

BULLETIN

OF THE

FLORIDA STATE MUSEUM

BIOLOGICAL SCIENCES

Volume 8

Number 2

THE AMERICAN CYPRINID FISHES OF THE
SUBGENUS LUXILUS (GENUS NOTROPIS)

Carter R. Gilbert



UNIVERSITY OF FLORIDA

Gainesville

1964

Numbers of the BULLETIN OF THE FLORIDA STATE MUSEUM are published at irregular intervals. Volumes contain about 300 pages and are not necessarily completed in any one calendar year.

OLIVER L. AUSTIN, JR., *Editor*

WALTER AUFFENBERG, *Managing Editor*

Consultant for this issue:

Donn Eric Rosen

Communications concerning purchase or exchange of the publication and all manuscripts should be addressed to the Managing Editor of the Bulletin, Florida State Museum, Seagle Building, Gainesville, Florida.

Published 2 June 1964

Price for this issue \$1.45

THE AMERICAN CYPRINID FISHES OF THE SUBGENUS *LUXILUS* (GENUS *NOTROPIS*)

CARTER R. GILBERT¹

SYNOPSIS: The cyprinid fishes of the subgenus *Luxilus* (genus *Notropis*) comprise three well-defined species groups of eight species and one subspecies. They occupy clear, small to medium-sized streams over most of temperate North America east of the Rockies, being absent only from areas southwest of the Red River drainage in Texas, the upper Missouri basin, the southern Piedmont plain, and peninsular Florida. The present study defines the subgenus, reviews its nomenclatural history, explains its patterns of variation, describes the various forms and their distributions, and discusses their probable zoogeographic and phylogenetic histories.

TABLE OF CONTENTS

Introduction	96	<i>Notropis zonistius</i>	126
Acknowledgements	97	<i>Notropis zonatus</i>	129
Materials	98	<i>Notropis pilsbryi</i>	133
Methods of Counting and		<i>Notropis cerasinus</i>	136
Measuring	99	<i>Notropis cornutus</i>	140
Hybridization	101	<i>Notropis albeolus</i>	151
Zoogeography and Phylogeny	104	<i>Notropis chrysocephalus</i>	157
Generic and Subgeneric		<i>Notropis chrysocephalus</i>	
Nomenclatural History	110	<i>chrysocephalus</i>	158
Subgeneric Diagnosis and		<i>Notropis chrysocephalus:</i>	
Specific Relationships	114	<i>chrysocephalus</i> × <i>isolepis</i>	166
Key to Species and Subspecies		<i>Notropis chrysocephalus</i>	
of the Subgenus <i>Luxilus</i>	117	<i>isolepis</i>	167
Species and Subspecies Accounts	122	Tables	173
<i>Notropis coccogenis</i>	122	References Cited	185

¹ This paper is a revision of a dissertation submitted to the University of Michigan in 1960 in partial fulfillment of the Ph.D. degree. The work was carried out while the author served as a teaching fellow in the Department of Zoology and as a research assistant in the Division of Fishes of the Museum of Zoology. Now at the University of Florida, he is Assistant Professor of Biological Sciences and Assistant Curator of Natural Sciences in the Florida State Museum. Manuscript received 5 July 1963.—Ed.

INTRODUCTION

Of the many species of cyprinid fishes inhabiting eastern North America, few are better known to the layman than the Common Shiner, *Notropis cornutus*. This is due to its abundance, wide distribution, large size, and striking coloration. Nevertheless the systematic relationships of the forms referred to this and to closely related species have long perplexed students of North American freshwater fishes.

The group that includes *Notropis cornutus* and its most closely related forms (here referred to as the subgenus *Luxilus*) is in a relatively early stage of evolution. Within the *Luxilus* complex may be found all stages of speciation, and in at least two cases considerable subjective judgment is needed to determine whether forms are incipient or actual species. The *Luxilus* group thus furnishes an excellent opportunity for observing and understanding the basic processes of change which occur during evolutionary history.

The members of the subgenus *Luxilus* have had an unstable nomenclatural history. Their recent evolution and consequent close inter-relationships have made the arrangement of species difficult. D. S. Jordan, who was mainly responsible for previous attempts to classify these groups, moved species back and forth among genera and subgenera, usually with little apparent reason.

Although morphological criteria have been the primary bases for the resolution of various taxonomic problems encountered in the present study, zoögeography, ecology, and clinal variation also have been taken into account. This has resulted in the recognition of 8 species and 1 subspecies instead of 6 species and 4 subspecies as in the currently accepted classification. Both arrangements are listed below.

Current classification	Proposed classification
<i>coccogenis</i> group	
<i>Notropis coccogenis</i> (Cope)	<i>Notropis coccogenis</i> (Cope)
<i>Notropis zonistius</i> (Jordan)	<i>Notropis. zonistius</i> (Jordan)
<i>zonatus</i> group	
<i>Notropis zonatus zonatus</i> (Agassiz)	<i>Notropis zonatus</i> (Agassiz)
<i>Notropis zonatus pilsbryi</i> Fowler	<i>Notropis pilsbryi</i> Fowler
<i>cornutus</i> group	
<i>Notropis cerasinus</i> (Cope)	<i>Notropis cerasinus</i> (Cope)
<i>Notropis cornutus cornutus</i> (Mitchill)	<i>Notropis cornutus</i> (Mitchill)

Current classification

Proposed classification

cornutus group (continued)*Notropis cornutus frontalis* (Agassiz)*Notropis albeolus* Jordan*Notropis cornutus chrysocephalus*
(Rafinesque)*Notropis cornutus isolepis*
Hubbs and Brown*Notropis albeolus* Jordan*Notropis chrysocephalus chrysoceph-*
alus (Rafinesque)*Notropis chrysocephalus isolepis*
Hubbs and Brown

The subgenus *Luxilus* is one of the widest ranging of the minor cyprinid groups in North America. Its species occur in fresh waters from the Gulf Coast north to 52° N. latitude in Manitoba and from Nova Scotia to the eastern slope of the Rocky Mountains. The only major area east of the Mississippi River from which it is absent is the southeastern Atlantic coastal plain from central North Carolina southward through peninsular Florida. To the southwest it does not occur beyond the Red River drainage.

All species ordinarily inhabit rather clear, small or medium-sized streams with gravel to rocky bottoms and moderate to swift gradients. Although some populations may be found living in extremely turbid waters, this is abnormal and usually temporary.

Hybridization between species of the *Luxilus* complex is frequent and occurs in many combinations both within the subgenus and with species of other subgenera and genera. These are reviewed, and the possible causes and effects of hybridization are discussed.

ACKNOWLEDGMENTS

This study was made possible by the aid and cooperation of many people. I am especially grateful to Dr. Reeve M. Bailey for his advice, criticism, and professional guidance throughout the course of the study; to my wife, Nancy, for her constant encouragement and invaluable help in the preparation and completion of this thesis; to Mrs. Elizabeth M. Anthony who prepared the drawings as well as the letters and margins for the distribution maps; to Dr. Ernest A. Lachner for much helpful advice regarding the preparation of this manuscript; and to Dr. Clarence L. Smith for field assistance and for most of the photographs included in this paper. I am indebted to the following persons for the use of specimens and equipment under their care: Dr. Edward C. Raney, Cornell University; Drs. Leonard P. Schultz, Ernest A. Lachner and William Ralph Taylor, United States National Museum; Dr. James E. Böhlke, Academy of Natural Sci-

ences of Philadelphia; Dr. Milton B. Trautman, Ohio State Archeological Museum; Dr. Royal D. Suttkus, Tulane University; Dr. Philip W. Smith, Illinois Natural History Survey; and Dr. Shelby D. Gerking, Indiana University. Sincere thanks are extended to Mrs. H. Williams Diamond, Jr., who helped type the manuscript; to Dr. Edward J. Crossman, Royal Ontario Museum of Zoology, for supplying certain locality records for Canada; to Dr. George A. Moore, Oklahoma State University, for several Oklahoma records; to Dr. Clark Hubbs, University of Texas, for all Texas records; to Dr. Frank B. Cross, University of Kansas, for several Kansas records; and to Dr. Ralph W. Yerger, Florida State University, for several Florida records. Appreciation is extended to Dr. Robert R. Miller, University of Michigan, for helpful advice and for the use of an unpublished list of hybrid fish combinations; to Dr. Karl F. Lagler, University of Michigan, for the use of equipment under his care; to Dr. Louella Cable, for the use of facilities at the U. S. government fish hatchery, Northville, Michigan; to Dr. Robert D. Ross, Virginia Polytechnic Institute, for supplying color notes for *Notropis albeolus*; and to Dr. William Ralph Taylor, for advice regarding the study. Finally, I am grateful to my fellow graduate students, Thomas L. Poulson, Teruya Uyeno, R. Jack Schultz and Howard F. Huddle for their help in the field and laboratory.

MATERIALS

The collections examined were selected to include samples from all parts of the ranges of the various forms, with special emphasis being placed on series from critical areas. Specimens have been examined or recorded from the following museum collections: Academy of Natural Sciences of Philadelphia (ANSP); Chicago Natural History Museum (CNHM); Cornell University (CU); Illinois Natural History Survey (INHS); Indiana University (IU); Kansas University (KU); Museum of Comparative Zoology, Harvard University (MCZ); Nova Scotia Provincial Museum (NSPM); Ohio State University (OSU); Royal Ontario Museum (ROM); Stanford University (SU); Texas Natural History Collection, University of Texas (TNHC); Tulane University (TU); University of Florida (UF); University of Michigan, Museum of Zoology (UMMZ); United States National Museum (USNM).

Locality records of specimens examined may be found in the original dissertation.

METHODS OF COUNTING AND MEASURING

To reduce sample bias usually no more than 10 specimens were counted from a single series, except in lots from certain critical or poorly collected areas, where larger numbers were used. As certain relative body proportions change with increase in size, body measurements were made only on specimens falling within certain size ranges in each species. For the larger forms (*N. cornutus*, *N. albeolus*, *N. chrysocephalus*, and *N. coccogenis*) specimens measuring approximately 60 to 80 mm in standard length were used; for the smaller species (*N. zonistius*, *N. cerasinus*, *N. zonatus*, and *N. pilsbryi*) the limits were 55 and 75 mm.

Counts and measurements were taken as outlined by Hubbs and Lagler (1947: 8-15) except that the mouth gape was determined by the transverse distance between the posterior angles of the mouth, instead of the greatest transverse distance across it. To eliminate difficulties in counting fine-scaled species, a new method was devised for taking scale counts on the anterior dorsal part of the body. The usual predorsal scale count on the dorsal midline directly in front of the dorsal fin is entirely satisfactory for coarse-scaled species, but overlaps and irregularities in fine-scaled forms make accurate determinations difficult. The scale rows along the side of the body are more regular than the predorsal scales, and provide a more accurate and effective assessment of differences in scale size among populations.

Anterior dorsal-lateral scale counts were made along the longitudinal row of scales lying approximately three-fourths of the distance from the lateral line to the mid-dorsal line. This varied from the third to the sixth row above the lateral line, depending on the size of the scales. The scales were counted from a point directly under the origin of the dorsal fin forward to their termination. The sum of this count and the body circumferential scale count is of great value in interpreting differences between the various species, particularly those in the *N. cornutus* species group.

Scale counts for both the circumferential and the caudal peduncle series are usually expressed as total numbers, but may also be written to indicate the relative disposition of scales above and below the lateral line. Thus a circumferential count written as 14-2-10 signifies 14 scales between and above and 10 scales between and below the lateral lines on each side of the body.

Proportional measurements are expressed in thousandths of the standard length (shortened hereafter to SL). These measurements were tabulated initially in the form of frequency distributions by major drainage areas for each member of the subgenus except *N. cerasinus*. When inspection revealed no consistent geographical variation in morphology except in *N. albeolus*, the proportional measurements for all the others were combined in the final tabulations.

Certain meristic counts for *N. cornutus*, *N. albeolus*, *N. c. chrysocephalus*, and *N. c. isolepis* were separated in the tables by major drainage areas. This was done because the wide ranges of these forms increases the possibilities for clinal or genetic variation. The better to show the overall differences between *N. cornutus* living east and west of the Appalachians, all populations in each of these two areas were combined, with three exceptions: Those in the upper Susquehanna and the St. Lawrence river systems are on or near the drainage divide between the Atlantic Ocean and the Mississippi; specimens from the streams in Maine and the Maritime provinces of Canada show rather unusual meristic characters. Counts from all areas were combined in the overall comparison of the *Luxilus* group.

Vertebral counts were determined from X-ray photographs. The procedures follow the methods discussed by Bailey and Gosline (1955). The Weberian apparatus, regarded as containing four fused vertebra, and the hypural plate were included in the counts. All photographs were made with type M film and a "hard ray" machine (Miller, 1957).

The angle of the mouth to the top of the head was determined with the aid of a special ocular as described by Smith (1956: 250). With the pointer set at a 0° reading, the fish is placed on the stage so that one crosshair (arbitrarily called the horizontal hair) in the ocular lies directly over the length of the lateral opening of the mouth, with the intersection of the crosshairs slightly anterior to the tip of the snout. The ocular is then rotated clockwise until the vertical crosshair touches the head at the posterior edge of the occiput. The angle is then read in degrees to the nearest half degree.

Inspection revealed that usually about 90 percent of the counts showed relatively little deviation from the mean of a normal distribution, while the extreme values dropped away rather sharply. As it is manifestly desirable to show this condition in a species account, the method shown in the following hypothetical examples was adopted to express it: A frequency distribution expressed as (22) 25 to 29 (33) indicates that 90 percent of the counts fall between 25 and 29, with

the extremes 22 and 33; a distribution expressed as (8) 9 or 10, usually 9, shows that less than 10 percent of the counts number 8 and, while a count of 10 is not particularly rare (more than 10 percent) 9 is a much more common value.

To determine possible sexual variation, approximately equal numbers of males and females were measured for the various morphometric characters. In most cases the means and range of variation differed so little and the overlap was so great that measurements were lumped in the final tabulations. Tables and lists of locality records in the original dissertation not regarded as essential have been omitted. Only new names or new combinations of names have been retained in the synonymy.

HYBRIDIZATION

Numerous hybrid combinations involving members of the *Luxilus* complex are known. Three of these, *N. c. chrysocephalus* \times *N. cornutus*, *N. c. chrysocephalus* \times *N. rubellus*, and *N. cornutus* \times *N. rubellus*, are the most common cyprinid hybrids in eastern North America. The *cornutus* \times *rubellus* hybrid was described by Jordan (1889a: 354) as a new species, *Notropis macdonaldi*, and the *chrysocephalus* \times *rubellus* cross was erroneously recorded by Forbes (1909: 386) and by Forbes and Richardson (1920: 149) as *Notropis pilsbryi*.

A number of papers have appeared dealing entirely or in part with various aspects of hybridization in certain species of *Luxilus*. Among the more comprehensive and important of these are Raney's (1940b) account of the comparative spawning behavior of *N. cornutus* and *N. rubellus* in New York, and Miller's (1962; 1963) papers dealing with the comparative morphology, sexual development, and hermaphroditism of *N. cornutus* \times *N. rubellus*. In my own (1961b) treatment of the relationships of *N. cornutus* and *N. c. chrysocephalus* I list the arguments for and against specific differentiation of *cornutus* and *chrysocephalus*, and favor their recognition as species, although the two forms often act as subspecies. This evidence is as follows:

1. Intergrading populations of subspecies normally show a perfect blending of morphological characters. Although this is approached in some associations containing both *cornutus* and *chrysocephalus*, in other populations the two forms remain morphologically distinct, with few apparent intermediates. In addition many populations within the zone of "intergradation" contain only one form.

This mosaic pattern is not concordant with the normal expectation for subspecies.

2. Competition is, in effect, nonexistent between subspecies, and where one has moved into a region formerly occupied solely by another, intergrading populations occur. The presence of isolated relict populations of *cornutus* surrounded by populations of *chrysocephalus* far to the south of the principal range, together with the observed gradual replacement of *cornutus* by *chrysocephalus* in parts of Ohio, indicate that competition exists where these fishes occur together.

3. *Chrysocephalus* apparently has disappeared from several mixed populations in southern Michigan following construction of dams near the mouths of the creeks where it formerly occurred. If *cornutus* and *chrysocephalus* were only subspecifically distinct, the phenotypic character of the populations would be expected to remain more or less constant.

4. The experimentally-verified differences in temperature tolerance between *cornutus* and *chrysocephalus* in the northern limits of their respective ranges are greater than one might normally expect in subspecies. The apparent preference of *cornutus* for headwaters and of *chrysocephalus* for the lower reaches of streams furnishes further evidence of this difference.

5. The distributional patterns of these forms suggest a long separation of *cornutus* and *chrysocephalus*, ample to permit evolution to the species level, and possibly dating back to late Pliocene.

Raney's paper includes a discussion of the morphology, fertility, hybrid vigor, and sex ratio of the *cornutus* \times *rubellus* hybrids. He decided, as did Hubbs and Brown (1929: 36-37), that hybridization between these species is accidental, and usually results from simultaneous spawning over the nests of other species, such as *Hybopsis micropogon*, *Semotilus atromaculatus*, and *Exoglossum maxillingua*. In the absence of such nests *rubellus* and *cornutus* spawn in different parts of the same riffle, *rubellus* in mid-water near the head, and *cornutus* on the bottom toward the base. Milt from *rubellus* males is washed downstream by the current, where it unites with eggs of *cornutus*. The latter observations are similar to those of Moore and Paden (1950: 92) for *Notropis pilsbryi* and *Dionda nubila*. Hybrids of this combination apparently arise as a result of the simultaneous

spawning of *Notropis pilsbryi* in riffles and *Dionda nubila* in pools at the bases.

The following is a list of the known hybrids involving members of the subgenus *Luxilus*. Some have been reported in the literature and are so indicated; those which have not yet appeared in the published record are indicated by catalog numbers only. I have made no attempt to verify the accuracy of all these identifications, nor have I included all literature references. Current nomenclature is used in all cases.

- Notropis albeolus* × *Notropis rubellus* (UMMZ 174754)
Notropis cerasinus × *Chrosomus oreas* (Raney and Lachner, 1946: 226)
Notropis chrysocephalus chrysocephalus × *Campostoma anomalum* (Trautman, 1957: 114)
Notropis chrysocephalus chrysocephalus × *Hybognathus nuchalis* (Luce, 1933: 116; O'Donnell, 1935: 482)
Notropis chrysocephalus chrysocephalus × *Hybopsis biguttata* (Luce, 1933: 115; O'Donnell, 1935: 482)
Notropis chrysocephalus chrysocephalus × *Hybopsis micropogon* (Trautman, 1957: 114)
Notropis chrysocephalus chrysocephalus × *Notropis chrosomus* (UMMZ 174833, UMMZ 175614)
Notropis chrysocephalus chrysocephalus × *Notropis cornutus* (Gilbert, 1961b: 181-192)
Notropis chrysocephalus chrysocephalus × *Notropis leuciodus* (UMMZ 175194)
Notropis chrysocephalus chrysocephalus × *Notropis rubellus* (Forbes, 1909: 386 [as *N. pilsbryi*]; Forbes and Richardson, 1920: 149 [as *N. pilsbryi*]; Hubbs, 1955: 10; Hubbs and Brown, 1929: 35-36; Hubbs and Moore, 1940: 96 [identification of *N. pilsbryi*]; Murray, 1938: 84; O'Donnell, 1935: 482; Trautman, 1948: 171 [in part]; Trautman, 1957: 114-115 [in part])
Notropis cornutus × *Campostoma anomalum* (Trautman, 1957: 114)
Notropis cornutus × *Chrosomus eos* (UMMZ 78827)
Notropis cornutus × *Chrosomus oreas* (Raney, 1950: 167)
Notropis cornutus × *Clinostomus elongatus* (Greeley, 1938: 51; Greene, 1935: 88-89; Koster, 1939: 207; Raney, 1940a: 7)
Notropis cornutus × *Clinostomus funduloides* (Raney, 1950: 167)
Notropis cornutus × *Hybopsis biguttata* (Taylor, 1954: 43)
Notropis cornutus × *Hybopsis micropogon* (Greeley, 1938: 51; Raney, 1940a: 7; Raney, 1940c: 135; Trautman, 1957: 114)
Notropis cornutus × *Notropis photogenis* (Greeley, 1938: 51)
Notropis cornutus × *Notropis rubellus* (Goldsborough and Clark, 1908: 35 [as *N. macdonaldi*]; Greeley, 1938: 51; Hubbs, 1955: 10; Hubbs and Brown, 1929: 35-36; Hubbs and Moore, 1940: 96 [identification of *N. macdonaldi*]; Jordan, 1889a: 354 [original description of *N. macdonaldi*]; Lachner, 1952: 436; Raney, 1940a: 7; Raney, 1940b: 361-367; Raney, 1940c: 135; Raney,

- 1950: 165, 167; Taylor, 1954: 43; Trautman, 1948: 171 [in part]; Trautman, 1957: 114-115 [in part])
- Notropis cornutus* × *Semotilus atromaculatus* (Bailey and Oliver, 1939: 172; Greeley, 1938: 51-52; Koster, 1939: 207; Raney, 1940a: 7; Raney, 1940c: 135; Simon, 1946: 91; Taylor, 1954: 42)
- Notropis cornutus* × *Semotilus corporalis* (Bailey, 1938: 150-151; Greeley, 1938: 52; Raney, 1940a: 7)
- Notropis pilsbryi* × *Dionda nubilus* (Moore and Paden, 1950: 92)
- Notropis pilsbryi* × *Notropis rubellus* (Cross, 1954: 313; Moore and Paden, 1950: 92)

ZOOGEOGRAPHY AND PHYLOGENY

The zoogeographic and phylogenetic history of a group of animals, often the subject of speculation, is usually reconstructed only with difficulty. Because the genus *Notropis* has evolved so recently, most of the forms linking the included natural groups are still extant and allow a relatively clear interpretation of the phylogenetic relationships. On the other hand, the high degree of speciation in the genus makes the zoogeographical relationships extremely complex.

The subgenus *Luxilus* probably evolved in the Mississippi basin, perhaps during the early to middle Pliocene. This hypothesis is based first on the present geographical distribution of the *Luxilus* complex and, second, on the assumption of a Miocene invasion of North America by the family Cyprinidae (Romer, 1945: 583).

The primary division within the subgenus most likely involved the precursor of *Notropis coccogenis* and *Notropis zonistius*. Judging from its present distribution, the *coccogenis* group probably evolved in the Tennessee River system. The marked differentiation of *coccogenis* and *zonistius* from the other species of *Luxilus* indicates that isolation from stocks in the Mississippi Valley lasted for a considerable time. The reasons for isolation, however, are unknown at present. Later, presumably still during the Pliocene, a segment of this stock reached the Chattahoochee River basin, there evolving into *N. zonistius*, while the stock remaining in the Tennessee system gave rise to *N. coccogenis*. Presumably this transfer was effected through a localized stream capture rather than by direct connection of the Chattahoochee with the Tennessee. No evidence indicates such a connection, and these river systems show little close faunal similarity.

Also during the Pliocene another segment of the Mississippi Valley stock presumably became isolated in the Ozark region. This eventually gave rise to the *zonatus* group, which includes *Notropis*

zonatus and *Notropis pilsbryi*. The cause of this isolation also is unknown, although it probably is related to the fact that the Ozarks contain clear, cool, rather swift-flowing streams. Unlike some other Ozarkian endemics, *Notropis zonatus* and *Notropis pilsbryi* have no immediate relatives living in upland areas east of the Mississippi River. Consequently these species are believed to be autochthonous for the Ozark region.

The distributions of *N. zonatus* and *N. pilsbryi* suggest a long separation between the Missouri and White river systems that has prevented gene interchange. This interpretation is supported by the parallel distribution patterns of other species pairs, such as *Etheostoma euzonum*-*E. tetrazonum*. The presence of *N. zonatus* in the Black River system strongly suggests that this river at one time was tributary to the Missouri, and that a reversal of flow has occurred rather recently, long after *zonatus* and *pilsbryi* separated. Records of *zonatus* from the headwaters of the St. Francis and Little rivers of southeastern Missouri are best explained on the basis of stream captures, although the possibility exists that these streams also once flowed to the north. Probably the most perplexing aspect of the zoögeography of these species has to do with the presence of *pilsbryi* in the Arkansas and Red river drainages. The distribution of several species (*Notropis spilopterus* and *Lepomis megalotis*) indicates a definite faunal relationship between the Illinois and Neosho rivers (tributaries of the Arkansas) and the Ozarkian tributaries of the Missouri River. The absence of *Notropis zonatus* from the Illinois and Neosho is an apparent contradiction, inexplicable save for the possibility that if *zonatus* did invade these river systems it could not compete with the well-established population of *pilsbryi*. Hubbs and Moore (1940: 94) have suggested the isolated populations of *pilsbryi* in the Red River system may have been introduced. It is equally possible that they represent relict populations, especially as they have been recorded from three separate localities in this drainage.

Prior to the Pleistocene epoch the drainage pattern of the Ohio Valley differed considerably from that of today. The Ohio River extended little east of Cincinnati, and what is now the upper Ohio flowed northward, probably to a river in the area of the present Lake Erie basin. Larger than either of these streams was the Teays River, a major prolongation of the Kanawha River. The Teays flowed northwestward across Ohio, Indiana, and apparently Illinois, and thence southward to the present Mississippi Valley. It occupied a wide, deep trench comparable in size with that of the lower Ohio River today (Flint, 1947: 166).

A number of species that are completely or largely restricted to the Roanoke River system, which drains into the Atlantic Ocean, have affinities not with other Atlantic coastal forms, but with species in the Ohio Valley. The headwaters of the Kanawha River are narrowly separated from those of the Roanoke over a fairly extensive area in western Virginia. Much of the present Roanoke fauna, including *Notropis cerasinus* and, possibly, *N. albeolus*, almost certainly reached this drainage by headwater transfer from the old Teays system during preglacial time (Wright, 1934: 65), though whether the invasions by these species occurred simultaneously cannot be determined.

Evolution of the common *N. cornutus*-*N. chrysocephalus* stock probably took place in the Mississippi Valley. This hypothesis is supported by the distribution pattern of these two species, which centers in this region. Some of the common *cornutus*-*chrysocephalus* stock is believed to have become separated from the main population in late Pliocene in one of the following areas: the Atlantic coast, the upper Mississippi Valley, the Great Plains, or the Great Lakes. The relative distributions of the two species suggest this segment evolved into *N. cornutus*, while that part of the population to the south became *N. chrysocephalus*.

There is little evidence that *N. cornutus* evolved in either the Mississippi Valley or on the Atlantic coast, except for its presence there today. Geological evidence (Flint, 1947: 163-167; and 1957: 168-170) indicates that before the Pleistocene the middle and upper parts of the Missouri did not flow into the Mississippi River as they do today, but instead "flowed north into the Souris-Assiniboine system, perhaps discharging via the Lake Winnipeg depression, the Nelson, and the Hudson Bay region. The advent of the ice sheet flowing from the northeast blocked all this drainage and detoured the Missouri along the ice margin." Contact was then established with the Kansas River below Kansas City, thus effecting a new outlet for the upper Missouri River. The upper Missouri therefore provided an isolated region where evolution of *Notropis cornutus* could have occurred, but its apparent absence from the upper Missouri drainage today argues strongly against this area as a place of origin.

Radforth (1944: 10-11) describes and pictures a hypothetical course for the Laurentian River, which drained the present Great Lakes region (with the possible exception of Lake Superior) in pre-Pleistocene time. Possibly a segment of the *cornutus*-*chrysocephalus* ancestral stock entered this river system during late Pliocene and there evolved into *N. cornutus*. This Laurentian center of origin for *N. cornutus*

appears to be the best of the several possibilities. In addition to other factors cited previously, spread to such distant areas as the Atlantic coast and the Rocky Mountains could have been accomplished most readily from a geographically intermediate area.

Following its initial invasion of the Atlantic coast the species spread southward, possibly to the Roanoke River. The population may then have become isolated from the remaining *cornutus* stock farther north, resulting in the eventual evolution of a new form, *Notropis albeolus*. The presence of other closely related species and subspecies pairs in the James and Roanoke systems, such as *Etheostoma longimanum*-*Etheostoma podostemone*, *Moxostoma rathbunae*-*Moxostoma hamiltoni*, and *Notropis procne* *procne*-*Notropis procne longiceps*, tends to confirm this idea. It is equally plausible, as indicated earlier, that *albeolus* reached the Atlantic coast via the Teays River. This is substantiated by the similarity in distribution pattern of this form with other species, such as *Notropis ardens* and *N. matinus*, which are restricted to the Roanoke and neighboring systems on the east coast, but whose affinities are with the Ohio Valley fauna. The differentiation of *albeolus* into two rather distinct forms, one occurring in the Roanoke and New drainages, the other in the Neuse, Tar, and Cape Fear systems, suggests that *albeolus* may even have evolved in some way from a union of stocks coming both from the Atlantic coast and the Ohio Valley.

The first glacial advance completely inundated the Laurentian River and thus split the range of *cornutus* into two major segments, one along the Atlantic coast, the other west of the glacier. Whether *cornutus* reinvaded the glaciated area during all the interglacial periods, which is a possibility, cannot be determined. Some remixing of segments of the Atlantic coastal and western populations of *cornutus* probably did occur during the Pleistocene, for no taxonomic separation can be made between the eastern and western populations of *cornutus* at the subspecific level. If these populations did not come into contact throughout the entire Pleistocene, the long period of isolation should have produced more pronounced morphological differences. Furthermore *cornutus* is so widespread and adaptable that it would be among the most likely species to expand into newly available territory.

Dispersal of *N. chrysocephalus* to various parts of the Mississippi Valley evidently occurred throughout the Pleistocene. The Mississippi River was then slightly cooler, less turbid, and less sluggish, and probably did not pose the barrier to small-stream fishes that it

does today. Certain parts of the Mississippi could have once acted as "filter bridges" for their movement.

Lowered ocean levels during the glacial periods permitted many freshwater streams to join before reaching salt water, for example those draining into the Gulf of Mexico from the Alabama system west to the Mississippi. During one of the glacial advances some *chrysocephalus* stock in the Mississippi Valley apparently moved through the lower reaches of the Mississippi into some of the Gulf coastal streams. When, with the retreat of the glacier, the sea level rose and restored the Mississippi to its former proportions, the *chrysocephalus* stock isolated in the coastal streams evolved into a new form, *isolepis*, here regarded as a well-defined subspecies of *chrysocephalus*. One can only speculate when the original invasion of the coastal streams by *chrysocephalus* occurred, but the estimated time necessary for a new form of this complex to evolve suggests it was probably during one of the first two glacial periods. Much later, after the morphological separation of *chrysocephalus* and *isolepis* was complete, the two forms came together again when the Alabama-Coosa system captured certain tributaries of the Tennessee. Van der Schalie (1945: 357-358) discusses the geological and malacological evidence showing the relationships of these two systems.

Notropis cornutus either survived in the upper Ohio Valley throughout the Pleistocene or reached there during one of the interglacial periods. Absence of this species from the upper Kanawha River system suggests a fairly recent invasion, either from headwater capture or through overflow streams from ponded lakes formed by the advancing Wisconsin glacier. The further advance of the Wisconsin ice sheet (Flint, 1947: 283) isolated the Ohio Valley populations of *cornutus* from both the Atlantic coast and the western populations.

As the Wisconsin ice sheet retreated, meltwater lakes formed at the glacial margin. Because the glacier prevented northward flow, the rising lakes began to cut outlets to the south. One of the largest, Lake Agassiz, covered an extensive area and drained into the Mississippi Valley by means of the Warren River outlet (Radforth, 1944: 13), near the present southern extremity of the Red River of the North. As the glacier retreated farther, a channel finally opened to the northeast, the origin of the Nelson River. This stream was situated at a lower elevation than the older Warren River, and thus formed a new outlet for Lake Agassiz, which consequently decreased

rapidly in area and was superseded by Lake of the Woods, Lake Winnipeg, and many lesser lakes.

Soon after formation of Lake Agassiz, there appeared farther to the east glacial lakes Duluth, Chicago, and Maumee, the precursors, respectively, of lakes Superior, Michigan, and Erie. These bodies, also plugged at their northern extremities, drained into the Mississippi Valley by way of the St. Croix outlet (Lake Duluth), the Fox and Chicago outlets (Lake Chicago) and the Fort Wayne outlet (Lake Maumee). With further glacial retreat changes continued until the present-day Great Lakes were eventually formed.

N. cornutus probably moved northward via the Warren River outlet into Lake Agassiz, and reinvaded the newly-formed Great Lakes from the south through glacial channels such as the St. Croix and Fox rivers (Greene, 1935: 15) and from the north via glacial Lake Agassiz through the Ft. William outlet in western Ontario (Underhill, 1957: 31). *Notropis cornutus* apparently was able to follow the retreating glacier more closely than many other species and, as a result, was again able to invade the east coast, this time via the Horseheads outlet (in the Lake Ontario drainage) into the Upper Susquehanna system (Bailey, 1945: 125-126). There it again mixed with the population of *cornutus* which had remained on the Atlantic coast presumably throughout the Pleistocene.

At this time ocean levels still were much lower than at present. The shallow bottom of Chesapeake Bay was above water, and all streams from the Susquehanna south to and including the James were interconnected. Although influence of the *cornutus* stock that crossed onto the Atlantic coast may have extended into the Chesapeake Bay area, the bulk of the western gene pool probably remained near the point of original entry. Proof that the preceding sequence of events occurred depends in large part on the usual absence of pigmentation on the chin and gular region in *cornutus* from the upper Susquehanna. This character, while not consistent enough to be taxonomically name-worthy, nevertheless is of value in the determination of zoögeographical relationships among populations. Pigment usually is lacking west of the Alleghenies, but not in coastal streams.

N. cornutus may possibly have utilized a temporary outlet between the forerunner of Lake Ontario and the Mohawk River. Apparently some species did enter the Mohawk in this way, but the history is blurred by the construction of the Mohawk-Erie canal across the drainage divide in the early 1800's. *Notropis cornutus* seems to have moved a considerable distance eastward from its western glacial refu-

gium, and this stock may have given rise, at least in part, to the present population in the Canadian maritime provinces.

With the openings of the Chicago and later the Maumee outlet into glacial lakes Chicago and Maumee, *N. chrysocephalus* also reached the Great Lakes drainage, there to live sympatrically with *Notropis cornutus*, possibly for the first time since the stocks separated in the Pliocene. Apparently *chrysocephalus* did not enter the Lake Ontario drainage till well after *cornutus*. By this time the Horseheads connection was broken, which prevented *chrysocephalus* reaching the Atlantic coast via the upper Susquehanna.

The general warming of streams in North America since the retreat of the Wisconsin ice sheet, and particularly with man's activities during the past century or so, has wrought significant changes in the relative distributions of *N. cornutus* and *N. chrysocephalus* which are still continuing. In the Ohio Valley at the height of the Wisconsin advance, *cornutus* was apparently the dominant, if not the sole representative of the *Luxilus* complex above roughly the mouth of the Wabash River. As stream conditions changed *chrysocephalus* invaded this area, and the resulting competition virtually eliminated *cornutus* from the lower Ohio Valley, though isolated relict populations remain in the lower Kanawha River system in southern West Virginia and in the White River system in southern Indiana. The gradual replacement of *cornutus* by *chrysocephalus* in eastern Ohio during the past 35 years has been well documented by Trautman (1957: 357).

GENERIC AND SUBGENERIC NOMENCLATURAL HISTORY

Luxilus Rafinesque, 1820a: 47-48 (original description of genus and subgenus; type species, *Luxilus chrysocephalus* Rafinesque, by subsequent designation of Jordan and Gilbert, 1877). Girard, 1856: 202-203 (name mistakenly allied with *Notemigonus*). Jordan, 1876a: 94 (*Luxilus chrysocephalus* synonymized with *Luxilus cornutus*). Jordan, 1876b: 286-287 (*Hypsilepis* synonymized with *Luxilus*). Jordan and Copeland, 1876: 134, 153 (type species said to be *Luxilus cornutus* (Mitchill), but that species was not among those included in *Luxilus* by Rafinesque; *Hypsilepis* a synonym). Jordan, 1877: 12, 28-31 (*Luxilus chrysocephalus* a synonym of *Luxilus cornutus*; review of Rafinesque's species; type species, *Luxilus cornutus*). Jordan and Gilbert, 1877: 86 (type species, *Luxilus chrysocephalus* Rafinesque). Jordan, 1882: 852-854 (*Luxilus* divided into three subgenera: *Luxilus*, *Coccotis*, and *Alburnops*). Jordan, 1885: 814 (subgenus of *Notropis*). Jordan, 1929: 82 (*Luxilus* restored to generic status).

Hypsilepis Agassiz, 1854: 359 (original description of genus *Hypsilepis*; type species, by original designation, *Leuciscus cornutus*; name attributed to

Baird). Cope, 1864: 279 (spelling emended to *Hypsilepis*). Jordan, 1876b: 283 (*Hypsilepis* synonymized with *Luxilus*). Jordan and Copeland, 1876: 153 (*Hypsilepis* synonymized with *Luxilus*).

Plargyrus Rafinesque, 1820a: 50-51 (substitute name for *Rutilus* if included species are not in that genus; type species, by absolute tautonymy, *Rutilus plargyrus*). Kirtland, 1845: 26 (refers to species *Leuciscus plargyrus*). Storer, 1846: 158 (refers to species *Leuciscus plargyrus*). Girard, 1856: 196 (*Plargyrus* accorded generic status). Jordan, 1876a: 94 (*Rutilus plargyrus* Rafinesque wrongly synonymized with *Luxilus kentuckiensis*). Jordan, 1876b: 281 (incorrectly allied with part of present subgenus *Cyprinella*). Jordan, 1877: 28-29 (*Plargyrus* Girard [not of Rafinesque] placed in synonymy of *Luxilus*; review of Rafinesque's species).

Coccotis Jordan, 1882: 852 (proposed as a subgenus of *Luxilus*; type species, by original designation, *Luxilus coccogenis*). Jordan, Evermann and Clark, 1930: 127 (generic status).

Coccogenia Cockerell and Callaway, 1909: 190-191 (proposed as a subgenus of *Notropis* on basis of scale characters; type species by original designation, *Notropis coccogenis*).

The genus *Notropis* Rafinesque (1818) is a large and diverse group, containing numerous closely related, morphologically similar forms. At various times in the past its principal components have been regarded as distinct, though poorly-defined genera. Gilbert (1884b) was the first to propose that a number of these be combined under the name *Notropis*. Jordan (1885b) relegated these groups to subgeneric status within the broad genus *Notropis*, where they have remained ever since despite sporadic efforts (Jordan, 1929; Jordan, Evermann and Clark, 1930) to separate them.

Although some of the chief subgroups of *Notropis* are difficult to separate and the relationships of some are not yet clear, several clusters of species share morphological characters and obviously constitute natural units. The subgenus *Luxilus* Rafinesque (1820a) is one such group. The species of *Luxilus* are characterized by common diagnostic features, but the diversity of their past assignment to genera shows that ichthyologists have not always recognized their close interrelationship. Some have been moved indiscriminantly from group to group without apparent reason.

Part of the difficulty regarding the status of *Luxilus* stems from the original description (Rafinesque, 1820a: 47-48) which, as is often true of Rafinesque's accounts, is quite general and vague. Of the four species he included in this group, only one (*L. chrysocephalus*) is now assigned to *Luxilus* as presently defined.

His description of *Rutilus plargyrus* in the same paper shows this species probably is identical to *L. chrysocephalus*, despite its assignment to a different genus. The description is accompanied by the following statement: "I call this genus *Rutilus* in the supposition that *Cyprinus rutilus* may be the type of it; if it should be otherwise, it may be called *Plargyrus*."

In 1817 Mitchill described *Cyprinus cornutus* from the Hudson River drainage in New York. This species is not closely related to the genus *Cyprinus*, a fact that was soon recognized, and it was assigned to the old-world genus, *Leuciscus*. Agassiz (1854), realizing that the affinities of *cornutus* were not with *Leuciscus* either, erected a new genus, *Hypsilepis* (this name has been attributed to Baird), with *cornutus* as type species.

Plargyrus Rafinesque was employed by Girard (1856: 31-32) to include the species *cornutus*. Girard states: "Since Rafinesque's genera are to be restored, his name *Plargyrus* is to take the precedence over the genus *Hypsilepis* of more modern coining. The name of *Plargyrus* was provided for in the *Ichthyologia Ohiensis*, to replace that of *Rutilus* in the eventuality that *Cyprinus rutilus* of Europe, which was the type of the genus *Rutilus*, should prove generically distinct from *Rutilus plargyrus* and similar American species, and which is the case." Girard evidently misunderstood the true relationships of *Luxilus chrysocephalus*, for he regarded this species as a close relative of *Notemigonus crysoleucas*, a species with no close relatives among the North American Cyprinidae.

Apparently Girard was alone in his use of the name *Plargyrus*, for subsequent investigators such as Putnam (1863), Cope (1864, 1867, 1869a, 1869b, 1870, and 1871), Abbott (1870 and 1874), and Jordan (1875) continued to use *Hypsilepis* (spelling changed to *Hypsilepis* by Cope, 1864) for *cornutus* and its related forms.

Jordan (1876a: 94), in his first review of Rafinesque's *Ichthyologia Ohiensis*, concluded that both *Luxilus chrysocephalus* and *Rutilus plargyrus* of Rafinesque were synonyms of *Hypsilepis cornutus*. The genera *Luxilus* and *Rutilus* both were described prior to *Hypsilepis*, however, and as *Rutilus* contains only old-world species not closely related to *N. cornutus*, *Hypsilepis* must obviously be placed in the synonymy of *Luxilus*. He made no mention of Girard's (1856) paper which resurrects *Plargyrus* as a genus for *cornutus*.

Jordan (1882: 852) redefined the genus *Luxilus* and included in it "three well-marked subgenera": *Luxilus*, *Coccotis*, and *Alburnops*. He defined *Luxilus* as "large species, with the scales very closely imbricated, and much deeper than long; the dorsal over the ventrals

and jaws even; type *L. cornutus*." In *Coccotis* he proposed to include "rather large species, with the scales less closely imbricated, but still deeper than long; dorsal behind ventrals and lower jaw projecting; type *L. coccogenis*." The third subgenus, *Alburnops*, he described as "small species with the scales normal; the jaws equal and the dorsal somewhat behind the ventrals; type *L. blennius*."

The name *Coccotis* was not used for many years, and its existence was overlooked by Cockerell and Callaway (1909) when they erected the subgenus *Coccogenia* for the sole reception of *N. coccogenis*, based entirely on a supposed difference in the character of its scales. The name has not been used since.

Jordan and Gilbert (1883) combined all the forms now considered to belong to *Notropis* and which have 2,4-4,2 teeth into the genus *Minnilus*. As extensive variation in dental arrangement exists among closely related species of Cyprinidae (Gibbs, 1957: 186), this scheme of classification was unrealistic and resulted in the splitting of a number of natural groups.

Jordan (1884: 284) again referred *cornutus* and its related forms, including *coccogenis*, to *Luxilus*. Gilbert (1884b: 210) proposed that *Notropis* Rafinesque (1818) replace *Minnilus* as the generic name for a number of species previously referred to many separate genera. In this Jordan (1885b: 810-814) concurred and published a subgeneric classification to distinguish the various groups within *Notropis*.

This system was followed with minor changes by virtually all ichthyologists until 1929, when Jordan again split *Notropis* and elevated its numerous subgenera to full generic status. He again regarded *Luxilus* as a genus for *cornutus* and its closest relatives, but he placed *N. coccogenis*, solely on the basis of scale characters, in the genus *Hydrophlox*, an artificial group containing a number of unrelated species.

Jordan, Evermann and Clark (1930) retained *Luxilus* as a genus. They also resurrected as a genus Jordan's *Coccotis*, which had been proposed as a subgenus 48 years earlier, and placed in it the species *coccogenis*, *zonistius*, *zonatus*, *brimleyi*, and *macdonaldi*. No reasons were given for setting up this group.

Few compilers and no practicing ichthyologists have followed either Jordan's or Jordan, Evermann and Clark's classification consistently. No structural or other basis has been discovered for a meaningful division at the generic level of this young and cohesive group. The current trend is to defer judgment on the relationships between the various subgenera of *Notropis* until a thorough systematic study is made of the entire genus.

SUBGENERIC DIAGNOSIS AND SPECIFIC
RELATIONSHIPS

The subgenus *Luxilus* is characterized by the following diagnostic features: anal rays modally 9 (10 in specimens of *N. zonistius* from southern part of range); pectoral rays 14 to 17; lateral-line scales usually 39 to 41; caudal peduncle scales usually 14 to 16 (7-2-5 to 7); peritoneum black or heavily speckled with black; pharyngeal teeth 2,4-4,2; dorsal fin inserted directly above or slightly behind anterior insertion of pelvic fin; anterior lateral-line scales and adjacent scales taller than wide, notably so in some forms; dark pigmentation present on scale pockets along side of body in most species, resulting in the appearance of black crescent-shaped vertical streaks; mouth large, terminal and oblique; size relatively large; body form in most forms more or less compressed.

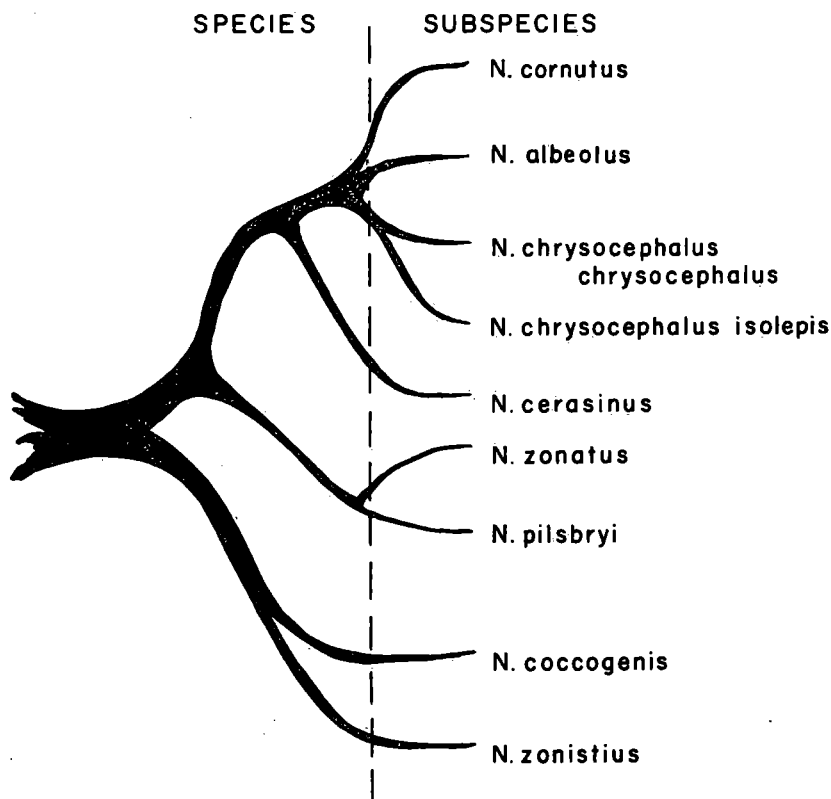


Figure 1. Hypothetical Phylogeny of the Subgenus *Luxilus*.

Three well-defined species groups are recognizable within the subgenus: The *coccogenis* group contains two species (*N. coccogenis* and *N. zonistius*), as does the *zonatus* group (*N. zonatus* and *N. pilsbryi*); the *cornutus* group consists of five forms (*N. cornutus*, *N. albeolus*, *N. chrysocephalus chrysocephalus*, *N. chrysocephalus isolepis*, and *N. cerasinus*). The first two species pairs are completely allopatric, but *cornutus* and its immediate relatives exhibit variable geographic relationships.

The *coccogenis* group is defined as follows: body strongly compressed or not; peritoneum heavily speckled with black pigment but never uniformly black; dorsal fin inserted slightly behind pelvic; scales along anterior-lateral part of body somewhat taller than wide; posterior borders of scales along side of body smooth and without scallops; nuptial tubercles weakly developed, nearly granular in some areas; tubercles present in two or three rows along lower jaw, present on tip of chin, on upper part of head concentrated mainly along side and tip of snout; tubercles either present or absent on top of head or back; tubercles present in both sexes, though poorly developed in females; crescentic vertical streaks moderately developed, not evident in some individuals; a red bar present on cheek or on margin of opercle and preopercle; caudal spot present or absent; a consistent pattern of dark pigmentation in the dorsal fin, either present or absent in the caudal fin; circumferential scales usually 13 to 16-2-10 to 12; caudal peduncle scales normally 7-2-5 or 6; no black lateral stripe on side of body.

The *zonatus* group has the following characters: body terete, not strongly compressed; peritoneum uniformly black; dorsal fin inserted slightly behind pelvic; scales along anterior-lateral part of body only slightly taller than wide; posterior edge of scales along side of body each with four or five definite scallops; nuptial tubercles weakly developed; tubercles granular, present in a single row along lower jaw, absent from tip of chin, present on top of head; tubercles present in both sexes, though weakly developed in females; crescentic vertical streaks absent from side of body; no red bar present on cheek or on margin of opercle and preopercle; caudal spot absent; no persistent pattern of dark pigmentation in either dorsal or caudal fin; circumferential scales usually 12 or 13-2-12 or 13; caudal peduncle scales normally 7-2-5 or 6; a distinct black lateral band present along side of body and encircling snout; a narrow, short secondary stripe running parallel and slightly dorsad to main lateral band.

The *cornutus* group may be diagnosed as follows: body deep and compressed, this character being quite variable among different popu-

lations of *albeolus*; peritoneum uniformly black; dorsal fin inserted directly above pelvic; scales along anterior-lateral part of body much taller than wide, becoming more pronounced with age; posterior edges of scales along side of body smooth and without scallops; nuptial tubercles well developed, the tips usually straight, sometimes curved forward; tubercles present in a single row along lower jaw, absent from tip of chin, present over entire head and along back as far as, and including, anterior part of dorsal fin; tubercles normally present only in breeding males (weakly developed in females of *N. cerasinus*); crescentic vertical streaks usually well developed along side of body, but either absent or weakly developed in *N. albeolus*; no red bar present on cheek or on margin of opercle and preopercle; caudal spot absent; no consistent pattern of dark pigmentation present in either the dorsal or caudal fins; circumferential scales usually 12 to 17-2-11 to 15; caudal peduncle scales usually 7-2-7 (7-2-5 or 6 in *N. cerasinus*); a black lateral stripe sometimes present on body of young but not consistently present throughout life.

The three species groups do not seem extremely close to one another. Their morphological differences are fairly sharp, and no connecting links exist between them. The relationships within each group, on the other hand, appear generally quite close, particularly in the *zonatus* and, to a lesser extent, the *coccogenis* groups. With one exception this holds true for the *cornutus* group also. *N. cerasinus*, although obviously much more closely related to *N. cornutus* and *N. chrysocephalus* than to any of the other species of *Luxilus*, differs notably from them in the character of the nuptial tubercles and their normal presence in females, in the slight difference in appearance of the scales, and in the number of caudal peduncle scales.

The closest relatives of *Luxilus* are those species of *Notropis* that share with it the largest number of similar or identical morphological characters. To base a relationship on only one or two shared features can be misleading. Some of the most constant diagnostic characters in the forms of *Luxilus*—pharyngeal tooth counts, anal ray counts, color of peritoneum, shape of scales along side of body, size of eye, and relative position of dorsal and anal fins—vary considerably among other closely related *Notropis* species.

Notropis ariommus seems rather close to the subgenus *Luxilus*. This species has in common with *Luxilus*: 2,4-4,2 teeth, a black peritoneum, large eye, dorsal fin inserted slightly posterior to the pelvics, and crooked parallel stripes running along the upper side of the back. In addition *ariommus* lives under ecological conditions quite similar to those preferred by all forms of *Luxilus*, particularly *N. zonatus* and

N. pilsbryi, which it resembles superficially so closely that it has been confused with *zonatus* in the literature (Evermann and Hildebrand, 1916: 444).

N. ariommus differs from typical forms of *Luxilus* in the form of the scales on the side of the body, which are normal in shape instead of high and diamond-shaped. From *N. zonatus* and *N. pilsbryi* it also differs in lacking prominent scallops on the posterior edge of the lateral scales and the black stripe along the side of the body.

While no other *Notropis* species shares so many features with *Luxilus* as *ariommus* does, *Notropis pyrrhomelas* of the headwater areas of the southern Piedmont Plain, which Gibbs (1957) placed in the subgenus *Cyprinella*, shares the following characteristics with *N. coccogenis* and *N. zonistius*: Dark pigmentation on the dorsal fin; a dark crescent-shaped blotch of pigment in the fork of the caudal; high diamond-shaped scales on the side of the body; a large eye; a prominent dark scapular bar; a peritoneum heavily flecked with black; and 10 anal rays. The last character is found in only a few populations of *zonistius*. *N. pyrrhomelas* differs from *coccogenis* and *zonistius* in having a 1,4-4,1 dental formula. The similarities suggest fairly close ties between the subgenera *Cyprinella* and *Luxilus*.

KEY TO SPECIES AND SUBSPECIES OF THE SUBGENUS *LUXILUS*

- 1a. A dark band on dorsal fin (may be orange-red in young). Peritoneum heavily speckled with dark melanophores, but not uniformly black. A red stripe usually present in life on cheek or on margin of opercle and preopercle. Nuptial tubercles in two or three rows along lower jaw extending to tip of chin. Dorso-lateral scales heavily margined with dark. Circumferential scales usually 13 to 15-2-10 to 12 2
- 2a. Black band on posterior half of dorsal fin almost parallel to distal margin. A wide black border in fork area of caudal fin. No caudal spot. Prominent red bar at margin of opercle and preopercle. Body more slender and terete. No nuptial tubercles on top of head, back, or dorsal fin. Angle between mouth and top of head usually 50 to 52°. Vertebrae 40 to 42, usually 41 *Notropis coccogenis*
Tennessee, Savannah, Catawba and New drainages; Alabama, Tennessee, Georgia, South Carolina, North Carolina, and Virginia.

- 2b. Dark diagonal band (orange-red in young individuals, black in adults) on dorsal fin, not paralleling distal margin, but beginning on lower third of anterior margin and terminating at middle of posterior margin. No black border in fork area of caudal fin. Caudal spot present, about equal to diameter of eye. Faint red bar sometimes present on cheek. Body deeper and more compressed. Nuptial tubercles present on top of head, back, and dorsal fin. Angle between mouth and top of head usually 57 to 61°. Vertebrae 38 to 40, usually 39. Anal rays usually 10 in specimen from southern part of range. *Notropis zonistius*
Chattahoochee and upper Savannah drainages of Alabama, Georgia, and Florida.
- 1b. No dark band on dorsal fin. Peritoneum uniformly black. No red stripe on cheek or on margin of opercle and preopercle. Nuptial tubercles in single row along lower jaw not extending to tip of chin. Dorso-lateral scales usually not broadly margined with dark pigment. Circumferential scales usually 12 to 17-2-11 to 15 3
- 3a. A prominent black stripe along length of body and encircling snout; a thin but distinct black stripe parallel to and slightly above this stripe on body. Body slender and terete. No black crescent-shaped bars on side of body. Insertion of dorsal fin slightly behind insertion of pelvic. Nuptial tubercles weakly developed, granular. Lateral scales with 4 or 5 prominent scallops on posterior margin 4
- 4a. No black pigment on posterior-dorsal margin of opercle or on area bounded by or between opercle and anterior part of lateral line. Pigment covering cleithrum usually very dark in adults. Area between lateral line and lateral stripe on middle part of body unpigmented. Pigment unequally distributed on caudal peduncle, very little present below lateral line. Fairly dense pigment around edges of dorso-lateral scales, forming parallel crooked lines that run length of back. Breeding colors usually more pronounced *Notropis zonatus*
Missouri, Black, St. Francis, and Mississippi drainages; Missouri and Arkansas.
- 4b. Black pigment present on posterior-dorsal margin of opercle and on area between opercle and anterior part

of lateral line. Pigment present only on upper half of cleithrum, usually relatively light in adults. Area between lateral line and lateral stripe on middle part of body pigmented. Pigment equally distributed above and below lateral line on caudal peduncle. Little pigment present around edges of dorso-lateral scales, with no parallel crooked lines along back. Breeding colors usually more subdued *Notropis pilsbryi*

Red, Arkansas and White river systems excluding the Black River; Arkansas, Missouri, eastern Kansas, and eastern Oklahoma.

- 3b. No prominent black stripe along length of body and head (some darkly pigmented juveniles have an indistinct dark stripe). Body usually deep and compressed (often slender and terete in *N. albeolus*). Black crescent-shaped bars usually present on side of body (ordinarily absent in *N. albeolus*). Insertion of dorsal fin directly above insertion of pelvic. Nuptial tubercles well developed, not granular. Lateral scales without prominent scallops on posterior margin....5

- 5a. Black, crescent-shaped marks on side of body very prominent, numerous, and distinct. Dark upper half of head sharply contrasting with light lower half, particularly in breeding males. Nuptial tubercles present in both sexes though much better developed in males; tips of tubercles in breeding males curved forward at tips. Scales on dorso-lateral part of body with a fine line about a quarter of the way from and paralleling outer edge. Caudal peduncle scales usually 14 or 15 (7-2-5 or 6). Size relatively small, not exceeding 90 mm.

..... *Notropis cerasinus*

Roanoke and New river systems in Virginia and North Carolina.

- 5b. Black, crescent-shaped marks on side of body usually prominent and distinct, though less so than in *N. cerasinus* (marks ordinarily absent in *N. albeolus*). Dark upper half of head not contrasting so sharply with lighter lower half. Nuptial tubercles normally present only in males; tubercles not curved forward at tips. Scales on dorso-lateral part of body without line paralleling outer edge. Caudal peduncle scales usually 16 (7-2-7). Size larger, reaching 175 mm.6

- 6a. Scales relatively large, the anterior dorso-lateral scales usually 13 to 16, circumferential scales usually 24 to 29. Scale pockets in dorso-lateral area with considerable dark pigment, forming three or four prominent straight or crooked parallel stripes along length of back; these meet posterior to the dorsal fin, forming distinct "V's." No broad, light area lateral to mid-dorsal stripe in breeding male. Mid-dorsal stripe not attaining a bright golden hue in live breeding males; narrow longitudinal stripe not present beneath parallel stripes on side of back. Pigment usually present on chin and anterior part of gular area7

- 7a. Parallel dark lines along dorso-lateral part of back crooked, sometimes fairly indistinct. Predorsal and anterior dorso-lateral scale rows always crooked. Anterior dorso-lateral scales (13) 14 to 16 (19); circumferential scales (23) 26 to 29 (32)

.....*Notropis chrysocephalus chrysocephalus*

Northeastern Oklahoma east to northern Georgia and north to southeastern Wisconsin and western New York. Intergrading with *isolepis* in central Alabama.

- 7b. Parallel dark lines along dorso-lateral part of back straight, always distinct. Predorsal and anterior dorso-lateral scale rows straight and even, rarely crooked. Anterior dorso-lateral scales (12) 13 or 14 (15); circumferential scales (23) 24 to 28

.....*Notropis chrysocephalus isolepis*

Southeastern Oklahoma and northeastern Texas to west-central Georgia and the Gulf coast. Intergrading with *chrysocephalus* in central Alabama.

- 6b. Scales relatively small, the anterior dorso-lateral scales usually 17 to 25, circumferential scales usually 26 to 35. Scale pockets in dorso-lateral area with little or no dark pigment; no parallel longitudinal stripes running along back. A broad, light stripe lateral to mid-dorsal stripe, particularly evi-

dent in breeding male. Mid-dorsal and narrow longitudinal stripes (the latter just below broad, light stripe) attaining a brilliant golden hue in live breeding males, disappearing soon after death (not yet observed in *N. albeolus*). Pigment either present or absent on chin and anterior part of gular area 8

- 8a. Scales smaller; those in anterior dorso-lateral region (16) 19 to 24 (30), those in circumferential series (26) 30 to 35 (39). Crescent-shaped bars usually present on side of body. General tone of body silvery-bronze. Dorsal region without a definite greenish cast in life. Breeding males with prominent, broad, dorso-lateral light stripe and much red on fins, less on body. Body usually deep and compressed

.....*Notropis cornutus*

Northern United States and southern Canada from northeastern Colorado to southeastern Saskatchewan and the Atlantic coast as far south as southern Virginia.

- 8b. Scales larger; those in anterior-dorso region (15) 17 to 19 (23), those in circumferential series (24) 26 to 30 (33). Crescent-shaped bars usually absent on side of body. General tone of body silvery with a definite greenish caste in life. Breeding males with the broad dorso-lateral light stripe not particularly evident; little or no red on fins, none on body except occasionally on tip of snout. Body usually slender and terete, more so in specimens from Roanoke and New river systems; less so in specimens from Neuse, Tar and Cape Fear systems

.....*Notropis albeolus*

Roanoke, New, Neuse, Tar and Cape Fear drainages in North Carolina, Virginia, and West Virginia.

Notropis coccogenis (Cope)

Warpaint Shiner, figures 2, 14D, map 1.

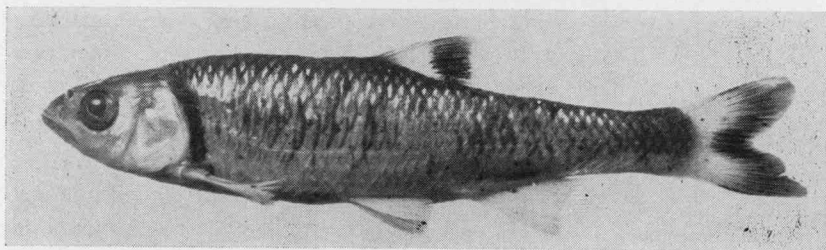


Figure 2. Adult male *Notropis coccogenis*, UMMZ 131488, 113 mm SL, from Cosby Creek, Cocke County, Tennessee.

- Hypsilepis coccogenis* Cope, 1867: 160 (original description; type locality Holston River, Virginia).
Leuciscus coccogenis, Günther, 1868: 253 (description; specimens from Virginia in British Museum).
Luxilus coccogenis, Jordan and Copeland, 1876: 153 (upper Tennessee River).
Minnilus coccogenis, Jordan and Gilbert, 1883: 188 (description; range).
Notropis coccogenis, Jordan, 1885b: 814 (range).
Hydrophlox coccogenis, Jordan, 1929: 83 (description; range).
Coccotis coccogenis, Jordan, Evermann and Clark, 1930: 127 (reference to original description; range).
Notropis brimleyi Bean, 1903: 913-914 (original description; Cane River, North Carolina; based on atypical specimen of *N. coccogenis*).
Hydrophlox brimleyi, Jordan, 1929: 83-84 (description; range).
Coccotis brimleyi, Jordan, Evermann and Clark, 1930: 127 (reference to original description).

TYPE. A series of 100 specimens (ANSP 3561-3660) bearing the data "Holston River, Virginia, collected by E. D. Cope," have been assumed to represent the syntypes of *Hypsilepis coccogenis* Cope (Fowler, 1910: 285). Jordan and Evermann (1896b: 285) listed as the type a specimen (USNM 36849), also collected by Cope, from the "Holston River, North Carolina." As the Holston River closely approaches but does not enter North Carolina, the label on the latter specimen is assumed to be partly in error and should probably read Virginia. Neither the U. S. National Museum nor Academy of Natural Sciences of Philadelphia has any record showing how or when this specimen was transferred, although judging from the entry in the National Museum catalogue Cope himself probably sent it late in 1884. The readily explained difference in locality data, the fact that Jordan and Evermann presumably had a valid reason for labeling the

specimen as "type," and the similarity in quality of preservation of specimens from the ANSP and USNM series strongly indicate that they were collected at the same time. Therefore, I think it logical to assume that the National Museum specimen is from Cope's original type series, and I hereby designate it as a lectotype of *Hypsilepis coccogenis*. The lectotype specimen is well preserved and is typical of *N. coccogenis*. Following are the more important meristic counts: anterior dorso-lateral scales 16; circumferential scales 14-2-10; lateral-line scales 39; caudal peduncle scales 7-2-6; pectoral rays 15 on each side; anal rays 9; pharyngeal teeth 2,4,4,2.

An examination of the syntypes in the Academy of Natural Sciences revealed they actually comprise five species. In addition to 90 paratypes of *Hypsilepis coccogenis* which have been recatalogued as ANSP 3561-3650, the following are also present: *Notropis ariommus* (6 specimens)—ANSP 3651-3656; *Notropis rubricroceus* (2 specimens)—ANSP 3657-3658; *Notropis chrysocephalus chrysocephalus* (1 specimen)—ANSP 3659; *Notropis galacturus* (1 specimen)—ANSP 3660.

DIAGNOSIS. An attenuate and terete, moderately large species of *Luxilus*, reaching 116 mm SL (Fowler, 1936: 192). *Notropis coccogenis* differs from other members of its subgenus, except *N. zonistius*, in the following characters: 2 to 3 rows of nuptial tubercles on lower jaw, extending to tip of chin (figure 14D); dorso-lateral scales outlined with dark pigment; peritoneum speckled with dark pigment, not appearing uniformly black. *N. coccogenis* is unique among forms of *Luxilus* in having: outer third of dorsal fin with a moderately oblique band which nearly parallels distal edge of fin; lower two-thirds of dorsal fin yellowish; a wide black border on posterior edge of caudal fin; a red maxillary spot; a prominent red bar at margin of opercle and preopercle; nuptial tubercles present on side and tip of snout, absent from top of head and back; an extremely well-developed black scapular bar; lower jaw usually projecting slightly.

A comparison of *N. coccogenis* and *N. zonistius* is presented in table 1.

DESCRIPTION. Fin ray and scale row counts and proportional measurements are listed in tables 4 and 9 to 15. Characters mentioned in the diagnosis are not repeated in the following description:

Angle of mouth to top of head usually 50° to 52° (range 46° to 55°); anterior dorso-lateral scales 15 to 18 (19); circumferential scales 25 to 29 (32) (relative distribution of circumferential scales usually 13 to 15-2-10 to 12; range 13-2-10 to 17-2-13); sum of anterior dorso-lateral and circumferential scales (40) 41 to 46 (50); caudal peduncle scales 14 to 16, usually 15; anal rays (8) 9 or 10, usually 9; pectoral

rays 14 to 16 (17), usually 15; vertebrae 40 to 42, usually 41; back dark olive; pockets of some scales along side of body with dark pigment, forming a few vertical crescent-shaped bars; breast, belly, and side metallic-silvery, with a rosy hue in breeding males; prominent gray-blue mid-dorsal stripe present; snout and upper lip red in breeding males; lower fins white; nuptial tubercles weakly developed, present in both sexes, but better developed in males; tubercles present on upper surface of pectoral fin and on side and tip of snout, absent from rest of head and back; females metallic-silvery, with only traces of red markings.

VARIATION. Hildebrand (1932: 63-64) compared the holotype of *Notropis brimleyi* Bean (USNM 50601) with specimens of *N. coccogenis*, and concluded that differences in appearance of the lower jaw in these two forms (projecting in *coccogenis*, included in *brimleyi*) warrant specific separation. His conclusions are not substantiated by the present study; examination of many individuals of *coccogenis* reveals that the supposed differences fall within the normal range of variation of the species.

Sexual dimorphism is less pronounced than in some *Luxilus* forms. Males are usually large, with most individuals over 100 mm long belonging to this sex, although one of the largest examples reported by Outten (1957: 75) was a female. During the breeding season males are more brightly colored than females, particularly as regards the red on the snout and side of the body. Although nuptial tubercles are present in both sexes, they are somewhat better developed in adult males.

DISTRIBUTION. The center of distribution of *Notropis coccogenis* is in the upper half of the Tennessee River system in eastern Tennessee, western North Carolina, northern Georgia and western Virginia, with a relict population present in the Tennessee system of western Alabama. It occurs in the headwaters of the Savannah River in North and South Carolina (Pickens, 1928: 30), of the Catawba River in North Carolina, and (one record) of the New River in north-western North Carolina (USNM 162281). Its presence in the Catawba and New systems may possibly be due to introduction. Its apparent absence from the upper Elk drainage in south-central Tennessee is possibly due to inadequate collecting.

Contrary to numerous accounts (Jordan and Evermann, 1896a; Jordan and Evermann, 1896b), *N. coccogenis* is not known from the Cumberland River system in Kentucky. Specimens recorded by Woolman (1892: 283) from the Big Sandy River of Kentucky have not been located, and from the known distribution this record is probably in

error. A reexamination of material recorded by Fowler (1922: 12; 1923: 11) from the Dan River, Virginia, and from the Neuse River system, North Carolina, shows these specimens are *Notropis albeolus*.

LIFE HISTORY AND ECOLOGY. Most of the following information has been taken from Outten's (1957: 68-84) detailed study of this species' life history.

Notropis coccogenis is an inhabitant of the swift riffles and flowing pools of medium to large upland streams. It occurs characteristically in the middle to upper levels of water and prefers a bottom composed of rocks and gravel.

Most individuals attain maturity when 2 years old. At this time they usually are about 75 mm SL, with the male averaging slightly larger than the female.

Outten observed spawning activity in the French Broad River system of North Carolina from early June to middle July when the water temperature was 68° or higher. This is somewhat later than the period of spawning for *N. cornutus* and *N. chrysocephalus* in Michigan. As the temperatures that *N. coccogenis* requires for breeding do not appear appreciably different from those for *cornutus* and *chrysocephalus*, the late spawning of *coccogenis* may be due to the cooler stream temperatures at the high elevations of the Tennessee uplands.

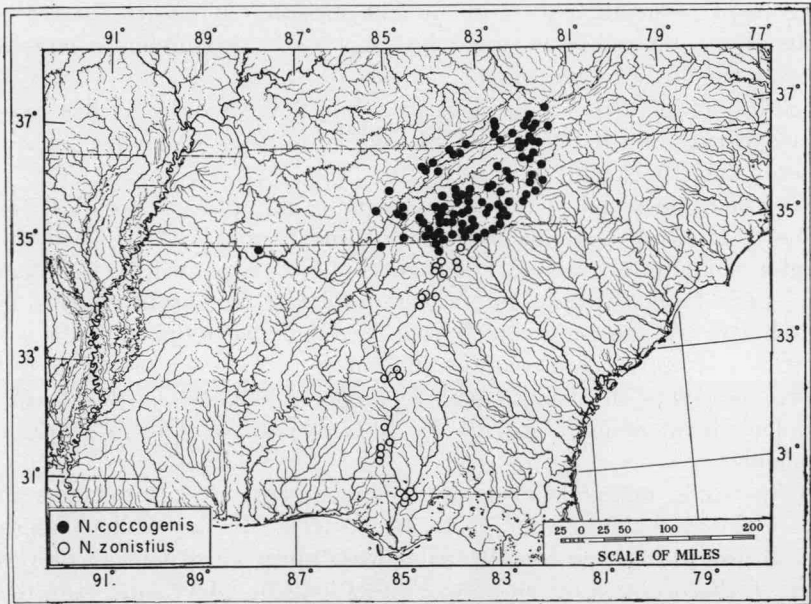
Spawning takes place in rapids 6 inches or more in depth or in more slowly flowing water up to 4 feet deep. In the shallow rapids small groups of up to 8 or 10 males were observed to hold territories over *Hybopsis micropogon* nests 2½ feet long by 2 feet wide, with the largest male occupying the upstream position. Occasionally one of the females lingering in a group farther back in the pools moved forward near a male. After remaining side by side a short time, they settled to the bottom where, with considerable vibration of their bodies, they spawned. This behavior is similar to that Raney (1940a: 7-8) observed for *Notropis cornutus* in New York.

Age-growth studies show the main increase in length to take place in the first and second years of life. During the first year males and females show little size difference, but in the second and third years males grow considerably more than females. Apparently little or no difference in growth rates occurs during the fourth year.

Counts of males and females in each age group show equal numbers of each sex present during the first year of life, but a higher proportion of females among older fish (66.2 percent in the second year of life, 76 percent in the third). This is paralleled by my observations on breeding populations of *N. cornutus* and *N. chryso-*

cephalus in Michigan and by those of Pfeiffer (1955: 101) on *N. rubellus*, in which females appear always to dominate markedly.

N. coccogenis feeds on terrestrial and aquatic animals, principally insects, with occasional small amounts of vegetable matter, usually taken at the surface or in the upper water levels. Food seems selected largely according to its relative abundance, with little or no species-preference evident.



Map 1.

Notropis zonistius (Jordan)

Bandfin Shiner, figures 3, 14B, map 1.

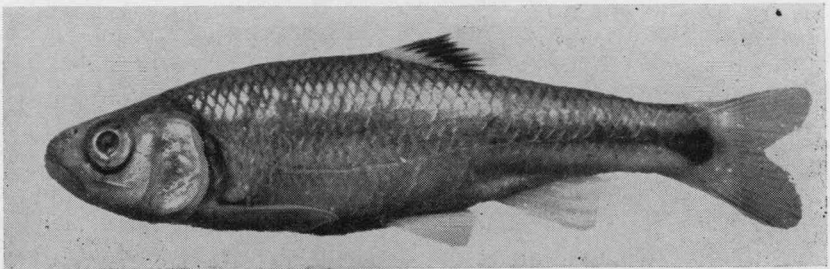


Figure 3. Adult male *Notropis zonistius*, UMMZ 175580, 85 mm SL, from Cane Creek, Dahlonega, Lumpkin County, Georgia.

Codoma eurystoma Jordan and Brayton, 1878: 42, 84-85 (partim, type series contained specimens of *N. zonistius* and *C. eurystoma* [= *N. venustus*]).

Luxilus zonistius Jordan, 1880: 239-240 (original description; type series consists of young specimens forming part of Jordan and Brayton's type series of *Codoma eurystoma*; holotype USNM 23452, 68.5 SL; type locality Suwannee Creek, Gwinnett County, Georgia).

Minnilus zonistius, Jordan and Gilbert, 1883: 188-189 (description; range).

Notropis zonistius, Jordan, 1885b: 814 (list; range).

Coccotis zonistius, Jordan, Evermann and Clark, 1930: 128 (reference to original description; range).

Hydrophlox zonistius, Schrenkeisen, 1938: 127 (characters; related to *Hydrophlox coccogenis*; northern Georgia).

DIAGNOSIS. A deep, compressed, small species of *Luxilus*, the males rarely exceeding 85 mm SL. *Notropis zonistius* differs from other members of its subgenus, except *N. coccogenis*, in the following characters: 2 to 3 rows of weakly-developed nuptial tubercles on lower jaw, extending to tip of chin (figure 14B); dorso-lateral scales outlined with dark pigment; peritoneum speckled with dark pigment, not appearing uniformly black. *N. zonistius* is unique among forms of *Luxilus* in having: dorsal fin with a strongly oblique black band (orange-red in younger specimens) beginning on lower third of anterior margin and terminating at middle of posterior margin; a distinct caudal spot, about equal to diameter of eye; a faint red bar along cheek.

N. zonistius and *N. coccogenis* are compared in table 1.

DESCRIPTION. Fin ray and scale row counts and proportional measurements are listed in tables 4 and 9 to 15. Characters mentioned in the diagnosis are not repeated in the following description:

Body deep and compressed; mouth large, terminal, and oblique, usually forming an angle of 57° to 61° with top of head (range 51° to 61.5°); anterior dorso-lateral scales 15 to 18 (19); circumferential scales (25) 27 to 30 (relative distribution of circumferential scales usually 15 or 16-2-11 or 12; range 13-2-10 to 16-2-13); sum of anterior dorso-lateral and circumferential scales (40) 43 to 48 (49); caudal peduncle scales 13 to 15, usually 14; anal rays (8) 9 or 10, usually 9; pectoral rays 14 to 16, usually 15; vertebrae 38 to 40, usually 39; color of body olivaceous to steel-blue above; side of body with considerable coppery luster; pockets of some scales along side of body with dark pigment, forming a few vertical crescent-shaped bars; prominent gray-blue mid-dorsal stripe; tubercles on upper part of head best developed on side and tip of snout, granular on top of head, back, anterior part of dorsal fin, and upper surface of pectoral fin; tubercles present on posterior edges of scales on upper half of body.

The following color description by Reeve M. Bailey is based on live specimens (UMMZ 157882) collected 23 August 1939 from a tributary of the Chattahoochee River 2.5 miles southwest of Chipley, Harris County, Georgia: side silvery, tinged with pinkish-orange on lower parts in large adults; upper parts dark olivaceous; lower fins white; dorsal fin white, with a band in middle, the band pink in young, reddish-orange in small adults, becoming entirely black in large adults; narrow reddish edge at base of caudal fin in smaller breeding males; tail bright red in large adult, with a whitish base and distal margin; lowermost ray of caudal fin whitish; reddish-orange bar extending upward and downward from base of pectoral, this bar black in breeding males; cheek pale silvery blue.

VARIATION. Nuptial tubercles are present in both males and females, but they are better developed in the males. Though no detailed comparison of breeding colors has been made between the sexes, one may assume that the male colors are more pronounced, as in other species of *Luxilus*.

Notropis zonistius apparently is the only species of *Luxilus* with a gradient in anal ray count (table 13). Specimens from the southern part of the range have a modal count of 10, as compared to 9 in specimens from farther north. This situation is comparable to that found in *Notropis cummingsae*, in which individuals from upland areas usually have 9 anal rays and those from lowland areas 10 or 11 (Hubbs and Rañey, 1951: 18), and in *Notemigonus crysoleucas*, in which specimens from farther south have a greater modal number of anal rays than those farther north (Schultz, 1927).

Martin (1949: 65) has shown that "a fast growing group of individuals may have relatively large body parts, such as head and fins." Thus in individuals developing in a warm environment, the anal fin grows more rapidly into a longer fin with more fin rays than in individuals from colder waters. As the variation in anal-ray counts in *N. zonistius* probably has an environmental rather than a genetic basis, the populations differing in this character have not been accorded subspecific status.

DISTRIBUTION. *Notropis zonistius* is restricted to small tributaries of the Chattahoochee River system in Georgia, Alabama, and Florida and the upper Savannah River system in Georgia. The single record from the Savannah system (CU 25170) is probably the result of stream capture, although the species may have been introduced there.

LIFE HISTORY AND ECOLOGY. Nothing has appeared in the literature regarding the life history of *N. zonistius*. In view of its close

taxonomic relationship to *N. coccogenis*, it is probably similar or identical to that species in many aspects of its life history.

N. zonistius inhabits clear water with a rather swift current and apparently prefers pools at the base of riffles to the swifter areas. Various field records and my limited field experience with it suggest it also prefers slightly smaller streams than does *N. coccogenis*.

Notropis zonatus (Agassiz)

Bleeding Shiner, figures 4, 5A, 14A, map 2

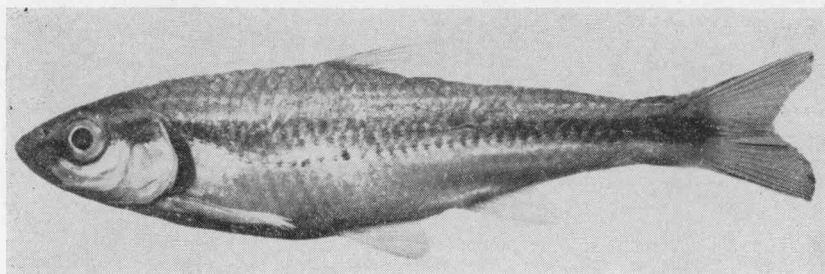


Figure 4. Adult *Notropis zonatus*, UMMZ 148446, 82 mm SL, from Huzzah Creek, Crawford County, Missouri.

Alburnus zonatus Agassiz, in Putnam, 1863: 9 (original description; type locality Osage River, presumably in Missouri).

Leuciscus zonatus, Günther, 1868: 253-254 (description; Osage River).

Minnilus zonatus, Jordan and Copeland, 1876: 154 (Osage River).

Chiola zonata, Jordan and Gilbert, 1883: 183 (in part; Osage River; description based on *Notropis dorsalis piptolepis*).

Notropis zonatus, Jordan, 1885b: 814 (in part; description; range).

Hydrophlox zonatus, Jordan, 1929: 83 (in part; description; Ozark region).

Coccotis zonatus, Jordan, Evermann and Clark, 1930: 128 (range; synonymy).

Notropis zonatus zonatus, Hubbs and Moore, 1940: 91-99, pl. 1, fig. C (general account; comparisons; distribution; synonymy).

TYPE. No holotype was designated for this species, but 13 syntypes exist, collected in 1854 by George Stolley from the Osage River, presumably in Missouri. One of these, an adult 65 mm SL (UMMZ 174594) I designate as lectotype of *Alburnus zonatus*. The specimen is typical of the species and shows all the distinguishing pigmentary characters plainly. Three of the paratypes are in the University of Michigan collections (UMMZ 86915), the other nine at Harvard University (MCZ 1914).

NOMENCLATURE. The authorship of *Alburnus zonatus*, as well as of several other species of North American freshwater fishes originally

described in a paper written by F. W. Putnam in 1863, has been the subject of considerable debate. As each of the new names is followed by "Agassiz, MS. (Nov. sp.)," most succeeding references have cited Agassiz as their describer. Some still contend that Putnam is the authority, as he wrote the paper and at no place in the text is it stated clearly that Agassiz was responsible for anything other than coining the new specific names. In view of the disagreement the authorship of these species is best cited as "Agassiz, *in* Putnam."

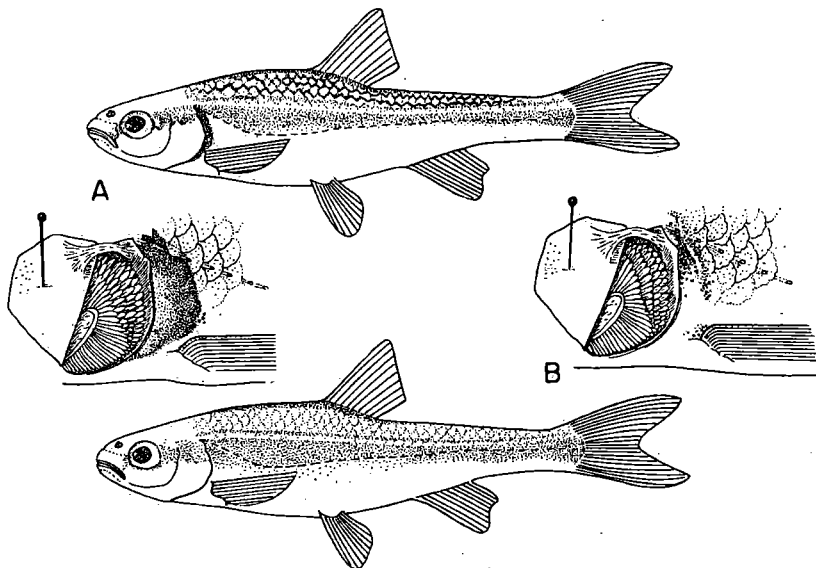


Figure 5. Pigmentation patterns of: A. Adult *N. zonatus*, UMMZ 152697, 68 mm SL, from Barren Fork, Tuscumbia, Miller County, Missouri. B. Adult *N. pilsbryi*, UMMZ 80987, 65.5 mm SL, from Elk River, Grove, Delaware County, Oklahoma.

Past references to *N. zonatus* often apply entirely, or in part, to another species, *N. pilsbryi*. These forms were regarded as identical (Hubbs and Brown, 1929: 36; Hubbs and Ortenburger, 1929: 81-82) until 1940, when Hubbs and Moore pointed out several well-defined morphological differences in addition to differences in range. They regarded the two forms as only subspecifically distinct, but presented evidence indicating that this was possibly a conservative separation.

DIAGNOSIS. A small species of *Luxilus*, rarely exceeding 85 mm SL. Distinguished from other species of *Luxilus* (except *N. pilsbryi*) by: A prominent black lateral stripe that encircles snout and is present at all ages; a well-developed, narrow, secondary lateral stripe situ-

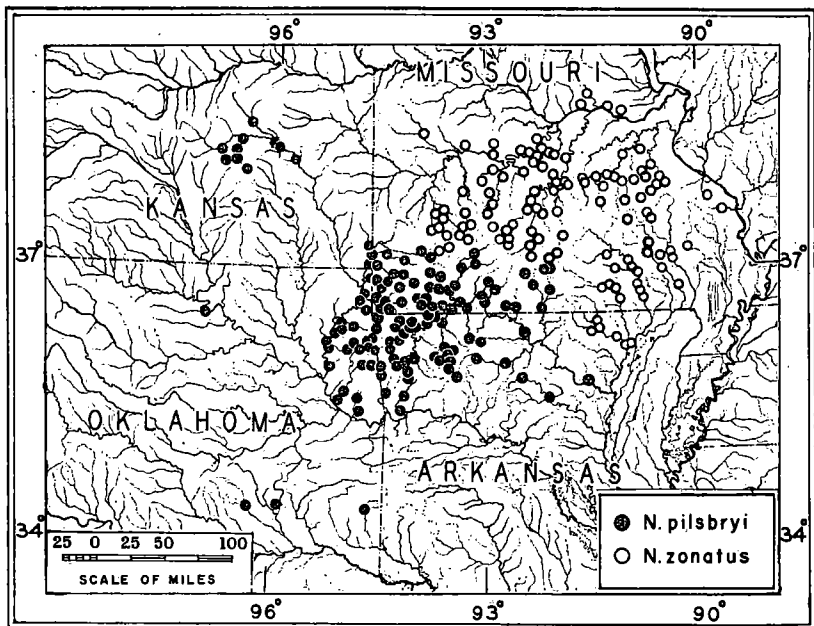
ated parallel and dorsad to the main lateral stripe; a jet-black predorsal streak; few apical radii on scales; four or five prominent scallops on posterior margin of those scales situated in or close to the lateral line; weakly developed nuptial tubercles on top of head and back, present in one row along lower jaw and absent from tip of chin; body slender and terete at all sizes.

Distinguished from *N. pilsbryi* by the following pigmentary characters (see figure 5A and table 2): Lateral stripe on posterior part of opercle curved sharply upward, not bordering upper half of posterior margin; lateral dark stripe extending little or not at all below lateral line posterior to head and anterior to caudal peduncle, and absent from a small area above middle part of lateral line; black pigment present over all of cleithral area dorsad to pectoral insertion, becoming jet-black in breeding individuals; pigment in lateral stripe on caudal peduncle unequally distributed around lateral line, more present above than below; pigment more dense around edges of dorso-lateral scale pockets, forming crooked parallel lines along side of back, the stripes converging posteriorly with those from opposite side of body; red and black pigment usually more pronounced, particularly in breeding males.

DESCRIPTION. Counts and measurements are given in tables 5 and 9 through 15. All distinctive pigmentary characters of the species are analyzed in table 2 and are shown in figure 5A. Characters mentioned in the above diagnosis are not repeated in the following paragraph:

Anterior dorso-lateral scales 14 to 16 (18); circumferential scales (25) 26 to 28 (29); sum of anterior dorso-lateral and circumferential scales (39) 40 to 44 (46); an olive area about $2\frac{1}{2}$ times as wide as mid-dorsal stripe (not so sharply defined as in *N. cornutus*) extending along body on either side of mid-dorsal stripe; side of body silvery with an intense black stripe running from snout to end of caudal peduncle, this stripe often overlain with a plumbeous coloration which disappears in preservative; mid-dorsal stripe black, slightly more than half as wide as eye, and extending around base of dorsal fin; breast, belly, and lower side of head silvery, becoming flame-red in breeding males; back olivaceous; lips, preopercular bar, and pectoral axil bright blood-red in breeding males; top of head dark gray to black, especially dark in breeding individuals; branchiostegals ordinarily colorless, becoming deep red in breeding males; fins ordinarily pale, becoming orange-red in breeding males except for gray borders; red most pronounced in dorsal fin, with some green beneath; red often more reduced in area and/or intensity in other fins, and in low breeding males largely

confined to the submarginal bands; nuptial tubercles weakly developed, granular in all but highest breeding males, in which they project slightly; four or five tubercles present in single row on lower jaw and absent from chin; tubercles present on snout and upper part of head, but apparently absent from predorsal area of back and dorsal fin.



Map 2.

DISTRIBUTION. Restricted to tributaries of the lower Missouri River in Missouri, to the Black, St. Francis, and Little river systems in Missouri and Arkansas, and to a few small tributaries of the Mississippi River in eastern Missouri.

The Bleeding Shiner is common in the lower (eastern) half of the Osage system, and is generally distributed throughout the Gasconade and Meramec drainages. It has crossed the lower Missouri in several places and has become established in at least four small tributaries flowing into this river from the north.

The record of *N. zonatus* for eastern Tennessee (Evermann and Hildebrand, 1916: 444) was based on specimens of *N. ariommus*. Specimens recorded as *N. zonatus* by Cockerell (1908: 170) from Boulder, Colorado, are *N. cornutus*.

LIFE HISTORY AND ECOLOGY. *N. zonatus* is typically an inhabitant of small to medium-sized Ozarkian streams with a gravel or rubble bottom and clear, rapidly-flowing water. In these situations it often is the most abundant fish species present. Hubbs and Moore (1940) reported this species, as well as *N. pilsbryi*, to be most common in moderately swift pools, but my observations indicate it is equally at home in or near the base of swift riffles, where it often is associated with *N. ariommus telescopus*. This habitat is somewhat different from that preferred by either *N. chrysocephalus* or *N. cornutus*, both of which characteristically live slightly farther away from the bases of riffles and rarely occur on the riffles except during spawning time. This apparent preference of *zonatus* for swifter water is reflected in its more streamlined form, as contrasted to the deeper, more compressed appearance of *chrysocephalus* and *cornutus*.

N. zonatus commonly lives with *N. chrysocephalus chrysocephalus*, but has been found only once with *N. cornutus*. At no time have *N. zonatus* and *N. pilsbryi* been found together, though the two occur within a few miles of each other in a number of places.

No accounts of either spawning or food habits in *N. zonatus* have been published. Its breeding habits are presumably similar to those of the closely related *N. pilsbryi* in the Illinois River system of Oklahoma, which Moore and Paden (1950: 92) have reported on.

Notropis pilsbryi Fowler

Duskystripe Shiner, figures 5B, 6, map 2.

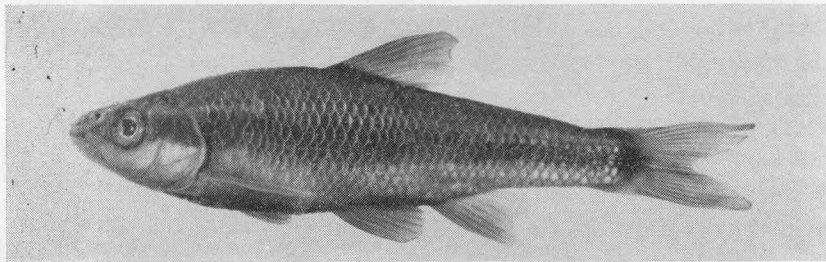


Figure 6. Adult male *Notropis pilsbryi*, USNM 161632, 74.5 mm SL, from Spring Creek, Cherokee County, Oklahoma.

Notropis zonatus, Jordan, 1885b: 814 (misidentification in part; description; range).

Hydrophlox zonatus, Jordan, 1929: 83 (misidentification in part; description; Ozark region).

Coccotis zonatus, Driver, 1942: 276 (misidentification in part; key).

Notropis pilsbryi Fowler, 1904: 245-246, fig. (original description; compared with *N. leuciodus*; holotype, ANSP 24514, 72.5 mm SL; type locality, White River system at Rogers, Arkansas).

Notropis zonatus pilsbryi, Hubbs and Moore, 1940: 91-99, pl. 1, figs. A and B (general account; comparisons; distribution; synonymy).

Notropis zonata pilsbryi, Cross, 1954: 309 (Cedar Creek and Cottonwood River, Kansas; Jennings [1942] record for *N. cornutus frontalis* based on this species).

Notropis cornutus frontalis, Jennings, 1942: 365 (Rock Creek, Chase County, Kansas).

NOMENCLATURE. Although adequately described by Fowler (1904: 245-246) the taxonomic relationships of *Notropis pilsbryi* have often been misunderstood. This is evident from Fowler's original description, which compares the species with *Notropis leuciodus*, and also from the identification by Forbes and Richardson (1920: 149) of the hybrid combination *Notropis cornutus (chrysocephalus)* \times *Notropis rubellus* as "*Notropis pilsbryi*." Hubbs and Ortenburger (1929: 81-82) and Hubbs and Brown (1929: 36) relegated *pilsbryi* to the synonymy of *N. zonatus*, a decision with which Fowler concurred. Although Jordan, Evermann and Clark (1930: 124) and Schrenkeisen (1938: 123) list *pilsbryi* as a full species, their works were merely compilations and were not based on original information. Hubbs and Moore (1940) correctly demonstrated the distinctness of *pilsbryi* and *zonatus*, and their findings have been followed since.

DIAGNOSIS. A small species of *Luxilus*, rarely exceeding 85 mm SL. Distinguished from other species of its subgenus (except *N. zonatus*) by: A prominent dusky-black lateral stripe that encircles snout and is present at all ages; a well-developed narrow secondary lateral stripe situated parallel and dorsad to main lateral stripe; a jet-black predorsal streak; few apical radii on scales; four or five prominent scallops on posterior margin of those scales situated in or close to lateral line; weakly developed nuptial tubercles on top of head and back, present in one row along lower jaw, and absent from tip of chin; body slender and terete at all sizes.

Distinguished from *N. zonatus* by the following pigmentary characters (see figure 5B and table 2): Lateral stripe on posterior part of opercle not curved sharply upward, extending straight across and bordering upper half of posterior margin; lateral dark stripe extending below lateral line for entire distance posterior to head; black pigment in cleithral area extending ventrally only about halfway to pectoral insertion; pigment in lateral stripe on caudal peduncle equally distributed above and below lateral line; pigment around edges of dorso-lateral scales not particularly dense, not forming parallel lines

running along dorso-lateral part of back; red and black pigment not especially pronounced in breeding specimens.

DESCRIPTION. Counts and measurements are given in tables 5 and 9 through 15. All distinctive pigmentary characters of the species are analyzed in table 2 and are shown in figure 5B. Characters mentioned in the above diagnosis are not repeated in the following paragraph:

Body slender and terete at all sizes; anterior dorso-lateral scales (14) 15 to 17 (18); circumferential scales (24) 25 to 29 (30); sum of anterior dorso-lateral and circumferential scales (39) 41 to 45 (48); an olive area about $2\frac{1}{2}$ times as wide as mid-dorsal stripe (not so sharply defined as in *N. cornutus*) extending along body on either side of mid-dorsal stripe; side of body silvery, with a dusky-black stripe running from snout to end of caudal peduncle, this stripe often overlain with a plumbeous coloration which disappears in preservative; mid-dorsal stripe black, slightly more than half as wide as eye, and extending around base of dorsal fin; breast, belly, and lower side of head silvery, becoming reddish in breeding males; back olivaceous; lips, preopercular bar, and pectoral axil reddish in breeding males; top of head dark gray to black; branchiostegals ordinarily colorless, becoming reddish in breeding males except for gray borders; nuptial tubercles weakly developed, granular in all but highest breeding males in which they project slightly; four or five tubercles present in single row on lower jaw and absent from chin; tubercles present on snout and upper part of head, but apparently absent from predorsal area of back and dorsal fin.

DISTRIBUTION. In the White River system (excluding the Black River) in Arkansas and Missouri and in a few tributaries of the Arkansas and Red rivers in Arkansas, Kansas, and Oklahoma.

N. pilsbryi probably is the most abundant cyprinid in the White River system, particularly in clear, upland tributaries. It is also common in many streams draining into the Illinois and Neosho rivers, tributaries of the Arkansas, although it seems rather scarce in some parts of the Neosho system. It is found in the lower reaches of the Illinois River and has been reported from the Arkansas River itself (Hubbs and Moore, 1940: 94). Its presence in the Red River system has been suggested by Hubbs and Moore (1940: 94) to be due to introduction, but its occurrence in three widely separated localities in this drainage suggests natural distribution.

LIFE HISTORY AND ECOLOGY. *Notropis pilsbryi* occupies the same type of habitat as the closely related *N. zonatus*. Its occurrence in

the turbid Arkansas River may be explained by the presence of springs in the river bed (Hubbs and Moore, 1940: 94).

Moore and Paden (1950: 92) published the following observations of spawning behavior in "*N. zonatus pilsbryi*" in the Illinois River system in Oklahoma, together with an account of possible hybridization with *Dionda nubila*:

"May 3, 1947, was one of those beautiful balmy spring days (air temperature 22°C., water 20°C.) with a perfectly clear sky and no wind. As we approached a long stretch of riffle, shortly after mid-day, a considerable area of water appeared to reflect a beautiful crimson. Approaching closer, to about 20 feet, a most unusual sight greeted our eyes. An area of about 10 by 6 feet in gently flowing water about 1 or 1½ inches deep was occupied by thousands of male *zonatus* lying so close to each other that it seemed there was no room for more. They were so beautiful that the eye at first failed to detect the occasional less brilliant female, and surely there were not very many lying between the males. Their activities made the surface of the water quite rough and so the whole process of spawning escaped us. The males were rolling from side to side so that their brilliant crimson underparts made the water appear to be on fire. When we stepped into the riffle the minnows scattered. By means of a screen we were able to collect eggs, presumed to be of this species, from the redd.

"Below the riffles occupied by *Notropis zonatus* was a deeper area (about 2 by 2½ feet) from which our seines took a considerable number of *Dionda* in breeding color. No evidence of the spawning of the Ozark minnow was obtained but it seems quite possible that spermatozoa of *Notropis zonatus* could be carried by the current into the spawning area of *Dionda nubila* where they might fertilize the eggs of that species."

Notropis cerasinus (Cope)

Crescent Shiner, figures 7, 14C, map 3.

Hypsilepis cornutus cerasinus Cope, 1867: 159 (original description; type locality headwaters of Roanoke River, Virginia).

Minnilus cornutus cerasinus, Jordan and Gilbert, 1883: 187 (description; range).

Notropis megalops cerasinus, Jordan, 1889b: 121-123 (description; comparison with *N. megalops albeolus*; abundant in Roanoke River system).

Notropis cerasinus, Jordan and Evermann, 1896a: 256 (range; synonymy).

Notropis cornutus cerasinus, Fowler, 1910: 284, pl. 18, fig. 31 (comparisons; status; types in ANSP).

Luxilus cornutus cerasinus, Jordan, 1929: 82 (description; range).

Luxilus cerasinus, Jordan, Evermann and Clark, 1930: 128 (reference to original description; range).

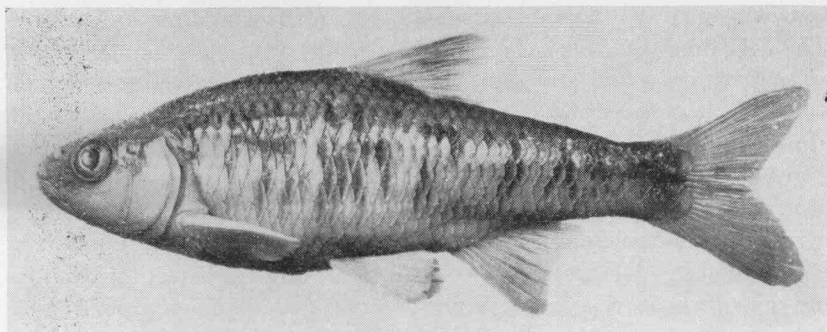


Figure 7. Adult male *Notropis cerasinus*, UMMZ 174710, 81 mm SL, from Cub Creek, Appomatox, Appomatox County, Virginia.

TYPE. Cope (1867: 159) did not designate a holotype for *Hyp-silepis cornutus cerasinus*. The syntypic series (ANSP 3791-3833) consists of 43 specimens, of which I designate an adult male, 73 mm SL, as lectotype; this specimen is now catalogued as ANSP 3791. The remainder of the series contains 8 paratypes of *Notropis cerasinus* (ANSP 3792-3799) and 34 specimens of *Notropis albeolus* (ANSP 3800-3833).

DIAGNOSIS. A small species of *Luxilus*, not exceeding 87.5 mm SL, distinguished by: Relatively large scales, the sum of anterior dorso-lateral and circumferential scales usually 41 to 47; caudal peduncle scales (12) 13 to 15 (16), usually 14 (range 5-2-5 to 7-2-7); body deep and compressed; upper half of head darkly pigmented, contrasting sharply with lighter lower half, particularly in breeding males; considerable red pigment on body and fins of nuptial males, possibly more than in any other form of *Luxilus*; scale pockets on side of body heavily pigmented, particularly in breeding males, with many scales appearing entirely black, forming vertical crescent-shaped bars which are more pronounced than in any other member of the subgenus; scales in dorsal region with a thin black line parallel to and approximately one-fifth of way in from posterior edge; nuptial tubercles present in both sexes, but less well developed in females; four or five tubercles present in a single row on lower jaw, not reaching tip of chin (see figure 14C); tubercles covering top and side of head, back and anterior part of dorsal fin; tubercles on head curved forward at tips.

DESCRIPTION. Fin ray and scale row counts and body proportions appear in tables 6 and 9 through 15. A comparison of *N. cerasinus* with other members of the *Notropis cornutus* species group is presented in table 3. Characters mentioned in the diagnosis are not repeated in the following paragraph:

Lateral-line scales and those in surrounding area much taller than wide, this character more pronounced in older fish, particularly in adult males; anterior dorso-lateral scales (14) 15 to 20 (22); circumferential scales (23) 24 to 28 (30); sum of anterior dorso-lateral and circumferential scales (37) 41 to 47 (51); vertebrae (38) 39 (40); angle of mouth to top of head averaging 57.5° (range 52.5° - 62.5°); color of dorsal region olive-brown, becoming steel-blue in breeding males; mid-dorsal stripe gray-blue, slightly more than half as wide as eye and extending around base of dorsal fin; red on cheek, opercle, lips and snout of breeding males.

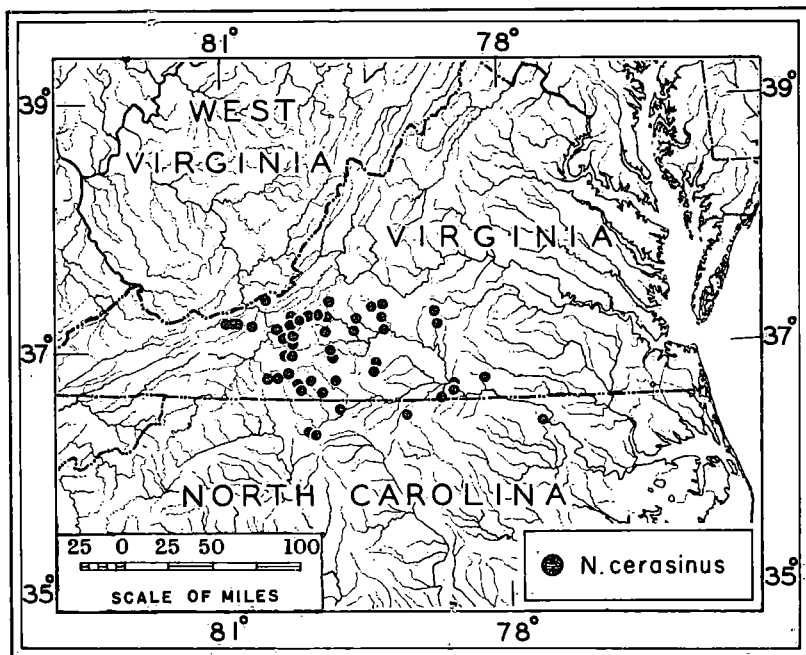
VARIATION. Raney (1947: 126) described the sexual dimorphism in breeding specimens of *N. cerasinus*. The following is a summary of his findings:

1. Males are more brilliantly colored than females, both with regard to red pigment on fins and body and other dark colors on the body.
2. Nuptial tubercles are better developed in males.
3. Males have a relatively small, non-protruding anal papilla; in females this structure is quite swollen and protrudes posteriorly.
4. Males have longer pectoral and pelvic fins than females.

DISTRIBUTION. Limited to the upper part of the Roanoke River drainage in Virginia and North Carolina and to a few eastern tributaries of the New River system in Virginia, *N. cerasinus* has the most restricted range of any *Luxilus* species. Unlike its near relative, *N. albeolus*, it is usually confined to headwater streams. Fowler's records (1922: 9, 12; 1923: 10; and 1945: 29) of *N. cerasinus* from the James River system are based on specimens of *N. cornutus*.

LIFE HISTORY AND ECOLOGY. Raney's (1947) paper is the only published work on the life history or ecology of this species. Concerned also with several other species of Cyprinidae, it is quoted in part here: "On June 21, 1946, in Otter River, Roanoke River system, 4 miles northeast of Bedford, Bedford County, Virginia, three minnows, *Notropis cerasinus*, *Notropis ardens ardens* and *Chrosomus oreas*, were observed over a *Nocomis leptcephalus* nest. The stream was a rather fast falling, clear mountain brook, about 75 feet wide

on the average, with long, moderately fast riffles and short, shallow pools. The temperature of the water was 70°F., and air 75°F., at 12:30 p.m.



Map 3.

"The nest was located near the head of a riffle in moderately swift water 18 inches deep, . . . about 20 feet from the bank. . . . A large male *Notropis cerasinus* was observed at the head of the nest. . . . Other male *cerasinus* soon moved in over the nest and established territories. They darted nervously about, attempting to drive away the smaller males of *Chrosomus*, which were well established over the nest. . . . On the other hand, *cerasinus* males did not often clash with male *ardens*, which were conspicuous just over them. . . . Female *cerasinus* occasionally appeared about the periphery of the nest, but spawning was not seen. The behavior over the nest was in general much like that of a related species, *Notropis cornutus*, as reported by Raney (1940a: 8)."

Actual spawning had not yet taken place when the observations ended. From all indications the spawning act probably is similar to that of *N. cornutus*.

Breeding individuals of *N. cerasinus* are usually found from middle to late June, those of the closely related *N. albeolus* from 2 to 3 weeks earlier. This may in part be accounted for by the cooler temperatures of the headwater streams *cerasinus* inhabits. The difference in spawning time may be one explanation for the apparent lack of hybrids between the two species.

Notropis cornutus (Mitchill)

Common Shiner, figures 8, 9A, 14F, 15D, 15E, map 4.

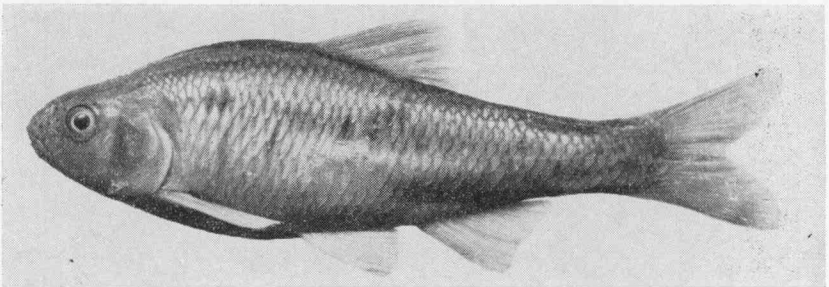


Figure 8. Adult male *Notropis cornutus*, UMMZ 121835, 106 mm SL, from Lost Creek, Defiance County, Ohio.

- Cyprinus cornutus* Mitchill, 1817: 289 (original description [July 1817]; type locality Wallkill River, New York).
- Leuciscus cornutus*, DeKay, 1842: 207-208, pl. 29, fig. 92 (description; ecology; New York).
- Hypsolepis cornutus*, Storer, 1855: 284-285, pl. 2, fig. 3 (description; Massachusetts).
- Plargyrus cornutus*, Girard, 1856: 196 (in part; in list of species; *Argyreus rubripinnis* a synonym).
- Hypsilepis cornutus*, Cope, 1864: 279 (comparison of specimens from Michigan with those from Susquehanna and Delaware drainages).
- Hypsilepis cornutus cornutus*, Cope, 1867: 159-160 (description; Susquehanna River drainage, Pennsylvania).
- Luxilus cornutus*, Jordan, 1876b: 286-287 (in part; description; range; synonymy).
- Minnilus cornutus cornutus*, Jordan and Gilbert, 1883: 187 (description; range).
- Minnilus cornutus*, Gilbert, 1884a: 14 (Ellis, Kansas).
- Notropis cornutus*, Jordan and Evermann, 1896a: 256 (in part; range; reference to original description).
- Nototropis cornutus*, Ruthven, 1906: 108 (Porcupine Mountains, Michigan).
- Notropis cornutus cornutus*, Hubbs, 1926: 46 (intermediate in appearance between *N. cornutus chrysocephalus* and *N. cornutus frontalis*; Atlantic coast drainage).

- Luxilus cornutus cornutus*, Jordan, 1929: 82 (range; intermediate in appearance between *L. cornutus frontalis* and *L. cornutus chrysocephalus*).
- Notropis cornuta*, Hubbs, 1955: 10 (in part; hybridization with *N. rubella*).
- Cyprinus megalops* Rafinesque, 1817: 121 (original description [December 1817]; type locality Hudson River system, New York).
- Notropis megalops*, Jordan, 1885a: 123 (in part; *Plargyrus bowmani* and *Plargyrus argentatus* are synonyms).
- Cyprinus melanurus* Rafinesque, 1817: 121 (original description; type locality Hudson River drainage, New York).
- Cyprinus haematopterus* Rafinesque, 1820b: 6 (original description; type locality Hudson River system, New York).
- Cyprinus trivittatus* Rafinesque, 1820b: 6 (original description; type locality Fish and Wallkill creeks, New York).
- Leuciscus vittatus* DeKay, 1842: 212, pl. 34, fig. 108 (original description; type locality Mohawk River system, New York).
- Argyreus rubripinnis* Heckel, 1843: 50 (original description; pharyngeal teeth figured).
- Leuciscus spiralingus* Valenciennes, in Cuvier and Valenciennes, 1844: 321-323 (original description; type locality New Jersey).
- Leuciscus plargyrus*, Kirtland, 1845: 26, pl. 8, fig. 2 (misidentification in part; description; Ohio).
- Leuciscus diplemia*, Kirtland, 1846: 276, pl. 22, fig. 3 (misidentification in part; description; ecology; Ohio).
- Leuciscus frontalis* Agassiz, 1850: 368 (original description; comparison with *Leuciscus cornutus* and *Leuciscus gracilis*; type locality Montreal River, Keeweenaw Point, Lake Superior, Michigan).
- Plargyrus frontalis*, Girard, 1856: 196 (Lake Superior).
- Hypsolepis frontalis*, Putnam, 1863: 7 (in Harvard collection).
- Notropis cornutus frontalis*, Evermann and Goldsborough, 1907: 96 (Lake Superior region, Canada).
- Luxilus cornutus frontalis*, Jordan, 1929: 82 (description; range).
- Notropis cornuta frontalis*, Schelske, 1957: 38 (lists probably erroneous record from Verdigris River system, Kansas).
- Leuciscus gracilis* Agassiz, 1850: 370 (original description; comparison with *Leuciscus cornutus* and *Leuciscus frontalis*; type locality Lake Huron).
- Plargyrus gracilis*, Girard, 1856: 196 (Lake Huron).
- Plargyrus typicus* Girard, 1856: 196 (in part; name replaces Rafinesque's *Rutilus plargyrus*).
- Plargyrus bowmani* Girard, 1856: 196 (original description; type locality Sweetwater River, Nebraska).
- Plargyrus argentatus* Girard, 1856: 212 (original description; type locality James River system, Virginia).
- Hypsilepis cornutus cyaneus* Cope, 1867: 160 (original description; type locality Montreal River, Keeweenaw Point, Lake Superior, Michigan).
- Minnilus cornutus cyaneus*, Jordan and Gilbert, 1883: 188 (description; range).
- Notropis megalops cyaneus*, Jordan, 1885b: 814 (in list; synonymy).
- Notropis cornutus cyaneus*, Jordan and Evermann, 1896b: 283 (description; reference to original description; northern Michigan).
- Notropis zonatus*, Cockerell, 1908: 170 (misidentification; Boulder, Colorado).

- Notropis universitatis* Evermann and Cockerell, 1909: 187 (original description; type locality Boulder, Colorado).
Hydrophlox universitatis, Schrenkeisen, 1938: 127 (related to *Hydrophlox coccogenis*; Colorado).
Notropis cerasinus, Fowler, 1922: 9 (misidentification in part; James River at Midway Mills, Virginia).
Notropis cornutus cerasinus, Fowler, 1923: 10 (misidentification in part; James River system, at Kyle, Virginia).
Notropis cornutus chrysocephalus, Jones, 1929: 32 (misidentification; Iowa).
Notropis cornutus: *chrysocephalus* \times *frontalis*, Hubbs and Brown, 1929: 36-38 (in part; discussion of intergradation; hybridization with *Notropis rubellus*; records for Ontario).

TYPE. Mitchill did not designate a type specimen for this species. As *Notropis cornutus* has often been confused with *N. chrysocephalus*, particularly in areas where the two species occur sympatrically, I feel that selection of a neotype is desirable. I therefore designate as neotype of *Cyprinus cornutus* Mitchill (1817) an adult female (UMMZ 174540), 69 mm SL, collected in the Wallkill River, 3 miles southwest of New Paltz, Ulster County, New York, 2 June 1936 by John R. Greeley and Reeve M. Bailey. Five other topotypes (UMMZ 114107) were collected with the neotype.

The more important meristic counts for the neotype are: Anterior dorso-lateral scales 20, circumferential scales 34, lateral-line scales 40, caudal-peduncle scales 16, pectoral rays 16-16, anal rays 9.

NOMENCLATURE. *Notropis cornutus* has been described as new and named eleven times. Types are extant for only five of these nominal species; I have examined them as follows:

- Leuciscus frontalis* Agassiz (MCZ 1751)—holotype
Leuciscus gracilis Agassiz (MCZ 1752)—two syntypes
Platygyrus bowmani Girard (ANSP 3236)—holotype
Hypsilepis cornutus cyaneus Cope (ANSP 3950-3959)—ten syntypes
Notropis universitatis Evermann and Cockerell (USNM 64151)—holotype

From 1885 to 1896 the specific name *megalops* was used in place of *cornutus*. The change was instituted by Jordan on the grounds that Mitchill's (1817: 289) brief diagnosis of *Cyprinus cornutus*, which was published in July or August, 1817, did not constitute an adequate description. Though Mitchill published a detailed description of the species 6 months later, Rafinesque in the meantime had described the same form as *Cyprinus megalops*. Jordan (*in* Jordan and Evermann, 1896b: 281) later reversed himself, and in 1916 the matter was finally resolved by the International Commission of Zoological Nomenclature,

which ruled (Jordan, 1916: 28) that a diagnosis, no matter how brief, constitutes a description providing there is no reasonable doubt as to the identity of the species involved.

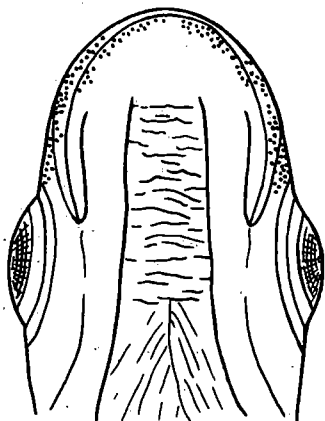
DIAGNOSIS. A species of *Luxilus* distinguished from other members of the subgenus by the following characters: Anterior dorso-lateral scales relatively small, numbering (16) 18 to 24 (30); circumferential scales (26) 30 to 35 (39); sum of anterior dorso-lateral and circumferential scales (42) 48 to 59 (69); mid-dorsal stripe gray-blue, turning to brilliant golden in live breeding males; a light olive stripe, slightly wider than dorsal stripe extending along body on either side of dorsal stripe (figure 15D); below this is another dark stripe, the same width as the dorsal stripe, which also becomes brilliant golden in breeding males; pigment usually absent from chin and gular region (figure 9A), particularly on specimens from west of the Alleghenies.

Further distinguished from the closely related *N. albeolus* by the following characters: Anterior dorso-lateral and circumferential scales smaller (for counts see preceding paragraph, table 7, and tables 9 through 11); considerable red pigment always present on body and fins of nuptial males, usually absent or subdued in breeding females; color of dorsal region olive-brown; scale pockets along side of body usually with considerable pigment, forming prominent crescent-shaped bars, particularly in breeding males; side of body with a bronzy aspect in life, as contrasted to the more silvery aspect of *N. albeolus*; body deep and compressed; maximum size apparently somewhat larger.

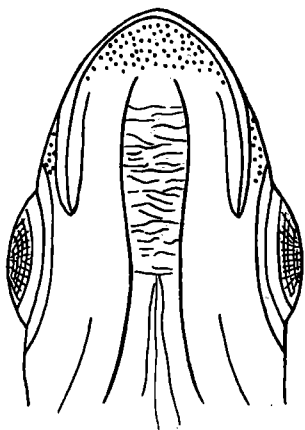
DESCRIPTION. Fin ray and scale row counts and body proportions were taken on varying numbers of specimens; these appear in tables 6, 7, and 9 through 15. Characters mentioned in the diagnosis are not repeated in the following paragraph:

One of the largest forms of *Notropis*, the males sometimes attaining a length of 175 mm or more; sides of body silvery-bronze, with a pink wash in breeding males; breast and belly silvery, with little or no pink in breeding males; pigment wholly or partly absent on chin and gular region in most populations west of the Appalachian Mountains, variable in most populations east of the mountains; top of head blue-brown, becoming deep blue-gray in breeding males; sides of head lighter gray than top; branchiostegals ordinarily colorless, but light rosy in breeding males; dorsal fin slightly dusky, often becoming notably darkened in breeding males; other fins normally plain; breeding males pink or red on distal third or fourth of all fins.

VARIATION. Geographical variation is noteworthy only in number of anal rays, pigmentation on chin and gular area, and in size of anterior dorso-lateral scales. No where is variation consistent enough to be deemed worthy of taxonomic recognition.



A



B

Figure 9. A. *Notropis cornutus*. Individuals living west of the Alleghenies usually lack pigment on the gular areas and most of the chin; those from the Atlantic side often have pigment here. B. *Notropis chrysocephalus chrysocephalus*. This pattern remains rather consistent throughout most of the range of this form. It is often lacking in specimens from the Tennessee River drainage.

Populations in Maine, Nova Scotia, and, presumably, New Brunswick often have many individuals (usually 40 to 60 percent) with 8 anal rays, a variation found only occasionally in other parts of the range (table 13). An analysis of other morphological characters from the Maine-New Brunswick-Nova Scotia area reveals surprisingly low anterior dorso-lateral and circumferential scale counts (table 7), though, as discussed below, they fall within the overall variation of this form. In no other way do these fish differ from typical *cornutus*.

The chin and anterior part of the gular area are unpigmented in populations west of the Appalachian Mountains, but this character shows little apparent consistency in populations east of the Appalachians. Only in the upper Susquehanna River system is pigment consistently absent and, as discussed in the zoogeographical section, this is of value in determining phylogenetic relationships. There can be little doubt that this character is largely under genetic control, a premise substantiated by the fact that this part of the head usually is pigmented in specimens of *N. chrysocephalus* living sympatrically with *N. cornutus*. In many populations over the northern part of the

range specimens of *cornutus* are heavily pigmented not only on the underside of the head, but over the entire body. This heavy pigmentation, often so intense that individuals are almost black, is without doubt a direct result of environmental conditions. Many northern waters are clear but heavily stained or tea-colored, which apparently causes an expansion and multiplication of melanophores over the entire body.

The size of the predorsal scales shows the greatest geographic variation of any character encountered in this species. Within a given population scale size is usually more or less uniform. This is not invariable, and in several series scale size has been found to vary considerably. There may even be great variation between populations in adjacent streams. Scale size generally decreases gradually from south to north, a gradient that is particularly noticeable in Atlantic coast populations. Northeastern populations, however, show an abrupt increase in average scale size (a decrease in scale counts), which reverses the trend seen in other coastal populations of *cornutus*.

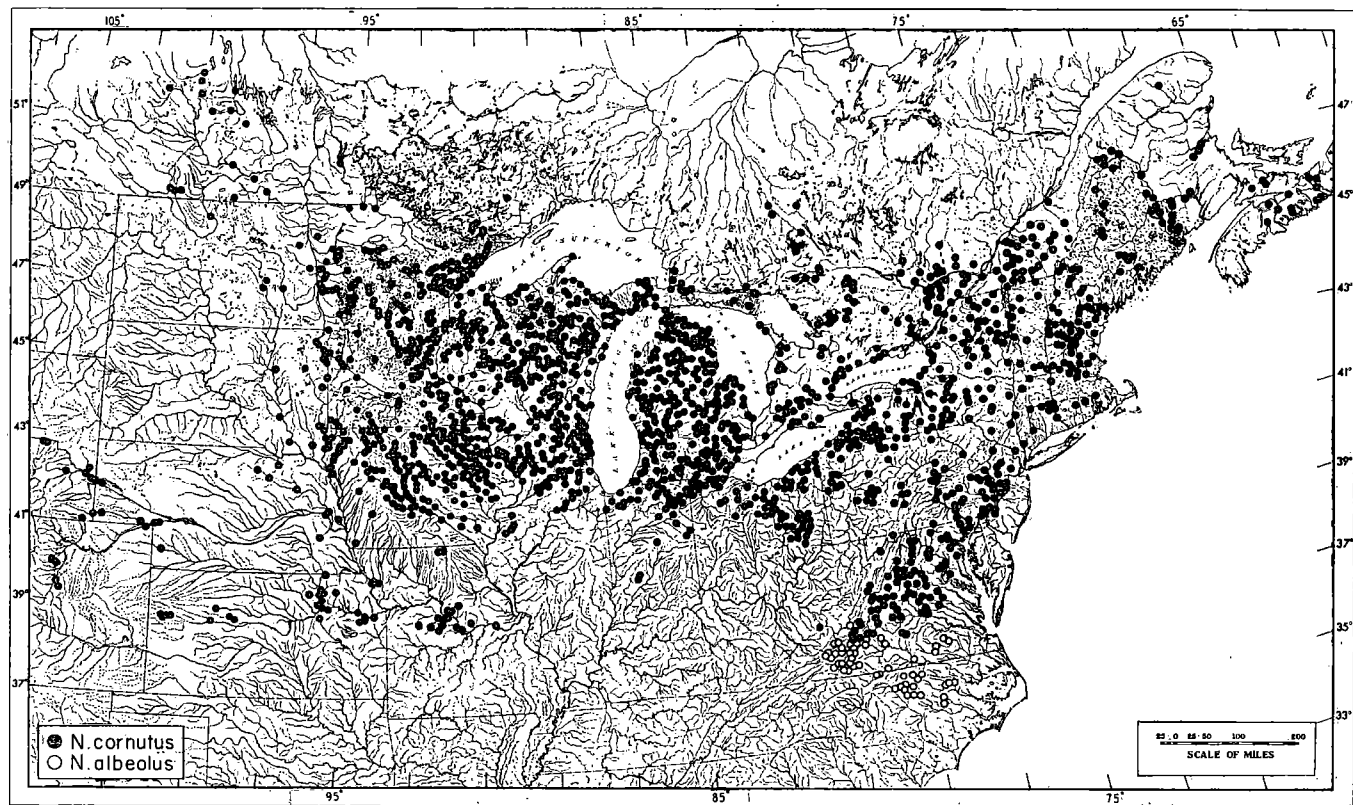
Individuals on the Atlantic coast have larger anterior dorso-lateral and circumferential scales, on the average, than those living west of the Appalachians. In the upper Susquehanna River system scale size averages somewhat smaller than for other coastal populations, a further indication of a post-Wisconsin invasion of the Susquehanna by western populations of *cornutus*. Difference in scale size has been the basis for a subspecific separation of populations from opposite sides of the Appalachians (Hubbs, 1926: 45-46). The desirability of maintaining this separation, however, has been questioned by some authors (Hubbs and Brown, 1929: 39; Greeley, 1938: 67), and their observations are confirmed by the present study.

Sexual dimorphism is pronounced in this species, as in most other nest-building or territorial cyprinids, such as *Semotilus atromaculatus*, *Campostoma anomalum*, and *Hybopsis biguttata*. Some differences are not evident until the breeding season, when males develop a deep red coloration on body and fins, as well as prominent nuptial tubercles on the head, back, anterior part of the dorsal fin, and upper surface of the pectoral fin. Females, in contrast, have a more subdued coloration and usually lack tubercles. Other sexual differences are present throughout the year and become pronounced in males only during the breeding season. This is particularly true of the black crescent-shaped markings on the side of the body, which become notably darker and more prominent. Also the mid-dorsal stripe and the narrow, light, parallel, longitudinal stripes on the lower part of the back become relatively lighter, contrasting markedly with the

rest of the body, and present a definite golden caste in life (Raney, 1940a: pls. 1-4). The golden color disappears shortly after death, and the stripes again appear darker than the surrounding areas. Similar changes have been noted by Lachner (1952: 438) for *Hybopsis biguttata*. Other sexual differences are present at all seasons: The adult male has a deeper and more compressed head and body, longer pectoral and pelvic fins (table 6), a greater amount of fatty tissue on the fins, and reaches a larger maximum size (Raney, 1940a: 5).

DISTRIBUTION. Occurs over a large part of the northern half of the United States and southern Canada from northeastern Colorado, southeastern Wyoming, eastern parts of North and South Dakota and southeastern Saskatchewan eastward in the southern parts of the Hudson Bay drainage, the upper Mississippi and Ohio valleys, and the Great Lakes-St. Lawrence drainage to the Atlantic coast as far south as south-central Virginia.

On the Atlantic slope it ranges from the Gaspé Peninsula and Nova Scotia as far south as the James River system in Virginia; it is common in the St. Lawrence and Great Lakes drainages and occurs in the southern part of the Hudson Bay drainage. The northernmost record is from a tributary of the Red River of the North in Manitoba (Keleher, 1956: 265); the westernmost records are from Wyoming and Colorado. As indicated by Radforth (1944: 89) the northern limits of its range coincide closely with the 65° F. July isotherm. It occurs in the upper part of the Mississippi River drainage, including parts of the Missouri and Ohio systems, but is not recorded from the Missouri River system in Montana, and is known from this system in North and South Dakota only from the James River and other eastern tributaries. It occurs sparingly in the lower Missouri system of Nebraska, Iowa, and Missouri, with most records in central Missouri. In the Platte system it is known mostly from upland tributaries in northeastern Colorado, southeastern Wyoming, and western Nebraska, with a few scattered records from the lowest parts of this drainage. In the Kansas River system it is abundant in places, the westernmost records being from isolated spring-fed streams. It is absent from the greater part of the Ohio River system, but is found in headwater tributaries in Indiana, Ohio, Pennsylvania and New York, being especially common and widespread in the Allegheny and Shenango drainages of New York and Pennsylvania. Isolated relict populations occur to the south in the lower Kanawha River system of West Virginia (Paint Creek, Fayette County), and in a tributary of the middle part of the White River in Indiana (Mill Creek, Hendricks and Morgan counties).



Map 4.

A specimen of *N. cornutus* in the United States National Museum (USNM 86211) bears the locality "vicinity of Medicine Hat, Alberta". The presence of several eastern species such as *Semotilus corporalis* and *Pimephales notatus* in the same collection suggests the locality data may have been transposed.

A single specimen supposedly collected in the Black River, Clark National Forest, Missouri (UMMZ 117557) also is regarded as suspect. There are no other records of this species from the Black River basin, and the next closest populations are in the Missouri River system approximately 150 miles to the north. *N. chrysocephalus*, which was taken in the same collection, is common throughout the Black drainage and, from the known relative distribution of these two forms it is rather unlikely that they should occur sympatrically so far south. This record may have resulted either from an introduction or, more likely, from an accidental transfer of specimens in the laboratory.

Two records of *N. cornutus* from the Arkansas River drainage in Kansas (UMMZ 122075, Winfield, Cowley County; KU, Rock Creek, near Iola, Allen County) are also thought to be due to transposed data. Other collections from Kansas have been found with faulty labeling, and until these records are substantiated it seems best to treat them as erroneous.

The populations in the headwaters of the Platte and Kansas rivers, those from the middle part of the White River, Indiana, and in the lower Kanawha River system, West Virginia, are the most interesting and significant ones in the range. Apparently *N. cornutus* once was much more widely distributed than at present, and its disappearance from large areas of the Great Plains can be attributed to the drying this area has undergone since the Wisconsin glacier retreated northward.

The absence of *N. cornutus* from a large part of the Ohio River system is due partly to natural conditions and partly to man's influence. Trautman (1957:357) has shown that *cornutus* is now missing from areas where man's activities have caused the streams to warm and silt and the flowing springs to disappear. Commonly it has been replaced by *N. chrysocephalus*, which reflects the two species' close ecological relationship and the tolerance of *chrysocephalus* for warmer, more turbid conditions. Early collections from the Ohio River system show that *chrysocephalus* has long been the dominant form and evidently started to replace *cornutus* before man started altering the landscape. Apparently a warming of the streams occurred, and though *cornutus* probably could have survived had no other factor been involved, *chrysocephalus* was favored by

the warmer conditions and largely dispossessed it in the southern part of its range. As these species occupy similar ecological niches, competition apparently extirpated *cornutus* from most of the Ohio Valley.

The presence of isolated populations of *cornutus* in the middle part of the White River system in south-central Indiana and in the lower Kanawha River system of West Virginia strongly supports this view. Although these populations may have been introduced by man, the evidence strongly favors their presence as natural. Though populations of *chrysocephalus* live only short distances away (see maps 4 and 5), there is no evidence that it has ever occurred in these pockets occupied by *cornutus*. I collected in these areas in August and September 1958, some 25 years after the *cornutus* colonies were discovered, and failed to find *chrysocephalus*. Apparently some barrier has prevented its moving in here as it has elsewhere.

In the Indiana population the barrier is almost certainly ecological. Mill Creek is unusual in having a shifting-sand bottom almost throughout its length, with short stretches of rubble and gravel riffle in a few places where sand has not covered the bottom. *N. cornutus* undoubtedly spawns in these limited stretches and has been able to survive by this thin margin. Apparently the stream is fed by a number of small springs, for on 26 August 1958 the water temperature in a shallow, unshaded section of the stream was only 70° F., much lower than might be expected considering the weather at the time. This stream is also one of the few places in southern Indiana where *Rhinichthys atratulus* can still be found. The habitat in Mill Creek is marginal for *cornutus* and has not allowed the population to reach large numbers. Paradoxically it has also permitted the species to survive, for the long stretches of shifting sand bottom have apparently effectively barred the movement of *chrysocephalus* into the area.

The reasons for *chrysocephalus*' absence from Paint Creek in the lower Kanawha system are less obvious. The area where *cornutus* was collected appears suitable for *chrysocephalus*, which has been collected near the mouth of Paint Creek. Thus some barrier, either physical or ecological, must exist in the lower half of the stream. In its lower reaches Paint Creek is a gravel-bottomed stream consisting almost entirely of shallow riffles with few or no deep pools. Perhaps this habitat is unsuitable for *chrysocephalus*.

LIFE HISTORY AND ECOLOGY. *N. cornutus* prefers small to medium-sized streams with clear, cool, weedless water, a moderate to swift current, and alternating pools and riffles, the latter with a gravel or

rubble bottom. Though the species is confined to this type of habitat over most of its range, populations in prairie and plains areas, particularly in Missouri, Iowa, and Nebraska, tolerate extreme turbidity and seasonally warm water provided a rubble or gravel bottom and a good current are still present. These factors seem more critical for spawning than clarity of water. Two other fishes, *Rhinichthys cataractae* and *Hybognathus hankinsoni*, which are commonly thought to be limited to clear, cool waters, are also able to survive under these same conditions of turbidity and high temperatures.

N. cornutus is usually found at the head or foot of riffles, most often the latter, but it tends to avoid the actual riffle except at spawning time. It likewise avoids still waters, though individuals may occasionally be found in them, especially if a slight current is present.

Although this species is generally a stream fish, it is also common in lakes in the northern part of its range. The apparent geographical bias probably has several causes. Lakes are relatively few in the southern part of its range and ecologically unsuitable. The northern lakes differ in usually having clean, weedless, wave-washed shores with gravel or rubble bottoms, thus in part duplicating the preferred stream conditions. The species is not known to spawn in lakes, and apparently enters them from feeder streams. Strangely neither *cornutus* nor *chrysocephalus* occurs, except as strays, in western Lake Erie where ecological conditions similar to those of inland streams permit the presence of such usually stream-inhabiting fishes as *Noturus flavus*, *Etheostoma blennioides*, and *Etheostoma flabellare*.

Because *cornutus* is so common and so easily observed, much has been written about its ecology and life history. Numerous food study accounts exist, many of which Adams and Hankinson (1928) reviewed. Largely carnivorous, it apparently prefers aquatic insects and their larvae. The diet is controlled largely by food availability, and plant material is not uncommon fare. This shiner usually feeds at the surface or in the upper water levels, but it may also take food on the bottom. This versatility in feeding habits probably partly explains its great success as a species.

Numerous accounts of its spawning behavior have appeared. Raney (1940a) reviewed all prior literature and also presented detailed new observations. The species may spawn from mid-May to mid-July, the time depending mainly on the water temperature; a minimum of at least 64° F. apparently must be attained before spawning can occur (Raney 1940a: 4). Although spawning has been observed in water as warm as 83° F., this is unusual, for spawning is normally completed before such temperatures are reached.

Spawning takes place usually in shallow to moderately deep riffles (3 to 8 inches) with a gravel or rubble bottom. The fish may excavate small depressions in gravel or sand in running water, or utilize the nests built by other species, even when these are in pools. It appears to prefer the nests of other species when available, with those of such nest-building forms as *Exoglossum maxillingua*, *Semotilus atromaculatus*, *Semotilus corporalis*, *Camptostoma anomalum*, and species of *Hybopsis* (subgenus *Nocomis*) most frequently utilized.

Males arrive first on the riffles, sometimes in large numbers (Fowler, 1909; 540; Raney 1940a: 5). There each individual attempts to hold a small territory. Females meanwhile remain a short distance downstream, usually in the first pool. When ready to breed the females move upstream, take a position over a male, and shortly thereafter the spawning act is consummated.

Notropis albeolus Jordan

White Shiner, Figures 10, 11, 15C, 15F, map 4

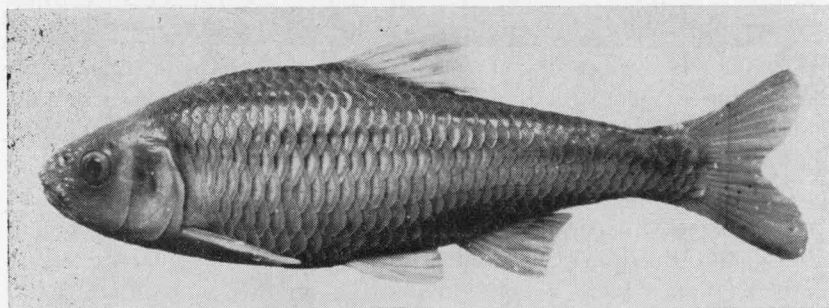


Figure 10. Adult male *Notropis albeolus*, CU 20322, 120 mm SL, from South Fork, Roanoke River, Allegheny Springs, Roanoke County, Virginia. (This specimen is typical of those in the Neuse, Tar, and Cape Fear drainages.)

Hypsilepis cornutus cornutus, Cope, 1870: 459 (misidentification; Neuse River, North Carolina).

Luxilus cornutus, Jordan, 1876b: 286-287 (misidentification in part; range).

Notropis cornutus, Goldsborough and Clark, 1908: 35 (misidentification; Horsepen Creek, Virginia).

Notropis megalops, Jordan, 1888: 58-59 (misidentification in part; description; range).

Notropis megalops albeolus Jordan, 1889b: 123, 125, 129 (original description; comparison with *N. megalops*; type locality Roanoke River, near Roanoke, Virginia; also in Tar and Neuse river drainages, North Carolina).

Notropis albeolus, Evermann and Cox, 1896: 305, 309 (synonymy; Neuse River system, North Carolina).

Luxilus cornutus albeolus, Jordan, 1929: 82 (description; range).

Luxilus albeolus, Jordan, Evermann and Clark, 1930: 129 (range; reference to original description).

Notropis cornutus albeolus, Fowler, 1945: 29 (Roanoke and Neuse rivers, North Carolina).

Notropis coccogenis, Fowler, 1922: 12 (misidentification; tributary of Dan River, Virginia).

TYPE. *Notropis megalops albeolus* was described on the basis of specimens David Starr Jordan collected in the Roanoke River at Roanoke, Virginia, 31 July-2 August 1888. Although no types were designated, the United States National Museum has a series of 16 specimens with the following data: "Roanoke River, Roanoke, Virginia, 1888, U. S. Fish Commission, D. S. Jordan;" the catalogue entry is dated 8 April 1889. As these seem to comprise at least part of the syntypic material of *N. albeolus*, I hereby designate as lectotype of *Notropis megalops albeolus* an adult, 76 mm SL, which retains the original catalogue number (USNM 40177). Fourteen other specimens of the original syntypic series now become paratypes and are recatalogued as USNM 177840. The remaining individual is *Notropis ardens*, and has been recatalogued under that name.

DIAGNOSIS. A species of *Luxilus* distinguished from other members of the subgenus by the following characters: Red pigment usually lacking on body and fins of nuptial males, always absent in females; dark pigmentation absent from dorsal and caudal fins; scale pockets along side of body with little or no pigment, resulting in few or no crescent-shaped bars; side of body silvery in life; no prominent, parallel, longitudinal stripes running along length of dorso-lateral region of body (figure 15C); a light olive stripe, slightly wider than dorsal stripe, extending along length of body on either side of mid-dorsal stripe.

N. albeolus is further distinguished from the closely related *N. cornutus* by the following characters: scales relatively large, those in the anterior dorso-lateral series (15) 17 to 20 (23); those in the circumferential series (24) 26 to 30 (33); sum of anterior dorso-lateral and circumferential scales (41) 43 to 50 (55); color of dorsal region olive-green; side of body silvery in life, as contrasted to the more bronzy aspect of *N. cornutus*; broad light stripes on either side of mid-dorsal stripe less evident in breeding males; body usually slender and terete in northern populations, body form in southern populations not appreciably different from *N. cornutus*; maximum size apparently somewhat smaller, adult males attaining a maximum length of about 130 mm.

A comparison of *N. albeolus* and *N. cornutus* is presented in tables 3, 6, 7, and 9 through 15, and in figures 15C through 15F.

DESCRIPTION. Fin ray and scale row counts and proportional measurements are listed in tables 6 through 15. Characters mentioned in the diagnosis are not repeated in the following paragraph:

Mid-dorsal stripe grayish-black, slightly more than half as wide as eye, and extending around base of dorsal fin; a light streak about the same width as dorsal streak extending along body on either side of dorsal streak (this character not nearly so clearcut and distinct as in *N. cornutus*); below each of these light streaks is another dark streak of the same width and slightly lighter color than the dorsal streak (this and the preceding character evident only in breeding males); pigment on chin and anterior part of gular region either present or absent; pinks and reds usually absent on body, rarely present on snout of breeding males; pink or red coloration usually absent from all fins at all ages, occasionally present on dorsal, caudal, anal, and pelvic fins of breeding males; dorsal fin slightly dusky, but never greatly darkened in breeding males; other fins plain; nuptial tubercles present over head, the tips pointing straight upward, possibly not as well developed as in *N. cornutus* and *N. chrysocephalus* (relatively few tuberculate specimens of *albeolus* have been examined).

VARIATION. *Notropis albeolus* exhibits the most interesting morphological variation found in any form of *Luxilus*. Differences in body proportions in particular contribute to a rather perplexing problem involving its correct taxonomic status. In general specimens from the New and Roanoke drainages seem similar in appearance, as do those from the Neuse, Tar, and Cape Fear systems. This similarity is particularly noticeable in body shape; specimens from the New and Roanoke tend to be more slender and terete, those from the other drainages are usually deeper and more compressed. Proportional measurements for individuals from the New and Roanoke aver-

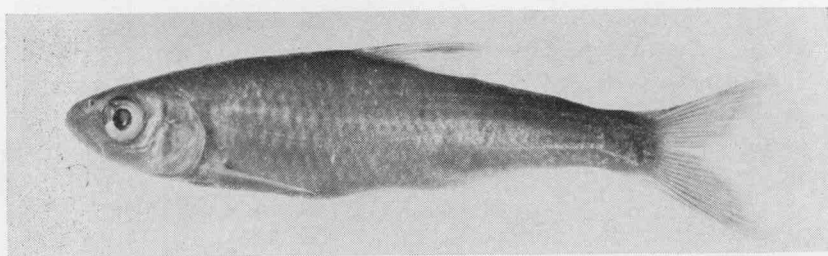


Figure 11. Adult *Notropis albeolus*, USNM 101339, 76.5 mm SL, from Waqua Creek at highway 140, Brunswick County, Virginia.

age less for a number of characters, particularly depth of body, depth of head, and distance from dorsum to lateral line (table 6). Also depth of caudal peduncle, length of head, mouth gape, width of body, width of head, width of eye, length of upper jaw, and all fin lengths average proportionately slightly less; the caudal peduncle, on the other hand, averages slightly longer. Although these differences are usually rather marked, atypical specimens can be found in both the northern and southern populations (figure 10).

Morphological differences of the above magnitude exist among individuals of *N. cornutus*. In that form these differences can always be explained by environment, slender-bodied fish usually being found where a shortage of food exists. As food is apt to be scarcer in cool, relatively sterile northern streams, slender-bodied individuals of *cornutus* tend to occur to the north. The morphological differences in *albeolus* cannot be explained by environment. While streams of the Roanoke and New River systems are in general clearer, swifter, and presumably somewhat more sterile than those of the Neuse, Tar, and Cape Fear drainages, this can hardly explain such sharp differences in body proportions. In addition the closely related *Notropis cerasinus*, a common species in the headwaters of the Roanoke, is characterized by a body form fully as deep and compressed as either that of *N. cornutus* or of the southern population of *N. albeolus*. This strongly suggests that the differences in body form in *albeolus* have a genetic rather than an environmental basis. Consequently *N. albeolus* may best be regarded as containing two distinct races, one inhabiting the New and Roanoke drainages, the other the Neuse, Tar, and Cape Fear systems.

The slight difference in scale counts between the two races is subject to considerable overlap. Table 7 shows specimens from the New and Roanoke drainages average about one scale more in the dorso-lateral and circumferential scale series than do those from the other systems. The upper limit (55) for this count in specimens from the more northern drainages is 4 more than for specimens from the Neuse, Tar, and Cape Fear; the lower limit (42) is 1 more.

The crescent-shaped markings that occasionally appear on the side of the body are more common in specimens from the southern drainages. Other kinds of variation apparently occur equally in both races.

The lack of red pigment on both the body and fins, including the breeding males, is one of this fish's most distinctive characters. Though this feature holds true most of the time, Robert D. Ross informs me in a letter that occasionally breeding males from both the

New and Roanoke show some red on the fins or body. Large adult males taken in the Tar River 20 August 1946 by Reeve M. and Joseph R. Bailey (UMMZ 147583) also showed some red on the caudal fin. Red pigment when present occurs only on the tips of the fins, not including the pectorals. I have never seen specimens of *albeolus* so colored, so I cannot assess possible differences from *cornutus* in distribution of red on the fins. Apparently the only part of the body on which red pigment appears is the snout.

Some individuals, particularly those from the Neuse, Tar, and Cape Fear systems, have a few vertical crescent-shaped bars along the side similar to those in *cornutus*, *cerasinus*, and *chrysocephalus*. Such specimens are extremely difficult to distinguish in preservative from sparsely pigmented individuals of *cornutus*.

Analysis of vertebral variation in *albeolus* (table 8) shows that specimens from the Roanoke and New river systems usually have 40 vertebrae, individuals from the Neuse generally 39. Specimens from the Tar drainage have either 39 or 40 vertebrae with equal frequency. The Cape Fear population could not be analyzed because of lack of material. At first glance the differences in vertebral counts appear to be directly correlated with variation in body depth, though the presence of either 39 or 40 vertebrae in Tar River specimens indicates otherwise. Possibly these counts reflect ecological differences between the several streams.

RELATIONSHIPS. The forms *albeolus* and *cornutus* are so close to the species-subspecies line in their degree of evolution that it is difficult to decide their proper taxonomic relationship. In the past *albeolus* has been treated both as a subspecies and, in recent years, as a species, which Moore (1957: 126) has questioned.

I myself have had doubts about the correct taxonomic status of *albeolus*. My first inclination (1961a: 2411) was to regard it as a subspecies of *N. cornutus*, primarily because not all preserved specimens of the two forms can be distinguished. This situation is by no means unique, and may be noted in other North American Cyprinidae, for example in species of the genus *Hybopsis* (subgenus *Nocomis*). Members of this group are very similar in over-all appearance, and several forms are positively distinguishable only by means of the number and arrangement of the nuptial tubercles on the heads of breeding males. Thus though only a small percentage of individuals of these species can be told apart, the constant differences in the character of the tubercles leaves little doubt that their relationships are at the specific level. Many other pertinent examples exist in fishes, as well as in other groups of animals.

The fact that some individuals of *cornutus* and *albeolus* cannot be distinguished does not disprove their specific distinction. Differences in color and in other features of body pigmentation, in size of the anterior dorso-lateral scales, and in body shape all argue for specific recognition.

DISTRIBUTION. Restricted to the Roanoke River system (including the Chowan) in Virginia and North Carolina, parts of the New River system in Virginia and West Virginia, and to the upper parts of the Neuse, Tar, and Cape Fear systems in North Carolina.

The apparent scarcity of *albeolus* from the more lowland tributaries of the Neuse, Tar, and Cape Fear drainages probably is due mainly to lack of collecting. Most of the specimens examined from these systems were taken during the spring when the streams are usually high, particularly those in the area below the Fall line. Recent autumn collections from the lowland areas indicate that this species is, in fact, fairly common there.

In recent years *N. albeolus* apparently has come to occupy a much more extensive area of the New River system than formerly. Jordan (1889b: 140-141) did not record it in his 1888 collections from Reed Creek, near Wytheville, Virginia, yet the species is plentiful there today. Carl L. Hubbs failed to take it in Wolf Creek, Bland County, Virginia in 1936, where it was collected both in 1953 and 1956 (UMMZ 169176 and UMMZ 174433). A series of 25 specimens (USNM 177876), Frank J. Schwartz collected in the Greenbrier River near Caldwell, Greenbrier County, West Virginia 13 October 1956 also represents a record for an area where this form was not previously recorded, despite rather intensive collecting both by Hubbs and John Addair during the 1930's. Although these range extensions may have resulted from human introduction, the fish could equally plausibly have found their way without help.

LIFE HISTORY AND ECOLOGY. No detailed work on the ecology or life history of *N. albeolus* has been published. The only data that have appeared consist of general habitat descriptions or collection sites.

This species seems to prefer the same habitat as *N. cornutus*, cool, clear, medium-sized streams with alternating riffles, flowing pools, and a rubble to rocky bottom. Although it is usually collected at the foot of riffles in midwater, it may on occasion be found in quite dissimilar situations. Some 28 specimens (UMMZ 174749) I collected in the Otter River, Campbell County, Virginia on 12 June 1956 were living in very warm, turbid, swift water on a bottom com-

posed entirely of shifting sand. Interestingly I also found here the closely related *Notropis cerasinus*, which is ordinarily restricted to headwaters of the Roanoke and New systems. Possibly both species had temporarily moved or been washed out of a nearby tributary where conditions were more to their liking.

Populations of *albeolus* in the Neuse, Tar, and Cape Fear drainages are found more frequently in turbid situations than are those in the New and Roanoke systems. This probably reflects ecological differences rather than racial dissimilarities in physiological tolerances, which are nevertheless possible, especially in view of the rather marked morphological differences between the two races.

N. albeolus probably breeds in late April or early May, an estimate based largely on circumstantial evidence. All spring collections I examined were taken either in early April, late May, or early June, and none contained gravid females or high tuberculate males.

Notropis chrysocephalus

Striped Shiner.

DIAGNOSIS. A species of *Luxilus* distinguished from the closely related *Notropis cornutus* by: larger scales, those in the anterior dorso-lateral series (12) 13 to 16 (19); circumferential scales (23) 24 to 29 (32); sum of anterior dorso-lateral and circumferential scales (36) 37 to 45 (48); dorso-lateral scale pockets darkest around edges, which, with the intensification of pigment caused by the overlapping scales, results in three parallel stripes running lengthwise along dorso-lateral part of back and meeting posterior to dorsal fin, thus forming distinct "V's" when seen from above; pigment usually present on chin and gular region; mid-dorsal stripe not turning brilliant golden in breeding males; dorso-lateral part of back without a light olive stripe extending along back just lateral to dorsal stripe.

DESCRIPTION. A large species of *Luxilus*, the males sometimes attaining a length of 175 mm or more; body and head deep and compressed, especially in adult males; pectoral fin rays 15 to 17 (18); lateral-line scales (36) 37 to 40 (42); dorsal region brown; scale pockets along side of body with considerable pigment on some scales forming a number of vertical crescent-shaped bars; side of body metallic-bronze in life; mid-dorsal stripe gray-black, slightly more than half as wide as eye, and extending around base of dorsal fin.

Notropis chrysocephalus chrysocephalus (Rafinesque)

Northern Striped Shiner, figures 9B, 12, 15B, map 5.

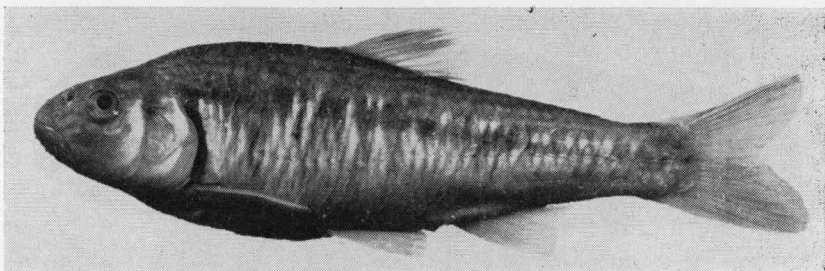


Figure 12. Adult male *Notropis chrysocephalus chrysocephalus*, UMMZ 154507, 140 mm SL, from Clear Creek, Wildie, Rockcastle County, Kentucky.

Luxilus chrysocephalus Rafinesque, 1820a: 48 (original description; type locality Kentucky).

Notropis cornutus chrysocephalus, Hubbs, 1926: 46 (recognized as a distinct form; intergradation with *N. c. frontalis*; name *frontalis* applied to *chrysocephalus* by Jordan and Evermann; nominal forms *plumbeolus* and *gibbus* of Cope are synonyms; Great Lakes drainage).

Luxilus cornutus chrysocephalus, Jordan, 1929: 82 (description; range).

Notropis chrysocephalus chrysocephalus, Gilbert, 1961a: 2411-2412 (general account).

Notropis chrysocephalus, Larimore and Smith, 1963: 323, 328, 332-333, 335, 338-339, 343, 345, 358, fig. 31 (Champaign County, Illinois).

?*Rutilus plargyrus* Rafinesque, 1820a: 50-51 (original description; type locality Kentucky).

Leuciscus plargyrus, Kirtland, 1845: 26-27, pl. 8, fig. 2 (in part; description; range; Ohio).

Luxilus plargyrus, Jordan, 1876a: 94 (review of Rafinesque's species).

?*Leuciscus gibbosus*, Storer, 1846: 166 (in part; description; Huntsville, Alabama).

?*Hypsolepis gibbosus*, Agassiz, 1854: 359 (Storer's *Leuciscus gibbosus* placed in genus *Hypsolepis*).

?*Plargyrus gibbosus*, Girard, 1856: 196 (in part; list of related species; Alabama).

Plargyrus typicus Girard, 1856: 196 (in part; name replaces Rafinesque's *Rutilus plargyrus*).

Plargyrus cornutus, Girard, 1856: 196 (misidentification in part; list of species).

Hypsolepis cornutus, Putnam, 1863: 7 (misidentification in part; in Harvard collection).

Leuciscus cornutus, Günther, 1868: 249 (misidentification in part; specimens in British Museum from Michigan, Lake Erie, and Miami River).

Hypsolepis cornutus, Cope, 1869b: 372-373 (misidentification in part; description; variation; range; Pennsylvania).

Luxilus cornutus, Jordan, 1876a: 94 (misidentification; review of Rafinesque's

- species; *Luxilus chrysocephalus* Rafinesque synonymized with *Cyprinus cornutus* Mitchell).
- Minnilus cornutus*, Jordan and Swain, 1883: 249 (misidentification; Clear Fork of Cumberland River, Kentucky).
- Notropis cornutus*, Gilbert, 1884b: 202 (misidentification; restoration of genus name *Notropis*; East Fork of White River, Indiana).
- ?*Cyprinus cornutus*, Call, 1896: 15 (misidentification; Falls of the Ohio, Louisville, Ky.; possibly refers to another species since *Notropis megalops* also listed).
- Notropis cornutus cornutus*, Knapp, 1953: 61 (misidentification; replaces *N. cornutus isolepis* immediately to north).
- Notropis cornuta*, Hubbs, 1955: 10 (misidentification in part; hybridization with *N. rubella*).
- Alburnops plumbeolus* Cope, 1864: 282 (original description; type locality Saginaw River, Flint, Michigan).
- Hypopsis plumbeolus*, Jordan, 1876b: 283 (description; range).
- Minnilus plumbeolus*, Jordan and Gilbert, 1883: 192 (description; range).
- Luxilus plumbeolus*, Jordan, 1884: 294 (description; range; synonymy).
- Hypsilepis frontalis*, Cope, 1864: 279 (misidentification; description; southeastern Michigan).
- Hypsilepis cornutus frontalis*, Cope, 1867: 159 (misidentification; description; Holston River, Virginia).
- Minnilus cornutus frontalis*, Jordan and Gilbert, 1883: 187 (misidentification; description; range).
- Notropis megalops frontalis*, Jordan, 1885b: 814 (misidentification; in list; synonymy).
- Notropis cornutus frontalis*, Jordan and Evermann, 1896a: 256 (misidentification; range; reference to original description).
- Hypsilepis cornutus gibbus* Cope, 1867: 158 (original description; type locality southeastern Michigan).
- Minnilus cornutus gibbus*, Jordan and Gilbert, 1883: 187 (description; range).
- Hypopsis lacertosus* Cope, 1869a: 230-232 (original description; type locality Bear Creek, tributary to Middle Fork of Holston River, Virginia).
- Alburnops lacertosus*, Jordan, 1878: 420 (range).
- Hydrophlox lacertosus*, Jordan and Brayton, 1878: 64, 84-85 (Holston River, Virginia).
- Minnilus lacertosus*, Jordan and Gilbert, 1883: 192 (description; headwaters of Tennessee River).
- Luxilus lacertosus*, Jordan, 1884: 294 (description; range; synonymy).
- Notropis lacertosus*, Jordan, 1885b: 814 (range).
- Luxilus cornutus lacertosus*, Schrenkeisen, 1938: 129 (headwaters of Tennessee River).
- Notropis megalops*, Jordan, 1885a: 123 (misidentification in part; *Plargyrus typicus* a synonym).
- Notropis cornutus: chrysocephalus* \times *frontalis*, Hubbs and Brown, 1929: 36-39 (in part; discussion of intergradation; hybridization; records for Ontario).

TYPE. Rafinesque designated no type specimen for this species. As *N. chrysocephalus* has often been confused with *N. cornutus*, par-

ticularly in areas where the two species occur sympatrically, I feel the selection of a neotype is desirable. I therefore designate as neotype of *Luxilus chrysocephalus* Rafinesque (1820) an adult male (UMMZ 174539) 99 mm SL, collected in a creek about 6 miles SSW of Danville, off highway 35, Lincoln County, Kentucky 5 April 1953 by R. M. Bailey and party. Six other topotypes (UMMZ 165232) were collected with the neotype.

The more important meristic counts for the neotype are: Anterior dorso-lateral scales 14, circumferential scales 28, lateral-line scales 38, caudal-peduncle scales 16, pectoral rays 17-17, anal rays 9.

NOMENCLATURE. The "large-scaled form" of *N. cornutus* has long been recognized by ichthyologists. Many chose to regard it merely as a variant of *cornutus*, although some separated it subspecifically. Consequently the identification of *N. chrysocephalus* in the literature often must be resolved by geography. Cope (1864: 279) believed Agassiz's description of *Hypsilepis frontalis* was based on this species, and as a result the name *frontalis* was incorrectly applied for more than 50 years. Not until 1926 did Hubbs point out that *frontalis* represents the fine-scaled northern form, and that the name *chrysocephalus*, which Jordan (1876a: 94) had placed in the synonymy of *Cyprinus cornutus* Mitchill, applied to the coarse-scaled southern form.

Cope's (1867: 158) description of *Hypsilepis cornutus gibbus* possibly was based on the hybrid *Notropis cornutus* \times *Notropis chrysocephalus*. Although Cope recorded only 16 predorsal scales for this form, individuals of the cross sometimes have almost as large scales as does *chrysocephalus*. Unfortunately the types of *gibbus* apparently no longer exist so this question is impossible to resolve.

An examination of the seven syntypes of *Alburnops plumbeolus* Cope (ANSP 2055-2061) shows that six specimens are *N. chrysocephalus*, the other *Notropis heterodon*. To fix the status of the specific name *plumbeolus* and to prevent possible confusion with *Notropis heterodon* I designate as lectotype of *Alburnops plumbeolus* a specimen 40.5 mm SL, catalogued as ANSP 2055. Five specimens become paratypes (ANSP 2056-2060), while the last is recatalogued as *Notropis heterodon* (ANSP 2061).

Cope (1869a: 230-232) described *Hybopsis lacertosus* on the basis of five specimens from Bear Creek, a tributary of the Middle Fork of the Holston River, Virginia. Nothing in the original description indicates how this form differs from *Notropis c. chrysocephalus* or *Notropis coccogenis*, the species of *Luxilus* occurring in this area, although the name "lacertosus" signifies a slender body. Unfortunately,

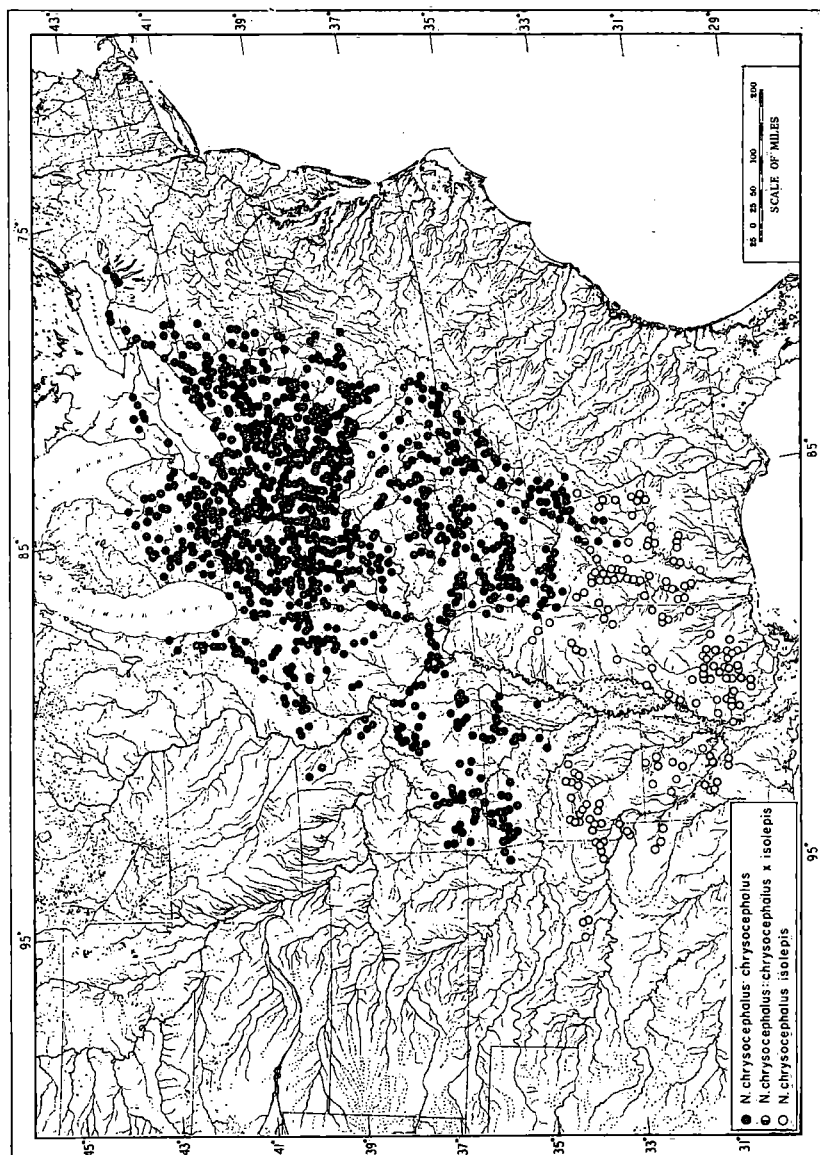
the types (ANSP 2835-2839) are in extremely poor condition, the bodies having become too decomposed as to be of aid in recognition. The heads, including the pharyngeal teeth are still intact, as are most of the fins. The head is deep in all specimens, in no case does the lower jaw project notably beyond the upper, and there is no sign of a black band on any dorsal fin. As all the above characters are indicative of *Notropis chrysocephalus*, I regard *Hybopsis lacertosus* Cope as a synonym of that species.

DIAGNOSIS. A subspecies of *N. chrysocephalus* distinguished from *N. c. isolepis* by: Slightly smaller scales, those in anterior dorso-lateral series (13) 14 to 16 (19); circumferential scales (23) 26 to 29 (32); sum of anterior dorso-lateral and circumferential scales (38) 40 to 45 (48); predorsal and anterior dorso-lateral scale rows more crooked and uneven; anterior dorso-lateral stripes crooked, more poorly defined, and not uniformly parallel (figure 15B); pigment usually present on chin and gular region (figure 9B often absent in specimens from Tennessee drainage).

DESCRIPTION. Fin ray and scale row counts and body proportions were taken on varying numbers of specimens. These appear in tables 6 and 9 through 15. Characters mentioned in the description of *Notropis chrysocephalus* and in the diagnosis are not repeated in the following paragraph:

Arrangement of circumferential scales above and below lateral line (11-2-10) 12-2-12 to 14-2-13 (15-2-15); dorso-lateral scale pockets darkest around edges which, with the intensification of pigment caused by the overlapping scales, results in three crooked, fairly well-defined parallel stripes running lengthwise along dorso-lateral part of back; side of body silvery-bronze with a deep rose-red in breeding males; breast and belly silvery with little or no pink in breeding males; branchiostegals colorless, with a decided rosy wash underlain with gray in breeding males; distal third or fourth of dorsal, caudal, anal, and pelvic fins pink in breeding females, deep pink to red in breeding males, except for extreme distal edges which are white; outer fifth of pectoral fin rosy, distal edge white in nuptial males; basal two-thirds of dorsal fin normally pallid, with a pinkish blush in nuptial males; basal two-thirds to three-fourths of anal, pelvic, pectoral, and caudal fins pallid.

VARIATION. Relatively little morphological variation occurs in this subspecies. Populations containing individuals with slightly smaller scales are found throughout the range, but the resultant high counts fall well within the normal range of variation for the species and pose no nomenclatural problem. A series of 35 specimens from the Coosa



Map 5.

River system, Alabama (UMMZ 175746) which showed the highest counts for any individuals of this form exhibited a number of abnormalities such as deformed fins and "bulldog" snout. These anomalies were also found in other species from the same locality, suggesting that some factor such as the chemical composition of the water was responsible, probably during early embryological development.

Occasionally the ordinary dark pigment on the anterior dorso-lateral scale pockets is either faint or virtually absent. In such cases *chrysocephalus* approaches *cornutus* in appearance and looks like a hybrid between these two species. The resemblance is merely superficial, for such individuals are found in areas where it seems unlikely that *cornutus* has ever occurred. As these are typical *chrysocephalus* in all other respects, the suppression of pigment along the upper side of the body apparently is of no special significance.

Individuals occasionally lack pigment on the chin and gular region. This is particularly common in the Tennessee River system, where the pigment is wholly or partially absent in approximately half the individuals.

DISTRIBUTION. Found throughout a large part of east-central United States from the upper Coosa River system in Alabama and Georgia and the lower Mississippi River drainage in Alabama, north-eastern Mississippi, Tennessee, northern Arkansas, and northeastern Oklahoma, northward to the lower Great Lakes region from south-eastern Wisconsin to western New York.

Common in the upper Coosa River system of Georgia and Alabama, but becomes increasingly less common in the lower parts of that drainage. It is abruptly replaced by *N. c. isolepis* a short distance north of the confluence of the Coosa and Tallapoosa rivers, with no apparent evidence of intergradation. It also occurs in the easternmost tributaries of the Cahaba and Black Warrior rivers and is replaced by *isolepis* in the lower parts of these drainages also. Collections are at present not extensive enough to permit an accurate picture of the relationships of the two forms, although intergradation is proved by a series of 16 specimens (UMMZ 168613) from the headwaters of the Black Warrior system.

Found in the headwaters of the Illinois and Neosho rivers (tributaries of the Arkansas) in northeastern Oklahoma, northwestern Arkansas, and southwestern Missouri. It has not yet been recorded from Kansas, but should occur in the extreme southeast corner of that state. To the east *chrysocephalus* is common throughout most of the White and Black river systems of northern Arkansas and southern Missouri, but occurs sparingly in the St. Francis River system and other small

tributaries of the Mississippi River in eastern Arkansas and Missouri.

Apparently absent from western Tennessee west of the Tennessee River system, although it is quite common throughout most of the Tennessee drainage itself in Tennessee, extreme northeastern Mississippi, northern Alabama, northwestern Georgia and southwestern Virginia. It has not yet been reported from North Carolina.

To the north it is one of the most abundant cyprinids in the Ohio River system, except for the upper Kanawha (New) River drainage, where it is practically absent—the single record for this drainage (USNM 177878) is believed an introduction.

Common in tributaries of the Gasconade and Meramec rivers in Missouri, it is rare in the Osage drainage of that state. It is found in some of the smaller tributaries of the Mississippi River in eastern Missouri both north and south of the Missouri River, and occurs in a few scattered localities in northeastern Missouri. There are as yet no records for Iowa. It is common in the Illinois River system in Illinois and in suitable habitats of the more eastern and southern parts of the state, but it has not yet been found west of the Illinois drainage.

It occurs throughout most of the lower Great Lakes region and is entirely absent only from the Lake Superior drainage. Its apparent absence from the more northern tributaries of the other Great Lakes seems to be related primarily to temperature, as its northern distributional limit coincides closely with the 70°F July isotherm (Radforth, 1944: 89). In the Lake Michigan basin it is known from extreme southeastern Wisconsin, northeastern Illinois, northern Indiana, and from western Michigan. It occurs sparingly in the Lake Huron basin, having been recorded only from certain tributaries of Saginaw Bay in Michigan and from a few localities in Ontario. It is widespread and common throughout most of the Lake Erie drainage. In the Lake Ontario basin its occurrence is spotty, with all known records coming from streams flowing into the south side of the lake.

The lack of records from any streams draining into the Atlantic Ocean indicates that this species probably was a late entrant into the Great Lakes drainage and failed to reach the Horseheads Outlet into the upper Susquehanna River system (Bailey, 1945: 125-126) before this connection was eliminated.

In recent times *N. chrysocephalus* seems to have replaced the closely related *N. cornutus* throughout much of the latter's former range. This is substantiated by the presence of isolated populations of *cornutus* in West Virginia and Indiana, and by Trautman's (1957) observations over the past 35 years on the relative distribution of

these two species in Ohio. A more complete discussion of the relationships of the two forms appears in the account of *cornutus* and in the section on zoogeography and phylogeny.

LIFE HISTORY AND ECOLOGY. *N. c. chrysocephalus* prefers an environment similar to that of *N. cornutus*. Both are ordinarily found in small to medium-sized streams having clear, weedless water, a moderate to swift current, and alternate pools and riffles, the latter with a gravel and/or rubble bottom. Individuals usually are found at the head or foot of riffles, more often the latter, but tend to avoid the riffles themselves except at spawning time. They likewise avoid quiet water, but individuals occasionally may be found there especially if a slight current is present.

As a rule *chrysocephalus* seems somewhat more tolerant than *N. cornutus* of warm, turbid conditions and has replaced it in a number of places where the environment has been so modified. The apparent preference of *chrysocephalus* for warmer waters is shown by the distribution of the two species when both occupy the same stream; the main body of the *cornutus* population is more apt to occur toward the headwaters, *chrysocephalus* usually is more common in the lower parts (Trautman, 1939: 285). When an obstruction was built across one such stream (Gilbert, 1961b: 188) *N. cornutus* took over completely, apparently because that segment of the population of *chrysocephalus* occurring toward the headwaters could not compete successfully unless continually reinforced from the main population downstream.

N. chrysocephalus is rarely found in lakes, partly because they are scarce throughout most of the species' range. Only to the north is *chrysocephalus* found with any consistency in standing waters, and here clear, gravel or rubble-bottomed, wave-washed shores are usually present. As in *N. cornutus*, spawning probably does not occur in the lakes themselves, but in tributary streams.

References to food habit studies of *N. cornutus* listed by Adams and Hankinson (1928) refer in part to *N. chrysocephalus*. Further accounts of the food habits of *chrysocephalus* are discussed by Langlois (1954). These studies reveal no apparent differences in food habits between *cornutus* and *chrysocephalus*.

Raney (1940a) described in detail the spawning behavior of *N. cornutus* and assembled the literature on breeding both in this form and *N. chrysocephalus*. This shows no essential differences in spawning behavior between the species, a finding supported by my own observations and those of others (Hankinson, 1932; Lachner, 1952). Whatever differences exist in spawning requirements most likely involve optimum temperatures and/or ranges of spawning temperature.

The northern limits of distribution of the two species seem to indicate that such differences do exist. Both species hybridize with other species with roughly equal frequency.

Notropis chrysocephalus: *chrysocephalus* \times *isolepis*

Notropis megalops, Gilbert, 1891: 157 (not of Rafinesque; in part; collections from area of intergradation in Black Warrior River system, Alabama).

The only collection I have seen that contains positively identified intergrades (UMMZ 168613) is from Blackburn Fork (9 miles southwest of Oneonta, Alabama), a headwater tributary of the Black Warrior River. Further collecting will probably reveal intergrading populations in a number of localities, most likely in other headwater tributaries of the Black Warrior and Cahaba systems. Other areas where intergrades might occur are the lower Coosa drainage where the two subspecies appear to be allopatric, the headwaters of the Tallapoosa River, the more westerly headwater gulf tributaries bordering the Tennessee River drainage, and the Arkansas River system in Arkansas.

The chief basis for identification of UMMZ 168613 as an intergrading population is the presence of typical individuals of both subspecies together with intermediates. Several specimens have pronounced, straight, dorso-lateral stripes running along the side of the back, while in others these stripes are crooked and poorly defined. The predorsal and anterior dorso-lateral scale rows in the former (*isolepis* type) individuals are regular and even, while these rows are irregular and uneven in the latter (*chrysocephalus* type) specimens.

The subspecies *chrysocephalus* and *isolepis* are readily distinguished not only on the basis of the criteria discussed above, but also by notable differences in both the anterior dorso-lateral and circumferential scale counts (tables 9 through 11). These differences by themselves are not sufficiently great to permit identification of small series of intergrades, such as the above.

The apparent scarcity of intergrading populations of *chrysocephalus* and *isolepis*, together with the rather unusual distribution of these forms in the Coosa system, suggest that these forms are close to the specific level of separation. I maintain them as subspecies because, in addition to the intergrading population previously cited, specimens of *isolepis* living well out of the area of potential intergradation occasionally have rather uneven anterior dorso-lateral stripes, causing the individual to appear more or less intermediate. Also past collections from near the known area of intergradation usually contain too few specimens or the individuals are too small to permit accurate identi-

fication. Hence some series of specimens identified to subspecies may actually consist of intergrades.

Notropis chrysocephalus isolepis Hubbs and Brown

Southern Striped Shiner, figures 13, 14E, 15A, map 5.

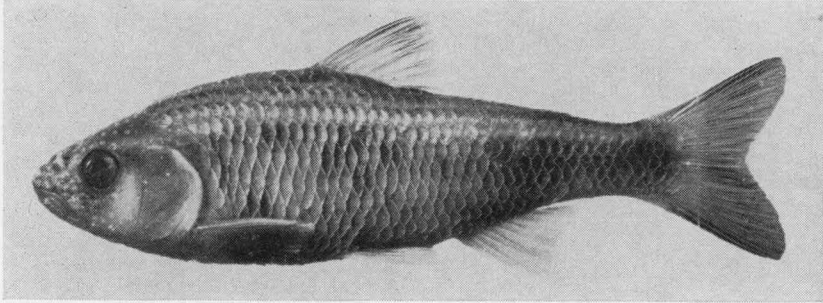


Figure 13. Adult male *Notropis chrysocephalus isolepis*, UMMZ 161262, 95 mm SL, from Vernon, Jackson Parish, Louisiana.

?*Leuciscus gibbosus* Storer, 1845: 48 (original description inadequate for positive identification; no type specimens; type locality Tuscaloosa, Alabama).

?*Plargyrus gibbosus*, Girard, 1856: 196 (in part; list of related species; Alabama).

Luxilus cornutus, Jordan, 1876b: 286-287 (misidentification in part; description; range; synonymy).

Notropis cornutus, Jordan and Evermann, 1896a: 256 (misidentification in part; range; reference to original description).

Notropis megalops, Gilbert, 1891: 157 (misidentification in part; Black Warrior and North rivers, Alabama).

Notropis cornutus isolepis Hubbs and Brown, in Ortenburger and Hubbs, 1927: 129-131 (original description; holotype, UMMZ 73090, 101 mm SL; four paratopotypes, UMMZ 73091; type locality Mountain Fork R., 10 mi. southeast of Broken Bow, McCurtain Co., Oklahoma; comparison with related forms; counts; range).

Luxilus cornutus isolepis, Jordan, Evermann and Clark, 1930: 128 (range; synonymy).

Notropis cornuta isolepis, Hubbs, 1951: 490 (first records for Texas).

Notropis chrysocephalus isolepis, Gilbert, 1961a: 2411-2412 (general account).

DIAGNOSIS. A subspecies of *Notropis chrysocephalus* distinguished from *N. c. chrysocephalus* by: Slightly larger scales, those in anterior dorso-lateral series (12) 13 or 14 (15); circumferential series (23) 24 to 28; sum of anterior dorso-lateral and circumferential scales (36) 37 to 41 (43); predorsal and anterior dorso-lateral scale rows very straight and even; anterior dorso-lateral stripes usually straight, well-defined,

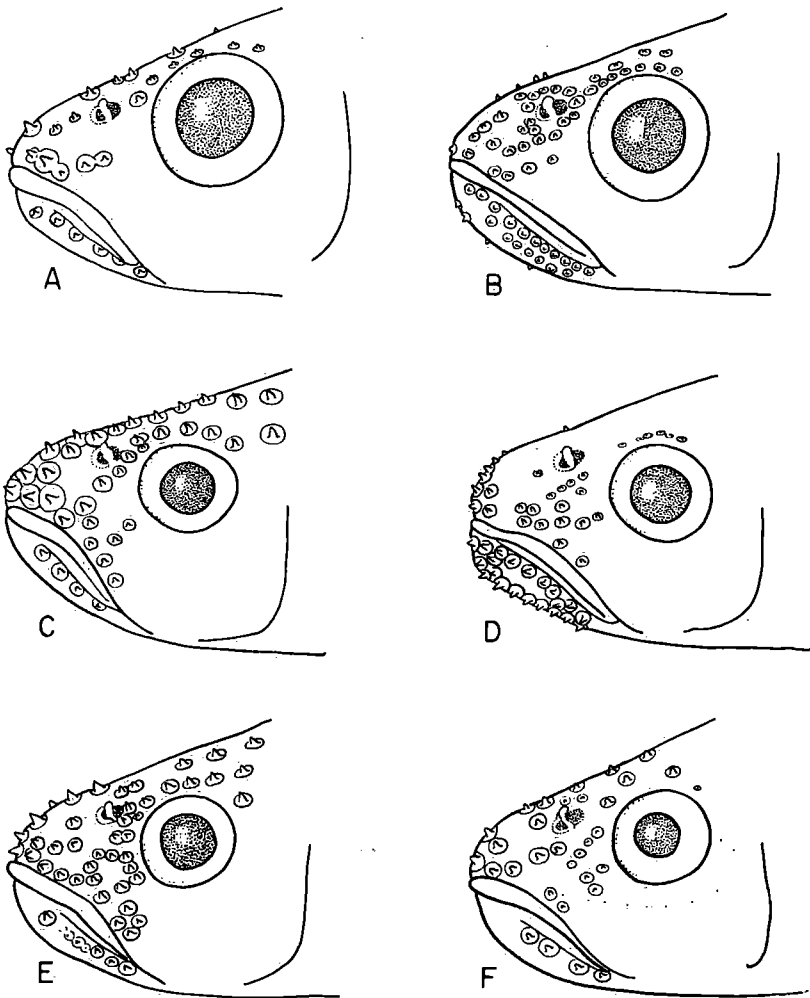


Figure 14. Tubercle patterns in *Luxilus*: A. *Notropis zonatus*, UMMZ 116373; B. *N. zonistius*, UMMZ 157882; C. *N. cerasinus*, UMMZ 174710; D. *N. cocco-genis*, CU 18558; E. *N. chrysocephalus isolepis*, UMMZ 161262; F. *N. cornutus*, UMMZ 95626.

and uniformly parallel; pigment always present on chin and gular region, often with a streak of black running posteriorly down gular membrane.

A comparison of *N. c. isolepis* and *N. c. chrysocephalus* is presented in table 3.

DESCRIPTION. Body proportions and counts of fin rays and scale rows are listed in tables 6 and 9 through 15. Characters mentioned in the description of *Notropis chrysocephalus* and in the above diagnosis are not repeated in the following paragraph.

Arrangement of circumferential scales above and below lateral line (10-2-11 or 11-2-10) 11-2-11 to 13-2-13 (15-2-13); dorso-lateral scale pockets darkest around edges which, with the intensification of pigment caused by the overlapping scales, results in three straight, well-defined, parallel stripes running lengthwise along dorso-lateral part of back, the stripes converging posteriorly with those from opposite side to give the appearance of long, narrow, parallel "Vs" when viewed from above (figure 15A); pigment always present on chin and gular area.

The following color description is based on an adult male (UMMZ 161262) collected on 6 June 1949 from a tributary of the Ouachita River 0.3 mi. southeast of Vernon, Jackson Parish, Louisiana: snout, branchiostegals, lower surface of head, and belly rosy, shading to scarlet along sides of body; dorsal and caudal fins of breeding males washed with yellowish, outer margin clear, bordered inside by a narrow band of crimson; distal half of pectoral, pelvic, and anal fins brilliant scarlet, except for the edges which are clear; proximal half of anal fin cream, distal half a brilliant scarlet except for the narrow border which is colorless; proximal half of pectoral and pelvic fins slaty gray, distal half scarlet, with the border colorless.

VARIATION. This form shows relatively little geographic variation. Occasionally an unevenness is evident in the arrangement of the predorsal and anterior dorso-lateral scales, but this is slight and never approaches the usual situation in *N. c. chrysocephalus*. Anal ray counts vary to some extent, the extremes in this subspecies being the greatest encountered in any form of *Luxilus*. A specimen with 7 anal rays (UMMZ 128116) was found from the Red River drainage of Arkansas, and one with 12 anal rays (UMMZ 161396) from a tributary of the Mississippi River in northern Mississippi; other specimens in these series have normal counts. Occasional populations contain an unusually high percentage of individuals with an anal ray count other than 9, a condition also encountered in certain populations of *Notropis cornutus*. Counts of 31 specimens of *isolepis* (UMMZ 157780)

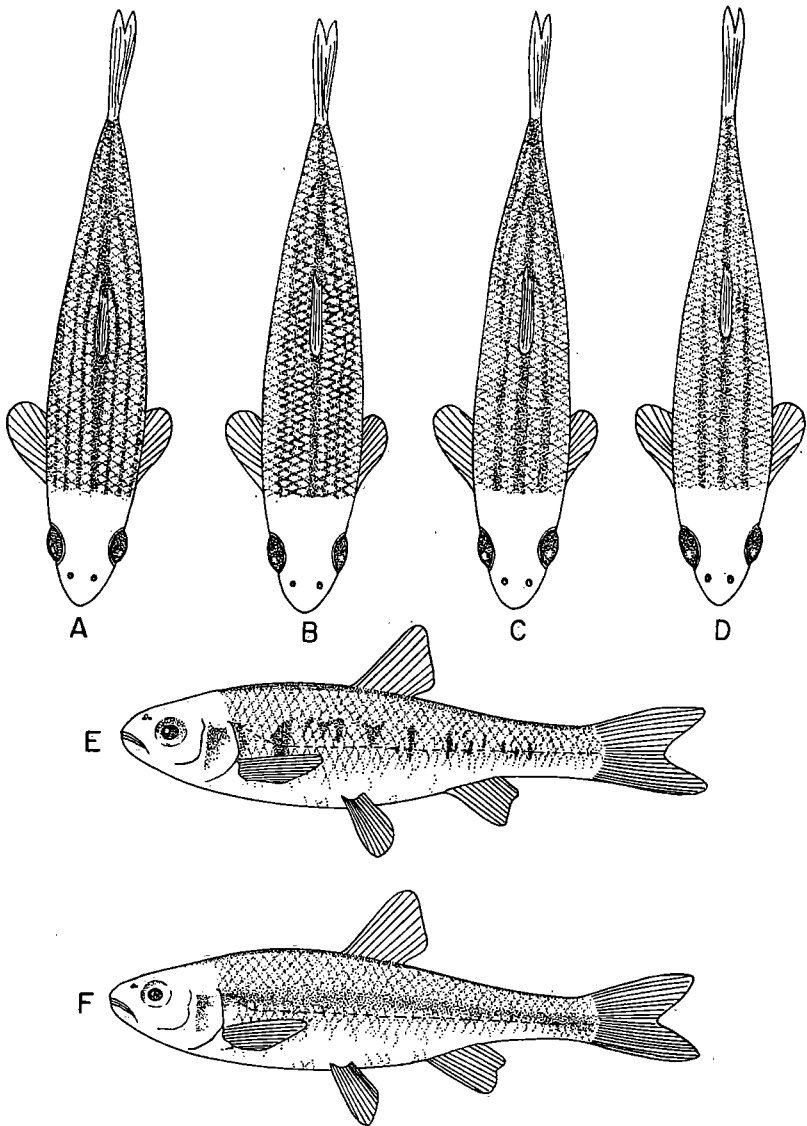


Figure 15. Pigmentation patterns and arrangement of dorso-lateral scales in *Luxilus*. A. *Notropis chrysocephalus isolepis*, UMMZ 161262, Red River drainage, Louisiana. B. *N. c. chrysocephalus*, UMMZ 100877, Wabash River drainage, Indiana. C. *N. albeolus*, CU 20322, Roanoke River drainage, Virginia. D. *N. cornutus*, UMMZ 9526, St. Lawrence River drainage, New York. E. *N. cornutus*, UMMZ 174813, James River drainage, Virginia. F. *N. albeolus*, UMMZ 174749, Roanoke River drainage, Virginia.

from the Chickasawhay drainage in Mississippi show 14 with 9 anal rays and 17 with 10.

Sexual variation is pronounced in *N. c. isolepis*, as in the closely related *N. cornutus* and *N. c. chrysocephalus*. Differences presumably are identical to those occurring in the latter form and very similar to those in the former. Breeding males develop a deep red coloration on body and fins, the black crescent-shaped markings on the side of the body become notably darker and more pronounced, and prominent nuptial tubercles develop on the head, back, anterior part of the dorsal and upper surface of the pectoral fins. Females have a more subdued coloration and usually lack tubercles. Adult males also develop a deeper and more compressed head, have slightly longer pectoral and pelvic fins, and an increased amount of adipose tissue surrounding the fin rays, but apparently do not differ in other respects from the females (table 6).

RELATIONSHIPS. *N. c. chrysocephalus* is the only form of *Luxilus* that occurs with *N. c. isolepis* in the Gulf drainage. Both are found in the Coosa River system and, although they occur in adjacent tributary streams a few miles apart, they have not yet been found together. Specimens from one collection taken in an eastern tributary of the neighboring Black Warrior system have been identified as intergrades, and several other collections in the same drainage have been identified as *N. c. chrysocephalus*. Perhaps transfer of *chrysocephalus* into the Black Warrior has been effected through a localized stream capture. The apparent lack of intergradation of *chrysocephalus* and *isolepis* in the Coosa basin is difficult to explain, though this may in some way be related to the fact that, in this area at least, the ranges of the two forms appear to be separated by the so-called Fall Line which marks the transition from an upland to a lowland environment (Fenneman, 1938: 126-131). On the other hand these forms may be incipient species which, because of ecological similarities, have each prevented the other from moving into the areas it occupies. Should this explanation be correct the intergradation in the Black Warrior drainage would be difficult to explain.

DISTRIBUTION. Confined to tributaries of the Gulf of Mexico from the eastern half of the Red River system (including the Ouachita River) in Texas, Louisiana, Arkansas and Oklahoma, eastward to the Tallapoosa drainage in western Georgia (UF 9563).

Its range west of the Mississippi River is, with one exception, restricted to the Red River system. A single record from the Arkansas drainage in Arkansas (USNM 165878) is interpreted as the result of either human introduction or localized stream capture. This form

apparently is fairly common in favorable habitats in southern Arkansas, extreme southeastern Oklahoma, and extreme northeastern Texas, but farther west is known only from the Blue River system of south-central Oklahoma. To the east it occurs in a number of smaller tributaries of the Mississippi River in western Mississippi, and recently has been recorded as far north as southwestern Tennessee (USNM 179780-179781). It probably does not normally occur in any independent river system east of Mobile Bay, although there are unpublished records (not verified by me) from the Escambia and Choc-tawhatchee drainages in Alabama. In the Coosa River system *isolepis* occurs as far north as Chilton County, Alabama; here its range dovetails with that of *N. c. chrysocephalus*. It is one of the most common fishes in upland tributaries to the Gulf of Mexico.

LIFE HISTORY AND ECOLOGY. No studies dealing with the life history and ecology of *N. c. isolepis* have been made. The form probably differs little, if at all, from *N. c. chrysocephalus* in these regards.

TABLE 1

Comparison of *Notropis coccogenis* and *Notropis zonistius*

Character	<i>Notropis coccogenis</i>	<i>Notropis zonistius</i>
Position of band on dorsal fin	Confined to posterior part of fin; almost parallels distal margin	Not confined to posterior part of fin; slopes obliquely forward and intersects lower third of anterior margin
Color of dorsal band	Black at all ages	Orange-red in young; black in adults
Caudal spot	Absent	Present
Black border on distal margin of caudal fin	Present	Absent
Red bar on side of head	Prominent; situated at margin of opercle and pre-opercle	Not prominent (often absent); situated on cheek
Nuptial tubercles on top of head and back	Absent	Present
Body form	Attenuate and tereete	Deep and compressed
Angle of mouth to top of head	Usually 49 to 53°	Usually 57 to 61°
Number of vertebrae	40 to 42; usually 41	38 to 40; usually 39
Maximum length of males	Ca. 115 mm.	Ca. 85 mm.

TABLE 2

Comparison of pigmentary characters in
Notropis zonatus and *Notropis pilsbryi*

Character	<i>Notropis zonatus</i>	<i>Notropis pilsbryi</i>
Pigment on posterior-dorsal part of opercle	Not bordering posterior-dorsal margin	Bordering posterior-dorsal margin
Pigment on cleithral area	Extending ventrally to pectoral insertion; becoming quite dark	Extending ventrally about halfway to pectoral insertion; not becoming particularly dark
Relation of lateral stripe to lateral line (anterior to caudal peduncle)	Not extending below lateral line	Extending below lateral line
Distribution of pigment on caudal peduncle	Unequally distributed; more present above lateral line than below	Equally distributed above and below lateral line
Dorso-lateral stripes on back	Present	Absent
Red pigmentation on body and fins	Usually more pronounced	Usually less pronounced
Black pigmentation on body	More intense; appearing deep black	Less intense; appearing more dusky

TABLE 3
Comparison between forms of the *Notropis cornutus* species group

Character	<i>N. cornutus</i>	<i>N. albeolus</i>	<i>N. c. chrysocephalus</i>	<i>N. c. isolepis</i>	<i>N. cerasinus</i>
Anterior dorso-lateral scales	(16) 18 to 24 (30)	(15) 17 to 20 (23)	(13) 14 to 17 (19)	(12) 13 or 14 (15)	(14) 15 to 19 (22)
Circumferential scales	(26) 30 to 35 (39)	(24) 26 to 30 (33)	(23) 26 to 29 (32)	(23) 24 to 28	(23) 25 to 28 (30)
Sum of anterior dorso-lateral and circumferential scales	(42) 48 to 59 (67)	(41) 43 to 50 (55)	(38) 40 to 44 (48)	(36) 37 to 41 (43)	(37) 41 to 47 (51)
Caudal peduncle scales	(13) 15 or 16 (18); usually 16	(13) 15 or 16 (17)	(12) 15 or 16 (17); usually 16	(14) 15 or 16; usually 16	(12) 13 to 15 (16); usually 14
Parallel stripes on anterior dorso-lateral part of back	Absent	Absent	Present; crooked	Present; straight	Absent
Crescent-shaped bars on side of body	Present	Usually absent	Present	Present	Present
Reds on body and fins of breeding males	Present and widespread	Usually absent; occasional on snout and fins	Present and widespread	Present and widespread	Present and widespread
Color of dorsum	Olive-brown	Olive-green	Olive-brown	Olive-brown	Olive-brown
Nuptial tubercles present in:	Males only	Males only	Males only	Males only	Both sexes
Appearance of nuptial tubercles on upper part of head	Straight at tips	Straight at tips	Straight at tips	Straight at tips	Curved forward at tips
Body form	Deep and compressed	Usually slender and terete in northern race; usually deep and compressed in southern race	Deep and compressed	Deep and compressed	Deep and compressed
Maximum size of males	Ca. 175 mm.	Ca. 130 mm.	Ca. 175 mm.	Ca. 175 mm.	Ca. 90 mm.

TABLE 4. COMPARISON OF PROPORTIONAL MEASUREMENTS
(EXPRESSED IN THOUSANDTHS OF STANDARD LENGTH)
FOR *Notropis coccogenis* AND *Notropis zonistius*

<i>Notropis coccogenis</i>					<i>Notropis zonistius</i>			
	Sex	No.	Range	Mean	Sex	No.	Range	Mean
Standard length			61-84 mm.				57.5-75 mm.	
Length of pectoral fin	M	19	182-201	193	M	8	197-224	204
	F	21	177-210	188	F	6	193-218	200
	*	66	174-210	190	*	37	187-234	204
Length of pelvic fin	M	19	139-161	153	M	8	159-186	169
	F	21	134-169	154	F	6	159-168	164
	*	66	134-169	153	*	37	156-186	166
Length of head	*	35	241-281	263	*	24	259-285	271
Depth of head	*	35	153-190	163	*	24	177-204	189
Width of head	*	35	128-146	136	*	24	136-161	152
Interorbital width	*	35	82-95	88	*	24	92-104	96
Mouth gape	*	35	43-59	52	*	24	57-73	67
Diameter of eye	*	35	66-81	74	*	24	68-82	74
Length of snout	*	35	66-85	76	*	24	67-79	73
Length of upper jaw	*	35	96-115	106	*	24	93-112	103
Distance from mid-dorsum to lateral line	*	35	131-168	149	*	28	162-203	180
Depth of body	*	40	192-244	215	*	24	217-284	256
Width of body	*	35	119-159	134	*	24	140-168	153
Length of caudal peduncle	*	35	181-224	204	*	24	173-231	206
Depth of caudal peduncle	*	35	85-102	95	*	24	104-119	109
Predorsal length	*	35	497-536	520	*	24	494-528	516
Prepelvic length	*	35	472-521	503	*	24	494-515	502
Preanal length	*	35	659-704	665	*	24	655-684	675
Length of dorsal fin	*	35	200-233	216	*	24	220-264	239
Length of anal fin	*	35	174-208	188	*	24	187-242	208
Length of caudal fin	*	29	266-300	279	*	22	279-315	296
Angle of mouth to top of head	*	58	46°-54°	50.5°	*	40	50°-61.5°	58°

* Summation of sexed males and females and additional unsexed adult specimens.

TABLE 5. COMPARISON OF PROPORTIONAL MEASUREMENTS
(EXPRESSED IN THOUSANDTHS OF STANDARD LENGTH)
FOR *Notropis zonatus* AND *Notropis pilsbryi*

	<i>Notropis zonatus</i>				<i>Notropis pilsbryi</i>			
	Sex	No.	Range	Mean	Sex	No.	Range	Mean
Standard length			54-76 mm.				55-74 mm.	
Length of pectoral fin	M	13	200-225	208	M	14	190-216	203
	F	13	183-216	203	F	13	184-210	198
	*	40	183-225	205	*	42	181-216	199
Length of pelvic fin	M	13	160-182	171	M	14	159-196	168
	F	13	158-179	171	F	13	151-174	166
	*	40	153-182	170	*	42	146-196	167
Length of head	*	38	259-284	269	*	36	251-284	265
Depth of head	*	51	161-186	174	*	49	154-183	168
Width of head	*	32	116-142	133	*	34	129-136	134
Interorbital width	*	32	80-89	84	*	34	75-86	80
Mouth gape	*	32	47-63	54	*	34	50-56	53
Diameter of eye	*	32	70-82	77	*	34	71-82	78
Length of snout	*	40	70-80	74	*	43	65-81	71
Length of upper jaw	*	32	80-94	88	*	34	78-90	88
Distance from mid-dorsum to lateral line	*	32	131-158	146	*	34	133-154	140
Depth of body	*	51	199-260	229	*	49	174-273	221
Width of body	*	32	115-145	131	*	34	126-157	135
Length of caudal peduncle	*	32	192-245	229	*	36	199-239	220
Depth of caudal peduncle	*	40	86-103	96	*	40	85-111	95
Predorsal length	*	32	460-505	488	*	34	470-504	493
Prepelvic length	*	32	464-508	487	*	34	475-497	487
Preal length	*	32	643-674	662	*	34	659-683	672
Length of dorsal fin	*	32	200-255	240	*	34	226-253	236
Length of anal fin	*	32	178-208	198	*	34	175-208	194
Length of caudal fin	*	32	240-315	290	*	34	262-321	290
Angle of mouth to top of head	*	39	46.5°-56°	51°	*	40	46°-56°	50.5°

* Summation of sexed males and females and additional unsexed, adult specimens.

TABLE 6. COMPARISON OF PROPORTIONAL MEASUREMENTS (EXPRESSED IN THOUSANDTHS OF STANDARD LENGTH)
BETWEEN MEMBERS OF THE *Notropis cornutus* SPECIES GROUP

	<i>N. cornutus</i>				<i>N. albeolus</i> (southern race)				<i>N. albeolus</i> (northern race)				<i>N. chryscephalus</i> <i>chryscephalus</i>				<i>N. chryscephalus</i> <i>isolepis</i>				<i>N. cerasimus</i>			
	Sex	No.	Range	Mean	Sex	No.	Range	Mean	Sex	No.	Range	Mean	Sex	No.	Range	Mean	Sex	No.	Range	Mean	Sex	No.	Range	Mean
Standard length (in mm.)			60-82				58-81				59-80				60-84				60-80				53-78	
Length of pectoral fin	M	57	170-236	206	M	18	183-231	205	M	13	166-211	193	M	24	176-230	202	M	18	174-234	205	M	18	193-233	218
	F	47	176-220	196	F	16	182-223	196	F	13	163-198	190	F	19	174-218	194	F	19	177-225	196	F	21	187-223	213
	*	137	164-240	202	*	58	170-231	202	*	78	159-213	190	*	95	172-237	197	*	83	175-236	205	*	53	187-233	215
Length of pelvic fin	M	57	157-206	172	M	18	160-192	180	M	13	158-188	171	M	24	149-197	173	M	18	158-198	175	M	18	164-204	187
	F	46	152-185	164	F	16	155-187	174	F	13	155-181	167	F	19	151-190	167	F	19	150-191	169	F	21	184-204	185
	*	136	144-211	168	*	58	145-192	177	*	78	147-192	169	*	95	142-206	168	*	83	150-199	174	*	55	158-204	185
Length of head	*	87	225-291	263	*	51	232-287	260	*	74	230-285	249	*	67	251-286	269	*	59	249-292	269	*	46	238-292	262
Depth of head	*	96	155-215	181	*	51	160-202	182	*	74	147-200	163	*	67	151-197	180	*	59	167-197	183	*	44	169-205	188
Width of head	*	56	119-155	138	*	41	126-155	138	*	30	109-140	123	*	36	124-163	144	*	38	130-153	148	*	37	129-169	141
Interorbital width	*	36	75-106	92	*	18	74-95	87	*	22	72-104	85	*	41	90-103	95	*	31	86-104	94	*	41	77-101	89
Mouth gape	*	62	43-78	62	*	25	50-80	63	*	13	31-61	49	*	62	46-70	56	*	57	47-71	58	*	32	45-77	63
Diameter of eye	*	55	61-86	75	*	32	60-94	77	*	15	60-87	71	*	41	65-94	80	*	50	65-90	78	*	32	63-89	74
Length of snout	*	87	59-79	70	*	40	60-83	71	*	54	59-76	67	*	67	66-82	74	*	59	63-86	72	*	46	54-82	68
Length of upper jaw	*	66	73-96	86	*	39	70-101	89	*	46	68-95	83	*	62	84-107	95	*	54	83-105	95	*	40	73-102	89
Distance from mid-dorsum to lateral line	*	82	135-193	160	*	29	155-207	176	*	40	126-185	150	*	62	137-196	169	*	56	143-199	174	*	36	150-204	173
Depth of body	*	87	210-295	260	*	51	235-316	269	*	74	189-256	230	*	67	213-305	263	*	58	225-309	261	*	41	238-330	274
Width of body	*	42	122-170	145	*	15	130-161	141	*	32	113-158	128	*	45	109-139	126	*	46	116-171	133	*	33	118-175	143
Length of caudal peduncle	*	75	171-257	222	*	52	182-238	206	*	61	195-241	214	*	62	172-244	217	*	57	168-244	211	*	42	190-250	216
Depth of caudal peduncle	*	79	82-120	101	*	48	95-116	105	*	62	79-114	96	*	62	90-117	100	*	59	94-123	106	*	43	97-123	110
Predorsal length	*	36	471-554	496	*	13	464-517	487	*	29	465-511	487	*	30	464-515	494	*	31	450-512	294	*	41	456-516	493
Prepelvic length	*	32	457-508	486	*	5	460-485	475	*	12	445-480	464	*	30	464-509	495	*	27	453-519	493	*	41	448-520	485
Preanal length	*	31	647-693	665	*	5	655-675	670	*	14	636-695	658	*	30	640-718	692	*	27	633-709	688	*	41	652-708	672
Length of dorsal fin	*	57	201-280	241	*	48	205-283	246	*	32	196-266	238	*	62	205-269	249	*	54	222-278	254	*	44	240-287	266
Length of anal fin	*	50	164-221	197	*	40	170-232	203	*	22	160-220	192	*	62	159-215	194	*	49	174-214	198	*	41	171-244	208
Length of caudal fin	*	52	238-339	299	*	30	265-337	306	*	25	248-320	286	*	62	248-342	295	*	49	232-364	302	*	35	274-331	299
Angle of mouth to top of head (in degrees)	*	67	53-63.5	57.7	*	30	51.5-61.5	57.3	*	41	47-58	53.1	*	36	53.5-65	59.0	*	33	52.5-64	58.0	*	27	52.5-62.5	57.

* Summation of sexed males and females and additional unsexed adult specimens.

TABLE 7. COMPARISON OF IMPORTANT AREAS OF DIFFERENTIATION FOR SUM OF ANTERIOR DORSO-LATERAL AND CIRCUMFERENTIAL SCALE COUNTS IN *Notropis cornutus* and *Notropis albeolus*

Area	Anterior dorso-lateral scales																No.	Mean
	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30		
<i>albeolus</i>																		
New & Roanoke drs.	1	2	38	55	48	21	7	3	—	—	—	—	—	—	—	—	175	18.46
Tar, Neuse & Cape Fear drs.	2	6	39	63	45	15	6	—	1	—	—	—	—	—	—	—	177	18.23
<i>cornutus</i>																		
Atlantic coast*	—	3	29	84	137	159	139	103	43	34	13	2	1	—	1	—	748	20.40
Maine-Maritime dr.	—	1	9	16	35	34	34	14	6	4	3	2	—	—	—	—	158	20.16
St. Lawrence dr.	—	—	2	10	14	17	20	20	7	10	1	1	—	—	—	—	102	20.90
upper Susquehanna dr.	—	—	—	—	—	3	17	16	30	15	9	5	3	1	1	—	100	23.12
west of Alleghenies	—	—	5	27	100	211	287	333	213	142	74	28	12	4	1	1	1438	21.85
Area	Circumferential scales																No.	Mean
	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39		
<i>albeolus</i>																		
New & Roanoke drs.	—	2	12	31	47	39	36	7	—	1	—	—	—	—	—	—	175	28.43
Tar, Neuse & Cape Fear drs.	1	5	31	54	32	35	15	3	1	—	—	—	—	—	—	—	177	27.68
<i>cornutus</i>																		
Atlantic coast*	—	—	—	5	8	46	126	175	179	127	60	17	4	1	—	—	748	31.60
Maine-Maritime dr.	—	—	1	—	4	27	54	34	24	8	5	—	1	—	—	—	158	30.59
St. Lawrence dr.	—	—	—	—	—	—	18	18	20	23	9	11	2	1	—	—	102	32.32
upper Susquehanna dr.	—	—	—	—	—	—	13	13	21	24	13	12	1	1	—	2	100	32.70
west of Alleghenies	—	—	—	—	—	8	69	165	279	348	255	178	88	33	7	8	1438	33.17

(Continued)

TABLE 7 (continued)

Area	Sum of above counts																			over		No.	Mean
	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	60		
<i>albeolus</i>																							
New & Roanoke drs.	—	2	4	15	22	36	28	30	11	19	3	1	2	1	1	—	—	—	—	—	—	175	47.01
Tar, Neuse & Cape Fear drs.	2	4	13	26	26	39	34	18	11	2	2	—	—	—	—	—	—	—	—	—	—	177	45.88
<i>cornutus</i>																							
Atlantic coast*	—	—	—	—	1	4	20	56	53	83	106	125	102	73	53	23	26	12	7	3	1	748	52.00
Maine-Maritime dr.	—	1	—	—	—	1	17	18	21	20	25	18	11	12	3	4	3	2	1	1	—	158	50.74
St. Lawrence dr.	—	—	—	—	—	—	—	3	5	12	14	12	9	12	8	11	12	2	1	—	1	102	53.22
upper Susquehanna dr.	—	—	—	—	—	—	—	—	—	1	4	4	7	11	23	16	15	4	7	2	6	100	55.82
west of Alleghenies	—	—	—	—	—	—	1	5	13	35	73	120	187	209	224	160	149	123	57	35	47	1438	55.02

* south of Maine.

TABLE 8. COMPARISON OF VERTEBRAL COUNTS IN *Notropis albeolus*
BY DRAINAGE SYSTEMS

Drainage	Vertebrae					No.	Mean
	37	38	39	40	41		
Neuse	—	7	31	8	—	46	39.02
Tar	1	—	9	7	—	17	39.29
Cape Fear	—	—	1	—	—	1	39.00
Roanoke	—	—	4	23	6	33	40.06
New	—	—	1	16	3	20	40.10

TABLE 11. COMPARISON OF SUM OF ANTERIOR DORSO-LATERAL AND CIRCUMFERENTIAL SCALES IN THE FORMS OF *Luxilus*

[illegible]

TABLE 12. COMPARISON OF LATERAL-LINE SCALES IN THE FORMS OF *Luxilus*

Form	Lateral-line scales								No.	Mean
	36	37	38	39	40	41	42	43		
<i>N. cornutus</i>	1	24	165	326	234	53	5	2	810	39.18
<i>N. albeolus</i>	—	22	66	80	28	14	—	—	210	38.69
<i>N. chrysocephalus</i>										
<i>chrysocephalus</i>	2	90	255	249	69	14	1	—	680	38.50
<i>N. chrysocephalus</i>										
<i>isolepis</i>	—	39	80	46	7	—	—	—	172	38.12
<i>N. cerasinus</i>	—	—	4	27	21	6	—	—	58	39.48
<i>N. zonatus</i>	—	—	9	18	31	19	2	4	83	39.99
<i>N. pilsbryi</i>	—	—	1	13	18	21	8	—	61	40.36
<i>N. coccogenis</i>	—	—	—	10	28	26	12	5	81	40.68
<i>N. zonistius</i>	—	6	17	33	16	12	2	1	87	39.24

TABLE 13. COMPARISON OF ANAL RAYS IN THE FORMS OF *Luxilus*

Form	Anal rays						No.	Mean
	7	8	9	10	11	12		
<i>N. cornutus</i>	—	100	749	20	—	—	869	8.91
<i>N. albeolus</i>	—	—	83	4	1	—	88	9.07
<i>N. chrysocephalus chrysocephalus</i>	—	49	530	10	1	—	590	8.94
<i>N. chrysocephalus isolepis</i>	1	7	146	26*	—	1	181	9.11
<i>N. cerasinus</i>	—	2	70	—	—	—	72	8.97
<i>N. zonatus</i>	—	4	101	5	—	—	110	9.01
<i>N. pilsbryi</i>	—	3	67	4	—	—	74	9.01
<i>N. coccogenis</i>	—	4	98	13	—	—	115	9.08
<i>N. zonistius**</i>	—	5	110	88	—	—	203	9.41

* 17 specimens in one collection

** Of 62 specimens from Florida, 53 had ten anal rays.

TABLE 14. COMPARISON OF VERTEBRAE IN THE FORMS OF *Luxilus*

Form	Vertebrae								No.	Mean
	36	37	38	39	40	41	42			
<i>N. cornutus</i>	2	—	2	36	136	55	6	237	40.08	
<i>N. albeolus</i>	—	1	7	46	54	9	—	53	39.54	
<i>N. chrysocephalus</i>										
<i>chrysocephalus</i>	—	—	6	53	48	7	—	114	39.49	
<i>N. chrysocephalus isolepis</i>	—	—	2	35	10	1	1	49	39.27	
<i>N. cerasinus</i>	—	—	3	22	8	—	—	33	39.15	
<i>N. zonatus</i>	—	—	—	4	22	2	—	28	39.93	
<i>N. pilsbryi</i>	—	—	—	6	16	1	—	23	39.78	
<i>N. coccogenis</i>	—	—	—	—	4	36	10	50	41.12	
<i>N. zonistius</i>	—	—	5	32	9	—	—	46	39.09	

TABLE 15. COMPARISON OF ANGLE OF SNOUT TO TOP OF HEAD
IN THE FORMS OF *Luxilus*

Form	46°	48°	50°	52°	54°	56°	58°	60°	62°	No.	Mean
	47.5°	49.5°	51.5°	53.5°	55.5°	57.5°	59.5°	61.5°	63.5°		
<i>N. cornutus</i>	—	—	—	10	12	15	11	10	9	67	57.65°
<i>N. albeolus</i> (southern race)	—	—	1	4	2	11	9	3	—	30	57.33°
<i>N. albeolus</i> (northern race)	1	5	9	11	6	8	1	—	—	41	53.13°
<i>N. chrysocephalus chrysocephalus</i>	—	—	—	5	6	8	7	6	4	36	59.06°
<i>N. chrysocephalus isolepis</i>	—	—	—	3	5	7	7	6	5	33	57.85°
<i>N. cerasinus</i>	—	—	—	3	8	4	8	2	2	27	57.41°
<i>N. zonatus</i>	5	8	9	6	8	2	—	—	—	38	51.21°
<i>N. pilsbryi</i>	5	10	8	8	4	1	—	—	—	36	50.70°
<i>N. coccogenis</i>	5	11	26	15	1	—	—	—	—	58	50.50°
<i>N. zonistius</i>	—	—	1	2	2	6	10	7	—	28	57.94°

REFERENCES CITED

Abbott, Charles C.

- 1870. Notes on fresh-water fishes of New Jersey. *Am. Naturalist*, 4(2): 99-117.
- 1874. Notes on the cyprinoids of central New Jersey. *Am. Naturalist*, 8(6): 326-338.

Adams, Charles C., and Thomas L. Hankinson

- 1928. The ecology and economics of Oneida Lake fish. *Roosevelt Wild Life Ann.*, 1(3-4): 239-548, figs. 175-244, 4 pls., 1 map.

Agassiz, Louis

- 1850. Lake Superior: Its physical character, vegetation, and animals, compared with those of other and similar regions . . . with a narrative of the tour by J. Elliot Cabot and contributions by other scientific gentlemen. Gould, Kendall and Lincoln, Boston, xii + 48 pp., 8 pls., many figs.
- 1854. Notice on a collection of fishes from the southern bend of the Tennessee River, Alabama. *Am. Jour. Sci. and Arts*, 17(2): 297-308 and 353-365.

Bailey, Joseph R., and James A. Oliver

- 1939. The fishes of the Connecticut watershed. *New Hampshire Fish and Game Dept., Surv. Rept.*, 4: 150-189, figs. 57-80.

Bailey, Reeve M.

- 1938. The fishes of the Merrimack drainage. *In: Biological survey of the Merrimack watershed.* *New Hampshire Fish and Game Dept., Surv. Rept.*, 3: 149-185, 12 figs.
- 1945. Review of: Some considerations on the distribution of fishes in Ontario. By: Isobel Radforth. *Copeia*, 1945(2): 125-126.

Bailey, Reeve M., and William A. Gosline

- 1955. Variation and systematic significance of vertebral counts in the American percid fishes of the family Percidae. *Misc. Publ. Mus. Zool., Univ. Mich.*, 93: 1-44.

Bean, Barton A.

- 1903. Notice on a collection of fishes made by H. H. Brimley in Cane River and Bollings Creek, North Carolina, with a description of a new species of *Notropis* (*N. brimleyi*). *Proc. U. S. Nat. Mus.*, 26(1339): 913-914.

Beckman, William C.

- 1952. Guide to the fishes of Colorado. *Univ. Colorado Mus., Leaflet* 11: 1-110, many figs.

Call, R. Ellsworth

- 1896. Fishes and shells of the Falls of the Ohio. *Mem. Hist. Louisville*, 1: 9-20.

Cockerell, T. D. A.

- 1908. The fishes of the Rocky Mountain region. *Univ. Colorado Studies*, 5(3): 159-178.

Cockerell, T. D. A., and Otis Callaway

1909. Observations on the fishes of the genus *Notropis*. Proc. Biol. Soc. Wash., 22: 189-196.

Cope, Edward Drinker

1864. Partial catalogue of the cold-blooded vertebrata of Michigan, Pt. I. Proc. Acad. Nat. Sci. Phila., 16: 276-285.
1867. On the genera of fresh-water fishes *Hypsilepis* Baird and *Photogenis* Cope, their species and distribution. Proc. Acad. Nat. Sci. Phila., 19: 158-166.
- 1869a. On the distribution of fresh-water fish in the Allegheny region of south-western Virginia. Jour. Acad. Nat. Sci. Phila., Ser. 2, 6(5): 207-247, pls. 22-24.
- 1869b. Synopsis of the Cyprinidae of Pennsylvania. Trans. Am. Phil. Soc., 13: 351-399, pls. 10-13.
1870. (*reprinted in 1877*). A partial synopsis of the fishes of the fresh waters of North Carolina. Trans. Am. Phil. Soc., 14: 448-495.
1871. Recent reptiles and fishes. Report on the reptiles and fishes obtained by the naturalists of the expedition. In: U. S. Geological Survey of Wyoming and Continuous territory (1870), pp. 432-442.

Cross, Frank Bernard

1954. Fishes of Cedar Creek and the South Fork of the Cottonwood River, Chase County, Kansas. Trans. Kans. Acad. Sci., 57(3): 303-314.

DeKay, James E.

1842. New York fauna. Part 1, Zoology; part 4, Fishes. Albany, 415 pp., 79 pls.

Driver, Ernest C.

1942. Name that animal. Kraushar Press, Northampton, Mass., 527 pp., many pls.

Ellis, Max W.

1914. The fishes of Colorado. Univ. Colorado Stud., 11(1): 1-136, 12 pls.

Evermann, Barton W., and Theodore D. A. Cockerell

1909. Descriptions of three new species of Cyprinoid fishes. Proc. Biol. Soc. Wash., 22: 185-188.

Evermann, Barton W., and Ulysses O. Cox

1896. The fishes of the Neuse River basin. Bull. U. S. Fish Comm. (1895), 15: 303-310.

Evermann, Barton W., and Edmund Lee Goldsborough

1907. A checklist of the freshwater fishes of Canada. Proc. Biol. Soc. Wash., 20: 89-119.

Evermann, Barton W., and Samuel F. Hildebrand

1916. Notes on the fishes of east Tennessee. Bull. U. S. Bur. Fisheries (1914), 34: 431-457.

Fenneman, Nevin M.

1938. Physiography of eastern United States. McGraw-Hill Book Co., New York, v-xiii + 714 pp. and 196 figs.

Flint, Richard Foster

1947. Glacial geology and the Pleistocene Epoch. John Wiley and Sons, New York, 589 pp., 88 figs., 30 tables, 6 pls.
1957. Glacial and Pleistocene geology. John Wiley and Sons, New York, v-xiii + 553 pp., many figs. and tables, 5 pls.

Forbes, Stephen A.

1909. On the general and interior distribution of Illinois fishes. Bull. Illinois St. Lab. Nat. Hist., 8: 381-437, maps 1-103.

Forbes, Stephen A., and Robert E. Richardson

1920. The fishes of Illinois. Second edition. Ill. St. Jour. Co., Springfield, vol. 3, cxxxi + 357 pp., many figs. and color pls., separate vol. of 103 maps.

Fowler, Henry W.

1904. Notes on fishes from Arkansas, Indian Territory and Texas. Proc. Acad. Nat. Sci. Phila., 56: 242-249, 1 fig.
1909. A synopsis of the Cyprinidae of Pennsylvania. Proc. Acad. Nat. Sci. Phila. (1908), 60: 517-553.
1910. Notes on the variation of some species of the genus *Notropis*. Proc. Acad. Nat. Sci. Phila., 62: 273-293, pls. 15-21.
1922. Records of fishes for the southern and eastern United States. Proc. Acad. Nat. Sci. Phila., 74: 1-27, 2 pls.
1923. Records of fishes for the southern states. Proc. Biol. Soc. Wash., 36: 7-34.
1936. Fresh-water fishes obtained in North Carolina in 1930 and 1934. Fish Culturist, 15(10): 192-194.
1945. A study of the fishes of the southern Piedmont and coastal plain. Monog. Acad. Nat. Sci. Phila., 7: i-vi, 1-408, figs. 1-313.

Gibbs, Robert 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(3): 185-195.

Gilbert, Carter Rowell

- 1961a. A systematic and geographical study of the subgenus *Luxilus* (family Cyprinidae). Dissertation Abstracts, 21(8): 2411-2412.
- 1961b. Hybridization versus intergradation: an inquiry into the relationship of two cyprinid fishes. Copeia, 1961(2): 181-192.

Gilbert, Charles H.

- 1884a. Notes on the fishes of Kansas. Bull. Washburn Coll. Lab. Nat. Hist., 1(1): 10-16.

- 1884b. A list of fishes collected in the East Fork of White River, Indiana, with descriptions of two new species. *Proc. U. S. Nat. Mus.*, 7(423): 199-205.
1891. Notes on explorations made in Alabama during 1889, with notes on the fishes of the Tennessee, Alabama, and Escambia rivers. *Bull. U. S. Fish Comm.* (1889), 9: 143-159, pl. 43.

Girard, Charles

1856. Researches upon the Cyprinoid fishes inhabiting the fresh waters of the United States, west of the Mississippi Valley from specimens in the Museum of the Smithsonian Institution. *Proc. Acad. Nat. Sci. Phila.*, 8: 165-213.

Goldsborough, Edmund Lee, and H. Walton Clark

1908. Fishes of West Virginia. *Bull. U. S. Bur. Fisheries* (1907), 27: 29-39, 1 fig.

Greeley, John R.

1938. Fishes of the area with annotated list. In: A biological survey of the Allegheny and Chemung watersheds. *Suppl. 27th Ann. Rept. N. Y. St. Cons. Dept.* (1937): 48-73, col. pls. 1-2, 3 figs.

Greene, C. Willard

1935. The distribution of Wisconsin fishes. *Wisconsin St. Cons. Comm.*, Madison, 235 pp., 96 maps.

Günther, Albert

1868. Catalogue of the Physostomi. . . . Catalogue of the fishes in the British Museum. Taylor and Francis, London, vol. 7, xx + 512 pp.

Hankinson, Thomas L.

1932. Observations on the breeding behavior and habits of fishes in southern Michigan. *Papers Mich. Acad. Sci.* (1931), 14: 411-425.

Heckel, Joh. Jakob

1843. *Abbildungen und Beschreibungen der Fische Syriens, nebst einer neuen Classification und Charakteristik Sammtlicher Gatlingen der Cyprinen.* Stuttgart, 258 pp., 23 pls.

Hildebrand, Samuel F.

1932. On a collection of fishes from the Tuckaseegee and upper Catawba river basins, N. C., with a description of a new darter. *Jour. Elisha Mitchell Sci. Soc.*, 48(1): 50-82, pl. 3, figs. 1-2.

Hubbs, Carl L.

1926. A check-list of the fishes of the Great Lakes and tributary waters, with nomenclatorial notes and analytical keys. *Misc. Publ. Mus. Zool., Univ. Mich.*, 15: 1-77, pls. 1-4.
1955. Hybridization between fish species in nature. *Systematic Zool.*, 4(1): 1-20.

Hubbs, Carl L., and Dugald E. S. Brown

1929. Materials for a distributional study of Ontario fishes. Trans. Roy. Can. Inst. (1929), 17: 1-56.

Hubbs, Carl L., and Karl F. Lagler

1947. Fishes of the Great Lakes Region. Bull. Cranbrook Inst. Sci., 26: i-xi, 1-109, many figs.
1958. Fishes of the Great Lakes Region. Bull. Cranbrook Inst. Sci., 26: i-xi, 1-213, many figs. 44 color pls. (revised edition).

Hubbs, Carl L., and George A. Moore

1940. The subspecies of *Notropis zonatus*, a cyprinid fish of the Ozark upland. Copeia, 1940(2): 91-99.

Hubbs, Carl L., and A. I. Ortenburger

1929. Fishes collected in Oklahoma and Arkansas in 1927. Publ. Univ. Okla. Biol. Surv., 1(3): 45-112, pls. 6-13.

Hubbs, Carl L., and Edward C. Raney

1951. Status, subspecies, and variation of *Notropis cummingsae*, a cyprinid fish of the southeastern United States. Occ. Papers Mus. Zool., Univ. Mich., 535: 1-25, 1 pl.

Hubbs, Clark

1951. Records from east Texas of three species of fish, *Semotilus atromaculatus*, *Notropis cornuta*, and *Microperca proleptaris*. Texas Jour. Sci., 3(3): 490.

Jennings, Dolph

1942. Kansas fish in the Kansas State College Museum at Manhattan. Trans. Kans. Acad. Sci., 45: 363-366.

Jones, David T.

1929. Notes on fishes taken in the vicinity of Vinton, Iowa. Copeia, 171: 29-34.

Jordan, David Starr

1875. Synopsis of the genera of fishes to be looked for in Indiana. Ann. Rept. Geol. Surv. Indiana (1874): 197-228.
1876a. Concerning the fishes of the Ichthyologia Ohienensis. Bull. Buffalo Soc. Nat. Sci., 3: 91-97.
1876b. Manual of the vertebrates of the northern United States . . . 1st ed., Jansen, McClurg and Co., Chicago; 342 pp.
1877. Contributions to North American Ichthyology. . . I. Review of Rafinesque's memoirs on North American fishes. Bull. U. S. Nat. Mus., 9: 1-53.
1878. A catalogue of the fishes of the fresh waters of North America. Bull. U. S. Geol. and Geog. Surv. Terr., 4: 407-442.
1880. Description of new species of North American fishes. Proc. U. S. Nat. Mus. (1879), 2(84): 235-241.

1882. Report on the fishes of Ohio. Section IV. Rept. Geol. Surv. Ohio, 4 (Zool. and Bot., Pt. I), pp. 737-1002.
1884. Manual of the vertebrates of the northern United States . . . 4th ed., Jansen, McClurg and Co., Chicago, 406 pp.
- 1885a. Identification of the species of Cyprinidae and Catostomidae, described by Dr. Charles Girard, in the Proceedings of the Academy of Natural Sciences of Philadelphia for 1856. Proc. U. S. Nat. Mus., 8(500): 118-127.
- 1885b. A catalogue of the fishes known to inhabit the waters of North America, north of the Tropic of Cancer, with notes on the species discovered in 1883 and 1884. Ann. Rept. Comm. Fish and Fisheries (1885): 787-973.
1888. A manual of the vertebrate animals of the northern United States . . . 5th ed., A. C. McClurg and Co., Chicago, iii + 375 pp.
- 1889a. 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. (1888), 11(723): 351-362, pls. 43-45.
- 1889b. Report of explorations made during the summer and autumn of 1888, in the Allegheny region of Virginia, North Carolina and Tennessee, and in western Indiana, with an account of the fishes found in each of the river basins of those regions. Bull. U. S. Fish Comm. (1888), 8: 97-173, pls. 13-15.
1916. The nomenclature of American fishes as affected by the opinions of the International Commission on Zoological Nomenclature. Copeia, 29: 25-28.
1929. Manual of the vertebrate animals of the northeastern United States inclusive of marine species . . . 13th ed., World Book Co., Yonkers-on-Hudson, N. Y., xxx + 446 pp., 1 map, 15 figs.
- Jordan, David Starr, and Alembert W. Zrayton
1878. Contributions to North American ichthyology. Based primarily on the collections of the United States National Museum. III. A. on the distribution of the fishes of the Allegheny region of South Carolina, Georgia, and Tennessee, with descriptions of new and little known species. Bull. U. S. Nat. Mus., 12: 7-95.
- Jordan, David Starr, and Herbert E. Copeland
1876. Check list of the fishes of the fresh waters of North America. Bull. Buffalo Soc. Nat. Sci., 3: 133-164.
- Jordan, David Starr, and Barton Warren Evermann
- 1896a. A check-list of the fishes and fish-like vertebrates of North and Middle America. Rept. U. S. Comm. Fish and Fisheries (1895): 207-584.
- 1896b. The fishes of North and Middle America . . . Bull. U. S. Nat. Mus., 47(1): i-lx, 1-1240.
- Jordan, David Starr, and Howard Walton Clark
1930. Check list of the fishes and fishlike vertebrates of North and Middle America, north of the northern boundary of Venezuela and Colombia. Rept. U. S. Fish Comm. (1928), 2: 1-670.

Jordan, David S., and Charles H. Gilbert

1877. On the genera of North American fresh-water fishes. Proc. Acad. Nat. Sci. Phila., 29: 83-104.

1883. Synopsis of the fishes of North America. Bull. U. S. Nat. Mus., 16: i-lvi, 1-1018.

Jordan, David S., and Joseph Swain

1883. List of fishes collected in the Clear Fork of the Cumberland, Whitley County, Ky., with descriptions of three new species. Proc. U. S. Nat. Mus., 6(378): 248-251.

Keleher, J. J.

1956. The northern limits of distribution in Manitoba for cyprinid fishes. Canadian J. Zool., 34: 263-266.

Kirtland, Jared P.

1845. Descriptions of the fishes of the Ohio and its tributaries (continued). Boston Jour. Nat. Hist., 5: 21-32, pls. 7-9.

1846. Descriptions of the fishes of Lake Erie, the Ohio River, and their tributaries. Boston Jour. Nat. Hist., 5: 265-276.

Knapp, Frank T.

1953. Fishes found in the freshwaters of Texas. Ragland Studio and Litho. Printing Co., Brunswick, Ga., vii + 165 pp., 190 figs.

Koster, William J.

1939. Some phases of the life history and relationships of the cyprinid, *Clinostomus elongatus* (Kirtland). Copeia, 1939 (4): 201-208.

Lachner, Ernest A.

1952. Studies on the biology of the cyprinid fishes of the chub genus *Nocomis* of northeastern United States. Am. Midland Naturalist, 48(2): 433-466.

Langlois, Thomas H.

1954. The western end of Lake Erie and its ecology. J. W. Edwards, Ann Arbor, Michigan, 479 pp., 72 figs.

Larimore, R. Weldon, and Philip W. Smith

1963. The fishes of Champaign County, Illinois, as affected by 60 years of stream changes. Bull. Ill. Nat. Hist. Surv., 28(2): 299-382, figs. 1-70.

Livingstone, D. A.

1953. The fresh water fishes of Nova Scotia. Proc. Nova Scotian Inst. Sci., 23(1): 1-90, figs. 1-36.

Luce, Wilbur M.

1933. A survey of the fishery of the Kaskaskia River. Bull. Ill. Nat. Hist. Surv., 20: i-iii, 71-123, figs. 1-12.

Martin, W. R.

1949. The mechanics of environmental control of body form in fishes. Univ. Toronto Stud., Biol. Ser. 58, Publ. Ont. Fish. Res. Lab., 70: 1-91, figs. 1-24.

Miller, Robert Rush

1957. Utilization of x-rays as a tool in systematic zoology. *Systematic Zool.*, 6(1): 29-40.

Miller, Rudolph J.

1962. Sexual development and hermaphroditism in the hybrid cyprinid, *Notropis cornutus* x *N. rubellus*. *Copeia*, 1962(2): 450-452.
1963. Comparative morphology of three cyprinid fishes: *Notropis cornutus*, *Notropis rubellus*, and the hybrid, *Notropis cornutus* x *Notropis rubellus*. *Am. Midland Naturalist*, 69(1): 1-33.

Mitchill, Samuel L.

1817. Report on the ichthyology of the Walkill, from specimens of fishes presented to the Society (Lyceum of Natural History) . . . by Dr. B. Akerly *Am. Monthly Mag. and Crit. Review*, vol. 1, no. 4, pp. 289-290.

Moore, George A., and John M. Paden

1950. The fishes of the Illinois River in Oklahoma and Arkansas. *Am. Midland Naturalist*, 44(1): 76-95.

Murray, Merritt J.

1938. Survey of some northern Indiana streams with special reference to trout production. *Invest. Indiana Lakes and Streams*, Indiana Dept. Cons., 1(7): 80-99, 7 figs.

O'Donnell, D. John

1935. Annotated list of the fishes of Illinois. *Bull. Ill. Nat. Hist. Surv.*, 20: 473-491, figs. 1-2.

Ortenburger, A. I., and Carl L. Hubbs

1927. A report on the fishes of Oklahoma, with descriptions of new genera and species. *Proc. Okla. Acad. Sci.* (1926), 6(19): 123-141.

Outten, L. M.

1957. A study of the life history of the cyprinid fish *Notropis coccoensis*. *Jour. Elisha Mitchell Sci. Soc.*, 73(1): 68-84.

Pfeiffer, Roman A.

1955. Studies on the life history of the Rosyface shiner, *Notropis rubellus*. *Copeia*, 1955(2): 95-104.

Pickens, A. L.

1928. Fishes of upper South Carolina. *Copeia*, 167: 29-32.

Putnam, F. W.

1863. List of the fishes sent by the Museum to different institutions, in exchange for other specimens, with annotations. *Bull. Mus. Comp. Zool.*, 1(1): 1-16.

Radforth, Isobel

1944. Some considerations on the distribution of fishes in Ontario. *Contr. Roy. Ont. Mus. Zool.*, 25: 1-116, figs. 1-32.

Rafinesque, C. S.

1817. First decade of new North-American fishes. *Am. Monthly Mag. and Crit. Review* (December, 1817), art. 5, no. 14, 2(2): 120-121.
- 1820a. *Ichthyologia Ohiensis*, or natural history of the fishes inhabiting the River Ohio and its tributary streams, preceded by a physical description of the Ohio and its branches. W. C. Hunt, Lexington, Ky., 90 pp.
- 1820b. *Annals of Nature* or annual synopsis of new genera and species of animals, plants, etc. discovered in North America. First Annual Number for 1820, printed for the author, Lexington, Kentucky, pp. 4-6.

Raney, Edward C.

- 1940a. The breeding behavior of the common shiner, *Notropis cornutus* (Mitchill). *Zoologica*, 25(1): 1-14, 4 pls.
- 1940b. Reproductive activities of a hybrid minnow, *Notropis cornutus* x *Notropis rubellus*. *Zoologica*, 25(3): 361-367, 1 table.
- 1940c. Nests under the water. *Bull. N. Y. Zool. Soc.*, 43(4): 127-135.
1947. *Nocomis* nests used by other breeding cyprinid fishes in Virginia. *Zoologica*, 32(3): 125-132, 1 pl.
1950. Freshwater fishes. In: *The James River basin, past, present and future*. Va. Acad. Sci., Richmond, pp. 151-194.

Raney, Edward C., and Ernest A. Lachner

1946. *Thoburnia hamiltoni*, a new sucker from the upper Roanoke River system in Virginia. *Copeia*, 1946(4): 218-226.

Romer, Alfred S.

1945. *Vertebrate Paleontology*. Univ. of Chicago Press, Chicago, 687 pp., 377 figs., 4 tables.

Ruthven, A. G.

1906. The cold-blooded vertebrates of the Porcupine Mountains and Isle Royale, Michigan. In: *An ecological survey in northern Michigan*. ("A Report from the University Museum, University of Michigan, published by the State Board of Geological Survey as part of the Report for 1905"), pp. 107-112.

Schelske, Claire

1957. An ecological study of the fishes of the Fall and Verdigris rivers in Wilson and Montgomery counties, Kansas, March, 1954 to February, 1955. *Emporia St. Res. Studies*, 5(3): 31-56.

Schrenkeisen, Ray

1938. *Field book of fresh-water fishes of North America north of Mexico*. G. P. Putnam's Sons, New York, xii + 312 pp., frontisp. and many figs.

Schultz, Leonard P.

1927. Temperature-controlled variation in the Golden shiner, *Notemigonus crysoleucas*. *Pap. Michigan Acad. Sci., Arts and Letters* (1926), 7: 417-432, tabs. 1-9, figs. 1-3.

Scott, W. B., and E. J. Crossman

1959. The freshwater fishes of New Brunswick: a checklist with distributional notes. Contr. Roy. Ont. Mus., Div. Zool. and Paleontology, 51: 1-37.

Simon, James R.

1946. Wyoming fishes. Bull. Wyoming Game and Fish Dept., 4: 1-129, figs. 1-92.

Smith, C. Lavett

1956. A simple microscope protractor. Copeia, 1956(4): 250.

Storer, David Humphreys

1845. (No title). Proc. Boston Soc. Nat. Hist., 2: 47-50.
1846. A synopsis of the fishes of North America. Mem. Am. Acad. Arts and Sci., 2: 253-550.
1855. A history of the fishes of Massachusetts (part 2). Mem. Am. Acad. Arts and Sci., 5: 122-168, 16 pls.

Taylor, William Ralph

1954. Records of fishes in the John N. Lowe collection from the Upper Peninsula of Michigan. Misc. Publ. Mus. Zool., Univ. Mich., 87: 1-50.

Trautman, Milton B.

1939. The effects of man-made modifications on the fish fauna in Lost and Gordon creeks, Ohio, between 1887-1938. Ohio Jour. Sci., 39(5): 275-288
1948. A natural hybrid catfish, *Schilbeodes miurus* x *Schilbeodes mollis*. Copeia, 1948(3): 166-174.
1957. The fishes of Ohio. Ohio St. Univ. Press, Columbus, xvii + 683 pp., 172 maps, 172 figs., 7 color pls.

Valenciennes, A. (in Cuvier and Valenciennes)

1844. Histoire Naturelle des Poissons. Paris, vol. 17, 497 pp., col. pls. 487-519.

Van der Schalie, Henry

1945. The value of mussel distribution in tracing stream confluence. Papers Michigan Acad. Sci., Arts and Letters, 30: 355-373.

Woolman, Albert J.

1892. Report of an examination of the rivers of Kentucky, with lists of the fishes obtained. Bull. U. S. Fish. Comm. (1890), 10: 249-288, pl. 51.

Wright, Frank J.

1934. The newer Appalachians of the South. Part I. Between the Potomac and New Rivers. Denison Univ. Bull., Jour. Sci. Lab., 29(1): 1-105, pls. 1-28, figs. 1-3.

Contributions to the BULLETIN OF THE FLORIDA STATE MUSEUM may be in any field of biology. Manuscripts dealing with natural history or systematic problems involving the southeastern United States or the Caribbean area are solicited especially.

Manuscripts should be of medium length—50 to 200 pages. Examination for suitability is made by an Editorial Board.

The BULLETIN is distributed worldwide through institutional subscriptions and exchanges only. It is considered the responsibility of the author to distribute his paper to all interested individuals. To aid in this, fifty copies are furnished the author without cost.

PREPARATION OF MANUSCRIPT

Highly recommended as a guide is the volume:

Conference of Biological Editors, Committee on Form and Style.

1960. Style manual for biological journals.

Amer. Inst. Biol. Sci., Washington. 92 p.

Manuscripts should be typewritten with double spacing throughout, with ample margins, and on only one side of the paper. The author should keep a copy; the original and a carbon must be submitted. Tables and legends of figures should be typed on sheets separate from the text. Several legends or tables may be placed on a single sheet.

Illustrations, including maps and photographs, should be referred to as "figures." All illustrations are reduced to a maximum of 4-1/4 by 7-1/8 inches. Size scales, wherever they are necessary, should be incorporated into the figure.

References to literature should conform with the bibliographic style used in recent numbers of the BULLETIN. Spell out in full the titles of non-English serials and places of publication.

Footnote material should be kept to a minimum. However, provide copy for a footnote detailing the title, affiliations, and address of the author (see recent numbers of the BULLETIN).

Manuscripts must be accompanied by a synopsis—a brief and factual summary (not a mere description) of the contents and conclusions, which points out the presence of any new information and indicates its relevance. In it list all new organisms described and give their ranges; indicate all taxonomic changes proposed. The synopsis, written in full sentences, should be concise, but completely intelligible in itself without references to the paper, thereby enabling the busy reader to decide more surely than he can from the title alone whether the paper merits his reading. The synopsis will be published with the paper. It does not replace the usual conclusions or summary sections. It may also serve as copy for the abstracting services.

Manuscripts and all editorial matters should be addressed to:

Managing Editor of the BULLETIN
Florida State Museum
Seagle Building
Gainesville, Florida