	12.03		
P1L	M(221)	135-229	189.1	12.63	13.6661	<.001
	F(200)	136-208	172.6	12.08		
P2L	M(221)	87-151	132.4	9.15	2.0855	<.05
	F(200)	103-190	130.4	10.16		
BWP	M(219)	115-164	138.9	9.01	2.3770	<.05
	F(192	111-163	136.7	9.83		

Range, mean, and standard deviation are in thousandths of standard length.

Nuptial tuberculation: A composite description is given of male nuptial tuberculation. The description was obtained from examination of 55 specimens, 57.0-100.5 mm SL, in highly tuberculate condition.

Cephalic tubercles are small and grainy and often difficult to discern from sensory papillae. Cephalic tubercles are concentrated in the supraorbital region and dorsally above the postocular commissure. The mid-occipital region posterior to the orbits has few tubercles. A moderate number of tubercles are present between the orbits. The preorbital, postorbital, and opercular regions are generally devoid of or with scant tuberculation. Snout tubercles are moderate in number and very tiny. The infraorbital and ventral surfaces are usually devoid of tubercles.

Body tuberculation on the nape and dorsolateral scales anterior to the dorsal insert is best developed with 6-10 small tubercles distributed on the scale periphery and 2-3 grainy tubercles in the scale centrum. Mid-lateral scales from the head to below the dorsal insert are usually without tubercles. Tubercles on the posterior dorsal and posterior dorsolateral scales are not as large as those on anterior scales and usually possess 4-10 tubercles on the scale periphery. Breast scales occasionally have 1-2 larger tubercles on each scale edge. The belly and posterior ventral scales lack tubercles.

Fin tuberculation: The pectoral fins have small, posteriorly directed tubercles on the dorsal surface of rays 2 through 8, 9, 10, or 11, more strongly developed on rays 2-6. Each branch of rays 2-6 has uniserial rows of tubercles extending nearly to the end of the ray with one tubercle per ray segment. Rays 7-11 generally possess

tubercles restricted to the basal portion of the ray (i.e., proximal to branching). Tubercles appear to originate from the posterior side of the ray when ray projected at 90 from the body. Tubercles are rarely on the ventral surface and then are restricted to the basal portion of the ray. Pelvic fin tubercles are on rays 2 through 4, 5, or 6, are very tiny, and generally restricted to distal branches. Distribution is one tubercle per segment and tubercles are visible only under intense light in the most highly tuberculate specimens. The anal fin has tiny tubercles on rays 2 through 5 or 6, usually on the distal branches but occasionally on the basal portion of rays 2-3. These tubercles are tiny but larger than pelvic tubercles and distributed one per ray segment. The dorsal fin has tubercles on rays 2 through 5 or 6 distally, although occasionally on the basal portion of the ray. Distribution is one tubercle per ray segment and size is comparable to pelvic tubercles.

A nuptial pad (sensu Branson, 1962) was present on all mature males examined which were captured from mid-April through early June. Location and appearance of the pad is as described by Branson (1962) for Hybopsis x-punctata and by Jenkins and Burkhead (1984) for H. monacha. In H. dissimilis, the pad may extend to the ventral surface, covering the branchiostegals and isthmus region with discrete patches. The nuptial cheek pad apparently does not develop in females.

Sensory and trophic anatomy. Davis and Miller (1967) figured the dorsal surface of the brain for Hybopsis dissimilis and provided measurements of each brain region. Additionally, external and internal cephalic taste buds were counted and proximal width and

length measured. Taste buds on barbels were also counted and length and width measured. The presence or absence of compound taste buds on the pectoral fin was noted. Specimens of H. dissimilis examined during this study invariably had compound taste buds on both the dorsal and ventral surfaces of the first interradial membrane of the pectoral fin with those on the dorsal surface slightly larger than the ventral counterparts. Additionally, I observed compound taste buds in the membranes between rays 1-2, 2-3, and 3-4 of the pelvic fin but most commonly on the interradial between 1-2 on the dorsal surface. Taste buds were also observed on interradials 1-2 and 2-3 of the anal fin. The cephalic lateral-line system of Hybopsis dissimilis was figured in Reno (1969b) and mean pore counts for canals presented as follows: infraorbital canal 12.5 (11-14); postocular commissure 3.3 (2-4); cephalic lateralis 2.9 (2-4); supraorbital canal 10.2 (8-11); supratemporal canal 5.5 (3-7), and preoperculomandibular canal 8.3 (8-10). These counts were made from H. dissimilis and H. harryi specimens. Davis and Miller (1967) presented a figure of the brain of Hybopsis dissimilis compiled from specimens of both H. dissimilis and H. harryi. Mean facial and optic lobe widths as per cent of total brain length were given as 13.0 and 28.1, respectively. Mean external and internal taste bud numbers for five cephalic regions were as follows: tip of snout 14.8/0.0; anterior nasal rosette 17.0/2.4; posterior nasal rosette 7.0/4.2; posterior of retina 6.9/13.6; and anterior of cerebellum 5.0/22.2.

The mouth is inferior with lips of moderate thickness which lack striae. Barbels range from a small, almost rectangular stub to a well

developed, tapered, druse-like extension of the lip symphysis. Secondary papillae on the barbel range from a few poorly developed buds to many well developed, elongate papillae. The sensory bristles of Branson (1962), located in the sulcus between upper lip and head, are usually absent but occasionally appear as small buds. Taste buds located ventrally on the lips and isthmus are numerous but small.

Gill rakers: 4(1), 5(3), 6(6), 7(10), 8(13), 9(4), 10(1), 11(1), 12(1); dorsal rakers (usually 3-4) short to medium in length and acutely pointed; ventral rakers rudimentary, blunt or knobby. Etnier and Starnes (ms) gave counts of 5-10 gill rakers which were best developed dorsad.

Pharyngeal teeth were figured by Cope (1868). All specimens examined (n = 31) during this study were 4-4. Apparently all teeth are hooked during early life stages but may be worn to a flat grinding surface by the first spawning season. The two posterior dorsal teeth of each arch are especially susceptible to wear and become acutely tipped with a smooth, flat grinding surface basad.

The intestinal tract is short to moderate in length and usually uncoiled. Occasionally, an accessory loop protrudes at the anterior-most segment of the last descending portion of the intestine. Total intestinal length in 38 specimens (64.2-112.7 mm SL; $\bar{x}$ = 85.6) ranged from 77% to 110% ($\bar{x}$ = 94%) of standard length. The inner surface of the intestine is ridged in the herringbone pattern described for Hybopsis monacha by Jenkins and Burkhead (1984). The peritoneal lining is brownish or black with scattered melanophores and sometimes a silver to white background coloration.

Other internal structures. The gas bladder is large and two chambered with mean total length 29.7% (22.9%-32.7%; n = 15) of SL. Average length of the anterior chamber is 10.9% (8.3%-13.4%) of SL while the posterior chamber averages 18.8% (14.6%-22.3%) of SL.

Vertebral counts are summarized in Table II-10 (p. 44) and include some specimens radiographed and counted by Jenkins and Lachner (1971). Specimens from USNM 116420, which were part of the Jenkins and Lachner Hybopsis dissimilis counts, were redetermined to be Pimephales notatus (Rafinesque). This explains the absence of specimens with total vertebral counts of 39 from Table II-10 (p. 44), as the five 39's of Jenkins and Lachner were all from P. notatus. Total vertebrae counts: 40(16), 41(15); precaudal vertebrae: 20(1), 21(21), 22(9); caudal vertebrae: 18(2), 19(20), 20(9).

Coloration. Freshly captured adults and juveniles are usually olive to khaki green above the lateral band. A charcoal to bluish black mid-lateral band with darkened oval to slightly oblong spots is usually present and conspicuous. The mid-dorsal line is broken with dark dashes interrupted by paler areas which sparkle like gold when observed under water. The lateral band extends from the posterior terminus, a small to medium caudal spot located at the caudal base, along the body through the opercle and eye to the anterior terminus at the lachrymal groove. The lateral band encompasses the lateral-line and 1/2 scale row above and below. It is generally widest directly below the dorsal insert and narrower posterior to the caudal peduncle. Diffuse lateral pigmentation on the scale periphery may extend three rows diagonally below the lateral-line. The venter is creamy to white

and virtually unpigmented with the exception of occasional melanophores along the anal base and the mid-ventral line posterior to the anal fin.

A distinctly paler region extends from about 1 1/2 scale rows above the lateral band for about 3 scale rows and is caused by reduction in background pigment. Further dorsolaterally, pigmentation returns to the darker coloration and scales appear cross-hatched due to increased coloration on the scale periphery. Dorsolaterally, w- and x-shaped spots occur randomly and are found most often posterior to the dorsal insert and above the lateral pale zone.

Cephalic pigmentation generally is an olive to charcoal background coloration composed of tiny, uniform melanophores. Pre- and postorbital regions are distinctly paler while the internareal region is darker due to the underlying nasal rosette. Below the orbit and on the ventral cephalic surface, melanophores are usually absent, the region immaculate.

Fin pigmentation: The dorsal fin has no interradial pigment and all rays are outlined with melanophores, including the branches of each major ray. Anal fin rays 1 or 2 through 5, 6, or 7 are pigmented on the basal half of each ray and sometimes to the distal margin in highly pigmented individuals. Ray 7, when pigmented, never has melanophores in the posterior branch of the ray. The pelvic fins are not strongly pigmented as rays 1 or 2 through 4 have only a sprinkling of melanophores on the medial portion of the ray. Occasionally ray 5 and/or 6 is pigmented while rays 7 and 8 are virtually always unpigmented. Pectoral fin rays 1 through 9 are usually strongly pigmented,

and rays 10, 11, and rarely 12 may be weakly outlined. During peak nuptial development, males have much denser, darker concentrations of melanophores on the posterior side of each pigmented ray. This sexual dimorphism is well enough developed that the sexes can be distinguished during underwater observations using this character. As in all other fins, no interradial pigment is present.

C. Hybopsis harryi Hubbs and Crowe, 1956

Ozark chub

Common Name and Types

Hubbs and Crowe (1956) described Hybopsis dissimilis harryi from streams draining the Ozark Mountain range in Arkansas and Missouri. The holotype is an 81.5 mm SL male (UMMZ 167083) collected from the White R. 3.0 miles SE of Mano, Barry Co., MO on 7 August 1940 with a 73 mm standard length paratopotype (UMMZ 151368). No common name has previously been applied to this form, therefore, the name Ozark chub, referring to the restricted geographic region of the species, is suggested.

Synonomy

Hybopsis dissimilis (Kirtland). Jordan and Gilbert, 1886:4 (White R., AR); Meek, 1894:248 (distribution AR; partial synonomy); Meek, 1895:78, 90, 92 (distribution AR; White R., AR); Jordan and Evermann, 1896:315, 318-319 (in part, in key; description; distribution); Meek, 1908:151 (in part, distribution); Martin and Campbell, 1953:46, 48, 51, 53 (abundance and habitat, Black R., MO); Pflieger,

1968:4 (MO checklist; in key); Moore, 1968:68, 69-70 (in part, in key; distribution); Eddy, 1969:102 (in part; in key; distribution); Reno, 1969a (in part, nomenclatorial review); Reno, 1969b (in part, description, discussion, and figures cephalic lateral-line system); Pflieger, 1971:262, 333-334 (partial synonomy; distribution; habitat; zoogeography); Buchanan, 1973a:28 (AR checklist); Buchanan, 1973b:3, 33, map 41 (in key; distribution AR); Green and Beadles, 1974:23 (checklist Current R., AR; habitat); Clay, 1975:141-142 (in part, distribution); Pflieger, 1975:104, 137-137 (description; distribution MO; habitat; biology; figured and in key); Bounds, et al., 1977:22-23 (Randolph Co., AR); Cashner and Brown, 1977:40 (distribution Buffalo R., AR); Frazier and Beadles, 1977:39 (Sylamore Cr., AR); Johnson and Beadles, 1977:59 (distribution Eleven Point R., AR); Eddy and Underhill, 1978:72-73 (in part, in key; distribution); Boschung, et al., 1983:Fig. 164, 421-422 (in part, description; distribution; related species; habitat; biology; color photo); Cooper, 1983:92 (in part, distribution); Mayden, 1985a:205 (in part, zoogeography).

Hybopsis watauga Jordan and Evermann. Jordan,1889:355-356 (in part, original description; comparison with H. dissimilis; distribution); Meek, 1894;249 (in part, distribution AR; partial synonomy); Meek, 1895:82, 90, 92 (description; S. Fork Little Red R., AR; distribution AR); Jordan and Evermann, 1896:315, 319 (in part, in key; description; distribution); Meek, 1908:151 (in part, distribution).

Erimystax watauga. Jordan, et al., 1930:138 (in part, distribution).

Erimystax dissimilis. Jordan, et al., 1930:138 (in part, distribution), Eddy and Surber, 1947:151 (in part, description and distribution); Patriarche and Campbell, 1958:256 (Clearwater Lake, MO).

Hybopsis dissimilis harryi. Hubbs and Crowe, 1956:2, 4, 6 (original subspecies description, Holotype UMMZ 167083; in key; distribution); Harris, 1980a:184 (systematics, distribution).

Hybopsis (Erimyxtax) dissimilis. Davis and Miller, 1967 (in part, brain morphology; habitat; distribution; feeding habits).

Hybopsis (Erimystax) dissimilis harryi. Jenkins and Lachner, 1971:6, 7, 12 (vertebral counts; differences subspecies of H. dissimilis).

Diagnosis

Hybopsis harryi is distinguished from other members of Erimystax by its elongate, double looped gut. It differs from H. cahni and H. x-punctata by the presence of mid-lateral and/or mid-dorsal dark spots. Hybopsis harryi differs from H. insignis by having oval mid-lateral spots and smaller scales (usually 45-51 in lateral-line). Hybopsis insignis has quadrate mid-lateral blotches and usually 37-47 lateral line scales. Hybopsis harryi is similar to H. dissimilis but distinguished by its shorter head ($\bar{x}$ = 233 TSL), broader connection of the opercular membranes ($\bar{x}$ = 63 TSL), greater ventral scalation ($\bar{x}$ = 76%), more numerous (9-16) and smaller (< pupil diameter) lateral spots, and higher total vertebrae counts (41-43). Hybopsis dissimilis has mean head length of 245 TSL, mean isthmus width of 52 TSL, mean

ventral scalation of 53%, 6-12 mid-lateral blotches usually equal to or larger than pupil diameter, and total vertebral counts of 40 or 41.

Description

The body is elongate, slightly compressed laterally, and tapered gradually from the pelvics posteriad to the caudal fin. The snout is bluntly rounded and overhangs the subterminal, ventral mouth. The eyes are medium in size, located laterally and directed somewhat dorsally. A terminal labial barbel, small to medium in size, is present. The upper lip is expanded anteriad and the lower jaw included. Pharyngeal teeth are 4-4. Scales in the lateral-line range 43-52. The mid-lateral band has 4-16 distinct oval spots (occasionally absent), generally smaller than pupil diameter. The mid-dorsal line has 3-10 darkened dashes. Dorsolateral pigment spots are present on the periphery of dorsolateral scales and usually occur as one or two horizontal rows beginning at approximately the dorsal insertion and extending posteriad to peduncle. No interradial fin pigment is present. The dorsal profile from the dorsal fin insertion to the snout is gently curved.

External morphology. Morphometry: Fin shape and placement and body form are illustrated in Figure II-8 (p. 40). Proportional data for measured variables and means for meristic variables are presented in Table II-8 (p. 40). Sexually dimorphic variables are presented in Table II-12.

Meristics: Range, mean, and standard deviation for meristic variables are given in Table II-8 (p. 41) and distribution is

Table II-12. Sexually Dimorphic Variables of Hybopsis harryi.

Variable	Sex(N)	Range[a]	Mean[a]	SD[a]	t-value	P
PRL	M(67)	461-531	484.5	13.62	2.6622	<.01
	F(93)	466-524	490.4	14.01		
PDL	M(67)	506-577	540.0	13.56	3.4931	<.001
	F(93)	502-599	532.8	12.28		
CPL	M(67)	195-248	223.9	11.80	2.0090	<.05
	F(93)	184-241	220.1	11.87		
BDD	M(67)	156-196	181.5	8.94	2.6481	<.01
	F(93)	156-203	177.1	11.00		
DFL	M(67)	167-216	194.6	10.84	4.5149	<.001
	F(92)	166-210	186.9	10.32		
AFL	M(67)	119-178	154.0	12.01	3.0534	<.005
	F(92)	124-172	148.5	10.82		
P1L	M(67)	152-213	191.1	13.17	11.7313	<.001
	F(93)	150-197	170.5	9.13		
P2L	M(67)	114-158	136.5	9.34	2.4641	<.05
	F(93)	109-159	133.0	8.44		

[a]Range, mean, and standard deviation are in thousandths of standard length.

presented in Table II-9 (p. 42). Meristic variables show no significant sexual dimorphism.

Nuptial tuberculation: Twenty-four male specimens captured from 10 April through the last of May were examined for nuptial tuberculation and a composite description is presented. Specimens ranged from 63.8-81.6 mm SL and were taken from throughout the range of the species.

Cephalic nuptial tuberculation, size, and distribution are generally the same as for Hybopsis dissimilis. Tubercles are, perhaps, somewhat smaller in H. harryi during peak development.

Fin tuberculation: Pectoral fin tubercles are present dorsally on rays 2 through 10 or 11 with occasional development on rays 1 and 12-15. Tubercles are most strongly developed anteriorly with each branched ray 2 through 6 supporting tubercles to the distal margin. Rays 7 through 11, 12, 13, 14, or 15 have reduced distal tubercles and coverage is restricted primarily to the basal portion of each ray (medial to branching). Distribution is as in other Erimystax with one tubercle per ray segment. Basal ray tubercles are on the posterior portion of the ray (with fin extended 90 from body) and are directed posteriad. Tubercles occasionally are present on the ventral surface of rays 2 through 6 but are small and poorly developed. Pelvic fin tubercles are usually small and located on the dorsal surface of rays 2 through 5 and occasionally on 1, 6, and 7. Tubercles are best developed on the distal 1/2 of each ray and extend medially to the middle of the basal ray portion. Tubercles are distributed one per

segment and occasionally occur on the ventral surface of rays 2 through 5 or 6 but are smaller than the dorsal counterparts. Dorsal fin tubercles are always present on rays 2 through 5 and, occasionally, rays 1 and 6 through 8. Tubercles are tiny and usually restricted to the distal 1/2 of the ray. Anal rays 2 through 6 or 7 possess small tubercles on the distal 1/2 of rays and the distribution is one tubercle per segment.

A nuptial pad is present in all mature, nuptial males examined. Location and appearance are as described for Hybopsis dissimilis. Females do not develop the nuptial pad and only occasionally are nuptial tubercles observed on the body and fins. When present in females, tubercles are tiny, irregular in distribution, and poorly developed.

Sensory and trophic anatomy. Davis and Miller (1967) used specimens of Hybopsis dissimilis and H. harryi in preparing the figured brain morphology of H. dissimilis. The composite nature of the H. dissimilis brain figure was discussed in the account of that species. Compound taste buds on the pectoral fin of H. harryi are found on both dorsal and ventral surfaces of the interradial membrane 1-2 and are usually quite small. Approximately 50% of specimens examined also exhibit small compound tastebuds on the ventral surface of all interradial membranes through ray 12. Pelvic fins have taste buds on both dorsal and ventral surfaces between rays 1 and 2 and they are usually present on the dorsal surface between the distal branches of ray 2. Anal and dorsal fin taste buds are very small and limited to the interradial membrane between rays 1 and 2.

Reno's (1969b) work on the cephalic lateral-line system was discussed in the Hybopsis dissimilis account. As in Davis and Miller (1967), Reno used a combination of H. harryi and H. dissimilis in his analysis.

The mouth is inferior with lips of moderate thickness, the upper noticeably expanded at the anterior midline and described as "shield shaped" by Hubbs and Crowe (1956). Lips lack definite striae but possess many small to medium size taste buds. Barbels range from small stubs to long, slender, acutely pointed structures with a few poorly to well developed sensory papillae. Sensory bristles (Branson, 1962) in the lip sulcus are usually absent. Taste buds in the center of the isthmus often appear as well developed papillae.

Gill rakers: 8(4), 9(11), 10(5) with the dorsal rakers medium in length and acutely pointed and the ventral rakers reduced to knobs.

All pharyngeal arches examined (n = 28) were 4-4. The teeth are hooked but apparently well worn at an early age so they appear acutely tipped with a smooth, flat to slightly concave grinding surface. Teeth from specimens of H. harryi are distinctly more worn than those from comparable size H. dissimilis, perhaps owing to the predominately herbivorous diet of H. harryi (Harris, msC).

The intestinal tract is usually long with at least two loops extending from side to side across the ventral surface of the anterior gut. Intestinal length in 66 specimens (71.7-102.8 mm SL, $\bar{x}$ = 87.2) ranges from 149% to 282% ($\bar{x}$ = 225%) of standard length. The inner intestinal surface has a ridged, herringbone pattern and the

peritoneal lining is a uniform, finely pigmented, dark brown to black color with occasional streaks of silver background coloration.

Other internal structures. The gas bladder is two chambered and large, averaging 31.2% (27.9%-33.4%; n = 10) of SL. The anterior chamber average length is 11.0% (9.0%-13.1%) while the posterior chamber averages 20.2% (16.5%-22.0%). Vertebral counts are: Precaudal 21(6), 22(20), 23(2); Caudal 19(5), 20(16), 21(7); Total 41(8), 42(15), 43(5). These counts include all materials examined by Jenkins and Lachner (1971).

Coloration. Live or freshly preserved specimens are yellow-green, tan, or gray dorsally. A prominent bluish black to charcoal lateral band extends from the lachrymal groove posteriad to the caudal peduncle and may extend onto the caudal fin in the form of 3-4 darkly outlined central caudal rays. Darker lateral spots occur in the lateral band and number from 4-16. They are usually round to slightly oblong in shape and equal to, or smaller than the pupil in size. Anteriad, the lateral band encompasses the lateral-line plus one scale row above and below and appears widest at mid-body. Posteriad, the band tends to narrow and at the peduncle is restricted to the lateral-line. A paler pigmented area composed of the two scale rows immediately above the lateral band occurs on the dorsolateral surface. Above the paler band and extending to the dorsal mid-line, a darker background coloration of charcoal to yellow green occurs. The mid-dorsal stripe is not well developed except for the 4-5 predorsal and 3-7 postdorsal spots or dashes. Two horizontal rows of spots occur on each dorsolateral surface and are composed of pigment concentrations

on the posterior edge of each scale in the row. Although variable in both occurrence and length, these rows of spots are usually located on the third and fourth scale rows above the lateral-line and immediately above the dorsolateral pale area. The more ventral row originates below the dorsal insertion while the more dorsal generally begins about halfway between the head and dorsal fin. Ventrolateral body pigmentation extends through scale rows 2-4 below the lateral-line with the more ventral scales lightly peppered on the periphery with tiny melanophores. The anal insert is sometimes outlined with melanophores that extend posteriad along the mid-ventral line. The remainder of the ventral surface is creamy to white.

Cephalic background coloration is a rather uniform charcoal gray composed of tiny melanophores except in the lighter pre- and post-orbital areas. A thin line of pigment generally occurs below the orbit and the ventrolateral and ventral cephalic regions were creamy or white and devoid of pigmentation.

Fin pigmentation: The dorsal fin has no interradial pigment and all rays are outlined with melanophores, usually to the distal margin. Anal rays 1 or 2 through 5, 6, or the anterior half of 7 are outlined on the basal 2/3. Usually rays 1 through 6 are pigmented. Pelvic rays 1 or 2 through 5 are weakly to moderately outlined on the medial portion of the ray. Pectoral rays 1 through 8, 9, or 10 are moderately to strongly outlined. Interradial pigment occurs between rays 1 and 2 in approximately 50% of specimens examined. Males develop concentrations of melanophores on the posterior side of pigmented rays

during spawning season and are easily differentiated from females using this character.

D. Hybopsis insignis Hubbs and Crowe, 1956

Blotched chub

Analysis

Specimens of Hybopsis insignis Hubbs and Crowe (1956) totaling 577 individuals from 23 populations were examined during this study. Of these, complete data sets of 29 meristic and morphometric variables were obtained from 510 individuals and subjected to multigroup discriminant analysis. Canonical analysis of discriminance indicated group centroids are unequal ($F = 7.20$; $P<0.001$). CV1 described 52% of total variation while variates 2 and 3 accounted for 10% and 8%, respectively. Correlations between meristic and morphometric variables and the first three canonical variates are presented in Table II-13. CV1 had a relatively high negative correlation with upper lip width and somewhat lower correlations with lateral-line scales, circumbody scales, and upper lip length. CV2 had high negative correlations with isthmus width and orbit width. CV3 had the highest positive correlation with lateral-line scales and caudal peduncle length and a high negative correlation with predorsal scales.

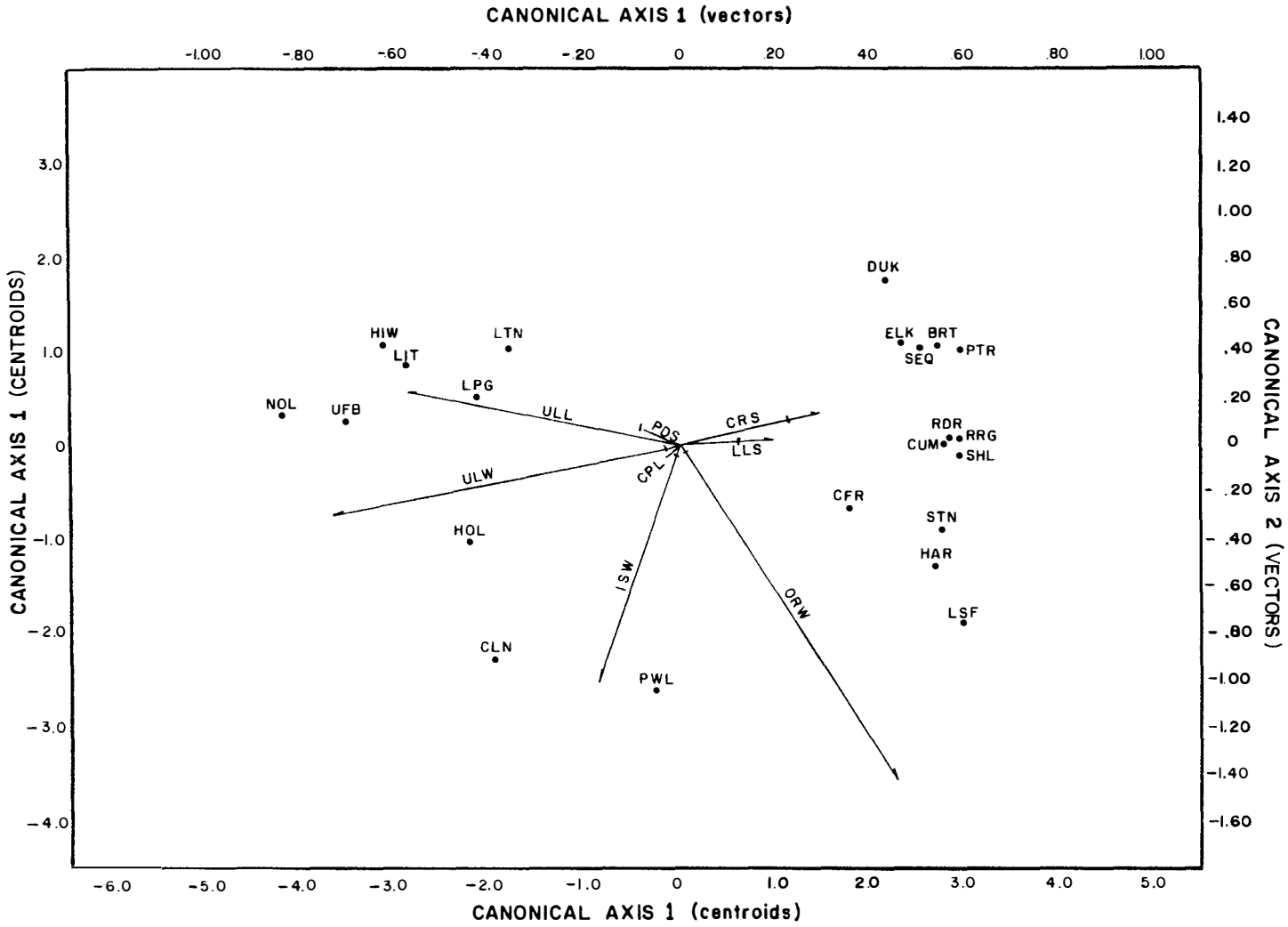
Two dimensional canonical graphs based on all variables were prepared for the 23 population centroids by plotting canonical axes 1 versus 2, 2 versus 3, and 1 versus 3. The best discrimination in canonical space was provided by canonical axes 1 versus 2 (Figure II-10). Vectors for the variables ULW, ULL, LLS, CRS, ISW, and ORW were

Table II-13. Correlations between Canonical Variates and Morphometric + Meristic Variables of *Hybopsis insignis*.

Variable	Canonical Variate 1	Canonical Variate 2	Canonical Variate 3
PRL	-0.054	-0.067	-0.123
PDL	0.033	-0.127	0.121
CPL	0.038	-0.115	0.210*
HDL	-0.049	-0.079	-0.084
SNL	-0.046	-0.034	-0.032
ULL	-0.222*[a]	-0.001	-0.090
GPW	-0.182	0.033	-0.082
IOW	-0.008	0.050	0.058
ORW	0.023	-0.244*	-0.150
BDD	-0.118	-0.140	0.043
CPD	-0.190	-0.160	0.040
ISW	-0.213	-0.292*	-0.091
DFL	-0.029	-0.154	0.141
AFL	-0.113	-0.038	-0.005
P1L	-0.140	-0.030	-0.048
P2L	-0.133	-0.077	-0.061
POL	-0.125	-0.025	0.026
ULW	-0.493*	-0.057	-0.096
BWP	-0.095	-0.050	0.011
LLS	0.286*	0.081	0.252*
ALL	0.064	-0.085	0.012
BLL	0.059	0.016	-0.064
CRS	0.236*	0.047	-0.144
CPS	-0.021	-0.090	-0.040
PDS	0.021	0.086	-0.243*
PBS	-0.029	0.001	0.164
LP1	0.016	-0.030	0.035
LP2	-0.002	0.039	0.032
ANR	0.024	0.024	0.039

[a]The * indicates highly correlated variables.

Figure II-10. Population centroids and variable vectors of Hybopsis insignis in canonical space determined from the meristic and morphometric data set. Vectors show contributions of raw data (⟶) and z-scores (⟶|).


CANONICAL AXIS 1 (vectors)
-1.00
-.80
-.60
-.40
-.20
0
.20
.40
.60
.80
1.00
CANONICAL AXIS 1 (CENTROIDS)
3.0
2.0
1.0
0
-1.0
-2.0
-3.0
-4.0
CANONICAL AXIS 2 (VECTORS)
1.40
1.20
1.00
.80
.60
.40
.20
0
-.20
-.40
-.60
-.80
-1.00
-1.20
-1.40
-1.60
-6.0
-5.0
-4.0
-3.0
-2.0
-1.0
0
1.0
2.0
3.0
4.0
5.0
CANONICAL AXIS 1 (centroids)
DUK
HIW
LTN
LIT
ELK
BRT
SEQ
PTR
LPG
NOL
UFB
ULL
POS
CRS
LLS
RDR
RRG
CUM
SHL
ULW
CPL
CFR
STN
HOL
HAR
MSI
ORW
LSF
CLN
PWL

drawn from the grand centroid and illustrated the relative contributions for both raw and z-score variables. Population centroids with 95% confidence circles indicate patterns of interactive variability among populations (Figure II-11).

Principal components analysis (PCA) of morphometric variables revealed PC1, PC2, and PC3 account for 77.6%, 7.1%, and 3.5% of total morphometric variation, respectively. Loadings of variables on the first three principal components are summarized in Table II-14. PC1 was a general size component while PC2 reflected variation in upper lip width and PC3 accounted for variation in anal and pelvic fin lengths. Plots of all possible configurations of the first three principal components were compared and PC1 versus PC2 appeared to provide the best discrimination among populations (Figure II-12). PCA using all variables added no additional discrimination.

Population means for the ten variables with high loadings in the multivariate analyses are presented in Table II-15. Comparisons among population means for the eight variables using the Gabriel multiple-comparison procedure are presented in Table II-16.

Discussion

Hubbs and Crowe (1956) described two subspecies of the blotched chub: *Hybopsis i. insignis* and *H. insignis eristigma*. Thirteen of the populations analyzed were *H. i. insignis* sensu Hubbs and Crowe and included the Red, Harpeth, Stones, Roaring, Caney Fork, Little South Fork, Cumberland, Duck, Buffalo, Shoal Creek, Elk, Paint Rock, and Sequatichie populations. Eight populations were *H. insignis eristigma*

Figure II-11. Population centroids and 95% confidence circles of Hybopsis insignis in canonical space determined from the meristic + morphometric data set. Only confidence circles of outlier populations are plotted.

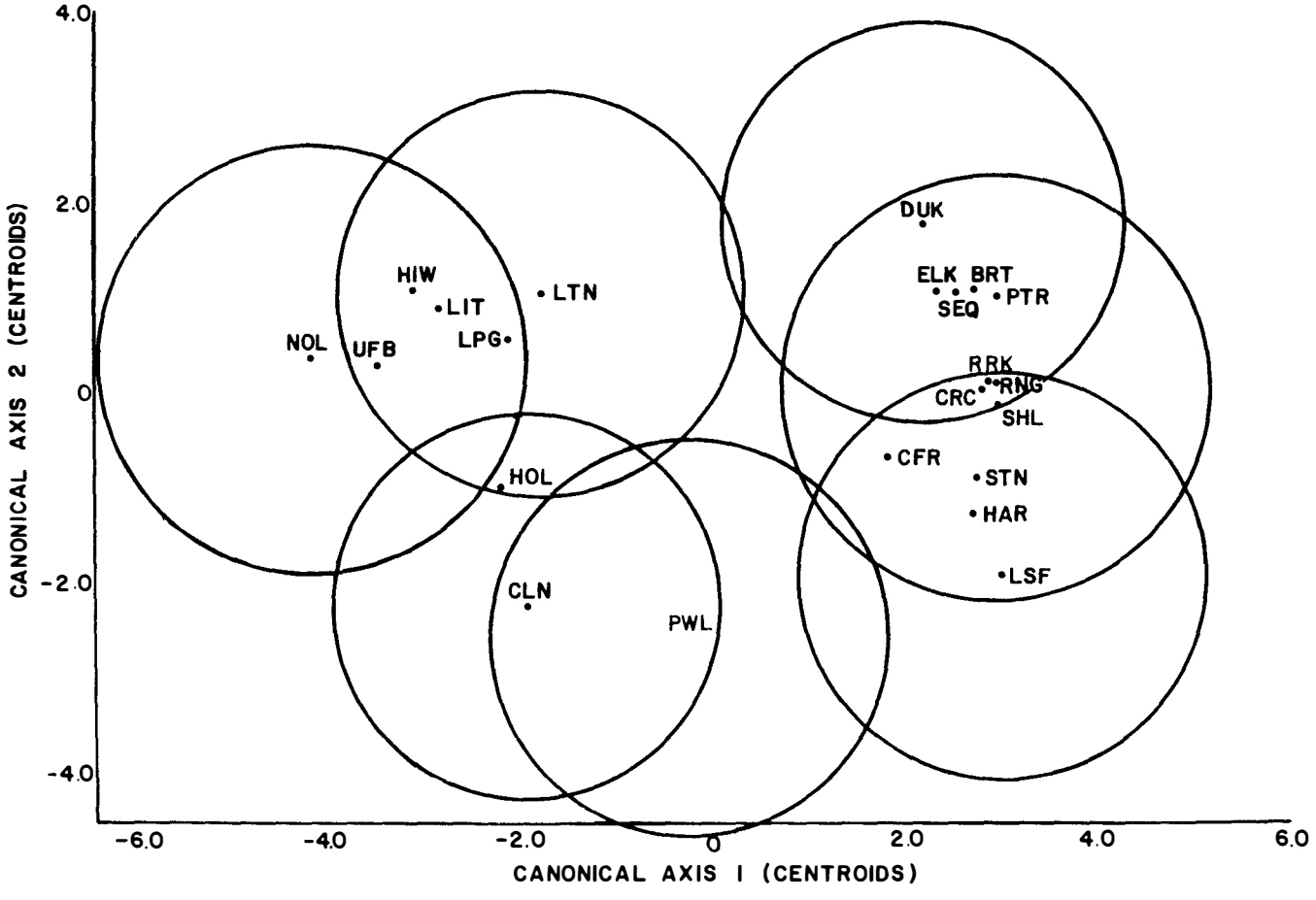

4.0
2.0
0
-2.0
-4.0
-6.0
-4.0
-2.0
0
2.0
4.0
6.0
CANONICAL AXIS 2 (CENTROIDS)
CANONICAL AXIS 1 (CENTROIDS)
HIW
LIT
LTN
NOL
UFB
LPG
HOL
CLN
PWL
DUK
ELK
BRT
SEQ
PTR
RRK
RNG
CRC
SHL
CFR
STN
HAR
LSF

Table II-14. Loadings of Morphometric Variables on Principal Components of *Hybopsis insignis*.

Variable	Principal Component 1	Principal Component 2	Principal Component 3
PRL	0.249	-0.080	0.111
PDL	0.231	-0.318	0.033
CPL	0.215	-0.344	0.089
HDL	0.251	-0.101	0.058
SNL	0.243	-0.054	0.069
ULL	0.230	0.277	-0.020
GPW	0.230	0.234	0.096
IOW	0.200	-0.229	0.345
ORW	0.228	-0.226	0.002
BDD	0.238	0.042	0.237
CPD	0.245	0.118	0.102
ISW	0.210	0.256	0.249
DFL	0.237	-0.209	-0.219
AFL	0.226	0.025	-0.533*
P1L	0.237	0.061	-0.362
P2L	0.231	0.055	-0.471*
POL	0.232	0.022	0.058
ULW	0.158	0.627*[a]	0.075
BWP	0.246	0.022	0.142

[a]The * indicates highly correlated variables.

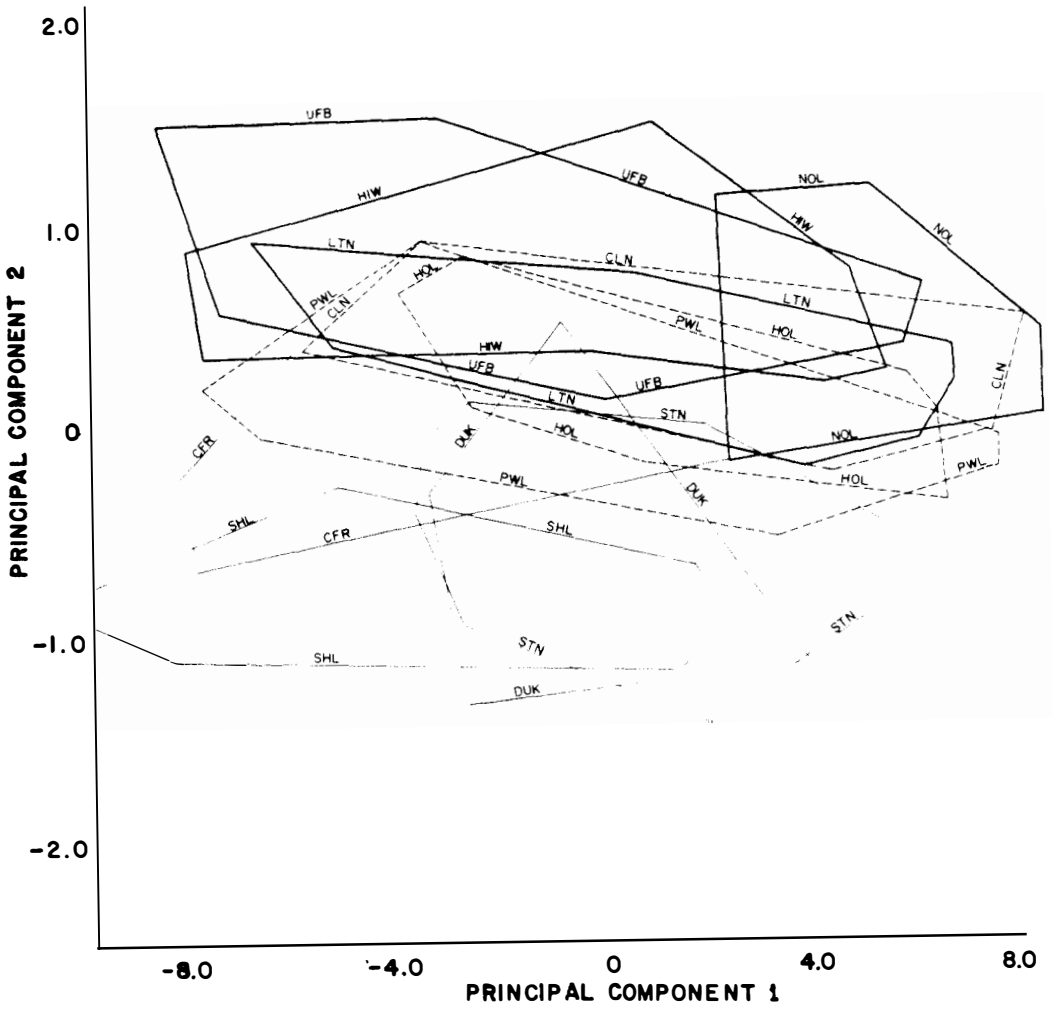


Figure II-12. Population polygons of Hybopsis insignis on principal component axes determined from the morphometric data set. Only outlier populations are plotted and heavy solid lines represent H. insignis eristigma, light solid lines represent H. i. insignis, and dashed lines represent intergrades.

Table II-15. Population Means for Morphological[a] and Meristic Variables of *Hybopsis insignis* with High Loadings in Multivariate Analyses.

Population	ULW	ULL	LLS	CRS	PDS	ISW	ORW	CPL	AFL	P2L
RDR	12	58	42.4	31.3	17.4	75	73	216	184	153
HAR	15	62	41.9	31.4	17.8	82	83	217	170	148
STN	13	58	42.1	31.5	18.2	81	81	215	168	140
CFR	15	61	41.3	31.2	17.6	72	79	206	186	157
RNG	12	60	41.0	31.8	18.1	76	79	207	172	150
CRC	13	63	42.2	31.3	17.0	82	80	225	168	147
LSF	12	60	41.0	30.5	17.8	75	87	212	172	152
BRT	13	59	43.7	31.3	17.9	60	80	230	170	148
DUK	15	62	42.5	31.0	17.1	76	75	222	162	136
SHL	11	57	43.3	30.4	17.4	67	74	229	175	148
ELK	15	61	42.0	30.2	17.0	70	75	215	165	141
PTR	13	61	43.2	30.2	17.6	66	77	220	185	153
SEQ	14	62	43.1	30.3	17.2	68	78	220	183	151
PWL	18	64	41.0	28.8	16.2	87	82	233	177	153
CLN	21	69	40.0	29.1	16.9	93	78	214	180	154
HOL	20	69	40.9	29.7	17.1	84	76	221	186	158
HIW	22	77	39.6	28.8	17.5	88	76	215	192	165
LTN	21	74	39.6	29.1	16.9	73	80	207	192	162
LIT	23	73	40.2	29.5	17.0	86	76	231	188	161
LPG	21	69	40.5	29.3	17.3	81	76	217	183	153
PIG	21	73	39.0	29.0	18.0	85	83	221	218	186
UFB	23	72	39.3	29.2	17.8	95	78	206	191	167
NOL	22	71	40.6	29.6	18.0	102	75	216	183	152

[a]Morphometric means are in thousandths of standard length.

Table II-16. Gabriel Multiple-Comparison of Hybopsis insignis Population Means.

Variable	ULW[a]	ULL[a]	ISW[a]	LLS[a]
F-value	74.7	47.4	29.4	19.9
Low Value	SHL	SHL	BRT	UFB
	RDR	STN	PTR	HIW
	RRG	RDR	SHL	LTN
	LSF	RNG	SEQ	CLN
↑	STN	LSF	ELK	LIT
P	PTR	BRT	CFR	LPG
O	BRT	PTR	LTN	NOL
P	CRC	CFR	LSF	HOL
U	SEQ	ELK	RDR	PWL
L	ELK	SEQ	DUK	LSF
A	CFR	HAR	RRG	RRG
T	HAR	DUK	STN	CFR
I	DUK	CRC	LPG	HAR
O	PWL	PWL	CRC	ELK
N	HOL	CLN	HAR	STN
S	CLN	LPG	HOL	CRC
↓	LPG	HOL	LIT	RDR
	LTN	NOL	PWL	DUK
	NOL	UFB	HIW	SEQ
	HIW	LIT	CLN	PTR
	LIT	LTN	UFB	SHL
	UFB	HIW	NOL	BRT

[b] Lines connect homogenous subsets.

[a] Morphometric means in thousandths of standard length.

sensu Hubbs and Crowe and included the Hiwassee, Little Tennessee, Little Pigeon, upper French Broad, Nolichucky, and Holston. The Clinch and Powell populations were considered by Hubbs and Crowe to be intergrades between the two subspecies.

The canonical graph of Figure II-10 (p. 73) showed two distinct clusters composed of populations HIW, LTN, LIT, LPG, UFB, and NOL on the negative side of canonical axis 1 and populations RDR, HAR, STN, CFR, RNG, LSF, CUM, DUK, BRT, SHL, ELK, PTR, and SEQ to the positive side of canonical axis 1. Three populations, HOL, CLN, and PWL, formed a transformation series between the two large clusters. The negative cluster was formed by populations representing Hybopsis insignis eristigma sensu Hubbs and Crowe while the positive cluster populations were H. i. insignis. Populations HOL, CLN, and PWL correspond to possible intergrades between the two subspecific taxa.

Based on PCA of morphological variables, populations assort into two groups (Figure II-12). Populations from the western and northern part of the species range comprised one group and included RDR, HAR, STN, CFR, RNG, CRC, LSF, BRT, DUK, SHL, ELK, PTR, and SEQ while eastern populations form group two and included HIW, LTN, LIT, LPG, PIG, UFB, NOL, HOL, and CLN. The Powell River population was intermediate in form between the two groups.

Additional evidence of the intermediacy of the Powell population was indicated by results of the Gabriel multiple-comparison test (Table II-16). Two groups were defined by multiple comparison of upper lip width and upper lip length means. Based on upper lip length, the Powell population assorted with Hybopsis insignis

eristigma populations but based on upper lip length, the Powell population assorted with *H. i. insignis* populations.

Two hypotheses are available to explain the observed variation between the groups of populations. The first hypothesis recognizes the presence of a single polytypic species with subspecies represented by the eastern and western groups and a zone of intergradation in the Powell, Clinch, and Holston drainages. The other hypothesis recognizes the eastern and western groups as discrete evolutionary species with the Powell-Clinch-Holston populations representing a zone of hybridization. The polytypic species hypothesis is most acceptable based on two factors. First, if two species are involved, hybrid populations are expected to possess members expressing both parental phenotypes as well as the intermediate hybrid phenotype. Examination of the Powell-Clinch-Holston populations by canonical graphs and comparison of variables among individuals show the presence of intermediate forms only. Second, hybrid zones are usually quite narrow (Wiley, 1981), whereas, zones of intergradation are geographically broader. The Powell-Clinch-Holston populations occupy a relatively broad portion of the geographic range of this taxon. The historical range of the species and subspecies is shown in Figure II-13.

There is reason to argue the classification of the Holston population as intergrades due to the morphological similarity to *eristigma* populations (Figures II-10, p. 73; II-11, p. 76; and II-12). Comparison of generalized distances between group centroids (Table II-17) showed the Holston population most similar to the Little Pigeon (an *eristigma*) and Clinch (intergrade) populations. Holston was also more

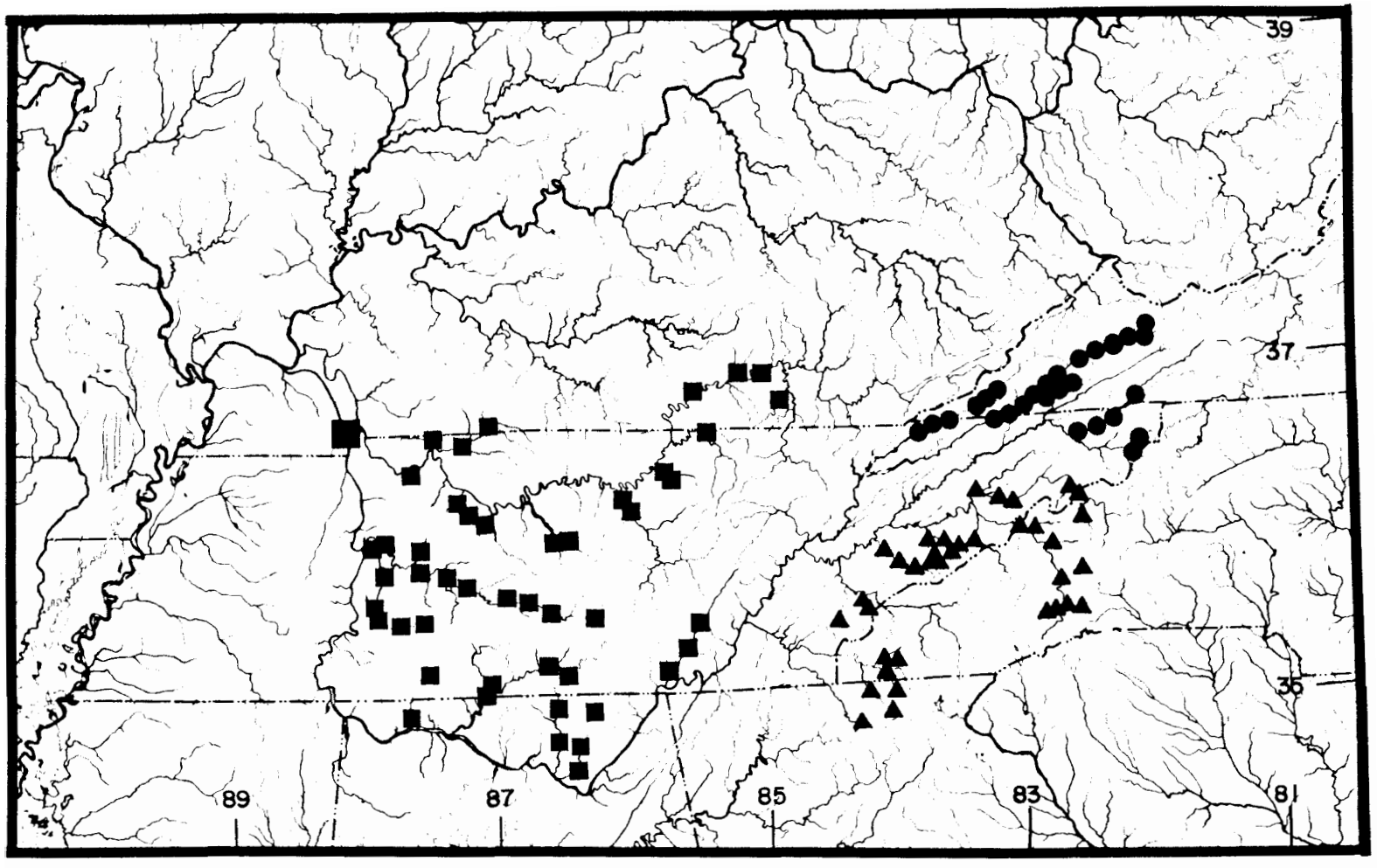


Figure II-13. Distribution of Hybopsis insignis. Squares represent H. i. insignis, triangles represent H. insignis eristigma, and circles represent intergrades.

Table II-17. Generalized Distances among Powell, Clinch, and Holston Populations of *Hybopsis insignis*.

Population	Generalized Distance		
	PWL	CLN	HOL
RDR	5.708	5.794	5.802
HAR	5.353	5.453	6.491
STN	6.148	5.809	6.496
CFR	5.811	5.489	5.519
RNG	6.155	6.063	6.306
CRC	5.464	6.543	6.254
LSF	5.521	5.866	6.539
BRT	5.997	6.731	6.486
DUK	5.884	6.265	6.106
SHL	5.140	6.042	5.715
ELK	5.361	5.768	6.037
PTR	5.775	6.263	6.174
SEQ	5.328	5.831	6.018
PWL	0.000	3.351	4.012
CLN	3.351	0.000	2.781
HOL	4.012	2.781	0.000
HIW	5.685	3.974	3.732
LTN	6.162	5.043	4.916
LIT	4.935	4.180	3.401
LPG	4.840	3.600	2.769
UFB	5.622	3.628	3.885
NOL	7.426	5.491	4.788

similar to the Hiwassee, Little, and upper French Broad (all eristigma) populations than the Powell intergrade population. Alternatively, the Powell population, considered the most intermediate in form between insignis and eristigma, was more similar to the Clinch and Holston than any other populations and Clinch shared closer similarity with the Powell and Holston than other populations.

Geisser classification was performed to analyze affinities of individuals and populations. Geisser classifcation probabilities correctly placed 83% of individuals (421 of 510) in their a priori designated population. All insignis specimens (n = 226) were classified within the 13 insignis populations. Only one of 218 specimens was classified outside the seven a priori eristigma populations. For the 80 specimens of the three putative intergrade populations, 65 were classified to the correct population, seven others classified within Clinch-Powell-Holston, six to eristigma populations, and two to insignis populations. Interestingly, two Holston specimens assorted with the Powell population but none with Clinch. Four Holston specimens and one each from Powell and Clinch fell within eristigma populations. Single specimens from the Powell and Clinch populations were most similar to insignis populations.

Phenotype of a species is genetically restricted to a range of form but expression of this form is influenced by environmental and ecological factors (Barlow, 1961; Endler, 1982; Snelson, 1972; and others). Whether the two forms of Hybopsis insignis are ecophenotypic variants or genetic variants is impossible to discern with absolute

certainty. My opinion leans toward genetic variants based on the nature of the key character for discrimination, upper lip width.

Table II-18 summarizes morphometric means for the combined populations of H. i. insignis, the intergrade populations, and H. insignis eristigma. The intergrades were more similar to the nominate subspecies in variables of length such as PRL, PDL, CPL, and HDL, but favor H. i. eristigma in descriptors of body robustness such as BDD, CPD, and ISW. Intergrades were more like eristigma in the width of the upper lip, a key character in distinguishing the subspecies. Intergrades were intermediate between the subspecies in the characters ULL, GPW, AFL, P1L, P2L, and BWP.

Hubbs and Crowe (1956) differentiated the two subspecific taxa based on the characters upper lip width and jaw length. They described insignis as having the upper lip scarcely expanded on the mid-line and jaw length which usually was 3.7-4.0 in head length. On the other hand, eristigma possessed an upper lip notably expanded on the midline and a larger mouth in which the upper lip was usually 3.2-3.4 in head length.

Results of this analysis indicate that upper lip width was, perhaps, the best discriminator of the subspecific taxa (Tables II-16, p. 81; and II-18). Hybopsis insignis eristigma had a much thickened upper lip that averaged >20 TSL for all populations while the insignis populations had a thin upper lip averaging <16 TSL. Upper lip length was also a good discriminator as insignis averaged <63 TSL/population and eristigma populations averaged >68 TSL. Additionally, eristigma was a more robust form with a deeper caudal peduncle, greater body

Table II-18. Variable Means and Standard Deviations for Hybopsis i. insignis, Intergrades, and H. insignis eristigma.

Variable	insignis Mean (SD)	Intergrades Mean (SD)	eristigma Mean (SD)
		Morphometrics	
PRL	494 (17)	506 (15)	514 (14)
PDL	531 (15)	528 (15)	519 (22)
CPL	219 (13)	216 (15)	214 (13)
HDL	254 (9)	263 (10)	263 (8)
SNL	100 (6)	104 (6)	104 (7)
ULL	60 (4)	70 (6)	73 (5)
GPW	52 (5)	59 (6)	63 (5)
IOW	46 (5)	44 (5)	46 (5)
ORW	78 (5)	77 (4)	77 (4)
BDD	186 (11)	205 (11)	203 (15)
CPD	77 (4)	89 (4)	87 (5)
ISW	73 (10)	92 (12)	87 (11)
DFL	206 (13)	211 (11)	210 (11)
AFL	173 (13)	182 (12)	190 (17)
P1L	203 (13)	215 (14)	227 (18)
P2L	147 (10)	154 (9)	163 (15)
POL	89 (6)	99 (9)	98 (6)
ULW	13 (2)	21 (3)	22 (3)
BWP	145 (9)	154 (13)	157 (11)
		Meristics	
LLS	42.5 (1.8)	40.4 (1.5)	39.7 (1.5)
ALL	6.9 (0.4)	6.9 (0.4)	6.7 (0.5)
BLL	6.2 (0.5)	6.1 (0.5)	6.0 (0.5)
CRS	30.9 (1.4)	29.4 (1.3)	29.1 (1.3)
CPS	15.7 (0.7)	15.9 (0.4)	15.8 (0.5)
PDS	17.5 (1.1)	17.3 (1.0)	17.4 (1.0)
PBS	75.1(12.9)	76.0(13.9)	75.6(12.4)
LP1	16.1 (0.8)	16.1 (0.8)	16.0 (0.8)
LP2	8.0 (0.3)	7.9 (0.5)	7.9 (0.3)
ANR	7.0 (0.1)	7.0 (0.1)	7.0 (0.1)
LTB	7.5 (1.0)	8.4 (1.3)	7.6 (1.1)
DBL	7.7 (1.0)	7.7 (1.2)	7.5 (1.2)

depth (BDD) and a wider body at the pelvic fins than insignis. Also, eristigma possessed longer pectoral, pelvic, and anal fins than insignis, especially in males. Males of the Nolichucky and upper French Broad populations possessed exaggerated anal fins that were sickle shaped and often had a lower lobe of the caudal fin that was much longer than the upper lobe (Figure II-14). Hybopsis i. insignis tended to be shorter predorsally and longer postdorsally than eristigma giving them a somewhat humped appearance (Figure II-14).

In summary, multivariate analyses revealed two morphotypes within Hybopsis insignis. These morphotypes are accorded subspecific status as H. i. insignis and H. insignis eristigma based on intermediacy of the Powell, Clinch, and Holston River populations. Figure II-13 shows distribution of these taxa.

Zoogeographic evidence appears to support these conclusions. Several taxa appear endemic or virtually endemic to headwaters of the Tennessee River in the Blue Ridge physiographic province (Starnes and Etnier, 1986). These taxa include Hybopsis insignis eristigma, Phenacobius crassilabrum, Etheostoma chlorobranchium, E. swannanoa, E. blennioides gutselli, and Phoxinus oreas, among others. Bogan and Parmalee (1983) found a similar distribution in the unionid mussel Epioblasma torulosa with E. torulosa gubernaculum inhabiting the headwaters of the Tennessee River and E. t. torulosa found in the lower reaches of the Tennessee River. The gubernaculum form graded into the torulosa form at about Knoxville (Ortmann, 1920 and 1925).

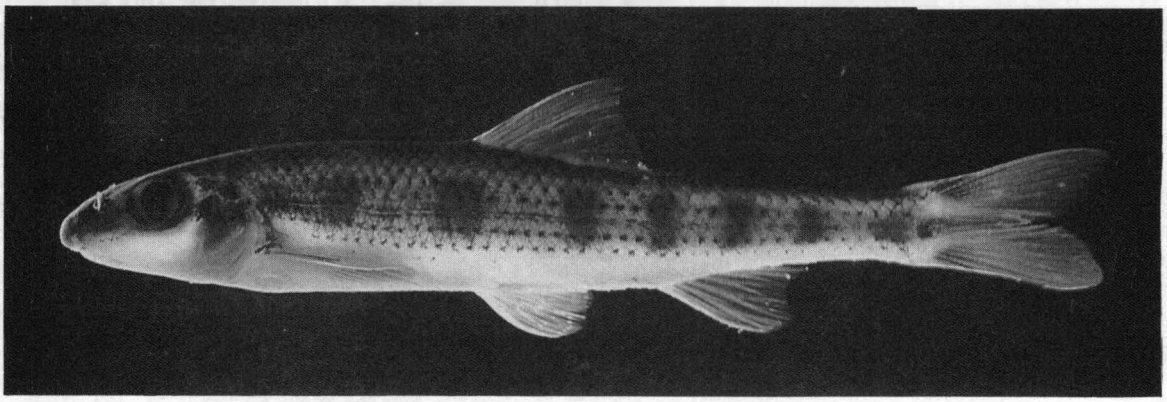
Starnes and Etnier (1986) hypothesize that these cold-adapted taxa differentiated during glacial maxima, then in postglacial times,

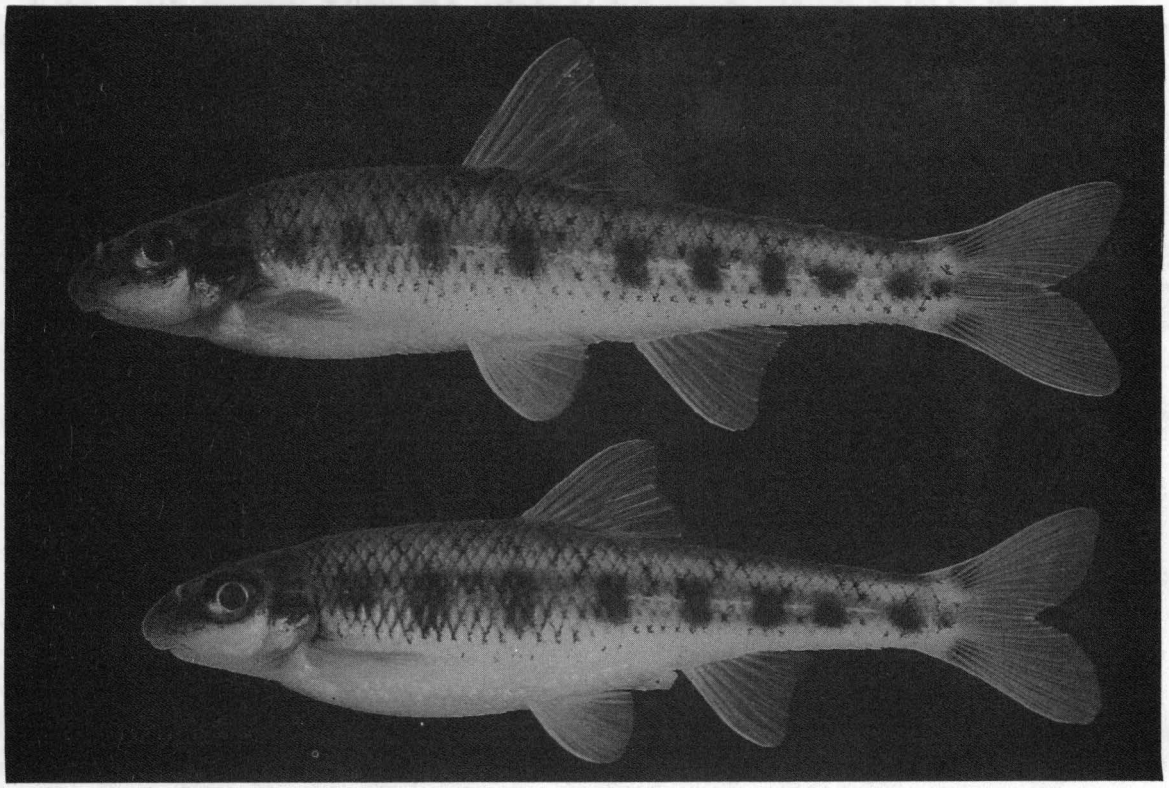
Figure II-14. Photographs of Hybopsis insignis.

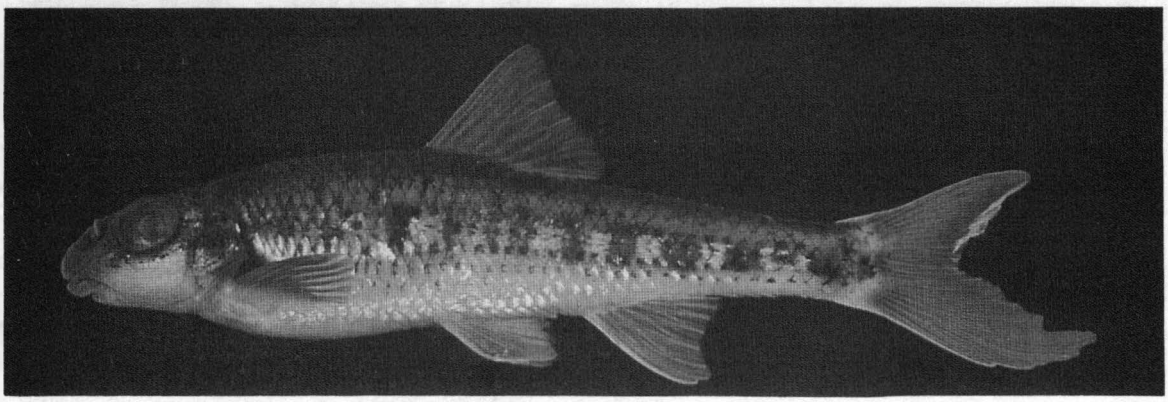
Figure II-14 A. Hybopsis insignis insignis - Blotched chub. TN, Perry Co. Buffalo River. 73.3mm SL.

Figure II-14 B. Hybopsis insignis eristigma - Blotched chub. Tn, Blount Co. Little River. Upper: 60.2mm SL male. Lower: 54.5 mm SL female.

Figure II-14 C. Hybopsis insignis eristigma - Blotched chub. NC, Henderson Co. 64mm SL.







retreated upstream following preferred temperatures to higher altitudes. With respect to Hybopsis insignis, the insignis form may have evolved in the lower Tennessee River system while the eristigma form evolved in the upper Tennessee River. During postglacial warming, the insignis form may have dispersed upstream via the main river before encountering the remnant populations of eristigma in the Powell-Clinch-Holston region. Subsequent climatic and/or ecological changes apparently eliminated this species and many others from the mainstream and western tributaries of the upper Tennessee River. The Powell-Clinch-Holston apparently has maintained ecological conditions similar to those during the time of secondary contact. The upper Clinch and upper Powell rivers are a well known refugia for rare unionid mussels such as Quadrula intermedia, Q. sparsa, Lexingtonia dollabelloides, Lemiox rimosus, Fusconaia cuneolus, F. cor, and several species of Epioblasma. Additionally, the Powell-Clinch-Holston system is the known historical range of Hybopsis cahni.

Synonomy

Hybopsis dissimilis (Kirtland). Jordan, 1889:355-356 (comparison with H. watauga); Jordan and Evermann, 1896:315, 318 (in key; description; range); Smith, 1907:102-103 (description; distribution NC); Evermann and Hildebrand, 1916:445 (distribution E. TN); Evermann, 1918:318, 319, 326, 347, 367 (distribution TN and KY; literature review); Fowler, 1922:24 (Paint Rock R., AL).

Hybopsis watauga Jordan and Evermann. Kirsch, 1893:262 (Caney Fork R., TN); Smith, 1907:102 (possible occurrence in NC); Evermann, 1918:329, 347, 367 (literature review).

Hybopsis insignis Hubbs and Crowe, 1956. Original description, subspecies, distribution, in key; Moore, 1968:69-70 (in key, distribution); Smith-Vaniz, 1968:29, 41, 130, 160 (distribution AL; partial synonomy; figure); Reno, 1969a:68 (nomenclatorial history); Reno, 1969b:739, 746-753, 762, 765-766, 770 (cephalic lateral-line system; biology; figure); Dahlberg and Scott, 1971:16, 59 (checklist GA; annotated list); Comiskey and Etnier, 1972:141, 144 (distribution Big S. Fork Cumberland R., TN and KY, zoogeography); TVA, 1973:Table 5 (distribution, standing crop, frequency occurrence, Buffalo R., TN); Hitch and Etnier, 1974:83 (distribution Nottely River, GA); Menhinnick, et al., 1974:30 (distribution and status NC); TVA, 1975:Tables 5-7 (distribution, standing crop, frequency occurrence Duck R. system, TN); Ramsey, 1976:54, 60 (distribution and status AL); Burr, 1980:64 (distribution KY); Harris, 1980b:188 (systematics; distribution; habitat; biology); Branson, et al., 1981:81 (distribution and status KY); Branson and Schuster, 1982:61, 63, 64 (distribution Little S. Fork Cumberland R., KY); Starnes and Starnes, 1985: 333 (associated with Noturus eleutherus).

Hybopsis insignis insignis. Hubbs and Crowe, 1956:2-5, 7-8 (original description; in key; distribution); Jenkins and Lachner, 1971:4, 6-7 (scale radii; vertebral counts); Jenkins, et al., 1972:49 (habitat; distribution; zoogeography); Stauffer, et al., 1982:30 (checklist central and northern Appalachian Mts.).

Hybopsis insignis eristigma. Hubbs and Crowe, 1956:2-5, 7-8 (original description; in key; distribution); Jenkins and Lachner, 1971:6-7 (scale radii; vertebral counts); Jenkins, et al., 1972:49, 97 (habitat; distribution; zoogeography); Stauffer, et al., 1982:30 (checklist central and northern Appalachian Mts).

Hybopsis (Erimystax) insignis. Davis and Miller, 1967 (distribution; brain morphology; sensory structures; biology).

Diagnosis

Hybopsis insignis differs from H. cahni and H. x-punctata in having mid-lateral and mid-dorsal dark blotches. It differs from H. dissimilis and H. harryi in having quadrate mid-lateral blotches, larger scales (usually 37-46 in lateral line), and fewer total vertebrae (37-40). Hybopsis disssimilis and H. harryi possess oval mid-lateral blotches, usually 43-51 lateral-line scales, and 40-43 total vertebrae.

Description

The body is elongate, loaf-shaped in anterior cross section, and tapered from the pelvics posteriad to the caudal. It is slightly compressed laterally, posterior of the dorsal fin. The snout is rounded and moderately overhangs the subterminal, ventral mouth. The eyes are medium size, located dorsolaterally, and directed somewhat posteriad. The terminal labial barbels are moderately to well developed. Pharyngeal teeth are 4-4. Within the mid-lateral band, 5-12 distinctive quadrate, columnar to square mid-lateral blotches are present. The mid-dorsal line has 3-11 darkened dashes. Randomly

distributed dorsolateral spots appear as x- or comma-shaped melanophores on the scale periphery. No interradial fin pigment is present. The dorsal profile from the dorsal insert to the snout is slightly to moderately curved.

External morphology. Morphometry: Fin shape and placement as well as general body physiognamy are illustrated in Figure II-14. Proportional data for morphometric variables are presented in Table II-19.

Meristics: Table II-19 summarizes countable characters with mean, range, and standard deviation, and Table II-20 gives meristic distributions.

Sexual dimorphism: Results of the t-test to summarize sexually dimorphic variables are presented in Table II-21. Variables with levels of probablility $P<0.05$ are considered significantly different. Females are shorter predorsally but males have longer post dorsal and caudal peduncle lengths. Females possess significantly longer head and snout lengths and larger mouths. Dorsal, anal, and pelvic fins are significantly longer in males.

Nuptial tuberculation: The following is a composite drawn from examination of 72 mature males from throughout the range of the species. Cephalic tubercles generally are sparse or absent pre- and postorbitally and dorsally near the mid-occipital. Heaviest tubercle concentrations occur above the eyes and in the opercular region. Medium, evenly spaced tubercles occur on sides of the head from the opercles anteriad to the maxillary sulcus extending onto the snout.

Table II-19. Range, Mean, and Standard Deviation of Variables of *Hybopsis insignis*.

Variable	N	Range[a]	Mean[a]	(SD)[a]
		Morphometrics		
STL	577	41.30-86.00	59.28	(7.67)
PRL	577	450-550	502	(18.7)
PDL	577	305-571	528	(18.8)
CPL	577	152-271	218	(14.1)
HDL	577	228-296	258	(9.9)
SNL	577	67-120	102	(6.5)
ULL	577	47-88	66	(7.5)
GPW	577	36-77	57	(6.9)
IOW	577	30-60	45	(5.0)
ORW	577	66-96	78	(4.8)
BDD	577	153-242	194	(15.4)
CPD	577	65-99	82	(6.6)
ISW	517	52-119	81	(13.3)
DFL	576	171-238	208	(11.1)
AFL	576	123-288	180	(15.8)
P1L	577	145-295	213	(18.3)
P2L	576	106-240	153	(13.5)
POL	577	68-126	94	(8.0)
ULW	550	6-36	18	(5.1)
BWP	529	120-184	151	(11.5)
		Meristics		
LLS	576	36-47	41.2	(2.1)
ALL	576	5-8	6.9	(0.4)
BLL	576	5-7	6.1	(0.5)
CRS	576	26-36	30.0	(1.6)
CPS	577	12-17	15.8	(0.6)
PDS	575	14-21	17.4	(1.1)
PBS	576	50-99	75.8	(13.1)
LP1	577	13-19	16.1	(0.8)
LP2	576	5-9	8.0	(0.3)
ANR	576	6-8	7.0	(0.1)
LTB	566	5-12	7.7	(1.1)
DBL	558	3-11	7.6	(1.1)

[a] Range, mean, and standard deviation of morphometric variables (except standard length) are in thousandths of standard length.

Table II-20. Frequency Distribution of Meristic Variables of Hybopsis insignis.

Frequency Distribution

Lateral Line Scales

36	37	38	39	40	41	42	43	44	45	46	47
2	11	37	75	91	102	108	74	39	19	11	7

Scales Above Lateral Line

5	6	7	8
1	95	468	12

Scales Below Lateral Line

5	6	7
35	443	98

Circumbody Scales

26	27	28	29	30	31	32	33	34	35	36
8	21	67	112	168	87	82	21	8	1	1

Circumpeduncle Scales

12	13	14	15	16	17
1	7	19	75	472	3

Predorsal Scales

14	15	16	17	18	19	20	21
1	20	89	211	166	74	11	3

Per Cent Ventral Scalation

40	45	50	55	60	65	70	75	80	85	90	95	100
2	6	29	7	81	11	76	39	153	22	127	21	1

Table II-21. Sexually Dimorphic Variables of Hybopsis insignis.

Variable	Sex(N)	Range	Mean (SD)	t-value	P
PRL[a]	M(200)	450-533	492.4 (17.09)	3.5865	<.001
	F(181)	459-550	499.2 (19.95)		
PDL	M(200)	491-571	535.7 (14.61)	5.5055	<.001
	F(181)	305-568	524.8 (23.50)		
CPL	M(200)	195-261	222.9 (12.65)	4.7138	<.001
	F(181)	168-271	216.4 (14.22)		
HDL	M(200)	228-283	254.5 (9.64)	2.6171	<.01
	F(181)	232-282	257.2 (10.07)		
SNL	M(200)	81-116	101.5 (6.14)	3.4042	<.001
	F(181)	82-120	103.6 (6.20)		
ULL	M(200)	47-81	64.6 (7.66)	3.8724	<.001
	F(181)	51-88	67.6 (7.63)		
GPW	M(200)	36-74	55.7 (6.95)	3.4388	<.001
	F(181)	41-77	58.1 (7.11)		
BDD	M(200)	159-224	190.1 (13.67)	3.8033	<.001
	F(181)	160-242	196.5 (18.69)		
DFL	M(200)	180-238	210.6 (10.88)	3.7288	<.001
	F(181)	171-236	206.3 (11.49)		
AFL	M(200)	139-244	182.0 (15.10)	2.0521	<.05
	F(181)	123-242	178.7 (15.76)		
P1L	M(200)	169-264	217.2 (17.47)	6.6283	<.001
	F(181)	145-277	205.3 (17.31)		
CPS	M(200)	12-17	15.7 (0.72)	2.2345	<.05
	F(181)	13-17	15.8 (0.54)		

[a]Range, mean, and standard deviation of morphometric variables are in thousandths of standard length.

The snout tip has poor tubercle development. Ventral cephalic tubercles are generally poorly developed.

The anterior dorsal and dorsolateral regions are tubercled with three to eight medium tubercles located peripherally on each scale and one to two tubercles on the scale centrum. Anterior ventral scales (below the lateral-line) normally are devoid of tubercles, except in the mid-pectoral region. Here, prominent single tubercles are displayed on the central periphery of each scale. Posterior dorsal and dorsolateral tubercles are fewer and smaller than the on anterior regions while ventrally, posterior to the pelvic fins, tubercles are more prominent in size and number.

Pectoral rays 1 through 9, 10, 11, or 12 have tubercles on the dorsal surface. Tubercles on the first ray are generally smaller and appear randomly distributed on the posterior field of the ray. Rays 2 through 6, 7, or 8 have one tubercle per segment on each branch of the primary ray meaning four rows are present distally on each ray. The remaining tubercled rays are restricted to the primary ray before branching. The ventral surface sometimes has poorly developed tubercles on rays 2 through 8, usually restricted to the primary ray.

Pelvic fins are tubercled dorsally on rays 1 or 2 through 4 or 5. Tubercles are small, distributed one per ray segment, and are best developed distally. Occasionally, tubercles occur ventrally on rays 2-4 but appear randomly distributed and do not form rows.

Anal fin tubercles are found on rays 1 or 2 through 4, 5, 6, or 7 and are best developed distally. Tubercles are small, usually one per

segment (occasionally two) and absent from the primary ray before branching.

Dorsal fin tubercles appear on rays 1 or 2 through 5, 6, 7, or 8 and are usually very small. Tubercles are distributed one per segment on the primary ray and secondary branches but do not extend to the distal margin of the ray.

The nuptial cheek pad was present on all mature males examined from early April until early July. Location and appearance are as described previously for Hybopsis dissimilis and by Branson (1962) and Jenkins and Burkhead (1984).

Sensory and trophic anatomy. Ranges and mean pore counts for each canal of the lateral-line system are taken from Reno, 1969b. From eight specimens of Hybopsis insignis, the following counts were obtained: infraorbital canal 11-13 (11.9); postocular commissure 2 (2.0); cephalic lateralis 3 (3.0); supraorbital canal 8-10 (9.6); supratemporal canal 5-6 (5.2); preoperculomandibular canal 7-9 (7.9).

Numbers of external and internal taste buds for five cephalic regions determined from serial sections are presented from the work of Davis and Miller (1967): tip of snout (14.1/0.0); anterior nasal rosette (29.6/3.3); posterior nasal rosette (12.8/5.4); posterior of retina (5.8/23.7); and anterior of cerebellum (5.7/27.9). Also, compound taste buds are present on the interradial membranes of the pectoral fins. Mean facial and optic lobe widths expressed as a per cent of total brain length are 17.0 and 27.4, respectively, for Hybopsis insignis (Davis and Miller, 1967).

Gill rakers: 4(2), 5(11), 6(10), 7(11), 8(3); dorsal rakers (3-4) short and acutely pointed; ventral rakers rudimentary, blunt or knobby. Etnier and Starnes (ms) give counts of 5-9.

Pharyngeal teeth are 4-4 in 36 specimens examined.

The intestinal tract is s-shaped and short to medium in length. Occasionally, an accessory loop protrudes from the anteriormost segment of the descending gut following the second 180 bend. Total intestinal length in 93 blotched chubs (SL 40.85-79.65 mm) ranges from 0.88 to 1.32 X SL (x = 1.03) (Harris, msD).

Other internal structures. The gas bladder is two chambered and smaller in size than in other species of Erimystax. Average total length of both chambers is 21.3% (19.0%-24.7%; n = 15) of SL. The anterior chamber mean length is 8.5% (6.9%-9.5%) of SL and the posterior chamber averages 12.8% (11.2%-15.2%) of SL.

Vertebral counts are summarized in Table II-10 (p. 44) and include all specimens of Lachner and Jenkins (1971). Total vertebrae: 37(2), 38(25), 39(47), 40(5); precaudal vertebrae: 19(41), 20(38), 21(1); caudal vertebrae: 18(7), 19(49), 20(23).

Coloration. Freshly captured specimens are olive to dark grey dorsally. A lateral band three scale rows wide is present with 5-12 conspicuous black blotches ranging from columnar to square to slightly rounded. The mid-lateral band extends from a small, inconspicuous basicaudal spot anteriad through the opercle and eye to terminus just posterior to the lachrymal groove. A distinctly paler region 1 1/2 scale rows wide occurs above the lateral band and is due to reduced background pigment. Darker background pigmentation resumes dorsally

and scale edges are lined with small melanophores giving a cross-hatched appearance. The mid-dorsal line has 3-11 conspicuous spots. Additional small spots and x-shaped markings occur on the dorsal and lateral surfaces, often manifested as four or five rows of spots along the lateral band. A dark bar is present on most individuals at the dorsal surface of the pectoral insert. Pigmentation rarely extends more than three rows below the lateral-line and the venter is creamy to white.

Cephalic background color is charcoal to tan. Distinct pale regions occur pre- and postorbitally. Dark bars due to the nasal rosettes occur between the nares. Some populations have dark speckling on the dorsum of the head. Below the orbits and the lachrymal groove, the head is immaculate.

Fin pigmentation: Pectoral rays 1 through 8, 9, 10, or 11 are pigmented but no interradial pigment is present. During spawning season, males have denser, darker concentrations of melanophores on the posterior side of each pigmented ray. Pelvic rays 1 or 2 through 3, 4, 5, or 6 usually are weakly pigmented medially. Anal rays 1 or 2 through 5 or 6 are weakly pigmented, with melanophores usually restricted to the basal half of the ray. Dorsal rays 1-7 and the first half of branched ray 8 are moderately to strongly pigmented but no interradial pigment is present.

E. *Hybopsis insignis insignis* Hubbs and Crowe, 1956

The holotype (UMMZ 157702) is a 59 mm standard length adult taken 22 October 1942 from the Tennessee River at the head of Blood River Island, Calloway County, KY.

Diagnosis

Hybopsis i. insignis is differentiated from *H. insignis eristigma* by its narrower ($\bar{x}$ = 13 TSL) and shorter upper lip ($\bar{x}$ = 60 TSL). Additionally, *H. insignis* has a longer postdorsal length ($\bar{x}$ = 531 TSL), and shorter fin lengths for the anal ($\bar{x}$ = 173 TSL), pectoral ($\bar{x}$ = 203 TSL), and pelvic ($\bar{x}$ = 147 TSL) fins. In *H. insignis eristigma*, the upper lip is expanded on anterior midline ($\bar{x}$ = 22 TSL) and is longer ($\bar{x}$ = 73 TSL). Also, postdorsal length is shorter ($\bar{x}$ = 519 TSL), and lengths for the anal ($\bar{x}$ = 190 TSL), pectoral ($\bar{x}$ = 227 TSL), and pelvic ($\bar{x}$ = 163 TSL) fins are longer than in *H. i. insignis*.

Description

The description is generally as for *Hybopsis insignis* with the following additions or exceptions. Morphometric and meristic variables are summarized in Tables II-18 and II-20. Fin placement and general body morphology are shown in Figure II-14 (p. 90). Mid-lateral blotches in *H. i. insignis* tend to be taller than wide giving the blotches a columnar appearance. Also, dorsolateral spotting is reduced which lends to the subspecies appearing paler than its Blue Ridge counterpart. The two lobes of the caudal fin are virtually equal in length in all populations. The dorsal profile from snout tip

to dorsal insert of many individuals appears relatively sharply angled due to the shorter predorsal distance.

F. Hybopsis insignis eristigma Hubbs and Crowe, 1956

The holotype of H. insignis eristigma is a 62 mm SL adult, UMMZ 129320 that was collected with two paratopotypes (UMMZ 177282) on 31 August 1937 from the West Prong of the Little Pigeon River at the TN Hwy 71 crossing 2.0 miles west of Pigeon Forge.

Diagnosis

See the diagnosis of Hybopsis i. insignis for comparison of the subspecies.

Description.

The description is generally as for Hybopsis insignis with the following additions or exceptions. Summations of morphometric and meristic variables are presented in Tables II-18 (p. 88) and II-20 (p. 97). Fin placement and morphology can be seen in Figure II-14 (p. 90).

Mid-lateral blotches tend to be relatively square in most specimens or with a slightly rounded appearance, especially posteriad, in some. Background pigmentation, dorsolateral spotting, and ventrolateral spotting are more dense and more numerous giving the subspecies a darker appearance than H. i. insignis. Many populations possess dark punctations on the dorsum of the head. The anal fin and lower lobe of the caudal fin are much elongated in some males of H. insignis eristigma (Figure II-14, p.90), especially in the upper French Broad population. Finally, the dorsal profile is more gently sloped from

snout tip to dorsal insert owing to relatively longer predorsal length.

G. Hybopsis x-punctata Hubbs and Crowe, 1956

Gravel chub

Analysis

Six hundred forty four Hybopsis x-punctata from 29 populations were examined during the course of this study. Complete data for 29 meristic and morphometric variables were obtained for 598 specimens from 27 populations and these were subjected to MDA. Tests of overall discrimination (= equality of group centroids) by MDA MANOVA indicated population centroids were not equal ($F = 7.28$; $P<0.001$).

The first five canonical variates from the meristic and morphometric data set accounted for 78.6% of total variation with variates 1 and 2 explaining 50% and 11%, respectively. Correlations between variables and the first three canonical variates are presented in Table II-22. CV1 was an expression of circumpeduncle scales primarily with lesser loadings for the variables circumferential scales, scales below lateral-line, and caudal peduncle depth. CV2 again had a high loading for circumpeduncle scales and had lower correlations with predorsal scales, upper lip width, orbit width, and caudal peduncle length. CV3 had high negative correlation with variables caudal peduncle length and post dorsal length.

From the total data set, two dimensional canonical graphs for 27 population centroids were constucted for canonical axes 1 versus 2, 2 versus 3, and 1 versus 3. The best discrimination in canonical space

Table II-22. Correlations between canonical variates and morphmometric + meristic variables of Hybopsis x-punctata.

Variable	Canonical Variate 1	Canonical Variate 2	Canonical Variate 3
PRL	0.097	0.156	-0.339
PDL	0.181	0.156	-0.479*
CPL	0.171	0.211	-0.605*
HDL	0.084	0.077	-0.311
SNL	0.039	0.065	-0.324
ULL	0.085	0.178	-0.321
GPW	0.102	0.167	-0.245
IOW	0.171	-0.019	-0.354
ORW	-0.014	0.204	-0.331
BDD	0.219	0.062	-0.304
CPD	0.256	0.029	-0.357
ISW	0.081	0.121	-0.198
DFL	0.218	0.033	-0.364
AFL	0.203	-0.021	-0.431
P1L	0.129	0.087	-0.326
P2L	0.177	0.029	-0.393
POL	0.171	0.076	-0.317
ULW	0.080	0.231	-0.092
BWP	0.117	0.097	-0.311
LLS	0.100	0.143	-0.265
ALL	0.208	-0.031	0.218
BLL	0.242	0.142	0.048
CRS	0.319*[a]	0.059	0.323
CPS	0.535*	0.426*	0.304
PDS	0.122	0.245*	-0.035
PBS	0.094	0.101	-0.067
LP1	0.034	-0.119	-0.112
LP2	0.003	-0.069	-0.061
ANR	0.026	-0.016	0.009

[a]The * indicates highly correlated variables.

is supplied by canonical axes 1 versus 2 (Figure II-15). Vectors for the variables CPS, PDS, CRS, LLS, and BLL were constructed with origin at the grand centroid and show relative contributions of raw and z-score variables to canonical discrimination. Group centroids with 95% confidence circles are illustrated in Figure II-16.

The first three canonical variates based on morphological variables explained 73% of total variation. CV1 expressed caudal peduncle depth while CV2 loaded heavily for caudal peduncle length and predorsal length.

Results of PCA using morphometric and meristic variables yielded essentially the same results as canonical analysis with high loadings on scale variables.

PCA of morphological variables showed PC1-3 account for 84.0%, 4.0%, and 2.3%, respectively, for a total of 90%. Table II-23 gives the loadings of variables on PC1-3. PC1 was a general size component, PC2 had a high positive loading for upper lip width, and PC3 contrasted the high negative loading of orbit width with a similar positive loading for upper lip width. Plots of individuals on PC1 versus PC2 are presented as population polygons in Figure II-17. Shearing of principal components added little to discrimination.

Population means for variables with high correlations or loadings in the multivariate treatments are listed in Table II-24. Results of the Gabriel multiple-comparison test of population means for significant variables are presented in Table II-25.

Figure II-15. Population centroids and variable vectors of Hybopsis x-punctata in canonical space determined from the meristic + morphometric data set.

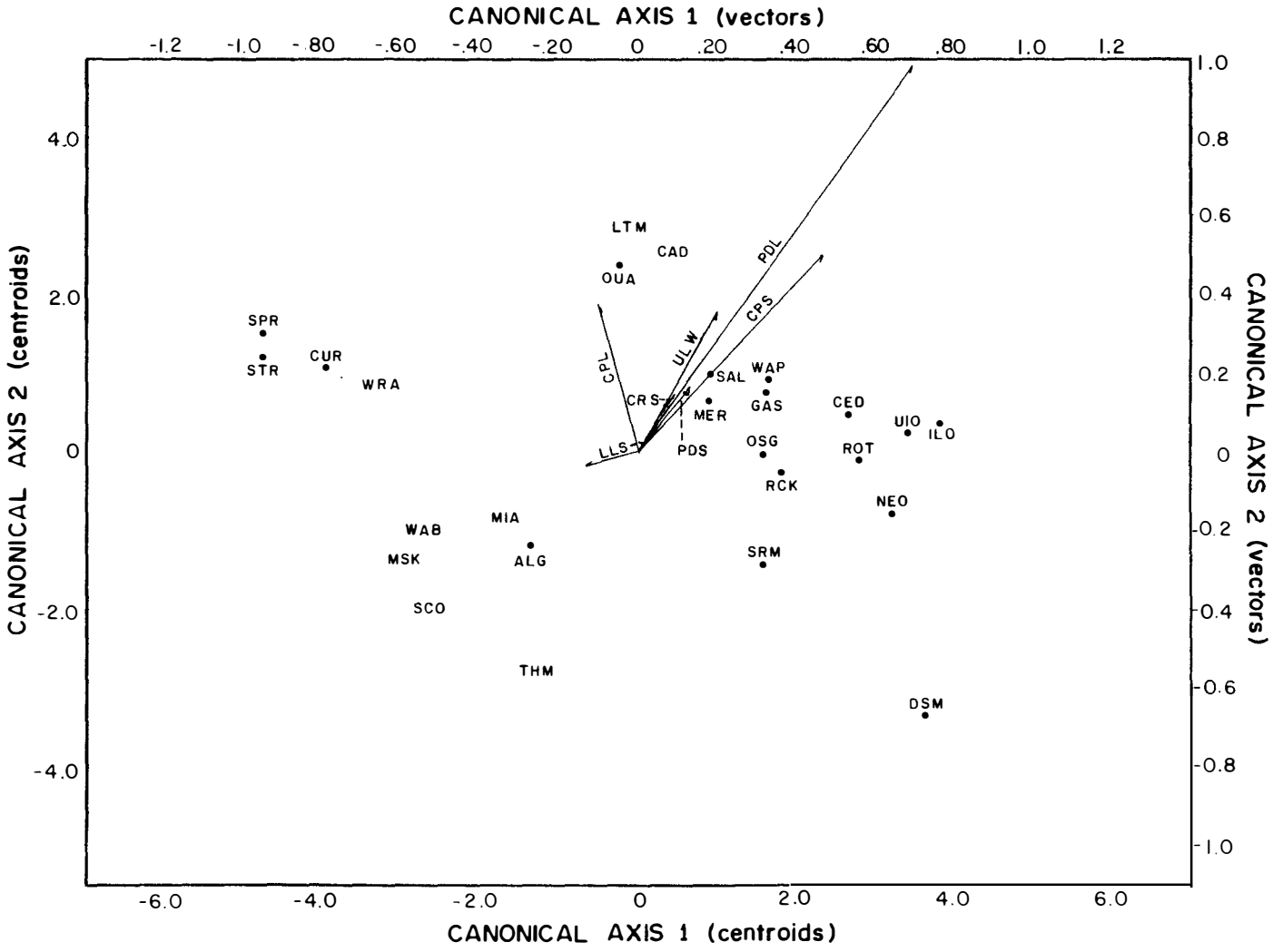

CANONICAL AXIS 1 (vectors)
-1.2
-1.0
-.80
-.60
-.40
-.20
0
.20
.40
.60
.80
1.0
1.2
CANONICAL AXIS 2 (centroids)
4.0
2.0
0
-2.0
-4.0
CANONICAL AXIS 2 (vectors)
1.0
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1.0
-6.0
-4.0
-2.0
0
2.0
4.0
6.0
CANONICAL AXIS 1 (centroids)
LTM
CAD
OUA
PDL
CPS
ULW
CPL
CRS
LLS
PDS
SAL
WAP
GAS
MER
CED
UIO
ILO
OSG
ROT
RCK
NEO
SRM
SPR
STR
CUR
WRA
WAB
MSK
MIA
ALG
SCO
THM
DSM

Figure II-16. Population centroids and 95% confidence circles of Hybopsis x-punctata in canonical space determined from the meristic + morphometric data set.

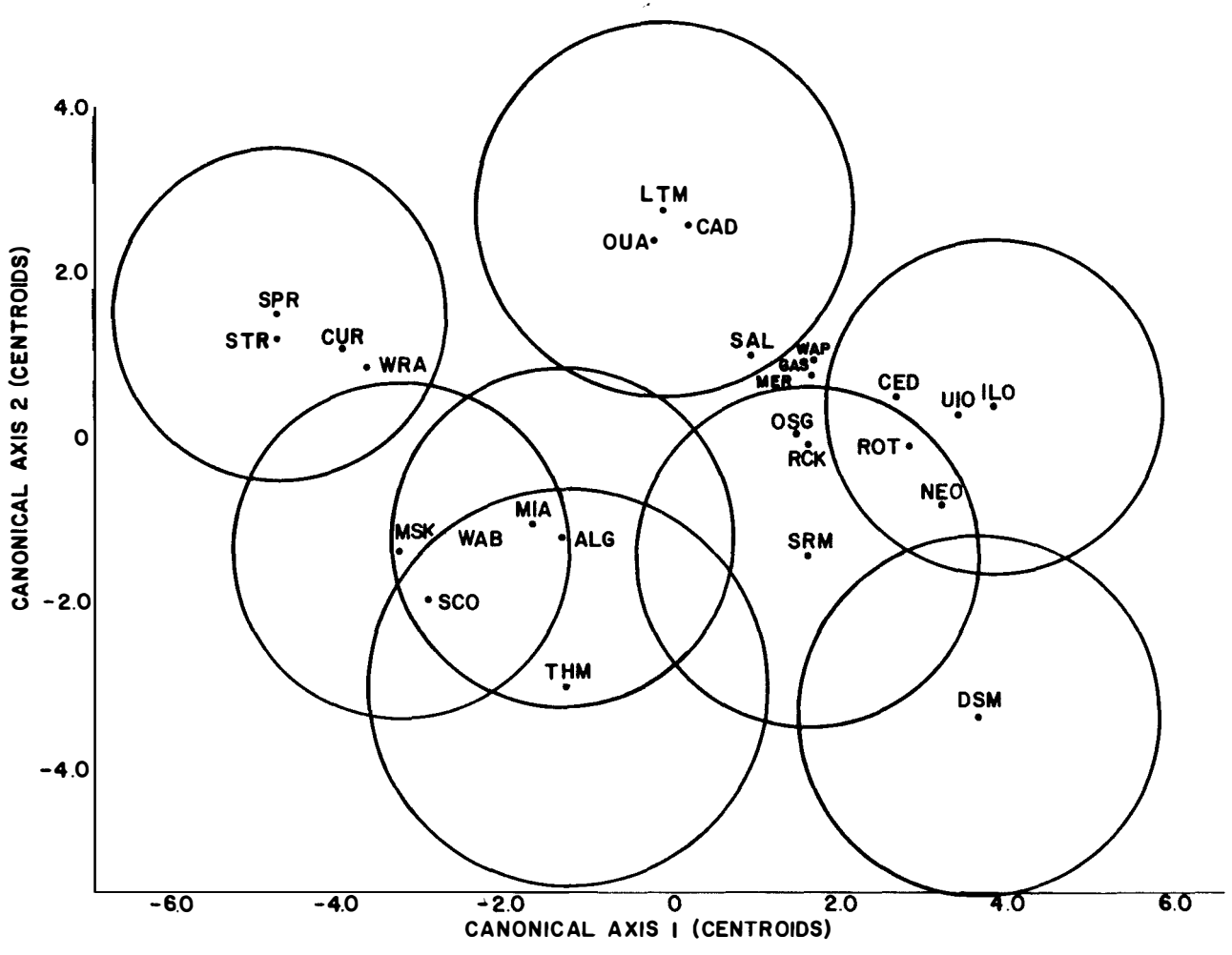

4.0
2.0
0
-2.0
-4.0
CANONICAL AXIS 2 (CENTROIDS)
-6.0
-4.0
-2.0
0
2.0
4.0
6.0
CANONICAL AXIS 1 (CENTROIDS)
LTM
CAD
OUA
SPR
STR
CUR
WRA
SAL
WAP
GAS
MER
CED
UIO
ILO
OSG
RCK
ROT
NEO
MIA
MSK
WAB
ALG
SRM
SCO
THM
DSM

Table II-23. Loadings of Morphometric Variables on Principal Components of Hybopsis x-punctata.

Variable	Principal Component 1	Principal Component 2	Principal Component 3
PRL	0.242	0.060	-0.244
PDL	0.241	-0.123	-0.031
CPL	0.225	-0.135	-0.043
HDL	0.243	0.081	-0.229
SNL	0.236	0.183	-0.213
ULL	0.230	0.171	-0.113
GPW	0.230	0.196	0.012
IOW	0.223	-0.213	-0.003
ORW	0.219	0.218	-0.560*
BDD	0.236	-0.065	0.159
CPD	0.235	-0.163	0.214
ISW	0.213	0.221	0.051
DFL	0.235	-0.269	0.151
AFL	0.225	-0.342	0.199
P1L	0.231	-0.132	0.084
P2L	0.235	-0.235	0.122
POL	0.236	-0.020	-0.032
ULW	0.174	0.641*[a]	0.595*
BWP	0.241	0.098	0.022

[a]The * indicates highly correlated variables.

Figure II-17. Population polygons of Hybopsis x-punctata on principal component axes determined from the morphometric + meristic data set.

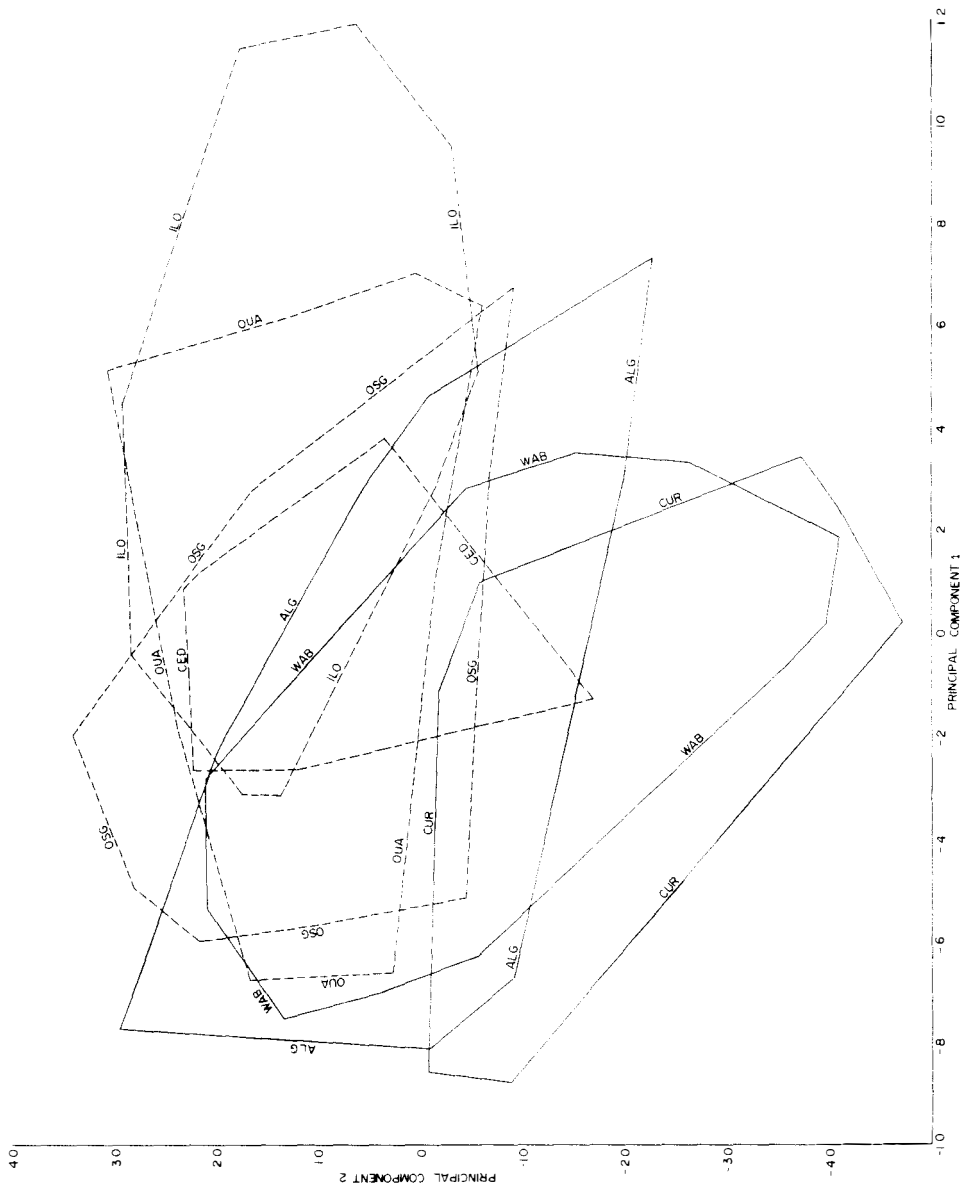

PRINCIPAL COMPONENT 2
PRINCIPAL COMPONENT 1
ILO
QUA
OSG
CED
ALG
WAB
CUR

Table II-24. Population Means for Variables of Hybopsis x-punctata with High Correlations in Multivariate Analyses.

Population	CPS	CRS	PDS	CPL[a]	CPD	PDL	ORW	ULW
ALG	13.6	30.6	16.5	218	84	530	76	10
MUS	12.6	29.6	15.8	201	84	522	79	12
SCO	12.7	29.6	15.8	200	89	516	80	13
MIA	12.0	30.3	17.0	200	89	516	76	11
GRK	12.0	28.0	15.0	186	92	510	73	--
WAB	13.0	29.8	16.1	198	85	510	78	11
THM	12.8	29.4	16.1	207	87	518	72	12
ROT	16.0	29.9	16.6	201	91	533	71	12
UIO	15.6	29.9	16.9	223	89	543	70	12
WAP	16.2	31.2	17.0	209	85	524	78	11
RCK	15.6	30.1	16.1	200	88	527	71	13
CED	15.9	30.8	16.8	227	90	549	71	12
DSM	15.8	30.0	15.6	197	102	522	75	12
SRM	15.6	30.5	15.9	198	95	522	77	12
GAS	15.9	30.4	17.2	203	87	524	73	11
OSG	15.7	30.8	16.7	205	90	529	75	12
MER	15.8	30.6	16.9	206	86	527	74	12
WRA	12.7	28.2	16.2	206	79	522	81	12
STR	12.9	27.7	17.3	207	81	516	81	13
SPR	13.0	28.2	15.7	202	80	509	83	13
CUR	13.2	28.2	16.6	202	82	508	85	14
ILO	15.7	32.5	17.4	209	92	538	70	13
NEO	15.8	32.8	17.0	204	95	534	71	13
OUA	15.9	31.9	17.4	211	85	522	77	14
LMR	16.0	32.5	17.8	209	87	513	80	15
CAD	15.9	32.3	17.4	210	84	526	77	15
SAL	16.0	29.8	16.5	189	86	513	74	12
WRI	12.6	29.4	15.9	205	80	524	76	13
TRI	16.0	30.8	16.3	217	86	541	68	14

[a] Morphometric means are in thousandths of standard length.

Table II-25. Gabriel Multiple-Comparison of Hybopsis x-punctata Population Means.

Variable	CPS	ULW	CPD	CRS
F-value	62.5	31.8	31.5	27.8
Low value	MIA [a]	UIO	WRA	STR
	WRI	ILO	WRI	SPR
	MUS	CED	SPR	CUR
	SCO	ROT	STR	WRA
	WRA	NEO	CUR	WRI
↑	THM	RCK	ALG	THM
	STR	THM	CAD	MUS
P	WAB	GAS	MUS	SCO
O	SPR	MER	WAP	WAB
P	CUR	OSG	WAB	ROT
U	ALG	WRI	OUA	UIO
L	UIO	MIA	MER	RCK
A	RCK	ALG	THM	MIA
T	SRM	OUA	LMR	GAS
I	OSG	SRM	GAS	SRM
O	ILO	CAD	RCK	ALG
N	MER	WAP	SCO	MER
S	NEO	WAB	UIO	CED
↓	CAD	MUS	OSG	OSG
	OUA	SCO	CED	WAP
	GAS	LMR	ROT	OUA
	CED	STR	ILO	CAD
	LMR	WRA	NEO	ILO
	ROT	SPR	SRM	LMR
	WAP	CUR	DSM	NEO

[a]The lines connect homogenous subsets.

Discussion

Hubbs and Crowe (1956) described Hybopsis x-punctata as a polytypic species composed of the nominal subspecies and H. x-punctata trautmani. Hybopsis x. x-punctata was differentiated as having a blunt, straight, short snout and deeper caudal peduncle with distribution defined as northwestern Arkansas, northeastern Oklahoma, southeastern Kansas, southern Missouri and scattered populations in the Mississippi drainage of Illinois, Wisconsin, Iowa, and southeastern Minnesota. Hybopsis x-punctata trautmani was described as having a pointed, down-curved, long snout and slender caudal peduncle and occurring in the Ohio River basin of Illinois, Indiana, Ohio, New York, Pennsylvania, and Kentucky with isolated populations in the Thames River, Ontario and the Lake Erie drainage of northern Ohio.

Examination of the canonical graphs (Figures II-15, p. 108; II-16, p. 110) indicated division of the 27 populations into two groups differentiated, primarily, on the basis of caudal peduncle scales, scales above and below the lateral-line, and lateral-line scales. The two groups roughly correspond in geographic distribution to the subspecies of Hubbs and Crowe with the group on the negative side of canonical axis 1 representing H. x-punctata trautmani and the positive canonical axis 1 group representing H. x. x-punctata. Examination of Table II-24 shows Ohio River and White River (AR and MO) drainage populations with modal caudal peduncle scale counts of 12 or 13. Hereafter, the Current, Strawberry, Spring, and main channel White River populations (AR and MO) will be referred to as the Ozarkian populations (after Thornbury, 1965) to avoid confusion with the White

River, IN population. Ouachita River, Neosho River, Missouri River and upper Mississippi River drainage populations possess 15 or 16 scales around the peduncle. Other variables are less definitive in separating the taxa. Certain trends are observable, such as the tendency of Ohio and Ozarkian populations to possess a more slender caudal peduncle, shorter postdorsal length, and larger eye (Table II-24) but certainly do not withstand rigorous population by population statistical analysis.

Geisser classification probabilities using morphometric and meristic variables correctly assigned 77% of individuals (463 of 598) to their a priori populations. Of the 227 specimens from the Ozark, Ohio, and Thames populations, 76% (172 of 227) were classified to the correct a priori population and 97% (219 of 227) classified within one of these 11 populations. Eight specimens were placed within putative x. x-punctata populations and included two to the Ouachita and Osage Rivers and one each to the Meramec, Gasconade, Salt, and Rock rivers.

There were 16 putative x. x-punctata populations from which 371 specimens were analyzed. Geisser classification correctly placed 78% (291 of 371) to a priori populations and all but two specimens to one of the 16 x. x-punctata populations. The two misclassified specimens were assigned to the Thames and White River, AR populations of x. trautmani. Clearly, the placement of 97% and 99.5% of specimens within the correct populations indicates two distinct taxa based on all variables analyzed. Geisser classification probabilities were recalculated using only morphometric variables to determine the

contribution of body morphology (without scale counts) to discrimination of the taxa. Seventy-two per cent of trautmani specimens were classified to the correct a priori population and 92% were classified within a trautmani population. Of the 18 specimens placed in x-punctata populations, seven went to the Meramec, five to the Osage, three to the Caddo and one each to the Salt and Rock populations. Ninety-seven percent of x-punctata specimens classified within x-punctata populations. Ten specimens were placed in trautmani populations including four to the Wabash, three to the Scioto, two to the Allegheny, and one to the White River, IN.

Particularly interesting among results from the morphology based Geisser analysis is the contribution of the Missouri River tributaries, the Osage, Gasconade, and Meramec rivers. Of the 18 putative trautmani specimens classified to x-punctata populations, 12 resembled Osage or Meramec populations while four resembled Ouachita River tributaries and one each to the Rock and Salt rivers. Ten putative x-punctata specimens were classified to trautmani populations including seven from the Osage-Gasconade-Meramec triumvirate and three from Ouachita River tributaries. This suggests considerable morphological overlap between the Missouri River tributary populations and the trautmani phenotype with somewhat lesser morphological congruence between the Ouachita River populations and the trautmani phenotype. These data lead one to suspect the Osage-Gasconade-Meramec as a region of intergradation with Ohio drainage trautmani and perhaps the Ouachita drainage as a zone of intergradation with Ozark drainage trautmani.

Inter- and intra-population variation in key variables is such that morphological definition of taxa and zones of intergradation or hybridization is difficult with the data at hand. The key character of caudal peduncle scales clearly separates Hybopsis x-punctata populations into two taxonomic groups. A conservative stance is taken in recognizing the two taxa as subspecies. Overall morphological intermediacy as discerned from MDA analysis and Geisser classification suggests populations from the Missouri River tributaries, (Osage, Gasconade, and Meramec rivers), are intergrades between the two subspecies. Additional morphological evidence suggests a similar status for Ouachita River populations. However, until additional detailed analysis of individual populations is complete, these populations are recognized as Hybopsis x-punctata x-punctata based on caudal peduncle scale counts. Therefore, the populations comprising H. x. x-punctata include the Caddo, Saline, Little Missouri and mainstem of the Ouachita River; the Neosho (Grand) drainage of Oklahoma, Arkansas, Kansas, and Missouri; the Osage, Gasconade, and Meramec rivers of the Missouri River drainage; and the Salt, Des Moines, Cedar, Wapsipinicon, Iowa, Root, and Rock rivers of the upper Mississippi River drainage. Hybopsis x-punctata trautmani populations occur in the Current, Spring, Strawberry, and White rivers in the Arkansas and Missouri Ozarks; the Ohio River tributaries which include the Wabash, Miami, Scioto, Muskingum, and Allegheny rivers and tributaries; and finally the Thames River, Ontario, Canada.

Data in Table II-24 (p. 115) and visual information provided in Figures II-15 (p. 108) and II-16 (p. 110) indicate a degree of

morphological differentiation between the Ozark and upper Ohio-Thames populations of Hybopsis x-punctata trautmani. This is recognized as differentiation on the racial level that is expressed by the Ozarkian race having a more slender caudal peduncle and larger eye than the Ohio-Thames race.

Summary of morphological variable means and meristic variable distributions are presented for the two subspecific taxa in Tables II-26 and II-27, respectively. Hybopsis x. x-punctata is a more robust form with deeper body and caudal peduncle depths. Hybopsis x-punctata trautmani has a longer head and snout and larger eye. Hybopsis x. x-punctata is proportionally shorter predorsally and longer postdorsally while H. x. trautmani tends to be more equal in pre- and postdorsal lengths. Linear scale counts such as lateral-line and predorsal scales show little differentiation between the taxa. Circumferential scale counts reveal that trautmani has either larger scales or smaller body dimensions to house scales because these counts (caudal peduncle, circumferential, above lateral-line, and below lateral-line) are lower than those for x-punctata.

The distributions of the subspecies, as herein defined (Figure II-18), are not firmly supported by current regional zoogeographic hypotheses or distributions of other species. Alternative hypotheses are presented to explain the distribution of Hybopsis x-punctata subspecies.

Establishment of the two morphotypes probably occurred by division of the prototypic form into an eastern population in the preglacial Teays system and a western population in the preglacial

Table II-26. Range, Mean, and Standard Deviation of Variables of *Hybopsis x. x-punctata* and *H. x-punctata trautmani*.

Variable	x-punctata		trautmani	
	Range	Mean (SD)	Range	Mean (SD)
		Morphometrics[a]		
PRL	437-533	499 (15)	467-547	510 (15)
PDL	493-474	531 (15)	476-566	516 (15)
CPL	160-249	208 (15)	167-236	203 (13)
HDL	229-276	255 (9)	194-293	265 (12)
SNL	82-119	102 (6)	91-130	109 (7)
ULL	49-73	60 (5)	50-75	62 (5)
GPW	39-65	52 (5)	38-63	52 (5)
IOW	35-57	44 (4)	33-62	43 (4)
ORW	62-87	73 (5)	66-90	80 (5)
BDD	173-248	203 (12)	160-227	191 (12)
CPD	77-105	89 (5)	70-97	84 (5)
ISW	31-97	72 (9)	49-104	72 (9)
DFL	174-253	215 (13)	181-246	208 (12)
AFL	137-212	174 (14)	140-209	171 (14)
P1L	155-244	203 (15)	164-250	204 (15)
P2L	120-288	152 (11)	124-176	150 (10)
POL	81-113	95 (6)	75-110	92 (6)
ULW	5-20	13 (3)	7-19	12 (2)
BWP	115-173	147 (10)	118-170	147 (11)
		Meristics		
LLS	37-47	40.9 (1.6)	36-45	40.2 (1.5)
ALL	6-8	7.0 (0.4)	5-8	6.5 (0.5)
BLL	5-7	6.1 (0.4)	5-7	5.5 (0.5)
CRS	27-36	31.3 (1.6)	26-34	29.3 (1.6)
CPS	13-17	15.8 (0.6)	11-16	12.9 (1.2)
PDS	14-20	16.9 (1.1)	13-19	16.1 (1.1)
PBS	40-90	53.1 (6.9)	40-80	50.2 (6.6)
LP1	14-18	16.1 (0.8)	13-19	16.1 (0.9)
LP2	7-9	8.0 (0.3)	7-9	8.0 (0.3)
ANR	6-7	7.0 (0.1)	6-7	7.0 (0.1)

[a] Morphometric means and standard deviations are in thousandths of standard length.

Table II-27. Frequency Distribution of Scale Variables of *Hybopsis x. x-punctata* and *H. x-punctata trautmani*.

Species	Frequency Distribution											
	Lateral-Line Scales											
	36	37	38	39	40	41	42	43	44	45	46	47
x-punctata	0	3	22	46	93	72	71	40	9	7	0	1
trautmani	1	8	22	48	66	52	28	11	3	1	0	0
	Scales Above Lateral Line											
	5			6			7			8		
x-punctata	0			30			311			23		
trautmani	1			112			124			3		
	Scales Below Lateral Line											
	5			6			7					
x-punctata	11			300			53					
trautmani	112			124			3					
	Circumbody Scales											
	26	27	28	29	30	31	32	33	34	35	36	
x-punctata	0	2	11	24	86	86	77	47	24	6	1	
trautmani	4	27	56	42	62	27	20	0	2	0	0	
	Circumpeduncle Scales											
	11		12		13		14		15	16		17
x-punctata	0		0		6		6		50	297		5
trautmani	1		126		50		27		26	10		0
	Predorsal Scales											
	13	14	15	16	17	18	19	20				
x-punctata	0	2	34	86	133	80	26	3				
trautmani	2	12	56	81	65	21	3	0				

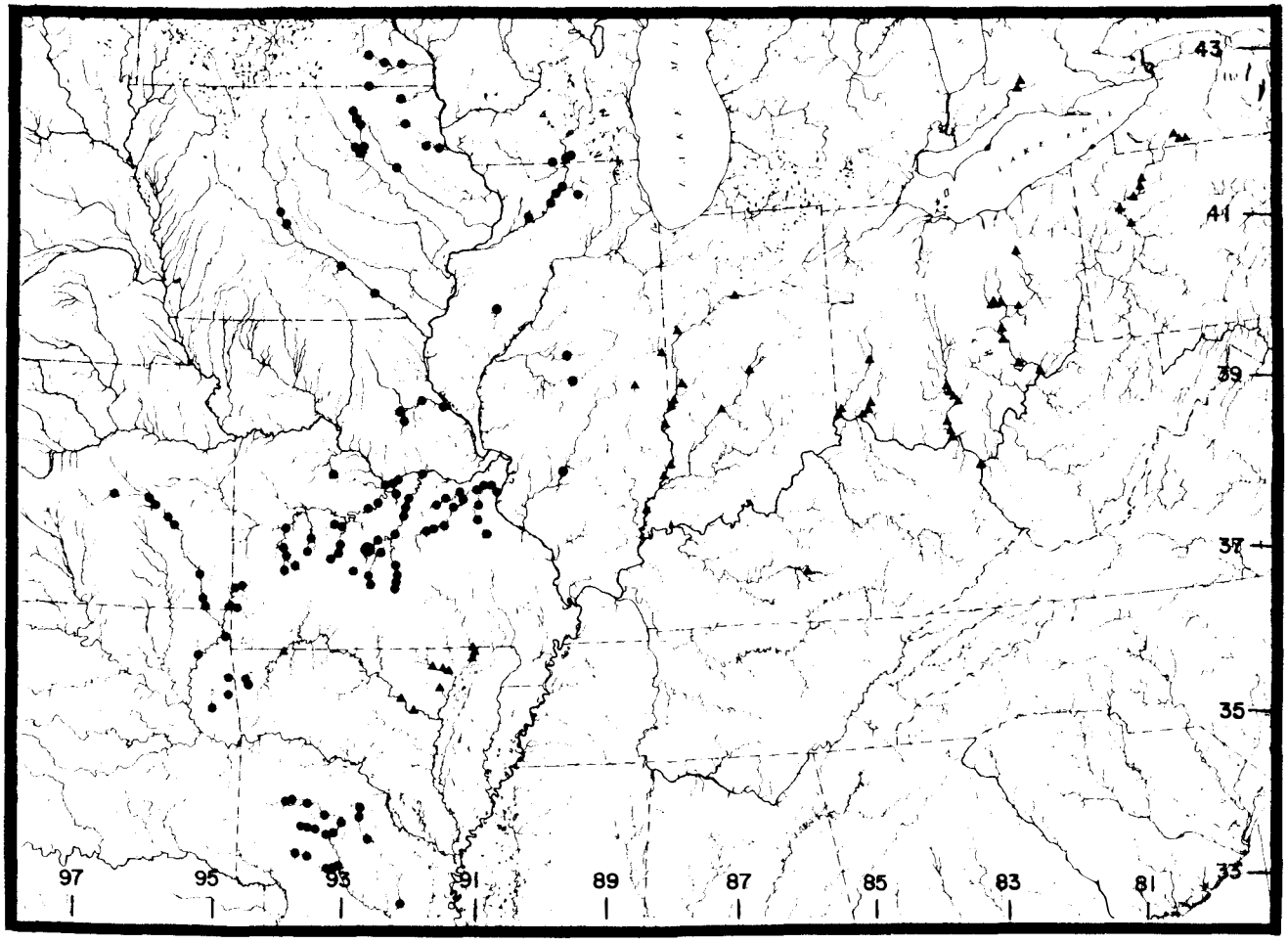


Figure II-18. Distribution of Hybopsis x-punctata. Circles represent H. x. x-punctata, and triangles represent H. x-punctata trautmani. Enlarged symbols indicate type locality.

upper Mississippi, Iowa, and/or Grand River systems (Pflieger, 1971; Mayden, 1985a) due to vicariance of unknown provenance. This east-west distribution or "highland track" (Mayden, 1985a) is generally supported by the distributions of many other species, species pairs, and subspecies of amphibians and fishes (Dowling, 1956; Etnier, 1976; Lachner and Jenkins, 1971; Mayden, 1985a; Page, 1974, 1983; and others).

The dispersal of Hybopsis x-punctata trautmani into Thames River of the Lake Erie drainage probably occurred via the Maumee outlet connecting the Wabash drainage with periglacial Lake Maumee (14,000 years before present) or early Lake Erie (12,000 ybp) (Bailey and Smith, 1981). The presence of H. x-punctata trautmani in the Ozark Highlands west of the present Mississippi River is somewhat enigmatic because H. x. x-punctata occurs to the south in the Ouachita Highland drainage, west in the Neosho drainage, and north in the Missouri and upper Mississippi drainages. Dispersal from the Ohio River drainage into the lower Mississippi may have occurred during glacial maxima when the Mississippi was cooler, less turbid, and less sluggish than at present (Gilbert, 1964). Connections between the Ohio and Mississippi probably existed in several locations as channels cut through Crowley's Ridge during high water levels (Robison, 1986). Pflieger (1971) suggested that small direct tributaries of the Mississippi and Ohio in the Mississippi Embayment provided habitats typical of small clear streams lining the eastern border of the Ozarks today. He visualized "tributary hopping" as a means of dispersing in stepwise fashion from tributary to tributary using the main channel

Mississippi. Subsequent dispersal occurred into the White River and tributaries.

The upper Mississippi River populations of Hybopsis x. x-punctata may have endured glacial advances in the driftless area of Wisconsin and, perhaps, unglaciated portions of the Grand River drainage (as depicted by Mayden, 1985a). The absence of Hybopsis x. x-punctata from the Ozarks and its presence in the Ouachita and Neosho drainages suggests that mainstream dispersal down the Mississippi River is not a viable explanation for present distribution. Pflieger (1971) noted shared distributions between the upper Arkansas (Neosho) and middle Missouri (Osage) systems for Notropis spilopterus, N. heterolepis, Noturus flavus, Percina phoxocephala, P. copelandi, Etheostoma nigrum, and E. microperca. He speculated upon a stream capture between the Osage and Spring river systems while noting there was little geological evidence (Bretz, 1965) for such an event. Recent analysis of the zoogeography of Ouachita Highland fishes (Mayden, 1985a) suggested the following alternative hypothesis. During pre-Wisconsinan glacial advances, part of the Grand River headwaters may have been diverted southward into the Plains Stream (Metcalf, 1966; Mayden, 1985a) providing H. x. x-punctata with access to the present day Neosho drainage. Subsequent stream capture by the Ouachita of a Plains Stream tributary (perhaps the Kiamichi River) prior to entrenchment of the Arkansas River introduced H. x. x-punctata into the Ouachita drainage. Geological corroboration for these hypotheses is currently lacking.

Synonomy

Ceratichthys dissimilis (Kirtland). Jordan, 1875:37 (genera, species IN); Nelson, 1876:45 (distribution IL); Jordan, 1878:62 (distribution IL).

Semotilus dissmilis Kirtland. Forbes, 1884:74 (Rock, Illinois and Ohio, Rivers IL).

Nocomis dissimilis (Kirtland). Jordan, 1877:377 (White R.,IN).

Hybopsis dissimilis (Kirtland). Jordan and Gilbert, 1886:11 (Washita (=Ouachita) and Saline Rivers, AR); Jordan, 1889:355-356 (comparison with H. watauga; distribution); Henshall, 1888:79 (Little Miami R., OH); Meek, 1891:122,138 (Gasconade, Little Piney Rivers, MO; Ouachita R., AR); Meek, 1892:234, 239, 242 (Cedar, Shellrock, Wapsipinicon, and Turkey Rivers, IO); Woolman, 1892:251, 258, 287 (Rolling Fork Salt R., KY; comparison with H. watauga; distribution KY).; Eigenmann and Beeson, 1894 (distribution IN); Meek, 1895:78, 90-92 (distribution AR); Evermann and Cox, 1896:410, 427 (distribution Missouri R. basin); Jordan and Evermann, 1896:315, 318-319 (in key; description and distribution, based in part on H. dissimilis); Osburn, 1901:62 (description; distribution OH, based in part on H. dissimilis); Evermann, 1902:96 (species list, Great Lakes drainage); Large, 1903:19 (in key; distribution IL); Forbes and Richardson, 1908:c, cv, cxi, 164-165 (description; distribution IL; biology; figure); Meek and Hildebrand, 1910:277-278 (in key; description; distribution; figure); Evermann, 1918:367 (Salt R. basin, KY).

Hybopsis dissimilis (Girard). Meek, 1892:109 (Cedar R. basin, IO).

Erimystax dissimilis (Kirtland). Hubbs and Greene, 1928:388 (species list Great Lakes drainage); Jordan, et al., 1930:138 (distribution; synonomy, based in part on H. dissimilis); Osburn, et al., 1930:172 (species list OH); Greene, 1935:77 (range; distribution WI); O'Donnell, 1935:481 (distribution IL); Aitken, 1936:32 (species list IO); Blatchley, 1938:53-54 (description; distribution IN, based in part on H. dissimilis); Hubbs and Lagler, 1939:17 (key to species of Great Lakes drainage); Eddy and Surber, 1947:151 (description; distribution, based in part on H. dissimilis); Moore and Paden, 1950:83 (Illinois R., AR and OK; habitat; relationship to H. dissimilis); Scott, 1958:16 (checklist Alaska and Canada); Dickinson, 1960:30-31 (key to WI fishes; line drawing).

Hybopsis watauga Jordan and Evermann. Eigenmann and Beeson, 1894:91 (distribution IN); Meek, 1894:249 (White R. at Eureka Springs, AR); Kirsch, 1895:37 (Eel R., IN); Meek, 1908:151 (distribution, IO). Blatchley, 1938:54 (description; distribution IN, based in part on H. dissimilis.

Erimystax new species Hubbs and Crowe. Gerking, 1945:50 (distribution IN).

Erimystax sp. Starrett, 1951:17 (abundance Des Moines R., IO).

Hybopsis sp. Harlan and Speaker, 1951:76 (description, habitat); Cleary, 1953:631 (abundance; distribution Iowa-Cedar R. drainage, IO); Gerking, 1955:69 (key to IN fishes); Bailey, 1956:357 (key to IO fishes).

Hybopsis x-punctata Hubbs and Crowe, 1956:2, 4, 7 (original description; subspecies; distribution; in key); Becker, 1961:242 (range reduction; turbidity); Deacon, 1961:380 (relative abundance Neosho R., KA); Nordlie, et al., 1961:255 (corrected distribution, MN); Branson, 1962:532, 536-538 (tuberculation; sensory structures; systematics; figure); Eddy, et al., 1963:115 (distribution Mississippi drainage, MN); Smith, 1965:7 (distribution and abundance, IL); Cross, 1967:89-90 (partial synonomy; description; distribution KA; biology; figure); Branson, 1967:133 (Neosho R.; Illinois R.; habitat); Davis and Miller, 1967:6, 8-9, 13-15, 24-27, 32-36 (range; brain morphology; sensory structures; biology); Phillips and Underhill, 1967:177-178 (distribution MN); Moore, 1968:68, 70 (in key; range); Pflieger, 1968:4, 33 (checklist MO; in key); Branson, et al., 1969:437 (distribution Spring R. drainage, OK, KA, MO); Reno, 1969a:68 (nomenclature); Reno, 1969b:739, 746-753, 762, 765-766, 770 (cephalic lateral-line system; biology; figure); Johnson and Becker, 1970:276 (status; distribution WI); Wiley and Collette, 1970:168 (nuptial tubercles, cites Branson, 1962); Pflieger, 1971:334-335 (partial synonomy; habitat; distribution MO; zoogeography); Smith, 1971:8-9 (distribution IL; range reduction due to siltation); Smith, et al., 1971:7, 14 (distribution upper Mississippi R.); Miller, 1972:242 (status WI); Buchanan, 1973a:28 (checklist AR); Buchanan, 1973b:4, 33, map 44 (checklist; distribution AR; in key); Miller and Robison, 1973:62, 67-68 (in key, figure, description; distribution; habitat; biology); Moore, 1973:2, 19 (history in OK); Scott and Crossman, 1973:380, 423-424 (in key; description; distribution; biology; partial synonomy; figure); Green

and Beadles, 1974:23 (relative abundance; biology; Current R.,AR); Balon, 1975:834 (reproductive guild as a non-guarding phytolithophil); Clay, 1975:138, 145 (in key; figure; description; range; distribution KY; subspecies); Cross and Collins, 1975:52 (description, distribution KA, habitat, biology, status KA); Denoncourt, et al., 1975:118 (checklist WVA); Geishler, et al., 1975:37 (checklist Illinois R., AR); Pflieger, 1975:104, 137-138 (in key; figure; description; etymology; habitat; biology; distribution MO); Whitaker and Wallace, 1975:456 (Wabash R. drainage, Vigo Co., IN); Hubbs and Pigg, 1976:116 (status OK); Bounds, et al., 1977:22-23 (checklist Randolph Co., AR); Johnson and Beadles, 1977:59 (Eleven Point R., AR); Dewey and Moen, 1978:40 (distribution Caddo R., AR); Harris and Douglas, 1978:56 (habitat; distribution upper Ouachita R., AR); Mills, et al., 1978:30 (distribution Big River, MO); Smith, 1979:75, 83-84 (in key; partial synonomy; figure; description; habitat; distribution IL; systematics); Burr, 1980:64 (distribution KY); Gilbert, 1980b:196 (figure; range; systematics; habitat; biology); Bailey and Smith, 1981:1550 (distribution Great Lakes drainage); Brenner, 1981:302 (Mercer Co., PA); Branson, et al., 1981:81 (status KY); Phillips, et al., 1982:118 (etymology; description; distribution); Fago, 1982:10-19, 24, map 16 (figure; distribution WI; abundance; habitat; status WI); Eaton, et al., 1982:191, 193 (distribution Allegheny R., NY and PA); Frietsche, 1982:29 (Little Missouri R., AR); Stauffer, et al., 1982:30-31 (checklist central and northern Appalachian Mountains); Becker, 1983:489-491 (figure, gut configuration, description, distribution WI, biology, status); Cooper, 1983:91, 93 (in key; figure;

range; distribution PA; biology); Brown and Armstrong, 1985:8 (relative abundance Illinois R., AR); Mayden, 1985a:200, 205-206 (zoogeography Ouachita and Ozark highlands).

Hybopsis x-punctata x-punctata Hubbs and Crowe, 1956:2, 4, 7 (in part, original description; range; in key); Eddy and Underhill, 1959:342 (corrected distribution, MN); Hubbs and Lagler, 1964:figure 125; Jenkins and Lachner, 1971:4-7 (scale radii; vertebral counts).

Hybopsis x-punctata trautmani Hubbs and Crowe, 1956:2, 4, 7 (in part, original description; range; in key); Hubbs and Lagler, 1957:3 (checklist Great Lakes drainage); Hubbs and Lagler, 1964:70, 79 (in key, range); Jenkins and Lachner, 1971:6-8 (vertebral counts); Trautman, 1957:307-309 (figure; description; distribution OH; habitat; ecology); Trautman, 1981:93, 285-287 (in key, figure; description; distribution OH; habitat; ecology; status OH).

Diagnosis

Hybopsis x-punctata differs from H. dissimilis, H. harryi, and H. insignis by lacking mid-lateral and mid-dorsal spots or blotches. It is discerned from H. cahni by the presence of distinctive dorsolateral and lateral punctations and x-shaped markings.

Description

The body is elongate, loaf-shaped in predorsal cross section, quadrate in postdorsal cross section, and tapered from the pelvics posteriad to the caudal fin. It is slightly compressed laterally posterior to the dorsal fin. The snout is rounded and overhangs a subterminal, ventral mouth. The eyes are medium size, located

dorsolaterally, and directed dorsally to somewhat posteriad. The terminal labial barbels are moderately to well developed, occasionally, with two per side. Pharyngeal teeth are 4-4. Scales are moderately large with 36-47 (38-44) in the lateral-line. A lateral band is present ranging from dusky to indistinct. The mid-dorsal stripe is weak and the dorsal and lateral regions covered with numerous x- or comma-shaped melanophores at scale junctions. No interradial fin pigment is present. The dorsal profile from dorsal insert to snout is slightly to moderately curved.

External morphology. Morphometry: Fin shape and placement as well as general body physiognamy are illustrated in Figure II-19. Proportional data for morphometric variables are in Table II-28.

Meristics: Tables II-28 and II-29 summarize countable variables with mean, range, standard deviation, and distribution.

Sexual Dimorphism. Morphometrics: Sexual dimorphism in morphometric characters is summarized in Table II-30 with results of t-tests. Males are longer postdorsally and in the caudal peduncle and broader in body width, interorbital width, and isthmus width. Dorsal and pectoral fin lengths are signifcantly longer in males. Females are longer predorsally and in the head region with longer snout length, lip length, and gape width.

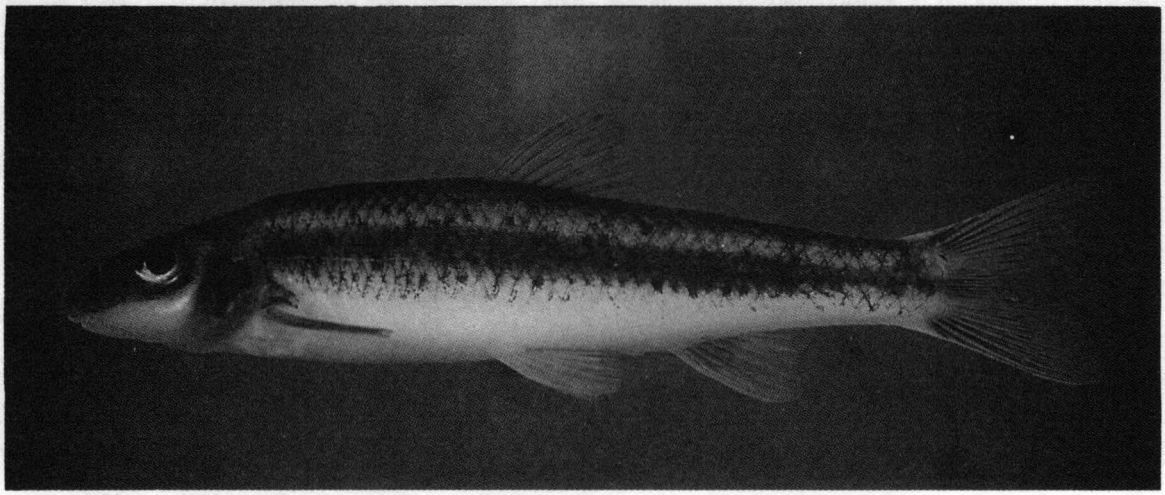
Nuptial tuberculation: Tubercle distribution is a composite obtained from observations of 85 mature males from throughout the range of the species. The head has reduced tuberculation in the mid-occipital, postorbital, and anteronarial regions. Tubercles are

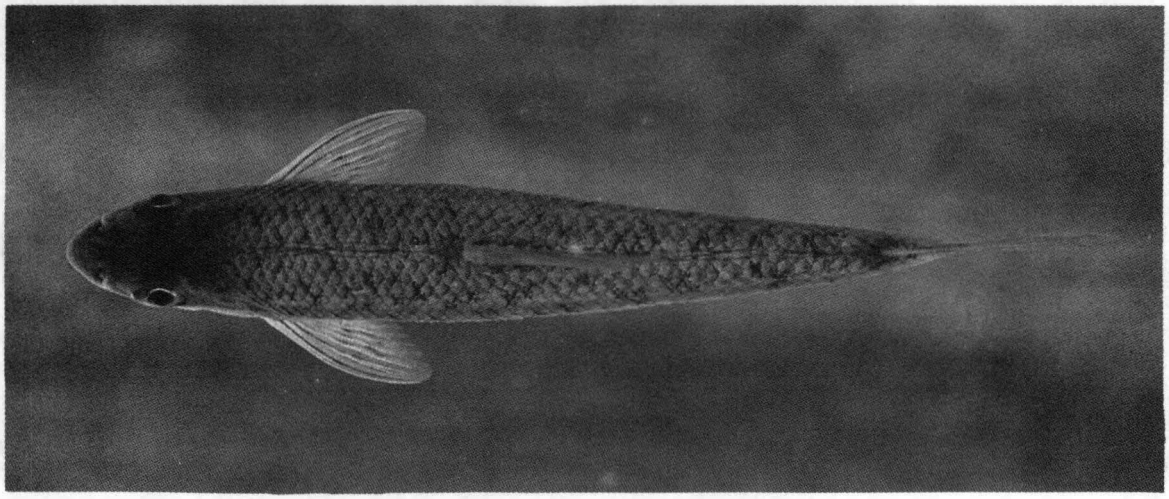
Figure II-19. Photographs of Hybopsis x-punctata.

Figure II-19 A. Hybopsis x. x-punctata. (Lateral aspect). IO, Winnishiek Co. Upper Iowa River at A-34 crossing. 70.9mm SL female.

Figure II-19 B. Hybopsis x. x-punctata. (Dorsal aspect). MO, Miller Co. Tavern Creek at MO Hwy. 133 crossing. 56.7mm SL

Figure II-19 C. Hybopsis x-punctata trautmani. (Lateral aspect). AR, Lawrence Co. Spring River at Ravenden. 67.3mm SL female.





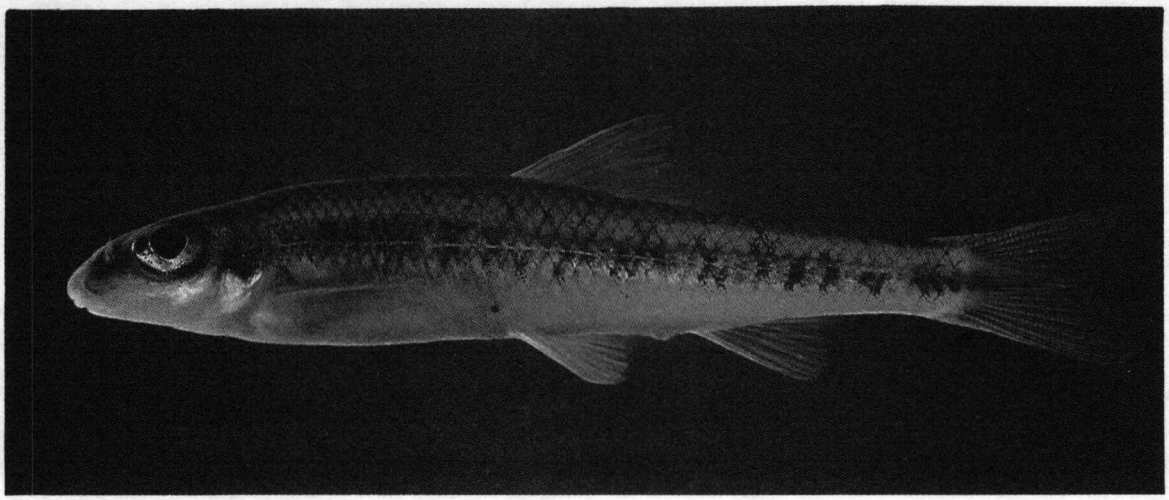


Table II-28. Range, Mean, and Standard Deviation of Variables of *Hybopsis x-punctata*.

Variable	N	Range	Mean	(SD)
		Morphometrics[a]		
STL	644	40.25-91.15	59.84	(9.39)
PRL	644	437-547	503	(16.2)
PDL	644	471-574	525	(16.7)
CPL	644	160-249	206	(14.0)
HDL	644	194-293	259	(11.3)
SNL	644	82-131	105	(7.1)
ULL	644	49-75	61	(4.6)
GPW	644	38-70	52	(4.8)
IOW	644	33-62	44	(3.7)
ORW	644	62-90	76	(5.6)
BDD	644	159-248	199	(14.0)
CPD	644	70-105	87	(6.0)
ISW	624	31-104	72	(8.7)
DFL	644	174-265	212	(13.7)
AFL	644	137-216	173	(14.0)
P1L	641	155-250	203	(14.8)
P2L	641	120-188	151	(10.3)
POL	644	75-114	94	(6.2)
ULW	641	4-20	12	(2.6)
BWP	638	115-173	147	(10.4)
		Meristics		
LLS	644	36-47	40.6	(1.6)
ALL	644	5-8	6.8	(0.5)
BLL	644	5-7	5.9	(0.5)
CRS	644	26-36	30.4	(1.8)
CPS	644	11-17	14.6	(1.7)
PDS	644	13-20	16.6	(1.2)
LP1	641	13-19	16.1	(0.8)
LP2	644	7-9	8.0	(0.3)
ANR	644	6-7	7.0	(0.1)

[a]Morphometric means and standard deviations (except standard length) are in thousandths of standard length.

Table II-29. Frequency Distribution of Meristic Variables of Hybopsis x-punctata.

Frequency Distribution

Lateral Line Scales

36	37	38	39	40	41	42	43	44	45	46	47
1	13	46	103	171	131	105	51	13	9	0	1

Scales Above Lateral Line				Scales Below Lateral Line		
5	6	7	8	5	6	7
1	155	462	26	131	455	58

Circumbody Scales

26	27	28	29	30	31	32	33	34	35	36
4	30	70	74	161	122	103	47	26	6	1

Circumpeduncle Scales

11	12	13	14	15	16	17
1	138	57	35	84	324	5

Predorsal Scales

13	14	15	16	17	18	19	20
2	15	102	184	208	101	29	3

Per Cent Ventral Scalation

40	45	50	55	60	65	70	75	80	85	90
36	55	360	75	80	8	13	3	8	0	1

Left Pectoral Rays							Left Pelvic Rays			Anal Rays	
13	14	15	16	17	18	19	7	8	9	6	7
2	10	131	319	154	23	2	17	592	36	6	638

Table II-30. Sexually Dimorphic Variables of Hybopsis x-punctata.

Variable	Sex(N)	Range	Mean (SD)	t-value	P
PRL[a]	M(203)	456-535	492.2 (15.91)	4.3098	<.001
	F(203)	465-547	502.2 (16.62)		
PDL	M(203)	484-574	533.0 (16.18)	4.9337	<.001
	F(203)	481-563	524.8 (17.06)		
CPL	M(203)	160-249	209.6 (14.90)	2.2044	<.05
	F(203)	171-242	206.4 (14.46)		
HDL	M(203)	225-277	255.1 (10.39)	4.2500	<.001
	F(203)	238-289	259.4 (10.18)		
SNL	M(203)	87-118	103.8 (6.63)	3.4319	<.001
	F(203)	90-122	106.0 (6.09)		
ULL	M(203)	50-72	59.4 (4.53)	6.0916	<.001
	F(203)	52-75	62.0 (4.28)		
GPW	M(203)	38-70	52.1 (5.08)	2.8483	<.05
	F(203)	43-64	53.4 (4.49)		
IOW	M(203)	35-55	44.0 (3.62)	2.6515	<.05
	F(203)	35-62	43.1 (3.56)		
ISW	M(201)	49-100	73.9 (9.41)	3.1609	<.005
	F(200)	31-104	71.1 (7.79)		
DFL	M(203)	183-265	213.0 (13.20)	3.2165	<.005
	F(203)	174-253	208.7 (13.64)		
P1L	M(203)	155-250	205.7 (13.58)	8.0547	<.001
	F(200)	164-228	195.2 (12.50)		
BWP	M(202)	124-173	149.8 (9.97)	2.0779	<.05
	F(200)	118-172	147.8 (9.68)		

[a] Means and standard deviations are in thousandths of standard length.

numerous, but small and grainy in the supraorbital, opercular, and interorbital areas.

Body tubercles are best developed anterior to the dorsal fin above the lateral band and scales have 14-25 grainy tubercles distributed over the entire scale. Some specimens have a preponderance of tubercles on the scale periphery. Dorsolateral scales posterior to the dorsal fin have tubercles usually restricted to the scale margin. Ventral scales anterior to the pelvic insertion have 1-3 enlarged tubercles at the center of the scale margin. Posterior ventral scales possess small tubercles on the scale margin.

Pectoral rays 1 or 2 through 9, 10, or 11 have tubercles that are best developed on rays 2 through 6, 7, or 8. Tubercles are uniserial with one per ray segment on the primary ray and each branch. Tubercles, if present on ray one, usually are smaller. Tubercles on rays 9-11 usually are restricted to the primary ray before branching.

Tubercles are uniserial on pelvic rays 2 through 4, 5, 6, or 7 and usually are absent from the proximal portion of each ray. They begin just before the first branching and are best developed on the distal portions of each ray.

Anal rays have small, uniserial tubercles usually on rays 2 through 6 or 7 distal to the primary ray.

Dorsal rays 1 or 2 through 6, 7, or 8 have tubercles on medial and distal portions distributed one or two per ray segment. They usually are very small and late developing.

A nuptial pad is present on all mature males examined from late March through late June. Location and appearance are as described by Branson (1962) and Jenkins and Burkhead (1984).

Sensory and trophic anatomy. Twenty-five specimens of Hybopsis x. x-punctata from the Ouachita and Neosho drainages were analyzed by Reno (1969b) for pores in the lateral-line system. Ranges and means obtained were: infraorbital canal 8-11 (9.9); postocular commissure 2-4 (3.0); cephalic lateralis 1-3 (2.6); supraorbital canal 6-11 (8.1); supratemporal canal 2-5 (2.7); and preoperculomandibular canal 6-9 (7.1).

Mean number of external and internal taste buds for five cephalic regions were analyzed by Davis and Miller (1967) from eight Neosho drainage specimens and one White River, AR specimen. Numbers obtained were: tip of snout (31.5/0.2); anterior nasal rosette (33.4/6.2); posterior nasal rosette (14.6/5.5); posterior of retina (7.8/17.8); and anterior of cerebellum (5.3/34.6). Mean facial and optic lobe width expressed as per cent of total brain length were 14.5 and 27.4, respectively (Davis and Miller, 1967).

Compound taste buds are present between the first and second pectoral and pelvic rays on both dorsal and ventral surfaces. Smaller taste buds are located distally on the dorsal surface interradially between branches. Most specimens have well developed sensory bristles on the lachrymal flap between the upper lip and snout.

Gill rakers: 3(2), 4(9), 5(12), 6(15), 7(9), 8(5); dorsal rakers are short, acutely pointed or blunt; ventral rakers are very short and blunt or rudimentary.

The intestinal tract ranges from simple s-shape to a modified s-shape with accessory loop ranging in length from a short protuberance to as long as the ascending portion of the gut. Total gut length of 71 Ouachita River drainage specimens is 0.75-1.30 X SL ($\bar{x}$ = 1.04) (Harris, msB).

Other internal structures. The gas bladder is large, two chambered, and averages 26.1% (24.8%-32.8%, n = 15) of SL. The anterior chamber averages 10.5% (8.4%-12.0%) of SL and the posterior chamber averages 17.5% (15.3%-21.1%) of SL. Vertebral counts are summarized in Table II-10 and include all specimens from Jenkins and Lachner (1971). Total vertebrae: 37(5), 38(36), 39(27), 40(1); precaudal vertebrae: 19(20), 20(45), 21(4); caudal vertebrae: 17(3), 18(26), 19(38), 20(2).

Coloration. Freshly captured specimens are olive to dark gray dorsally and white to cream ventrally. A dusky to bold lateral band is present from the lachrymal groove posterior to the caudal fin, most strongly pigmented from the posterior dorsal fin base posteriad to the caudal base. Anteriorly, the band is primarily restricted to lateral-line scales and 1-1 1/4 scale rows above. Posterior to the anal fin, the band constricts to the lateral-line scale row. The mid-dorsal band is thin and poorly to moderately pigmented.

Dorsolateral background pigment immediately above the lateral band is diffuse producing a pale zone 1 1/2 scale rows wide. Dorsally, background pigmentation is more concentrated. From one scale row below the lateral-line dorsad, x- and comma-shaped melanophores are

randomly distributed. These markings occur between scales rather than in the centrum of a scale.

Across the head, the band is relatively diffuse in the opercular region and through the eye. The band is generally quite distinct anterior to the eye before terminating at the lachrymal groove. Cephalic pigment is dark with pale zones in the pre- and postorbital regions. A thin line of pigment just below the eye extends to the snout, with the area ventral to this immaculate. Nares and the internarial area are darkened due to nasal rosettes.

Fin pigmentation: Pectoral rays 1 through 6, 7, 8, 9, or 10 are outlined with melanophores. During spawning, males have denser, darker concentrations on the posterior of each pigmented ray. Some populations have concentrations which appear as spotting when viewed from above. Pelvic rays 1 or 2 through 3, 4, or 5 are very sparsely outlined, usually on the medial portion of the ray. Anal rays 1 or 2 through 4, 5, 6, or 7 have melanophores usually restricted to the basal half of the ray. Dorsal rays 1 through 7 and the first branch of ray 8 are moderately to strongly outlined. The caudal fin of some populations has pigment spots forming one or two v-shaped rows with apex at the caudal base. Procurrent caudal rays are more heavily outlined than other rays, causing the outer edges of the caudal fin to be darker. Interradial pigment is absent on all fins.

H. Hybopsis x-punctata x-punctata Hubbs and Crowe, 1956

The holotype of the species and subspecies, UMMZ 152359, is a 67.7 mm SL adult collected from the Gasconade River at Starks Ford,

8.0 miles south of Richland, Pulaski County, MO on 28 August 1940. Pflieger (1971) corrected the locality data which Hubbs and Crowe (1956) erroneously listed as "Starks Fork of Gasconade River".

Diagnosis

Hybopsis x. x-punctata differs from H. x-punctata trautmani by having a modal count of 16 circumpeduncle scales to 12 for trautmani. Hybopsis x. x-punctata is shorter in predorsal length (x = 499 TSL), head length (x = 255 TSL), and snout length (x = 102 TSL) but longer postdorsally (x = 531 TSL) than trautmani. Hybopsis x. x-punctata is also more robust in body depth (x = 203 TSL) and caudal peduncle depth (x = 89 TSL).

Means in thousandths of SL for Hybopsis x-punctata trautmani variables are: predorsal length = 510, postdorsal length = 516, head length = 265, snout length = 109, body depth = 191, and caudal peduncle depth = 84.

Description

The description is generally as given for Hybopsis x-punctata. Many specimens of H. x. x-punctata are darker dorsally and seem to have more distinctive x-shaped markings than its eastern counterpart. These observations may be due, in part, to the clear waters from which most H. x. x-punctata were taken. This seems to heighten the expression of melanistic characters. Hubbs and Crowe (1956) referred to the short, straight muzzle of this subspecies as a means of differentiating the two forms.

I. Hybopsis x-punctata trautmani Hubbs and Crowe, 1956

The holotype for H. x-punctata trautmani, UMMZ 177278, is a 70 mm SL adult collected in the Waldoning [sic = Walhonding] River, Newcastle Township, Coshocton County, OH with six paratopotypes catalogued as UMMZ 177279 (Hubbs and Crowe, 1956). They were collected 20 October 1939 by M. B. Trautman and E. L. Wickliff.

Diagnosis

See diagnosis for Hybopsis x. x-punctata.

Description

The description is generally as for Hybopsis x. x-punctata. Hubbs and Crowe (1956) described the snout in H. x-punctata trautmani as relatively pointed and downcurved. The downcurve occurs anterior to the nares which makes the bulbous snout tip appear to sag. Many trautmani specimens appear pale and without prominent markings, however, this may be a function of time in preservative and/or water clarity at the time of capture (see H. x. x-punctata description).

Tubercule size in male Hybopsis x-punctata trautmani appears smaller at peak development than in H. x. x-punctata, although this was not quantified. Reduced tuberculation is also noted in the vertical fins of trautmani with no tubercles observed on the anal rays of any individuals.

J. Hybopsis cahni Hubbs and Crowe, 1956

Slender chub

Analysis

Hybopsis cahni is known historically from the Powell, Clinch, and Holston rivers of the upper Tennesee River system. A total of 53 specimens was examined, 19 from the Powell River and 34 from the Clinch River. The Holston population is known from but a single specimen taken during a preimpoundment survey for Cherokee Reservoir (Etnier, Starnes, and Bauer, 1979). Discriminant function analyses (DFA) based on all variables and morphological variables only for 17 Powell and 19 Clinch specimens indicated population centroids were significantly different. MDA MANOVA for all variables yielded $F = 7.06$ with $P<0.001$ and for morphological variables $F = 9.65$ with $P<0.001$. Based on correlations between variables and the discriminant functions for the two data sets, no single variable showed high discriminatory power. Because of the small sample size and inequality of group dispersions, results of MDA analysis for this species must be considered suspect. Geisser classification probabilities placed all individuals in the correct a priori population.

Principle components of morphological variables described >90% of total variation on the first three components with PC1-3 accounting for 77%, 10%, and 4%, respectively. PC1 is primarily a size component while PC2 contrasts relatively high positive loadings for postdorsal and caudal peduncle length with the negative loading for upper lip width. PC3 describes the variation contributed by interorbital width

and isthmus width. Individuals are graphed using the axes PC1 versus PC2 (Figure II-20) and show good discrimination but with considerable overlap of populations when outliers are connected to show population distribution. Variable loadings for the first three principal components as well as the discriminant functions for all variables and morphological variables are presented in Table II-31.

Ranges, means, and standard deviations are summarized for morphological variables for each population and populations combined in Table II-32. Distribution of meristic variables is presented in Table II-33. Morphometric means indicated the Clinch population was considerably longer in predorsal length, head length, and snout length. Clinch specimens also possessed a larger eye and had greater body width. The Powell population was longer postdorsally and had a longer caudal peduncle length. These differences were substantial but in view of results of the PCA (Figure II-20) they are considered racial differences that do not warrant taxonomic recognition. Distribution of the species is presented in Figure II-21.

Diagnosis

Hybopsis cahni differs from all other *Erimystax* by lacking mid-lateral and mid-dorsal blotches or spots and by lacking dorsolateral x-shaped or punctate markings. It is most similar to *Hybopsis x-punctata trautmani* but differs by having a longer, narrower caudal peduncle and more narrowly conjoined isthmus, in addition to the pigmentation differences stated above.

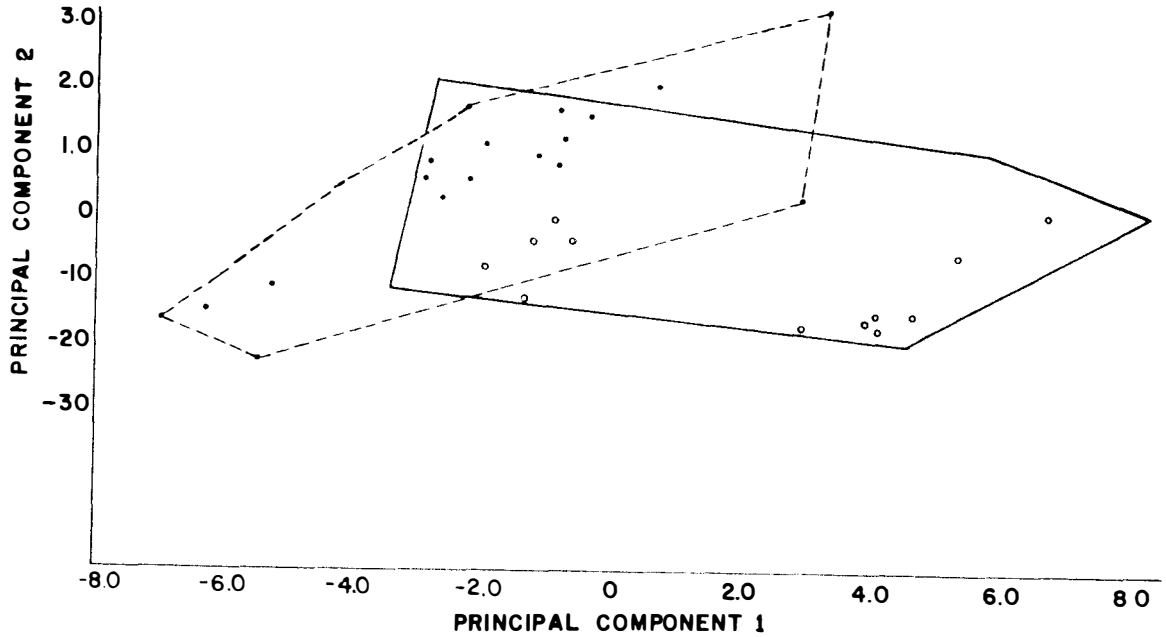


Figure II-20. Population polygons of Hybopsis cahni on principal component axes determined from the morphometric data set.

Table II-31. Discriminant Function (DF) and Principal Components (PC) Correlations with Variables of Hybopsis cahni.

Variable	DF1[a] (all)	DF1[b] (morph)	PC1	PC2	PC3
PRL	-0.172	-0.298	0.250	-0.095	-0.079
PDL	-0.035	-0.060	0.200	0.435*[c]	0.050
CPL	-0.006	-0.011	0.163	0.510*	0.051
HDL	-0.172	-0.296	0.256	-0.093	0.002
SNL	-0.174	-0.299	0.247	-0.174	0.023
ULL	-0.179	-0.309	0.232	-0.217	-0.161
GPW	-0.149	-0.256	0.247	-0.102	-0.045
IOW	-0.038	-0.066	0.190	0.284	0.555*
ORW	-0.169	-0.292	0.245	-0.145	-0.100
BDD	-0.118	-0.204	0.248	-0.033	0.052
CPD	-0.087	-0.150	0.247	0.027	0.046
ISW	-0.082	-0.142	0.208	-0.188	0.512*
DFL	-0.114	-0.196	0.237	0.165	-0.164
AFL	-0.044	-0.076	0.218	0.261	-0.221
P1L	-0.116	-0.200	0.240	0.047	-0.292
P2L	-0.076	-0.132	0.226	0.170	-0.356
POL	-0.130	-0.225	0.239	-0.117	0.271
ULW	-0.128	-0.220	0.185	-0.393*	-0.084
BWP	-0.141	-0.224	0.253	-0.106	0.079
LLS	0.045				
ALL	-0.072				
BLL	-0.004				
CRS	-0.060				
CPS	-0.041				
PDS	-0.086				
PBS	-0.001				
LP1	-0.049				
LP2	-0.002				
ANR	-0.031				

[a]DF1 (all) is discriminant function for meristic + morphometric variables.

[b]DF1 (morph) is discriminant function for morphometric variables.

[c]The * indicates highly correlated variables.

Table II-32. Range, Mean, and Standard Deviation of Variables of the Clinch, Powell, and Total Populations of Hybopsis cahni.

	Clinch		Powell		Total	
Variable	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)
			Morphometrics[a]			
PRL	487-553	526 (14)	453-532	494 (21)	453-553	514 (23)
PDL	467-531	500 (19)	486-554	529 (18)	467-554	511 (23)
CPL	186-242	212 (16)	203-243	224 (11)	186-243	216 (16)
HDL	249-286	270 (8)	244-275	254 (9)	244-286	265 (11)
SNL	104-126	115 (6)	98-119	105 (6)	98-126	111 (8)
ULL	50-78	63 (6)	51-66	56 (4)	50-66	60 (7)
GPW	43-66	55 (5)	42-53	48 (3)	42-66	53 (6)
IOW	39-59	45 (5)	40-50	45 (3)	39-59	45 (4)
ORW	72-91	81 (4)	69-85	74 (5)	69-91	79 (5)
BDD	158-212	181 (14)	166-190	175 (6)	158-212	179 (12)
CPD	66-79	74 (3)	67-82	74 (4)	66-82	74 (4)
ISW	51-81	63 (10)	49-78	60 (7)	49-81	61 (9)
DFL	180-234	198 (12)	188-216	201 (7)	180-234	199 (10)
AFL	154-184	168 (8)	161-198	178 (10)	154-198	171 (10)
P1L	185-222	202 (10)	172-222	198 (13)	172-222	200 (11)
P2L	127-160	142 (8)	139-163	149 (7)	127-163	145 (8)
POL	79-104	90 (6)	76-99	87 (5)	76-104	89 (6)
ULW	5-16	13 (3)	8-15	10 (2)	5-16	12 (3)
BWP	128-169	149 (14)	124-155	135 (8)	124-169	143 (13)
			Meristics			
LLS	39-47	42.2 (1.8)	39-45	42.1 (1.8)	39-47	42.2 (1.8)
ALL	6-7	6.7 (0.5)	6-7	6.3 (0.5)	6-7	6.6 (0.5)
BLL	5-7	5.8 (0.6)	5-6	5.7 (0.5)	5-7	5.8 (0.5)
CRS	26-32	29.7 (1.3)	26-32	28.6 (1.6)	26-32	29.3 (1.5)
CPS	12-14	12.2 (0.5)	12-13	12.1 (0.3)	12-14	12.2 (0.5)
PDS	15-19	17.4 (0.8)	15-18	16.6 (0.7)	15-19	17.1 (0.9)
PBS	40-60	46.7 (5.4)	40-60	48.2 (4.8)	40-60	47.2 (5.2)
LP1	14-17	15.5 (0.7)	14-16	15.2 (0.8)	14-17	15.4 (0.7)
LP2	7-9	8.0 (0.4)	8-9	8.1 (0.2)	7-9	8.0 (0.3)
ANR	6-8	7.0 (0.2)	7	7.0 (0.0)	6-8	7.0 (0.2)

[a]Morphometric means and standard deviations are in thousandths of standard length.

Table II-33. Frequency Distribution of Meristic Variables of Hybopsis cahni.

Population	Frequency Distribution								
	Lateral-Line Scales								
	39	40	41	42	43	44	45	46	47
Clinch	1	4	9	7	6	4	1	1	1
Powell	3	1	3	3	5	1	3	0	0
Total	4	5	12	10	11	5	4	1	1
	Above Lateral-Line		Below Lateral-Line			Circumpeduncle			
	6	7	5	6	7	12	13	14	
Clinch	10	24	10	21	3	28	4	2	
Powell	13	6	5	14	0	17	2	0	
Total	23	30	15	35	3	45	6	2	
	Circumbody Scales								
	26	27	28	29	30	31	32		
Clinch	1	0	7	3	13	9	1		
Powell	2	2	7	3	2	2	1		
Total	3	2	14	6	15	11	2		
	Predorsal Scales					Per Cent Ventral Scalation				
	15	16	17	18	19	40	45	50	55	60
Clinch	1	3	13	16	1	9	8	14	0	2
Powell	1	7	10	1	0	3	3	12	0	1
Total	2	10	23	17	1	12	11	26	0	3
	Pectoral Fin Rays				Pelvic Fin Rays			Anal Rays		
	14	15	16	17	7	8	9	6	7	8
Clinch	1	19	11	3	2	28	3	1	32	1
Powell	4	8	7	0	0	18	1	0	19	0
Total	5	27	18	3	2	46	4	1	51	1

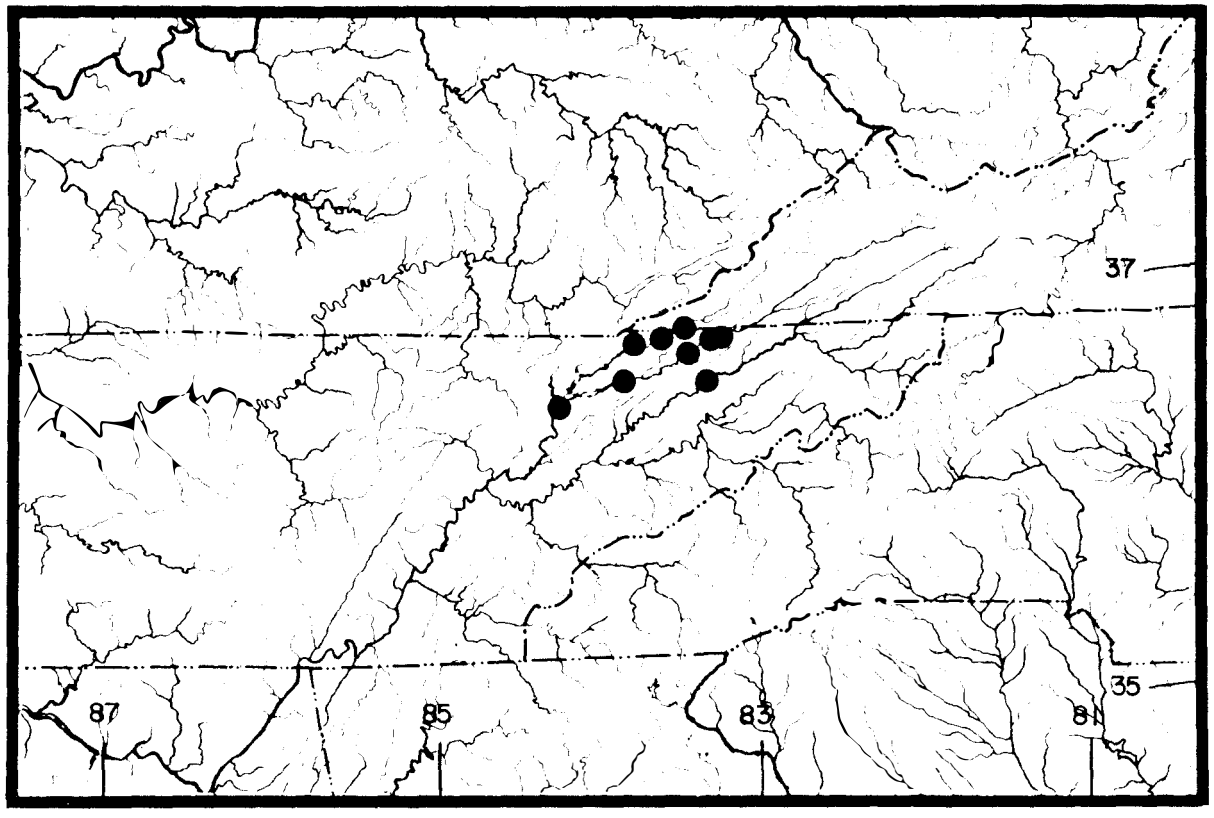


Figure II-21. Distribution of Hybopsis cahni.

Description

The holotype (UMMZ 157708) is a 62.3 mm standard length male collected 8 September 1939 from the Powell River 3.0 miles southeast of Harrogate at U. S. Highway 25E, Claiborne County, Tennessee. Four paratopotypes 49 to 51 mm standard length are catalogued as UMMZ 157709.

The body is elongate, oval in anterior cross section, tapers from the pelvics posterior to the caudal fin, and is slightly compressed laterally posterior to the dorsal fin. The snout is rounded and overhangs the inferior mouth. The eyes are medium in size, supralateral, and directed somewhat posteriad. The terminal labial barbels at end of each lip are small to moderate in size. Pharyngeal teeth are 4-4. Gill rakers were 3(3), 4(2), 5(3), 6(2) in 10 specimens examined. Scales are moderately large with 39-45 in the lateral-line. The gut is s-shaped and 0.71-0.91 of standard length ($\bar{x}$ = 0.82, n = 10).

Morphometry: Fin shape and placement and general body physiognamy are illustrated in Figure II-22. Proportional data for morphometric variables are summarized in Table II-32.

Meristics: Table II-32 and II-33 summarize countable characters.

Coloration: Freshly collected specimens are yellowish tan, olive, or brown dorsally and white to cream ventrally. The lateral band is prominent posterior to the dorsal fin and lacks enlarged spots or blotches. It encompasses the lateral-line plus one scale row above and below, becomes narrower on the peduncle, being restricted to the lateral-line, and then widens before reaching the weak to moderately

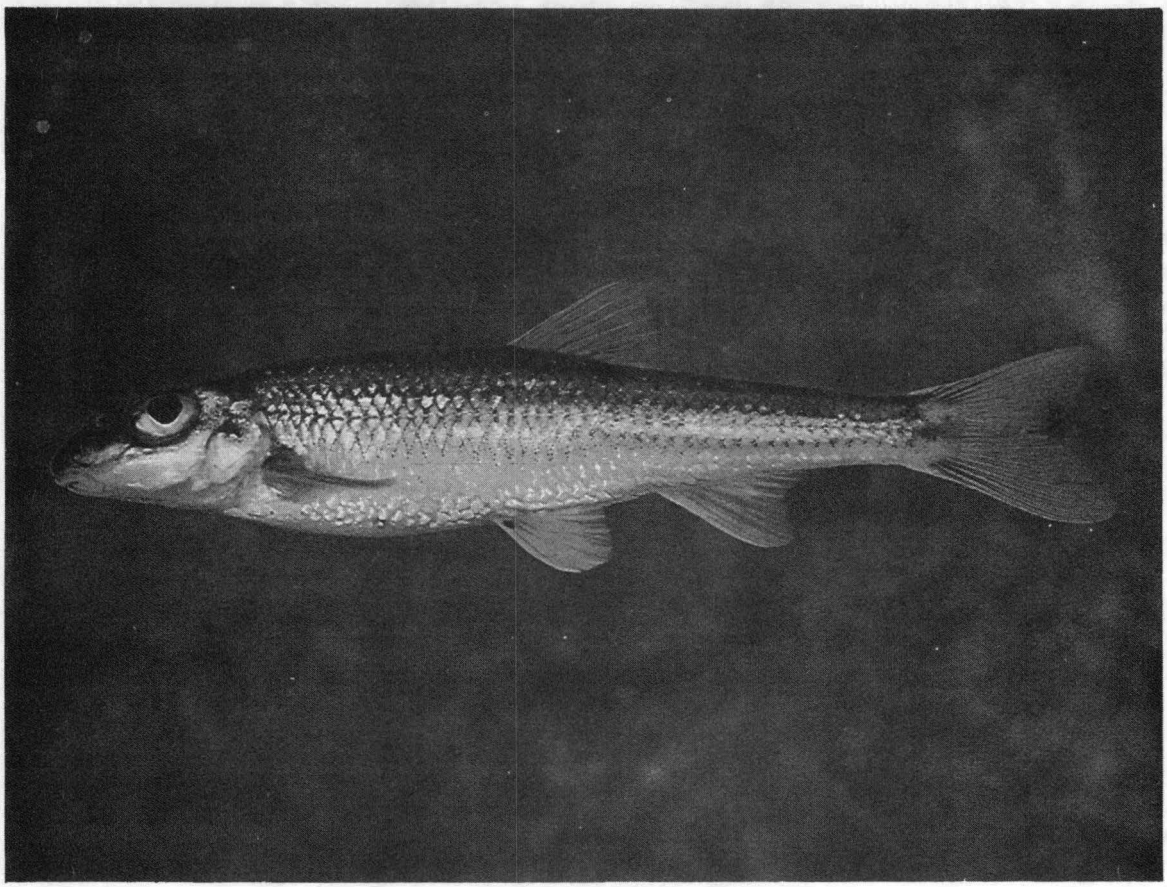


Figure II-22. Photograph of Hybopsis cahni.

dark basicaudal spot. Reduction of melanophores at scale junctions produces an alternating pattern of pale and dark v-shaped chevrons on the posterior lateral band. Anterior to the dorsal fin, the lateral band is diffuse through the eye onto the snout before termination at the lachrymal groove. A paler band occurs 1-1 1/2 scale rows above the lateral band due to smaller, less concentrated melanophores. Above the pale band, melanophores are more dense and evenly distributed producing a darker tan or gray color. The mid-dorsal stripe is moderately developed anterior to and poorly developed or absent posterior to the dorsal fin. Laterally, scattered melanophores occur on two or three scale rows below the lateral-line.

Cephalic pigmentation is a yellowish brown or gray with pale regions anterior and posterior to the orbits. Two dark crescents occur between the nares due to the internal nasal rosettes. Snout pigmentation is uniform.

Melanophores outline rays 1 through 8, 9, or 10 of the pectoral fins; 1 through 3, 4, or 5 medially and very sparsely on the pelvic fins; 1 through 5, 6, or 7 basally on the anal fin; and 1 through 7 plus the anterior branch of ray 8 on the dorsal fin. Interradial pigment is absent from all. The caudal fin is darkly pigmented from the basicaudal spot diffusing through middle rays 2 through 4, the next 2-3 rays on either side lack dark pigment, and the outer 4 rays on each side are outlined with dark pigment.

Sexual Dimorphism: The slender chub is sexually dimorphic in three characters based on results of Students t-test (Table II-34).

Table II-34. Sexually Dimorphic Variables of Hybopsis cahni.

Variable	Sex(N)	Range	Mean	SD	t-value	P
DFL[a]	M(9)	194-216	204.2	6.89	2.3247	<.05
	F(7)	188-204	196.7	5.71		
P1L	M(9)	190-213	202.0	6.91	4.9237	<.001
	F(7)	172-191	184.7	7.04		
PDS	M(9)	16-18	17.1	0.60	2.3620	<.05
	F(7)	16-17	16.4	0.53		

[a]Morphometric means and standard deviations in thousandths of standard length.

Males have significantly longer dorsal and pectoral fins and more predorsal scales than females.

Tuberculation: The following is a composite compiled from the descriptions of Etnier and Starnes (ms), Jenkins (1975), and Jenkins, Burkhead, and Haxo (ms) and six nuptial males collected 18 April 1978 from Clinch River (NLU 39505). Cephalic tubercles are moderate in size and density in the supraorbital and opercular regions. Tubercles are sparse to absent pre- and postorbitally, in the midoccipital region, and on the snout tip. Pectoral fins have tubercles on rays 2 through 8, 9, or 10 and they are well developed on rays 2 through 6. Distribution is uniserial with one per segment on each ray branch. Rays 7 through 10 have tubercles usually restricted to the primary ray before branching. The pelvic fin has small tubercles on rays 2 through 4, 5, or 6. Anal rays 2 through 4 have very tiny tubercles on the distal half and dorsal rays 2 through 5 or 6 have small, distally restricted tubercles. Body tubercles are more widely spaced than cephalic tubercles.

Synonomy

Hybopsis monaca (Cope). Evermann and Hildebrand, 1916:445 (Clinch R., TN).

Hybopsis cahni Hubbs and Crowe, 1956:2-3, 6 (in key; original description; range); Davis and Reno, 1966:307 (figure; description and morphometrics; Clinch R.; TN specimens); Davis and Miller, 1967:5, 7-9, 14-15, 24-26, 32-37 (range; taste buds; brain morphology; biology); Moore, 1968:68-69 (in key; description; range); Eddy, 1969:105

(description; range); Reno, 1969a:68 (nomenclature); Reno, 1969b:739, 746-753, 762, 765-766, 770 (cephalic lateral-line system; biology; figure lateralis system); Jenkins and Lachner, 1971:4, 6-8 (scale radii; vertebral counts); Jenkins, et al., 1972:48, 97 (range; zoogeography); Eddy and Underhill, 1978:75 (in key; range); Deacon et al., 1979:34 (figure; status); Etnier, et al., 1979:no pagination (Holston R., TN); Jenkins, et al., 1980:182 (figure; range; systematics; habitat; biology); Parker and Dixon, 1980:44-45 (figure; description; range; habitat; biology; status); Starnes and Etnier, 1980:B5-B6 (figure; description; range; habitat; biology; status); White, 1982:74-75 (figure; description; range; biology; status); Stauffer, et al., 1982:30-31 (checklist central and northern Appalachian Mountains); Ono, et al., 1983:235 (status).

K. Interspecific Relationships within *Erimystax*

Analysis

Analysis of intraspecific variation in four recognized species of *Erimystax* revealed the presence of a sibling species within *Hybopsis dissimilis*. Interest now turns to assessing the interspecific relationships of the five species in this study. MDA was performed using the five species as individual populations. From the pool of 1751 specimens, population sizes are *cahni* = 36, *dissimilis* = 437, *harryi* = 171, *insignis* = 510, and *x-punctata* = 597. Results of MDA with meristic and morphometric variables indicated the group centroids were signifcantly different ($F=127.62$; $P<0.001$).

Canonical variates 1 and 2 based on meristic plus morphomtric variables described 52% and 32% of total variation, respectively. Correlations among variables and the first two canonical variates are presented in Table II-35. CV1 described variation in lateral-line and predorsal scales. CV2 was a descriptor of variation in per cent ventral scalation and scales below the lateral-line. Centroids were graphed in canonical space using canonical axis one versus canonical axis two to visualize the relationships among species (Figure II-23). Vectors for high discrimination variables were plotted from the grand centroid. Group means for these variables were compared using the Gabriel procedure (Table II-36).

Results of Geisser classification (Table II-37) showed the procedure performed well, placing 97% of individuals within the correct a priori population. Two Hybopsis cahni specimens were classified with H. x-punctata indicating, similarity between those species. Strikingly, only one H. dissimilis specimen was placed with H. harryi which reinforces the recognition of the taxa as separate species. Hybopsis insignis was perhaps the most intermediate of the Erimystax as indicated by classification of some insignis to each species.

Canonical analysis using morphological variables described 97% of total variation on the first three canonical variates. CV1 accounted for 59% of total variation and had highest correlation with the variables caudal peduncle length and postdorsal length. CV2 described 22% of total variation and compared the high positive loading of upper lip width with the negative loading for caudal peduncle depth. Graphing

Table II-35. Correlations between Canonical Variates and Variables of Erimystax Species for Meristic + Morphometric and Morphometric Data Sets.

	All Data[a]		Morphological Data[b]	
Variable	Canonical Variate 1	Canonical Variate 2	Canonical Variate 1	Canonical Variate 2
PRL	0.256	-0.028	0.351	-0.123
PDL	0.276	-0.018	0.376*	-0.124
CPL	0.305	0.012	0.416*	-0.043
HDL	0.208	-0.037	0.289	-0.100
SNl	0.116	-0.032	0.159	-0.099
ULL	0.114	0.038	0.201	0.105
GPW	0.178	0.022	0.250	0.086
IOW	0.239	-0.019	0.331	-0.058
ORW	0.187	-0.004	0.260	-0.013
BDD	0.147	-0.029	0.199	-0.128
CPD	0.124	-0.039	0.161	-0.211*
ISW	-0.061	0.134	-0.107	0.146
DFL	0.193	-0.040	0.264	-0.138
AFL	0.129	0.028	0.175	0.026
P1L	0.127	0.036	0.169	0.025
P2L	0.123	0.018	0.162	-0.043
POL	0.249	-0.040	0.345	-0.125
ULW	-0.011	0.235	-0.039	0.391*
BWP	0.154	0.002	0.209	-0.043
LLS	0.577*[c]	0.013		
ALL	0.261	0.186		
BLL	0.393	0.427*		
CRS	0.177	-0.081		
CPS	0.122	0.105		
PDS	0.472*	0.052		
PBS	-0.027	0.514*		
LP1	0.273	-0.059		
LP2	-0.162	-0.361		
ANR	0.042	0.104		

[a]Derived from the meristic + morphometric data set.

[b]Derived from the morphometric data set.

[c]The * indicates highly correlated variables.

Figure II-23. Species centroids, 95% confidence circles, and variable vectors of Erimystax species in canonical space determined from the meristic + morphometric variable set.

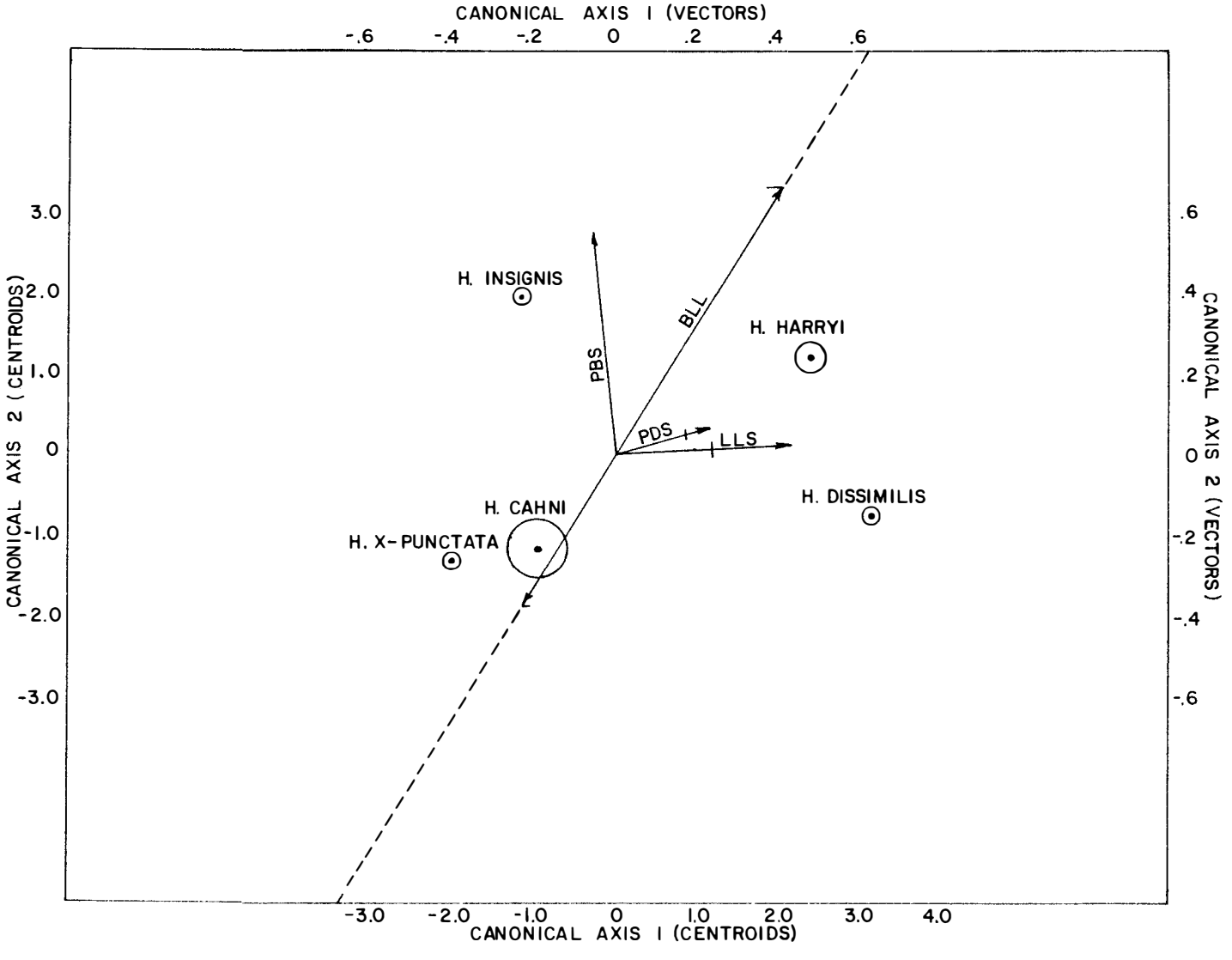

CANONICAL AXIS I (VECTORS)
-.6
-.4
-.2
0
.2
.4
.6
3.0
2.0
1.0
0
-1.0
-2.0
-3.0
CANONICAL AXIS 2 (CENTROIDS)
.6
.4
.2
0
-.2
-.4
-.6
CANONICAL AXIS 2 (VECTORS)
H. INSIGNIS
H. HARRYI
H. CAHNI
H. X-PUNCTATA
H. DISSIMILIS
PBS
BLL
PDS
LLS
-3.0
-2.0
-1.0
0
1.0
2.0
3.0
4.0
CANONICAL AXIS I (CENTROIDS)

Table II-36. Gabriel Multiple-Comparison of Erimystax Species Means.

Variable	LLS[a]	PDS	PBS
F-value	1122.3	771.8	711.2
High	harryi	harryi	harryi
	dissimilis	dissimilis	insignis
	cahni	insignis	dissimilis
	insignis	cahni	x-punctata
Low	x-punctata	x-punctata	cahni

[b] Lines connect homogenous subsets.

Variable	BLL	CPD	ULW
F-value	79.7	431.8	327.1
High	harryi	x-punctata	insignis
	dissimilis	insignis	harryi
	insignis	harryi	x-punctata
	x-punctata	dissimilis	cahni
Low	cahni	cahni	dissimilis

Variable	CPL	POL
F-value	85.0	20.1
High	harryi	x-punctata
	dissimilis	dissimilis
	insignis	insignis
	cahni	harryi
Low	x-punctata	cahni

[a] All species are significantly different for this variable.

Table II-37. Results of Geisser Classification Procedure of Erimystax Species Using Meristic + Morphometric Variables.

	cahni[a]	dissimilis	insignis	x-punctata	harryi
cahni[b]	34	0	0	2	0
dissimilis	1	430	0	5	1
insignis	1	5	478	22	4
x-punctata	4	0	4	589	0
harryi	3	3	2	0	163

[a]Columns represent taxa and number of specimens as interpreted by Geisser classification.

[b]Rows represent taxa and number of specimens as interpreted by taxonomic comparison.

Table II-38. Results of Geisser Classification Procedure of Erimystax Species Using Morphometric Variables.

	cahni[a]	dissimilis	insignis	x-punctata	harryi
cahni[b]	28	0	5	3	0
dissimilis	0	421	5	7	4
insignis	4	6	458	41	1
x-punctata	1	3	29	562	2
harryi	0	5	6	3	157

[a] Columns represent taxa and number of specimens as interpreted by Geisser classification.

[b] Rows represent taxa and number of specimens as interpreted by taxonomic comparison.

group centroids on canonical axes 1 versus 2 allowed visualization of species relationships in canonical space (Figure II-24). Variables with high correlations to canonical variates were plotted from the grand centroid and the group means for these variables compared by the Gabriel procedure (Table II-36). Hybopsis insignis appears more closely related to H. cahni and H. x-punctata based on Figure II-24.

Geisser classifcation based on morphological variables classified 93% of individuals to the correct a priori population (Table II-38). The morphological similarity between H. insignis and H. x-punctata was reflected by the misclassification of 41 (8% of total) insignis to x-punctata and 29 (5% of total) x-punctata to insignis.

Generalized distances among species of Erimystax generated from all variables and morphological variables are presented in Table II-39 and II-40. Generalized distances and visual assessment of canonical variates (Figure II-23) indicate Erimystax species are assignable to two species groups. The x-punctata species group is composed of H. x-punctata and H. cahni. Key definitive characters for the x-punctata group are lack of lateral and dorsal blotches and longer snout length. When H. x-punctata trautmani is compared with H. cahni (Tables II-26, p. 122; II-27, p. 123; and II-31, p. 147; II-32, p. 148), additional similarities include caudal peduncle scales (12), longer snout length (means 109 and 111, respectively), longer head length (265), large orbit width (80 and 79, respectively), shorter postdorsal length (516 and 511, respectively), and larger scales as reflected by scales above and below lateral-line.

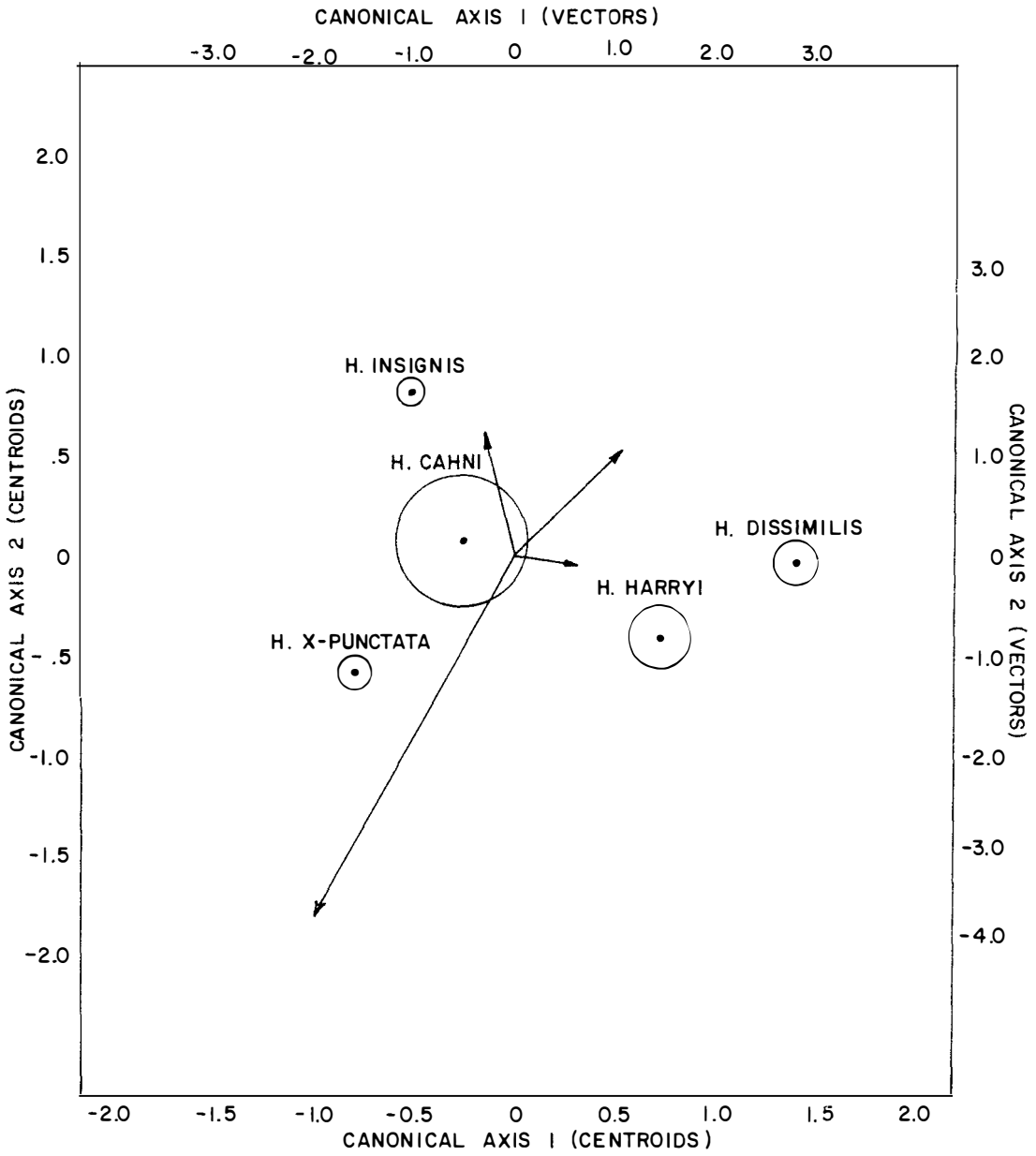


Figure II-24. Species centroids, 95% confidence circles, and variable vectors of Erimystax species in canonical space determined from the morphometric variable set.

Table II-39. Generalized Distances among Erimystax Species Based on Morphometric and Meristic Variables.

	cahni	dissimilis	insignis	x-punctata	harryi
cahni	0.000	5.884	5.508	3.872	7.229
dissimilis	5.884	0.000	5.832	5.679	5.023
insignis	5.508	5.832	0.000	4.302	5.611
x-punctata	3.872	5.679	4.302	0.000	6.474
harryi	7.229	5.023	5.611	6.474	0.000

Table II-40. Generalized Distances among Erimystax Species Based on Morphometric Variables.

	cahni	dissimilis	insignis	x-punctata	harryi
cahni	0.000	4.445	3.480	3.389	5.245
dissimilis	4.445	0.000	4.357	4.656	3.872
insignis	3.480	4.357	0.000	2.923	4.365
x-punctata	3.389	4.656	2.923	0.000	4.402
harryi	5.245	3.872	4.365	4.402	0.000

The dissimilis species group is composed of Hybopsis dissimilis, H. harryi, and H. insignis. The primary characters linking these species are the presence of lateral and dorsal blotches and modal counts of 16 scales around the caudal peduncle. Other meristic and morphometric characters form no pattern to distinguish the dissimilis group. Their cohesiveness as a group is based on overall similarity as depicted by generalized distances (Table II-39).

L. Phylogenetic Relationships of Erimystax

The chub genus Hybopsis posseses one of the most chaotic and tumultuous taxonomic histories of any North American fish taxon. This nomenclatural roller coaster has been reviewed in detail by Reno (1969), Clemmer (1971), and Jenkins and Lachner (1971). Current formal taxonomic alignment of Hybopis follows Jenkins and Lachner (1971) with minor exceptions as noted below.

Subgenus Hybopsis is composed of H. amblops, H. rubrifrons, H. hypsinotus, H. lineapunctata (see Clemmer and Suttkus, 1971), H. labrosa, H. zanema (see Jenkins and Lachner, 1980a, 1980b), H. sp. "thin lips" chub, and H. storeriana. Clemmer (1971) concluded the Hybopsis amblops complex (i.e., amblops, rubrifrons, lineapunctata and two members of Notropis) were closely related to Notropis but deferred nomenclatural change due to the instability that would result. Alignment of the amblops complex with Notropis would remove the type of Hybopsis and require generic regrouping of the remaining Hybopsis.

Subgenus Erimystax is sanctuary for H. dissimilis, H. x-punctata, H. insignis, H. cahni, H. monacha, and as mentioned in this study, H.

harryi. Notropis harperi was placed in Erimystax by Hubbs and Crowe (1956) and Jenkins and Lachner (1971) before reassignment to Notropis by Gilbert and Bailey (1972).

The species Hybopsis gelida and H. meeki are members of the subgenus Macrhybopsis while the monotypic subgenera Platygobio and Extrarius house H. gracilis and H. aestivalis, respectively. The nomen Oregonichtys has been variously used at the generic (Hubbs et al., 1974; Bond, 1974) and subgeneric (Long, 1980) level for H. crameri. Subgenus Yuriria for H. alta was elevated to generic status by Smith, et al. (1975).

Jenkins and Lachner (1971) indicated that the subgenera Platygobio, Macrhybopsis, and Erimystax were more closely allied to the genus Phenacobius than Hybopsis sensu sticto (the amblops group). They also suggested that Hybopsis s.s. was more closely related to the genus Notropis than Hybopsis sensu lato. Furthermore, Jenkins and Lachner predicted the dismemberment of Hybopsis s.l..

A wave of primarily osteological studies of cyprinid genera with cladistic analyses have spawned additional theories concerning relationships within Hybopsis and among other cyprinid genera. These include doctoral dissertations by Coad (1975), Coburn (1982), and Mayden (1985b). At present, general communication of the results of these studies is limited to oral presentations, abstracts, and manuscripts in preparation (Coburn, 1983; Mayden, 1983; Coburn and Cavender, 1985; Cavender and Coburn, 1985). At this point, it seems prudent to summarize the recent works of Coburn (1982) and Mayden (1985b) as they pertain to Erimystax and relatives.

Coburn 1982. Coburn pioneered cladistic analysis in deciphering higher relationships of North American cyprinids. His primary goal was to define of the subgenus Notropis and its component species and determine its relationship to other subgenera within Notropis. Although the primary thrust was in Notropis, it was necessary to analyze additional genera and species of North American cyprinids as outgroups (see Watrous and Wheeler, 1981) to polarize character states within Notropis.

Coburn did little in realigning species within subgenera of Hybopsis but presented several hypotheses of subgeneric relationships. Based on six synapomorphic characters, Coburn linked Phenacobius with the subgenera Extrarius and Erimystax. These are 1) transverse process on 4th Weberian rib heavy, 2) dentary with short, downwardly deflected gnathic ramus and high coronoid process, 3) metapterygoid with single articular process with hyomandibula, 4) ascending arm of preopercle reduced and horizontal arm long, 5) median portion of supratemporal canal crosses occipital, and 6) mesial margin of third pharyngobranchial deeply concave.

Five synapomorphies further unite Phenacobius and Extrarius. These are 1) short triangular basihyal, 2) stubby blunt anterior processes on urohyal, 3) dorsal process of anterior ceratohyal projects over upper hypohyal, 4) efferent pseudobranchial artery is enclosed in ascending wings of parasphenoid, and 5) dorsoposterior prong on the metapterygoid.

Hybopsis s.s., long considered closer to members of Notropis than Hybopsis s.l., was found to share three synapomorphies with members of

the Notropis heterolepis group. These characters include 1) elongate rod-shaped kinethmoid, 2) deep cleft in anterior ethmoid block, and 3) a deep maxilla. More recent work by Coburn and Cavender (1985) found synapomorphies of the jaws, pharyngeal pad, pharyngeal arch, dilator fossa, metapterygoid, and basihyal that unite the subgenus Macrhybopsis (Hybopsis gelida and H. meeki) with Hybopsis storeriana and the subgenus Extrarius. These four species were found to share synapomorphies of the infraorbitals with Erimystax. Additional data apparently led to allignment of Phenacobius with Exoglossum (Cavender and Coburn, 1985).

Mayden 1985b. Mayden analyzed phylogenetics of the subgenus Cyprinella of Notropis and in determining character polarities by outgroup analysis added considerable information to the foundation provided by Coburn. Three synapomorphies unite Agosia, Hybognathus, Exoglossum, Nocomis, Campostoma, Dionda, Platygobio, Phenacobius, and the subgenera Macrhybopsis (including Hybopsis storeriana), Extrarius, and Erimystax (including H. monacha). Mayden refers to this group as the "chub clade". The three derived characters include 1) an elongate, straight, anteriorly directed palatine, 2) a pre-ethmoid groove, and 3) a smooth, oval urohyal.

Within the chub clade, three characters are shared by Platygobio, Macrhybopsis, Extrarius, Erimystax, and Phenacobius. The synapomorphies are 1) a nuptial pad on the inter- and preopercles, 2) a short triangular basihyal, and 3) a single articular surface for the hyomandibular on the metapterygoid. Macrhybopsis and Platygobio share characters of pigmentation of the caudal fin and a thin, lamellate,

ventral horizontal plate of the urohyal. Extrarius, Phenacobius, and Erimystax are monophyletic, sharing the synapomorphies given by Coburn. Mayden defines an Erimystax-Phenacobius clade based on five derived characters: 1) a narrow caudal skeleton, 2) lachrymal skin flap with taste buds, 3) a ventrally deflected posttemporal cephalic canal, 4) broad plate-like second infraorbital bone, and 5) reduced dorsal cephalic tuberculation.

Erimystax is defined by the following synapomorphies: 1) a unique "stellate barbel", and 2) elongate basihyal. Within Erimystax, he envisions a trichotomy with E. monacha, E. x-punctata, and the clade composed of E. dissimilis, E. insignis, and E. cahni. The dissimilis-insignis-cahni clade is based on a narrowly developed maxillary process of the palatine.

Comments. Hypotheses of Mayden and Coburn concerning higher relationships of Erimystax are generally congruent except for Coburn's placement of Platygobio outside the open myodome clade. This decision was based on the fused posterior myodome opening which Mayden contends is derived in Platygobio based on an open posterior myodome in juveniles. This decision is justified by additional synapomorphies discussed earlier. Coburn did not examine Hybopsis gelida or H. meeki so no relationships of Macrhybopsis were proposed.

Cavender and Coburn (1985) interpret close relationship in Erimystax-Extrarius-Macrhybopsis while Mayden (1985b) prefers an Erimystax-Phenacobius-Extrarius clade. Coburn feels Erimystax and Extrarius are sister groups but Mayden interprets Phenacobius and Erimystax as more closely related. I would not pretend to pass

judgement on their interpretations. However, I would suggest the differences in interpretation are due to a several factors. First, cyprinid osteological study for North American taxa is in its infancy. Many of the characters which seem promising for defining clades will, with further study and analysis of additional specimens, be found not so informative. Secondly, these osteological studies have been performed with relatively few specimens from each species so that variation within a particular taxon cannot be adequately evaluated. Therefore, characters that are relative in nature, such as thickness, width, or minor departures in angulation, are not as conservative as presence-absence characters (i.e., the posterior myodome opening). I am sure as methodology advances, more technical means of comparing individual bones or bone structures will be devised. Computer based graphical comparisons would seem to offer an excellent means of comparing osteological characters. Basing taxonomic decisions on relative characters should await variational studies of these characters over the range of a taxon.

The Phenacobius-Erimystax clade of Mayden (1985b) is based on five synapomorphies which include lachrymal skin flap with taste buds and reduced dorsal cephalic tuberculation. These characters are subject to the range of variation discussed previously. In the study of Erimystax, I regularly examined the lachrymal region for taste buds (i.e., pappilae). They ranged in development from almost as large as maxillary barbels in Hybopsis x-punctata to non-existent in various H. dissimilis, H. harryi, and H. insignis populations. Regarding head tuberculation, Hybopsis monacha has much larger tubercles than other

members of Erimystax and Phenacobius. Many of these characters need further substantiation before they can be firmly accepted as synapomorphies uniting these groups.

The same questions are raised with the synapomorphies uniting species of Erimystax (Mayden, 1985b). A unique "stellate barbel" certainly expresses itself in some populations of Hybopsis x-punctata but can be virtually absent in other Erimystax populations. Pronouncement of the "stellate barbel" uniting Erimystax should await histological examination to assess structure.

Jenkins and Burkhead (1984) present considerable evidence relating Hybopsis monacha with the subgenus Cyprinella of Notropis. These, as well as characters suggested by Coburn (1982), Mayden 1985b), and this study, are summarized in Table II-41 comparing Erimystax, H. monacha, and Cyprinella. This information was consolidated form the work of Burkhead, et al. (1985), Pflieger (1975), Coburn (1982), Howell and Williams (1971), Jenkins and Burkhead (1984), Wallace and Ramsey (1981), Outten (1958), Gibbs (1963), Gibbs (1957), Gibbs (1961), Jenkins, et al. (ms), Etnier and Starnes (ms), and Lee, et al. (1980). Outgroups used to polarize character states for these taxa were taken from within the open posterior myodome clade of Mayden (1985b).

The following references to character numbers refer to Table II-41. Characters are referrable to three groups: 1) meristic, 2) sensory, and 3) reproductive. Meristic group character 1, pharyngeal dentition, is interpreted as a synapomorphy uniting Erimystax with H. monacha. Coburn (1982) has interpreted loss of teeth from the minor

Table II-41. Characters Used to Evaluate Phylogenetic Relationships among *Erimystax*, *Hybopsis monacha*, and *Cyprinella*.

Character	Erimystax	H. monacha	Cyprinella
1) Pharyngeal teeth	4-4	4-4	1,4-4,1
2) Anal rays	7	8	8-11
3) Lateral-line scales	38-50	53-61	32-43
4) Peduncle scales	12-16	15-19	14-16
5) Predorsal-postdorsal length	Post >	Pre >	Pre >
6) Eye diameter	67-79	49-51	60-80
7) Labial barbels	Yes	Yes	No
8) Pectoral sensory structures	Yes	Yes	No
9) Upper lip expanded	Yes	Yes	No
10) Interradial dorsal fin pigment	No	Yes	Yes
11) Head tubercles	Small Random	Large Rows	Large Rows
12) Pectoral tubercles ray 1	No	Yes	Yes
13) Breeding colors	No	Yes	Yes
14) Nuptial pad	Always	Some	Never
15) Ovum diameter	>1.5	1.0-1.3	0.8-1.4
16) Spawning	open substrate	crevice	crevice
17) Known hybrids	*Erimystax*	*Cyprinella*	*H. monacha*

row as the derived state based on the work of Nelson (1969) and Chu (1935). No clear polarization of character 2 was obtained from outgroups within the open myodome assemblage, as both seven and eight ray states were common. Looking outside the open myodome clade, eight or more anal rays is the rule. Reduction of anal ray numbers is tentatively interpreted as apomorphic with the seven ray condition a synapomorphy uniting Erimystax species.

Scale numbers are subject to ecophenotypic variation and thus hard to divide into discrete "groupings" for polarization. Outgroup members of the chub and Cyprinella assemblages generally have relatively low scale counts (i.e., larger scales). Using the count groupings for characters 3 and 4, Erimystax and Cyprinella counts are plesiomorphic and H. monacha counts represent the derived state. Again, these polarizations are considered tentative due to the general uncertainty of cyprinid relationships and problems associated with outgroups used for comparisons. Donoghue and Cantino (1984) have discussed the logic and limitations of outgroup methodology when relationships are uncertain. Polarization using outgroups that are relatively apomorphic within a lineage can cause serious misinterpretations of in-group relationships. For example, if the Erimystax-H. monacha-Cyprinella in-group were polarized using only members of the clade lacking the posterior myodome opening, character polarizations for meristics would be opposite of those presented above.

Character five can not be polarized due to insufficient information on outgroups. Erimystax species are considerably longer postdorsally than predorsally (or equal in Hybopsis cahni) whereas H.

monacha and Cyprinella species (for which data were available) are much longer predorsally. This may be a result of dorsal fin placement, dorsal profile, or differences in relative numbers of precaudal and caudal vertebrae (see Jenkins and Lachner, 1971). Eye diameter was not polarized due to insufficient data for outgroups. Hybopsis monacha has a considerably smaller eye than Erimystax. Also, its direction is more lateral than the dorsolateral, slightly posterior direction of the eyes in Erimystax. Character 7, labial barbels, has been discussed previously. Suffice to say that the heteromorphic assemblage known as Hybopsis has been defined based on the presence of a maxillary barbel which is a "variable and labile character...which may have arisen independently several times" (Jenkins and Lachner, 1971).

Compound taste buds on the pectoral fins (and other fins in some species) is a derived condition found in Hybopsis s.l. (Davis and Miller, 1967). Jenkins and Burkhead (1984) make no mention of these stuctures in H. monacha. This character may also have arisen independently several times in the Hybopsis lineage.

Character 9, the anteriomedial upper lip expansion (Jenkins and Burkhead, 1984), is interpreted as a synapomorphy linking Erimystax and Hybopsis monacha. Pigmentation between posterior dorsal fin rays (character 10) is interpreted as a synapomorphy linking H. monacha with Cyprinella.

Characters 11-17 are considered the reproductive group. Characters 11-13 are synapomorphies linking Hybopsis monacha with Cyprinella. The nuptial pad (character 14) is considered unique to

the Phenacobius-Erimystax-Macrhybopsis-Extrarius clade. It is quite variable in its expression among these taxa. I have never observed it missing in mature Erimystax (less H. monacha) and Phenacobius species. I also have observed many Extrarius males that appeared in peak reproductive condition but have yet to observe a nuptial jaw pad. Jenkins and Burkhead (1984) have observed the character in but two adult males of Hybopsis monacha. It is certainly a character that expresses phylogenetic information whose full content has yet to be revealed. Dionda has a nuptial pad in breeding males which is similar but considered convergent due to "different location and morphological dissimiliarities" (Mayden, 1985b). This character may be more primitive than currently recognized and differentially expressed by descendant taxa. Perhaps some lineages have retained the character fully while others express the state only occasionally in individuals that have inherited the primitive genotype. At present it is considered a synapomorphy linking H. monacha with Erimystax.

Coburn (1982) has opened the interesting possibility of using ovum diameter as a phylogenetic character. Data from his study reveal Cyprinella species ova diameters are generally in the 1.0 mm range (except Notropis pyrrhomelas = 1.4 mm) and Jenkins and Burkhead (1984) give a range of 1.0-1.3 mm for Hybopsis monacha. Analyses of Erimystax species reveal mean ovum diameters in the 1.5 mm range. Coburn (1982) has concluded that small ovum diameter is plesiomorphic but still the problem of separating ranges into distinct groups exists (as in scale count groups). Large ovum size is tentatively considered

a synapomorphy linking species of Erimsytax. Analysis of morphology of fertilized ova may prove useful as a phylogenetic character.

Recent information presented by Burkhead, et al. (1985) links Hybopsis monacha with Cyprinella in spawning behavior (character 16). These observations suggest classification of both as crevice spawners. My observations of Erimystax spawning behavior indicate that these species are open substrate spawners. Crevice spawning is considered a synapomorphy uniting H. monacha and Cyprinella.

Character 17 can not be polarized but is considered indicative of close relationship. Hybrids are known between Hybopsis monacha and Notropis (Cyprinella) galacturus (Burkhead and Bauer, 1983). Trautman (1957) hypothesized hybridization between H. (Erimystax) dissimilis and H. (Erimystax) x-punctata and I have observed putative hybrids between H. (Erimystax) dissimilis and H. (Erimystax) insignis.

Mayden (1985b) aligned Hybopsis s.s. with species currently in Notropis and recommended elevation of the subgenera of Hybopsis s.l. to generic rank. Should these recommendations be formalized, I would recommend the resurrection of Erimonax (Jordan, 1924) to at least the subgeneric level (after Jenkins and Burkhead, 1984) for H. monacha until relationships are resolved. Biochemical studies may shed additional light on the relationships of this complex assemblage.

4. MATERIAL EXAMINED

The following universities, museums, institutions, and individuals (abbreviations in parentheses) provided materials used in the multivariate analyses: Academy of Natural Sciences of Philadelphia (ANSP), Appalachian Environmental Laboratory (AEL), Arkansas State University (ASUMZ), Auburn University (AU), Cornell University (CU), Eastern Kentucky University (EKU), Field Museum of Natural History (FMNH), Florida State Museum (FSM), Illinois Natural History Survey (INHS), Iowa State Univeristy (ISU), Robert E. Jenkins (REJ), Mississippi State University (MSU), National Museum of Natural History (USNM), North Carolina State Museum (NCSM), Northeast Louisiana University (NLU), Ohio State University (OSUMZ), Oklahoma State University (OAM), Pennsylvania State University (PSU), Henry W. Robison (HWR), Royal Ontario Museum (ROM), Southern Illinois University (SIUC), Stanford University (SU), Wayne C. Starnes (WCS), Tulane University (TU), University of Alabama (UAIC), University of Georgia (UGA), University of Kansas (KU), University of Louisville (UL), University of Michigan (UMMZ), University of Minnesota (UM), University of Northern Iowa (UNI), University of Oklahoma (UOMZ), University of North Carolina-Charlotte (UNCC), and University of Tennessee (UT). Collection abbreviations followed by a question mark indicate the museum destination for uncatalogued material or collections presently at a museum awaiting curation.

A. Meristic and Morphometric Specimens

Hybopsis dissimilis (Kirtland) -- Spotted chub

Allegheny R. Drainage. NY: Cattaraugus Co.: NLU 31017, Allegheny R. 0.7mi W Portville (3); CU 62479, Allegheny R. at Rt. 219 (2); TU 4334, Allegheny R. at Allegheny (10); CU 62733, Allegheny R. at Vandalia (5); PA: Forest Co.: CU 6713, Allegheny R. 1.0 mi N Tionesta (2); Warren Co.: CU 9409, Allegheny R. 8.0 mi NE Tidioute (7); PSU 637, Allegheny R. near Warren (5); Venango Co.: USNM 161903, French Cr. at Rt 19 (2).

Muskingum R. Drainage. OH: Coshocton Co.: OSUMZ 11995, Walhonding R. (3); OSUMZ 963, Walhonding R. 1.0 mi above Six Mile Dam (1); OSUMZ 12757, Walhonding R. 1.0 mi above Six Mile Dam (1); OSUMZ 16920, Walhonding R. at Warsaw (1); OSUMZ 998, Walhonding R. at Walhonding (2); ROM 17378, Walhonding R. Newcastle Township (1); Ashland Co.: OSUMZ 511, Clear Fork Mohican R. Hanover Township (2); Muskingum Co.: OSUMZ 924, Muskingum R. at Ellis Dam (1).

Scioto R. Drainage. OH: Pickaway Co.: OSUMZ 18950, Scioto R. SE Jackson Township (2); OSUMZ 13574, Scioto R. Jackson Township (1); KU 11353, Big Darby Cr. at Rt. 104 (1); OSUMZ 8389, Big Darby Cr. 1.0 mi S Fox (5); CU 46838, Big Darby Cr. 1.0 mi S Fox (1).

Elk R. Drainage. WVA: Braxton Co.: CU 32504, Elk R. below Gassoway (10); CU 32284, Elk R. above Hyer (1); CU 32404, Elk R. 2.0 mi above Frametown (7); Kanawha Co.: AEL 288, Kanawha R. below London Locks (2); Webster Co.: AEL 627, Elk R. at Co Rd 7 (3).

Big Sandy R. Drainage. KY: Floyd Co.: UL 6654, Levisa Fork 5.0 mi SE Allen (10); Pike Co.: UT 44.1754, Russell Fork at US Hwy 80 (5); UL 6637, Levisa Fork at confl Russell Fork near Milland (4).

Kentucky R. Drainage. KY: Leslie Co.: UL 7163, Greasy Cr. 9.0 mi S Hyden (4); UL 10548, Middle Fork KY R. (6); Owsley Co.: UMMZ 177821, Redbird Cr. at confl Sexton Cr. 8.0 mi N Oneida (3); UMMZ 168879, Redbird Cr. at confl Sexton Cr. (3); Perry Co.: UL 11774, Middle Fork KY R. at Buckhorn (10); USNM 206474, Middle Fork KY R. (7).

Green R. Drainage. KY: Allen Co.: UL 11944, Barren R. 1.5 mi W Allen-Monroe Co. line (3); Barren Co.: UMMZ 154687, Peters Cr. 10.0 mi NE Scottsville (3); Green Co.: UMMZ 165281, Green R. at Greensburg (1); UL 11916, Green R. 15 mi upstream Greensburg (5); UL 11910, Green R. 6.0 mi downstream confl Pitman Cr. (8); Hart Co.: EKU 84, Green R. at KY Hwy 31W (7); Monroe Co.: USNM 206478, Salt Lick Cr. 1.0 mi E Akersville (10); Warren Co.: SU 3228, Barren R. at Bowling Green (3); USNM 63838, Barren R. at Bowling Green (3).

White R. Drainage. IN: County Unknown: USNM 20145, White R. (1); USNM 23448, White R. (2); Johnson Co.: INHS 73810, Cress Cr. 4.0 mi E Franklin (1).

Wabash R. Drainage. IN: Cass Co.: USNM 206511, Eel R. (1); Fulton Co.: USNM 69077, Tippecanoe R. at Marshland (2); USNM 66892, Tippecanoe R. at Marshland (7); USNM 66891, Tippecanoe R. at Marshland (2); USNM 40739, Tippecanoe R. at Marshland (1); Pulaski Co.: UGA 214, Tippecanoe R. (3); Starke Co.: USNM 69209, Bass Lake (1).

Red R. Drainage. KY: Logan Co.: SIUC ?, Red R. at Dot (1); TN: Robertson Co.: CU 22181, Red R. at Rt 41 (1); CU 22162, Sulphur Fork Cr. 5.0 mi S Adams (1); CU 23136, Sulphur Fork Cr. at Hills Mill, Rt 76 (2); CU 23134, Sulphur Fork Cr. at Hills Mill, Rt 76 (1).

Harpeth R. Drainage. TN: Cheatham Co.: UT 44.1109, Harpeth R. 1.5 mi N US Hwy 70 (1); CU 49952, Harpeth R. at US Hwy 70 (13); Uncat., Turnbull Cr. (2).

Stones R. Drainage. TN: Rutherford Co.: TU 19493, E. Fork Stones R. at Hwy 231 (10); CU 52868, E. Fork Stones R. at Hwy 231 (3).

Obey R. Drainage. TN: Jackson Co.: CU 51632, Blackburn Fork Roaring R. at Rt 135 (1); UMMZ 168200, Cumberland R. 6.5 mi NE of Gainesboro (1); Overton Co.: KU 14189, W. Fork Obey R. 5.0 mi W Alpine (1); UT 44.?, W. Fork Obey R. near Alpine (3); Pickett Co.: UMMZ 121732, Obey R. at Pryor Bend (1); UT 44.2095, Wolf R. at confl Town Branch Cr. 1.0 mi NE Byrdstown (2); Unknown Co.: USNM, Obey R. at Olympus (1).

Little S. Fork Cumberland R. Drainage. KY: McCreary-Wayne Co.: UT 44.436, Little S. Fork Cumberland R. at Hwy 92 (1); SIUC 2282, Little S. Fork Cumberland R. at Hwy 92 (2); SIUC 7284, Little S. Fork Cumberland R. at Ritner Ford (9); Uncat., Little S. Fork Cumberland R. at Ritner Ford (3); Wayne Co.: UT 44.436, Little S. Fork Cumberland R. 0.5 mi upstream confl Stone Dry Branch (3); TU 74570, Little S. Fork Cumberland R. at Parmleysville (1).

Duck R. Drainage. TN: Bedford Co.: UT 44.1569, Duck R. 2.0 mi NW Elbethel (10); Lewis Co.: NLU 47616, Buffalo R. at confl Grinder's Creek (10); NLU 43115, Buffalo R. at confl Grinder's Creek (4);

Marshall Co.: NLU 52963, Duck R. at RM 173.1 1.0 mi above Hardison Mill (8); NLU 50385, Duck R. at confl Caney Cr., RM 176.9 (6); Perry Co.: TU 101802, Buffalo R. at RM 54 (1); NLU 28631, Buffalo R. at Beardstown (7); Wayne Co.: NLU 28801, Buffalo R. at Hwy 13 (1).

Shoal Cr. Drainage. AL: Lauderdale Co.: MSU 6097, Shoal Cr. at Hwy 8 (1); UAIC 7178.01, Shoal Cr. at RM 13.9-15.9 (4); UAIC 7177.01, Shoal Cr. at Co. Rd 94 (5); TN: Lawrence Co.: MSU 6117, Shoal Cr. at Iron City (3); UAIC 4769.03, Shoal Cr. (4).

Elk R. Drainage. AL: Madison Co.: Uncat., Flint R. at RM 24.6-26.3 (2); TN: Lincoln Co.: UT 44.1556, Elk R. at Hwy 231/431 (5); TU 30256, Elk R. at Fayetteville (10).

Paint Rock R. Drainage. AL: Jackson Co.: UT 44.1619, Paint Rock R. at Co. Rd 4 (2); UT 44. ? , Paint Rock R. along Co. Rd 9 S Estillfork (10); USNM 248184, Paint Rock R. at confl Estill Fork and Hurricane Cr. (6); UAIC 7176.01, Paint Rock R. at RM 30.7 (2); UAIC 7172.01, Paint Rock R. at RM 17.3 (1); Unknown Co.: ANSP 84360, Paint Rock R. (8).

Holston R. Drainage TN: Sullivan Co.: UT 44.271, N. Fork Holston R. at Hwy 23 (10); Carter Co.: UMMZ 130823, Watauga R. at Hwy 37 (1); USNM 40468, Watauga R. at Elizabethton (2); VA: Scott Co.: Uncat., N. Fork Holston R. at Rt 778 (6); Smyth Co.: UMMZ 96883, N. Fork Holston R. above Saltville (3); VPI 892, Middle Fork Holston R. above Chilhowie (10).

Clinch-Powell R. Drainage. TN: Claiborne Co.: UT 44.1488, Powell R. at US Hwy 25E (5); FSM 17167, Powell R. at US Hwy 25E (7); NLU 50205, Powell R. at Buchanan Ford, RM 99.2 (10); UT 44.518, Powell

R. 3.5 mi SW US Hwy 25E (3); Hancock Co.: UT 44.1631, Clinch R. at Frost Ford, 3.7 mi NE Sneedville (15); NLU 39507, Clinch R. at Frost Ford (10); TU 96244, Clinch R. at Frost Ford (4); VA: Lee Co.: UMMZ 96928, Indian Cr. (1); Scott Co.: TU 70439, Copper Cr. 0.4 mi upstream confl Clinch R. (5).

Salt R. Drainage. KY: Marion Co.: Uncat., Rolling Fork Salt R. 2.0 km NE Jessietown (10).

Hybopsis harryi Hubbs and Crowe -- Ozark chub

Little Red R. Drainage. AR: Van Buren Co.: NLU 47891, Archey's Fork Little Red R. at Hwy 65 (1); WCS ?, Archey's Fork Little Red R. at Hwy 65 (1); NLU ?, Archey's Fork Little Red River downstream U.S. Hwy 65 xing (26); Unknown Co.: FMNH 859, Middle Fork Little Red R. at Kinderhook (1).

St. Francis R. Drainage. MO: Madison Co.: St. Francis R. at Rt C (1); NLU 53585, St. Francis R. at Hwy 34 (25).

Spring R. Drainage. AR: Fulton Co.: NLU 41045, S. Fork Spring R. 1.0 mi W Saddle (3); NLU 41033, S. Fork Spring R. 1.0 mi N Moko (2); NLU 42295, English Cr. at Hwy 289 (1); ASUMZ 5873, Myatt Cr. at Hwy 9 (3); ASUMZ 6286, Myatt Cr. at Hwy 289 (2); ASUMZ 5802, Myatt Cr. (1); ASUMZ 5825, Myatt Cr. (1); ASUMZ 5767, Myatt Cr. (2); NLU ? , Myatt Cr. at Hwy 289 (2).

Eleven Point R. Drainage. AR: Randolph Co.: ASUMZ 7279, Eleven Point R. at confl Diles Cr. (10).

Current R. Drainage. AR: Randolph Co.: TU 66785, Current R. 4.5 mi NW Success (10); ASUMZ 2474, Current R. (4); MO: Shannon Co.:

Uncat., Jacks Fork Current R. (1); KU 7641, Current R. at Round Springs State Park (3); KU 3311, Jacks Fork Current R. at Alley Springs State Park (3); UMMZ 157698, Current R. at confl Big Spring Branch (3) PARATYPES.

Black R. Drainage. MO: Reynolds Co.: KU 16572, W. Fork Black R. at Rt 21 (10); Wayne Co.: NLU 53583, Black R. at Hwy 49 (4); Unknown Co.: OAM 7225, Upper Black R. (5).

Upper White R. Drainage. AR: Independence Co.: NLU 20074, White R. at Lock and Dam 3, 15.0 mi NW Batesville (10); Izard Co.: NLU 13754, White R. 0.5 mi NW Guion (10); Marion Co.: NLU 26937, Buffalo R. at Hwy 14 (5); Newton Co.: NLU 26152, Big Cr. 0.2 mi SE Carver (6); Searcy Co.: NLU 25272, Buffalo R. at Hwy 65 (8); Stone Co.: NLU 13914, White R. at Lock and Dam 3 (20); MO: Barry Co.: UMMZ 151344, White R. 3.0 mi S Shell Knob (2) PARATYPES; UMMZ 167083, White R. 3.0 mi SE Mano (1) HOLOTYPE; Christian Co.: KU 10840, James R. at confl Wilson Cr. (1); Taney Co.: KU 10919, Beaver Cr. at Kissee Mills (2).

Hybopsis insignis Hubbs and Crowe -- Blotched chub

Red R. Drainage. TN: Montgomery Co.: CU 23257, Yellow Cr. at Rt. 13 (2); CU 50300, Confl Sulphur Fork Cr. and Red R. at Port Royal (2); KY: Logan Co.: SIUC ? , Red R. at Dot (15); SIUC ? , Red R. NE Smith Grove Church (1).

Lower Tennessee R. Drainage. KY: Calloway Co.: UMMZ 157702, Tennessee R. at Blood Island (1) HOLOTYPE; UMMZ 157703, Tennessee R. at Blood Island (1) PARATYPE.

Harpeth R. Drainage. TN: Cheatham Co.: CU 49953, Harpeth R. at Hwy 70 (10); UT 44.1225, Harpeth R. 2.0 mi N Hwy 70 (10); UMMZ 174467, Turnbull Cr. 1.0 mi W Kingston (5); UT 44.2569, Turnbull Cr. 0.6 mi E Craggie Hope (2).

Stones R. Drainage. TN: Rutherford Co.: CU 52869, E. Fork Stones R. at Hwy 231 (9); UT 44.560, E. Fork Stones R. at Hwy 231 (10); TU 33195, Stones R. at Walterhill, Hwy 231 (6).

Caney Fork R. Drainage. TN: Smith Co.: UMMZ 86294, Caney Fork R. at Lancaster (1) PARATYPE; NLU 25653, Smith Fork at Hwy 141 (3); SU 5152, Smith Fork at Lancaster (5).

Roaring R. Drainage. TN: Jackson Co.: UMMZ 168248, Roaring R. 2.0 mi upstream confl Cumberland R. (6) PARATYPES; KU 11540, Roaring R. at Rt 135 (3); UMMZ 125082, Blackman's Fork E of Gainesboro (1) PARATYPE.

Crocus Cr. Drainage. KY: Cumberland Co.: CU 51582, Crocus Cr. at Rt 704 (9); UMMZ 177970, Crocus Cr. at Rt 704 (3); UL 8038, Crocus Cr. (3).

Little S. Fork Cumberland R. Drainage. KY: Wayne-McCreary Co.: UT 44.289, Little S. Fork at Ritner Ford (5); SIUC 7285, Little S. Fork at Ritner Ford (5); Uncat., Little S. Fork at Ritner Ford (4); Uncat., Little S. Fork at Ritner Ford (5).

Duck R. Drainage. TN: Bedford Co.: UT 44.1570, Duck R. 5.7 mi NW Shelbyville (7); Maury Co.: UT 44.570, Duck R. at Kettle Mills (3); Hickman Co.: UT 44.1597, Duck R. 8.0 mi E Centerville (10); UT 44. ?, Piney R. 6.6 mi NW Centerville (1); Humphreys Co.: UT 44.1738, Duck R. 1.0 mi upstream confl Hurricane Cr. (10); UT 44.775, Buffalo R. 1.3

mi upstream of mouth (19); Lewis Co.: UT 44.502, Buffalo R. at confl Grinders Cr. (4).

Shoal Cr. Drainage. AL: Lauderdale Co.: USNM 36662, Shoal Cr. at Florence (1); AU 2916, Big Butler Cr. at Pruitton (2); UAIC 7178.02, Shoal Cr. at confl Butler Cr. (6); UAIC 7177.02, Shoal Cr. at Co. rd 94 NE of Florence (11); TN: Lawrence Co.: MSU 6117, Shoal Cr. at Iron City (5); UAIC 4771.03, Factory Cr. (1).

Elk R. Drainage. TN: Giles Co.: UT 44.2163, Elk R. 0.75 mi upstream Co. Rd 6234 (20); UT 44.2343, Richland Cr. at Co. Rd 4209 (10).

Paint Rock R. Drainage. AL: Jackson Co.: UT 44.2352, Paint Rock R. at Co. Rd 9 (3); UAIC 6341.04, Paint Rock R. 1.3 mi S Princeton (1); UAIC 6354.03, Paint Rock R. 12.0 mi NE Paint Rock (4); UAIC 6345.03, Paint Rock R. 0.6 mi S Swain (2); UAIC 6347.03, Paint Rock R. at confl Estille Fork and Hurricane Cr. (1); UAIC 7176.02, Paint Rock R. at RM 30.7 (5); Madison Co.: UAIC 7174.01, Paint Rock R. at RM 19.1 (8); Unknown Co.: ANSP 84360, Paint Rock R. (3).

Sequatchie R. Drainage. TN: Marion Co.: Uncat., Sequatchie R. 0.5 mi upstream confl Little Sequatchie R. (10); Uncat., Sequatchie R. at RM 17, Ketner's Mill (8); Sequatchie Co.: UF 15531, Sequatchie R. 1.5 mi NNE of Marion-Sequatchie Co. line (6); UMMZ 168138, Sequatchie R. 8.0 mi SSW Dunlop (1); TU 33463, Sequatchie R. at Hwy 127 (1).

Hiwassee R. Drainage. GA: Union Co.: UAIC 2556, Nottely R. at GA Hwy 180 (1); CU 62998, Toccoa R. at GA Hwy 60 (6); TU 38288, Toccoa R. at GA Hwy 60 (1); TU 37412, Toccoa R. 1.0 mi E GA Hwy 60 (6); TU 40757, Toccoa R. along GA Hwy 60 19.4 mi SE Morgantown (5); UG 759,

Suches Cr. (1); UG 742, Town Cr. (1); UT 44.577, Coosa Cr. at GA Hwy 76 (2); UMMZ 94592, Arkaqua Cr. (1); NC: Clay Co.: UMMZ 156368, Brasstown Cr. (4) PARATYPES; Cherokee Co.: NCSM 4814, Valley R. at Co. Rd 1515 (10); TU 25647, Valley R. 4.6 mi SW Marble (5).

Little Tennessee R. Drainage. TN: Monroe Co.: USNM 70587, Tellico R. at Tellico Plains (1); UT 44. ? , Citico Cr. 0.6 mi upstream confl Little Tennessee R. (7); UT 44.2219, Citico Cr. 3.8 mi upstream confl Little Tennessee R. (2); UT 44. ? , Citico Cr. (3); UT 44. ? , Citico Cr. (3).

Little R. Drainage. TN: Blount Co.: Uncat., Little R. at US Hwy 411 (10); UT 44.426, Little R. at US Hwy 411 (10); USNM 231228, Little R. at US Hwy 411 (5).

Little Pigeon R. Drainage. TN: Sevier Co.: UT 44.93, Little Pigeon R. at Sevierville (10); USNM 129320, W. Prong Little Pigeon R. (1) HOLOTYPE; NLU, 19062, W. Prong Little Pigeon R. at Hwy 441, Pigeon Forge (6); NLU 6142, W. Prong Little Pigeon R. at Pine Grove (6); USNM ? , Walden Cr. (4).

Pigeon R. Drainage. TN: Cocke Co.: UMMZ 131494, Cosby Cr. at Padgett Mill (1) PARATYPE.

French Broad R. Drainage. NC: Buncombe Co.: UMMZ 138558, French Broad R. 2.0 mi SW Skyland (1) PARATYPE; CU 10052, French Broad R. 2.0 mi SW Skyland (3); USNM 40613, Swannanoa R. at Black Mountain (1); UMMZ 156039, Cane Cr. 5.25 mi NE Fletcher (1) PARATYPE; UT 44.1894, Cane Cr. at Co. Rd 3138, 4.0 mi SE Skyland (7); CU 63423, Cane Cr. at Co. Rd 3116, 3.0 mi E. Fletcher (6); UMMZ 156067, Cane Cr. 0.25 mi N Henderson-Buncombe Co. line (9); Henderson Co.: UMMZ 156004,

Mills R. 1.5 mi W Mills River (2); UMMZ 156021, S. Fork R. 3.0 mi SW Mills River (10) PARATYPES; UT 44.1892, Mills R. at NC Hwy 280/191 (10); CU 63350, S. and N. Fork Mills R. at Co. Rd 1342 (7); CU 63134, S. Fork Mills R. 4.0 mi SW Mills River (5); Madison Co.: CU 22876, Ivy Cr. 6.5 mi SW Mars Hill(1); USNM 40606, Spring Cr. at Hot Springs (2) PARATYPES; SU 1025, Spring Cr. at Hot Springs (1).

Nolichucky R. Drainage. NC: Yancey Co.: UNCC 77-93, Cane R. 2.0 mi E Sioux (10); TN: Greene Co.: UT 44.1681, Nolichucky R. at RM 19.7 (10); UT 44. ? , Nolichucky R. at RM 44 (?), Unicoi Co.: UT 44.1682, N. Indian Cr. at confl Nolichucky R. (2).

Holston R. Drainage. TN: Carter Co.: UMMZ 157415, Elk R. 2.5 mi S Butler (1) PARATYPE; Johnson Co.: UMMZ 157433, Roan Cr. 1.4 mi upstream confl Little Doe Cr. (5); Sullivan Co.: UMMZ 157763, S. Fork Holston R. 1.0 mi S TN-VA line (4); UMMZ 157563, S. Fork Holston R. 0.5 mi upstream damsite (1) PARATYPE; UMMZ 157511, S. Fork Holston R. at confl Jacob Cr. (1); UMMZ 157535, S. Fork Holston R. at confl Fish Dam Cr. (1); VA: Washington Co.: TU 34581, S. Fork Holston R. at Hwy 91 (1); REJ, S. Fork Holston R. at Co. Rd 711 (4).

Clinch R. Drainage. VA: Russell Co.: NLU 20313, Little River above Duncan Branch (10); Scott Co.: CU 64106, Copper Cr. 0.25 mi upstream confl Clinch R. (10); CU 62828, Copper Cr. 2.5 mi upstream confl Clinch R. (10); TU 69245, Copper Cr. 2.5 mi NE Speers Ferry (10).

Powell R. Drainage. TN: Claiborne Co.: REJ, Powell R. 0.8 mi NW Hoop, RM 153.5 (1); NLU 50859, Powell R. at Buchanan Ford, RM 99.2 (1); NLU 50581, Powell R. at Buchanan Ford, RM 99.2 (5); UMMZ 112994,

Indian Cr. (1); NLU 50635, Powell R. at McDowell Ford, CO. Rd 2592 (2); VA: Lee Co.: UMMZ 103438 and 103439, Powell R. at confl Station Cr. (6); NLU 50325, Powell R. 1.9 mi upstream TN-VA line (5); NLU 50621, Powell R. 1.9 mi upstream TN-VA line (3); NLU 50497, Powell R. 2.5 mi upstream TN-VA line (2).

Hybopsis x-punctata Hubbs and Crowe -- Gravel chub

Allegheny R. Drainage. PA: Venango Co.: UMMZ 108121, Allegheny R. (1); Warren Co.: CU 6741, Allegheny R. 2.0 mi S Tidioute (1); PSU 32, Allegheny R. at Kinzua Dam (10); NY: Cattaraugus Co.: UMMZ 180963, Allegheny R. at confl Pierce Run (1); CU 62734, Allegheny R. at Vandalia (1); CU 62499, Allegheny R. 1.0 mi downstream Rt 219 (3); TU 7902, Allegheny R. at Allegany (7); CU 44619, Allegheny R. at S. Carrolton (1).

Muskingum R. Drainage. OH: Coshocton Co.: UMMZ 177278, Walhonding R. Newcastle Township (1) HOLOTYPE; UMMZ 177279, Walhonding R. Newcastle Township (5) PARATOPOTYPES; OSUMZ 12307, Walhonding R. (4); OSUMZ 12171, Walhonding R. (3); OSUMZ 1237, Tuscarawas R. Lafayette Township (5); Muskingum Co.: UMMZ 86018, Muskingum R. (2) PARATYPES; Washington Co.: UMMZ 87782, Muskingum R. west-central Muskingum Township (1); UMMZ 107290, Muskingum R. west-central Muskingum Township (6); UMMZ 87761, Muskingum R. at Lowell (2).

Scioto R. Drainage. OH: Athens Co.: OSUMZ 9-270, Hocking R. Troy Township (1); Lawrence Co.: OSUMZ 580, Ohio R. at Dam 29 (1); Pike Co.: OSUMZ 21226, Camp Cr. (10); UMMZ 87744, Scioto R. SW Scioto Township (1) PARATYPE; OSUMZ 15774, Scioto R. Newton-Camp Townships

(10); OSUMZ 13335, Scioto R. S Waverly (1); Ross Co.: OSUMZ 11284, Scioto R. Jefferson Township (2); UMMZ 87812, Scioto R. Springfield Township (1) PARATYPE; Scioto Co.: OSUMZ 17531, Scioto R. Rush Valley Township (4); OSUMZ 15365, Scioto R. Clay-Washington Townships (6).

Whitewater R. Drainage. IN: Franklin Co.: OSUMZ 28165, Whitewater R. Highland Township (1); OH: Clermont Co.: UMMZ 107775, Little Miami R. at Milford (1); Hamilton Co.: OSUMZ 11285, Whitewater R. (1).

Green R. Drainage. KY: Green Co.: USNM 63836, Green R. at Greensburg (1).

Wabash R. Drainage. IN: Cass Co.: USNM 125130, Eel R. at Logansport (1); Jackson Co.: OSUMZ 27727, E. Fork White R. Jackson Township (1); Knox Co.: USNM 66890, Wabash R. at Vincennes (1); USNM 40837, Wabash R. at Vincennes (2); USNM 40863, Wabash R. at Vincennes (4); USNM 40881, Wabash R. at Vincennes (2); Marion Co.: USNM 36746, White R. at Indianapolis (1); Martin Co.: OSUMZ 28824, E. Fork White R. Halbert Township (1); Owen Co.: USNM 175003, White R. at Gosport (2); USNM 36497, White R. at Gosport (7); Parke Co.: INHS 73971, Racoon Cr. at Coxville (1); Posey Co.: USNM 68952, Wabash R. at New Harmony (1); UMMZ 81328, Wabash R. at New Harmony (10) PARATYPES; Putnam Co.: OSUMZ 27384, Big Walnut Cr. (1); Unknown Co.: USNM 117359, White R. (1); UMMZ 100851, Salamonie R. near Monument City (6); Vermillion Co.: OSUMZ 27219, Brouillette's Cr. Clinton Township (2); UMMZ 27026, Big Vermillion R. Vermillion Township (7); Vigo Co.: ISU 363, Brouillette's Cr. at Shepardsville (1); ISU 362, Wabash R. 8.0 mi N Terre Haute (1); Warren Co.: OSUMZ 28896, Wabash R. Liberty

Township (2); INHS 77168, Big Pine Cr. 2.5 mi N Williamsport (4); ISU 361, Pine Cr. 5.0 mi W Attica (2); IL: Clark Co.: UT 44.1683, Wabash R. (1); Lawrence Co.: UMMZ 167084, Wabash R. at St. Francisville (1) PARATYPE; INHS 12036, Vermillion R. 4.0 mi E Westville (1).

Thames R. Drainage. Canada: Ontario: UMMZ 60436, Thames R. at Munsey Indian Reserve (4); ROM 8417, Thames R. (1); ROM 20018, Thames R. (4).

Root R. Drainage. MN: Fillmore Co.: UMMZ 157330, Root R. (2) PARATYPES; UM 14841, Root R. at Rushford (1); Olmsted Co.: UM 19696, N. Fork Root R. (5).

Upper Iowa R. Drainage. IO: Winnishiek Co.: NLU 53587, Upper Iowa R. at Hwy A 34 (25).

Turkey R. Drainage. IO: Clayton Co.: UNI D63-16, Volga R. at Osborn (2); UNI D68-3, Turkey R. at Osterdock.

Wapsipinicon R. Drainage. IO: Buchanan Co.: UMMZ 162817, Wapsipinicon R. Sumner Township (5).

Rock R. Drainage. IL: Ogle Co.: INHS 22347, Kyte R. 2.0 mi SE Chana (1); FMNH 84850, Rock R. 5.0 mi S Oregon (1); INHS 22312, Rock R. 2.5 mi NE Byron (9); INHS 22270, Rock R. 1.0 mi S Oregon (5); Winnebago Co.: INHS 3588, Rock R. 6.0 mi S Rockford (1); Whiteside Co.: INHS 22994, Elkhorn Cr. 1.0 mi NW Galt (3); WI: Rock Co.: UMMZ 200688, Turtle Cr. (3); MPM 15480, Rock R. (3).

Cedar R. Drainage. IO: Bremer Co.: UMMZ 177452, Cedar R. at Waverly (1); SU 4598, Cedar R. at Waverly (1); UMMZ 163781, Shellrock R. Washington Township (1); Butler Co.: UMMZ 163782, Shellrock R.

Dayton Township (2); Floyd Co.: NLU 53586, Cedar R. at US Hwy 218 (25).

Salt R. Drainage. MO: Pike Co.: UF 14590, Salt R. 8.0 mi NW Louisiana (1); UMMZ 148563, Salt R. 8.0 mi NW Louisiana (2); Ralls Co.: UMMZ 149379, Salt R. 6.0 mi N Center (10); FMNH 83581, Salt R. 6.0 mi N Center (7).

Gasconade R. Drainage. MO: Maries Co.: TU 54126, Gasconade R. 6.9 mi SE Vienna (1); Osage Co.: KU 5167, Gasconade R. at Rt 89 (1); Phelps Co.: TU 54141, Gasconade R. at Jerome (3); Pulaski Co.: KU 11040, Big Piney R. (7); UT 44.902, Roubidoux R. at MO Hwy 17 (4); UMMZ 152359, Starks Fork Gasconade R. 8.0 mi S Richland (1) HOLOTYPE; UMMZ 152382, Gasconade R. 6.0 mi NE Hazelgreen (6); Wright Co.: UMMZ 152154, Gasconade R. 2.0 mi W Manes (8); Texas Co.: KU 11052, Big Piney R. 2.5 mi N Houston (2).

Osage R. Drainage. MO: Cedar Co.: FMNH 87255, Sac R. (4); UMMZ 150115, Sac R. 1.5 mi E Stockton (5); Cole Co.: KU 11087, Osage R. 3.5 mi N St. Thomas (5); KU 11279, Osage R. 3.5 mi N St. Thomas (10); Dade Co.: UMMZ 151729, Turnback Cr. 4.0 mi E Greenfield (2) PARATYPES; UMMZ 151751, Sac R. 2.0 mi S Dadesville (1); Dallas Co.: UMMZ 150435, Niangua R. 5.0 mi SE Buffalo (3); TU 54224, Niangua R. at Hwy 7 (1); Hickory Co.: KU 7546, Pomme de Terre R. at Hermitage (1); Miller Co.: UT 44.1887, Tavern Cr. at Hwy 52 (10); UMMZ 152716, Osage R. at Tuscumbia (5); Osage Co.: UMMZ 188320, Big Maries R. at Hwy 63 (1); Polk Co.: UMMZ 150086, Little Sac R. at Hwy 123 (4) PARATYPES.

Meramec R. Drainage. MO: Crawford Co.: KU 11170, Huzzah Cr. E Steelville (2); KU 10631, Meramec R. 2.0 mi N Steelville (5); Franklin

Co.: UMMZ 149648, Bourbouse R. 3.0 mi NW Strain (3); UMMZ 149671, Meramec R. 4.0 mi E Sullivan (5); Jefferson Co.: KU 10083, Big R. at Morse Hill (2); NLU 31979, Big R. at Morse Hill (10); UMMZ 142179, Meramec R. 1.0 mi S Pacific (2); St. Francois Co.: KU 10099, Big R. 3.0 mi E Bonne Terre (4).

Upper White R. Drainage. AR: Carroll Co.: USNM 117356, White R. at Eureka Springs (1); Independence Co.: USNM 59211, White R. at Batesville (3) PARATYPES; NLU 13831, White R. at Batesville (5); KU 8744, White R. at Batesville (1); TU 43226, White R. at Batesville (4); TU 49240, White R. at Batesville (5); TU 49937, White R. at Batesville (7).

Strawberry R. Drainage. AR: Lawrence Co.: HWR 76-79, Strawberry R. at Hwy 115 (2); HWR 77-46, Strawberry R. at Hwy 115 (4).

Spring R. Drainage. AR: Lawrence Co.: NLU 41756, Spring R. at Ravenden (5); NLU 40533, Spring R. at Ravenden (5); Sharp Co.: NLU 42066, Spring R. at Williford (20).

Current R. Drainage. AR: Randolph Co.: ASUMZ 2273, Current R. (7); ASUMZ 2337, Current R. (1); TU 66786, Current R. 4.5 mi NW Success (10).

Illinois R. Drainage. AR: Washington Co.: WCS ? , Illinois R. at Hwy 16 (4); UT 44.1843, Illinois R. (1); OK: Adair Co.: USNM 203423, Barren Fork Cr. 1.0 mi E Baron (1); EKU 3, Barren Fork Cr. 1.0 mi E Baron (1); TU 2263, Illinois R. at Hwy 59 (4) PARATYPES; TU 38248, Illinois R. 9.0 mi E Chewey (1); Cherokee Co.: UOMZ 36394, Illinois R. 0.5 mi NE Tahlequah Bridge (4); UOMZ 26717, Caney Cr. (10); KU 2141, Illinois R. (3); UM 14773, Illinois R. (2).

Neosho R. Drainage. KA: Chase Co.: KU 2710, Cottonwood R. (10); S. Fork Cottonwood R. at Cottonwood (2); Cherokee Co.: KU 3584, Shoal Cr. at Hwy 26 (4); UMMZ 160378, Shoal Cr. 2.0 mi S Galens (1) PARATYPE; KU 15188, Shoal Cr. (2); KU 3607, Spring R. at Hwy 96 (5); Coffey Co.: KU 14438, Neosho R. (1); Labette Co.: KU 2907, Neosho R. (10); KU 14667, Neosho R. E Chetopa (4); Neosho Co.: UMMZ 97123, Neosho R. 12.0 mi NE Parsons (10); Woodson Co.: KU 2597, Neosho R. at Neosho Falls (2); OK: Mayes Co.: UMMZ 103097, Grand R. 4.0 mi E Choteau (10) PARATYPES.

Ouachita R. Drainage. AR: Clark Co. NLU 18374, Caddo R. at I-30 (5); NLU 18598, Caddo R. at I-30 (8); Hot Spring Co.: NLU 31876, Ouachita R. (10); Montgomery Co.: NLU 31241, S. Fork Caddo R. 0.5 mi S Hopper (5); NLU 38583, Ouachita R. at Hwy 270 (5); Ouachita Co.: NLU 25311, Little Missouri R. 10.0 mi NE Chidester (10); Pike Co.: UT 44.900, Caddo R. at Hwy 70 (7); Saline Co.: USNM 36462, Saline R. at Benton (4).

Hybopsis cahni Hubbs and Crowe -- Slender chub

Clinch R. Drainage. TN: Anderson Co.: UMMZ 103462, Clinch R. below Norris Dam (1) PARATYPE; UMMZ 103463, Clinch R. below Norris Dam (3) PARATYPES; Hancock Co.: UT 44.367, Clinch R. 0.3 mi downstream of Hwy 33, Kyle's Ford (1) UT 44. ? , Clinch R. 0.3 mi downstream of Hwy 33, Kyle's Ford (3); TU 71694, Clinch R. 3.7 mi NE Sneedville, Frost Ford (1); NLU 39505, Clinch R. 3.7 mi NE Sneedville, Frost Ford (10); UT 44.1630, Clinch R. at Frost Ford (10); UT 44. ? , Clinch R. at

Frost Ford (1); Union Co.: USNM 70580, Clinch R. at Walker's Ford (4).

Powell R. Drainage. TN: Claiborne Co.: UMMZ 157709, Powell R. 3.0 mi SE Harrogate (4) PARATYPES; UMMZ 157708, Powell R. 3.0 mi SE Harrogate (1) HOLOTYPE; USNM 231229, Powell R. at Hwy 25E (4); FSM 17166, Powell R. at US Hwy 25E (10).

B. Radiograph Material

The following material was x-rayed for determination of vertebral counts. This includes material used by Jenkins and Lachner (1971).

Hybopsis dissimilis Hubbs and Crowe -- Spotted chub

Allegheny R. Drainage. PA: Mercer Co.: USNM 161903, French Cr. (4).

Wabash R. Drainage. IN: Marshall Co: USNM 66892, Tippecanoe R. (6).

Buffalo R. Drainage. TN: Wayne Co.: USNM 247794, Buffalo R. (5); USNM 247864, Buffalo R. (7).

Holston R. Drainage. VA: Smyth Co.: USNM 195832, N. Fork Holston R. (8).

Hybopsis harryi Hubbs and Crowe -- Ozark chub

Current R. Drainage. MO: Ripley Co.: CU 32874, Current R. (2).

White R. Drainage. AR: Stone Co.: NLU 13914, White R. (20); MO: Barry Co.: CU 24242, White R. (5); Stone Co: Indian Cr. (1).

Hybopsis i. insignis Hubbs and Crowe

Cumberland R. Drainage. TN: Montgomery Co.: CU 50300, Cumberland R. (3).

Elk R. Drainage. TN: Lincoln Co.: CU 24676, Elk R. (3).

Harpeth R. Drainage. TN: Cheatham Co.: CU 49953, Harpeth R. (7).

Red R. Drainage. TN: Robertson Co.: CU 22177, Sulphur Fork Red R. (2).

Shoal Cr. Drainage. AL: Lauderdale Co.: USNM 36662, Shoal Cr. (1).

Stones R. Drainage. TN: Rutherford Co.: TU 19492, Stones R. (36).

Hybopsis insignis eristigma Hubbs and Crowe

Little R. Drainage. TN: Blount Co.: CU 41380, Little R. (1).

Little Pigeon R. Drainage. TN: Sevier Co.: Little Pigeon R. (6).

Little Tennessee R. Drainage. TN: Monroe Co.: Tellico R. (1).

Upper French Broad R. Drainage. NC: Buncombe Co.: CU 10052, French Broad R. (3); Henderson Co.: UT 44.1892, Mills R. (15).

Hybopsis x. x-punctata Hubbs and Crowe.

Allegheny R. Drainage. PA: Warren Co.: CU 6741, Allegheny R. (3).

Des Moines R. Drainage. IO: Wapello Co.: USNM 35837, DesMoines R. (1).

Gasconade R. Drainage. MO: Texas Co.: CU 32902, Big Piney R. (3); USNM 63222, Big Piney R.? (3); USNM 42832, Little Piney R.? (2).

Ouachita R. Drainage. AR: Clark Co.: USNM 36428, Ouachita R. (7); Ouachita Co.: NLU 25311, Little Missouri R. (15); Saline Co.: Saline R. (7).

Hybopsis x-punctata trautmani Hubbs and Crowe

Green R. Drainage. KY: Green Co.: USNM 63386, Green R. (1).

Spring R. Drainage. AR: Sharp Co.: NLU 42066, Spring R. (20).

Wabash R. Drainage. IN: Knox Co.: USNM 40837, Wabash R. (2); USNM 40863, Wabash R. (4); USNM 40881, Wabash R. (2); USNM 66890, Wabash R. (1); Posey Co.: USNM 68952, Wabash R. (1).

White R. Drainage. AR: Independence Co.: USNM 59211, White R. (5); Carroll Co.: USNM 117356, White R. (1).

White R. Drainage. IN: Marion Co.: USNM 6746, White R. (1); Unknown Co.: USNM 117359, White R. (1).

Hybopsis cahni Hubbs and Crowe -- Slender chub

Clinch R. Drainage. TN: Anderson Co.: UMMZ 103462-63, Clinch R. (4); USNM 70580, Clinch R. (5).

Powell R. Drainage. TN: Claiborne Co.: UMMZ 157709, Powell R. (4).

CHAPTER III

BIOLOGY OF THE GRAVEL CHUB, *Hybopsis x-punctata* (CYPRINIDAE), IN THE OUACHITA RIVER SYSTEM, ARKANSAS

1. INTRODUCTION

The subgenus *Erimystax* (Cyprinidae:*Hybopsis*), as currently recognized, is composed of five species: *H. cahni*, *H. dissimilis*, *H. harryi*, *H. insignis*, and *H. x-punctata*. Little is known of the biology of these species with the exception of *H. cahni* which is being studied by R. E. Jenkins and N. M. Burkhead (Jenkins, 1975; Burkhead and Jenkins, 1982). Life history investigations for the remaining four species were initiated for the purpose of 1) filling the void in knowledge concerning biological parameters such as age-growth, population dynamics, food habits, and reproduction; and, 2) comparing biological and ecological parameters among the *Erimystax* species for use in systematic decisions at the species level and issuing phylogenetic constructs.

2. PUBLISHED DATA

Many published accounts describing the habitat and/or microhabitat of the gravel chub have appeared in the literature. Perhaps the earliest observations were those of Forbes and Richardson (1908) who stated that the western gravel chub (*Hybopsis x. x-punctata*) in northern Illinois was taken in swift water over sand substrate. Moore

and Paden (1950:83) provided the following observations of the western gravel chub from the Illinois River, OK and AR:

> Specimens were most frequently taken from under flat rocks in shallow, fast water at the head of riffles. When disturbed [H. x-punctata] was observed to dart swiftly away to hide under the rocks. The retreat chosen was often too small to accomodate the entire body, but as soon as the head was hidden the fish became motionless. The crepuscular habit explains the usual absence of the species in ordinary seine hauls.

The writings of Trautman (1981:287) on habitat of the eastern gravel chub (Hybopsis x-punctata trautmani) in Ohio are also worthy of quotation:

> The gravel chub chiefly inhabited the large sand and gravel riffles and bars of moderate- or large-sized streams, where the current had deposited coarse sands and gravels and had kept these comparatively free of clayey silts and other injurious pollutants, and where the water depth was between 1'-4' (0.3-1.2 m) in summer and 2'-6' (0.6-1.8 m) in winter. Whereever silt was lacking the gravel chub was present in the largest numbers in the slower-flowing, deeper waters, but where silting was rapid the species was forced to abandon this and could then be found in shallower and swifter water which still contained a suitable sand and/or gravel habitat. When this latter habitat became silt covered, the relict population was forced into swifter waters where the bottoms consisted of large gravel and boulders, or the species disappeared entirely from that section. It avoided rooted aquatics and the larger species of algae and aquatic mosses; in fact little vegetation grew among the sand and gravel habitats frequented by the gravel chub.

Regarding the western gravel chub, Pflieger (1971,1975) added that it inhabits clear to moderately turbid streams with slight to moderate current, permanent flow and well defined, silt free gravel or rubble bottom riffles. Pflieger contended that, in the Ozarks, the

gravel chub was most abundant in the downstream sections of larger streams where gradient was less and water was warmer and more turbid than in the headwaters. Fago (1982) summarized the habitat of the western gravel chub in Wisconsin as streams 6-90 m wide, stream depth 0.5 m, water velocity 0.5 ft/sec to 1.5 ft/sec with slight to moderate turbidity (secchi disk visibility at depths to 1.0 foot). Other published habitat observations, which basically recapitulate some part of the above, include Cross, 1967; Cross and Collins, 1975; Deacon, 1961; Gilbert, 1980b; Green and Beadles, 1974; Harlan and Speaker, 1951; Harris, 1978; Johnson and Beadles, 1977; Miller and Robison, 1973; Scott and Crossman 1973; and Smith, 1979.

Becker (1983) reported the only substantive information on food habits. He apparently examined the digestive tract of a single Meramec R., MO gravel chub and found an abundance of desmids and diatoms of many species, as well as plant material and sand grains, but no animal matter. Davis and Miller (1967) suggested H. x-punctata feeds by probing under rocks and in crevices with its sensitive snout. A diet of small invertebrates was hypothesized for the gravel chub by Miller and Robison (1973) while Scott and Crossman (1973) suggested food probably consists of aquatic insect larvae.

Reproductive season and behavior are essentially unknown for Hybopsis x-punctata although Branson (1962) speculated that it spawned in the gravel of rapidly flowing riffles, often under gravel and rocks. He also supposed that males use their ventral fins and nuptial jaw thickening (= nuptial jaw pad) for maintaining contact with the females during spawning. Cross (1967) observed captured Neosho R., KA

gravel chubs freely extruding eggs or milt on 9 April 1953. These specimens were taken adjacent to a gravel bar in water 2-3 feet deep where the current was swiftest and the water temperature 60° F. Cross presumed spawning was limited to a short period in early spring. Branson, et al. (1969) stated that gravel chub spawning reached its peak between late April and mid-May (in the Spring River of KA, OK and MO) although it continued into June in the Illinois River, OK.

In most written accounts, age and growth data for the gravel chub has been limited to adult size range and maximum size. Trautman (1957, 1981) gave lengths for October young of year eastern gravel chubs as 1.1-2.4 inches (2.8-6.1 cm), one year olds 1.7-2.8 in (4.3-7.1 cm), breeding adults 2.5-3.8 in (6.4-9.7 cm) and largest specimen 3.9 in (9.9 cm). Becker (1983) calculated total length at annulus formation for five Age Class I and four Age Class II gravel chubs captured in MO (Louis CO.). The average (weighted) total length at formation of the first annulus was 54.7 mm and at annulus II, 81.4 mm. Gilbert (1980b) reported adult size as 64-89 mm SL.

Gravel chub population structure and abundance have generally not been addressed. Branson, et al. (1969) believed the gravel chub more abundant in the Arkansas River basin than previously reported because the species is not easily collected by seine due to its habit of diving into the gravel when startled. They stated that in localities where a seine might produce 5-10 specimens, electrofishing usually yields tens to hundreds. Other studies have reported total numbers of gravel chubs collected from specific localities to reflect relative

abundance (Branson, et al., 1969; Fago, 1982; Fruge, 1971; Harris, 1978; Myers, 1977; Raymond, 1975; and Reynolds, 1971).

3. STUDY AREA

The Caddo River at Caddo Valley, Clark County, Arkansas was the primary life history study site for the gravel chub, Hybopsis x-punctata. The stream was selected for its easy access, good water clarity for underwater observations, and the availability of large numbers of specimens collected on an almost monthly basis during an earlier ichthyofaunal survey of the Caddo River (Fruge, 1971). The Caddo River is a fifth order tributary of the Ouachita River and drains a total area of 1235 square kms (Yanchosek and Hines, 1979). The primary study site was 2.0 km above the mouth with an upstream drainage area of 1217 square kms. At the study site, river morphology consisted of shallow riffles alternating with deeper runs. Lentic habitat was restricted to small backwaters on the inside of bends in the river. The substrate was predominatly small to medium gravel with lesser amounts of sand and cobble.

The Caddo River was impounded in 1969 by the U.S. Army Corps of Engineers to form the 5643 hectare (ha) DeGray Lake and the 202 ha regulating pool. DeGray Lake was contructed for flood control and power generating capabilities and designed for hypolimnetic release below the spillway. In 1983 the spillway release was modified and hypolimnetic release discontinued.

Collections from sites in the Little Missouri and Ouachita Rivers were utilized to supplement monthly data from the Caddo River in the

analysis of population structure and age/growth. Locality information and museum numbers for specimens used in this study can be obtained from the author.

4. METHODS

This life history study used a combination of personal collections and field observations augmented by museum specimens. Analysis of 12 monthly samples was attempted but winter high water precluded collections for December. Samples were taken at one or two week intervals from April through June to more precisely determine spawning period. No distinction was made between collections from different years or rivers in analysis of results, so this study reflects the "generalized life history" of the gravel chub.

Collections were made using 2.4-m X 3.0-m and 2.4-m X 6.1-m seines with 0.6-cm mesh. Seining downstream with the current proved a successful means of obtaining gravel chubs, especially using the 6.1-m seine. From April through June, specimens were checked in the field for spawning condition by gently pressing the abdomen to extrude ova or milt. All specimens were preserved in 10% formalin and stored in 45% isopropanol.

Preserved specimens were sexed by examination of the gonads and then measured to the nearest 0.05 mm standard length (SL) using Helios dial calipers. This was followed by removal of gonads, digestive tract, liver, kidneys, gas bladder, and fat accumulations. Gonads were stripped of connective tissues and fat, blotted dry, and weighed to the nearest 0.001 g using a Mettler AE 160 digital electronic

balance. Specimens were blotted dry externally and inside the body cavity and weighed to the nearest 0.001 g to yield the adjusted body weight. Gonadosomatic index (GSI) was calculated as gonad weight X 100/adjusted body weight. Ten of the largest ova were removed from each female and measured to the nearest 0.01 mm using an ocular micrometer.

The terminology of Heins (1985) was utilized in the gross assessment of female reproductive condition. Individual females were classified into the following stages based on ovarian condition: (1) Latent (LA)--ovaries very small, thin, transparent to slightly translucent. Larger developing ova, if present, yolkless or vitellogenic but with nuclei visible. (2) Early maturing (EM)--ovaries small to moderate in size, translucent to white in color. Larger eggs relatively small with nuclei obscured by yolk deposition, often numerous and becoming white in color. (3) Late maturing (LM)--ovaries moderate in size to greatly enlarged and filling a large portion of the body cavity, white to cream in color. Larger maturing ova often numerous, sometimes as large as mature ova but not easily differentiated from smaller maturing ova, and white to yellow in color. (4) Mature (MA)--ovaries greatly enlarged, filling a major portion of the body cavity and usually distending the abdomen, and cream to yellow. Mature or ripe ova present, easily differentiated from maturing ova on the basis of size and color, and relatively numerous. Mature ova opaque, cream to yellow in color, becoming translucent with small oil globules visible. Ripe ova transparent yellow or amber with large oil globules, often with vitelline membranes elevated. (5) Partially

spent (PS)--ovaries noticeably smaller than mature ovaries; relatively small number of mature ripe ova present. (6) Spent (SP)--ovaries a compact white mass without mature ripe ova. Unspent mature ova are shriveled and brown or red and apparently being resorbed into the ovarian matrix. This category is added to 1-5 presented by Heins (1985). Females that were MA or PS were considered sexually mature.

In addition to the gonadosomatic index, reproductive condition in males was determined by gross examination of the testes, as well as secondary sexual characteristics, such as tuberculation, pectoral fin coloration, and development of the nuptual pad. Reproductively mature (MA) males had swollen, opaque white testes while latent (LA) males had small, translucent to white testes. Males with swollen testes and well developed secondary sexual characters were considered mature.

Monthly food habits were evaluated by removing gut contents anterior to the first bend in the digestive tract for a minimum of 10 specimens (when available) and identifying food items to the lowest possible taxon. Lowest taxon was often family or order due to pharyngeal mastication of the food items. Taxa were enumerated, lumped by order, and placed in vials of 70% isopropanol. Non- animal remains were placed in two groups: 1) plant material which included filamentous algae, roots, leaves, and bark; 2) periphytic detrital aggregate (PDA) (Bowen, 1981) which is a complex aggregation of detritus, diatomaceous algae, and bacteria. PDA is apparently equivalent or very similar to complexes defined by the terms scum flora (Lodge, et al., 1985), aufwuchs (Colinvaux, 1973, Burkhead, 1980) or periphyton (Colinvaux, 1973). Plant material and PDA were teased apart in a

dissection dish using needle and forceps and removed to their respective vials using a suction dropper. This allowed separation of the two components and high recovery of total gut contents. Biomass of food items was determined by drying food group samples to constant weight in individual preweighed dishes using a convection oven at 100° C. Dishes were cooled to room temperature and weighed to the nearest 0.001 g. In conjunction with food habit analysis, gut length was measured to the nearest 0.05 mm using dial calipers following the method of Snelson (1971).

Age and population structure were examined using length frequency histograms of large series of specimens. Age of population group members was verified by scale analysis following methods of Tesch (1971), Weatherley (1972), and Bagenal (1971). Ten scales were removed from the predorsal lateral region of each specimen examined, stained with alizarin in 2% KOH, and projected to the screen of a Bausch and Lomb scale reader. Total scale length and annular lengths were measured to the nearest 0.05 mm with calipers. Growth in terms of biomass was estimated by weighing a sample of each age class from each monthly sample.

Reproductive and feeding behavior were observed in the field by snorkeling when water clarity permitted. Approximately 30 hours were spent underwater observing gravel chub behavior. Eighteen visits were made to the Caddo River between 1981-1985 during the months April-August.

Data for water temperature and discharge were obtained from U.S. Geological Survey records (1970-1983a). These records are for the

Ouachita River at the U.S. Hwy 67 station, Hot Spring County, AR and are considered indicative of stream conditions for life history study locations. Temperature and discharge data are presented as monthly averages in this paper.

Summary statistics and Model I linear regression were performed using programs found in Brower and Zar (1984). Model II regression was performed using the geometric mean regression method (Ricker, 1973; Sokal and Rohlf, 1981) when both x and y variables were measured with error. Non-linear regression was performed using Statistical Analysis System (SAS) Version 5.

5. RESULTS

Food and Feeding Habits

Food. Stomach contents from 147 specimens of Hybopsis x-punctata were examined to determine diet composition. These represent samples of at least 10 specimens for the months January-November. No December collected specimens were available for examination. Tables III-1 and III-2 summarize the dietary analyses for biomass and numbers of food items.

The annual or total food biomass estimate for each food item is presented as: total biomass for each food item/ total biomass for all food items X 100 which = % annual biomass for each food item. This is column TOT of Table III-1. Per cent annual biomass is also presented by summing the monthly percentages of each food item and dividing by the number of months analyzed (= column CORR of Table III-1). Corrected biomass estimates (Table III-1) show PDA made up almost half

Table III-1 Per Cent Food Biomass from Monthly Samples of *Hybopsis x-punctata*.

Food Item	Month											Totals	
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Tot[a]	Corr[b]
Nematoda									0.7			0.1	0.1
Oligochaeta	1.3											0.1	0.1
Hydracarina						0.1						-	-
Ephemeroptera	1.8	2.4	9.4	26.2	3.1	2.4	1.4	22.8	46.4			10.4	10.5
Odonata							7.5					0.2	0.7
Plecoptera		1.9						5.6	2.1			0.8	0.9
Heteroptera					0.1							-	-
Megaloptera								13.2	6.5			1.5	1.8
Trichoptera	24.9	37.4	3.8	8.2		10.1	33.8	5.6	26.9		3.5	14.4	14.0
Coleoptera		1.1		1.6		0.6						0.4	0.3
Diptera	16.7	2.6	10.0	3.1	2.3	1.3		2.6	4.5		3.9	4.2	4.3
Lepidoptera		1.6	4.7	8.0	0.2	1.0	2.8	5.3	2.0			1.9	2.3
Fish Ova					0.9							0.1	0.1
Plant		1.8		4.0	71.3	40.7	1.4	15.1	2.1	16.8		14.6	14.0
PDA	55.2	51.2	72.1	47.9	10.5	27.6	23.9	26.2	6.2	65.8	92.6	45.3	43.6
Mollusca					14.4	15.5	29.1	3.7	2.7	17.4		5.8	7.5
# Examined	12	12	12	19	22	17	15	10	11	15	12	157	
# Empty	0	0	0	3	1	2	3	0	0	4	0	13	

[a]Annual total derived from sum of monthly biomass.
[b]Annual total derived from sum of per cent monthly biomass.

Table III-2. Number of Food Items from Monthly Samples of *Hybopsis x-punctata*.

Food Item	Month											Totals	
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Tot[a]	% Tot
Nematoda				1	1			1	5			8	0.7
Oligochaeta	3											3	0.3
Hydracarina						2		6	2			10	0.9
Ephemeroptera	3			3		1	1					8	0.7
Baetidae													
Baetis				10		2		22	36			70	6.4
Heptageniidae													
Stenonema		1	3	4		3		5	19			35	3.2
Oligoneuridae													
Isonychia				1				1	9			11	1.0
Odonata-Zygoptera							1					1	0.1
Plecoptera				3					3			6	0.6
Chloroperlidae													
Hastaperla								1	2			3	0.3
Perlidae													
Acroneuria								1	1			2	0.2
Perlesta				1								1	0.1
Heteroptera													
Corixidae					1							1	0.1
Megaloptera													
Corydalidae								1	1			2	0.2
Trichoptera	1		1					1			1	4	0.4
Helicopsychidae								1	2			3	0.3
Hydropsychidae	13	33		2		20	3		2	3		76	7.0
Hydroptilidae	7	1	1	1		9	2		2			23	2.0
Leptoceridae			2									2	0.2
Philopotamidae						4	2	2	73			81	7.4

Table III-2. (Continued)

Food Item	Month											Totals	
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Tot[a]	% Tot
Coleoptera		1		1		1		1				4	0.4
Diptera													
Chironomidae	374	73	67	36	20	55		26	8		10	669	61.5
Simuliidae				1	28	1	4	2	1			37	3.4
Tipulidae									1			1	0.1
Lepidoptera													
Pyralidae		1	1	2		3	3	3	2			15	1.4
Gastropoda						1		1	1	4		7	0.6
Pelecypoda													
Cyrenidae													
Corbicula			2				1					3	0.3
Fish Ova				1	4							5	0.5
Total	401	110	77	67	54	102	17	75	170	4	14	1088	

[a]Sum of monthly totals.

(43.6%) of the annual diet of the gravel chub while three additional food items, Trichoptera (14%), plant material (14%), and Ephemeroptera (10.3%) contributed 38.3% of the diet. Gastropoda (7.5%), Diptera (4.3%), Lepidoptera (2.3%), and Megaloptera (1.8%) rounded out the food items contributing more than 1% to the annual dietary biomass taken by Hybopsis x-punctata.

PDA was the largest contributor to diet biomass in nine of 11 months analyzed (Table III-1). It comprised >50% of stomach contents in the coldwater months of October-March but apparently was of reduced importance during late spring-summer when other food items may be more abundant. Plant material showed a large increase in May (71.3%) and June (40.7%) and this was attributed to blooms of filamentous Chlorophyta. Ephemeroptera (8 of 11 months), Trichoptera (9 of 11) and Diptera (9 of 11) were consistent and often significant parts of the monthly diet samples. Notable exceptions were the May sample in which Ephemeroptera and Trichoptera were absent and Diptera were present in small numbers, and the October sample in which all three orders were absent.

Feeding behavior. Gravel chubs were observed feeding in moderate current over gravel or small rock sustrates with patchy, attached, nonemergent vegetation (mostly Podostemon). Most feeding time was spent grazing or gleaning over the rock/gravel substrate apparently sucking up PDA and anything within the aggregate. Gravel chub feeding behavior was similar to that of stoneroller minnows and they were often observed feeding over the same habitat in mixed assemblages.

Gravel chubs were also observed grazing on the extremities of the vegetation but were never seen rooting into the vegetation as would be expected if they were seeking invertebrate prey. Occasionally, individuals would dart into the water column, apparently to take drift items, but they were never observed more than 8-10 cm above the stream bottom. On two occasions I witnessed chubs vigorously searching gastropod and Corbicula shells for food. Gravel chubs probably take advantage of natural mollusk mortality rather than actively preying on the living.

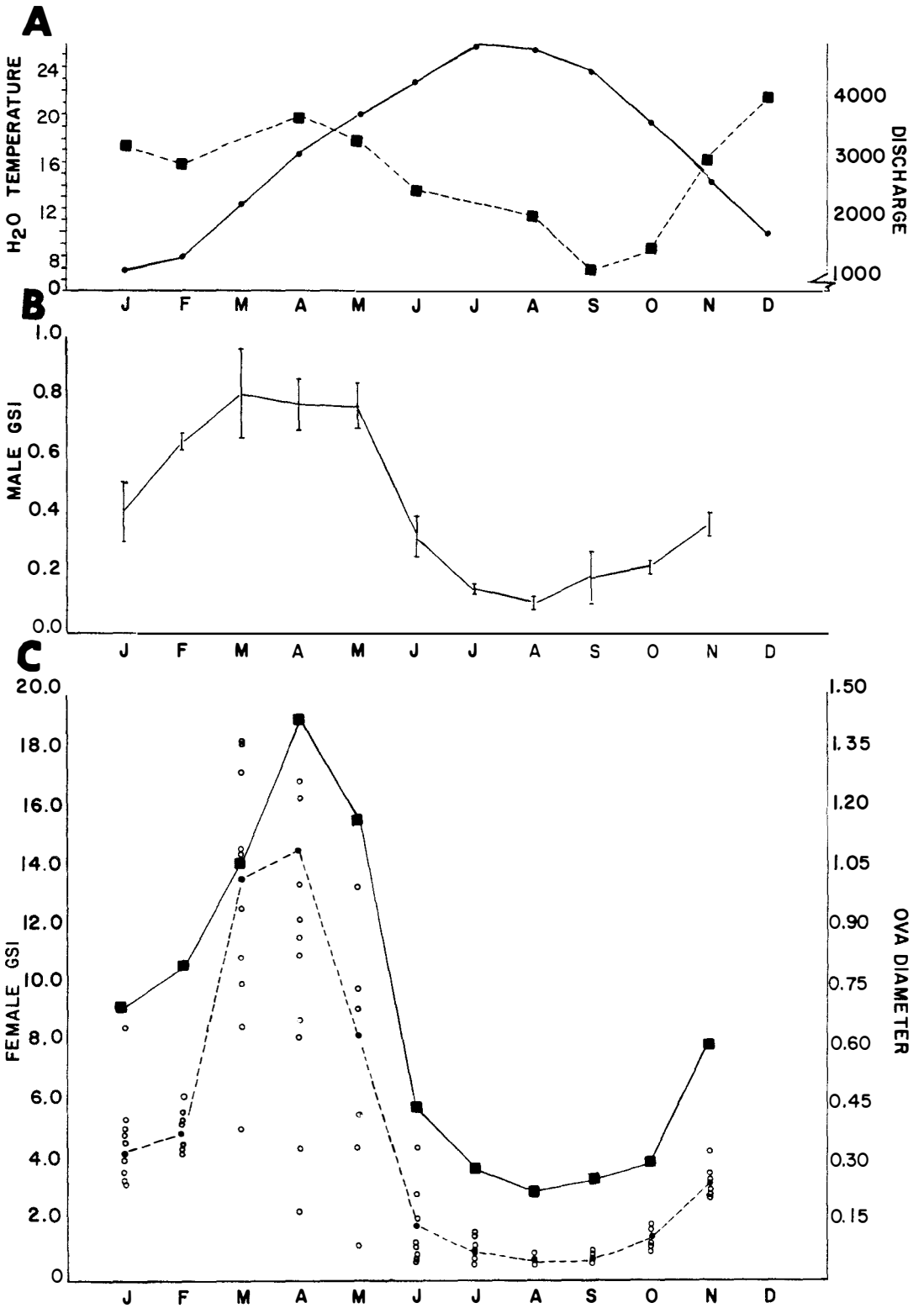
Although feeding behavior was not quantified, I estimate that 90% of feeding time consisted of gleaning or vacuuming food from rock or gravel substrates or vegetation. The remainder of feeding time was spent probing easily accessible rock crevices for food items or taking drift from the water column.

Gut length for Ouachita River drainage gravel chubs ranged from 0.75-1.30 X standard length (SL) with a mean of 1.04 (n=71). Gut morphology was modified from the simple s-shaped arrangement by an extra loop at the second 180° bend in the gut and ranged from a well developed accessory gut loop (as figured in Becker, 1983:489) to a small semi-loop (Becker, 1983:558).

Reproduction

Male. Testicular and ovarian development appeared relatively synchronous with peak GSI values for testes occurring from March to early May (Figure III-1). This suggests males were primed for spawning slightly before females and remain capable of spawning well

Figure III-1. Reproductive parameters of Hybopsis x-punctata. A. Mean water temperature (^{O}C) and discharge (cfs) of the Caddo River, AR for 1970-1983. B. Male H. x-punctata mean gonadosomatic index (GSI) with standard deviation. C. Female H. x-punctata mean GSI (solid circles) and mean ovum diameter (squares). Open circles represent individual female GSI values.


A
H2O TEMPERATURE
24
20
16
12
8
0
4000
3000
2000
1000
DISCHARGE
J F M A M J J A S O N D
B
MALE GSI
1.0
0.8
0.6
0.4
0.2
0.0
J F M A M J J A S O N D
C
FEMALE GSI
20.0
18.0
16.0
14.0
12.0
10.0
8.0
6.0
4.0
2.0
0
1.50
1.35
1.20
1.05
0.90
0.75
0.60
0.45
0.30
0.15
OVA DIAMETER
J F M A M J J A S O N D

past the female peak for reproduction. All testes from July-October were classified LA. A slow increase in testicular size began in November and continued through February, followed by rapid swelling to achieve maximum development that was maintained late March-May. Testes examined in June-July were much decreased in size indicating cessation of reproductive activity. Mean GSI values ranged from lows of 0.16 for July and 0.12 for August to highs of 0.81, 0.78, and 0.77 for March, April, and May, respectively.

January specimens did not exhibit the male secondary sexual characters of tuberculation, nuptial jaw pad, or pectoral fin pigmentation. Some individuals collected February 19 had tiny pectoral fin and dorsolateral body tubercles, a thin and poorly developed nuptial jaw pad, and a slight increase in size and intensity of interradial pectoral fin pigmentation. By mid-March, pectoral fin tubercles were moderate in size and tiny tubercles were present on the dorsal, anal, and pelvic fins. Dorsolateral body tubercles were more prominent and now occurred over the entire scale surface. Tubercles were also present dorsally and ventrally on body scales posterior to the dorsal fin. Cephalic tubercles were present as tiny granules. Pectoral fin pigmentation was much more pronounced and males were readily distinguished from females. Nuptial pads were present on all sexually mature males but were still thin and patchy. By mid- to late April, body and fin tuberculation were fully developed, interradial pectoral fin pigment was dense, and the nuptial jaw pad completely covered the region posterior and ventral to mouth corners and extended ventrad to the anterior branchiostegals. Secondary characters were static

through May but by mid-June the nuptial jaw pad was thinning, pectoral tubercles were patchy, most dorsolateral body tubercles had sloughed, but cephalic tubercles were still present. Pectoral pigmentation was still concentrated in males so that they were readily distinguished from females. July specimens had lost all secondary sexual characters.

Female. Based on GSI values and mean ovum diameter (Figure III-1), the peak reproductive period in female Hybopsis x-punctata lasted from early April until early May. Ovaries in January (n=11) and February (n=10) were LA or EM with GSI means of 4.28, 4.99 and mean ovum diameters of 0.70 mm, 0.81 mm, respectively (Figure III-1). A rapid increase in ovum diameter and ovarian weight occurred in March as all ovaries examined (n=10) were LM with a GSI of 13.62 and mean ovum diamter of 1.25 mm. April collections contained specimens that were LM, MA, and PS. Specimens obtained 4 April 1971 were LM and MA with GSI values ranging 4.47-28.72 and mean ovum diameter of 1.43 mm. Mature ova were generally >1.50 mm with a maximum size of 2.00 mm. Five specimens obtained 30 April 1976 contained MA and PS individuals with GSI values ranging from 2.39-17.06. Specimens from 20 May 1984 (n = 10) included two MA individuals and eight PS individuals. Mean ovum diameter was 1.17 mm and included ova from PS individuals which were apparently being resorbed into the ovarian matrix. Average GSI for May specimens was 8.24. All specimens examined from 17 June 1984 were SP or LA with mean ovum diameter of 0.44 mm and GSI of 1.95. Ovaries for July-October were LA with mean ovum diameters of 0.28, 0.23, 0.25, and 0.30; and GSI values of 0.95, 0.77, 0.72, and 1.48,

respectively. In November samples both LA and EM ovaries appeared as indicated by average GSI of 3.20 and mean ovum diameter of 0.60.

Fecundity. Ova counts were made for 12 adult females ranging in size from 49.9-79.3 mm SL captured 17 March 1971, 4 April 1971, 4 April 1976, and 12 April 1970 (Figure III-2). There was a high correlation ($r = 0.94$) between fecundity (F) and SL with the relationship expressed by the Model II linear regression equation $F = 12.71(SL) - 482.60$. Bagenal (1971) stated the importance of log-log transformations for stabilizing variation and aiding prediction. The logarithmic equation for these data is $\log_{10} F = 2.55(\log_{10} SL) - 2.10$ with a correlation coefficient of $r = 0.94$. It appears either model adequately describes the fecundity-standard length relationship.

Spawning. Thirteen attempts to observe spawning behavior were made on the following dates between 1982 and 1985: April 7, 11, 13, 18; May 16, 20, 23, 25, 29; June 5, 17; and July 22. Twenty hours were spent attempting to observe spawning behavior. Presumed spawning was observed on 13 and 18 April 1985 between 1300-1600 hours CST with water temperature 62-66° F. Both sexes were massed at the riffle heads in 40-60 cm of water over clean, small to medium gravel substrate. Numerous females with greatly distended abdomens were observed lying motionless on the substrate, usually in a slight depression or crevice created by larger gravel. Little feeding activity was seen from these females except for an occasional foray into the water column to take a drift item. Males grazed busily in close proximity to the resting females. Five presumed spawnings were observed on these two days. Three of these events began with males

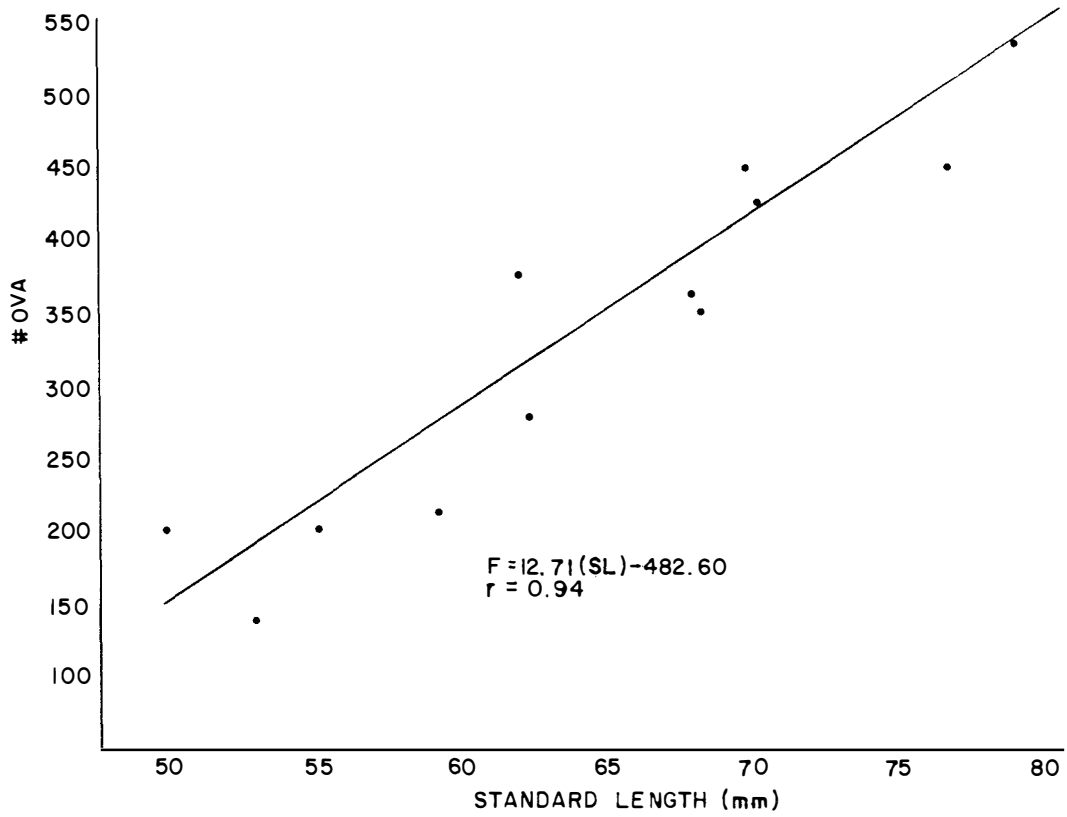


Figure III-2. Linear regression of standard length (SL) versus fecundity (F) for Hybopsis x-punctata.

assuming position on the substrate beside the female or in the water column slightly above the female but not in physical contact in either case. The females appeared to respond with a slow undulating body movement after which the male would move into contact with the female by first touching cheeks and then placing the body parallel to the female. This was followed by rapid body vibrations in unison during which gametes were assumed to be deposited. The presumed spawning act lasted less than two seconds and was followed by the pair rising into the water column and disengaging. Slight variations were observed during two other presumed spawns. During these acts, single females were swimming lazily just above the substrate when approached by a single male in one instance and two males in another. The females undulated slowly in both cases which was followed by male-female cheek touching and a dive into the substrate. Rapid body vibration ensued followed by disengagement. In the event with two males, both males appeared to take part in the spawning event.

The smallest reproductively mature female examined measured 49.9 mm SL while the smallest male was 56.4 mm SL. Most, if not all, individuals spawn at age 2 when they are >50 mm SL.

Age and Growth

Collections of Hybopsis x-punctata are generally small with the majority represented by <50 specimens. Large series of individuals were available for the months February, June, September, and October and analyses by length-frequency histograms are presented in Figure III-3. Table III-3 summarizes age and growth data for males, females,

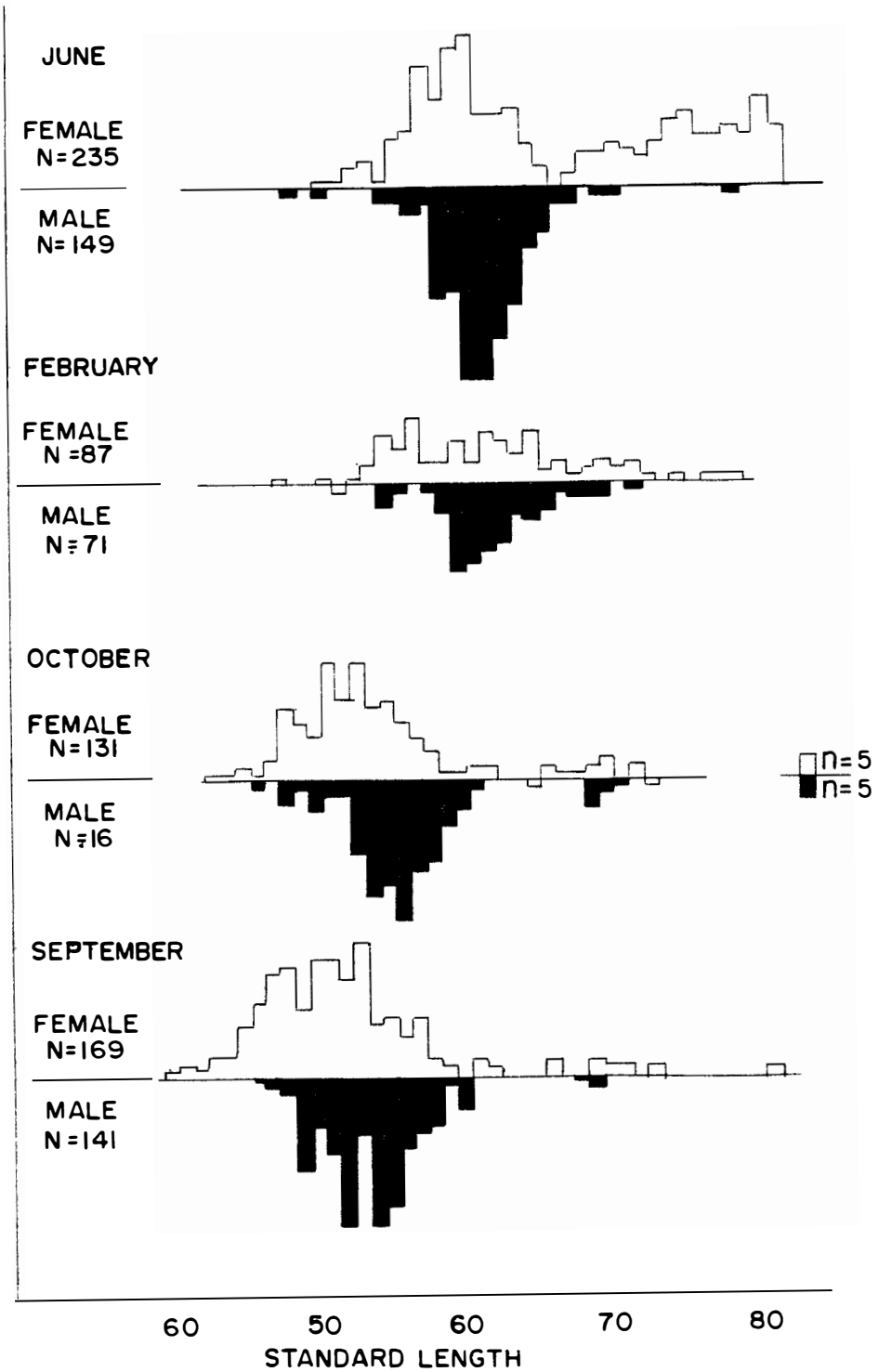


Figure III-3. Length-frequency histogram for Hybopsis x-punctata.

Table III-3. Mean Standard Length Based on Monthly Samples of Each Age Group of Male, Female, and Total Hybopsis x-punctata.

Age Group	Month		Females $\bar{x}$	Females n	Males $\bar{x}$	Males n	Total $\bar{x}$	Total n
	April	1						
	May	2						
	June	3						
	July	4					28.07	(16)
	August	5	47.74	(20)	50.22	(22)	49.75	(42)
1	September	6	50.51	(162)	53.34	(136)	51.73	(298)
	October	7	52.51	(120)	55.20	(105)	53.77	(225)
	November	8	54.89	(12)	59.08	(12)	56.99	(24)
	December	9						
	January	10	60.28	(24)	60.95	(22)	60.60	(46)
	February	11	59.25	(75)	61.41	(64)	60.24	(139)
	March	12	59.77	(32)	62.24	(13)	60.48	(45)
	April	13	56.34	(11)	60.54	(11)	58.44	(22)
	May	14	59.87	(25)	64.08	(18)	61.63	(43)
	June	15	61.12	(161)	62.02	(158)	61.56	(319)
	July	16	63.34	(21)	58.97	(5)	62.50	(26)
	August	17	66.18	(15)	66.53	(13)	66.34	(28)
2	September	18	67.15	(13)	67.54	(9)	67.31	(22)
	October	19	68.75	(21)	69.36	(16)	69.01	(37)
	November	20	67.67	(28)	67.26	(15)	67.52	(43)
	December	21						
	January	22	74.97	(3)	75.95	(1)	75.21	(4)
	February	23	71.90	(17)	69.43	(7)	71.18	(24)
	March	24	73.15	(4)	68.35	(3)	71.09	(7)
	April	25	70.35	(3)	73.57	(3)	71.96	(6)
	May	26	78.80	(10)	75.48	(2)	78.24	(12)
	June	27	78.47	(122)	77.05	(2)	78.45	(124)
	July	28	80.56	(14)	75.45	(3)	79.66	(17)
3	August	29						
	September	30	80.50	(1)			80.50	(1)
	October	31						
	November	32	80.38	(4)	75.70	(1)	79.44	(5)

and the sexes combined. Non-linear growth equations for standard length did not differ significantly between the sexes (Figure III-4). The relationship of age versus standard length in males is described by $L = 45.58 + 1.45A - 0.01A$ ($r = 0.90$) and for females by $L = 41.96 + 1.52A - 0.01A$ ($r = 0.96$). Age in months versus standard length for the entire sample is plotted in Figure III-5 using a moving average of threes and assuming no decrease in standard length (after Mayden and Burr, 1981). Age versus body weight for sexes combined is presented in Figure III-6 and is described by the linear equation $W = 0.559 + 0.179A$ ($r = 0.94$).

As April seemed to be the month of peak spawning, it was designated as month 1 for ageing purposes with May assigned as month 2. I have followed the suggestion of Everhart and Youngs (1981:68-69) by reporting annuli in Roman numerals and age groups in Arabic numerals where specimens 0 to 12 months old are in group 1, specimens 13 to 24 months old are in group 2 and so on.

Young of year (yoy) specimens were collected in early July (22-33 mm SL, $\bar{x} = 28.1$). Rapid growth occurred during the summer so that, by mid-September, sexes combined yoy had a mean SL of 51.7 mm. A bimodal distribution can be seen in September specimens with Age 1 and 2 individuals dominant. A single 42-month-old Age 3 individual (verified by scale analysis) was also present. The October population exhibited a similar bimodal grouping of Age 1 and 2 specimens. The February distribution was unimodal but June Age 2 and 3 groupings were distinctly visible. The most distinctive aspect of the June population data (Figure III-3) was the virtual absence of Age 3 males

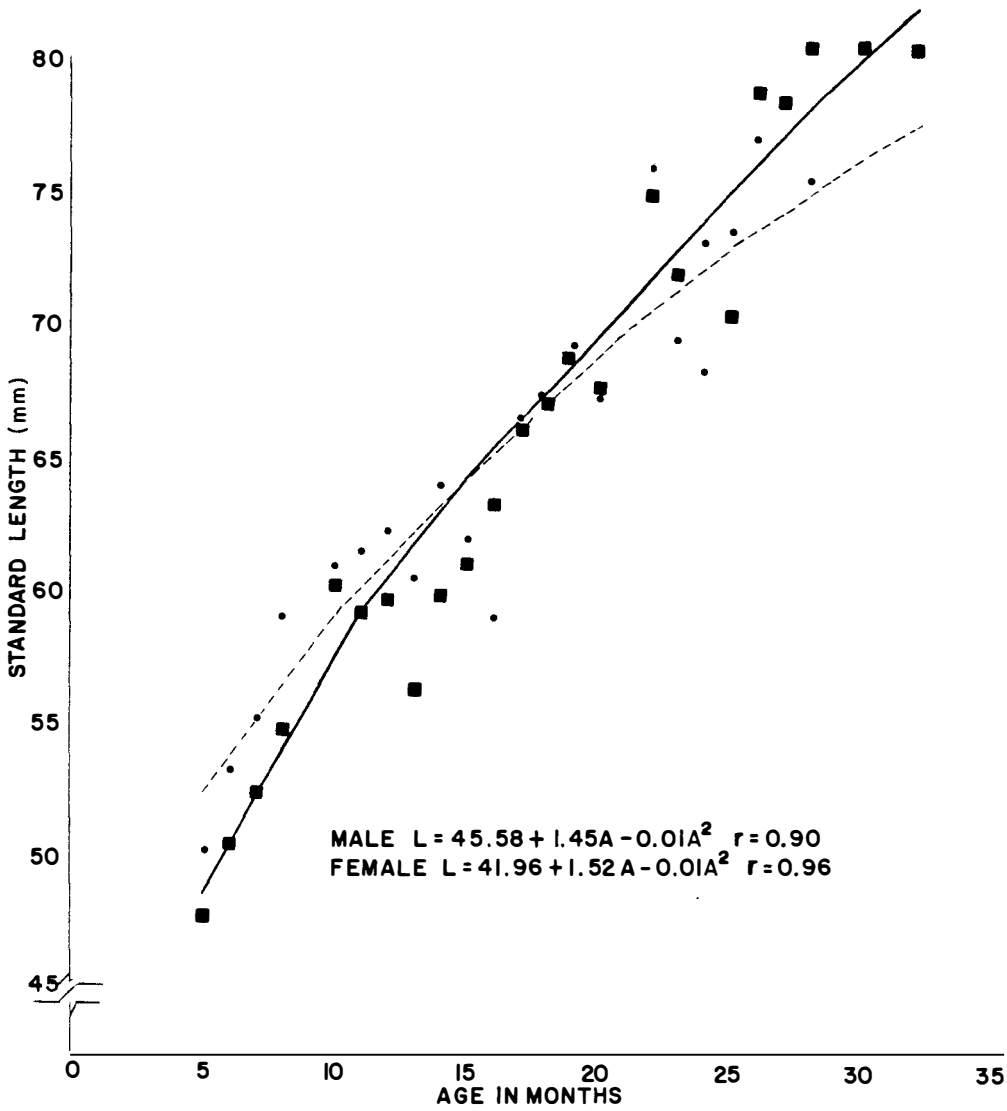


Figure III-4. Non-linear regression of age versus standard length for male (dashed line) and female (solid line) Hybopsis x-punctata. Mean monthly standard length for males (circles) and females (squares) are plotted.

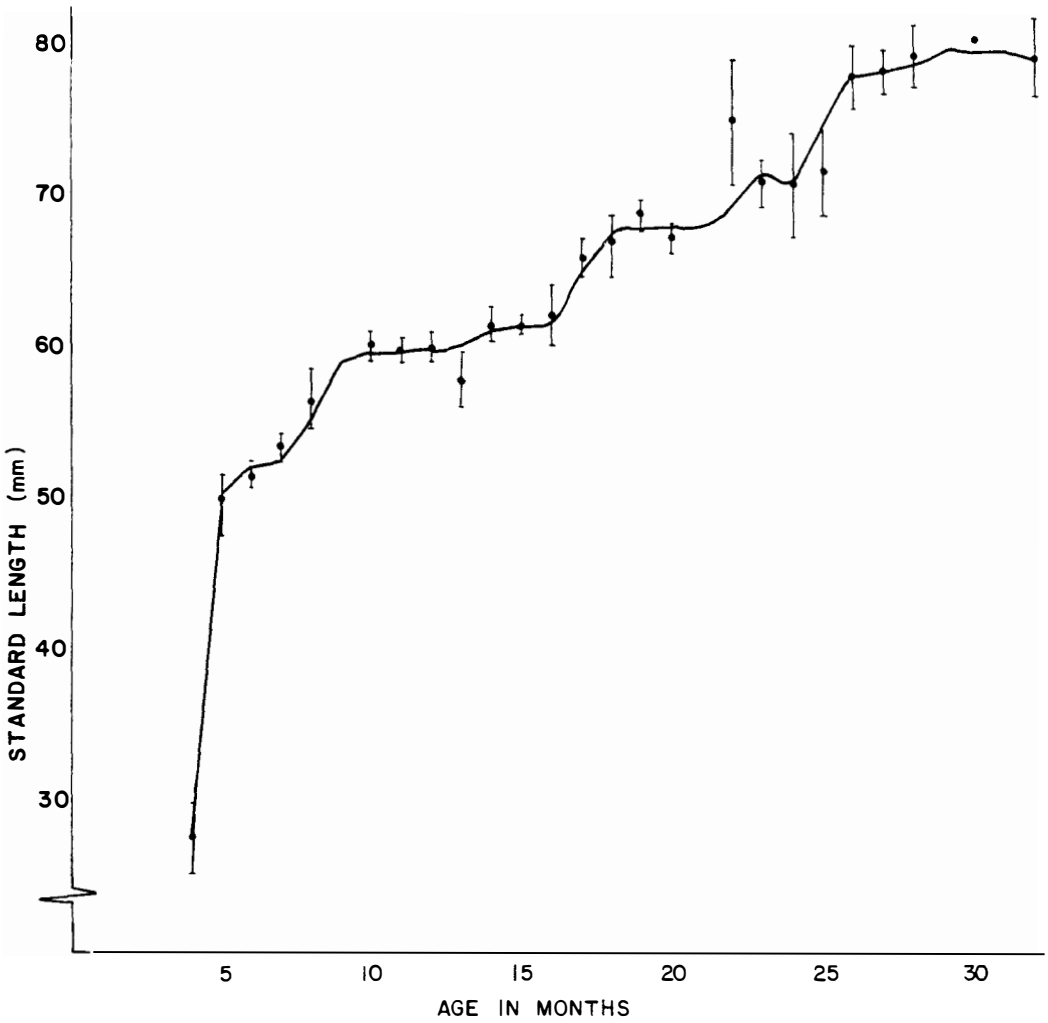


Figure III-5. Age versus mean standard length (circles) plotted as a moving average of three for Hybopsis x-punctata. Bars represent one standard deviation.

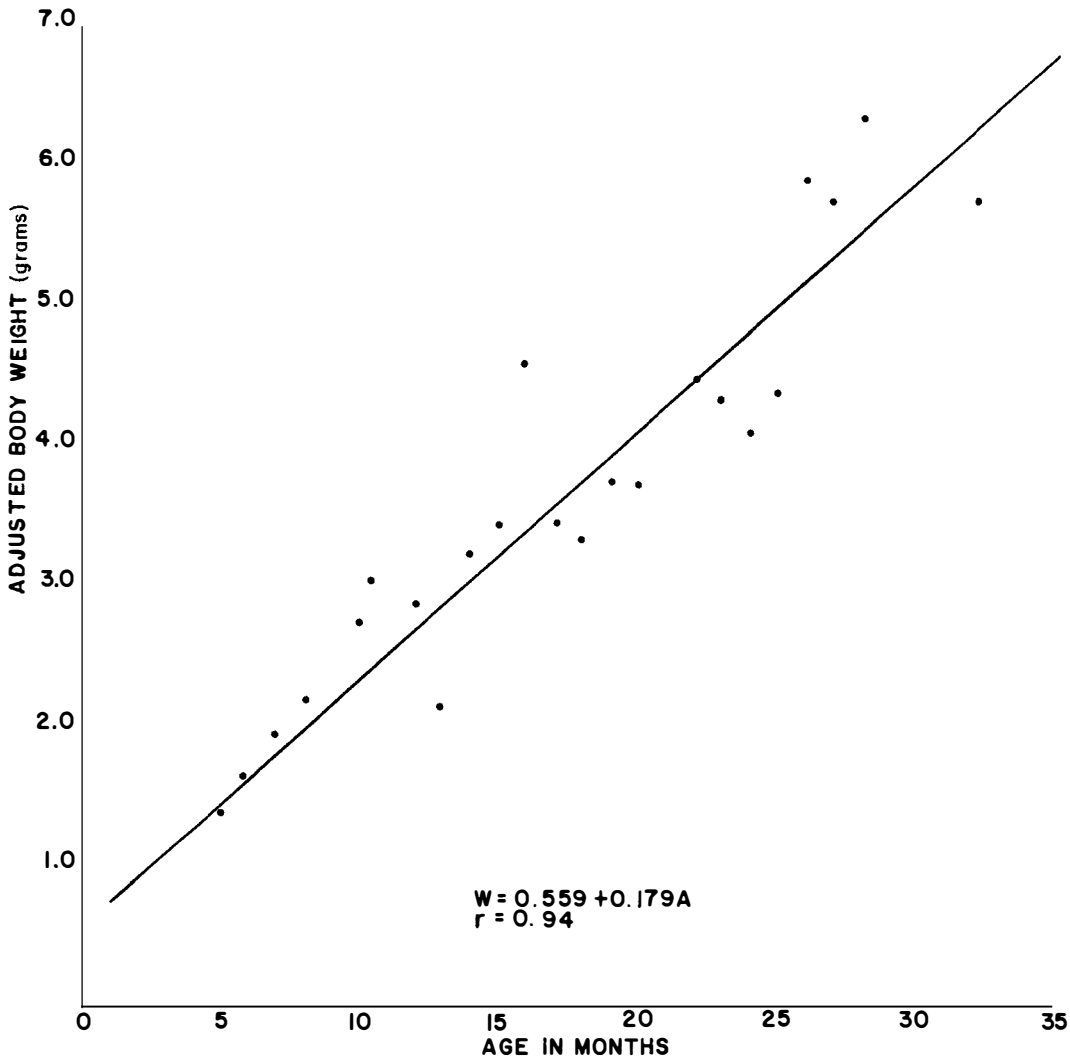


Figure III-6. Linear regression of age versus mean adjusted body weight for Hybopsis x-punctata.

which may indicate post spawning mortality or perhaps habitat segregation.

Growth trends in Table III-3 suggest that males were consistently larger than females until approximately month 20, when female standard length surpassed and dominated until the end of the growth table. The largest specimen examined during this study was an 89.2 mm SL female (month 26) while the largest male was 79.2 mm SL (also month 26).

Regression analysis of scale length-scale radius relationships from 43 specimens (Age 2 = 24, Age 3 = 19) collected 29 June yielded the regression line described by $Y = (0.92)X + 30.77$ (Y = SL; X = projected scale radius in mm at 120x) with $r = 0.89$. Back calculation of standard lengths at annulus formation resulted in an average SL of 61.80 mm at annulus I and 71.27 mm at annulus II. Assuming annulus deposition occurs in early spring, the back calculated average SLs are in close agreement with measured averages (sexes combined, Table III-3) of 61.4 mm for May Age 2 and 75.2 mm for May Age 3.

Population Dynamics

Sex ratio. An overall sex ratio of 3 females to 2 males was observed for all collections combined (n = 1559). Sex ratios for each age group are displayed in Table III-4 and relative survival of the sexes of each year class are presented in Table III-5. There were no collections in which females were outnumbered by males. Age groups 1 and 2 are more balanced (Table III-4) with females contributing 54.7% and 54.4%, respectively. Age group 3 shows a great disparity between the sexes as 93% (154 of 165 specimens) examined were female. Post

Table III-4. Sex Ratios of Hybopsis x-punctata for Each Age Group and the Total Sample.

	Age Group 1	Age Group 2	Age Group 3	Total Sample
Females	0.54	0.55	0.93	0.59
Males	0.46	0.45	0.07	0.41

Table III-5. Relative Survival of Year Classes of Male, Female, and Total Hybopsis x-punctata Expressed as Proportions of Age Class 1 ($1x^1$) and Age Class 2 ($1x^2$).

Sample	Age Group	# Individuals	Survival $1x^1$	$1x^2$
Males	1	374	1.000	____
	2	256	0.684	1.000
	3	11	0.029	0.043
Females	1	445	1.000	-----
	2	319	0.717	1.000
	3	154	0.346	0.483
Total	1	819	1.000	-----
	2	575	0.702	1.000
	3	165	0.201	0.287

spawning collections from June and July of Age 3 specimens were heavily skewed towards females with ratios of 61:1 and 5:1 respectively.

Survivorship. Survivorship calculations (Table III-5) show the drastic decline in survivorship from age 2 to age 3 in males.

Relative abundance. No quantitative samples were taken during this study to determine the density/unit area of gravel chubs at the Ouachita River system study sites. However, information on the relative abundance of the gravel chub in optimum habitat was obtained from data amassed during ichthyofaunal surveys of the Caddo (Fruge, 1971), Little Missouri (Myers, 1977), and middle Ouachita (Raymond, 1975) rivers. Data reported represent collections from the single site which yielded the most specimens of Hybopsis x-punctata during the respective river surveys. Generally, cyprinids were collected using 9-m X 3-m and 12-m X 3-m seines and the majority of specimens captured were preserved for laboratory identification (Douglas, pers. comm.). Although these collecting methods were not designed for accurate quantification, a reasonable indication of relative abundance was obtained.

The site on the Caddo River is the same as the primary site for this study, the Interstate Highway 30 crossing near Caddo Valley, AR. Data reported represent 13 collections made between July 1970 and April 1971. Myers (1977) and Raymond (1975) both collected the Little Missouri River at its confluence with the Ouachita River at Tate's Bluff, Ouachita County, AR. Myers reported nine collections between August 1972 and April 1974 while Raymond added three additional

collections in March, June, and July 1975. Data from Raymond and Fruge are summarized in Table III-6.

Both the Caddo and Ouachita sites support a diverse cyprinid assemblage with 15 and 19 species, respectively. At both sites, the bigeye shiner, Notropis boops and the steelcolor shiner, N. whipplei were the most abundant cyprinids. The gravel chub was third in relative abundance at the Ouachita-Little Missouri confluence (11.4%) and fifth in the Caddo River (6.2%).

DISCUSSION

Miller and Robison (1973) and Scott and Crossman (1973) speculated that food of the gravel chub consisted of small invertebrates. While present in specimens examined, invertebrates comprised only 43% of the estimated annual food biomass (Table III-1). Fifty eight per cent of the annual food budget is a combination plant material (14.0%) and a periphytic detrital aggregate (43.6%).

Several species of North American cyprinids are known or suspected to be "herbivorous" or "detritivorous" including Campostoma species (Burkhead, 1980; Kraatz, 1923; Schmulbach, 1957), Hybognathus species (Copes, 1975; Forbes and Richardson, 1920; Cross, 1950; Gilbert, 1980a; Lee, 1980; Burr, 1980; Pflieger, 1980), Notemigonus crysoleucas (Carlander, 1979; Snelson, 1975), Notropis mekistocholas (Snelson, 1971, 1980), Notropis nubilus (Smith, 1979; Pflieger, 1975), Phoxinus cumberlandensis (Starnes and Starnes, 1981) and P. erythrogaster (Phillips, 1969; Settles and Hoyt, 1976). All but Notemigonus have elongate, coiled guts which are associated with

Table III-6. Per Cent Relative Abundance of Selected Cyprinid Species from Sites on the Caddo and Ouachita Rivers.

Species	Caddo River	Ouachita River
Campostoma anomalum	12.6%	3.2%
Hybopsis x-punctata	6.2%	11.4%
Notropis atherinoides	0.5%	4.5%
N. boops	31.0%	49.3%
N. whipplei	34.6%	17.1%
Pimephales notatus	9.3%	4.7%
Others	5.8%	9.8%

herbivory/detritivory. Campostoma probably has the most elongate gut of any North American cyprinid (Burkhead, 1980) with a maximum gut length 7.94 times its total length (TL) (Kraatz, 1924). Becker (1983) reported gut lengths for the following species: Campostoma oligolepis 3.3-5.2 X TL; Cyprinus carpio 1.6 X TL; Hybognathus hankinsoni 3.8-4.1 X TL; Hybognathus nuchalis 5.4-5.8 X TL; Notropis nubilus 1.9-2.4 X TL. The gut length for Notropis mekistocholas is reported to be 1.4-2.4 X SL (Snelson, 1971).

The congeners Hybopsis aestivalis and H. storeriana are reported to be primarily insectivorous (Becker, 1983; Kinney, 1954; Starrett, 1950) with gut lengths 0.5-0.7 X TL (Becker, 1983). Hybopsis monacha was considered phyletically linked to Erimystax and the subgenus Cyprinella of Notropis (Jenkins and Burkhead, 1984). The gut of H. monacha was short and s-shaped, averaging 68.4% SL in eight adults examined (Jenkins and Burkhead, 1984). H. monacha was considered an insectivore by Jenkins and Burkhead although algae and detritus were found in five specimens taken during November. Hybopsis x-punctata gut length for Ouachita River drainage specimens was intermediate (0.75-1.30 X SL, $x = 1.04$, $n = 71$) between species classified as insectivores and detritivores.

Bowen (1979, 1981), (Burkhead (1980), Starnes and Starnes (1981) and Prejs (1984) provided useful summaries and thoughtful insight into the behaviour, biochemistry, and mechanics of herbivorous-detritivorous feeding in freshwater fishes. Bowen (1979) has shown that Tilapia mossambica can digest and assimilate periphytic detrital aggregate (PDA). Numerous workers have concluded that detritus is

either indigestible or of little food value and that detritivores must depend upon detrital microorganisms to meet nutritional requirements (Bowen, 1979). Bowen stated that most authors have reached this conclusion by microscopic examination of food and feces which shows no change in detrital form, and so they assumed it was not digested. Bowen disagreed and cited Gordon (1970) who reported 30-60% of organic carbon in detritus (from seawater) was hydrolyzed. Riley (1970) suggested the problem with detritus as a food source was lack of protein and that digestion of detritus would supply the consumer only with energy. Protein must be obtained by digestion of protein-rich organisms such as bacteria or invertebrates. Bowen suggested three adaptive strategies for detritivores to obtain sufficient dietary protein: 1) Selective feeding on protein-rich detrital aggregate; 2) Selective ingestion of protein-rich elements of detrital aggregate or 3) Complementing the detrital diet with protein-rich animal foods.

The quality of the PDA ingested by Hybopsis x-punctata is unknown. Based on the quantities of various food items found in the gut (Table III-1), it seems likely that the gravel chub utilizes strategy 3 (above) to obtain necessary dietary protein especially during the period of peak growth. During May-August, the per cent contribution of PDA to the diet ranged from 6.2-27.6 while invertebrates contributed 21.0-91.1%. By itself, PDA may be sufficient as a source of energy to sustain body function during cold water periods of no growth. Per cent dietary PDA for October, November, and January was 65.8, 92.6, and 55.2, respectively.

Food selection under natural conditions is expected to be a compromise between preference and availability and/or the cost of ingestion of a food type versus the benefit derived from it (Prejs, 1984). Optimal foraging models predict that organisms will consume with minimal energy cost to obtain maximum benefits (Schoener, 1971; Werner and Hall, 1974).

Food data for the gravel chub (Tables III-1, p. 208 and III-2, p. 209) suggest that it is an opportunistic omnivore which on an annual basis consumed relatively equal amounts of periphytic detrital aggregate and macrobenthic invertebrates. No quantitative data were available for invertebrate taxa or periphytic detrital aggregate but, based on visual observation, PDA appeared to be more abundant during the summer and early fall. Whether the increased percentage of macroinvertebrate biomass in stomach contents from May through September was due to selective feeding or simply greater density of invertebrates residing in the PDA matrix cannot be ascertained until quantitative studies are undertaken. An interesting relationship may exist between increased growth and increased invertebrate dietary intake in the gravel chub.

Observations of feeding behavior substantiated the classification of Hyboposis x-punctata as an opportunistic feeder. Very little probing or substrate picking was observed but, rather, an almost continuous gleaning of the substrate seemed to be the primary mode of feeding. When chubs encountered dead gastropods or asiatic clams, they would proceed to peck and probe until the shells housing the animals were cleaned. I concur with Davis and Miller's (1967)

hypothesis that x-punctata is primarily a cutaneous taste feeder, but observations of chubs darting up into the water column to take drift indicate sight plays a role in feeding strategy.

Although Balon (1975), when defining reproductive guilds in fishes, listed Hybopsis x-punctata as a non-guarding phyto-lithophil, I believe the gravel chub is a lithophilic spawner. All spawning observations I have made indicate the gravel chub spawns over clean swept rock or gravel substrate. My observations and those of Cross (1967) indicate gravel chubs spawn at water temperatures >17 C (above 60 F). I was not able to observe spawning from mid April through mid May, usually due to high water conditions and associated poor visibility. From Figure III-1 (p. 213), it is apparent that peak spawning for H. x-punctata coincides with the annual peak in discharge for Ouachita River streams. This would explain why, in over 50 underwater hours attempting to observe spawning behavior for Erimystax species, I have observed spawning on only three different occasions. A reproductive peak during high flows would be advantageous to these open substrate spawners with non-adhesive eggs as poor visibility would hinder predators. This would also explain the utility of the nuptial jaw pad in species recognition during spawning under conditions of high flow and poor visibility.

Initiation of spawning by increased water discharge in conjunction with rising water temperature has been noted in several groups of larger riverine fishes including Polyodon (Purkett, 1961; Hubert, et al., 1984), Catostomus (Barton, 1980; Edwards, 1983b), and Ictiobus (Edwards and Twomey, 1982; Edwards, 1983a). This is the

first implication of a small cyprinid with discharge initiated spawning and may indicate evolution of the ancestral Erimystax stock in large riverine environs.

Mature egg diameter of 1.5-2.0 mm was somewhat larger than reported ovum diameters for most other North American cyprinids (Becker, 1983; Campbell and MacCrimmon, 1970; Heins and Clemmer, 1976; Settles and Hoyt, 1976; Starnes and Starnes, 1981). In comparison with other North American cyprinids, the gravel chub seems to have traded high numbers of ova for larger size ova and theoretically larger, better developed larvae at hatching. If spawning occurs during high water spates, the first few days in the life of the larval chub are probably spent in turbid backwaters with a better chance for predator avoidance and rapid growth ensuring a better chance of survival.

Rapid growth from hatching through the first fall is common for small, short-lived cyprinids. Table III-3 (p. 221) and Figure III-4 (p. 223) indicated that yoy gravel chubs continued growth in standard length through December before undergoing cessation that continues until June (post-spawning) the following year. Another growth spurt occurred for these now age 1 individuals from June through October, followed again by winter slow growth. That males grew more rapidly than females during the first year (Table III-3, p. 221) was not surprising due to the energy females invest in ova production. Most females spawn during their first spring after birth and up to 20% of their adjusted body weight may be ova. Males also spawn during their first spring but only 1% of adjusted body weight is invested in

testes. The energy required for male secondary character development such as tubercles and nuptial jaw pads is unknown, but must surely be less than the total female investment in ova. The energy expended by males during spawning must be greater than that for females due to the female "resting position" prior to the spawn. Females eventually overtook males in standard length following spawning in year 2, and this may be attributed to ovarian atresia observed in virtually all post-spawning females that probably gave a protein boost for rapid growth. Females attained larger maximum size than males as indicated by maxima of 89.2 mm SL and 79.2 mm SL, respectively.

The maximum age recorded for gravel chubs during this study was 42 months, although few probably live beyond thirty months (Table III-3, p. 221). My data (Tables III-3, p. 221 and III-5, p. 227) indicated male population numbers declined rapidly following the second winter of life and relatively few individuals lived to spawn a second time.

CHAPTER IV

BIOLOGY OF THE OZARK CHUB, *Hybopsis harryi* (CYPRINIDAE), IN THE WHITE RIVER SYSTEM, ARKANSAS AND COMPARISON WITH ASPECTS OF THE BIOLOGY OF THE SPOTTED CHUB, *Hybopsis dissimilis*

1. INTRODUCTION

The subgenus *Erimystax* is composed of five species and until recently the biology of these species was virtually unknown. Jenkins (1975) and Burkhead and Jenkins (1982) published the available information on the slender chub, *Hybopsis cahni*, a threatened species of the upper Tennessee River drainage. Harris (msB) studied the biology of *H. x-punctata*, the gravel chub, in the first of three life history papers involving species of *Erimystax*. As stated previously (Harris, msB), the purpose of these studies is 1) to fill the void in knowledge concerning age and growth, population dynamics, food habits, and reproduction and 2) to compare biological and ecological parameters among *Erimystax* species for use in systematic decisions at the species level and for issuing phylogenetic constructs.

Until recently (Harris, msA), the Ozark and spotted chubs were considered subspecies of *Hybopsis dissimilis*. This study was pivotal in the decision to elevate the two taxa to species standing.

2. STUDY AREA

The primary study area for the Ozark chub was Buffalo River at the AR Hwy 14 crossing, Marion County, AR. Buffalo River is a fourth order tributary to the White River with a stream length of approximately 216 kilometers and total drainage area of 3582 square kilometers (Cashner and Brown, 1977). Drainage area above the Hwy 14 bridge is 2776 km (Sullavan, 1974). In 1972, the Buffalo River was designated as this country's first National Scenic River. It generally has not been significantly impacted by damming or channel modification and is flanked for much of its length by Buffalo River National Park lands.

At the study site, the river consisted of long stretches of medium depth runs interrupted by shallow riffles and narrow raceways. Substrate was predominately gravel-cobble with some patchy bedrock and sand. Water quality was very good and water clarity was excellent for underwater observation during late spring, summer, and fall.

Supplementary data, primarily used in population dynamics study and age-growth analysis, were gathered from additional localities in the Buffalo and White rivers. Localities and museum numbers for materials used in this study can be obtained upon request from the author.

Data for the spotted chub comes from specimens collected in the Duck and Buffalo Rivers, Tennessee River drainage, of west-central Tennessee. Duck River specimens were taken from Marshall and Humphreys counties. Total drainage area for Duck River at Hurricane

Mills, Humphreys County (ca 2.0 km above the mouth) was 6623 km . (USGS, 1970-1983b). Habitat consisted of long riffle/runs grading into deeper runs over gravel and sand substrate. Buffalo River specimens were taken in Lewis County at the confluence with Grinder's Creek. The river consisted of alternating riffles and runs with gravel, cobble, and bedrock substrate. Drainage area at this locality is <1170 sq. kms. (USGS, 1970-1983b).

3. PUBLISHED DATA

Very little published information is available for Hybopsis harryi. In their study of small fishes of the Black River and Clearwater Lake, MO, Martin and Campbell (1953) found H. harryi composed 0.7% of the small fishes collected from the Black River in 1947. Martin and Campbell observed that H. harryi was a bottom dwelling species found in riffle channels with moderate to fast current. They noted it was "the most common bottom-feeding species" in the riffles and occurred in pools.

Davis and Miller (1967) and Reno (1969b) based their hypotheses concerning H. dissimilis on examination of both H. harryi and H. dissimilis. Davis and Miller considered that "H. dissimilis" evolved as a sight feeding inhabitant of clear streams based on brain morphology and taste bud distribution/morphology. Reno noted the even distribution of superficial neuromasts in the head region and suggested "H. dissimilis" may live slightly above stream bottom where microcurrent reception by skin neurommasts is unabated and unmodified by surrounding obstacles.

Pflieger (1971) described the habitat of H. harryi as moderately large, clear streams with continuous, strong flow and clean gravelly or rocky bottoms with preferred habitat below riffles or in pools with noticeable current. In 1975, Pflieger repeated this habitat description, gave a maximum length of 4.5 inches (= in) for the species, and noted the coiled configuration of the digestive tract. Brief mention was made of distribution and habitat in Sylamore Creek (Frazier and Beadles, 1977) and the Eleven Point River, AR (Johnson and Beadles, 1977). No other published information was available.

Slightly more information was available for the spotted chub, Hybopsis dissimilis. Trautman (1957, 1981) gave the following age-length ranges for Ohio specimens: young of year 1.3-2.4 in (3.3-6.1 cm) in October; around year 1, 2.0-2.8 in (5.1-7.1 cm); breeding adults usually 2.5-4.0 in (6.4-10.0 cm); largest specimen 4.2 in (11.0 cm) long. Clay (1975) gave total length as 2.5-4.0 in. Jenkins, et al. (ms) stated that the species matures in one year and obtains a maximum age of two years and a few months. Eight yoy specimens from Tennesee taken 29 June averaged 35 mm SL. Sixty-one age 1 and 2 males ranged in size from 63-95 mm SL ($\bar{x}$ = 76 mm SL) while 43 age 1 and 2 females were 57-103 mm SL ($\bar{x}$ = 76.3 mm SL). Jenkins, et al. found the largest Virginia specimen to be a 114 mm SL female.

The first habitat observation published for the spotted chub was that of Kirtland (1850) stating "it is usually found in deep water at the foot of riffles." Clay (1975) gave preferred habitat as riffles with bottoms of clean sand and gravel in streams of moderate size, and described representative habitat of the species as the South Fork

Kentucky River near Booneville, KY. Also, Clay gave physical characters of this stream and listed some of the species associates of the spotted chub.

Trautman (1981:284) provided a detailed description of habitat:

> The spotted chub inhabited riffles and bars in streams of moderate size, 1'-4' deep, where favorable current deposited coarse sands and gravels and kept them free of silt. The largest numbers were usually found in deeper waters at the foot of riffles and in deeper gravel bottom pools present in the main portions of riffles. The species seemed to avoid aquatic vegetation and disappeared from a riffle when the gravel was coated with silt or other pollutants.

Trautman (1957, 1981) noted a similarity in the habitat of gravel and spotted chubs and supposed competition occurs between the two.

Cooper (1983) suggested the spotted chub spawned in the spring by broadcasting eggs over gravel riffles. Duck River, TN chubs were reported to spawn from mid-May through mid-June with an average fecundity of 400 (Harris, 1980a). Jenkins, et al. (ms) defined the spawning period as late April to late May in Virginia.

4. METHODS

The life history study of Hybopsis harryi used a combination of personal collections and field observations augmented by museum specimens. Analysis of 12 monthly samples was attempted but winter high water precluded collections for December, January, and March. Samples were taken at weekly or bimonthly intervals from April through June to more precisely determine spawning period. No distinction was made between collections from different years or rivers in analysis of

results, so this study reflects the "generalized life history" of the Ozark chub.

Only museum specimens were used to gain biological information on the spotted chub, Hybopsis dissimilis. Specimens were available for April, May, June, August, and November.

Collections were made using 2.4-m X 3.0-m and 2.4-m X 6.1-m seines with 0.6-cm mesh. Seining downstream with the current proved a successful means of obtaining Ozark chubs, especially using the 6.1-m seine. From April-June, specimens were checked in the field for spawning condition by gently pressing the abdomen to extrude ova or milt. All specimens were preserved in 10% formalin and stored in 45% isopropanol.

Detailed methodology for examination of reproductive, feeding, and age-growth characteristics was presented in Harris, msB. For preserved specimens, reproductive condition was determined by calculating the gonadosomatic index (GSI) expressed as gonadal weight/adjusted body weight. Ova diameters were measured to the nearest 0.01 mm using a dissecting scope and ocular micrometer. Live specimens were checked in the field by gently squeezing the abdomen to see if ova or milt were readily extruded.

The terminology of Heins (1985) is used to assess both female and male reproductive condition. Female ovarian condition descriptors include: 1) latent (LA); 2) early maturing (EM); 3) late maturing (LM); mature (MA); and partially spent (PS). One additional category is added to those of Heins. The category is spent (SP) and is recognized by ovaries appearing as a compact white or yellow mass with

reddish or dark brown mature ova that are shriveled and apparently being resorbed into the ovarian matrix. Male testes are described as mature (MA) or latent (LA) (Heins, 1985).

Gut contents from anterior to the first 180° bend were removed from a minimum of 10 specimens (when available) from each monthly sample. Animal items were identified to the lowest taxon and non-animal gut contents were classified as plant, including filamentous algae, roots, leaves, or bark, or PDA (Bowen, 1981). Dry weight biomass of animal items (grouped by order), plant, and PDA was determined to the nearest 0.001 g using a Mettler AE 160 electronic balance. In conjunction with food habit analysis, gut length was measured to the nearest 0.05 mm using dial calipers following the method of Snelson (1971).

In addition to the gonadosomatic index, reproductive condition in males was determined by gross examination of the testes as well as secondary sexual characteristics such as tuberculation, pectoral fin coloration, and development of the nuptual cheek pad. Reproductively mature (MA) males had swollen, opaque white testes; while latent (LA) males had small, translucent to white testes. Males with swollen testes and well developed secondary sexual characters were considered mature.

Age and population structure were examined using length frequency histograms of large series of specimens. Age of population group members was verified by scale analysis following methods of Tesch (1971), Weatherley (1972), and Bagenal (1971). Ten scales were removed from the predorsal lateral region of each specimen examined,

stained with alizarin in 2% KOH, and projected to the screen of a Bausch and Lomb scale reader. Total scale length and annular lengths were measured to the nearest 0.05 mm with calipers. Growth in terms of biomass was estimated by obtaining adjusted body weight of specimens of each age class from each monthly sample.

Reproductive and feeding behavior were observed in the field by snorkeling when water clarity permitted. Approximately 10 hours were spent underwater observing Ozark chub behavior. Four visits were made to the Buffalo River between 1982-1983 during the months May, June, July, and September.

Data for water temperature and discharge were obtained from U.S. Geological Survey records (1970-1983a, 1970-1983b). Data for the Buffalo River, AR were obtained from the U.S. Highway 65 station, Searcy County, AR and are considered indicative of stream conditions for life history study locations. Data for the Duck-Buffalo River, TN were obtained form the gauging station at Flat Woods on the Buffalo River, Perry County, TN. Temperature and discharge data are presented as monthly averages in this paper. Summary statistics and Model I linear regression were performed using programs found in Brower and Zar (1984). Model II regression was used when both x and y variables were measured with error as in the case of standard length versus fecundity (Ricker, 1973; Sokal and Rohlf, 1981).

5. RESULTS

A. Hybopsis harryi -- Ozark chub

Habitat and Associates

Habitat. Hybopsis harryi was observed at one time or another in virtually every microhabitat at the Hwy 14 study area. This species was most often observed in runs or riffle habitat over gravel substrate in water approximately 45-60 cm deep. It was not observed often or in large numbers in side channel lentic habitat or in the torrential raceways with bedrock and boulder substrate.

There appears to be microhabitat segregation between young of the year and adults chubs. Young were observed in backwaters and shoreline or sidechannel habitat where current velocity was slow. Adults were seldom observed in this habitat and appeared transient when they were seen there. There may be some microhabitat partitioning of the sexes during the period immediately prior to spawning as evidenced by collections dominated by one or the other sex from March and April.

Species Associates. Species most often collected or observed with H. harryi included Campostoma anomalum, Notropis greenei, N. telescopus, N. pilsbryi, N. galacturus, N. nubila, Micropterus dolomieui, Moxostoma spp., Hypentelium nigricans, Etheostoma euzonum, E. blennioides, Percina caprodes and P. evides. Hybopsis harryi was quite numerous in its preferred habitat and was subjectively determined to be second in numerical abundance to Campostoma anomalum. Ordinarily, this would not be reflected in capture data due to successful net avoidance capabilities of this elusive species.

Food and Feeding Habits

Food. Stomach contents from 118 adult and six young of year (yoy) specimens of Hybopsis harryi were examined. Summaries of biomass and countable food items are presented in Tables IV-1 and IV-2, respectively. In Table IV-1, the total biomass estimate is presented as: sum of monthly estimates for each item/sum of biomass for all food items (= grand sum biomass) X 100 which = per cent annual biomass for each food item (column TOT in Table IV-1). Annual biomass is also presented as the sum of monthly percentages of each food item divided by the total number of months for which specimens were examined (column CORR in Table IV-1), and is referred to as corrected annual biomass.

Feeding behavior. Ozark chubs were observed feeding in moderate current over gravel, rock, or bedrock substrates. They were most often in the runs between the base of a riffle and the head of the next in water 40-100 cm deep. My observations indicate they feed by grazing on the tops of rocks and between larger interstitial spaces. Numerous individuals were seen grabbing drift from the water column although they never ventured more than 10 cm from the stream bottom.

Gut morphology. Gut length was determined for 54 H. harryi (SL 71.9-120.1 mm). Length of the digestive tract ranged from 1.49-2.73 times standard length with $\bar{x}$ = 2.25 SL. Gut morphology differs from the simple s-shape by having two or more accessory loops as in Figure IV-1.

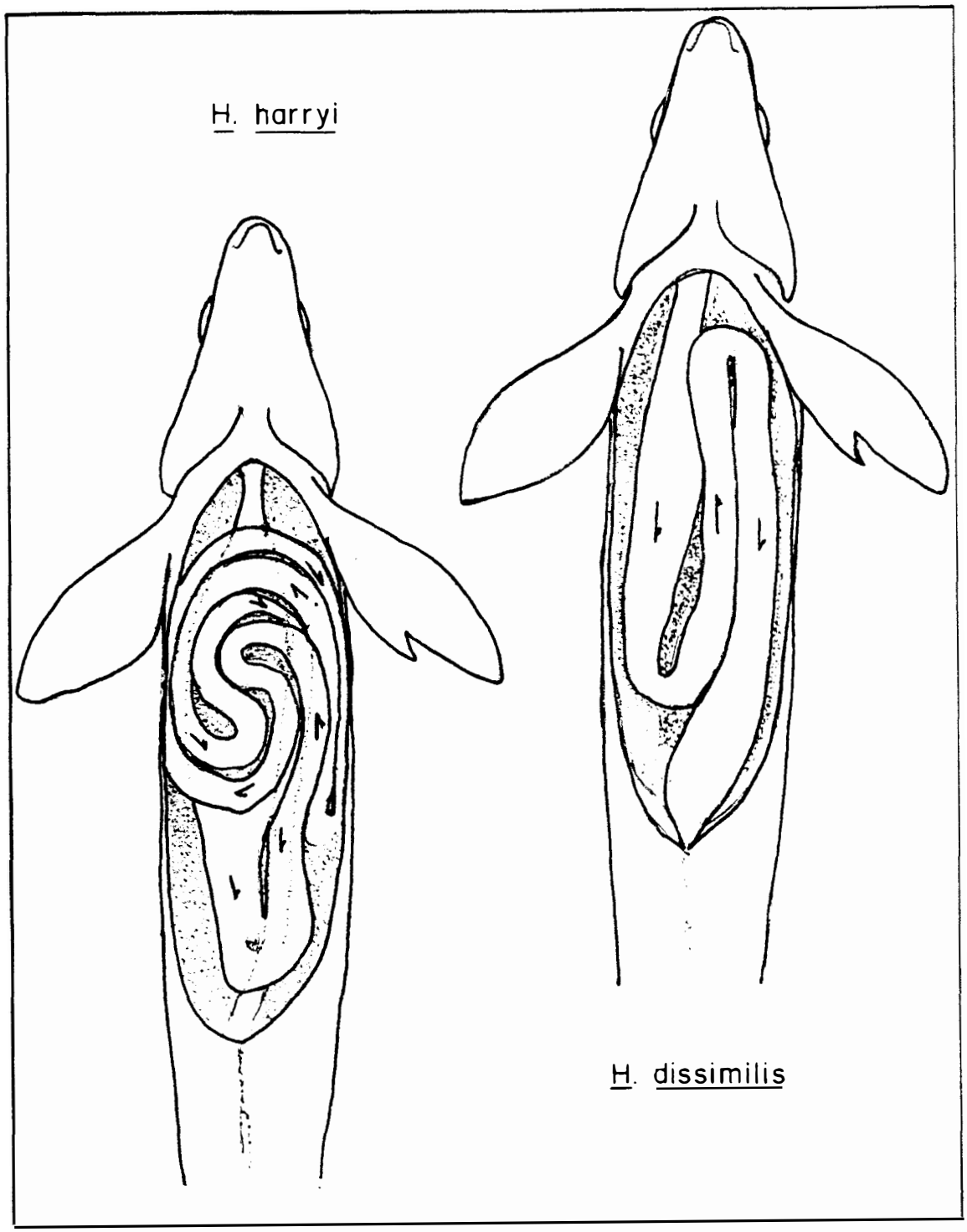


Figure IV-1. Gut morphology of Hybopsis harryi and H. dissimilis.

Table IV-1. Per Cent Food Biomass from Monthly Samples of Hybopsis harryi.

Food Item	Month										Totals	
	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Tot[a]	Corr[b]
Ephemeroptera			0.5		2.4	5.7	1.8	0.9		0.2	1.0	1.3
Odonata				0.6							0.1	0.1
Plecoptera			0.2	0.4			1.3				0.2	0.2
Megaloptera									3.2		0.1	0.4
Trichoptera	0.4			7.8	10.5	6.8	8.9	2.7			4.0	4.1
Diptera	1.0		0.8	4.2	1.5	2.6		0.4		0.1	1.3	1.2
Lepidoptera	0.7			2.4	6.0	2.9	1.0	2.7	0.2	1.8	1.9	2.0
Plant			0.8	24.2	19.7	45.4	59.8	4.6	72.6	1.2	18.2	25.4
PDA	97.7		97.7	60.3	59.8	36.5	26.0	88.3	20.9	96.7	72.9	64.9
Gastropoda						0.2		0.4	3.0		0.2	0.4
Scales	0.2										-	-
Unknown							1.1				0.1	0.1
# Examined	11		13	10	13	14	15	10	12	20	118	
# Empty	1		2	0	0	2	0	0	1	2		

[a]Annual total derived from sum of monthly biomass.

[b]Annual total derived from sum of per cent monthly biomass.

Table IV-2. Number of Food Items from Monthly Samples of Hybopsis harryi.

Food Item	Month									Totals	
	Feb	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Tot[a]	% Tot
Nematoda						1				1	0.2
Hydracarina						1				1	0.2
Ephemeroptera		1	1	2	3	3	2	2	1	15	3.5
Baetidae				1	1					2	0.5
Heptageniidae				1	1					2	0.5
Odonata-Zygoptera			1							1	0.2
Plecoptera			1			1				2	0.5
Trichoptera	1		4	1						6	1.4
Helicopsychidae						2				2	0.5
Hydropsychidae			5	13	1	2	2			23	5.4
Hydroptilidae		2	5	31	17	8	15	1		79	18.7
Leptoceridae			8			1				9	2.1
Coleoptera			1							1	0.2
Diptera											
Chironomidae	24	26	79	27	30	3	14		8	211	49.9
Simuliidae			1		6					7	1.7
Tipulidae				1						1	0.2
Lepidoptera											
Pyralidae	1		7	24	2	4	4	1	2	45	10.6
Gastropoda					1	1	1	1		4	0.9
Fish Scales	7								1	8	1.0
Unknown						1				1	0.2
Total	33	29	114	101	62	28	38	6	12	423	

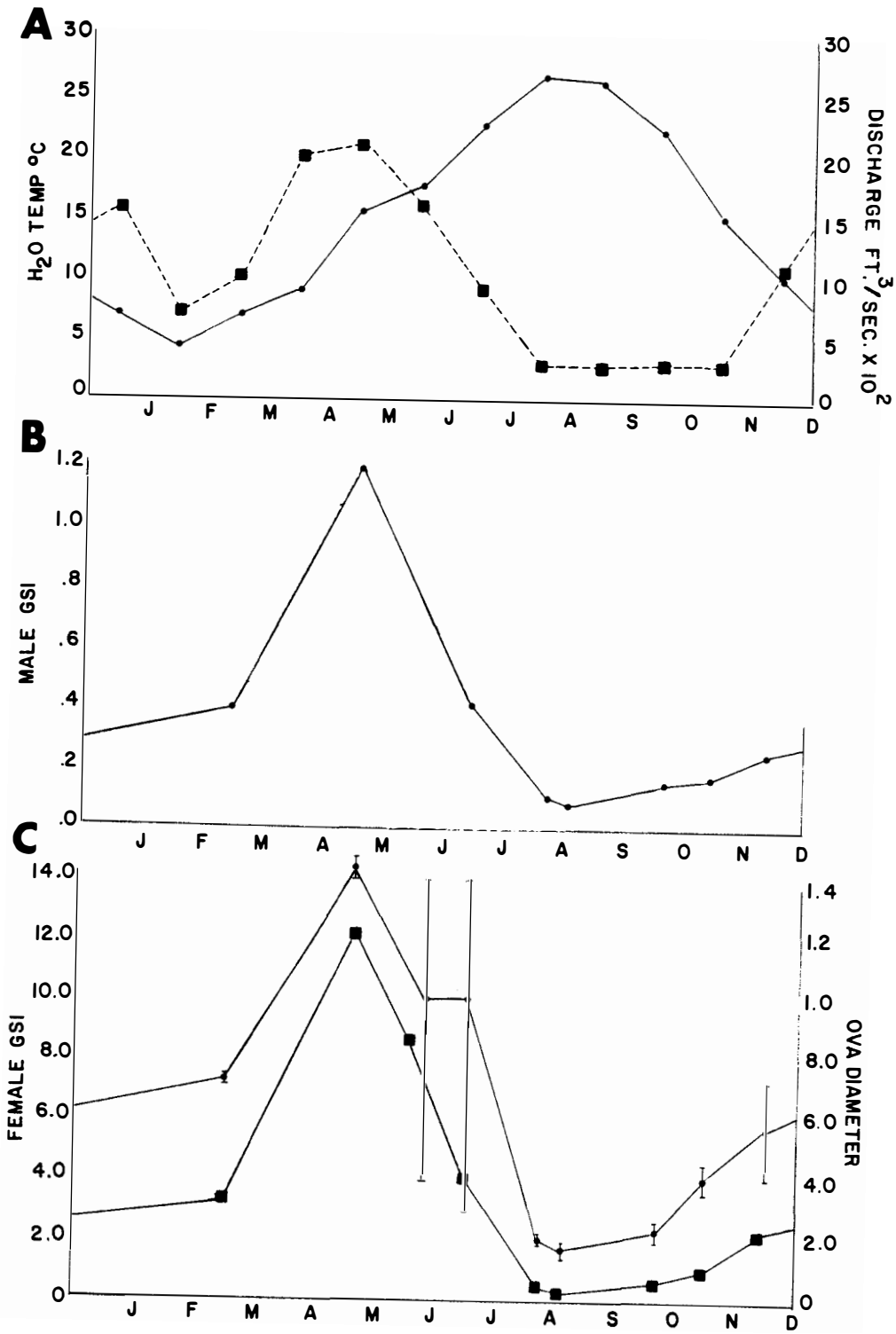
[a]Sum of Monthly totals.

Reproduction

Male. Gonadosomatic index values (Figure IV-2) indicated male peak reproductive development occurred in late April to early May. Lack of specimens from December, January, and March made it difficult to determine when increase in gonadal size and weight began. Rapid increase in mean GSI occurred from mid-February (mean GSI = 0.39) until a peak in mid-April (mean GSI = 1.19) followed by rapid decline through May (0.36), June (0.42), and July (0.12) before bottoming in August (0.08). Males captured 19 April 1983 readily released milt when the abdomens were gently squeezed. Only one of nine specimens captured 13 June 1982 was still running milt.

Secondary sexual characteristics were expressed beginning in late winter or early spring. Males captured in early February were generally without fin tubercles but minute tubercles were present on the periphery of dorsolateral body scales. The pectoral fins also lacked concentrated interradial pigmentation at this time. A single individual (of six examined) showed early development of the nuptial jaw pad. Specimens captured on 19 April had well developed pectoral fin tubercles on the dorsal surface while the dorsal, anal, and pelvic fins possessed typically minute tubercles restricted to the distal one half of rays. Nuptial jaw pads were well developed and pectoral fin interradial pigmentation was concentrated so that males were easily separated from females. Anterior dorso-lateral scales had 8-10 tubercles on the periphery of each scale with perhaps 5-6 tubercles located centrally. Posterior of the dorsal fin, tubercles were restricted to the periphery of each scale.

Figure IV-2. Reproductive parameters of Hybopsis harryi. A. Mean water temperature (circles) and discharge (squares) of the Buffalo River, AR for 1970-1983. B. Male Hybopsis harryi mean gonadosomatic index (GSI). C. Female H. harryi mean GSI (squares) and mean ovum diameter (circles) with standard deviation.


A
30
25
20
15
10
5
0
H_2O TEMP °C
DISCHARGE FT.^{3}/SEC. X 10^2
J F M A M J J A S O N D
B
1.2
1.0
.8
.6
.4
.2
.0
MALE GSI
J F M A M J J A S O N D
C
14.0
12.0
10.0
8.0
6.0
4.0
2.0
0
FEMALE GSI
1.4
1.2
1.0
8.0
6.0
4.0
2.0
0
OVA DIAMETER
J F M A M J J A S O N D

Specimens from May and June were generally as described for April. July specimens were without fin and body tubercles or, if present on the pectoral fin, they appeared in uneven rows as if being sloughed from the surface. Nuptial jaw pads, if present, appeared thin and patchy. By August, none of the males examined showed signs of secondary sexual characters.

Female. GSI values (Figure IV-2) suggest that females were in or near spawning condition by mid to late April. Nine reproductively mature females captured 19 April 1984 had an average GSI of 12.23 with individual values ranging 3.76-29.97. All individuals were MA with respect to ovarian development. Two immature females (55.85 and 54.50 mm SL) possessed EM ovaries and were not expected to participate in spawning that year. Mean ovum diameter for mature April specimens was 1.43 mm with a maximum observed size of 2.00 mm. Ova ready for spawning were >1.50 mm while the majority were in the 1.75-1.85 mm range. When checked for spawning condition in the field by gently squeezing the belly, only one of the nine specimens extruded ova.

Fifteen females captured 19 May 1984 were examined and two specimens were judged MA, while 13 were PS. When examined at capture, only one individual would extrude ova when pressured. Average GSI for nine weighed specimens was 8.92 with a range of 4.04-18.95. Additionally, nine yoy females were judged LA or EM and not participating in that years reproductive effort. Of eight females captured 31 May 1982, three were classified as PS and five as SP. Four yoy specimens 63.35-72.90 mm SL did not have mature ova and did not spawn. Average ovum diameter for May specimens was 1.03 mm. Size of ripe ova was the

same as for April specimens but the May average was lowered by the SP ovaries with ova ranging 0.2-0.4 mm in diameter. Four of the five females captured 13 June were SP while the other was PS.

July-September females remained LA as indicated by the low GSI and ovum diameter values in Figure IV-2. October and November individuals showed signs of slow, steady ovarian gain with average GSI of 1.07 and 2.25, respectively, and average ovum diameters of 0.41 and 0.57.

Fecundity. Number of ova showed a high correlation with standard length ($r = 0.97$) and is described by the Model II regression $F = 32.34(SL) - 2334.08$ as shown in Figure IV-3. When log transformed (as recommended by Bagenal, 1971), the relationship is described by the linear equation $\log_{10} F = 4.20(\log_{10} SL) - 5.46$ ($r = 0.95$).

Spawning. Seven attempts to observe spawning behavior were made on the following dates from 1982 through 1984: 19 April, 19 May, 30 May, 31 May, 2 June, 13 June, and 24 June. Approximately 13 total hours were spent in underwater observation. On 30 May 1983, a rather large congregation of Ozark chubs was observed in water 40-60 cm deep at the head of a riffle and immediately downstream for a distance of 10 m. Although actual spawning was not observed, behavior similar to that of prespawning gravel (Hybopsis x-punctata) and blotched (H. insignis) chubs was observed. Three mature chubs which appeared to be females were nestled on the substrate in shallow depressions or crevices between rocks. Presumed males approached the females on several occasions but neither made contact nor elicited any response from the reposed females. On 2 June 1983, two females were observed

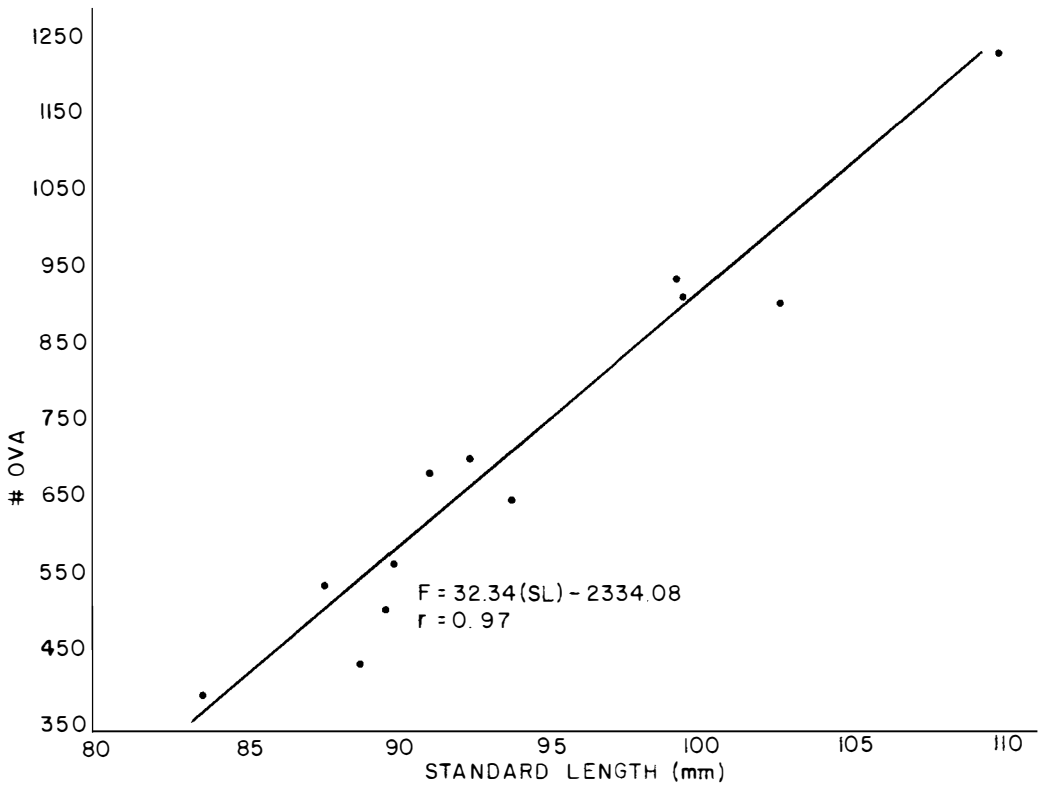


Figure IV-3. Linear regression of standard length (SL) versus fecundity (F) for Hybopsis harryi.

in the same behavior. One female, observed for 30 minutes, spent most of the time resting passively in substrate depressions. She was disturbed on several occasions by passing centrarchids (Lepomis and Micropterus dolomieui) but each time resettled to a bottom depression. During the observation time, the specimen remained within a one meter radius of where originally observed. One interaction with a presumed male was observed when the male entered the shallow depression, lay side to side with the female for five seconds, and then exited. Water level had dropped considerably since the earlier visit and Ozark chubs were dispersed throughout lentic habitat except for the shallowest riffles (<10 cm deep) and torrential raceways.

The smallest female specimen observed with mature ova was an individual 63.35 mm SL. The smallest male with secondary reproductive characters and mature testes measured 76.90 mm SL. Five of 22 (22.7%) yoy females examined from April, May, and June samples possessed mature ova and may have taken part in spawning activities. Only two of 21 yoy males (9.5%) examined were judged capable of participating in reproductive efforts.

Age and Growth

Collections of Hybopsis harryi are small, generally numbering fewer than 50 mature individuals. Figure IV-4 presents a combination of two collections (209 individuals) from late July and early August to illustrate population structure of the Ozark chub. Table IV-3 summarizes available data on age (in months) and growth (SL) for males, females, and the combined sexes. Linear equations for age

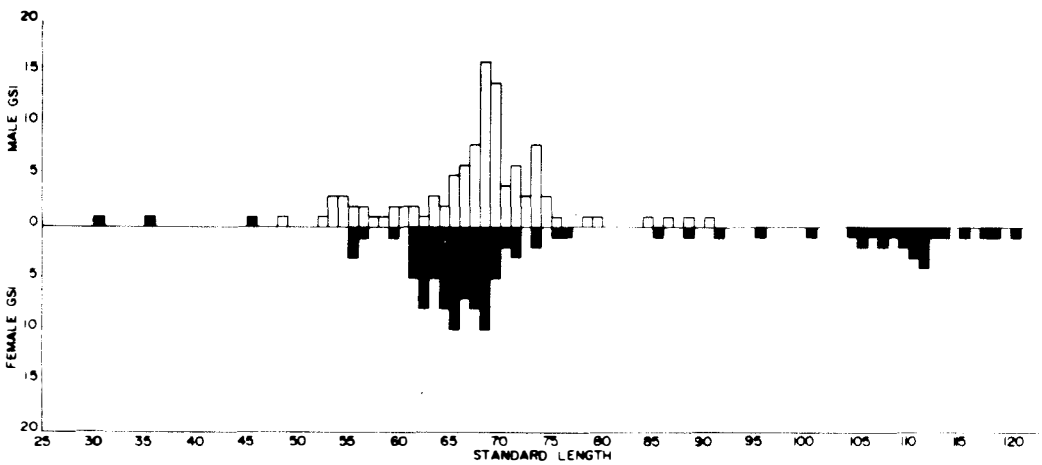


Figure IV-4. Length-frequency histogram for Hybopsis harryi. Solid bars represent females and open bars represent males.

Table IV-3. Mean Standard Length Based on Monthly Samples of Each Age Group of Male, Female, and Total *Hybopsis harryi*.

Age Group	Month		Males $\bar{x}$	Males n	Females $\bar{x}$	Females n	Total $\bar{x}$	Total n
	May	1						
	June	2					30.65	(5)
	July	3					38.37	(27)
	August	4	42.91	(9)	43.85	(15)	43.50	(24)
	September	5	51.55	(33)	51.48	(21)	51.52	(54)
1	October	6	54.95	(24)	56.37	(18)	55.52	(43)
	November	7	50.71	(64)	48.25	(67)	49.45	(131)
	December	8						
	January	9						
	February	10	59.58	(10)	50.99	(5)	56.72	(15)
	March	11	49.80	(13)	51.30	(14)	50.44	(28)
	April	12	62.10	(1)	58.03	(3)	59.05	(4)
	May	13	63.89	(17)	62.78	(14)	63.39	(31)
	June	14						
	July	15	66.88	(103)	66.29	(83)	66.62	(186)
	August	16	72.11	(12)	72.94	(20)	72.63	(32)
	September	17	81.72	(5)	83.50	(3)	82.39	(8)
2	October	18	85.03	(8)	83.09	(4)	84.38	(12)
	November	19	79.68	(3)	77.55	(1)	79.15	(4)
	December	20						
	January	21						
	February	22	86.60	(2)	89.42	(3)	88.29	(5)
	March	23						
	April	24	87.60	(7)	89.88	(6)	88.65	(13)
	May	25	86.55	(1)	90.18	(19)	90.00	(20)
	June	26	91.64	(8)	91.11	(4)	91.47	(12)
	July	27	94.48	(2)	101.45	(1)	96.80	(3)
	August	28	88.90	(4)	94.90	(7)	92.71	(11)
	September	29	91.40	(1)	103.50	(1)	97.45	(2)
3	October	30	93.45	(3)	94.10	(2)	93.71	(5)
	November	31						
	December	32						
	January	33						
	February	34						
	March	35						
	April	36			106.05	(2)	106.05	(2)
	May	37						
	June	38			114.15	(1)	114.15	(1)
4	July	39						
	August	40	111.30	(1)	111.42	(21)	111.41	(22)

Table IV-3. (Continued)

Age Group	Month	Males $\bar{x}$	Males n	Females $\bar{x}$	Females n	Total $\bar{x}$	Total n
	September 41						
	October 42			111.70	(1)	111.70	(1)

versus standard length did not vary significantly between the sexes ($F_s = 0.13 << F\ [1,43] = 4.08$). These equations are expressed as $SL = 40.83 + 1.87A$ ($r = 0.96$) for males and $SL = 40.00 + 1.93A$ ($r = 0.97$) for females and are shown in Figure IV-5. Age versus standard length for the combined sexes is plotted in Figure IV-6 using a moving average of threes and assuming no decrease in SL (after Mayden and Burr, 1981). Age versus body weight for the combined sexes is presented in Figure IV-7 and is described by the linear equation $W = 0.355A - 0.732$ ($r = 0.98$).

As noted previously, late April through May is the time of peak reproduction. Therefore, I have designated May as month 1 for aging purposes with June as month 2, etc. As suggested by Everhart and Youngs (1981:68-69), annuli are reported in Roman numerals and age groups in Arabic numerals where specimens between zero and 12 months are Age Group 1, specimens 13 to 24 months are in Age Group 2, and so on.

Young of year specimens were represented in June collections by five specimens ranging 25.75 - 33.65 mm SL, $x = 30.65$. Rapid growth continued until the onset of winter coldwater in November when growth slowed until the cessation of spawning activities in June (Figure IV-6). November yoy specimens were usually between 50-60 mm SL. As noted for Hybopsis x-punctata (Harris, msB), rapid growth appeared to coincide with warm water temperatures and assumed increase in the primary dietary constituent, periphytic detrital aggregate. July age 2 specimens averaged 66.6 mm SL ($n = 186$) which increased to 72.6 mm SL for August ($n = 32$) and 82.4 mm SL for September ($n = 8$). Data for

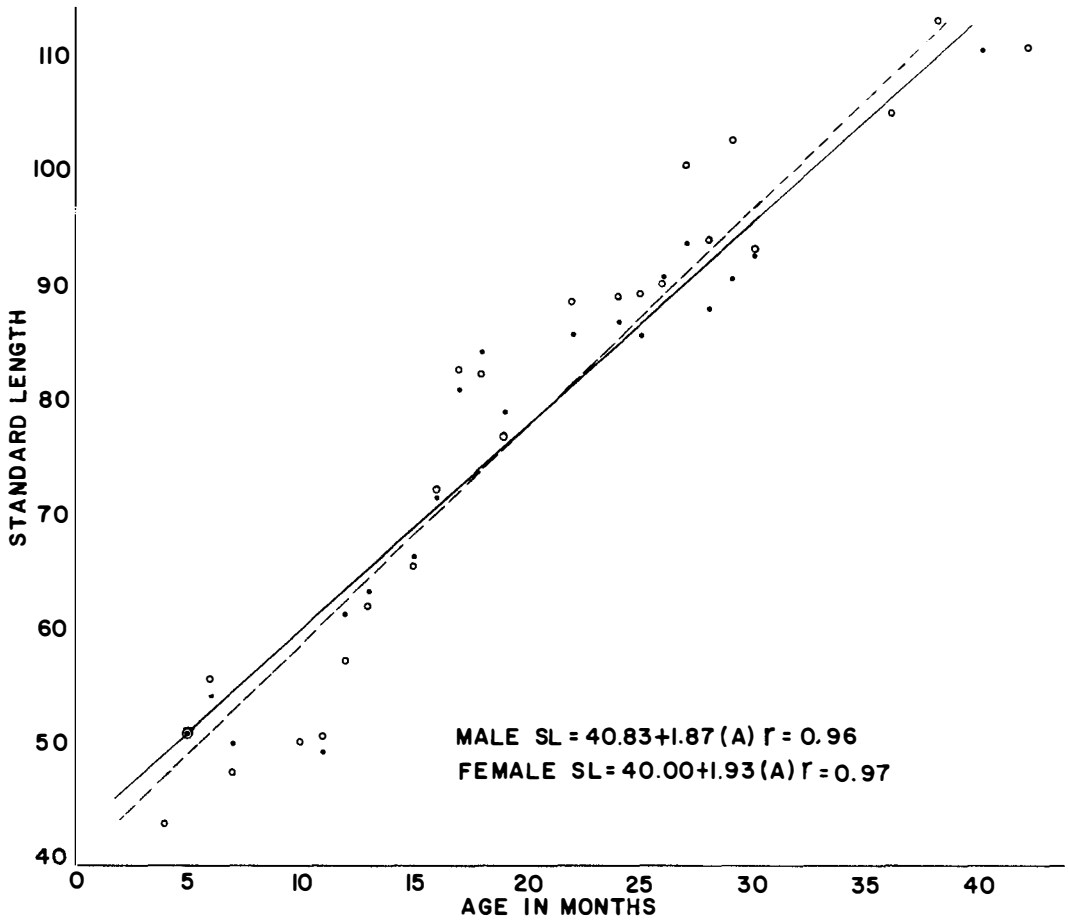


Figure IV-5. Linear regression of age (A) versus standard length (SL) for male (solid line) and female (dashed line) Hybopsis harryi. Mean monthly standard length for males (closed circles) and females (open circles) are plotted.

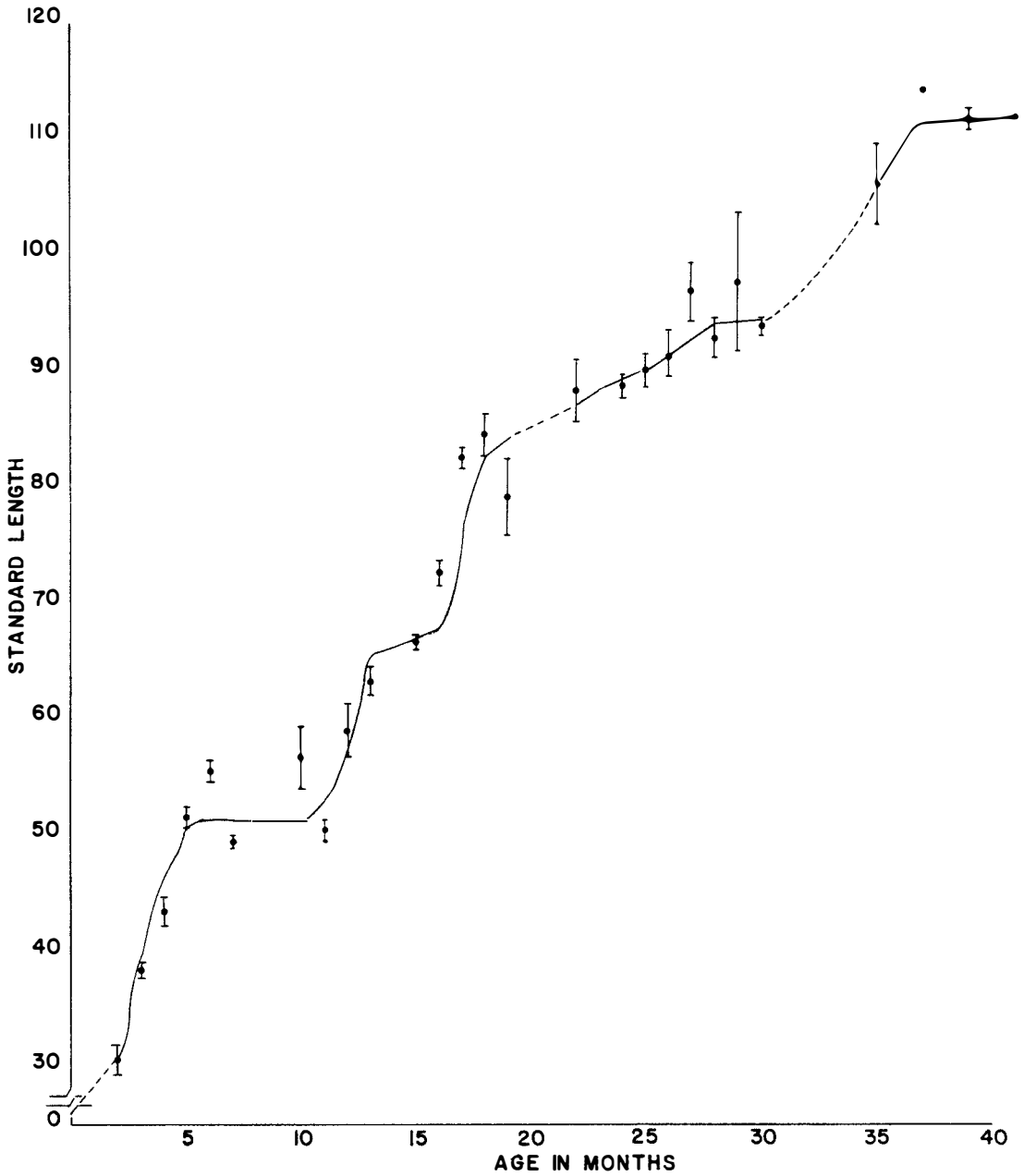


Figure IV-6. Age versus mean standard length plotted as a moving average of three for Hybopsis harryi. Bars represent + one standard deviation.

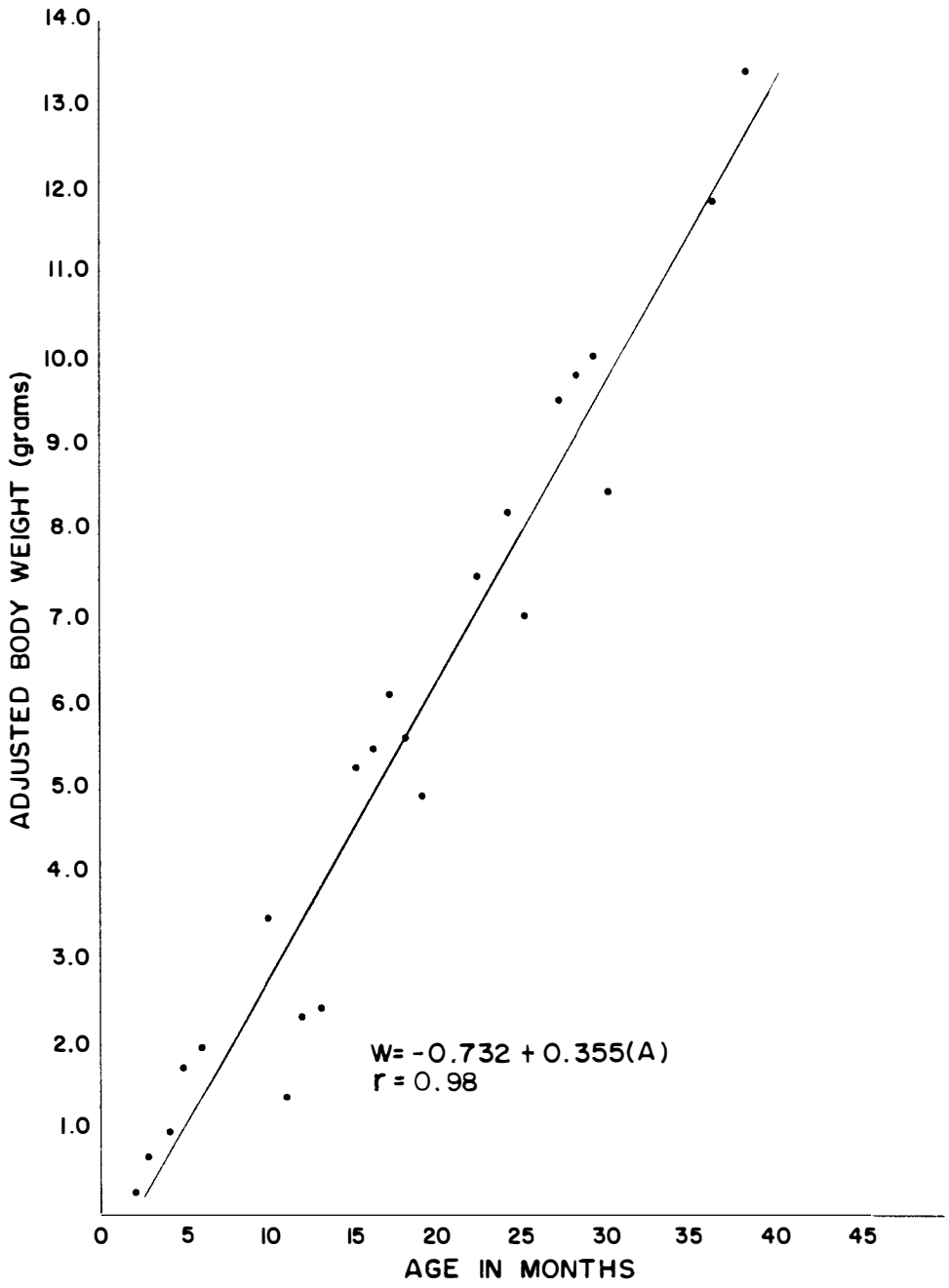


Figure IV-7. Regression of age (A) versus mean adjusted body weight (W) for Hybopsis harryi.

age 3 and 4 growth was confusing and inconclusive due primarily to the low numbers of individuals available for study.

Overall growth trends for the sexes (Figure IV-5) indicated males were larger than females until approximately age 20 months. The largest individual examined during this study was a 40-month-old female measuring 120.1 mm SL while the largest male was also 40 months old and 111.3 mm SL.

Linear regression was performed on scale length-scale radius data from 48 specimens (Age 2 = 18, Age 3 = 27, Age 4 = 3) collected 19 April, 31 May, 13 June, and 24 June. The data yielded the line described by the regression equation $Y = (0.92)X + 44.99$ ($r = 0.63$) where Y = SL and X = projected scale radius in mm at 120x. Back calculation of SL at annulus formation resulted in the averages 74.6 mm at age 2, 85.8 mm at age 3, and 102.2 mm at age 4.

Population Dynamics

Survivorship. Survivorship tables are presented in Table IV-4. Survivorship was high for age 2 specimens and was similar for the sexes. Both sexes showed significantly increased mortality by age 3, the males moreso than females. Age 4 males were rare within the cohort and surviving females represented approximately 8% of all females. The oldest specimen in this study was a 42 month-old-female whereas only one age 4 male, a 40-month-old individual, was found.

Sex Ratio. The male to female ratio observed in 667 specimens was 1:1 (Table IV-5). Males slightly outnumbered females in Age 1 and

Table IV-4. Relative Survival of Year Classes of Male, Female, and Total *Hybopsis harryi* Expressed as Proportions of Age Class 1 ($1x^1$), Age Class 2 ($1x^2$), and Age Class 3 ($1x^3$).

Sample	Age Group	# Individuals	Survival		
			$1x^1$	$1x^2$	$1x^3$
Males	1	154	1.000	-----	-----
	2	157	1.019	1.000	-----
	3	19	0.123	0.121	1.000
	4	1	0.006	0.006	0.053
Females	1	143	1.000	-----	-----
	2	134	0.937	1.000	-----
	3	36	0.252	0.269	1.000
	4	23	0.161	0.172	0.639
Total	1	297	1.000	-----	-----
	2	291	0.980	1.000	-----
	3	55	0.185	0.189	1.000
	4	24	0.080	0.082	0.436

Table IV-5. Sex Ratios for Each Age Group and the Total Sample of *Hybopsis harryi*.

	Age Group 1	Age Group 2	Age Group 3	Age Group 4	Total
Males	0.52	0.54	0.35	0.04	0.50
Females	0.48	0.46	0.65	0.96	0.50

2 samples representing 52% and 54% of the respective age groups. Females dominated Age 3 by almost 3.5:1 and Age 4 by greater than 9:1.

B. *Hybopsis dissimilis* -- Spotted chub

Food Habits

Gut contents of 43 adult spotted chubs were examined and results are presented as biomass (Table IV-6) and countable food items (Table IV-7). As discussed for the Ozark chub, biomass is summarized as a per cent of total biomass (TOT) and as a mean of the monthly per cent biomass for each food item (CORR).

Gut morphology. Gut length of 38 *H. dissimilis* (SL 63.4-112.7 mm) ranged 0.77-1.11 times SL with x = 0.94 SL. Gut morphology was basically s-shaped with varying lengths of an accessory loop (Becker, 1983) at the second 180 bend in the gut. This form is contrasted with that of the Ozark chub illustrated in Figure IV-1 (p. 247).

Reproduction

Although material was available from only five months of the year, the data collected allowed valuable observations concerning reproduction of this species. Gonadosomatic index values are presented in Figure IV-8 for males and females. Data for discharge and water temperature are also plotted in Figure IV-8.

Although March specimens were not available for either sex, it would appear that April was the peak reproductive month for the spotted chub based on condition of the females. Of seven females examined from three collections (11, 16, and 27 April) four were MA,

Table IV-6. Per Cent Food Biomass from Monthly Samples of Hybopsis dissimilis.

Food Item	Month					Totals	
	Apr	May	Jun	Aug	Nov	Tot[a]	Corr[b]
Oligochaeta			7.0	0.1	31.5	2.4	7.7
Ephemeroptera	7.6	28.4	11.9	2.7	3.1	6.9	10.7
Plecoptera	0.4		2.6	1.0		1.1	0.8
Megaloptera	1.3			0.6		0.6	0.4
Trichoptera	45.8	9.5	39.3	14.7		24.3	21.9
Coleoptera	10.6		0.8			2.2	2.3
Diptera	3.5	1.4	0.9	0.3	0.6	1.1	1.3
Lepidoptera			4.2			0.8	0.8
Gastropoda	1.2	4.7	1.2	0.2		0.9	1.5
Plant		8.4	12.4	58.0	14.8	33.9	18.7
PDA	29.6	47.6	19.7	22.5	50.0	25.9	33.9
# Examined	12	6	8	12	5	43	
# Empty	1	0	2	0	1	4	

[a]Annual total derived from sum of monthly biomass.

[b]Annual total derived from sum of per cent monthly biomass.

Table IV-7. Number of Food Items from Monthly Samples of *Hybopsis dissimilis*.

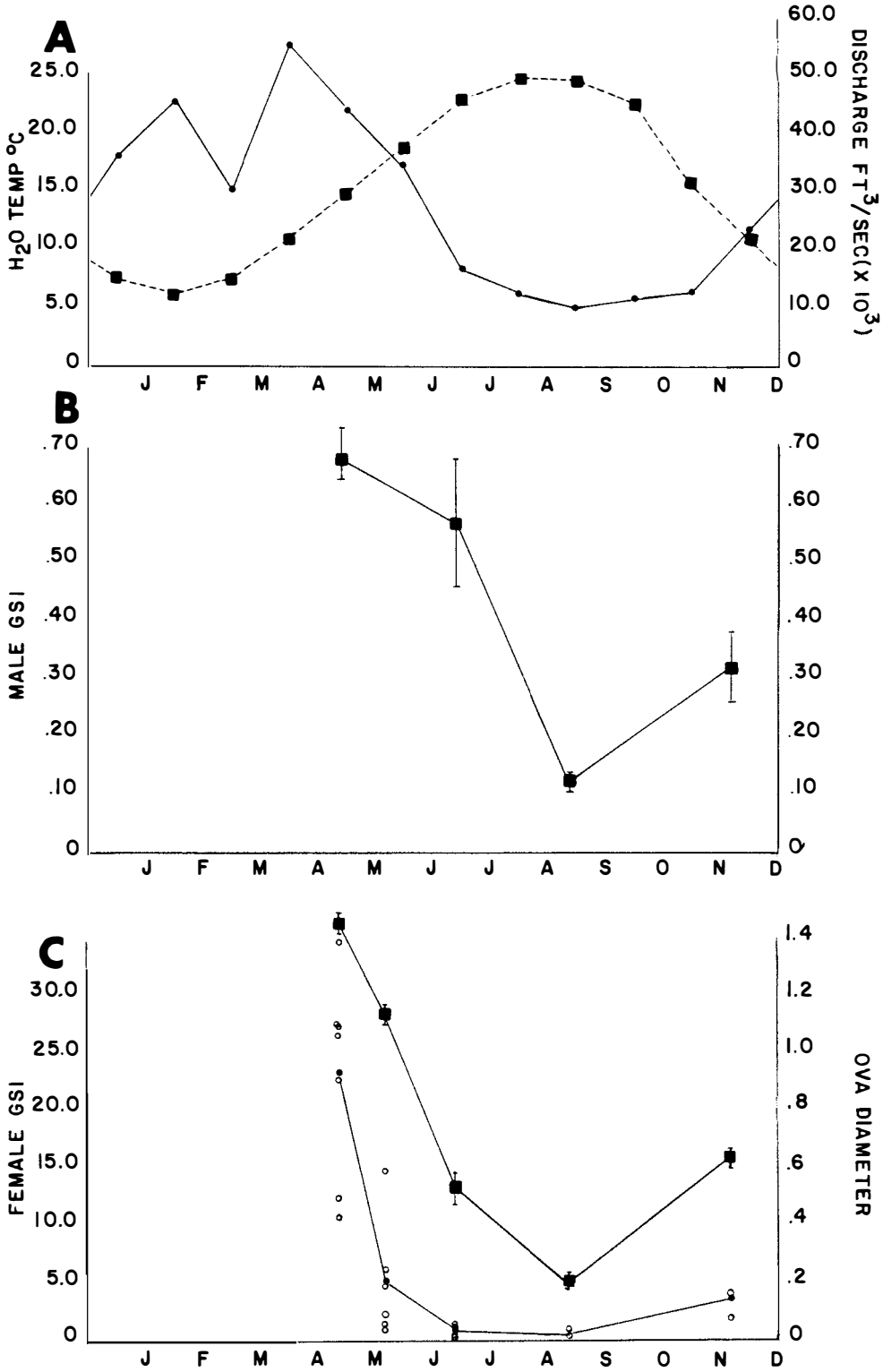
Food Item	Month					Totals	
	Apr	May	Jun	Aug	Nov	Tot[a]	% Tot
Oligochaeta			1	1	1	3	1.2
Hydracarina		1				1	0.4
Ephemeroptera	2		1	2	2	7	2.7
Baetidae			2			2	0.8
Ephemerellidae	2					2	0.8
Heptageniidae	2	1	4	3		10	4.1
Leptophlebiidae	1	3	1	4		9	3.7
Oligoneuridae							
Isonychia		1				1	0.4
Plecoptera	1		1	1		3	1.2
Perlidae							
Acroneuria				1		1	0.4
Perlesta				1			0.4
Megaloptera							
Corydalidae	1					1	0.4
Trichoptera		1				1	0.4
Hydropsychidae	4	1	13	1		19	7.0
Hydroptilidae	8		3	9		20	8.2
Leptoceridae	12	1	7	65		84	34.8
Psychomyiidae		20				20	8.2
Coleoptera			1			1	0.4
Psphenidae	1					1	0.4
Diptera							
Chironomidae	14	8	13	10	3	48	19.7
Simuliidae					1	1	0.4
Lepidoptera			1			1	0.4

Table IV-7. (Continued)

Food Item	Month					Totals	
	Apr	May	Jun	Aug	Nov	Tot[a]	% Tot
Gastropoda	2	1	1	1		5	2.0
Totals	50	38	49	100	7	244	

[a]Sum of monthly samples.

Figure IV-8. Reproductive parameters of Hybopsis dissimilis. A. Mean water temperature (squares) and mean discharge (circles) of the Buffalo River, TN from 1970-1983. B. Male Hybopsis dissimilis mean gonadosomatic index (GSI). Bars represent + one standard deviation. C. Female H. dissimilis mean GSI (closed circles) and mean ovum diameter (squares). Bars represent + one standard deviation and open circles are individual GSI values.


A
25.0
20.0
15.0
10.0
5.0
0
H2O TEMP °C
60.0
50.0
40.0
30.0
20.0
10.0
0
DISCHARGE FT3/SEC(X 10³)
J F M A M J J A S O N D
B
.70
.60
.50
.40
.30
.20
.10
0
MALE GSI
J F M A M J J A S O N D
C
30.0
25.0
20.0
15.0
10.0
5.0
0
FEMALE GSI
1.4
1.2
1.0
.8
.6
.4
.2
0
OVA DIAMETER
J F M A M J J A S O N D

two were LM, and one was PS. GSI values for April females were similar to those of April female Ozark chubs. Six females collected 5 May were equally divided between the PS and SP condition. All females (n = 5) from a 13 June sample were SP.

No May males were available, but May GSI was expected to be similar to or slightly below the April value as witnessed by the gradual decrease in GSI between April and June (Figure IV-8). A precipitous drop in GSI occurs after June as has been shown in other Erimystax species.

Male secondary sexual characteristics were fully displayed in the five April specimens examined. Pectoral tubercles and interradial pigment were well developed and nuptial jaw pads were thick and highly visible. Dorsal, anal, and pelvic tubercles were present but poorly expressed. Cepahalic tubercles were small but dense and body tuberculation, especially antero-dorsolaterally, was well developed. These covered the periphery and centrum of each scale above the lateral band anterior to the dorsal fin insertion. June specimens showed signs of losing secondary characters as pectoral tubercles were patchy and many had lost the spiny tubercle caps. Nuptial jaw pads were thin and patchy. August males showed no signs of secondary sexual characters.

Fecundity. Number of ova showed a high correlation with standard length (r =0.96) for the individuals analyzed. Available reproductive material was restricted to very small and very large individuals. The Model II linear regression was described by F = 23.04(SL) - 1198.30 as shown in Figure IV-9. Log transformation yields the equation log F =

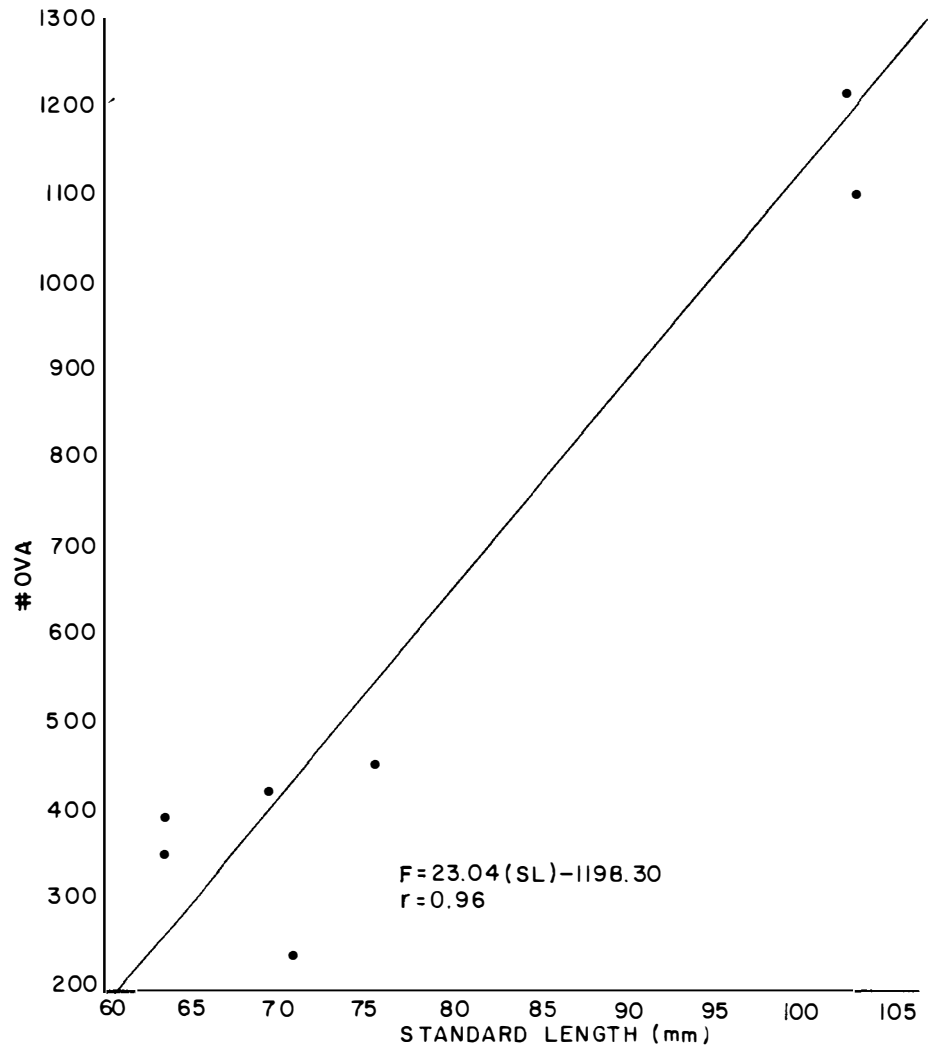


Figure IV-9. Regression of standard length (SL) versus fecundity (F) in Hybopsis dissimilis.

$2.92(\log_{10} SL) - 2.80$ ($r = 0.90$). The maximum ovum diameter measured was 1.75 mm and mature ova were 1.30-1.75.

6. DISCUSSION

Previous to this study, virtually nothing was known of the food and feeding habits of the Ozark and spotted chubs. Harris (1980a), based on examination of five specimens from the Duck River, TN, gave the diet of spotted chubs as snails and a wide variety of aquatic insect larvae with occasional terrestrial insects included. Observations on feeding behavior suggested picking the upper surface of stones as the primary means of obtaining food (Harris, 1980a; Jenkins and Burkhead, 1984).

Data for the Ozark chub (Tables IV-1, p. 248 and IV-2, p. 249) suggest that it is primarily a benthic herbivore/detritivore with plant material (predominately filamentous algae) and periphytic detrital aggregate (PDA) comprising slightly more than 90% of the annual diet. PDA was virtually the only food item ingested during the cold water months November, February, and April and was 97-98% of food biomass. With the onset of warmer water and greater algal productivity, the plant component increased in dietary importance to maxima of 45% and 60% for July and August. In no month did the combined plant-PDA component fall below 80% of total dietary intake. Intake of immature aquatic insects appears to be opportunistic as no taxon comprised more than 11% of a monthly food biomass sample. More than likely, most aquatic invertebrates are accidently taken with the PDA or algal matrix rather than deliberately searched for and consumed.

Observations on feeding behavior showed Ozark chubs fed primarily by grazing over the surface of rocks and gravel. This behavior encompassed approximately 90% of observation time while searching interstitial spaces or entering the water column to take drift items made up the remaining 10%. This type of feeding strategy appears energy conservative from the acquisition stand point as PDA is ubiquitious throughout the riverine system. The nutritional value of PDA and algae, especially in terms of supplying protein requirements, remains conjectural.

The PDA-plant component contributed slightly more than half (52%) of the corrected total biomass from the abbreviated sample of Hybopsis dissimilis. The largest contribution of PDA-plant for months analyzed was the 80% for August. Of special interest was the relative similarity of the plant component in both the Ozark and spotted chubs (Tables IV-1, p. 248 and IV-6, p. 267). Both data sets showed a modest plant contribution to the April diet, followed by rising amounts to the August peak (almost 60% for both) before decreasing to lowered November levels. Amounts of PDA in the spotted chub diet were lower for all months than those measured for the Ozark chub. Whether this reflects lesser amounts of PDA in the Duck-Buffalo system or selective feeding which eliminates quantities of PDA is unknown. Aquatic insect larvae, especially Trichoptera and Ephemeroptera, were significant contributors to the spotted chub diet, averaging 21.9% and 10.7% of the total diet. Invertebrates as a whole were quite abundant during the spring months, making up 80% and 78% of the April and June samples.

Harris (msB) discussed "herbivorous" and "detritivorous" components of the North American freshwater ichthyofauna and the apparent relationship between herbivores/detritivores and elongation of the digestive tract. The gut length of H. harryi (1.5-2.7 X SL; $\bar{x}$ = 2.25) is quite similar to other species considered herbivorous/detritivorous. On the other hand, the gut of H. dissimilis is considerably shorter, ranging 0.8-1.1 X SL with $\bar{x}$ = 0.94 and, as with H. x-punctata (Harris, msB), is intermediate between species classified as insectivores and detritivores/herbivores.

Bowen (1979, 1981), Burkhead (1980), Starnes and Starnes (1981), and Prejs (1984) provide summaries of available literature and insight into herbivorous/detritivorous feeding in freshwater fishes. Bowen (1979), citing (Riley, 1970), suggests PDA is a suitable source for carbohydrates to fulfill energy requirements of aquatic species but may lack necessary protein for growth. Bowen (1979) suggested three adaptive strategies for detritivores to obtain sufficient dietary protein: 1) Selective feeding on protein rich detrital aggregate; 2) selective ingestion of protein rich elements of detrital aggregate or 3) complementing the detrital diet with protein rich animal foods.

Harris (msB) has suggested that the gravel chub, Hybopsis x-punctata, utilizes strategy 3 to supply sufficient dietary protein for growth. Invertebrate contribution to gravel chub dietary biomass during months of peak growth ranged from a low of 31% for June to a peak of 91.8% in September. The Ozark chub also increased the percentage of invertebrate dietary biomass during growth months but to a much lesser degree than the gravel chub. Peak invertebrate food

intake for the Ozark chub occurred in June (20.4%) and fell through the summer to 7.1% in September. This may indicate that 1) low invertebrate intake (7.1-20.4%) provides sufficent protein for growth or 2) PDA-plant components supply enough protein for sustaining growth.

Harris (1980a) stated peak reproduction in the Duck-Buffalo River system occurred from mid-May through mid-June with average fecundity of 400. Reanalysis of Duck-Buffalo River specimens shows peak spawning probably occurs from mid-April to late May in that system with only sparse, scattered activity extending into June. This corresponds nicely with information gathered on Virginia populations (Jenkins, et al., ms).

Reproductive behavior of the Ozark chub appeared to be similar to that of Hybopsis x-punctata, the gravel chub (Harris, msB) and Hybopsis insignis, the blotched chub (Harris, msD). Although actual spawning of the Ozark chub was not witnessed, the location and pre-spawning behaviour were the same as in the other two species. Using the reproductive guilds of Balon (1975), the Ozark chub should be classified a non-guarding lithophilic spawner, as should the other members of the subgenus Erimystax.

Spawning for both the Ozark and spotted chubs occurs from early or mid-April to late May and appears to be initiated by high water levels and warming temperature. As shown in Figures IV-2 (p. 251) and IV-8 (p. 270), spawning occurs when water temperatures reach >15°C (>60°F) and river discharges are at or near their maximum. The same correlation occurs in Hybopsis x-punctata (Harris, msB) and in several genera of big river fishes such as Polyodon (Purkett, 1961; Hubert, et

al., 1984), Catostomus (Barton, 1980; Edwards, 1983b), and Ictiobus (Edwards and Twomey, 1982; Edwards, 1983a). This leads to speculation that the ancestral Erimystax stock may have evolved in a big river environment.

Diameter of mature ova for the two species, 1.50-2.00 mm for the Ozark chub and 1.30-1.75 mm for the spotted chub, was somewhat larger than reported values for other North American cyprinid species adapted to lotic habitats (Becker, 1983; Heins and Clemmer, 1976). I suspect newly hatched Erimsytax drift with the current until deposited to spend their first few weeks in food-rich slack water areas feeding upon microcrustaceans, midge larvae, and PDA until strong enough to sustain the rigors of their preferred riffle habitat. This has been somewhat substantiated by obervations and collections of very young Hybopsis insignis from these shallow lentic habitats. Additionally, many hours of observation in adult habitat of the Ozark chub immediately after peak spawning found no yoy present. A start as relatively large larvae would be an advantage allowing them to leave the potentially predator-filled nursery areas as soon as possible.

The coefficients for regression equations of SL versus fecundity of Hybopsis harryi and H. dissimilis were subjected to the F-test for significance. Results indicated they were not significantly different ($F_s = 4.25 < F_{.05}[1,13] = 4.67$). Comparison of the linear regression coefficients for age versus standard length in the two sexes of H. harryi (Figure IV-5, p. 261) showed they were not significantly different. The trend in H. x-punctata (Harris, msB) of males being larger than females until the end of the second growth season (ca

month 20) was also evident in the Ozark chub. This sexual size disparity was more noticeable in H. x-punctata as reflected in a signifcant difference between the regression coefficients of age versus standard length (Harris, msB).

There appeared to be differences in age at maturity between H. harryi and H. dissimilis, at least in two of the populations examined. Data from this study indicated that <25% of females and <10% of males reach reproductive maturity at 12 months. Jenkins et al. (ms) found 114 of 116 Virginia Hybopsis dissimilis specimens taken late April to mid-June to be mature..

Maximum age for the Ozark chub in this study was 42 months and females apparently had a greater survival rate than did males. Jenkins, et al. found maximum age of two years and a few months for the spotted chub in Virginia; hence, there may be significant differences in longevity for the two species.

CHAPTER V

THE BIOLOGY OF THE BLOTCHED CHUB, *Hybopsis insignis* (CYPRINIDAE), IN THE UPPER TENNESSEE RIVER SYSTEM

1. INTRODUCTION

This is the third in a series of studies dealing with life history and biology of species belonging to the subgenus *Erimystax* of *Hybopsis*. An earlier account reported on the biology of the gravel chub, *Hybopsis x-punctata*, from the Ouachita River drainage, Arkansas (Harris, msB). This was followed by a paper detailing life history aspects of the Ozark chub, *H. harryi*, compared with biological parameters of the spotted chub, *H. dissimilis* (Harris, msC). Previously, Jenkins (1975) and Burkhead and Jenkins (1982) provided information on the fifth member of *Erimystax*, *H. cahni*, the slender chub. These studies were initiated to provide basic biological data for phylogenetic analysis of *Erimystax* and *Hybopsis*.

2. STUDY AREA

The primary study area was Little River from the U.S. Hwy 411 bridge northeast of Maryville upstream to near Townsend, Blount County, Tennessee. Headwaters of Little River originate in the Great Smoky Mountains National Park and drain northwestward to empty into Fort Loudon Lake, formerly the Tennessee River. Drainage area, 27.8

km uptream from the mouth, at the Hwy 411 bridge is 697 km (USGS, 1970-1983b).

Water quality was good to excellent despite heavy recreational use during warm water months. Water clarity was generally excellent for underwater observations during most of the year except immediately following heavy rains. River morphology in most of the study area was alternating pool and riffle, occasionally separated by long runs. Substrate ranged from bedrock-boulder-small rock in the upper portion of the study area to predominately small gravel near the Hwy 411 bridge. Elevation of the study area was 337.4 m above mean sea level near Townsend and 259.1 m above msl at the Hwy 411 bridge (USGS, 1970-1983b).

3. PUBLISHED DATA

Observations concerning the biology of the blotched chub are few and represented primarily by comments on preferred habitat and relative abundance. Smith (1907) termed the species (listed as Hybopsis dissimilis) "not rare" in the Swannanoa River at Asheville and Spring Creek at Hot Springs, North Carolina. Typical habitat for the blotched chub is medium to large streams or small rivers in moderate to swift current with clean gravel, cobble or rock substrate (Comiskey and Etnier, 1972; Hitch and Etnier, 1974; Harris, 1980b; Branson and Schuster, 1982; Etnier and Starnes, ms; and Jenkins, et al., ms). Branson and Schuster (1982) designated a status of "special concern" for the species in the Little South Fork Cumberland River, KY.

Similarly, status of the blotched chub in Alabama was listed as "of special concern" (Ramsey, 1976).

TVA (1975) fish population estimates found Hybopsis insignis quite abundant in the Duck River, TN drainage with estimated number per stream mile ranging from 206-9930 and weight in pounds per stream mile ranging from 0.7-48.0. Specimens were collected from the Duck River between river miles 17 and 153 and the lower segments of Piney River and Fountain Creek. Greatest abundance was found at Duck River miles 96 and 147.3 Data for the Buffalo River, TN drainage (TVA, 1973) indicated the species was less abundant with a single estimate at river mile 62.9 showing 81 individuals/stream mile and 0.4 lbs/stream mile.

In a study of Hybopsis brain patterns, Davis and Miller (1967) found H. insignis has increased taste bud density on the snout tip and lips with associated increased size in the facial lobe of the brain. They postulated use of the lips for food detection or discrimination. Reno (1969b) examined Hybopsis cephalic lateral-line systems and visualized H. insignis groping about the stream bottom to acquire food rather than relying upon sight as the primary means of detecting food.

Davis and Miller (1967) found abundant algae, primarily diatoms and desmids, in the branchial cavities of six species of Hybopsis, including H. insignis, from the Powell River, TN. Harris (1980b) examined gut contents of five blotched chubs from the Duck River, TN and found filamentous algae and a wide variety of benthic invertebrates dominated by the mayfly genus Potamanthus.

Spawning season extends from late spring to early summer (Harris, 1980b). On 14 April, a Tennesee female was fully gravid; Virginia females collected 14-21 May were mostly gravid; early to mid June VA fish were partly to mostly spent; and some TN females had eggs freely flowing on 12 June with water temperature at 25 C (Jenkins, et al., ms).

Harris (1980b) gave adult size range as 45-77 mm standard length (SL). The largest known VA specimen was an 80 mm SL female (Jenkins, et al., ms) while Etnier and Starnes (ms) listed maximum total length as 100 mm. Virginia young of year ranged 23-39 mm SL in late July and 34-42 mm SL with mean of 38.4 in early August while mature fish collected 17 March through 21 June are summarized as: 44 males, 47-77 mm SL, x = 58.6; 51 females, 47-80 mm SL, x = 59.3 (Jenkins, et al, ms). Jenkins, et al. (ms) stated most individuals mature in one year but gave a size range 41-56 mm SL for immatures during the breeding period. They believed all blotched chubs were adults by two years and gave a maximum age of two years plus two or three months.

4. METHODS

This life history study used a combination of personal collections and field observations augmented by museum specimens. Analysis of 12 monthly samples was attempted but winter high water precluded collections for January and allowed collection of but one individual in February. Samples were taken or observations made at weekly or bimonthly intervals from April through June to more precisely determine spawning period. No distinction was made between collections

from different years in analysis of results, so this study reflects the "generalized life history" of the blotched chub.

Collections were made using 2.4-m X 3.0-m and 2.4-m X 6.1-m seines with 0.6-cm mesh. Seining downstream with the current proved a successful means of obtaining blotched chubs, especially using the 6.1-m seine. Electrofishing and application of ichthyocide were also attempted but proved unsuccessful. From April-June, specimens were checked in the field for spawning condition by gently pressing the abdomen to extrude ova or milt. All specimens were preserved in 10% formalin and stored in 45% isopropanol. Detailed methodology for examination of reproductive, feeding, and age-growth parameters was presented in Harris, msB. For preserved specimens, reproductive condition was determined by calculating the gonadosomatic index (GSI) expressed as gonadal weight/adjusted body weight X 100. Ovum diameter was measured to the nearest 0.01 mm using a dissecting scope and ocular micrometer. Reproductive condition of live specimens was determined by gently pressing the abdomen to check for expulsion of ova or milt.

The terminology of Heins (1985) is used to describe female and male gonadal reproductive condition. Female ovary condition descriptors include: 1) latent (LA), 2) early maturing (EM), 3) late maturing (LM), 4) mature (MA), and 5) partially spent (PS). The descriptor spent (SP) (Harris, msB) is added to those of Heins.

Male testes are described as mature (MA) or latent (LA). In addition to the gonadosomatic index, reproductive condition in males was determined by gross examination of the testes as well as secondary

sexual characteristics such as tuberculation, pectoral fin coloration, and development of the nuptual cheek pad (Branson, 1962).

Gut contents from anterior to the first bend in the gut were removed from a minimum of ten specimens (when available) from each monthly sample. Animal items were identified to the lowest possible taxon and non-animal items were classified as plant (includes filamentous algae, roots, leaves, and bark) or periphytic detrital aggregate, the PDA of Bowen (1981). Dry weight biomass of animal items (grouped by order), plant, and PDA was determined to the nearest 0.001 g using a Mettler AE 160 electronic balance. In conjunction with food habitat analysis, gut length was measured to the nearest 0.05 mm using dial calipers following the method of Snelson (1971).

Each specimen from monthly samples was aged by scale analysis following methods of Tesch (1971), Weatherley (1972), and Bagenal (1971). Ten scales were removed from the predorsal lateral region of each specimen examined, stained with alizarin in 2% KOH, and examined under a dissecting scope at 40X. Determination of size (SL) at annulus formation was attempted by back calculation. Stained scales were projected on the screen of a Bausch and Lomb scale reader (120X) and scale length and radius length were measured from the focus. Total scale length and annular lengths were measured to the nearest 0.05 mm with calipers. Growth in terms of biomass was estimated by weighing a sample of each age class from each monthly sample.

Reproductive and feeding behavior were observed in the field by snorkeling when water clarity permitted. Approximately 35 hours were

spent underwater observing blotched chub behavior. Fourteen visits were made to Little River between May 1979 and May 1983.

Data for water temperature and discharge were obtained from U.S. Geological Survey records (1970-1983b). These records were for the Little River at the U.S. Hwy 411 station, Blount County, TN and were considered indicative of stream conditions for life history study locations. Temperature and discharge data are presented as monthly averages in this paper.

Summary statistics and linear regression were performed using programs found in Brower and Zar (1984). Model II linear regression (GMR procedure) was used when both x and y variables were measured with error as in standard length versus fecundity (Ricker, 1973; Sokal and Rohlf, 1981). Testing of regression coefficients follows Sokal and Rohlf (1981:499-505).

5. RESULTS

Habitat and Associates

Habitat. Adult Hybopsis insignis were most often observed and/or collected from the heads of riffles with moderate to swift current and water ranging 30-60 cm deep. They also inhabited the base of these riffles where current slows and water deepens after exiting the shallow, swift raceways. Adult blotched chubs were seldom observed in torrential raceways or in slow-moving pool habitat. Young of year (yoy) chubs were found abundant in a shallow backwater with little to no current on 5 July 1980. By 10 July, most yoy had moved into the more typical adult habitat at the heads of riffles.

Associates. The following species were found in close association with Hybopsis insignis during underwater observations: Campostoma anomalum, Nocomis micropogon, Notropis leuciodus, N. telescopus, Phenacobius uranops, Hypentelium nigricans, Noturus eleutherus, Etheostoma rufilineatum, E. simoterum, E. zonale, Percina aurantiaca, P. burtoni, P. caprodes, and Cottus carolinae. The blotched chub was often observed in mixed cyprinid assemblages with Campostoma and Phenacobius.

Food and Feeding Habits

Feeding behavior. Blotched chubs exibited three primary modes of feeding. Gleaning the surfaces of rock and gravel substrate and probing interstitial spaces was the most often observed feeding behavior. The second most common method of food acquisition involved browsing on the tips and probing dense mats of Podostemon. It was not readily apparent if aquatic insects or plant material was the intended food item. A rather unique feeding behavior was the third mode observed which involved chubs searching submerged water willow (Justicia sp.) rooted to the substrate at the base but swept downstream by the current so that the distal plant tip was parallel to and but a few centimeters above stream bottom. Blotched chubs would begin at the plant base and search up the stalk and leaves to the tip of the plant, disengage from the plant, swim back to the plant base and begin the sequence again. It was not apparent if aquatic insects or attached algae were the food items sought but, apparently, Justicia was not ingested as it was not recovered in any of the guts examined.

Food. Gut contents from 113 blotched chubs were examined and results as biomass and countable food items are presented in Tables V-1 and V-2, respectively. In Table V-1, the total biomass estimate is presented as: sum of monthly estimates for each item/sum of biomass for all food items (= grand sum biomass) X 100 = per cent annual biomass for each food item (column TOT of Table V-1). Per cent annual biomass was also presented as the mean of the monthly percentages for each food item (column CORR of Table V-1) and termed corrected annual biomass.

Gut morphology. Gut length was measured for 93 Hybopsis insignis (SL 40.85-79.65 mm). Digestive tract lengths ranged from 0.88-1.32 of standard length with $\tilde{x}$ = 1.03. Gut morphology seldom deviated from the simple s-shaped form.

Reproduction

Female. Gonadosomatic index (GSI) values are presented in Figure V-1 along with mean monthly ovum diameter. Measurements showed most mature ova were spherical and greater than 1.5 mm in diameter with a maximum observed diameter of 1.85 mm. Data indicated female ovaries reached maximum size in mid-April (mean GSI 22.8, ovum diamter 1.58 mm) followed by a slight decrease in May (mean GSI 19.2, ovum diameter 1.54 mm) and a drastic decline in June (mean GSI 3.6). Mean GSI was at an annual low in August (0.8) and built slowly through the fall and winter before rapidly increasing from March through April in preparation for spawning.

Table V-1. Per Cent Food Biomass from Monthly Samples of Hybopsis insignis.

Food Item	Month											Totals	
	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Tot[a]	Corr[b]
Nematoda				2.1								0.3	0.2
Oligochaeta				0.5			0.1					0.1	0.1
Hydracarina			0.1			3.0		0.3				0.1	0.3
Ephemeroptera	20.0	0.9	2.1	7.2	3.5	18.5	4.0	1.3	5.0	10.3		5.4	6.6
Plecoptera			3.1									0.8	0.3
Trichoptera		12.7	0.1	3.5	5.1	6.0	7.7	6.7	2.4	5.9		4.2	4.6
Coleoptera						3.0	0.5					0.2	0.3
Diptera	80.0	73.6	86.1	35.7	32.9	19.2	20.2	71.8	35.0	26.1	8.8	45.3	43.7
Lepidoptera							1.0					0.2	0.1
Plant											5.9	0.1	0.5
PDA		12.7	8.7	51.0	58.5	50.3	66.5	20.1	57.6	57.7	85.3	43.3	42.6
# Examined	1	11	12	14	8	8	19	6	12	12	10	113	
# Empty	0	3	1	2	0	3	0	0	2	0	4	15	

[a]Annual total derived from sum of monthly biomass.

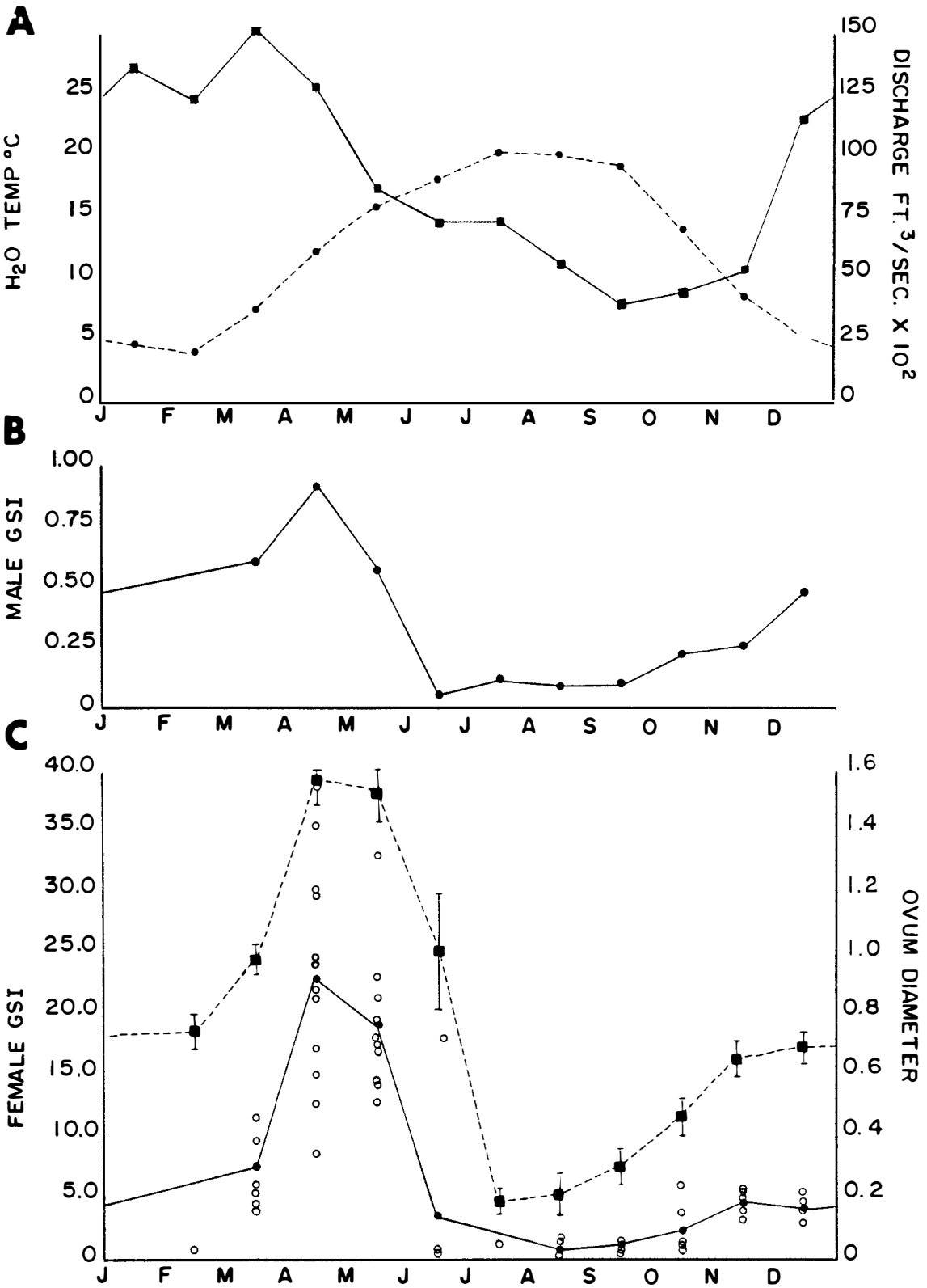
[b]Annual total derived from sum of per cent monthly biomass.

Table V-2. Number of Food Items from Monthly Samples of Hybopsis insignis.

Food Item	Month											Totals	
	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Tot[a]	% Tot
Nematoda				6								6	0.2
Oligochaeta							1					1	-
Hydracarina			2			3		1				6	0.2
Ephemeroptera	1	3	37	20	6	1	13		1	2		84	2.9
Baetidae			5	24	2	6	5	30	9			81	2.8
Heptageniidae						1			1	2		4	0.1
Oligoneuridae			1						1			2	0.1
Plecoptera													
Perlidae			6									6	0.2
Trichoptera		1	2	1	3		3		1	2		13	0.5
Brachycentridae				12						1		13	0.5
Hydropsychidae			1	1		6	3	1	3			15	0.5
Hydroptilidae		5	2		11	2	5	5				30	1.0
Leptoceridae								1				1	-
Psychomyiidae						2						2	0.1
Coleoptera						1	1					2	0.1
Diptera													
Chironomidae	7	199	260	159	36	35	103	41	210	26	11	1087	37.7
Simuliidae	10	3	123	282	151	198	309	316	94	10		1486	51.9
Tipulidae	1	8	7	1	3	2	8			5		35	1.2
Lepidoptera							1					1	-
Total	19	219	445	506	212	257	452	395	320	48	11	2884	

[a]Sum of monthly totals.

Figure V-1. Reproductive parameters of Hybopsis insignis. A. Mean water temperature (circles) and mean discharge (squares) of Little River, TN for 1970-1983. B. Male Hybopsis insignis mean gonadosomatic index (GSI). C. Female H. insignis mean GSI (solid circles) and mean ovum diameter (squares). Bars represent + one standard deviation and open circles are individual GSI values.


A
H2O TEMP °C
0
5
10
15
20
25
DISCHARGE FT.3/SEC. X 10²
0
25
50
75
100
125
150
J F M A M J J A S O N D
B
MALE GSI
0
0.25
0.50
0.75
1.00
J F M A M J J A S O N D
C
FEMALE GSI
0
5.0
10.0
15.0
20.0
25.0
30.0
35.0
40.0
OVUM DIAMETER
0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
J F M A M J J A S O N D

March females included three age 2 individuals whose ovaries were classified as LM (GSI 9.6-11.7) and four age 1 individuals with EM ovaries (GSI 4.0-6.0). In April, six age 2 and four age 1 females were classified as MA (GSI 17.0-38.7) while three age 1 specimens were LM (GSI 8.5-14.8). Examination of May specimens revealed five age 1 MA specimens (GSI 17.0-33.1) and two LM individuals (GSI 12.8-17.0). Age 2 females included two specimens that appeared PS and one which was MA. Ripe ova were abundant in all May ovaries. By early and mid-June three age 1 and one age 2 females were SP. July through October female ovaries were all classified as LA while November and December ovaries appeared EM.

All March through June age 2 females were mature and capable of participating in spawning. Of 21 age 1 females examined, three did not reach reproductive maturity in time for spawning. Mature specimens ranged in size from 43.95-60.25 mm SL. The three immatures were 40.80, 44.15, and 46.15 mm SL.

Fecundity. Number of ova showed a high correlation with standard length ($r = 0.96$) and was described by the Model II linear regression $F = 23.97(SL) - 1086.72$ as shown in Figure V-2. When log transformed (as recommended by Bagenal, 1971), the relationship was described by the linear equation $\log_{10} F = 3.42(\log_{10} SL) - 3.55$ ($r = 0.98$).

Measurements were made for all ova from four mature females collected 11 April (1) and 27 May (3) and results are presented in Figure V-3. As seen in this figure there were two complements of ova present during this time, one composed of ripe and mature ova, the other composed of maturing ova.

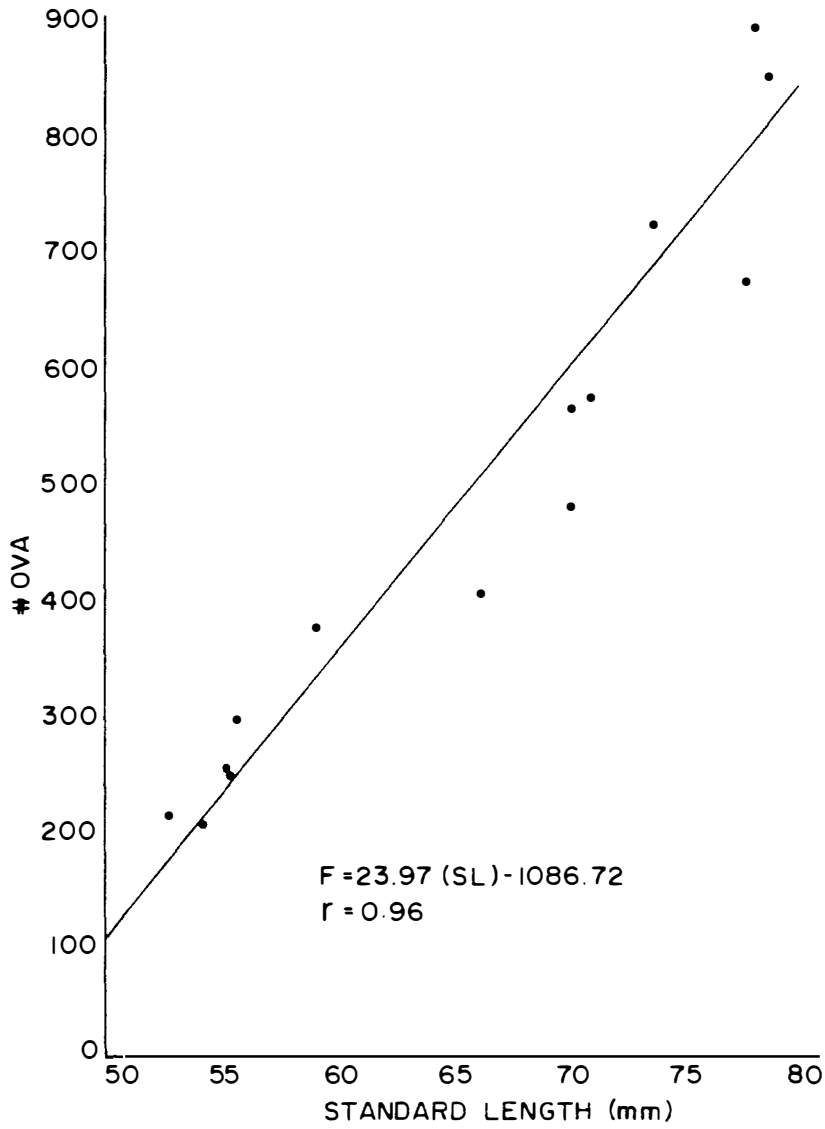


Figure V-2. Regression of standard length (SL) versus fecundity (F) for Hybopsis insignis.

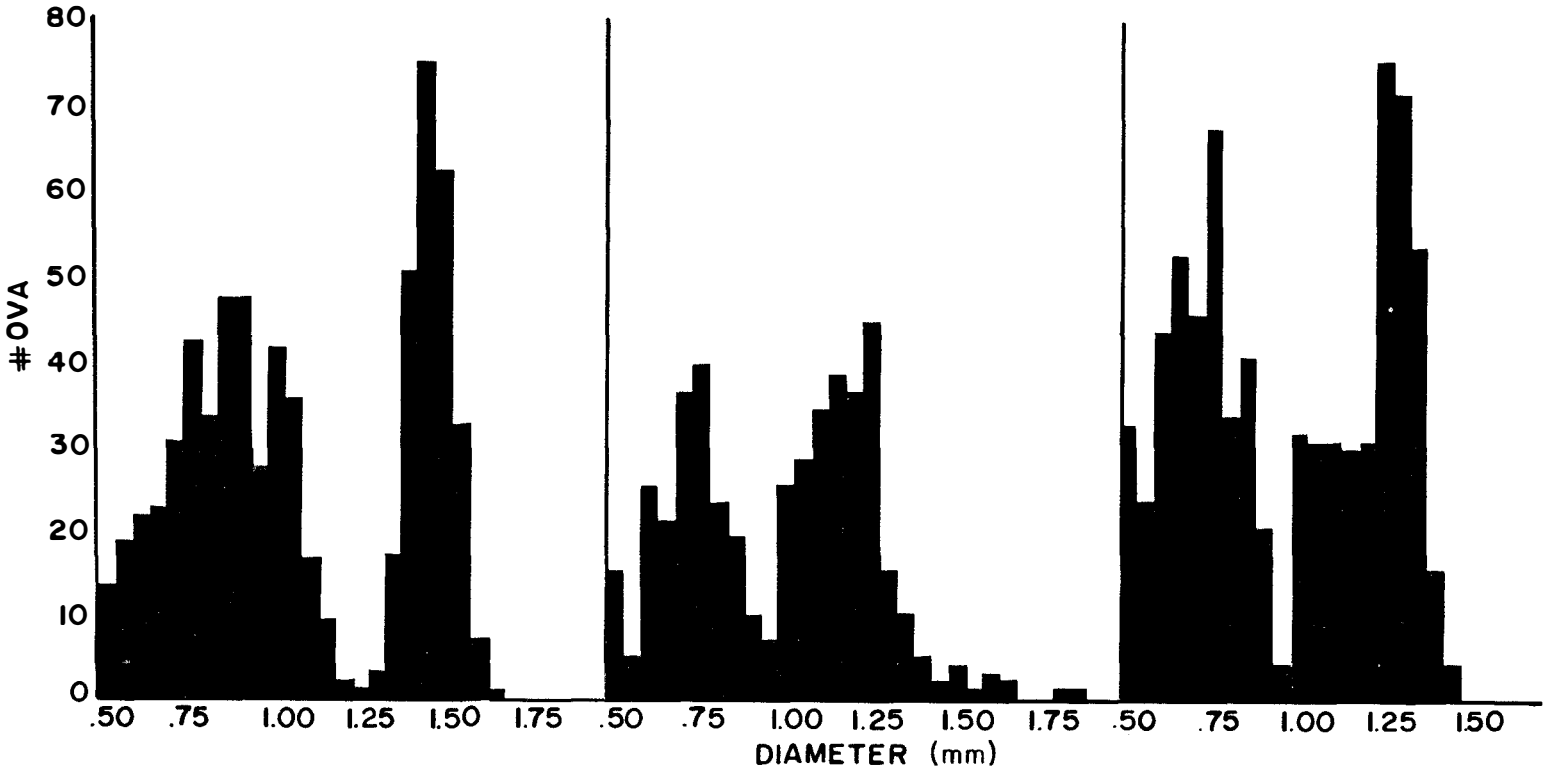


Figure V-3. Diameter frequency of ova from three female Hybopsis insignis.

Male. GSI values (Figure V-1) indicated male peak reproductive development occurred in mid-April (mean GSI = 0.9) and extended through early May (mean GSI = 0.6). By mid-June males were spent and testes judged LA. Testes remained LA through September at which time a slow gain in GSI began which culminated with spawning in April and May. Five males captured 11 April 1980 were reproductively mature and highly tuberculate but not running milt when the abdomen was gently pressed. Two males captured 27 May 1983 extruded milt when pressure was applied. All age 2 males collected March through June were mature and only two of 23 age 1 specimens were judged immature.

Secondary male sexual characteristics began to develop in late winter and early spring. Examination of a single male captured 19 February revealed very tiny tubercles on the most anterior pectoral fin rays. No cephalic or body tubercles were present. On 12 March, pectoral fin tubercles were moderately developed and very tiny tubercles were present on the pelvic, dorsal, and anal fins. Tubercles were present, but poorly developed, on the periphery of anterior dorsolateral body scales. Cephalic tubercles were poorly developed to absent. Concentrated melanin had begun to develop interradially in the pectoral fin. By 14 April, the pectoral fin, body, and cephalic tubercles were fully developed. Dorsal, anal, and pectoral tubercles were small to moderate in size but did not develop much larger. The nuptial pad (as figured by Branson, 1962) appeared as splotches around the sensory canals of the lower jaw but was not prominantly developed. Interradial pigmentation of the pectoral fin was well developed and males were easily differentiated from females using this

characteristic. All males from collections of 17 and 27 May showed fully developed male secondary characters. By 10 July, males had lost all fin tubercles and most head and body tubercles. The nuptial pads were present but appeared to be sloughing as some sensory papillae extended through this tissue. Males from collections of 26 August showed no signs of any secondary sexual characters.

Spawning. Attempts to observe spawning behavior were made on the following dates between 1979 and 1983: 11 April, 11 May, 15 May, 27 May (2), 28 May, 29 May, 2 June (2), 9 June, 12 June, and 16 June. Spawning behavior was witnessed on 11 May 1979, 28 May 1983, and 29 May 1980. The following was excerpted from field notes of observations taken on 28 May from 1200-1500 hours with water temperature of 59° F and air temperature of 68° F.

A large aggregation of perhaps 50 blotched chubs was observed in a five square meter area at the head of a Justicia covered shoal inundated by 10-20 cm of flowing water. The aggregation was in mid-channel in water 50-80 cm deep with gravel, rock, and cobble substrate and moderate current. Rooted and attached vegetation were absent from the spawning area. Females were resting on the substate in depressions between or behind larger rocks. They were easily differentiated from males by their swollen abdomens and smaller, less pigmented pectoral fins. Females would occasionally enter the water column, apparently to take drift items, and then settle back to their original resting spots. Males were moving about and feeding freely. On several occasions, males would approach from the side or behind and lie directly on top of or beside the female. If no response was

offered by the female within three or four seconds, the male would leave. On three separate occasions, females responded by rapid body quiver and the male would then join cheek to cheek, vent to vent with the female and both would vibrate rapidly for two or three seconds followed by the male leaving the depression. These were assumed to be spawning acts, although gamete depostion could not be observed.

Age and Growth

Age and growth data were analyzed using May as month 1 based on reproductive data. Table V-3 summarizes standard length measurements taken from 172 specimens of Hybopsis insignis. Age versus standard length is plotted in Figure V-4 using a moving average of three and assuming no decrease in standard length (after Mayden and Burr, 1981). When age versus standard length was compared between the sexes, they did not differ significantly ($F_s = .004 << F_{.05}[1,32] = 1.92$). Linear equations for age versus standard length were: SL = 41.08 + 1.29(A) for males and SL = 41.77 + 1.31(A) for females with r = 0.95 for both.

As seen in Figure V-4, young of year grew rapidly until the arrival of cold temperatures in October when growth slowed until the completion of spawning the following May. This trend of spring-summer growth and fall-winter cessation of growth appeared in each age class.

Scale length-scale radius data was obtained from 22 specimens (age 2 = 13, age 3 = 9) and subjected to linear regression analysis. The data yielded the line described by the regression equation SL = 25.45 + 1.028 (scale radius) (r = 0.69). Back calculation of standard

Table V-3. Mean Standard Length Based on Monthly Samples of Each Age Class of Male, Female, and Total *Hybopsis insignis*.

Age Group	Month		Females $\bar{x}$	n	Males $\bar{x}$	n	Total $\bar{x}$	n
	May	1						
	June	2					16.05	(1)
	July	3					26.27	(14)
	August	4	46.78	(8)	41.88	(6)	44.68	(14)
	September	5	48.25	(1)			48.25	(1)
1	October	6	50.73	(7)	51.32	(13)	51.11	(20)
	November	7	51.55	(1)	50.85	(2)	51.08	(3)
	December	8	52.55	(5)	52.37	(5)	52.46	(10)
	January	9						
	February	10						
	March	11	50.69	(4)	54.32	(7)	53.00	(11)
	April	12	53.90	(7)	58.74	(11)	56.86	(18)
	May	13	53.46	(8)	54.65	(3)	53.79	(11)
	June	14	56.63	(5)	54.73	(2)	56.09	(7)
	July	15			60.67	(3)	60.67	(3)
	August	16	67.58	(6)	65.03	(4)	66.56	(10)
	September	17	71.85	(4)	63.95	(1)	70.27	(5)
2	October	18	71.35	(2)	68.98	(3)	69.93	(5)
	November	19	71.48	(6)	68.25	(2)	70.68	(8)
	December	20						
	January	21						
	February	22	69.80	(1)			69.80	(1)
	March	23	73.77	(3)	69.34	(7)	70.67	(10)
	April	24	74.57	(6)	70.03	(3)	73.06	(9)
	May	25	69.45	(3)			69.45	(3)
	June	26	74.55	(1)			74.55	(1)
3	July	27	75.00	(1)	74.18	(4)	74.34	(5)
	August	28	78.20	(1)			78.20	(1)
	September	29						
	October	30	79.65	(1)			79.65	(1)

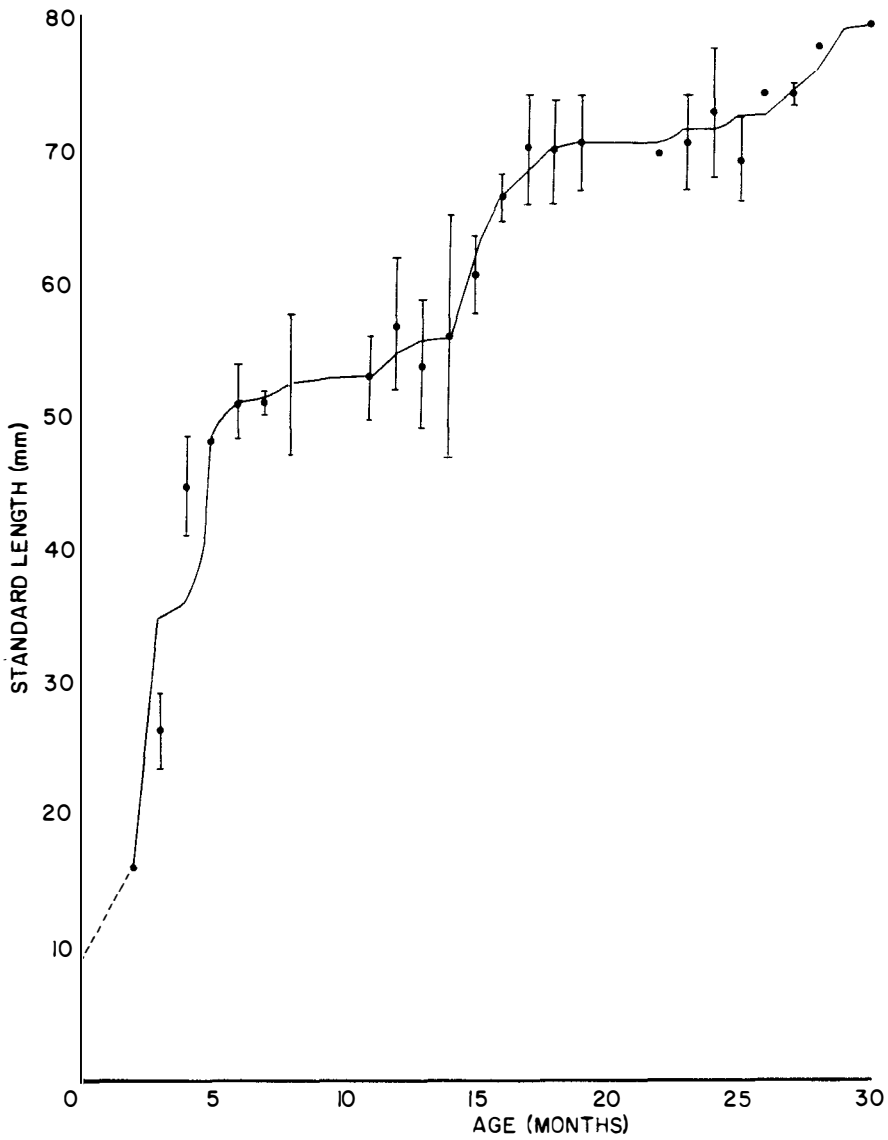


Figure V-4. Age versus standard length plotted as a moving average of three in Hybopsis insignis.

length at annulus formation resulted in averages of 58.01 at annulus I and 67.22 at annulus II.

The oldest individual examined during this study, a 30 month female, was also the largest specimen at 79.65 mm SL. The oldest males were 27 months and reached a maximum size of 75.05 mm SL. Of 157 sexable specimens, 81 were males and 76 were females for a ratio of approximately 1.1:1.

6. DISCUSSION

Harris (1980b) reported the diet of Hybopsis insignis was composed of filamentous algae and immature aquatic insects based on the analysis of five specimens from the Duck River, TN. Based on analysis of 113 specimens in this study (Table V-1, p. 289), the blotched chub annual diet was primarily composed of immature aquatic insects (56.2% corrected biomass) and periphytic detrital aggregate (PDA) (42.6% corrected biomass). The species is a combination detritivore/insectivore functioning as an opportunistic omnivore.

PDA composed greater than 50% of gut contents for the months May through December (excepting September). In May water temperatures rose above 60 F and there was a noticeable increase in PDA on rock surfaces. PDA remained abundant through early or mid-December when water temperatures have dropped considerably and the rock surfaces were swept clean by increased water discharge due to winter rains. Gut contents for February through April were low in PDA which probably reflects a lack of available PDA rather than selective feeding on aquatic insects.

Diptera were always the largest contributor to the aquatic insect portion of monthly dietary biomass with ranges of 8.8%-86.1% of total monthly intake (Table V-1). Chironomidae and Simuliidae were the principal numerical contributors to the dipteran component (Table V-2). The other major contributors to dietary biomass were immature Ephemeroptera and Trichoptera with annual corrected biomass shares of 6.6% and 4.6%, respectively.

Mean gut length in Hybopsis insignis was 1.03 X SL and gut configuration a simple s-shape. A cursory review of gut lengths for cyprinids considered insectivores showed ranges of 0.5-0.7 X TL (Becker, 1983). The gut length for the blotched chub was somewhat intermediate to lengths of insectivores and species considered herbivores/detritvores. The blotched chub gut was very similar in configuration and length to those of H. x-punctata (1.04) and H. dissimilis (0.94) (Harris, msB, msC). This similarity extended to the composition of dietary biomass with PDA-plant : aquatic invertebrates represented by 43.1% : 56.2% in H. insignis, 57.6% : 42.6% in H. x-punctata, and 52.6% : 47.4% in H. dissimilis. The lone member of Erimystax with a coiled gut configuration was H. harryi which had a mean gut length of 2.25 X SL. A shift towards herbivory/detritivory was reflected by the PDA-plant:aquatic invertebrate biomass data of 90.3%:9.8% (Harris, msC).

Bowen (1979, 1981), Burkhead (1980), Starnes and Starnes (1981), and Prejs (1984) discussed herbivorous/detritivorous feeding in freshwater fishes. Bowen (1979), citing Riley (1970), suggested PDA was a suitable source for carbohydrates to fulfill energy requirements

but might lack necessary protein for growth. Bowen suggested three adaptive strategies for detritivores to obtain sufficient dietary protein: 1) Selective feeding on protein-rich detrital aggregate; 2) Selective ingestion of protein-rich elements of detrital aggregate or ; 3) complementing the detrital diet with protein-rich animal foods.

Growth (in SL) in blotched chubs occurred from May through October (Figure V-3). Examination of diet biomass showed relatively equal quantities of PDA and animal foods during the growth months suggesting the blotched chub adapted strategy 3 (above) to meet protein requirements. Young of year blotched chubs underwent explosive growth during their first five months of life (Figure V-3). Preliminary data indicated very young chubs may feed primarily upon aquatic invertebrates, possibly to obtain necessary protein for early growth. I examined gut contents of 10 age three month chubs (20.95-30.30 SL) and found primarily immature dipterans and mayflies with very little PDA. Although biomass was not quantified, a conservative estimation puts the animal portion at >80% of gut contents. Further work is in progress to examine diet switching and growth patterns in yoy blotched chubs.

Feeding behavior in the blotched chub consisted primarily of "gleaning" rock surfaces with lesser amounts of time spent searching under and between stones or rooting in riffle weed (Podostemon) mats. A unique feeding behavior which consisted of stripping attached food from the surface of submerged water willow (Justicia) was observed but does not contribute significantly to total feeding time. It was

impossible to determine during underwater observation if aquatic insects were present in the PDA matrix. Removal of smooth surfaced, PDA-covered stones from the stream for examination seldom revealed aquatic insects on the exposed surface. On the other hand, riffle weed encrusted rocks always had invertebrates available on the exposed surface. It seems reasonable to assume blotched chubs satisfy energy needs by taking PDA matrix by gleaning and then switch to searching riffle weed mats when increased protein is needed.

Jenkins, et al. (ms) and this study indicated most 1 and 2-year-old individuals were reproductively mature. The peak reproductive period for blotched chubs occurred from late April through late May (Figure V-1, p. 291). Initiation of spawning was probably controlled by increased water temperature with reproduction occurring at water temperatures >59 F. A possible relationship between spawning initiation and peak stream discharge was discussed for Hybopsis x-punctata (Harris, msB), H. harryi and H. dissimilis (Harris, msC). The same relationship, apparently, does not exist for H. insignis (Figure V-1, p. 291). This suggests the following: 1) spawning in H. x-punctata, H. harryi, and H. dissimilis was initiated by water temperature coincidental to period of peak stream discharge or 2) spawning of the previous species was initiated by temperature and discharge and H. insignis has evolved different reproductive strategies which are not dependent on discharge initiated spawning.

Spawning behavior observed in Hybopsis insignis was similar to that observed in H. x-punctata (Harris, msB) and H. harryi (Harris,

msC). H. insignis is a non-guarding lithophilic spawner (Balon, 1975) as are other members of Erimystax.

Mature ova were generally in the 1.5 mm diameter range, which was similar to values for other Erimystax (Harris, msB, msC). This size is somewhat larger than reported values for other North American lotic cyprinids (Becker, 1983; Heins and Clemmer, 1976). Beginning as a large larva may allow quicker transition from predator-filled larval habitat to normal adult habitat. Following fertilization, ova or perhaps newly hatched larvae drift downstream until settling in lentic backwaters. Based on underwater observation, young spend their first one and a half to two months in these food rich backwater areas, gorging on aquatic insect larvae before moving out to normal riffle habitat in mid- to late July.

Linear regression coefficients for age versus standard length were not significantly different between the two sexes. Regression lines indicated females were larger than males throughout life although examination of monthly data (Table V-3, p. 299) showed males larger than females for four of seven months during the first 13 months of life. A larger sample might show blotched chub males larger than females during the first year of life, as was the case in Hybopsis x-punctata and H. harryi (Harris, msB, msC).

Growth was explosive for the first six months of life as yoy blotched chubs reach >60% of their maximum standard length (assuming average SL at six months = 50 mm and maximum SL as 80 mm) during this time. Little or no growth occurred during winter and early spring (Figure V-4). Estimates for standard length at annulus formation

agreed closely with data in Table V-3 (p. 299). Standard length at annulus I was calculated as 58.0 mm while data in Table V-3 (p. 299) showed mean SL of approximately 57.0 mm for April specimens. Calculated SL at annulus II was 67.2 mm while observed mean SL was 73.06 mm for April.

In this study, maximum age for the blotched chub was 30 months, which is similar to maximum age reported for H. x-punctata, H. dissimilis, and H. cahni (Harris, msB, msC; Jenkins, et al., ms). Hybopsis harryi lived a maximum of 42 months (Harris, msC). Maximum sizes recorded during this study were 79.65 mm SL for females and 75.50 mm SL for males. This compares with a maximum size of 86.00 mm SL recorded for a female from the Red River of the lower Cumberland River system (Harris, msA).

CHAPTER VI

SUMMARY

1. TAXONOMY

Results of this study indicate five species are members of the subgenus Erimystax including Hybopsis cahni Hubbs and Crowe, H. dissimilis (Kirtland), H. harryi Hubbs and Crowe, H. insignis Hubbs and Crowe, and H. x-punctata Hubbs and Crowe. Erimystax is defined by the following combination of characters: Pharyngeal teeth 4-4; anal rays 7; single small to large terminal, labial barbel on each side of mouth, often with enlarged sensory papillae; mouth inferior and subterminal; upper lip expanded anteriad; relatively large dorsolateral eyes directed somewhat posteriad; scales in lateral-line 36-53; lachrymal groove well developed; dark pigment on snout posterior of lachrymal groove and anterior of eye; pectoral fin with sensory papillae between first two rays; maxillary flap present, often bearing sensory papillae; nuptial males with nuptial pad; and sexes without nuptial coloration. Some authors (Hubbs and Crowe, 1956; Mayden, 1985b) include Hybopsis monacha in Erimystax but analysis of 17 character states during this study reveal that H. monacha is divergent from Erimystax in nuptial coloration, tuberculation, and spawning behavior. Although the exact position of H. monacha in cyprinid phylogeny remains uncertain, it is not considered a member of Erimystax.

Analysis of intraspecific variation in Hybopsis dissimilis reveals that the subspecies recognized by Hubbs and Crowe (1956) are trenchantly different in gut morphology, per cent ventral scalation, head length, orbit width, and aspects of coloration. These variables, in conjunction with differences in life history parameters, are considered sufficiently divergent to recognize these allopatric taxa as separate species. Hybopsis dissimilis is restricted to the Ohio, Tennessee, and Cumberland drainages east of the Mississippi River while H. harryi is found west of the Mississippi in the White River drainage of the Arkansas and Missouri Ozarks.

Variation within Hybopsis insignis is sufficient for recognition of two subspecies, H. i. insignis and H. insignis eristigma. Hybopsis i. insignis is longer in postdorsal length and has shorter mean fin lengths. Hybopsis insignis eristigma has a much wider and longer upper lip. Based on morphological intermediacy, the Clinch, Powell, and Holston River populations are considered intergrades between the subspecies. Hybopsis i. insignis is found in the lower Tennessee River drainage, south and west of Waldens Gorge, and in the Cumberland River drainage. Hybopsis insignis eristigma is found in eastern tributaries of the upper Tennessee River drainage, primarily in the Blue Ridge physiographic region.

Intraspecific variation in Hybopsis x-punctata is sufficient to recognize two subspecies, Hybopsis x. x-punctata and H. x-punctata trautmani. Differentiation is based primarily on number of caudal peduncle scales with modal counts of 16 in H. x. x-punctata and 12 in H. x-punctata trautmani. Additionally, H. x. x-punctata has a shorter

head, snout, and predorsal length and is more robust in body and caudal peduncle depth. Hybopsis x. x-punctata occurs in the Ouachita, Neosho, Missouri, and upper Mississippi drainages and H. x-punctata trautmani is found in the Thames, Ohio, and White (Arkansas and Missouri) river drainages. Some morphological intermediacy is seen in the Osage, Gasconade, and Meramec populations suggesting they might be intergrades between the two forms. Additional information is required before this hypothesis can be confirmed.

Comparison of interspecific variation among Erimystax species suggests alignment into two species groups. The dissimilis species group is composed of Hybopsis dissimilis, H. insignis, and H. harryi based on the presence mid-lateral and mid-dorsal spots or blotches and overall morphological similarity determined from multivariate analyses. The x-punctata species group is composed of Hybopsis x-punctata and H. cahni based on the absence of mid-dorsal and mid-lateral spots or blotches and the close morphological similarity of H. cahni and H. x-punctata trautmani.

2. LIFE HISTORY

Analyses of food habits indicate that three of four Erimystax species studied consume relatively equal amounts of plant material-periphytic detrital aggregate (PDA) and benthic invertebrates. Per cent annual biomass of plant-PDA and invertebrates for the three species is: Hybopsis x-punctata 58 : 42; H. dissimilis 53 : 47, and H. insignis 43 : 57. These species have simple s-shape guts with gut length approximately equal to standard length of the individual.

Hybopsis harryi feeds primarily on the plant-PDA component which accounts for 90% of the annual biomass consumed. The gut is coiled in H. harryi and usually twice as long as standard length in each individual.

In Erimystax, peak spawning occurs in April or May and appears restricted to a three or four week period in each species. Spawning may be activated by a combination of rising water temperature (usually >60° F) and increased discharge. Hybopsis x-punctata spawned from early April to early May in the Ouachita River drainage. Peak reproductive activity for H. harryi occurred from late April to late May in Buffalo River, Arkansas. Hybopsis dissimilis spawned from early April to early May in the Buffalo-Duck rivers, Tennessee. Peak spawning in Hybopsis insignis occurred from late April to late May in Little River, Tennessee. All Erimystax appear to spawn over clean gravel substrate at the head of riffles or in moderately swift runs. Observations suggest most spawning events involve one male and one female interactions. Ova are non-adhesive and are not buried during spawning. Larvae are thought to drift with the current to slackwater nursery pools until large enough to withstand the rigors of lotic adult habitat. Mature intraovarian ova range from 1.3-2.0 mm in diameter with an average ovum diameter of approximately 1.5 mm.

Early growth is explosive with species obtaining greater than 50% of adult standard length during the first seven or eight months of life. Males tend to attain greater mean standard length than females during the first 12 months but females usually catch and surpass males in mean standard length during months 13-24. Periods of rapid growth

for both sexes of each species occur during late spring through early fall. When water temperatures decrease during fall, winter, and early spring, growth rates also decrease. Females tend to have greater survival rates for the older age classes of each species. The sex ratio is approximately 1:1 for age class 1 but becomes highly skewed in favor of females in the later age classes. Maximum ages for species are: Hybopsis x-punctata 32 months, H. insignis 30 months, H. dissimilis 26-28 months (Jenkins, et al.), and H. harryi 42 months. Maximum size in standard length recorded for each species is: Hybopsis x-punctata 89.2 mm SL female; H. harryi 120.1 mm SL female; H. dissimlis 114.0 mm SL female (Jenkins, et al.); and H. insignis 86.0 mm SL female.

LITERATURE CITED

LITERATURE CITED

Aitken, W. W. 1936. Some common Iowa fishes. Iowa State Coll. Ext. Circ. No. 224.

Albrecht, G. E. 1978. Some comments on the use of ratios. Syst. Zool. 27:67-71.

_____. 1979. The study of biological versus statistical variation in multivariate morphometrics: the descriptive use of multiple regression analysis. Syst. Zool. 28:338-344.

_____. 1980. Multivariate analysis and the study of form, with special reference to canonical variate analysis. Am. Zool. 20:679-693.

Atchley, W. R. 1978. Ratios, regression intercepts, and the scaling of data. Syst. Zool. 27:78-83.

Atchley, W. R. and D. Anderson. 1978. Ratios and the statistical analysis of biological data. Syst. Zool. 27:71-78.

Atchley, W. R., C. T. Gaskins, and D. Anderson. 1976. Statistical properties of ratios. I. Empirical results. Syst. Zool. 25:137-148.

Bagenal, T. B. 1971. A short review of fecundity, pp. 89-111 in W. E. Ricker, ed. Methods for Assessment of Fish Production in Fresh Waters. Blackwell Scientific Publications, Oxford, England.

Bailey, R. M. 1956. A revised list of the fishes of Iowa, with keys for identification, pp. 326-377 in J. R. Harlan and E. B. Speaker, Iowa fish and fishing. Iowa State Cons. Comm., Des Moines.

Bailey, R. M. and G. R. Smith. 1981. Origin and geography of the fish fauna of the Laurentian Great Lakes basin. Can. J. Fish. Aquat. Sci. 38:1539-1561.

Bailey, R. M., J. E. Fitch, E. S. Herald, E. A. Lachner, C. C. Lindsey, C. R. Robins, and W. B. Scott. 1960. A list of common and scientific names of fishes from the United States and Canada. 2nd Ed. Am. Fish. Soc. Spec. Publ. No. 2.

Balon, E. K. 1975. Reproductive guilds of fishes: a proposal and definition. J. Fish. Res. Bd. Can. 32:821-864.

Barlow, G. W. 1961. Causes and significance of morphological variation in fishes. Syst. Zool. 10:105-117.

Barton, B. A. 1980. Spawning migrations, age, and growth, and summer feeding of white and longnose suckers in an irrigation reservoir. Can. Field-Nat. 94:300-304.

Becker, G. C. 1961. Fading fins. Trans. Wisconsin Acad. Sci., Arts, Lett. 50:239-248.

_____. 1983. Fishes of Wisconsin. Univ. Wisconsin Press, Madison.

Blatchley, W. S. 1938. The fishes of Indiana, with descriptions, notes on habits and distribution in the state. Nature Publishing Co., Indianapolis.

Bogan, A. E. and P. W. Parmalee. 1983. Tennessee's rare wildlife Volume II: The mollusks. Tennessee Wildlife Resources Agency, Nashville.

Bond, C. E. 1974. Keys to Oregon freshwater fishes. Oregon State Univ. Agri. Exp. Sta. Spec. Rept., Corvallis.

Bookstein, F.L., B. Chernoff, R. L. Elder, J. M. Humphries, G. R. Smith, and R. E. Strauss. 1985. Morphometrics in evolutionary biology: The geometry of size and shape change with examples from fishes. Acad. Nat. Sci. Philadelphia Spec. Publ. 15.

Boschung, H. T., J. D. Williams, D. W. Gotschall, D. K. Caldwell, and M. C. Caldwell. 1983. The Audubon Society guide to North American fishes, whales, and dolphins. Chanticleer Press, Inc., New York.

Bounds, S. M., J. K. Beadles, and B. M. Johnson. 1977. Fishes of Randolph County, Arkansas. Proc. Arkansas Acad. Sci. 31:21-25.

Bowen, S. H. 1979. A nutritional constraint in detritivory by fishes: the stunted population of Sarotherodon mossambicus in Lake Sibaya, South Africa. Ecol. Monogr. 49:17-31.

_____. 1981. Digestion and asssimilation of periphytic detrital aggregate by Tilapia mossambica. Trans. Am. Fish. Soc. 110:239-245.

Branson, B. A. 1962. Observations on the breeding tubercles of some Ozarkian minnows with notes on the barbels of Hybopsis. Copeia 1962:532-539.

_____. 1967. Fishes of the Neosho River system in Oklahoma. Am. Midl. Nat. 78:126-154.

Branson, B. A. and D. L. Batch. 1974. Fishes of the Red River drainage, eastern Kentucky. Univ. Kentucky Press, Lexington.

_____ and _____. 1983. Fishes of the South Fork of the Kentucky River, with notes and records from other parts of the drainage. Proc. SE Fishes Council 4(2):1-15.

Branson, B. A. and G. A. Schuster. 1982. The fishes of the wild river section of the Little South Fork of the Cumberland River, Kentucky. Trans. Kentucky Acad. Sci. 43:60-70.

Branson, B. A., J. Triplett, and R. Hartmann. 1969. A partial biological survey of the Spring River drainage in Kansas, Oklahoma and Missouri Part II: the fishes. Trans. Kansas Acad. Sci. 72:429-472.

Branson, B. A., D. F. Harker, Jr., J. M. Baskin, M. E. Medley, D. L. Batch, M. L. Warren, Jr., W. H. Davis, W. C. Houtcooper, B. Monroe, Jr., L. R. Phillippe, and P. Cupp. 1981. Endangered, threatened, and rare animals and plants of Kentucky. Trans. Kentucky Acad. Sci. 42:77-89.

Brenner, F. J. 1981. Impacts of impoundments on six small watersheds in Pennsylvania. Am. Fish. Soc. Warmwater Streams Symp. 1981:291-302.

Bretz, J. H. 1965. Geomorphic history of the Ozarks of Missouri. Missouri Geol. Surv. and Water Res., 2nd Ser. 41:1-147.

Brower, J. E. and J. H. Zar. 1984. Field and laboratory methods for general ecology, 2nd Ed. Wm. C. Brown Publishers, Dubuque.

Brown, A. V. and M. L. Armstrong. 1985. Propensity to drift downstream among various species of fish. J. Freshwater Ecol. 3:3-17.

Buchanan, T. M. 1973a. Checklist of Arkansas fishes. Proc. Arkansas Acad. Sci. 27:27-29.

_____. 1973b. Key to the fishes of Arkansas. Arkansas Game and Fish Comm., Little Rock.

Burkhead, N. M. 1980. The life history of the stoneroller minnow Campostoma a. anomalum (Rafinesque) in five streams in east Tennessee. Tennessee Wildlife Res. Agency Tech. Rept. No. 80-50.

Burkhead, N. M. and B. H. Bauer. 1983. An intergeneric hybrid, Hybopsis monacha X Notropis galacturus, from the Tennessee River drainage. Copeia 1983:1074-1077.

Burkhead, N. M. and R. E. Jenkins. 1982. Five-year status review of the slender chub, Hybopsis cahni, a threatened cyprinid fish of the upper Tennessee drainage. U. S. Fish Wildl. Serv. Rept., Newton Corner, Virginia.

Burkhead, N. M., R. E. Jenkins, W. H. Haxo, and S. P. McIninch. Abstr. 65th Ann. Meet. Am. Soc. Ichthyol. Herpetol. p. 47.

Burr, B. M. 1978. Systematics of the percid fishes of the subgenus Microperca, genus Etheostoma. Bull. Alabama Mus. Nat. Hist. No. 4.

_____. 1980. Hybognathus hankinsoni Hubbs, brassy minnow, p. 175 in D. S. Lee, et al Atlas of N. A. Freshwater Fishes, North Carolina State Mus. Nat. Hist., Raleigh.

Campbell, J. S., and H. R. McCrimmon. 1970. Biology of the emerald shiner, Notropis atherinoides Raf., in Lake Simcoe, Canada. J. Fish Biol. 2:259-273.

Carlander, K. 1969. Handbook of freshwater fishery biology, Vol. 1. Iowa State Univ. Press, Ames.

Cashner, R. C. and J. D. Brown. 1977. Longitudinal distribution of the fishes of the Buffalo River in northwestern Arkansas. Tulane Stud. Zool. and Biol. 19:37-46.

Cavender, T. M. and M. M. Coburn. 1985. Interrelationships of North American Cyprinidae, Part II. Abstr. 65th Ann. Meet. Am. Soc. Ichthyol. Herpetol. p. 49.

Chu, Y. T. Comparative studies on the scales and on the pharyngeals and their teeth in Chinese cyprinids, with particular reference to taxonomy and evolution. Biol. Bull. St. John's Univ., Shanghai, No. 2.

Clay, W. M. 1975. The Fishes of Kentucky. Kentucky Dept. Fish Wildlife Resources, Frankfort.

Cleary, R. E. 1953. An annotated check-list of the fishes of the Iowa-Cedar River drainage basin in Iowa. Proc. Iowa Acad. Sci. 60:626-635.

Clemmer, G. H. 1971. The systematics and biology of the Hybopsis amblops complex. Ph.D. Diss., Tulane University, New Orleans.

Clemmer, G. H. and R. D. Suttkus. 1971. Hybopsis lineapunctata a new cyprinid fish from the upper Alabama River system. Tulane Studies Zool. Bot. 17:21-30.

Coad, B. W. 1975. On the intergeneric relationships of North American and certain Eurasian cyprinid fishes (Cypriniformes, Cyprinidae). Ph.D. Diss., Univ. Ottawa, Toronto.

Coburn, M. M. 1982. Anatomy and relationships of Notropis atherinoides. Ph.D. Diss., Ohio State Univ., Columbus.

_____. 1983. Systematic relationships of the cyprinid taxa Hybopsis (Extrarius) aestivalis, Hybopsis (Erimystax) spp., and Phenacobius. Abstr. 92nd Ann. Meet. Ohio Acad. Sci. p. 5.

Coburn, M. M. and T. M. Cavender. 1985. Interrelationships of eastern North American cyprinids. Abstr. 65th Ann. Meet. Am. Ichthyol. Herpetol. p. 49.

Colinvaux, P. A. 1973. Introduction to ecology. John Wiley & Sons, Inc., New York.

Comiskey, C. E. and D. A. Etnier. 1972. Fishes of the Big South Fork of the Cumberland River. J. Tennessee Acad. Sci. 47:140-145.

Cooper, E. L. 1983. The Fishes of Pennsylvania and the Northeastern United States. Pennsylvania State Univ. Press, University Park.

Cope, E. D. 1868. On the distribution of fresh-water fishes in the Allegheny region of southwestern Virginia. J. Acad. Nat. Sci. Philadelphia. Ser. 2, Vol. 6:207-247.

_____. 1869. Synopsis of the Cyprinidae of Pennsylvania. Trans. Amer. Phil. Soc., 13, Pt. 3, 351-399.

_____. 1881. The fishes of Pennsylvania. Rept. Pennsylvania State Comm. Fish. 1879-1880:59-145.

_____. 1883. The fishes of Pennsylvania. Rept. Pennsylvania State Comm. Fish. 1881-1882:108-194.

Copes, F. 1975. Ecology of the brassy minnnow, Hybognathus hankinsoni Hubbs. Univ. Wisconsin, Stevens Point, Mus. Nat. Hist. Fauna and Flora Wisconsin Part III Rept. No. 10:46-72.

Corrucini, R. S. 1975. Multivariate analysis in biological anthropology: some considerations. J. Hum. Evol. 4:1-19.

_____. 1977. Correlation properties of morphometric ratios. Syst. Zool. 26:211-214.

Cross, F. B. 1950. Effects of sewage and of a headwaters impoundment on the fishes of Stillwater Creek in Payne County, Oklahoma. Am. Midl. Nat. 43:128-145.

_____. 1967. Handbook of fishes of Kansas. Univ. Kansas Mus. Nat. Hist. Misc. Publ. No. 45.

Cross, F. B. and J. T. Collins. 1975. Fishes in Kansas. Univ. Kansas Mus. Nat. Hist. Publ. Ed. Ser. No. 3.

Dahlberg, M. D. and D. C. Scott. 1971. The freshwater fishes of Georgia. Bull. Georgia Acad. Sci. 29:1-64.

Davis, B. J. and R. J. Miller. 1967. Brain patterns in minnows of the genus Hybopsis in relation to feeding habits and habitat. Copeia 1967:1-39.

Davis, B. J. and H. W. Reno. 1966. Rediscovery of the slender chub, Hybopsis cahni Hubbs & Crowe (Cyprinidae) at the type locality in Claiborne County, Tennessee. Copeia 1966:307.

Deacon, J. E. 1961. Fish populations, following a drought, in the Neosho and Marais des Cygnes rivers of Kansas. Mus. Nat. Hist. Univ. Kansas Publ. 13(9):359-427.

Deacon, J. E., G. Kobetich, J. D. Williams, and S. Contreras. 1979. Fishes of North America endangered, threatened, or of special concern: 1979. Fisheries 4:29-44.

DeKay, J. E. 1842. Zoology of New York. Vol. 3, Part 4, Fishes. W. White, A. White, and J. Visscher, Publ., Albany.

Denoncourt, R. F., E. C. Raney, C. H. Hocutt, and J. R. Stauffer. 1975. A checklist of the fishes of West Virginia. Virginia J. Sci. 26:117-120.

Dewey, M. R. and T. E. Moen. 1978. Fishes of the Caddo River, Arkansas after impoundment of Degray Lake. Proc. Arkansas Acad. Sci. 32:39-42.

Dickinson, W. E. 1960. Handbook of Wisconsin fishes. Milwaukee Public Mus. Pop. Sci. Handbook Ser. No. 8.

Dixson, D. A., B. A. Branson, and D. L. Batch. 1983. Correlation of fish distribution and stream order in the upper Cumberland and upper Kentucky Rivers based upon an information retrieval system. Trans. Kentucky Acad. Sci. 44:111-116.

Donoghue, M. J. and P. D. Cantino. 1984. The logic and limitations of the outgroup substitution approach to cladistic analysis. Syst. Bot. 9:192-202.

Dowling, H. G. 1956. Geographic relations of ozarkian amphibians and reptiles. SW Nat. 1:174-189.

Driver, E. C. 1942. Name that animal, a guide to the identification of the common land and freshwater animals of the United States, with special reference to the area east of the Rockies. Kraushar Press, Northampton.

Eaton, S. W., R. J. Nemecek, and M. M. Kozubowski. 1982. Fishes of the Allegheny River above Kinzua Dam. New York Fish and Game J. 29:189-198.

Eddy, S. 1957. How to know the freshwater fishes. Wm. C. Brown Co. Publishers, Dubuque.

_____. 1969. How to know the freshwater fishes, 2nd ed. Wm. C. Brown Co. Publishers, Dubuque.

Eddy, S. and T. Surber. 1943. Northern fishes with special reference to the upper Mississippi Valley. Univ. Minnesota Press, Minneapolis.

_____ and _____. 1947. Northern fishes with special reference to the upper Mississippi Valley, Rev. ed. Univ. Minnesota Press, Minneapolis.

Eddy, S. and J. C. Underhill. 1959. Recent changes and corrections for the Minnesota fish fauna. Copeia 1959:342-343.

_____ and _____. 1974. Northern fishes, with special reference to the upper Mississippi Valley. Univ. Minnesota Press, Minneapolis.

_____ and _____. 1978. How to know the freshwater fishes, 3rd ed. Wm. C. Brown Co. Publ., Dubuque.

Eddy, S., J. B. Moyle, and J. C. Underhill. 1963. The fish fauna of the Mississippi River above St. Anthony Falls as related to the effectiveness of this falls as a migration barrier. Proc. Minnesota Acad. Sci. 30:111-115.

Edwards, E. A. 1983a. Habitat suitability index models: Bigmouth buffalo. U. S. Dept. Int., Fish Wildl. Serv. FWS/OBS-82/10.34.

_____. 1983b. Habitat suitability index models: Longnose sucker. U. S. Dept. Int., Fish Wildl. Ser. FWS/OBS-82/10.35.

Edwards, E. A. and K. Twomey. 1982. Habitat suitability index models: Smallmouth buffalo. U. S. Dept. Int. Fish Wildl. Serv. FWS/OBS-82/10.13.

Eigenmann, C. H. and C. H. Beeson. 1894. The fishes of Indiana. Proc. Indiana Acad. Sci. 1893:76-108.

Endler, J. A. 1982. Problems in distinguishing historical from ecological factors in biogeography. Am. Zool. 22:441-452.

Etnier, D. A. 1976. Percina (Imostoma) tanasi, a new percid fish from the Little Tennessee River. Proc. Biol. Soc. Wash. 88:469-488.

Etnier, D. A. and W. C. Starnes. ms. The fishes of Tennessee.

Etnier, D. A., W. C. Starnes, and B. H. Bauer. 1979. Whatever happened to the silvery minnow (Hybognathus nuchalis) in the Tennessee River? Proc. SE Fishes Council 2(3):no pagination.

Everhart, W. H. and W. D. Youngs. 1981. Principles of fishery science. Cornell Univ. Press, Ithaca, NY.

Evermann, B. W. 1902. List of species of fishes known to occur in the Great Lakes or their connecting waters. Bull. U. S. Fish. Comm. 21:95-96.

_____. 1918. The fishes of Kentucky and Tennessee: a distributional catalogue of the known species. Bull. U. S. Fish. Comm. 35:295-368.

Evermann, B. W. and U. O. Cox. 1896. A report upon the fishes of the Missouri River basin. Rept. U. S. Comm. Fish. 1894:325-429.

Evermann, B. W. and S. F. Hildebrand. 1916. Notes on the fishes of east Tennessee. Bull. U. S. Bur. Fish. 34:431-451.

Fago, D. 1982. Distribution and relative abundance of fishes in Wisconsin. 1. Greater Rock River basin. Wisconsin Dept. Nat. Res. Tech. Bull. No. 136.

Forbes, S. A. 1884. A catalogue of the native fishes of Illinois. Ill. State Fish Comm. Rept. 1884:60-89.

Forbes, S. A. and R. E. Richardson. 1908. The Fishes of Illinois. Illinois State Lab. of Nat. Hist., Urbana.

Fowler, H. W. 1919. A list of the fishes of Pennsylvania. Proc. Biol. Soc. Wash. 32:49-74.

_____. 1922. Records of fishes for the eastern and southern United States. Proc. Acad. Nat. Sci. Philadelphia 74:1-27.

_____. 1940. A list of the fishes recorded from Pennsylvania. Pennsylvania Bd. Fish. Comm. Biennial Rept. for period ending 31 May 1940, p. 59-78.

_____. 1945. A study of the fishes of the southern Piedmont and Coastal Plain. Acad. Nat. Sci. Philadelphia Monograph No. 7.

Frazier, G. C. and J. K. Beadles. 1977. The fishes of Sylamore Creek, Stone County, Arkansas. Proc. Arkansas Acad. Sci. 31:38-41.

Frietsche, R. A. 1982. The warmwater fish community of a cool tailwater in Arkansas. Proc. Arkansas Acad. Sci. 36:28-30.

Fruge, D. W. 1971. Fishes of the Caddo River, west-central Arkansas. M.S. thesis, Northeast Louisiana Univ., Monroe.

Gerking, S. D. 1945. The distribution of the fishes of Indiana. Investigations Indiana Lakes and Streams 3:1-137.

_____. 1955. Key to the fishes of Indiana. Investigations Indiana Lakes and Streams 4:49-86.

Geishler, M. R. , E. D. Short, and P. D. Kittle. 1975. A preliminary checklist of the fishes of the Illinois River, Arkansas. Proc. Arkansas Acad. Sci. 29:37-39.

Gibbs, R. H., Jr. 1957. Cyprinid fishes of the subgenus Cyprinella of Notropis. I. Systematic status of the subgenus Cyprinella, with a key to the species exclusive of the lutrensis-ornatus complex. Copeia 1957:185-195.

_____. 1961. Cyprinid fishes of the subgenus Cyprinella of Notropis. IV. The Notropis galacturus-camurus complex. Am. Midl. Nat. 66:337-354.

_____. 1963. Cyprinid fishes of the subgenus Cyprinella of Notropis. The Notropis whipplei-analostanus-chloristius complex. Copeia 1963:511-528.

Gilbert, C. R. 1964. The American cyprinid fishes of the subgenus Luxilus (genus Notropis). Bull. Florida State Mus. 8:95-194.

_____. 1980a. Hybognathus hayi Jordan, cypress minnow, p. 176 in D. S. Lee, et al Atlas of N. A. Freshwater Fishes, North Carolina State Mus. Nat. Hist., Raleigh.

_____. 1980b. Hybopsis x-punctata Hubbs and Crowe, gravel chub, p. 196 in D. S. Lee, et al Atlas of N. A. Freshwater Fishes, North Carolina State Mus. Nat. Hist., Raleigh.

_____. 1980c. Notropis harperi Fowler, redeye chub, p. 270 in D. S. Lee et al Atlas of N.A. Freshwater Fishes, North Carolina State Mus. Nat. Hist., Raleigh.

Gilbert, C. R. and R. M. Bailey. 1972. Systematics and zoogeography of the American cyprinid fish Notropis (Opsopoeodus) emiliae. Occ. Pap. Univ. Mich. Mus. Zool. No. 664.

Gordon, D. C. 1970. Some studies on the distribution and composition of particulate organic carbon in the North Atlantic Ocean. Deep Sea Research 17: 233-243.

Green, J. F. and J. K. Beadles. 1974. Ichthyofaunal survey of the Current River within Arkansas. Proc., Arkansas Acad. Sci. 28:13-18.

Greene, C. W. 1935. The distribution of Wisconsin fishes. Wisconsin Cons. Comm., Madison.

Gunther, A. 1868. Catalogue of the fishes of the British Museum, Vol. 7, Royal British Museum, Publisher, London.

Harlan, J. R. and E. B. Speaker. 1951. Iowa fish and fishing. Iowa State Cons. Comm., Des Moines.

Harris, J. L. 1980a. Hybopsis dissimilis (Kirtland), streamline chub, p. 184 in D. S. Lee, et al. Atlas of North American Freshwater Fishes. North Carolina State Mus. Nat. Hist., Raleigh.

_____. 1980b. Hybopsis insignis Hubbs and Crowe, blotched chub, p. 188 in D. S. Lee, et al. Atlas of North American Freshwater Fishes. North Carolina State Mus. Nat. Hist., Raleigh.

_____. msA. Systematics and distribution of fishes currently allocated to Erimystax (Jordan), a subgenus of Hybopsis (Cyprinidae).

_____. msB. Biology of the gravel chub, Hybopsis x-punctata (Cyprinidae), in the Ouachita River system, Arkansas.

_____. msC. Biology of the Ozark chub, Hybopsis harryi (Cyprinidae), in the White River System, AR and comparison with aspects of the biology of the spotted chub, Hybopsis dissimilis.

_____. msD. The biology of the blotched chub, Hybopsis insignis (Cyprinidae) in the upper Tennessee River system.

Harris, J. L. and N. H. Douglas. 1978. Fishes of the mountain province section of the Ouachita River. Proc. Arkansas Acad. Sci. 32:55-59.

Heins, D. C. 1985. Life history traits of the Florida sand darter Ammocrypta bifascia, and comparisons with the naked sand darter Ammocrypta beani. Am. Midl. Nat. 113:209-216.

Heins, D. C. and G. H. Clemmer. 1976. The reproductive biology, age and growth of the North American cyprinid, Notropis longirostris (Hay). J. Fish. Biol. 8:365-379.

Hendricks, M. L., J. R. Stauffer,Jr., C. H. Hocutt, and C. R. Gilbert. 1979. A preliminary checklist of the fishes of the Youghiogheny River. Nat. Hist. Misc. No. 203.

Hendricks, M. L., J. R. Stauffer, Jr., and C. H. Hocutt. 1983. The zoogeography of the fishes of the Youghiogheny River system, Pennsylvania, Maryland, and West Virginia. Am. Midl. Nat. 110:145-164.

Henshall, J. A. 1888. Contributions to the ichthyology of Ohio. No. 1. J. Cincinnati Soc. Nat. Hist. 11:76-80.

Hitch, R. K. and D. A. Etnier. 1974. Fishes of the Hiwassee River system - ecological and taxonomic considerations. J. Tennessee Acad. Sci. 49:81-87.

Hocutt, C. H., R. F. Denoncourt, and J. R. Stauffer, Jr. 1979. Fishes of the Gauley River, West Virginia. Brimleyana 1:47-80.

Howell, W. M. and J. D. Williams. 1971. Notropis gibbsi, a new cyprinid fish from the Tallapoosa River system in Alabama and Georgia. Copeia 1971:55-64.

Hubbs, C. L. 1926. A check list of the fishes of the Great Lakes and tributary waters, with nomenclatorial notes and analytical keys. Misc. Publ. Univ. Michigan Mus. Zool. No. 15.

Hubbs, C. L. and W. R. Crowe. 1956. Preliminary analysis of the American cyprinid fishes, seven new, referred to the genus Hybopsis, subgenus Erimystax. Occ. Pap. Univ. Michigan Mus. Zool. No. 578.

Hubbs, C. L. and C. W. Greene. 1928. Further notes on the fishes of the Great Lakes and tributary waters. Pap. Michigan Acad. Sci., Arts, and Letters 8:371-392.

Hubbs, C. L. and K. F. Lagler. 1939. Keys for the identification of the fishes of the Great Lakes and tributary waters. Published by the authors, Ann Arbor.

_____ and _____. 1957. List of fishes of the Great Lakes and tributary waters. Michigan Fish. 1:1-6.

_____ and _____. 1958. Fishes of the Great Lakes Region. Rev. ed. Cranbrook Inst. Sci. Bull. 26.

_____ and _____. 1964. Fishes of the Great Lakes Region. Univ. Michigan Press, Ann Arbor.

Hubbs, C. L., R. R. Miller, and L. C. Hubbs. 1974. Hydrography, History, and Relict Fish of the North-Central Great Basin. Mem. California Acad. Sci. No. 7.

Hubbs, Clark, and J. Pigg. 1976. The effects of impoundments on threatened fishes of Oklahoma. Ann. Oklahoma Acad. Sci. 5:113-117.

Hubert, W. A., S. H. Anderson, P. D. Southall, and J. H. Crance. 1984. Habitat suitability index models and instream flow suitability curves: Paddlefish. U. S. Fish Wildl. Serv. FWS/OBS-82/10.80.

Humphries, J. M., F. L. Bookstein, B. Chernoff, G. R. Smith, R. L. Elder, and S. G. Poss. 1981. Multivariate discrimination by shape in relation to size. Syst. Zool. 30:291-308.

Jenkins, R. E. 1970. Systematic studies of the catostomid fish tribe Moxostomatini. Ph.D. Diss., Cornell Univ., Ithaca, New York.

_____. 1975. Status report on Hybopsis cahni, the slender chub. Endang. Spec. Off. Rpt., Washington.

Jenkins, R. E. and N. M. Burkhead. 1984. Description, biology and distribution of the spotfin chub, Hybopsis monacha, a threatened cyprinid fish of the Tennessee River drainage. Bull. Alabama Mus. Nat. Hist. 8:1-30.

Jenkins, R. E. and E. A. Lachner. 1971. Criteria for analysis and interpretation of the American fish genera Nocomis Girard and Hybopsis Agassiz. Smithsonian Contr. Zool. No. 90.

_____ and _____. 1980a. Hybopsis labrosa Cope, thicklip chub, p. 189 in D. S. Lee et al., Atlas of North American Freshwater Fishes. North Carolina State Mus. Nat. Hist., Raleigh.

_____ and _____. 1980b. Hybopsis zanema (Jordan and Brayton), Santee chub, p. 197 in D. S. Lee, et al., Atlas of North American Freshwater Fishes. North Carolina State Mus. Nat. Hist., Raleigh.

Jenkins, R. E., N. M. Burkhead, and W. S. Haxo. ms. The Fishes of Virginia.

Jenkins, R. E., E. A. Lachner, and F. J. Schwartz. 1972. The distributional history of the biota of the southern Appalachians Part III: Vertebrates. Virginia Poly. Inst. State Univ. Res. Div. Monogr. 4:43-117.

Johnson, B. M. and J. K. Beadles. 1977. Fishes of the Eleven Point River within Arkansas. Proc. Arkansas Acad. Sci. 31:58-61.

Johnson, M. and G. C. Becker. 1970. Annotated list of the fishes of Wisconsin. Wisconsin Acad. Sci., Arts, and Lett. 58:265-300.

Jordan, D. S. 1875. Synopsis of the genera of fishes to be looked for in Indiana. Ann. Rep. Geol. Surv. Indiana 6:197-228.

_____. 1876. A partial synopsis of the fishes of upper Georgia. Ann. Lyceum Nat. Hist. New York 11:307-377.

_____. 1877. On the fishes of northern Indiana. Proc. Acad. Nat. Sci. Philadelphia 29:42-82.

_____. 1878. A catalogue of the fishes of Illinois. Bull. Illinois State Lab. Nat. Hist. 1:37-70.

_____. 1882. Report on the fishes of Ohio. Rept. Geol Surv. Ohio 4:735-1002.

_____. 1889. Descriptions of fourteen species of fresh-water fishes collected by the U. S. Fish Commission in the summer of 1888. Proc. U. S. Nat. Mus. 11:351-362.

_____. 1920. The genera of fishes Part IV. From 1881 to 1920, thirty-nine years, with the accepted type of each. Stanford University.

_____. 1924. Concerning the genus Hybopsis of Agassiz. Copeia 1924:51-52.

_____. 1929. Manual of the vertebrate animals of the northeastern United States inclusive of marine species. 13th ed. World Book Co., Yonkers-on-the-Hudson, NY.

Jordan, D. S. and B. W. Evermann. 1896. The fishes of North and Middle America. Part 1. Bull. U. S. Nat. Mus. No. 47.

_____ and _____. 1900. The fishes of North and Middle America. Part IV. Bull. U. S. Nat. Mus. No. 47.

Jordan, D. S. and C. H. Gilbert. 1883. Synopsis of the fishes of North America. Bull. U. S. Nat. Mus. No. 16.

_____ and _____. 1886. List of fishes collected in Arkansas, Indian Territory, and Texas in September, 1884, with notes and description. Proc. U. S. Nat. Mus. 9:1- 25.

Jordan, D. S., B. W. Evermann, and H. W. Clark. 1930. Check list of the fish and fishlike vertebrates of North and Middle America north of the boundary of Venezuela and Columbia. Rept. U. S. Comm. Fish. 1928.

Kinney, E. C., Jr. 1954. A life history of the silver chub, Hybopsis storeriana (Kirtland), in western Lake Erie with notes on associated species. Diss. Abstr. 20(6):1978-1980.

Kirsch, P. H. 1893. Notes on a collection of fishes from the southern tributaries of the Cumberland River in Kentucky and Tennessee. Bull. U. S. Fish Comm. 11:259-268.

_____. 1895. A report upon explorations made in Eel River basin in the northeastern part of Indiana in the summer of 1892. Bull. U. S. Fish Comm. 14:31-40.

Kirtland, J. P. 1841. Descriptions of the fishes of the Ohio River and its tributaries. Boston J. Nat. Hist. 3(1840):338-352, pls 4-6.

_____. 1850. Fishes of Ohio, Leuciscus dissimilis Kirtland--spotted minnow. The Family Visitor 1(24):189.

Kraatz, W. C. 1923. A study of the food of the minnow Campostoma anomalum. Ohio J. Sci. 23:265-283.

_____. 1924. The intestine of the minnow Campostoma anomalum (Rafinesque), with special reference to the development of its coiling. Ohio J. Sci. 24:265-298.

Kuhne, E. R. 1939. A guide to the fishes of Tennessee and the mid-south. Tennessee Dept. Cons., Nashville.

Lachner, E. A. and R. E. Jenkins. 1971. Systematics, distribution and evolution of the Nocomis biguttatus species group (family Cyprinidae:Pisces) with a description of a new species from the Ozark upland. Smithsonian Contr. Zool. 91:1-28.

Large, T. 1903. A list of the native fishes of Illinois, with keys. Rept. Illinois State Fish Comm. 1900-1902.

Lee, D. S. 1980. Hybognathus regius Girard, eastern silvery minnow, p. 179 in D. S. Lee, et al Atlas of N. A. Freshwater Fishes, North Carolina State Mus. Nat. Hist., Raleigh.

Lodge, D. M., A. L. Beckel and J. J. Magnuson. 1985. Lake-bottom tyrant. Nat. Hist. 94(8):32-37.

Long, J. J. 1980. Hybopsis crameri (Snyder), Oregon chub, p. 183 in Atlas of North American Freshwater Fishes. North Carolina State Mus. Nat. Hist., Raleigh.

Martin, R. G. and R. S. Campbell. 1953. The small fishes of Black River and Clearwater Lake, Missouri in J. L. Funk, et al, eds. The Black River Studies 26:45-66. Univ. Missouri, Columbia.

Mayden, R. L. 1983. Phylogenetic analysis of the subgenus Cyprinella, genus Notropis (Cyprinidae). Abst. 63rd Ann. Meet. Am. Soc. Ichthyol. Herpetol. p. 11.

_____. 1985a. Biogeography of Ouachita highland fishes. SW Nat. 30:195-211.

_____. 1985b. Phylogenetic studies of North American minnows, with emphasis on the genus Cyprinella (Teleostei:Cypriniformes). Ph.D. Diss., Univ. Kansas, Lawrence.

Mayden, R. L. and B. M. Burr, 1981. Life history of the slender madtom, Noturus exilis, in southern Illinois (Pisces:Ictaluridae). Occ. Pap. Mus. Nat. Hist. Kansas No. 93:1-64.

Mayr, E., E. G. Linsley, and R. L. Usinger. 1953. Methods and principles of systematic zoology. McGraw-Hill, New York.

Meek, S. E. 1891. Report of explorations made in Missouri and Arkansas during 1889, with an account of the fishes observed in each of the river basins examined. Bull. U. S. Fish. Comm. 9:113-141.

_____. 1892. A report upon the fishes of Iowa, based upon observations and collections made during 1889, 1890, and 1891. Bull. U. S. Fish. Comm. 10:217-248.

_____. 1894. A catalogue of the fishes of Arkansas. Ann. Rept. Geol. Surv. Arkansas 2:215-276.

_____. 1895. Report of investigations respecting the fishes of Arkansas, conducted during 1891, 1892, and 1893, with a synopsis of previous explorations in the same state. Bull. U. S. Fish Comm. 14:67-94.

_____. 1908. List of fishes known to occur in the waters of Indiana. Rept. Indiana Comm. Fish and Game 1907-1908:134-171.

Meek, S. E. and S. F. Hildebrand. 1910. A synoptic list of the fishes known to occur within 50 miles of Chicago. Field Mus. Nat. Hist. Zool. Ser. 7:223-238.

Menhinnick, E. F., T. M. Burton, and J. R. Bailey. 1974. An annotated checklist of the freshwater fishes of North Carolina. J. Elisha Mitchell Soc. 90(1):24-50.

Metcalf, A. L. 1966. Fishes of the Kansas system in relation to zoogeography of the Great Plains. Publ. Mus. Nat. Hist. Univ. Kansas 17:23-189.

Miller, R. J. and H. W. Robison. 1973. The Fishes of Oklahoma. Oklahoma State Univ. Press, Stillwater.

Miller, R. R. 1972. Threatened freshwater fishes of the United States. Trans. Am. Fish. Soc. 101:239-252.

Mills, P. A., C. H. Hocutt and J. R. Stauffer, Jr. 1978. The pre-impoundment fish fauna of Big River (Meramec drainage, Missouri). Trans. Missouri Acad. Sci. 12:25-35.

Moore, G. A. 1957. Fishes, pp. 31-210 in W. F. Blair, A. P. Blair, P. Brodkorb, F. R. Cagle, and G. A. Moore, eds. Vertebrates of the United States. McGraw-Hill Book Co., Inc., New York.

_____. 1968. Fishes, pp. 21-165 in W. F. Blair, A. P. Blair, P. Brodkorb, F. R. Cagle, and G. A. Moore, eds. Vertebrates of the United States. McGraw-Hill Book Co., Inc., New York.

_____. 1973. Discovery of fishes in Oklahoma (1852-1972). Proc. Oklahoma Acad. Sci. 53:1-26.

Moore, G. A. and J. M. Paden. 1950. The fishes of the Illinois River in Oklahoma and Arkansas. Am. Midl. Nat. 44:76-95.

Myers, J. W. 1977. Fishes of the Little Missouri River, southwest Arkansas. M.S. thesis, Northeast Louisiana Univ., Monroe.

Neff, N. A. and L. F. Marcus. 1980. A survey of multivariate methods for systematics. Am. Mus. Nat. Hist., New Hork.

Nelson, E. W. 1876. A partial catalogue of the fishes of Illinois. Bull. Illinois Mus. Nat. Hist. 1:33-52.

Nelson, G. J. 1969. Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. Bull. Am. Mus. Nat. Hist. 141:479-552.

Nordlie, F., J. C. Underhill, and S. Eddy. 1961. New distributional records of some Minnesota fishes. Minnesota Acad. Sci. 29:255-258.

O'Donnell, D. J. 1935. Annotated list of the fishes of Illinois. Illinois Nat. Hist. Surv. Bull. 20:473-500.

Olund, L. J. and F. B. Cross. 1961. Geographic variation in the North American cyprinid fish, Hybopsis gracilis. Univ. Kansas Mus. Nat. Hist. Publ. 13(7):323-348.

Ono, R. D., J. D. Williams, and A. Wagner. 1983. Vanishing fishes of North America. Stone Wall Press, Inc., Washington.

Ortmann, A. E. 1920. Correlation of the shape and station in freshwater mussels. Proc. Am. Phil. Soc. 19:269-312.

_____. 1925. The naiad-fauna of the Tennessee River system below Walden Gorge. Am. Midl. Nat. 9:321-372.

Osburn, R. C. 1901. The fishes of Ohio. Ohio Acad. Sci. Spec. Pap. No. 4.

Osburn, R. C., E. L. Wickliff, and M. B. Trautman. 1930. A revised list of the fishes of Ohio. Ohio J. Sci. 30:169-176.

Outten, L. M. 1958. Studies of the life history of the cyprinid fishes Notropis galacturus and rubricroceus. J. Elisha Mitchell Sci. Soc. 74:122-134.

Page, L. M. 1974. The subgenera of Percina (Percidae: Etheostomatini). Copeia 1974:66-86.

_____. 1981. The genera and subgenera of darters (Percidae, Etheostomatini). Occas. Pap. Mus. Nat. Hist. Univ. Kansas No. 90.

_____. 1983. Handbook of darters. T. F. H. Publications, Neptune City, NJ.

Parker, W. and L. Dixon. 1980. Endangered and threatened wildlife of Kentucky, North Carolina, South Carolina and Tennessee. North Carolina Agri. Ext. Ser., Raleigh.

Patriarche, M. H. and R. S. Cambell. 1958. The development of the fish population in a new flood-control reservoir in Missouri, 1948-1954. Trans. Am. Fish. Soc. 87:240- 258.

Pflieger, W. L. 1968. A check-list of the fishes of Missouri with keys for identification. Missouri Dept. Cons. D-J Series No. 3.

_____. 1971. A distributional study of Missouri fishes. Publ. Mus. Nat. Hist. Univ. Kansas 20: 225-570.

_____. 1975. The Fishes of Missouri. Missouri Dept. Cons., Jefferson City.

_____. 1980. Hybognathus nuchalis Agassiz, central silvery minnow, p. 177 in D. S. Lee, et al Atlas of N. A. Freshwater Fishes, North Carolina State Mus. Nat. Hist., Raleigh.

Phillips, G. L. 1969. Diet of the minnow Chrosomus erythrogaster (Cyprinidae) in a Minnesota stream. Am. Midl. Nat. 82:99-109.

Phillips, G. L. and J. C. Underhill. 1967. Revised distribution records of some Minnesota fishes, with addition of two species to the faunal list. J. Minnesota Acad. Sci. 34:177-180.

Phillips, G. L., W. D. Schmid, and J. C. Underhill. 1982. Fishes of the Minnesota Region. Univ. Minnesota Press, Minneapolis.

Pimentel, R. A. 1979. Morphometrics, the multivariate analysis of biological data. Kendall/Hunt Publishing Co., Dubuque.

Prejs, A. 1984. Herbivory by temperate freshwater fishes and its consequences. Env. Biol. Fishes 10:281-296.

Purkett, C. A., Jr. 1961. Reproduction and early development of the paddlefish. Trans. Am. Fish. Soc. 90:125-129.

Ramsey, J. S. 1976. Freshwater fishes, pp. 53-65 in H. T. Boschung, ed. Endangered and Threatened Plants and Animals of Alabama. Bull. Alabama Mus. Nat. Hist. No. 2.

Raymond, L. R. 1975. Fishes of the hill province section of the Ouachita River, from Remmel Dam to the Arkansas-Louisiana line. M.S. thesis, Northeast Louisiana Univ., Monroe.

Reno, H. W. 1969a. A partial nomenclatural review of Hybopsis (Pisces:Cyprinidae). Proc. Oklahoma Acad. Sci. 48:65-71.

_____. 1969b. Cephalic lateral-line systems of the cyprinid genus Hybopsis. Copeia 1969:736-773.

Reynolds, J. T. 1971. Fishes of the Saline River, south central Arkansas. M.S. thesis, Northeast Louisiana Univ., Monroe.

Ricker, W. E. 1973. Linear regression in fishery research. J. Fish. Res. Board Canada 30:409-434.

Riley, G. A. 1970. Particulate organic matter in seawater. Advances in Marine Biol. 8:1-118.

Robins, C. R., R. M. Bailey, C. E. Bond, J. R. Brooker, E. A. Lachner, R. N. Lea, and W. B. Scott. 1980. A list of common and scientific names of fishes from the United States and Canada, 4th ed. Am. Fish. Soc. Spec. Publ. No. 12.

Robison, H. W. 1986.. Zoogeographic implications of the Mississippi River Basin, pp. 267-285 in C. H. Hocutt and E. O. Wiley, eds. The Zoogeography of North American Freshwater Fishes. John Wiley & Sons, Inc., New York.

Ross, R. D. 1959. Drainage evolution and distribution problems of the fishes of the New (upper Kanawha) River system in Virginia, Part IV-Key to the indentification of fishes. Virginia Poly. Inst. Tech. Bull. 146.

Ross, R. D. and J. E. Carico. 1963. Records and distribution problems of fishes of the North, Middle, and South Forks of the Holston River, Virginia. Virginia Poly. Inst. Tech. Bull. No. 161.

SAS, 1985. SAS user's guide: statistics, version 5 edition. SAS Institute, Inc., Cary, North Carolina.

Schoener, T. W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2:369-404.

Schmulbach, J. C. 1957. The life history of the central stoneroller, Campostoma anomalum pullum Agassiz. M.S. thesis, Southern Illinois Univ., Carbondale.

Scott, W. B. 1958. A checklist of the freshwater fishes of Canada and Alaska. Royal Ontario Museum, Toronto.

Scott, W. B. and E. J. Crossman. 1973. Freshwater Fishes of Canada. Bull. Fish. Res. Bd. Can. 184:1-966.

Settles, W. H. and R. D. Hoyt. 1976. Age structure, growth patterns and food habits of the southern redbelly dace Chrosomus erythrogaster in Kentucky. Trans. Kentucky Acad. Sci. 37:1-10.

Smith, H. M. 1907. The fishes of North Carolina. North Carolina Geol. and Econ. Surv., Vol. 2., Raleigh.

Smith, M. L., T. M. Cavender, and R. R. Miller. 1975. Climatic and biogeographic significance of a fish fauna from the late Pliocene-early Pleistocene of the Lake Chapala Basin (Jalisco:Mexico). Stud. Cenozoic Paleo. Strat. Univ. Michigan Pap. Paleo. 12:29-38.

Smith, P. W. 1965. A preliminary annotated list of the lampreys and fishes of Illinois. Illinois Nat. Hist. Surv. Biol. Notes No. 54.

_____. 1971. Illinois Streams: a classification based on their fishes and an analysis of factors responsible for disappearance of native species. Illinois Nat. Hist. Surv. Biol. Notes No. 76.

_____. 1979. The fishes of Illinois. Univ. Illinois Press, Urbana.

Smith, P. W., A. C. Lopinot, and W. L. Pflieger. 1971. A distributional atlas of upper Mississippi River Fishes. Illinois Nat. Hist. Surv. Biol. Notes No. 73.

Smith-Vaniz, W. F. 1968. Freshwater fishes of Alabama. Agri. Exp. Sta., Auburn Univ.

Snelson, F. F., Jr. 1970. Systematics of some minnows of the subgenus Lythrurus, genus Notropis (Pisces:Cyprinidae). Ph.D. Diss., Cornell Univ., Ithaca, New York.

_____. 1971. Notropis mekistocholas, a new herbivorous cyprinid fish endemic to the Cape Fear River, basin, North Carolina. Copeia 1971:449-462.

_____. 1972. Systematics of the subgenus Lythrurus genus Notropis (Pisces:Cyprinidae). Bull. Florida State Mus. Biol. Sci. 17:1-92.

_____. 1975. Patterns of gut elongation in American cyprinids. Abstr. Amer. Soc. Ichth. & Herp., Williamburg, Virginia. p. 117.

_____. 1980. Notropis mekistocholas, Cape Fear shiner, p. 287 in D. S. Lee, et al Atlas of N. A. Freshwater Fishes, North Carolina State Mus. Nat. Hist., Raleigh.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry, 2nd ed. W. H. Freeman and Co., San Francisco.

Starnes, L. B. and W. C. Starnes. 1985. Ecology and life history of the moutain madtom, Noturus eleutherus (Pisces:Ictaluridae). Am. Midl. Nat. 114:331-341.

Starnes, W. C. and D. A. Etnier. 1980. Fishes, pp. BI-III, B1-B134 in D. C. Eagar and R. M. Hatcher, eds. Tennessee's Rare Wildlife Volume I: The vertebrates.

Starnes, W. C. and D. A. Etnier. 1986. Drainage evolution and fish biogeography of the Tennessee and Cumberland River drainages, pp. 325-361 in C. H. Hocutt and E. O. Wiley eds. Zoogeography of North American Freshwater Fishes. John Wiley & Sons, Inc., New York.

Starnes, W. C. and L. B. Starnes. 1981. Biology of the blackside dace Phoxinus cumberlandensis. Am. Midl. Nat. 106:360-371.

Starrett, W. 1950. Food relationships of the minnows and darters of the Des Moines River, Iowa. Ecology 31:216-233.

_____. 1951. Some factors affecting the abundance of minnows in the Des Moines River, Iowa. Ecology 32:13-27.

Stauffer, J. R., Jr., B. M. Burr, C. H. Hocutt, and R. E. Jenkins. 1982. Checklist of the fishes of the central and northern Appalachian Mountains. Proc. Biol Soc. Wash. 95:27-47.

Strauss, R. E. 1985. Evolutionay allometry and variation in body form in the South American catfish genus Corydoras (Callichthyidae). Syst. Zool. 34:381-396.

Strauss, R. E. and F. L. Bookstein. 1982. The truss: body form reconstruction in morphometrics. Syst. Zool. 31:113-135.

Sullavan, J. N. 1974. Drainage areas of streams in Arkansas: White River basin. U. S. Geol. Surv. and Arkansas State Highway Comm., Little Rock.

Sullivan, R. M. 1985. Phyletic, biogeographic, and ecologic relationships among montane populations of least chipmunks (Eutamias minimus) in the southwest. Syst. Zool. 34:419-448.

Swift, C. C. 1970. A review of the eastern North American cyprinid fishes of the Notropis texanus species group (subgenus Alburnops) with a definition of the subgenus Hydrophlox, and materials for a revision of the subgenus Alburnops. Ph.D. Diss., Florida State Univ., Tallahassee.

Tesch, F. W. 1971. Age and growth., pp. 98-127 In W. E. Ricker, ed. Methods for Assessment of Fish Production in Freshwaters. Blackwell Scientific Publications, Oxford, England.

Thornbury, W. D. 1965. Regional geomorphology of the United States. John Wiley and Sons, New York.

Trautman, M. B. 1957. The fishes of Ohio. Ohio State Univ. Press, Columbus.

_____. 1981. The fishes of Ohio, revised edition. Ohio State Univ. Press, Columbus.

TVA. 1970. Tennessee Valley streams: their fish, bottom fauna, and aquatic habitat. Powell River Drainage Basin. Div. Forestry, Fisheries, and Wildlife Dev., Fisheries and and Waterfowl Res. Branch, Norris.

_____. 1973. Tennessee Valley streams: their fish, bottom fauna, and aquatic habitat. Buffalo River Drainage Basin. Div. Forestry, Fisheries, and Wildlife Dev., Fisheries and Waterfowl Res. Branch, Norris.

_____. 1975. Tennessee Valley streams: their fish, bottom fauna, and aquatic habitat. Duck River Drainage Basin. Div. Forestry, Fisheries, and Wildlife Dev., Fisheries and Waterfowl Res. Branch, Norris.

U. S. Geological Survey. 1970-1983a. Water Resources Data-Arkansas--Water Years 1970-1983. U.S. Govt. Printing Office, Washington, D.C.

_____. 1970-1983b. Water Resources Data-Tennessee--Water Years 1970-1983. U.S. Govt. Printing Office, Washington, D.C.

Wallace, R. K. and J. S. Ramsey. 1981. Reproductive behavior and biology of the bluestripe shiner (Notropis callitaenia) in Uchee Creek, Alabama. Am. Midl. Nat. 106:197-200.

Watrous, L. E. and Q. D. Wheeler. 1981. The out-group comparison method of character analysis. Syst. Zool. 30:1-11.

Weatherley, A. H. 1972. Growth and ecology of fish populations. Academic Press, New York.

Werner, E. E. and D. J. Hall. 1974. Optimal foraging and the size selection of prey by bluegill sunfish (Lepomis macrochirus). Ecology 55:1042-1052.

Werner, R. G. 1980. Freshwater fishes of New York state: a field guide. Syracuse Univ. Press, Syracuse.

Whitaker, J. O., Jr., and D. C. Wallace. 1975. Fishes of Vigo County, Indiana. Indiana Acad. Sci. 84:449-499.

White, C. P. 1982. Endangered and threatened wildlife of the Chesapeake Bay Region: Delaware, Maryland, & Virginia. Tidewater Publ., Centreville, Maryland.

Wiley, E. O. 1977. The phylogeny and systematics of the Fundulus nottii species group (Teleostei:Cyprinodontidae). Occ. Pap. Mus. Nat. Hist. Univ. Kansas 66:1-31.

_____. 1981. Phylogenetics: The theory and practice of phylogenetic systematics. John Wiley & Sons, Inc., New York.

Wiley, M. L. and B. B. Collette. 1970. Breeding tubercles and contact organs in fishes: Their occurrence, structure, and significance. Bull. Am. Mus. Nat. Hist. 143:145-216.

Williams, J. D. 1975. Systematics of the percid fishes of the subgenus Ammocrypta, genus Ammocrypta, with descriptions of two new species. Bull. Alabama Mus. Nat. Hist. No. 1. 56 p.

Woolman, A. J. 1892. Report of an examination of the rivers of Kentucky, with lists of the fishes obtained. Bull. U. S. Fish Comm. 10:249-288.

Yanchosek, J. J. and M. J. Hines. 1979. Ouachita River Drainage Areas. U. S. Geol. Surv. Open File Rept. 80-334 compiled in cooperation with the Arkansas Highway Trans. Dept., Little Rock.

Zorach, T. 1972. Systematics of the percid fishes, Etheostoma camurum and E. chlorobranchium new species, with a discussion of the subgenus Nothonotus. Copeia 1972:427-447.

VITA

John Lowrey Harris, the son of John Roland and Elizabeth Ann Webster Harris, was born in Mansfield, Louisiana on November 23, 1953. He attended Mansfield Elementary School and was graduated from Mansfield High School in May 1971. The following September he entered Southern State College, Magnolia, Arkansas on an athletic scholarship and in May 1975 received a Bachelor of Science degree in Biology. In September 1975, he accepted a teaching assistantship at Northeast Louisiana University, Monroe and began work toward a Master of Science in biology which was conferred in August 1977.

In September 1977, he entered The Graduate School of The University of Tennessee and began work toward a Ph.D. degree while serving as a graduate teaching assistant in the Department of Zoology. He took full time employment with the Environmental Division of the Arkansas Highway and Transportation Department in October 1980 while continuing to work toward the Ph.D. degree. He received the Doctor of Philosophy, with a major in zoology in June 1986.

The author is a member of the American Society of Ichthyologists and Herpetologists, the American Malacological Union, the Society of Systematic Zoology, the Southeastern Fishes Council, and the Arkansas Academy of Science. Mr. Harris will continue to be employed by the Arkansas Highway and Transportation Department following graduation.