BULLEIN

of the FLORIDA STATE MUSEUM Biological Sciences

Volume 17 1972 Number 1

SYSTEMATICS OF THE SUBGENUS LYTHRURUS, GENUS NOTROPIS (PISCES: CYPRINIDAE)

Franklin F. Snelson, Jr.



Numbers of the BULLETIN OF THE FLORIDA STATE MUSEUM, BIOLOGICAL SCIENCES, 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

Consultants for this issue: CARTER R. GILBERT ROBERT E. JENKINS

Communications concerning purchase or exchange of the publication and all manuscripts should be addressed to the Managing Editor of the Bulletin, Florida State Museum, Museum Road, University of Florida, Gainesville, Florida 32601.

This public document was promulgated at an annual cost of \$2653.08 or \$2.70 per copy. It makes available to libraries, scholars, and all interested persons the results of our researches in the natural sciences, emphasizing the Circum-Caribbean Region.

SYSTEMATICS OF THE SUBGENUS Lythrurus, GENUS Notropis (PISCES: CYPRINIDAE)

Franklin F. Snelson, Jr. 1

Synopsis: The subgenus Lythrurus Jordan is diagnosed and its nomenclature discussed. Closely related to the atherinoides series of the subgenus Notropis Rafinesque, Lythrurus is composed of four species groups distinguished on the basis of tuberculation, vertebral number, and pigmentation. These groups are as follows: (1) the fumeus complex, includes only Notropis fumeus Evermann; (2) the ardens complex, includes N. ardens (Cope) and N. lirus (Jordan); (3) the umbratilis complex, includes N. umbratilis (Girard) and subspecies; and (4) the roseipinnis complex, which is revised herein.

Members of the roseipinnis complex are distributed primarily in streams of the eastern Gulf Coast. All forms are closely related and distinguished chiefly on measurements and pigmentation, especially that of the fins. N. b. bellus (Hay) shows little geographic variation and is distributed throughout most of the Mobile Bay basin. It is absent above the Fall Line in the Coosa River system. Above the Fall Line in the Black Warrior River system it is replaced by a strongly differentiated new subspecies, N. b. alegnotus. These two forms appear to have interbred and formed intergrade populations around Tuscaloosa, Alabama.

N. roseipinnis (Hay) is distributed in Gulf Coastal streams from Mobile Bay west through Lake Pontchartrain and in the Bayou Pierre, Big Black, and Yazoo drainages of the Mississippi Valley. This species exhibits striking geographic variation, much of an east-west clinal nature. Though they have not been collected together, N. b. bellus and N. roseipinnis live in close proximity in the lower Mobile Bay drainage. Here they are strongly differentiated, but more westerly populations of N. roseipinnis approach N. b. bellus in many features.

N. atrapiculus, a new form previously confused with N. b. bellus and N. roseipinnis, is distributed in streams along the eastern Gulf Coast from the Escambia to the Apalachicola drainage. It is allopatric from its two close relatives and is intermediate or interjacent between them in most differentiating characters. Because of its intermediacy and the resulting weak differentiation, its proper taxonomic status is de-

batable. As nothing suggests whether it is more closely related to N. b. bellus or to N. roseipinnis, atrapiculus is accorded specific rank.

¹This is the first in a series of papers dealing with the systematics of the subgenus Lythrurus. This study is part of a dissertation submitted to the Graduate School of Cornell University in partial fulfillment of the requirements for the Ph.D. degree. The author is currently Assistant Professor of Biological Sciences at Florida Technological University, P. O. Box 25000, Orlando, Florida 32816. Manuscript accepted 20 June 1971. Ed.

Snelson, Franklin F., Jr. 1972. Systematics of the Subgenus *Lythrurus*, Genus *Notropis* (Pisces: Cyprinidae) Bull. Florida State Mus., Biol. Sci., Vol. 17, No. 1, pp. 1-92.

TABLE OF CONTENTS

YNOPSIS	1
NTRODUCTION	2
ACKNOWLEDGEMENTS	3
METHODS AND SIGNIFICANCE OF CHARACTERS STUDIED	
MATERIAL EXAMINED	
Systematics Accounts	17
Surgenus Luthrurus	Ľ
Notropis bellus bellus 2	20
Notronis hellus alegnotus new subspecies	37
Notropis bellus: bellus x alegnotus	43
Notropis roseipinnis	45
Notropis atrapiculus new species	58
EVOLUTION OF THE roseipinnis Species Complex	
LITERATURE CITED	
Tables	

INTRODUCTION

Taxonomic and evolutionary problems are characteristic of groups that have undergone recent radiation, and the North American minnow genus *Notropis* is no exception. The limits of the genus are quite subjective, and "lumpers" and "splitters" continue to debate the status of peripheral yet closely related genera. Several well-defined lineages within the genus merit subgeneric status, but many species do not fit into any subgeneric scheme yet proposed. Forms included in the genus present examples of all levels of divergence, including the especially troublesome category of incipient or semispecies (Gilbert, 1961). Intrageneric hybridization is not uncommon.

Students of *Notropis* have recently made significant progress in unraveling systematic and evolutionary problems. Some of the more important works in this regard have been studies of subgenera or species groups containing assemblages of closely related forms, for example the subgenus *Cyprinella* (Gibbs, 1957a, b, and other papers), the subgenus *Luxilus* (Gilbert, 1961, 1964), the *N. hypselopterus* complex (Bailey and Suttkus, 1952; Suttkus, 1955), portions of the subgenus *Hydrophlox* (Suttkus and Raney, 1955a,b,c), and portions of *Hydrophlox* and the *N. texanus* species group (Swift, 1970).

The object of this study is to clarify the systematics of an additional

group of closely related *Notropis* species assigned to the subgenus *Lythrurus*. As currently constituted, *Lythrurus* contains the following forms¹:

Notropis fumeus Evermann
Notropis umbratilis umbratilis (Girard)
Notropis umbratilis cyanocephalus (Copeland)
Notropis ardens ardens (Cope in Günther)
Notropis ardens lythrurus (Jordan)
Notropis ardens matutinus (Cope)
Notropis lirus (Jordan)
Notropis bellus bellus (Hay)
Notropis bellus alegnotus new subspecies
Notropis roseipinnis Hay
Nortropis atrapiculus new species

The included forms are distributed primarily along the eastern Gulf Coast and in the Mississippi Valley. The Atlantic slope and the Great Lakes basin have each been invaded by only one species, *N. ardens* and *N. umbratilis* respectively. Most of the species prefer small, clear streams, where they are often abundant. Maximum length attained usually is less than 2½ inches, and most of the species have small scales and bright red breeding colors.

ACKNOWLEDGEMENTS

This study was carried out under the guidance of Edward C. Raney. In addition to his interest and encouragement, Dr. Raney allowed unrestricted access to his voluminous library. Clifford O. Berg and Richard B. Root served as minor committee members and greatly stimulated my interest and imagination. My graduate program and this study were supported by a National Institutes of Health Predoctoral Graduate Fellowship awarded by the Division of General Medical Sciences. Funds for computer analysis of certain data were provided through NSF Grant GB 4865 X to Edward C. Raney. Royal D. Suttkus had previously recognized many of the systematic problems concerning *Lythrurus* species, but generously suggested that I pursue this study.

I am grateful to the following curators or staff and their institutions (abbreviations used throughout the text) for granting specimen loans, laboratory facilities, and numerous other courtesies: James E. Böhlke and James C. Tyler, Academy of Natural Sciences of Philadelphia (ANSP); John S. Ramsey and Ron J. Gilbert, Auburn University (AU); Edward C. Raney, Cornell University (CU); Joseph R. Bailey, Duke University (DU); Ralph W. Yerger and Camm C. Swift, Florida State University (FSU); Philip W. Smith, Illinois Natural History Survey (INHS); Craig E. Nelson, Indiana University (IU); William M. Palmer, North Carolina State Museum

¹Certain nomenclatural modifications of this list will be required, but except for members of the *roseipinnis* complex, I prefer to use currently accepted nomenclature until justification for name changes has been published. Certain nomenclatural changes have been anticipated by Bailey et al. (1970).

(NCSM); Neil H. Douglas, Northeastern Louisiana University (NLU); Milton B. Trautman, Ohio State University (OSU); George A. Moore and Rudolph J. Miller, Oklahoma State University (OSUMZ); Kirk Strawn and J. Van Conner, Texas A and M University (TAMU); Clark Hubbs, University of Texas Natural History Collection (TNHC); Royal D. Suttkus and Glenn H. Clemmer, Tulane University (TU); Ernest A. Lachner and Stanley H. Weitzman, United States National Museum (USNM); Herbert T. Boschung, Jr., Benjamin R. Wall, Jr., and James D. Williams, University of Alabama (UAIC); Donald C. Scott and Michael Dahlberg, University of Georgia (UG); Frank B. Cross, University of Kansas (UK); William M. Clay, University of Louisville (UL); Reeve M. Bailey and Robert R. Miller, University of Michigan Museum of Zoology (UMMZ); Loren Hill, University of Oklahoma (UOMZ); William S. Woolcott, University of Richmond (UR); and David A. Etnier, University of Tennessee (UT). Material from the Fannye A. Cook collection (AF), housed at the Mississippi State Game and Fish Commission Museum in Jackson, was examined while on loan to various workers at the University of Alabama.

The following generously provided field assistance: Lee Barclay, J. J. Chambers, Glenn H. Clemmer, Ron J. Gilbert, W. Mike Howell, James H. Hunt, Robert E. Jenkins, Bruce W. Menzel, William M. Palmer, John S. Ramsey, James D. Williams, and Thomas E. Yarbrough. Nomenclatural matters were discussed with Reeve M. Bailey, William I. Follett, Carter R. Gilbert, Carl L. Hubbs, Ernest A. Lachner, Ralph W. Taylor, and James C. Tyler. Bruce W. Menzel freely gave help and advice in organizing data for computer analysis and in the statistical interpretation of results.

I am indebted to the following colleagues for many favors: Robert C. Cashner, Glenn H. Clemmer, J. Van Conner, Llewellyn M. Ehrhart, Carter R. Gilbert, W. Mike Howell, Robert E. Jenkins, Robert A. Kuehne, Maurice F. Mettee, Jr., George A. Moore, William M. Palmer, William L. Pflieger, John S. Ramsey, Harley W. Reno, Robert D. Ross, Clarence L. Smith, William F. Smith-Vaniz, Royal D. Suttkus, Camm C. Swift, Benjamin R. Wall, Jr., James D. Williams, David L. Thomas, Milton B. Trautman, and Timothy Zorach. The line drawings are by Merry F. Wirtz, and graphs are by George Batik. Photographic copy work is by Douglas M. Payne and Lorran R. Meares.

Both my parents and parents-in-law indirectly contributed to this work in numerous ways. Deepest thanks go to my wife Earline for her labors toward the completion of the original dissertation.

METHODS AND SIGNIFICANCE OF CHARACTERS STUDIED

Unless specified otherwise, counting and measuring procedures follow Hubbs and Lagler (1958:19-26). The expression of meristic data in the form (8) 9-11 (13) indicates that the extreme values for this character were 8 and 13, and that 85-95 percent of the observed counts were between 9 and 11.

All meristic characters were analyzed initially by drainage and occasionally on an upstream-downstream tributary basis also. When no significant intra- or interdrainage variation was apparent, the data were pooled for presentation in tables or text.

Many morphometric and secondary sexual characters of *Lythrurus* species exhibit seasonal variation. Such characters were evaluated only in specimens collected during the breeding season. Unless a more specific meaning is indicated, the terms "breeding", "spawning", "nuptial",

and "reproductive" are used to indicate only that the specimens under consideration were deemed to be in or near spawning condition on the basis of gonadal development and/or full expression of secondary sexual characters.

FIN RAY COUNTS.—The dorsal, pelvic, and caudal fin rays showed only rare deviation from the counts of 8, 8, and 19 respectively, and detailed analyses were discontinued early in the study. The number of pectoral fin rays, counted only on the left side, proved to be of relatively little systematic value. N. b. alegnotus differs from other members of the roseipinnis complex in having slightly fewer pectoral fin rays; otherwise, Lythrurus species have usual counts of 13 or 14. The number of anal fin rays shows interesting patterns of geographic variation within species but is of limited use in distinguishing between species. The subgenus as a whole is characterized by high anal ray counts, usually 10-13. Certain populations of N. roseipinnis have the highest anal ray counts $(\bar{x}=12.1)$ recorded for the genus.

SCALE COUNTS.—Counts of the body and caudal peduncle circumferential scales are written in the form 7-2-5=14, indicating seven scales above and between the lateral lines and five scales below and between the lateral lines. The dorsal component of the body circumference scale count was made around the body at the point, slightly in advance of the pelvic fin insertion, where the lateral line dipped to its lowest level.

Predorsal scales of Lythrurus species are small, partially embedded, and often nonimbricate. Furthermore the anterior dorsolateral area of the body is variably naked in N. atrapiculus and N. roseipinnis. In addition, breeding males of several species have thickened skin and enlarged tubercles on the nape, often extending along the notal ridge to the dorsal fin origin. These and other considerations make the usual predorsal scale count and the anterior dorsolateral scale count of Gilbert (1964) impossible to apply consistently in Lythrurus. Consequently, number of predorsal scale rows was used as an index of predorsal scale In making this count, previously applied in the genus by Bailey and Suttkus (1952), Suttkus (1955), and Suttkus and Clemmer (1968), the posteroventrally oblique scale rows crossing an imaginary line between the dorsal fin insertion and cleithrum were enumerated. first row counted was the one including the first predorsal scale; the last row counted was the one including the first (anterior-most) lateral line scale. Single scales interposed between two otherwise regular rows were not counted. Two or more scales in a regular, oblique series were considered a row even if that series terminated before crossing the dorsal midline or the lateral line. This count is easily made, relatively objective, and consistently applicable to all species studied. However, because the line of enumeration passes low on the sides anteriorly, it is less sensitive to variation in scale size along the predorsal midline than is the usual predorsal scale count.

In Lythrurus the systematic utility of scale counts is reduced by extensive intraspecific variation. In some instances, a single species shows variation spanning that within the whole subgenus. When species differ in scale numbers, the differences are usually only modal. Large samples were needed to elucidate all but the grossest intraspecific variation.

SQUAMATION.—Cursory observations indicate that all forms of Lythrurus have the breast partly to completely covered with small, partially embedded scales. The predorsal midline is usually fully scaled, but occasionally there are narrow, naked interspaces between nonimbricate scales or naked patches of varying sizes. Because of difficulties in objective evaluation, no attempt was made to quantify breast or nape squamation.

Squamation tends to be reduced on the anterior dorsolateral part of the body. In its weakest form, this reduction is expressed as narrow imbrication of thin, partially embedded scales. Intermediate stages of reduction are characterized by scales on the upper anterior sides of the body being nonimbricate and isolated from one another by naked interspaces of varying sizes. Maximum reduction is characterized by the upper anterior sides of the body being naked. Size of the naked area varies; in extreme cases it is triangular in shape, with its base at the head and its apex extending posteriorly to just below the dorsal fin origin.

Five arbitrary classes of anterior dorsolateral scale reduction were distinguished and numbered as follows: (0) no reduction; scales fully (though weakly) imbricate, with no naked interspaces; this is the typical condition in N. b. bellus; (1) weak reduction; scales not fully imbricate, with narrow naked interspaces; (2) moderate reduction; scales not imbricate, with moderate naked interspaces; (3) strong reduction; scales few and scattered, with naked interspaces larger than average scale diameter: (4) naked: scales absent from an area of varying size on the anterior dorsolateral part of the body; this is the extreme condition, developed in some populations of N. roseipinnis and occasionally in N. atrapiculus. The symbols (+) and (-) were used with each of the five index values, indicating specimens that did not exactly conform to the typical condition for a given category. In the final analysis, index values were assigned arbitrary numerical values as follows: 0=0; 0(+)=0.3; 1(-) = 0.7; 1 = 1; 1(+) = 1.3; 2(-) = 1.7; 2 = 2; 2(+) = 2.3; 3(-) = 1.72.7; 3=3; 3(+)=3.3; 4(-)=3.7; 4=4; 4(+)=4.3. The index of reduction was recorded only from the left side of specimens over 40 mm SL. The index considers only the size of the naked interspaces between scales, and not scale size *per se*. Scale size usually, but not necessarily, decreases with the increase in the scale reduction index.

PHARYNGEAL TEETH.—The pharyngeal teeth of most Lythrurus forms showed only nominal variation from the usual count of 2,4-4,2. Only N. b. alegnotus shows a significant tendency for one tooth to be lost from the minor row on one or both sides.

GILL RAKERS.—The gill rakers on the lower limb of the first branchial arch were counted on the right side for ease of handling. Any raker that straddled the angle of the arch was counted. The number of gill rakers shows no ontogenetic change in *N. amoenus* (Abbott) or *N. atherinoides* Rafinesque (Snelson, 1968). This appears to be the case in *Lythrurus* species, but regression analyses were not performed. Only rarely were rakers counted in specimens below 40 mm SL.

The length, number, and structure of gill rakers are useful taxonomically in the study of certain shiners (Snelson, 1968, 1971), especially in cases where morphological or ecological clues suggest trophic divergence. Gill raker characters were of relatively little significance in *Lythrurus*, where the species share basically similar trophic adaptations. All species are characterized by a few (usually 6-8) rather short rakers, which showed no significant incidence of unusual structure (cf. Snelson, 1968:791). Gill-raker characters showed little or no geographic variation.

Vertebrae.—Vertebral numbers were determined from radiographs. The total count includes the Weberian apparatus (4) and the urostylar vertebra (1). The first vertebra bearing a well-developed hemal spine was considered the first caudal vertebra; all those anterior to it were counted as trunk vertebrae. Number of vertebrae proved useful in confirming the suspected close relationship between N. ardens and N. lirus and added evidence for distinguishing these two species as a group from the remainder of the subgenus. N. roseipinnis exhibits east-west clinal variation in vertebral numbers.

Measurements.—Measurements were taken with dial calipers to the nearest 0.05 mm. All measurement conversions were made arithmetically. The opercular membrane was excluded from the head length and postorbital head length measurements. Fleshy orbit length was the greatest transverse distance between the fleshy margins of the orbit, excluding any marginal skin that grew inward over the cornea. Postdorsal length was taken from the insertion of the dorsal fin to the caudal base. Body width was the maximum dimension, measured between the pectoral and pelvic fin bases. Prepelvic and preanal measurements were

taken from the insertion of the first ray of those fins to the tip of the upper lip.

The use of morphometric data in *Lythrurus* is complicated by several sources of variation; most conspicuous are allometric, sexual, and seasonal components. Seasonal variation was minimized by measuring only breeding specimens. Allometric variation was minimized by measuring specimens within a limited size range. The complicating effects of sexual dimorphism in certain measurements (see below) usually were eliminated by utilizing only breeding males for both intra- and interspecific comparisons.

Morphometrics usually proved to vary little over the range of a species. However distinct east-west clinal variation was discovered in certain measurements of *N. roseipinnis*, and *N. lirus* also exhibited geographic variation in some proportions.

LATERAL LINE SYSTEM.—Only three forms of the subgenus Lythrurus, N. b. alegnotus, N. fumeus, and N. lirus, show a tendency for the
lateral line on the body to be reduced. This reduction seems attributable to delayed development and takes the form of certain scale pores
being poorly and irregularly formed or absent. Reduction is strongest
on the caudal peduncle, where the affected scales may be isolated or
in a continuous series.

The great variability of this character precluded any meaningful quantitative analysis. While it is evident that overall development of the lateral line improves with size, the relationship between number of pored or unpored scales and size seems to follow no orderly pattern. Extent of lateral line reduction varies considerably between different populations of the same species, further complicating analysis. The overall trend toward reduction of the lateral line is most weakly expressed in *N. fumeus* and most strongly developed in *N. b. alegnotus*, *N. lirus* being somewhat intermediate.

In examination of the cephalic lateral line, the terminology, abbreviations, and counting procedures of Illick (1956) and Reno (1966, especially figs. 1 and 3) are followed with a few alterations. A common pore at the junction of the supratemporal (ST) and infraorbital (IO) canals was excluded from the count of both canals. In pore count formulas, the broad separation of the ST canal at the dorsal midline is indicated by a comma; otherwise, interruptions along the length of a canal are indicated by a plus (+) sign.

The IO canal as defined by Illick (1956) is composed of two segments. The IO segment extends posteriorly to the dermosphenotic bone, and the postocular commissure (POC) extends from the dermosphenotic bone to the junction of the ST canal (Reno, 1966). In fishes having the

supraorbital (SO) canal joining the IO canal at the dermosphenotic bone, it is convenient to include the pores anterior to this juncture in the IO canal and those posterior to it in the POC. However in most North American cyprinids the SO canal does not join the IO canal, and it is often difficult to decide whether a certain pore should be included in the IO canal or the POC. Consequently I follow Illick (1956) in including all pores anterior to the juncture of the ST canal and the POC in the count of the IO canal.

In the subgenus *Lythrurus*, only *N. ardens* has the cephalic laterosensory system fully formed in the adult stage. The system tends toward reduction in all other members of the subgenus. Reductive tendencies are expressed mainly in the development of the ST and IO canals. The SO and preoperculomandibular (POM) canals show little modification and are formed in the fashion typical of the genus (see Illick, 1956:figs. 28-30, and Reno, 1966:fig. 1).

The ST canal of all species is broadly interrupted at the dorsal midline. Incomplete development of the ST canal leaves secondary interruptions, usually between the normal positions of the first and second pores. These interruptions appear as incompletely closed pores (or slits) or open troughs. Occasionally this canal is absent on one or both sides. Reduction of the ST canal is strongest in N. b. alegnotus and N. lirus. In these two forms 52 and 60 percent respectively of the specimens examined had ST pores reduced from the typical number of 2 to 1 on one or both sides, suggesting that reductive tendencies are in the process of eliminating one pore and a portion of the canal. In other species secondary interruptions are occasional, but complete formation is the typical condition in adults.

Lekander (1949), Harrington (1955), and Swift (1970) have noted that the IO is ontogenetically the last cephalic lateral line canal to form and therefore is susceptible to retarded formation (neoteny) and other reductive tendencies. Irregularities in the presence and number of infraorbital ossicles is not uncommon. Reno (1966) demonstrated that the IO canal and some of its associated ossicles are absent in *Notropis buchanani* Meek.

In the subgenus *Lythrurus*, any or all of infraorbital bones 2 through 4 may occasionally be incompletely formed, leaving breaks or open slits in the canal. Such interruptions usually are below the eye at the junction of IO₂ and IO₃, or behind the eye at the junction of IO₃ and IO₄. Occasionally the POC is poorly formed, disconnected from the ST and/or cephalic lateralis (CL) canals, or absent. The most characteristic feature of IO canal neoteny is reduction or absence of the dermosphenotic bone. This small canal-bearing bone, when present, lies free in the skin over

the sphenotic (autosphenotic) bone posterodorsad to the eye. Harrington (1955), Reno (1966), and others have noted that this element is already a vestige; and its extreme reduction or absence is not surprising since the associated section of the IO canal is one of the last to form during ontogeny (Lekander, 1949; Swift, 1970; H. W. Reno, pers. comm.).

The condition of the IO canal at the position of the dermosphenotic bone was classified in one of three categories: (1) complete, the IO and POC segments of the canal continuous; (2) partially interrupted, the IO and POC segments being connected by an open trough or slit; (3) incomplete, the IO and POC branches entirely separate. Ossification of the dermosphenotic bone was studied on specimens cleared and stained by the method of Taylor (1967).

In N. ardens the IO canal is complete in about 95 percent of the specimens examined, and the dermosphenotic bone is present and fully formed. In a second group of forms, N. b. alegnotus, N. fumeus, and N. lirus, the IO canal is almost always incomplete at the position of the dermosphenotic bone; and the bone is usually absent or very weakly ossified. In the remaining species of the subgenus, the IO canal ranges from incomplete to complete at the position of the dermosphenotic bone; and the bone either is absent or present but poorly formed. and stained specimens reveal that the IO canal may be complete even though the dermosphenotic bone is weakly ossified or absent. The canal in such cases apparently is formed primarily of connective tissue. N. b. bellus is representative of this third grouping of species. sented in Table 1 indicate that canal closure is correlated with size. Most smaller specimens have the IO canal completely or partially interrupted; in larger ones the probability that the canal will be closed increases, but even at maximum adult sizes, a substantial portion of the population will retain the juvenile condition.

Some additional species of *Notropis* exhibiting irregularities in the development of the cephalic lateral line canals are *N. bifrenatus* (Cope) (Harrington, 1955), *N. altipinnis* (Cope) (Snelson, 1968:798), *N. chalybaeus* (Cope), *N. texanus* (Girard), *N. welaka* Evermann and Kendall (Swift, 1970), and *N. alborus* Hubbs and Raney (Snelson, 1971). Except for *N. chalybaeus* and *N. texanus*, these species are not intimately related and none are closely related to species of *Lythrurus*. Not only does canal reduction not follow phylogenetic lines, it is not directly correlated with obvious ecological parameters. For example, *N. bifrenatus*, *N. chalybaeus*, and *N. welaka* inhabit Coastal Plain creeks characterized by dark-stained acid waters, low gradients, and, often, abundant vegetation. *N. lirus* and *N. b. alegnotus*, with an equally reduced cephalic

lateral line, live in upland streams of the riffle-pool type, usually with clear water, hard bottoms, and moderate to fast current. *N. alborus* and *N. altipinnis* occupy roughly intermediate conditions in the periodically turbid streams in the Piedmont province along the central Atlantic slope.

The SO canal pores are modally 8 in all forms of the subgenus. The ST pore count is modally 2,2 in most species except when reduction of portions of the canal creates anomalous counts. The IO pore counts of all forms are quite similar, with only N. b. alegnotus showing any departure from the norm. The POM canal exhibits the greatest intra- and interspecific variation in pore counts. Cephalic lateral line pores are moderate to moderately large in species of Lythrurus. The largest pores are in the upland species N. lirus, and the second largest are in the low-land species N. fumeus.

PIGMENTATION.—Details of pigmentation are of primary importance in the systematics of certain *Notropis* groups. The following pigmentary characters are of special significance in the subgenus *Lythrurus*: (1) anterior basidorsal spot, (2) pigment on fin interradial membranes, (3) darkened scales on sides of body, (4) bar- or chevron-shaped markings on body, (5) lip and chin pigmentation, (6) midlateral stripe on body, (7) pigmentation of scale pockets on anterior dorsolateral part of body, (8) cleithral pigment, and (9) extension of pigment below lateral line. Characters (2), (3), (4), (8), and (9) exhibit their maximal and most consistent development during the breeding season; and for these characters, only specimens in breeding condition are considered in detail.

In this genus of over 110 species, an anterior basidorsal spot is found only in two species of *Lythrurus*, *N. ardens* and *N. umbratilis*. This spot is located on the dorsal fin at its anterior insertion and is formed by a concentration of melanophores over the rays and interradial membranes. It is not to be confused with a concentration of pigment on the body at the bases of the first one or two dorsal rays. The latter type of spot is developed in several other species of *Notropis*.

Despite its uniqueness, the anterior basidorsal spot apparently has not been a stable character during the evolution of *Lythrurus*. *N. lirus* does not retain the spot of its relative *N. ardens*, and all forms of the *roseipinnis* complex lack the spot seen in the related *umbratilis* complex. Even within the *umbratilis* complex, there is geographic variation in the development of the spot, suggesting that it is in the process of being lost for the third independent time.

An attempt was made to evaluate quantitatively the chevron-shaped markings and bars present on the sides of the body in some members of the subgenus. An arbitrary index was established as follows: (0) no bars or chevrons present; (1) one or the other of these markings weakly de-

veloped; (2) moderately developed; and (3) strongly developed. Plus or minus signs were appended to the index when deemed appropriate. In addition, the body bars of *N. ardens* were counted. A count of 5-4 indicates five bars before and four bars behind the dorsal fin origin. The results of this analysis were only of general use, as these pigmentary features showed conspicuous ecological, geographic, sexual, and seasonal variation. Moreover *N. ardens* was bilaterally asymmetrical in position and number of body bars in about half the specimens studied.

Fin pigmentation patterns are important characters in the subgenus Cyprinella (Gibbs, 1957a, b, and other papers) and in the hypselopterus-signipinnis-euryzonus complex of Notropis (Bailey and Suttkus, 1952; Suttkus, 1955). The subgenus Lythrurus is divisible into two groups on the basis of the presence or absence of melanin deposits in fin interradial membranes (excluding from consideration the anterior basidorsal spot). Within the group possessing fin interradial pigment, the umbratilis complex is distinguished from the roseipinnis complex in having rather patternless suffusions of melanin in the fins of spawning males only. In the roseipinnis complex, fin melanin is present in both sexes year round (intensified during the spawning period), and deposition patterns are specific.

Details of fin pigmentation are important differentiating characters in the *roseipinnis* complex. Although present throughout the year, fin pigmentation is best and most uniformly developed in breeding material, to which the analysis was limited. Fin pigment was evaluated through an index derived by counting those anal and pelvic fin interradial membranes bearing melanin. An interradial membrane was recorded as pigmented if it was solid black or if it bore even a single melanophore that was not touching a ray. Pigment on the membrane in the branch of a ray was tabulated with the preceding interradial membrane; i.e., anal membrane number one was tabulated as being pigmented if there was pigment on the membrane between the first and second principal rays and/or if there was pigment on the membrane between the branch(es) of the second ray. The number of pigmented anal and pelvic interradial membranes were added to give a total index value.

A specimen of N. b. b ellus with terminal pigment bands completely through its anal and pelvic fins might have a fin pigment index of 9 (pigmented anal membranes) + 7 (pigmented pelvic membranes) = 16 (total). The fin pigment pattern for a breeding male N. roseipinnis from the Pascagoula drainage might be as follows: (1) heavy pigment concentration in the tips of the first two anal interradial membranes, a few scattered melanophores in the third interradial membrane, and no melanophores on the following membranes; and (2) a few scattered

melanophores in the first pelvic interradial membrane and no melanophores on the following interradial membranes. The fin pigment index for this hypothetical specimen would be 3+1=4. In addition to this index, subjective features such as intensity and pattern of fin pigmentation are also significant but are not expressed quantitatively.

Fin pigment differences within the *roseipinnis* complex are determined genetically. Nevertheless, it is evident that melanophore concentrations vary phenotypically in response to some environmental factors. For example, pigment usually is better developed in specimens from dark-stained water. To compensate for the variation introduced by ecological differences, large samples of breeding specimens from many different collecting sites within each drainage were studied. To elucidate patterns of ontogenetic change in the fin pigmentation index, regression analyses were performed, considering the total fin pigment index as the dependent variable and standard length as the independent variable.

Breeding Coloration.—Two major difficulties in treating breeding coloration objectively in *Notropis* are: (1) color is developed best in breeding males, and the intensity, quality, and pattern of coloration may vary according to the state of sexual ripeness; and (2) coloration may be influenced by environmental conditions. Despite these drawbacks, breeding coloration has proved useful in several investigations of *Notropis* (e.g., Gibbs, 1957a; Gilbert, 1964; Snelson, 1968).

In Lythrurus coloration was helpful in separating N. fumeus, which has yellow pigment limited to the rays of the fins. With the exception of N. lirus, the remaining species are characterized by having red pigment developed primarily on the interradial membranes of fins and in varying amounts on the head and body. N. lirus apparently develops weak, ephemeral coloration ranging from yellow or gold through pink or red.

Breeding Tuberculation.—In recent years considerable emphasis has been placed on tuberculation as a systematic character, not only in cyprinids but in other groups as well (e.g., Vladykov, 1963, for Salmonidae; Collette, 1965, for Percidae; and Huntsman, 1967, for Catostomidae). The evaluation and practical use of tuberculation characters are complicated by several factors. First, tubercles are usually found only in, or are best developed in, adult males captured during the breeding season. Only a few large cyprinids (e.g., Nocomis, Lachner and Jenkins, 1971) have tubercle "spots" evident in both sexes throughout the year. A number of series must be surveyed to assure that maximum tubercle development has been observed. Koehn (1965) documented the developmental sequence of tuberculation for Notropis lutrensis (Baird and Girard) and showed that patterns differ according to the state of sexual

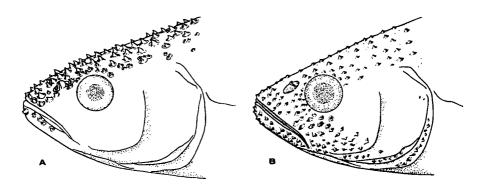


FIGURE 1.—Patterns of head tuberculation in the subgenus Lythrurus. Both drawings are composites from several adult breeding males. A.—N. ardens. CU 22997; Cumberland dr., Tennessee. 2 June 1953. This pattern is typical of all forms of the ardens species complex, except that N. lirus has fewer, more-prominent mandibular tubercles. B.—N. umbratilis cyanocephalus. INHS uncat.; Wabash dr., Illinois. 21 June 1961. This pattern is typical of all forms of the roseipinnis species complex. Gulf Coast populations of N. fumeus exhibit a similar pattern but have snout tubercles more reduced.

readiness. Finally Branson (1962) and Snelson (1968:784) have pointed out the difficulty of differentiating very small tubercles from sensory structures. Despite these complications, tuberculation has proved highly significant in establishing the taxonomic status of many closely related or otherwise very similar species (e.g., Gibbs, 1957b; Huntsman, 1967; Lachner and Jenkins, 1967, 1971; Snelson, 1968; Howell and Williams, 1971).

Two major patterns of head tuberculation occur in the subgenus Lythrurus. The N. ardens and N. lirus pattern (Fig. 1A) is characterized by (1) large, close-set, antrorse tubercles on the head dorsum; (2) a variable complement of mandible tubercles, either a few scattered at the chin tip (lirus) or several tubercles in a single row (ardens); and (3) the usual absence of tubercles elsewhere laterally and ventrally on the head. The other pattern of head tuberculation (Fig. 1B) is typical of the remainder of the subgenus except for Mississippi Valley populations of N. fumeus. This pattern is characterized by (1) moderate-sized, scattered, erect tubercles on the head dorsum; (2) tubercles arranged in two rows along each mandible; and (3) a general profusion of tubercles on lateral and ventral areas of the head.

In pectoral fin tuberculation, *N. fumeus* is distinguished from other members of the subgenus by its small, dense tubercles that form a fine shagreen over the rays. Other forms in the subgenus have larger, coarser

tubercles that usually do not form a shagreen. The largest pectoral fin tubercles in the subgenus are those of *N. ardens*.

The number of chin and lower jaw tubercles exhibits both geographic and ontogenetic variation in *N. lirus*. Mandibular tubercles were enumerated by counting each tubercle tip, not each base. In some cases a single, unusually large tubercle base may be biconic, terminating in two separate points.

Sexual Dimorphism.—The species of *Lythrurus* exhibit strong sexual dimorphism. As is typical for most cyprinids, the most striking differences involve coloration and tuberculation. The breeding colors of females are more subdued than those of males. Tubercle development in breeding females varies within the subgenus, but it is always very weak when compared with males. Females may have poorly developed head tubercles but rarely have body tubercles. Fin tubercles are always absent.

Certain pigmentation features also exhibit sexual dimorphism. The bars of N. ardens and the chevrons of N. umbratilis are best and most consistently developed in reproductive males. Darkened scales on the flanks of N. b. bellus usually are present only in males. Melanism is exhibited only by breeding males of N. umbratilis and, to a lesser degree, N. b. bellus. In the umbratilis complex, melanin is deposited in fin interradial membranes of breeding males only. In the roseipinnis complex fin membrane pigment is present year round in both sexes but is intensified in breeding males.

An enlarged urogenital papilla is characteristic of breeding females of all species of *Lythrurus*. The structure protrudes posteriorly to about the anal fin origin and has no consistent shape or ornamentation. In males the urogenital papilla is not enlarged. This character facilitates external sexing throughout most of the year.

Sexual dimorphism in body size is widespread among fishes. In North American cyprinids males usually are larger than females when territoriality is expressed, especially in the form of paternal nest building and defense. When territoriality is reduced or absent and spawning more gregarious, body size is more nearly equal, or females may be the larger sex. To check for sexual dimorphism in size, record was made of the length and sex of the largest specimen in every collection that contained mature males and females. When the largest male and female in a collection differed by less than a millimeter, no size difference was recorded. If there were no difference between the maximum size attained by each sex, one would assume that a male would be the larger sex in roughly half of the collections examined and a female would be the larger in the other half. A 2X2 Chi-square analysis (Snedecor and

Cochran, 1967) was used to determine if the observed values departed significantly from this expected 50:50 ratio. For example, of 73 collections of N. b. bellus containing mature adults of both sexes, the largest male was one millimeter or more longer than the largest female in 57; and the reverse was true in 16. The Chi-square analysis shows that the observed data depart significantly from expected values, suggesting that males are usually larger than females.

The species of *Lythrurus* are sexually dimorphic in several proportional measurements. Samples for direct sexual comparison were drawn from a relatively small geographic area (a single drainage when possible) in order to eliminate confounding geographic variation. Only breeding adults in 10-mm size classes were measured, thereby minimizing problems of allometry. Means for each measurement were compared statistically with Student's *t*-test (Snedecor and Cochran, 1967).

Results of these analyses are summarized in Table 2. As in many cyprinids, males tend to have significantly larger fins than females; the pectoral fin is the only exception in *Lythrurus*. Body depth and width measurements are usually greater in breeding females because enlarged ovaries distend their body cavities. Males of most species have deeper and/or longer caudal peduncles than do females, and the orbit is always larger in females than in males.

In Clinostomus funduloides Girard the fins are placed more posteriad in females than in males (i.e., females have greater predorsal, prepelvic, and preanal lengths) (Deubler, 1955). Miller (1963:24) found the dorsal fin of female Gila crassicauda (Baird and Girard) to be located more posteriorly than that of males, and he further stated that this is generally the case in American cyprinids. Subsequently, this matter has been given little attention. Jenkins and Zorach (1970) found no sexual difference in relative dorsal fin position of Notropis bifrenatus. Of the eight forms included in Table 2, females of four have the dorsal fin located more posteriad than that of males; and females of all have greater prepelvic and preanal lengths.

The significance, if any, of isolated instances of sexual dimorphism in proportions (e.g., the longer head of female *N. fumeus*) (Table 2) is enigmatic. Perusal of the data indicates that most of these differences probably are not maintained throughout the range of the species involved.

MATERIAL EXAMINED

The institutions from which material was examined are noted in the Acknowledgments section. Specimens studied are listed at the end of the account of each form treated. Collections are recorded by museum number and are arranged according to drainage (and occasionally subsystem), state, and county. Complete locality

data are given only for new taxa, species of spotty or rare occurrence, important distributional records, or collections considered significant for some other reason. Both material actually studied and that merely identified for use as distributional data are included. In addition to standard abbreviations for compass directions and states, the following abbreviations are used in recording materials: airmi. = airmiles, br. = branch, co. = county, cr. = creek, dr. = drainage, fk. = fork, hwy. = highway, jct. = junction, mi. = miles, par. = parish, r. = river, rdmi. = road miles, rt. = route, and trib. = tributary.

SYSTEMATIC ACCOUNTS

Subgenus Lythrurus Jordan

Lythrurus Jordan, 1876:271-2, 285 (original description; type species Semotilus diplemia Rafinesque [now Notropis umbratilis cyanocephalus (Copeland), see below] by subsequent designation of Jordan and Copeland, 1877, and Jordan and Gilbert, 1877).

Nomenclature and History.—When Jordan described Lythrurus, the name Semotilus diplemia Rafinesque (1820:50) was associated with the redfin shiner; and Jordan's account (1876:285-6) of the species he called Lythrurus diplaemius (emended spelling) clearly refers to this minnow. However, as early as 1877, Jordan (1877b:30) realized that Rafinesque's description fit the redfin shiner poorly. Subsequently, Jordan and Meek (1884) and Jordan (1885b) dissociated the name diplemia from the redfin shiner. Gilbert (1891) proposed that Rafinesque's name be considered a synonym of Semotilus atromaculatus (Mitchill), and ensuing published accounts have followed this practice.

Taken out of context, the proposal of Semotilus diplemia Rafinesque as the type species of Lythrurus Jordan would render the latter name either unidentifiable or a synonym of Semotilus. In either case it would not be available as a genus group name for the shiners treated herein. As Jordan obviously intended the redfin shiner to be the type of Lythrurus, I accept as valid the emended type species designation (Jordan and Evermann, 1896a; Jordan, 1919:386) in which this intent is specified. Thus the type species of Lythrurus Jordan is the form now called Notropis umbratilis cyanocephalus (Copeland). This action is justified by Article 70a of the International Code of Zoological Nomenclature. In this case, nomenclatural stability and uniformity are best served by selecting as the type species "... the nominal species actually involved, which was wrongly named in the type-designation..."

Jordan (1876) originally described Lythrurus as a genus and included two species, L. diplaemius (Rafinesque) (now N. u. cyanocephalus) and L. ardens (Cope). The major features he used to distinguish his new genus from Notropis (his Minnilus—these two names were used interchangeably for the same group of fishes until about 1885) were

smaller scales; the presence of bright red breeding colors, especially on the fins; and the presence of masticatory surfaces on the pharyngeal teeth.

Nominal forms were added to the genus by Jordan (1877a), Jordan and Copeland (1877), and Jordan (1878). By the time Hay (1881) described three new species and briefly reviewed the group, eight nominal forms were included. Hay pointed out that the tooth characters supposedly distinguishing Lythrurus from Notropis (his Minnilus) were too variable to be relied upon as generic characters, and furthermore that genera defined on the basis of such characters appeared to cut across natural phyletic lines. For the first time he reduced Lythrurus to a subgenus of Notropis. Jordan vacillated between calling Lythrurus a genus (Jordan, 1882) and a subgenus (Jordan and Gilbert, 1883) until 1885 when he (Jordan, 1885b) followed Gilbert's (1884) lead in reducing all the then-recognized genera of shiners to subgeneric status under Notropis. Most workers have since maintained Lythrurus as a subgenus. The move by Jordan (1929) and Jordan, Evermann, and Clark (1930) to re-elevate all the subgenera of Notropis was never widely followed.

By 1885 the subgenus Lythrurus was constituted in essentially modern terms, except for the erroneous inclusion of Notropis metallicus Jordan and Meek (Jordan, 1885b). The single exception was the poorly known N. fumeus, which was maintained with species of the subgenus Notropis as late as 1930 (Jordan et al., 1930). Not until the name fumeus was revived were the ties between N. fumeus and Lythrurus appreciated (Ortenburger and Hubbs, 1926; Hubbs and Ortenburger, 1929) and established (Hubbs and Black, 1940).

Diagnosis.—The subgenus *Lythrurus*, like most subgenera in *Notropis*, is not recognizable as a phylogenetic unit on the basis of a single or few diagnostic characters. Instead the group is diagnosed by a combination of characters.

Anal fin rays usually 10-13 (occasionally 9 in N. ardens); pectoral fin rays usually 12-15; lateral line scales usually 37-50; body circumference scales usually 26-38. Scales rather small, especially so predorsally; exposed area of scales on sides of body usually not notably deeper than long (except in some populations of N. umbratilis); scale imbrication moderate to strong except on anterior dorsolateral part of body, where squamation is reduced and imbrication weak or lacking. Mouth moderately large, terminal, and oblique; snout shape from moderately acute to bluntly rounded (latter condition typical of N. fumeus); eye moderate to moderately large, positioned laterally on head. Fins moderate to moderately large, with angles moderately acute and narrowly rounded; anterior rays of depressed dorsal fin usually exceed posterior

rays; posterior border of extended anal fin usually slightly to moderately falcate. Body shape ranging from slender and terete to deep and compressed. Pharyngeal teeth usually 2,4-4,2 (often only one tooth in one or both minor rows of N. b. alegnotus). Cephalic lateral line system tending to be reduced; IO canal most susceptible to reduction, often interrupted at position of dermosphenotic bone. Gut short, simple, "S"shaped; peritoneum silvery, spotted with light to heavy concentrations of melanophores. Anterior basidorsal spot present or absent; fin interradial membranes with or without deposits of melanin. Nuptial tubercles of males moderately small to moderately large and usually well developed over head (except for some populations of N. fumeus) and body (except for N. ardens and N. lirus). Bright breeding colors usually developed; color usually red, best developed on fins, variously developed on body; breeding colors yellow or gold in N. fumeus and in some populations of N. lirus. Urogenital papilla of breeding females enlarged and protruding posteriorly to about anal fin origin. Adult size usually less than 60 mm SL, except larger in N. ardens.

Species Groups.—I consider *Lythrurus* to be composed of four fairly discrete species complexes. The composition and characters of these groups are given in Table 3. The form variously referred to in the literature as *N. fumeus* or *N. fumeus fumeus* from the Ouachita Mountains (called the Ouachita Mountain shiner in my dissertation) requires additional study before it can be assigned to a species group. It seems certain that it will be included within either the *fumeus* or *umbratilis* complex. When this decision is reached, the diagnosis of the appropriate group will need to be expanded accordingly.

RELATIONSHIPS.—The subgenus Lythrurus is closely related to the atherinoides series of the subgenus Notropis (see Snelson, 1968, for a characterization of the latter). The two groups agree in dorsal fin position, high anal ray counts, pharyngeal tooth counts, and general physiognomy. The major features in which Lythrurus has diverged from the atherinoides series are as follows: (1) development of smaller scales, (2) tendency toward a reduction in squamation on anterior dorsolateral part of the body, (3) development of bright breeding colors, (4) trend toward reduction of the cephalic laterosensory system, (5) tendency toward stronger development of breeding tubercles, (6) development of an enlarged urogenital papilla in breeding females, and (7) more reduced body size. Of these differences, Lythrurus species clearly represent the derived or advanced condition in (2) and (4); and substantial arguments could be made for considering Lythrurus advanced in all six characters.

N. fumeus comes close to bridging the morphological gap between

the atherinoides series and the subgenus Lythrurus. It agrees favorably with the former, especially such species as N. amoenus and N. atherinoides, in pigmentation and general physiognomy; and it exhibits few of the specializations that distinguish other members of Lythrurus. Nevertheless the small scales, high anal ray counts, reduced cephalic lateral line, tuberculation (of some populations), xanthic breeding colors, enlarged urogenital papilla (females only), and small size of this species show conclusively that it is more closely related to species of the subgenus Lythrurus than to any member of the subgenus Notropis.

Notropis bellus bellus (Hay) 1881

PRETTY SHINER

Figure 3B

Minnilus bellus Hay, 1881:510-11 (original description; in synopsis and key to subgenus Lythrurus). Hay, 1883:74 (distribution). Jordan and Gilbert, 1883: 198-9 (in key; description).

Notropis alabamae Jordan and Meek, 1884:476-7 (original description). Jordan, 1885a:548 (N. alabamae incorrectly synonymized with N. lirus). Jordan, 1885b:27, footnote 2 (N. alabamae incorrectly synonymized with N. lirus).

Notropis bellus. Jordan, 1885b:27 (listed; range). Jordan and Evermann, 1896a: 559 (listed). Jordan and Evermann, 1896b:258, 297 (in key; description). Fowler, 1945:30 (listed from Alabama Dr.). Eddy, 1957:118, 130, fig. 296 (in key; characters; range). Howell, 1957:236-45, map 31 (in key; characters; Ala. records, in part; sympatry with N. roseipinnis erroneous). Cook, 1959:33, 38, 107, 120-1 (in key; spawns in late June; description; compared with N. roseipinnis; distribution). Boschung, 1961:274, 281-2 (first records from Coosa R. system; station 44 record based in part on hybrid N. b. bellus x N. lirus; habitat; range, partly in error). Schrenkeisen, 1963:124 (range, in part; characters). Ramsey, 1965:24, 93 (distribution, in part). Williams, 1965:23-4, 85 (records and distribution in Tallapoosa R. system). Tucker, 1967:90, 192, map 51 (partial synonymy, habitat; distribution; records from Mobile basin; possible competitive exclusion with N. roseipinnis). Moore, 1968:74, 80 (in key; characters; range). Wall, 1968:17, 40, 43-6, fig. 3 (first report from Tennessee Dr.; distinguished from N. ardens; counts; Bear Cr. system records; complementary distribution with N. ardens in Bear Cr.; all in part). Smith-Vaniz, 1968:36, 43-4, 124-5, 130, fig. 77 (in key; partial synonymy; range, except for reference to new form in Chattahoochee, which is N. atrapiculus; zoogeography).

Lythrurus bellus. Jordan, Evermann, and Clark, 1930:126 (listed; synonymy). Misidentifications. Wall, 1968:17 (N. fumeus as N. bellus from Bear Cr., in part).

Types.—The type series was specified as USNM 27426, with the following data: Catawba Creek and tributaries at Artesia, Lowndes County, Mississippi (Tombigbee drainage); March and April 1880; collector, O. P. Hay (Hay, 1881:488-9, 511). Two jars bearing the number USNM 27426 have been located; one jar contains a single specimen, the other three. Jar labels indicate that the single, isolated specimen is "the type"; and I herein select it as lectotype. This poorly preserved, nearly scaleless specimen is about 45 mm SL. Anal rays number 9, a rare count for N. b. bellus, but in body shape and especially in fin pigmentation the specimen is typical of the subspecies. The three other specimens originally cataloged as USNM 27426 are lectoparatypes, now USMN 203332. Other specimens from the type series, not

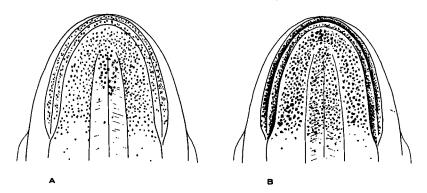


FIGURE 2.—Lower jaw and gular pigmentation in adults of two species of the rosei-pinnis complex. A.—N. bellus bellus. CU 53133; Tallapoosa dr., Alabama. B.—N. roseipinnis. TU 25833; Pearl dr., Louisiana.

examined by me, are cataloged as Stanford University 756 (6) and 2526 (1) (Böhlke, 1953). Thus, of the 36 specimens Hay (1881) reported from Artesia, only 11 have been located. Hay's four specimens from Macon, Mississippi, were not found.

As noted by Smith-Vaniz (1968:43), the name Notropis alabamae Jordan and Meek (1884:476-7) is correctly a synonym of N. b. bellus and not N. lirus as indicated by Jordan (1885a:548) and subsequent workers. This species was described from six specimens taken in a tributary of the Alabama River at Montgomery, Alabama, by M. McDonald. I selected one adult about 45 mm SL as lectotype of Notropis alabamae Jordan and Meek. It retains the original number, USNM 35297. Five lectoparatypes are recataloged as USNM 203323. Jordan and Evermann (1896b:298) erroneously listed USNM 35295 as part of the type series of N. alabamae. Pantosteus (= Catostomus) delphinus is cataloged under this number.

DIACNOSIS.—See Tables 16 and 17 and the Comparisons section of the species account.

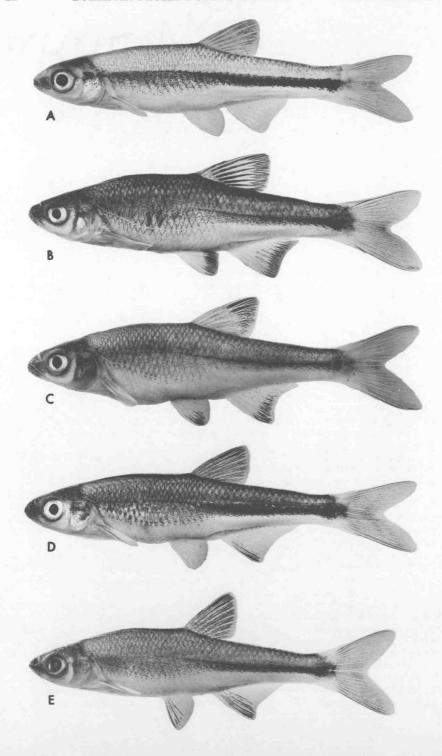
Description.—Certain counts are presented in Tables 1 and 4-10. Measurements are presented in Table 14. General physiognomy and pigmentation are shown in Fig. 3B. Details of chin and fin pigmentation are illustrated in Figs. 2A and 4I-L.

Body circumference scales (15) 16-19 (21), modally 17, above lateral line and (9) 11-13 (15), modally 11, below. Caudal peduncle scales 5-8 above lateral line and 5-8 below, with usual counts of 7 and 5 respectively. Pharyngeal tooth counts from throughout range as follows in 41 specimens: 1,4-4,1 (in 1 specimen); 1,4-4,2 (4); 2,4-4,1 (1); 2,4-3,2 (1); 2,4-4,2 (33); and 3,4-4,2 (1).

Scales moderately imbricate over most of body. Predorsal scales reduced in size but imbrication only slightly or not at all reduced. Anterior dorsolateral scale reduction index usually one or less (Table 11), indicating that naked interspaces between scales, when present, are very narrow.

Lower jaw rarely included within upper (32 specimens). Chin tip usually terminates equal with (107 specimens) or protrudes slightly beyond (123 specimens) tip of the upper lip. Chin tip occasionally protrudes strongly (69 specimens). Fleshy orbit length roughly equal to snout length. Body deep and compressed. Body depth tends to show weak positive allometry in breeding males. Dorsal fin large in adult breeding males; other fins moderately large.

Lateral line on body complete and decurved, reaching lowest point over or slightly before pelvic fin base. Supratemporal canal broadly interrupted at dorsal midline and occasionally with secondary interruptions. Pore count formulas for ST



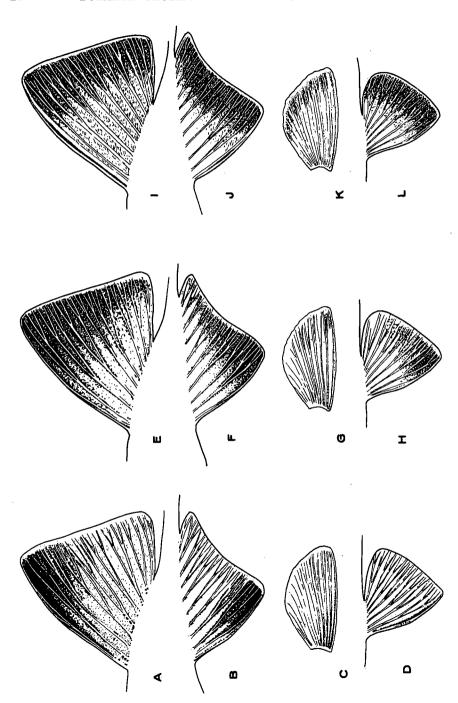
canal, in order of their frequency, were 2,2 (in 135 specimens); 2,3 (18); 3,2 (14); 3,3 (8); 1+2,2+1 (8); 1,2 (5); 1+2,2 (3); 1,1 (3); 1+2,3 (2); 2,1 (2); 2,2+1 (2); 2,4 (1); 1+2,1 (1); and 1,2+1 (1). Supraorbital canal incomplete (not joining postocular commissure) but only rarely (3 of 201 specimens) interrupted along its course; pore counts for 198 specimens were 7 (in 7 specimens), 8 (144), 9 (41), and 10 (6); $\bar{x}=8.2$. Preoperculomandibular canal only rarely (3 of 441 specimens) interrupted along its length; pore counts are presented in Table 10. Dermosphenotic bone reduced or absent. In adults infraorbital canal ranges from interrupted to complete at position of this bone. Pore counts for adults with complete IO canals were 11 (in 2 specimens), 12 (22), 13 (33), 14 (26), 15 (17), 16 (7), 17 (2), and 18 (1); $\bar{x}=13.6$. In adults with IO canal partially or fully incomplete most frequent pore count formulas were 11+3 (in 38 specimens), 10+2 (27), 10+3 (18), 11+2 (18), 12+3 (12), 11+4 (7), and 12+2 (6). Number of IO pores before dermosphenotic disjuncture (when present) 9 (in 3 specimens), 10 (51), 11 (68), 12 (21), 13 (6), and 14 (2); $\bar{x}=10.9$.

Lips typically little or no darker than snout tip and chin. Usual pattern of chin and gular pigmentation illustrated in Fig. 2A. Pigment extending posteriorly along mandibles to near angle of mouth but limited to anterior portion of gular area. Typically no darkened preorbital blotch and no dark band passing around snout. Superficial pigmentation of snout, top of head, and temporal-upper opercular areas uniformly dark and scattered. In breeding males pigment over posterior margin of cleithrum usually forming dusky bar of varying intensity. Cleithral pigment reduced in females and nonreproductive specimens.

Dusky middorsal stripe moderately developed before dorsal fin but weaker posteriorly. Stripe not surrounding dorsal fin base, though pigment laterad to dorsal fin may be slightly duskier than surrounding areas. In females, scales on upper anterior sides of body usually outlined by pigment. Suffusions of pigment under centers of scales occasionally obscuring crosshatched pattern. In some cases males resemble females; but often, especially during breeding season, general increase in melanism obscures crosshatched effect. About 65 percent of breeding males examined had a few conspicuously darkened scales on flanks. Slight concentrations of pigment over myosepta on anterior dorsolateral part of body producing faint chevron-shaped markings in about 20 percent of breeding males examined. Darkened scales and chevrons accentuated by increased melanism of breeding males; both features rarely developed in females. Bar-like markings never developed on body.

Poorly defined dusky stripe present midlaterally on caudal peduncle. Posteriorly, it is one or two scale rows wide, weak to moderate in intensity, and has diffuse borders. Stripe broadens and fades over and anterior to anal fin; only an occasional suggestion of weak lateral stripe continuing forward to head and across opercle to eye. Stripe may broaden slightly over hypural plate, but discrete caudal spot absent. Pigment usually extends slightly (females) to far (breeding males) below lateral line at midbody, primarily along scale borders. Discrete punctulations above and below each lateral line pore lacking. Melanophores weakly to moderately developed along anal fin base and in a double row along ventral surface of caudal peduncle. Anterior basidorsal spot absent.

FIGURE 3.—A.—N. bellus alegnotus, weakly tuberculate adult male 47.6 mm SL. UAIC 2504; Black Warrior dr., Alabama. 19 March 1967. B.—N. b. bellus, tuberculate adult male 52.2 mm SL. CU 16027; Tallapoosa dr., Alabama. 12 June 1949. C.—N. atrapiculus, tuberculate adult male 50.7 mm SL. CU 53157; Conecuh-Tallapoosa dr., Alabama. 22 May 1968. D.—N. roseipinnis, tuberculate adult male 44.9 mm SL. TU 45468; Pascagoula dr., Mississippi. 16 April 1967. E.—N. roseipinnis, tuberculate adult male 44.4 mm SL. TU 15453; Pearl dr., Louisiana. 21 April 1957.



FIN PIGMENTATION.—The following description is based on breeding adults. Fin pigment is intensified during the reproductive season, and patterns of deposition are then readily discernible. Fin melanin is reduced in nonbreeding specimens, especially juveniles, but basic patterns of deposition remain essentially unchanged through the year.

Dorsal fin of breeding males margined with dark band formed by concentration of melanin on interradial membranes in and about secondary branches of rays (Figs. 3B, 4I). Band uniform in width and intensity throughout. In some specimens basal half of fin lightly dusted with melanophores (Fig. 4I). In others basal pigment dark and separated from dusky terminal band by light zone extending through middle of fin, resulting in double-banded appearance (Fig. 3B).

Dorsal fin of breeding females weakly pigmented and often not appearing dusky to unaided eye. Melanophores usually sparsely scattered over basal half of fin.

Terminal band faintly represented by pigment in and about crotches of rays.

Anal fin of breeding males bordered by dark band formed by heavy melanin deposits on interradial membranes in and about secondary branches of rays (Figs. 3B, 4J). Band extending length of fin, uniform in width and intensity. Central part of fin clear (small males) or dusted with melanophores (large males).

In breeding females terminal band of anal fin reduced, often invisible to unaided eye. Pigment representing band scattered lightly along margin of fin. Re-

mainder of fin immaculate.

All principal caudal rays bordered by melanophores in both sexes. In breeding males some or all interradial membranes may be dusky, especially around fork area

and near tips of fin lobes. Females rarely have caudal interradial pigment.

Pectoral fin pigmentation attaining maximal development only in large males in advanced breeding condition. First (unbranched) pectoral ray bordered by pigment along most of length. Succeeding several rays variably and weakly bordered, mostly along basal portion. Narrow dusky band, about one-half the intensity of bands in other fins, extends around edge of fin (Fig. 4K). Development of band diminishes sharply with size and sexual development. In subadult males or males of reduced sexual readiness, only dusky spot remains in fork of first branched ray at apex of fin. This stage similar to maximal development of pectoral fin pigment in breeding males of N. atrapiculus (Fig. 4G). Females may or may not possess weak apical spot, and pectoral fin never fringed with pigment.

Pelvic fins of breeding males margined by dark band formed by interradial pigment in and about branches of rays (Figs. 3B, 4L). Band extends entirely through fin, uniform in width and intensity. Basal three-fourths of fin immaculate. In females this band weak or invisible to unaided eye, but reduced pigment visible with

magnification.

The high index of fin pigmentation in breeding males of N. b. bellus (Table 12) correlates with the bands of pigment entirely through their anal and pelvic fins. Small breeding males show a weak tendency for the pelvic fin band to be reduced, but typically once a male begins to exhibit secondary sexual characters, pigment representing the bands is developed (though sometimes faintly) in both fins. The lack

FIGURE 4.—Fin pigmentation in adult breeding males of three members of the roseipinnis species complex. From top to bottom, fins are the dorsal, anal, left pectoral (dorsal view), and left pelvic. All drawings are composites from several specimens. Details of ray structure and number are not entirely accurate. A-D.—N. roseipinnis. CU 15622 (30 March 1948) and TU 51439 (19 April 1968); Pascagoula dr., Mississippi. E-H.—N. atrapiculus. CU 16214 (13 June 1949) and TU 2593 (2 June 1951); Escambia dr., Alabama. I-L.—N. bellus bellus. CU 16027 (12 June 1949), CU 53133 (25 May 1968), and TU 25963 (21 June 1962); Tallapoosa dr., Alabama.

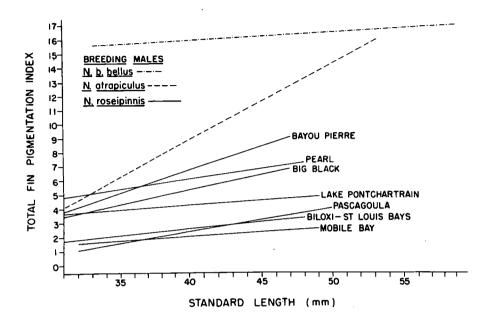


FIGURE 5.—Calculated regression lines for ontogenetic change in the total fin pigment index of breeding males of three members of the *roseipinnis* species complex. Statistical data for each line are presented elsewhere (Snelson, 1970: appendix).

of noteworthy ontogenetic change and reduced individual variation are reflected in a regression line with very little slope and a low residual variance (Fig. 5; Snelson, 1970: Appendix).

Breeding females lag in development of fin pigment (Table 13). Pigment representing the anal and pelvic fin bands is incompletely formed at small sizes, is added rapidly with increasing size, and the total pigment complement is complete or nearly so in large adults. Nevertheless at any given size females vary more than males in this index. Consequently the regression line for ontogenetic change in the total fin pigment index begins at a low value, increases rapidly, and levels off asymptotically; and there is more variation about the line than in males (Fig. 6; Snelson, 1970: Appendix).

BREEDING COLORATION

Males.—Red color on fins may vary in intensity from pale to bright (probably depending on sexual readiness) and in hue from flame to wine red (depending on extent to which erythrophores are masked by melanin deposits). Membranes of dorsal fin washed with pale red. Erythrophores visible microscopically throughout most of fin but obscured in proximal and distal portions by heavy melanin deposits. Thus red color usually conspicuous to unaided eye only in zone through middle of fin. Red pigment lightly washed over distal one-third to one-half of anal and pelvic fin membranes. Distal melanin deposits obscure erythrophores, and color appears as poorly defined red bands proximal to black marginal band. Caudal fin membranes lightly washed with orange-red. Pectoral fin occasionally with light red wash bordering first ray.

Iris faintly washed with orange-red. Some specimens with pale reddish slash

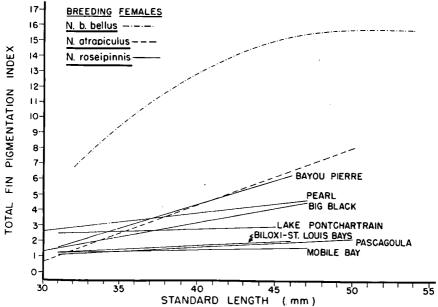


FIGURE 6.—Calculated regression lines for ontogenetic change in the total fin pigment index of breeding females of three members of the *roseipinnis* species complex. Statistical data for each line are presented elsewhere (Snelson, 1970: appendix).

along posterior margin of preopercle. Faint orange spot usually present on body at base of pectoral fin.

All fresh breeding males I have studied have lacked red pigment on the body, even under microscopic examination, but John S. Ramsey and Camm C. Swift both inform me (pers. comms.) that males of this form occasionally have a light wash of orange or pink on the dorsolateral aspect of the body. Hay (1881) and Howell (1957:237) state that the species has a "flame"-colored belly, but this needs verification. In life the body of both sexes is olive dorsally, silver with gray-blue iridescence laterally, and white ventrally.

FEMALES.—Breeding females have relatively dull colors. The dorsal fin usually is faintly washed with orange-red. Weak suffusions of erythrophores are present on the caudal and anal fins of some specimens.

Breeding Tuberculation.—The tuberculation of all members of the *roseipinnis* complex is basically very similar. To avoid redundant descriptions, the tuberculation of N. b. bellus is described in detail, and other forms are described only as they differ.

Males.—Pectoral fin rays 1 through about 8 or 10 bear small tubercles dorsally. Some tubercles usually present along midlength of ray 1, but number and distribution variable. Tuberculation maximally developed on rays 2 through about 6. Small tubercles originate near bases of rays, becoming slightly larger and more numerous distally. Full development occurs just proximal to and at first (major) branching point of ray. Here tubercles slightly retrorse, arranged in irregular bi- or triserial pattern with about 8-14 tubercles per fin ray segment. (In general, larger males tend to have a few more tubercles per ray segment than smaller males). Distal to branching point, weak single or double row of tubercles follows each ray branch to near edge of fin.

A few tubercles occasionally present on second rudimentary ray of dorsal fin. Otherwise, dorsal, caudal, anal, and pelvic fin rays normally lack tubercles.

The pattern of head tuberculation of all members of the roseipinnis complex is basically like that of N. umbratilis cyanocephalus (Fig. 1B). Numerous moderately small, erect tubercles scattered over top of head from occiput to snout tip. Poorly defined hiatus occasionally present between snout tip and head dorsum tubercles, Tubercles extending laterally on temporal area to upper just anterior to nostrils. They may be slightly larger and more concentrated along upper rim of orbit, but seldom form a discrete row. Snout, preorbital, and suborbital areas bear numerous scattered, erect tubercles. In many specimens suborbital tubercles terminate posteriorly near angle of preopercle (as in Fig. 1B). Large males of this form more prone than any other member of roseipinnis complex to develop postorbital tubercles. Roughly half the large breeding males examined had few tubercles scattered over subopercle and lower part of opercle, and several specimens had few tubercles on middle of opercle and immediate postorbital area. Interopercle and exposed portions of branchiostegal rays bear rows of well-developed tubercles, and a series rims posterior edge of opercle on opercular membrane. Each mandible bears double row of tubercles, a laterally directed row along outer edge of dentary bone, an inner, ventrally or ventrolaterally directed row along inner border. Outer row usually continuous around chin tip to join counterpart from opposite side. Inner row often does likewise, but may terminate anteriorly near first preoperculomandibular canal pore. Few tubercles occasionally scattered over gular area. Lips typically nontuberculate. Tubercles on lateral and ventral parts of head approximately equal to those on top in size and development.

Tuberculation of body scales weak and variable posterior to imaginary line between dorsal and anal fin origins. Anterior to this line and below lateral line, 1 to 5 (usually 2 to 3) erect or slightly antrorse tubercles along margins and occasionally over centers of scales in prepelvic area. Tuberculation of belly and breast variable. In some specimens these areas nontuberculate; in others, both areas armed with tubercles arranged 1 or 2 per scale. Scales above lateral line on sides of body bear about 4 to 7 erect or slightly antrorse tubercles. These usually line posterior margin of each scale but occasionally are more randomly scattered, especially near head. Tubercles weakly developed near dorsal fin origin, but becoming larger, stronger, and more numerous anteriorly along middorsal line. On nape, erect or slightly antrorse tubercles numerous, about as large as those on head dorsum, and not closely

associated with scale margins.

FEMALES.—Few small, weak tubercles usually scattered along nape and over top of head of breeding females. Irregular single or double row of weak tubercles often extends along mandible. Otherwise head areas tuberculated in males usually naked in females. Body and fins usually nontuberculate.

Comparisons.—N. b. bellus is compared with other forms of the roseipinnis complex in Tables 16 and 17 and in succeeding Comparisons sections.

N. b. bellus is sympatric and syntopic with N. lirus near the Fall Line in the Coosa River system and in the upper Cahaba River system. Except for a few putative hybrids (CU 53341, CU 53353, TU 23595), these two are most readily distinguished by the following features: (1) Chin pigment of lirus is restricted to a thin black band around the tip of the lower jaw; cf. with Fig. 2A for b. bellus. (2) Breeding males of lirus have large, antrorse tubercles on top of the head and few tubercles on lateral and ventral areas of the head. One or two prominent tubercles at the chin tip are characteristic. Head dorsum tubercles of b. bellus are moderate in size and erect, and lateral and ventral head areas are

generously supplied with tubercles. (3) The body of *lirus* is elongate and slender; that of b. bellus is deep and robust. (4) A broad, dark midlateral stripe is developed in *lirus* but absent from b. bellus. (5) Fin interradial pigment is lacking in *lirus* but strongly developed in b. bellus.

N. b. bellus is sympatric and occasionally syntopic with N. fumeus in the Bear and Yellow creek systems of the Tennessee drainage. Juveniles of these forms are occasionally troublesome to separate but adults can be distinguished most readily as follows: (1) fumeus has a dark midlateral stripe that is absent in b. bellus; (2) chin pigmentation of fumeus is lighter and less extensive than that of b. bellus (Fig. 2A); (3) fin interradial pigment is lacking in fumeus, well developed in b. bellus. Moreover fumeus has yellow rather than red breeding colors, smaller and weaker head tubercles, and minute pectoral fin tubercles arranged in a dense shagreen.

N. ardens and N. umbratilis cyanocephalus also occur in the Tennessee drainage, and the former is occasionally syntopic with N. b. bellus in the Bear and Yellow Creek systems. Both are readily distinguished from N. b. bellus by their possession of an anterior basidorsal spot.

Sexual Dimorphism.—Sexual dimorphism is strongly developed in N. b. bellus and is most pronounced during the breeding season. Sexual differences in tuberculation, breeding coloration, and fin pigmentation have been summarized above. No sexual dimorphism in meristic characters was noted.

Sexual dimorphism in morphometric characters is summarized in Table 2. A sample of 36 breeding males and 33 breeding females from the Tombigbee River system was used for statistical comparison with Student's t-test. All specimens measured were 40-50 mm SL. Mean SL for males was 45.49 mm; mean SL for females was 46.09. Levels of probability greater than 0.1 were considered not significant (ns). Following each character is given (first) the range and mean for males, (second) the range and mean for females, and (third) the probability that the two means are significantly different. Predorsal length: 518-563, 538.1; 507-552, 535.0; ns. Postdorsal length: 474-506, 489.6; 470-502, 485.6; <0.1. Prepelvic length: 465-501, 482.6; 480-514, 492.7; <0.001. Preanal length: 620-655, 638.2; 629-661, 647.9; <0.001. Head length: 224-258, 239.9; 228-247, 239.4; ns. Head depth: 163-191, 175.9; 168-187, 177.6; ns. Postorbital head length: 95-117, 103.9; 94-109, 103.2; ns. Snout length: 66-79, 71.2; 64-74, 69.7; <0.05. Upper jaw length: 78-94, 85.3; 81-92, 85.4; ns. Gape width: 53-71, 63.1; 53-72, 61.2; ns. Fleshy orbit length: 66-79, 72.7; 68-80, 74.2; <0.05. Fleshy interorbital width: 85-102, 93.6; 85-102, 92.6; ns. Body depth: 233-280, 254.4; 229-282, 254.4; ns. Body width: 123-158, 139.1; 131-164, 148.0; <0.001. Caudal peduncle

length: 204-248, 223.9; 214-242, 222.8; ns. Caudal peduncle depth: 97-118, 105.8; 93-107, 100.0; <0.001. Dorsal fin length: 219-268, 234.5; 201-234, 220.7; <0.001. Anal fin length: 201-244, 226.6; 195-229, 212.9; <0.001. Pectoral fin length: 166-205, 178.0; 167-194, 179.8; ns. Pelvic fin length: 144-168, 155.3; 141-162, 150.1; <0.001. Males usually have deeper and more compressed bodies than females. The lack of a significant difference in body depth in this analysis is because the abdomens of the females measured were distended with eggs.

The urogenital papilla of breeding females is enlarged and protrudes posteriorly to about the anal fin origin. In males the papilla is not enlarged. This difference is maintained to some degree throughout the warmer months of the year and facilitates external sexing. Breeding males usually are duskier than females. Darkened scales and chevron-shaped markings were present on the sides of the body in about 60 and 20 percent respectively of the breeding males examined. Both features are rarely developed in females.

Males attain larger adult size than females. Of 73 collections examined, a male was the largest specimen in 57, a female in 16. The Chi-square analysis gives a highly significant value of 23.0 (probability much less than 0.005), indicating that males are larger in significantly more than half the cases. The largest male examined was 59.5 mm SL; the largest female was 57.5 mm SL.

Geographic Variation.—N. b. bellus shows no trenchant geographic variation in the various subsystems of the Mobile Bay drainage (see Tables). Although modes may shift slightly from one system to another, the differences are regarded as insignificant in view of the extensive intrapopulation variation. The Tennessee drainage population has the highest index of anterior dorsolateral scale reduction (Table 11); but otherwise, the differences between it and the Tombigbee population, its presumed ancestral stock, are slight. Additional comments on geographic variation within the Black Warrior system are presented under the account of Intergrades.

Habitat and Distribution.—N. b. bellus maintains sizeable populations in a wide variety of environmental situations. It is primarily an inhabitant of small to moderately large streams of low to moderate gradients. Water conditions range from clear to heavily, sometimes continuously, turbid. It usually is taken over sand, silt, or clay bottoms but occasionally is present over harder bottoms of gravel or bedrock. Vegetation may or may not be present. This form usually avoids the darkstained, acid water of the lower Coastal Plain, but its absence from such streams in the lower Mobile Bay basin may be influenced more by competition with N. roseipinnis than by ecological tolerances (see below).

N. b. bellus seems to be relatively tolerant of pollutants detrimental to many fishes. It is the most abundant fish in Shades Creek (Birmingham, Alabama), a highly disturbed and polluted stream whose depauperate fauna is marked by an absence of darters and the presence of only three other minnows, Notemigonus crysoleucas (Mitchill), Pimephales notatus (Rafinesque), and Semotilus atromaculatus (Mitchill) (W. M. Howell, pers. comm.).

This form is indigenous to the Mobile Bay basin, where it is widespread over the middle and upper Coastal Plain of all drainage systems (Fig. 7). In the Coosa system, it stops abruptly at the Fall Line and is replaced upstream by N. lirus; but in the Cahaba and Tallapoosa systems, it is sparingly distributed above the Fall Line. With two minor but problematic exceptions, this form is restricted to the Coastal Plain in the Black Warrior system. It is replaced at the Fall Line by intergrade populations and above by N. b. alegnotus. One exceptional locality for N. b. bellus is just above the Fall Line in the Hurricane Creek system in Tuscaloosa County, Alabama (UAIC 326). This creek otherwise seems to be inhabitated by intergrades and, consequently, the locality data for UAIC 326 are questionable. The second problematical record is from Lost Creek in Walker County, Alabama (CU 53348). The locality data for this collection are not in question. Lost Creek is far removed from other populations of N. b. bellus, and material tentatively identified as N. b. alegnotus has been taken in its upper reaches. I suspect that this Lost Creek series of N. b. bellus is the result of a recent introduction.

The existence of N. b. bellus in the Bear Creek system (extreme northwestern Alabama and northeastern Mississippi) of the Tennessee drainage was first reported by Wall (1968) and Smith-Vaniz (1968:124). Both authors note that its presence there is attributable to headwater stream piracy between the Tennessee and Tombigbee drainages. Geological evidence suggests that sections of the present-day Bear Creek were originally part of the Buttahatchee River system (Tombigbee drainage) before being captured by the Tennessee. Nocomis leptocephalus bellicus (Girard), Notropis baileyi Suttkus and Raney, N. b. bellus, N. chrusocephalus isolepis Hubbs and Brown, Noturus funebris Gilbert and Swain, and Etheostoma s. stigmaeum (Jordan) are present in the Bear Creek system. These forms are either indigenous to the Mobile Bay basin or present there but absent throughout most of the Tennessee basin; and, according to Wall (1968), they represent part of the captured fauna. Smith-Vaniz (1968:124) adds Notropis stilbius (Jordan) and Noturus gyrinus (Mitchill) to the list. N. b. bellus is also present in Yellow Creek, another tributary of the Tennessee River adjacent to

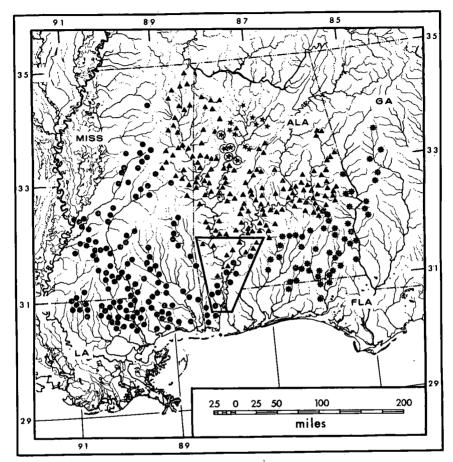


FIGURE 7.—The distributions of the members of the roseipinnis complex. N. atrapiculus (asterisks), N. b. bellus (triangles), N. bellus: bellus x alegnotus (circled stars), N. bellus alegnotus (stars), and N. roseipinnis (circles). Imprecise localities and broadly overlapping symbols are not plotted. The distributions of N. b. bellus and N. roseipinnis within the inset area are shown in detail in Fig. 8.

Bear Creek in northeastern (Tishomingo County) Mississippi. Studies in progress by R. D. Caldwell (pers. comm.) indicate that the Yellow Creek population may have originated through an introduction.

Except for Bear and Yellow creeks, N. b. bellus is not known outside the Mobile Bay basin. All previous records of N. bellus from Gulf Coast systems east of Mobile Bay are based on N. atrapiculus. The specimens representing Howell's (1957) single record of N. bellus from the Perdido drainage are apparently lost. The record is probably based on either N. atrapiculus or N. roseipinnis.

The detailed distribution of N. b. bellus and N. roseipinnis in the

lower Mobile Bay basin is plotted in Fig. 8. The ranges of these two species interdigitate and closely approach one another, as first pointed out by Tucker (1967). In central Monroe County, Alabama, N. b. bellus is common in the Flat Creek system, while N. roseipinnis is common in the Limestone Creek system. The mouths of these creeks in the Alabama River are about two miles apart. The species have been taken in close proximity in southern Clarke County, but in this case in streams flowing in opposite directions (N. b. bellus in Tombigbee River tributaries, N. roseipinnis in Alabama River tributaries). They have not yet been collected together.

In four collections of N. b. bellus (TU 32486, TU 32595, TU 40443, TU 45501) from the area of distributional proximity, I have singled out a total of 6 (of a combined total of 259) specimens that are somewhat anomalous in their characters. The absence of sympatric collections of N. b. bellus and N. roseipinnis and the nature of the characters of these specimens prompt me to consider them anomalous N. b. bellus rather than hybrids.

The allopatric distribution of these two forms may be attributable to strong habitat segregation, competitive displacement, or some combination of these. N. b. bellus may not tolerate the dark-stained, acid waters of the low Coastal Plain. Such habitats are typical of N. roseipinnis. On the other hand, Tucker (1967:192) hypothesized that the contiguous distribution of these two forms was a consequence of competitive displacement. N. roseipinnis is largely restricted to the lower Coastal Plain in the Mobile Bay system. It is not found as far upstream as might be predicted from its ubiquitous distribution in more westerly drainages (Fig. 7). Perhaps competition with N. b. bellus is the factor restricting the distribution of N. roseipinnis in the Mobile basin.

REPRODUCTION.—Heretofore nothing has been published on the reproductive habits of members of the *roseipinnis* complex. I made the following observations in Calebee Creek, Co. Hwy. 229 bridge, 14.4 airmi. W. Tuskegee (T17N, R21E, Secs. 26 and 27), Macon Co., Ala.; Tallapoosa R. system; 25 May 1968.

Large numbers of N. b. bellus were milling over three nests of Lepomis megalotis (Rafinesque) in water about 1 foot deep and approximately 2 to 3 feet from shore at the edge of a pool. The area, approximately 20-foot square, was strewn with a few limbs and stumps. No current was detectable over the nests. Several seine hauls showed most of the shiners in the vicinity of the nests to be large tuberculate males with milt running freely. Shiners returned almost immediately after the seine passed over the nest and otherwise seemed oblivious to my presence.

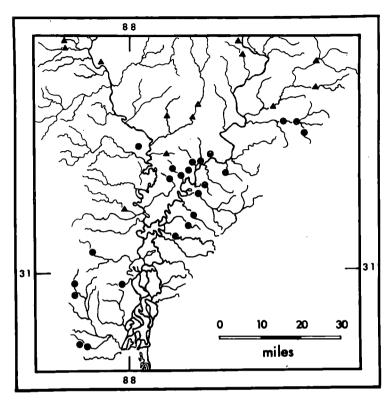


FIGURE 8.—The distributions of N. b. bellus (triangles) and N. roseipinnis (circles) in the lower Mobile Bay basin in Alabama (inset area in Fig. 7). Imprecise localities and broadly overlapping symbols are not plotted.

The nest closest to shore was watched between 1:00 and 1:45 PM. An estimated 15-20 shiners swarmed continuously over the nest, centering most of their activity 4 to 6 inches above the bottom. The larger specimens, obviously males, were more consistent in their occupancy of the nest area than smaller specimens (probably females and/or juveniles), which dashed in for a short while and then disappeared. No single male dominated the entire nest; instead 3 or 4 large individuals patroled most vigorously. These large males, all fins erect, milled over the nest constantly, making short dashes after smaller individuals that darted into the area and occasionally after each other. Each chase was pursued only a few inches and no ritualized fighting was seen. Smaller specimens (probably females) milled near the surface in deeper water a foot or two from the nest. I saw no spawnings, and subsequent laboratory examination of the females suggested that most were not ripe.

The male sunfish was considerably more wary than the shiners. He

moved onto the nest only three times during the observations and each time stayed only a few minutes. The sunfish ignored the shiners milling immediately above him. The shiners shifted the center of their activity slightly from the middle of the nest toward its edge but otherwise seemed unperturbed by the sunfish's presence. Water temperature over the nest was 78°F at the end of the observation period, air temperature 85°F.

Hunter and Hasler (1965) described the reproduction of N. umbratilis over the nests of Lepomis cyanellus Rafinesque.

MATERIAL EXAMINED

TENNESSEE DRAINAGE.

Bear Creek system.—ALABAMA, Franklin Co.: TU 40589, UAIC 2095, 2304, 2323, 2331. Marion Co.: TU 40530, UAIC 1775, 1776, 2521, 2878. Winston Co.: CU 53350.

Yellow Creek system.—Mississippi, Tishomingo Co.: UAIC 2637 (Yellow Cr., 1 mi. E. Holts Spur, T3S, R9E, Sec. 35).

MOBILE BAY DRAINAGE.

Tombigbee River system.—Mississippi, Chickasaw Co.: UAIC 2292, 2633. Clay Co.: TU 38548, 39414, UAIC 2291. Itawamba Co.: CU 24881, UAIC 2091, 2293, 2294, 2295. Kemper Co.: UAIC 1896, 2159, UMMZ 113871. Lee Co.: TU 2445. Lowndes Co.: TU 38536, 40214, 40485, 48836, UAIC 2026, 2290. Monroe Co.: UAIC 1005, 1006, 2634. Noxubee Co.: TU 3761, UAIC 2160, 2161, 2162. Oktibbeha Co.: UAIC 2632, USNM 165997. Pontotoc Co.: UMMZ 154362. Prentiss Co.: UAIC 2089, 2653. Tishomingo Co.: UAIC 2297, 2641. Winston Co.: UAIC 2163, 2630, 2631. Alabama, Choctaw Co.: UAIC 125 B (Souwilk Cr., 0.9 mi. N Bolinger, Ala. Rt 29), 142 (1 mi. S Gilberton, Ala. Rt. 29, TION, R3W, Sec. 6), 494, UMMZ 135891. Clarke Co.: TU 2625 (Bassett Cr., ca. 0.5 mi. E Whatley, Hwy. 84), 32486 (Bassett Cr., trib. Tombigbee R., 2 mi. W Suggsville), 32529 (trib. Salt Cr., 5 mi. S Jackson, Hwy. 15), 41422 (Salt Cr., 4.5 mi. S Jackson, Hwy. 15), 43197 (2.0 mi. WNW Coffeeville and Rt. 69, Co. Rt. 1), 45501 (Rabbit Cr., 2.7 mi. NE Jackson nr. Hwy. 10 bridge), UAIC 431 (Bashi Cr., 2 mi. N Campbell), 1839 (Salt Cr., ca. 4 mi. S Jackson on FAS Rd., T6N, R2E, Sec. 34), 2028 (spring, trib. Rabbit Cr., 2.6 mi. E off U. S. Hwy. 43, N of Jackson on Co. Rt. 10). Fayette Co.: UAIC 1581. Greene Co.: CU 15499, UAIC 1771, 1887, 1889, 1897, 1898, 2047, 2048, 2049, 2050, 2587. Greene-Pickens Co. line: UAIC 2164. Greene-Sumter Co. line: UAIC 1470. Lamar Co.: UAIC 2185, 2186. Marengo Co.: TU 32444, UAIC 428, 430. Marion Co.: CU 25711, TU 19071, 30231, UAIC 789, 2006, UMMZ 175346. Pickens Co.: TU 48866, UAIC 888, 1891, 1892, 2022, 2023, 2183, 2184. Sumter Co.: CU 15545, TU 7499, 48902, UAIC 490, 1890, 2156, UMMZ 163737. Tuscaloosa Co.: UAIC 821, 1058, 1062, 1863, 2842. Washington Co.: UAIC 496 (Bilboa Cr., U. S. Hwy. 43, 1 mi. SE McIntosh). Winston Co.: UAIC 1593.

Black Warrior River system.—ALABAMA, Greene Co.: CU 52866, UAIC 111, 112, 113, 114, 115, 329. Hale Co.: CU 21169, UAIC 73, 74, 75, 158, 159, 161, 162, 163, 164, 258, 259. Perry Co.: UAIC 260. Tuscaloosa Co.: CU 33223, UAIC 326 (Big Cottondale Cr., T21S, R9W), 679, 683, 686, 687, 689, 692, 1218, 1584, UAIC uncat. (Cribb's Mill Cr., trib. Cypress Cr., ca. 2 mi. SW Tuscaloosa, T22S, R10W, Sec. 16). Walker Co.: CU 53348 (Lost Cr., Hwy. 69 bridge, 3.9 airmi. NNE center Oakman, T15S, R8W, Sec. 3).

Alabama River system.—Alabama, Autauga Co.: UAIC 2114, 2120. Butler

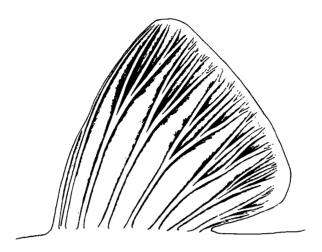


FIGURE 9.—Pattern of dorsal fin pigmentation in a breeding adult male paratype of *N. bellus alegnotus*, 48.1 mm SL (CU 53354). The dorsal fin typically contains eight rays rather than seven as shown.

Co.: TU 3197. Chilton Co.: UAIC 2305, 2306. Clarke Co.: UAIC 2341 (Cane Cr., 3 mi. S Lower Peach Tree, T10N, R5E, Sec. 35). Dallas Co.: TU 32632, 32672, 35205, UAIC 2127, 2307, 2308, 2365, 2367, 2390, 2391, 2402. Dallas-Lowndes Co. line: UAIC 2403. Dallas-Wilcox Co. line: UAIC 2362. Elmore Co.: TU 15247, UAIC 2115, 2117. Lowndes Co.: UAIC 124, 134 A, 540, 541, 542, 2404. Marengo Co.: UAIC 2039, 2041. Monroe Co.: TU 2635 (trib. Alabama R., 17.3 mi. S Camden, Hwy. 11), 32595 (Robinson Cr., trib. Flat Cr., 3.9 mi. N Tunnel Springs, Hwy. 47), 44446 (Flat Cr., 8.6 mi. NW Monroeville, Hwy. 41), UAIC 524 (Flat Cr., 2 mi. N Beatrice, Ala. Rt. 100), 2372 (Robinson Cr., Ala. Hwy. 47, 3 mi. NE Tunnel Springs, T8N, R8E, Sec.4), USNM uncat. (Robinson Cr., trib. N. Fk. Flat Cr., S of Beatrice, Ala. Rt. 21). Montgomery Co.: UAIC 130, 140, 815, 2406, 2407. Perry Co.: TU 25963, UAIC 2122, 2123, 2128. Wilcox Co.: TU 2571, 3059, 3429, 32457 (Bear Cr., trib. Alabama R., 3.1 mi. NW Lower Peach Tree, Co. Hwy. 1), 32616, 44505, UAIC 525, 527, 531, 533, 535, 536, 538, 539, 2342 (Bear Cr., 3 mi. N Lower Peach Tree, Co. Rt. 1, T11N, R4E, Sec. 1), 2343, 2344, 2345, 2346, 2363.

Cahaba River system.—Alabama, Bibb Co.: CU 46493, TU 35097, UAIC 403, 813, 2590, 2629. Dallas Co.: TU 35070. Jefferson Co.: CU 53347, UAIC 950, 1862, 2577. Perry Co.: TU 32689, 32695, UAIC 963. Shelby Co.: CU 53339.

Coosa River system.—Alabama, Chilton Co.: UAIC 663, 664. Elmore Co.: TU 23589, UAIC 666, 2118.

Tallapoosa River system.—ALABAMA, Bullock Co.: UAIC 1472, 1473, 1565 (Old Town Cr., nr. Mt. Hilliard Church, NE Union Springs, T14N, R22E, Sec. 1). Chambers Co.: AU 1418, 1421, UAIC 1377. Clay Co.: UAIC 1508. Cleburne Co.: UAIC 1366, 1495, 1503. Coosa Co.: UAIC 1359. Elmore Co.: AU 24, UAIC 822, 1279, 1281, 1356, 1357, 1362, 1363. Lee Co.: CU 46248, 53191, UAIC 1237, 1372, 1479, 1528, 1529, 1670, UMMZ 111152, 111159, 124116, 162590. Macon Co.: AU 84, 115, CU 14043, 15999, 16027, 53133, TU 30937, UAIC 1368, 1371, 1373, 1480, 1482, 1512, 1513, 1516, 1669, UMMZ 111151. Macon-Montgomery Co. line:

UAIC 1234. Montgomery Co.: TU 9503, UAIC 1217, 1232, 1238. Randolph Co.: AU 1419, UAIC 1378. Tallapoosa Co.: AU 12, UAIC 1486, 1487, UMMZ 111153.

Notropis bellus alegnotus, new subspecies

Figure 3A

Notropis bellus. Howell, 1957:240-1, map 31 (UAIC 214, Lost Cr. system). Notropis roseipinnis. Howell, 1957:248, map 32 (UAIC 209, Lost Cr. system).

TYPES:—Holotype: CU 53346, a tuberculate adult male 42.3 mm SL; Tombigbee (Black Warrior) dr., Ala., Jefferson Co., Five Mile Cr., trib. to Valley Cr., at U. S. Hwy. 11 bridge, 5.0 airmi. SW of jct. Ala. Hwy. 150 and U. S. Hwy. 11 in Bessemer; T19S, R5W, Sec. 36; 19 May 1969; Franklin F. Snelson, Jr. and Bruce W. Menzel (FFS-69-7).

Paratypes: 98 specimens collected with the holotype, cataloged as follows: CU 53354 (68), TU 58810 (10), UMMZ 197674 (10), and USNM 204313 (10).

Counts of the holotype are as follows: anal rays 10; pectoral rays 13; lateral line scales 39; body circumference scales 17-2-11=30; predorsal scale rows 20; caudal peduncle scales 5-2-4=11; IO canal incomplete at dermosphenotic bone, with pores 12+2; POM canal pores 13; index of anterior dorsolateral scale reduction 3; and index of fin pigmentation 0+0=0. Measurements of the holotype, expressed as thousandths of SL, are as follows: predorsal length 556; postdorsal length 467; prepelvic length 496; preanal length 644; head length 238; head depth 162; postorbital head length 94; snout length 72; upper jaw length 84; gape width 55; fleshy orbit length 70; fleshy interorbital width 88; body depth 223; body width 138; caudal peduncle length 224; caudal peduncle depth 106; dorsal fin length 202; anal fin length 202; pectoral fin length 158; and pelvic fin length 139.

DIACNOSIS.—See Tables 16 and 17 and the Comparisons section of the species account.

DESCRIPTION.—Certain counts are presented in Tables 4-10. Measurements are presented in Table 14. General physiognomy and pigmentation are shown in Fig. 3A. Details of dorsal fin pigmentation are illustrated in Fig. 9.

Body circumference scales 15-17 (19), modally 17, above lateral line and (10) 11-13 (14), modally 11 or 12, below. Caudal peduncle scales 5-7, modally 5 or 6, above lateral line and 4-5, modally 5, below. Pharyngeal tooth counts of 25 specimens 1,4-4,1 (in 7 specimens); 1,4-4,2 (4); 2,4-4,1 (4); and 2,4-4,2 (10).

Scales moderately to weakly imbricate except predorsally where imbrication and scale size reduced. On upper anterior sides of body, partially embedded scales nonimbricate, separated from one another by moderate to large naked interspaces. Index of anterior dorsolateral scale reduction averages 2.37 (Table 11).

Tip of lower jaw usually equal to (31 specimens) or projects slightly beyond (29 specimens) tip of upper lip. Chin occasionally included within upper lip (10 specimens), only rarely projecting strongly beyond it (3 specimens). Fleshy orbit length approximately equal snout length. Body relatively slender and compressed. Posterior border of extended anal fin straight to slightly falcate.

Lateral line on body decurved, reaching lowest point slightly in advance of pelvic fin. Lateral line with many scale pores weakly developed or absent, especially on caudal peduncle, where unpored scales occur singly or in series containing up to 10 scales. No orderly relationship between number of pored or unpored scales and size. Supratemporal canal strongly reduced, in various stages of incomplete formation in many adult specimens. The ST canal broadly interrupted at dorsal midline. Pore count formulas, in order of their frequency, 2,2 (in 13 specimens); 1,1 (12); 2,1 (5); 3,2 (4); 1,2 (2); 2,3 (2); 2,0 (1); 0,1 (1); 1,0 (1); and 3,2+1 (1). Of specimens examined 52 percent had ST pores reduced to 1 or 0 on one or both sides. Supraorbital canal incomplete (not joining postocular commissure) but fully formed and without interruptions in all adults examined; pore counts for 42 specimens were

Scapular bar absent.

7 (in 1 specimen), 8 (32), and 9 (9); $\bar{x}=8.2$. Preoperculomandibular canal well developed and without interruptions along its length; pore counts are given in Table 10. Dermosphenotic bone usually small and poorly ossified or absent, and infraorbital canal typically disconnected from postocular commissure over position of bone. Rarely (6 of 83 specimens) closure of canal complete at this point; pore counts for these 6 specimens 13 (in 2 specimens), 14 (3), and 15 (1); $\bar{x}=13.8$. Most frequent IO pore count formulas for specimens with interrupted canals 11+2 (20 specimens), 12+2 (13), 12+3 (10), 11+1 (6), 11+3 (4), 10+2 (3), and 13+2 (3). Number of IO pores anterior to dermosphenotic interruption 9 (in 1 specimen), 10 (8), 11 (31), 12 (28), 13 (7), and 14 (2); $\bar{x}=11.5$.

Lips heavily pigmented, conspicuously darker than more sparsely pigmented chin and snout tip. Gular and chin pigment forming no consistent pattern; some specimens approaching N. b. bellus (Fig. 2A), but most with melanophores randomly scattered over chin. Deep-lying pigment over lachrymal bone usually creating dark preorbital blotch. This blotch and the heavily pigmented lips usually forming dark band passing around snout tip. Superficial pigment on head dorsum rather uniformly scattered. Pigment reduction behind, between, and in front of nostrils, and on snout tip results in narrow, often tapering, dusky bar extending forward between nostrils to merge with thin transverse band of pigment just behind upper lip. These features of snout pigmentation most prominent in juveniles and subadults.

Dusky middorsal stripe weak and ill-defined, developed from head to tail but not surrounding dorsal fin base. Pigment rather uniformly scattered on anterior dorsolateral area of body; scales not clearly outlined and crosshatched appearance Bars, chevrons, and darkened scales never present on body of either sex. Plumbeous lateral stripe originates at base of tail and passes forward to head. On caudal peduncle stripe dark and about one scale row wide; on trunk stripe broader (to about two and one-half scale rows wide) and slightly weaker and more diffuse. Upper margin of stripe discrete, falling along midlateral horizontal myoseptum; lower margin discrete on caudal peduncle but diffuse anteriorly. Lateral stripe usually continuing forward across upper half of opercle. At midbody pigment stops at lateral line or extends up to one scale row's distance below the (latter condition in some large breeding males). Discrete punctulations adjacent to lateral line pores absent. Lateral stripe may expand slightly over or just in advance of hypural plate, but discrete caudal spot absent. Melanophores moderately to weakly developed along anal fin base and in double row along ventral margin of caudal pedunele. Anterior basidorsal spot absent.

FIN PROMENTATION.—Though breeding material is used for the basis of the following description, N. b. alegnotus contrasts with the nominal subspecies in show-

ing little seasonal variation in the intensity of fin pigmentation.

All rays of dorsal fin with thin black borders basally. Proximal half of interradial membranes usually immaculate but occasionally with a few scattered melanophores (never enough to appear dusky to unaided eye). Pigment borders becoming progressively darker and thicker distally, their outside margins becoming blurred. In area of ray branching, dusky color bleeds off irregularly onto interradial membranes (Figs. 3A, 9). Extent of pigment diffusion variable, but melanophores rarely extend farther than a ray's thickness onto membrane. Consequently, principal interradial membrane never completely covered with pigment. Secondary interradial membranes darkened in same manner and by deposition of melanin in ray crotches. Occasionally, heavy pigmentation in and around major branching points of rays forms weakly defined series of submarginal blotches. Narrow, clear band fringes distal edge of fin. Except for being generally lighter, dorsal fin pigmentation of breeding females like that of males.

Anal fin of breeding males usually immaculate (Fig. 3A) but occasionally with few melanophores scattered along margins of first several rays. Rarely (8 of 62 specimens) ray border pigment heavier, bleeding slightly onto first few interradial membranes at apex of fin. Anal fin of breeding females pigmented like that of males except that interradial pigment was never observed.

All principal caudal rays bordered by melanophores in both sexes. Breeding males occasionally have a few melanophores scattered over interradial membranes near tips of caudal lobes or near fork. Interradial pigment rarely present in females.

First pectoral ray bordered by melanin along entire length, next several rays weakly bordered along basal portions. Sexes similar.

Pelvic fin of breeding males usually immaculate (Fig. 3A), but occasionally with a few melanophores scattered along borders of first several rays. Rarely (4 of 62 specimens) ray border pigment darker, bleeding slightly onto interradial membranes at apex of fin. Pelvic fin of breeding females pigmented like that of males except that no interradial pigment was seen.

As N. b. alegnotus usually lacks interradial pigment in the anal and pelvic fins, the index of fin pigmentation is uniformly very low (Tables 12 and 13) and was not subjected to regression analysis. The few males showing a slight amount of interradial pigment in the tips of the anal and/or pelvic fins were not all large (ranged from 40 to 48 mm SL), although the highest pigmentation index (3+3=6) did come from the largest male examined (48.1 mm SL).

BREEDING COLORATION

Males.—Except for narrow, colorless marginal band, dorsal fin of breeding males flushed with brilliant red, contrasting conspicuously with heavy black pigment bordering rays. Viewed microscopically, erythrophores visible on membranes, absent from rays. Caudal fin washed with red-orange, only about half as bright as dorsal fin; color restricted primarily to membranes. Anal fin devoid of color in all males studied except two with interradial pigment. In these, trace of orange mixed in among melanophores at apex of fin. Pelvic fins lacked red color in all males examined, even in specimens with interradial melanin. Approximately half of males studied had faint streak of red in membrane following first ray of pectoral fin.

Iris of breeding males washed with pale yellow-orange. Otherwise, no bright pigment visible, even microscopically, on head or body. In life, lips and preorbital area conspicuously darker than remainder of head. Venter is white, dorsum olive. Side up to midlateral horizontal myoseptum dominated by silvery band, paralleled along its upper margin by narrow pinkish or purplish iridescent line.

FEMALES.—Breeding females are less vivid than males. Dorsal and caudal fins faintly washed with orange-red, but fading quickly to yellow-green in preservative.

BREEDING TUBERCULATION

Males.—Pectoral fin tuberculation of this form is similar to that of N. b. bellus except that, where maximally developed (on rays 2 through about 5), tubercles are more randomly arranged (seldom in linear series) and average slightly smaller. In some specimens the arrangement approaches a coarse shagreen.

The description of head tuberculation of N. b. bellus applies equally well to N. b. alegnotus with these exceptions: (1) Tubercles on the head dorsum are usually erect, but isolated tubercles may be slightly antrorse or even slightly retrorse. (2) The tendency for suborbital and interopercular tubercles to encroach backward and upward onto the lower opercle is not so well developed in this form. (3) The most noticeable difference is that N. b. alegnotus has better-developed tubercles on the ventral aspect of the head. Those lining the opercular membrane, branchiostegal rays, and interopercle are numerous, close-set, and strong. Jaw rami tubercles are especially formidable, about 50 percent larger than those on the head dorsum.

Body tuberculation agrees with that described for N. b. bellus with these exceptions: (1) Belly and breast tuberculation is less variable and usually well developed

on both areas, with 1 or 2 moderate-sized, erect tubercles per scale. (2) Tubercles lining the posterior margins of body scales range from erect to distinctly retrorse and are only rarely weakly antrorse. (3) Middorsal and nape tubercles range from erect to moderately antrorse, but the antrorse condition was observed more frequently than in the nominal subspecies.

FEMALES.—The tubercle description of females of the nominal subspecies applies equally well to this form.

COMPARISONS.—N. b. alegnotus is compared with other members of the roseipinnis complex in Tables 16 and 17. In addition to the differences noted there. N. b. alegnotus shows average differences from N. b. bellus in the following more subtle features: (1) Subspecies bellus has a well-developed lateral line; alegnotus has pores poorly formed or absent from some scales. (2) The cephalic lateral line of alegnotus is more reduced, though pore counts of the POM and IO canals average higher. (3) The number of ST canal pores was reduced from two to one or zero on one or both sides of the head in 52 percent of the alegnotus examined: the corresponding figure for bellus was 6 percent. (4) The IO canal is complete or incomplete at the dermosphenotic bone in bellus; it is usually incomplete, rarely complete, in alegnotus. (5) Pectoral fin tubercles are slightly smaller and more close-set in alegnotus. (6) In alegnotus tubercles on the underside of the head are approximately 50 percent larger than those on top; they are approximately equal in bellus. (7) Red color in the dorsal fin of bellus is usually subdued; the dorsal fin of alegnotus is bright red.

N. b. alegnotus is syntopic with no other species of Lythrurus. N. ardens is present in the upper Locust Fork of the Black Warrior system but has not yet been taken in proximity with N. b. alegnotus. The two are easily distinguished by the presence of an anterior basidorsal spot in N. ardens. The only other Lythrurus species that could be confused with N. b. alegnotus are N. fumeus and N. lirus. These species are similar to N. b. alegnotus in having a dusky lateral stripe, but both are readily distinguished from it by the absence of the peculiar pattern of dorsal fin pigmentation (Fig. 9). Furthermore N. fumeus has yellow rather than red fins and more reduced breeding tubercles on the head. N. lirus is distinctive in having chin pigment restricted to the tip of the lower jaw and in possessing large, antrose head tubercles and a few enlarged tubercles on the chin tip.

Sexual Dimorphism.—Sexual dimorphism is well developed in N. b. alegnotus and is most pronounced during the breeding season. Sexual differences in breeding tuberculation and coloration have been summarized. No sexual dimorphism in meristic characters was noted.

Sexual dimorphism in morphometric characters is summarized in

Table 2. A sample of 24 breeding males and 26 breeding females from Five Mile Creek was used for statistical comparison with Student's ttest. All specimens measures were 40-55 mm SL. Mean SL for males was 43.92 mm; mean SL for females was 46.01. Levels of probability greater than 0.1 were considered not significant (ns). Following each character is given (first) the range and mean for males, (second) the range and mean for females, and (third) the probability that the two means are significantly different. Predorsal length: 529-564, 548.7; 531-569, 555.2; <0.025. Postdorsal length: 465-506, 477.9; 451-486, 467.5; <0.001. Prepelvic length: 471-504, 491.5; 485-519, 507.0; <0.001. Preanal length: 622-644, 635.4; 635-660, 648.7; < 0.001. Head length: 221-249, 234.8; 225-248, 236.0; ns. Head depth: 151-166, 159.2; 153-169, 160.5; ns. Postorbital head length: 90-102, 96.8; 91-105, 97.1; ns. Snout length: 65-78, 70.5; 66-81, 70.8; ns. Upper jaw length: 77-88, 81.3; 76-88, 81.5; ns. Gape width: 53-67, 58.7; 50-68, 59.7; ns. Fleshy orbit length: 65-76, 70.8; 69-79, 72.8; <0.025. Fleshy interorbital width: 82-97, 89.4; 83-93, 89.7; ns. Body depth: 196-235, 220.4; 194-244, 226.4; <0.1. Body width: 127-143, 136.5; 126-165, 148.3; < 0.001. Caudal peduncle length: 216-251, 233.0; 215-236, 223.7; <0.001. Caudal peduncle depth: 94-113, 104.7; 93-106. 98.9; <0.001. Dorsal fin length: 194-225, 205.5; 192-224, 203.5; ns. Anal fin length: 184-216, 198.5; 177-199, 189.1; <0.001. Pectoral fin length: 157-182, 165.1; 155-187, 168.3; ns. Pelvic fin length: 131-150. 142.7; 130-152, 138.8; <0.005. Body depth and width measurements were influenced by the distended body cavities of the gravid females.

The urogenital papilla of females is enlarged and protrudes posteriorly to about the anal fin origin. In males the papilla is not enlarged. This difference is developed to some extent throughout the year but is most pronounced during the reproductive season.

Available material is insufficient to test for sexual dimorphism in size by the method employed elsewhere in this study. Cursory observations suggest that females reach a slightly larger size than males. If true, this would contrast with N. b. bellus, in which the male is the larger sex.

GEOGRAPHIC VARIATION.—No significant geographic variation is evident among the samples at hand.

DISTRIBUTION AND HABITAT.—N. b. alegnotus is known from several widely scattered localities above the Fall Line in the Black Warrior River basin of Alabama (Fig. 7). It has been found in both the Mulberry Fork and Locust Fork systems, the two major branches of the upper Black Warrior, and in the Valley Creek system, a direct tributary of the River itself.

From the Lost Creek system (Lost and Wolf creeks) in Walker County, Alabama, 30 specimens are available. Because most of these

are poorly preserved young or juveniles, important diagnostic details are largely undeveloped or otherwise not visible. In general appearance and, most importantly, pattern of fin pigmentation, the few adequately preserved adults appear to agree satisfactorily with other populations of N. b. alegnotus. Nevertheless the nature of the study material precludes definitive analysis of these populations, and their identity must remain tentative pending examination of adequate series of (preferably breeding) adults.

The single series of N. b. alegnotus from Mud Creek was taken in April, 1966. On 15 May 1969 Bruce W. Menzel and I revisited this locality only to find the creek devoid of all aquatic life, apparently because of extensive strip mining in the watershed.

Except for the Lost Creek system, N. b. alegnotus is quite common in the streams it occupies. At the times of my observations it was numerically dominant in Five Mile, Marriott, and Crooked Creeks. These streams are small (15-30 ft. wide) and composed of long, deep, relatively slow-flowing pools alternating with shorter sections of riffles and shallows. They have clear, white water, hard bottoms (ranging from sand-gravel to bedrock), beds of water willow (Justicia) in shoal areas, and moderate gradients. N. b. alegnotus was found commonly in the deeper, slower parts of pools and runs immediately downstream from shoals. Strong currents were conspicuously avoided, as were large deep pools without perceptible current in Crooked Creek.

ETYMOLOGY.—The name alegnotus is a compound of the Greek a (not) and legnotos (with a colored border) and is treated as an adjective. The name refers to the absence of black marginal bands in the fins.

MATERIAL EXAMINED

None of the material listed below is designated as paratypes.

MOBILE BAY DRAINAGE.

Black Warrior River system.—Alabama, Blount Co.: UAIC uncat. (James Cr., trib. Mulberry Fork, T13S, R3W, Sec. 9), 3340 (unnamed cr. feeding lake just off Co. Hwy. 8, ca. 1.5 mi. SW Hayden, T13S, R2W, Sec. 29). Cullman Co.: CU 53345, UAIC uncat. (both same locality: Marriott Cr., trib. Mulberry Fork, along Hwy. I. 65, 9.3 rdmi. S jct. I. 65 and U. S. Hwy. 278 nr. Cullman, T11S, R3W, Sec. 32). Jefferson Co.: UAIC 1932 (Mud Cr., ca. 0.5 mi. W community of Mud Creek, T19S, R6W, Sec. 9), 1934, 2504, 3041 (all same locality: Five Mile Cr., trib. Valley Cr., U. S. Hwy. 11 bridge, 5.0 airmi. SW jct. Ala. Rt. 150 and U. S. Hwy. 11 in Bessemer, T19S, R5W, Sec. 36), 3317 (Turkey Cr., trib. Locust Fork, 1 mi. W Morris, Co. Hwy. 144, T15S, R3W, Sec. 2), 3318 (Crooked Cr., trib. Locust Fork, ca. 4.5 mi. W Morris, Co. Hwy. 144, T15S, R3W, Secs. 16, 17), 3326 (Hogeland Cr., trib. Locust Fork, ca. 1.5 mi. NE Warrior, T14S, R2W, Sec. 6). Walker Co.: CU 53349, TU 26923, UAIC 214 (all same locality: Wolf Cr., Hwy. 69 bridge, 2.8 airmi. S center Oakman, T16S, R8W, Sec. 9), UAIC 91 (West Branch Wolf Cr., 2 mi. W

Corona, Ala. Rt. 18, T15S, R9W, Sec. 27), 209 (Lost Cr., 0.5 mi. E Carbon Hill, U. S. Hwy. 78, T13S, R9W, Sec. 32), 210 (Lost Cr. 4 mi. E Carbon Hill, Hwy. 118, T14S, R9W, Sec. 2). Winston Co.: UAIC 3870 (Rock Cr., 1.5 mi. ENE Upshaw, ca. 1.0 mi. SW Co. Hwy. 41, T9S, R6W, Sec. 11), 3872 (Boone Cr., 1.5 mi. N Addison, ca. 0.5 mi. W Co. Hwy. 41, T9S, R6W, Sec. 28).

Notropis bellus: bellus x alegnotus

INTERGRADES

Notropis bellus. Howell, 1957:239-40, 243, 245, map 31 (UAIC 89 and 208, North R. and Hurricane Cr. systems).

Notropis roseipinnis. Howell, 1957:248, map 32 (UAIC 167, 168, 170, 206, 208, North R. system).

Characters.—On the basis of geographic location and morphological characters, populations at the Fall Line in the Black Warrior River system are considered intergrades between N. b. bellus and N. b. alegnotus. In meristic features, intergrades are most like bellus in caudal peduncle scales (Table 8), anal rays (Table 9), POM canal pores (Table 10), and IO canal pores before the dermosphenotic disjuncture ($\bar{x} = 10.5$). Intergrades are intermediate in number of pectoral fin rays (Table 9). They are similar to alegnotus in the index of anterior dorsolateral scale reduction (Table 11). In morphometric characters, intergrades are most like bellus in caudal peduncle length and are similar to alegnotus in predorsal length and in having smaller fins. Intergrades are interjacent in body and head depth, prepelvic length, and upper jaw length. They are extreme in having a more slender caudal peduncle than either subspecies (Table 14).

Fin pigmentation of breeding adults in the intergrade populations is superficially similar to that of N. atrapiculus (Figs. 3C, 4E-H). Unlike alegnotus, the anal and pelvic fins of intergrades usually bear interradial pigment; but unlike bellus, there are no terminal bands through the fins. Instead, interradial pigment is well developed near the apex of the fin and becomes weaker posteriorly. Consequently fin pigment index values of intergrades are interjacent between those of the two subspecies (Tables 12, 13). In nuptial males the pectoral fin band typical of the nominal subspecies is absent, and dorsal fin pigmentation is intermediate and superficially similar to that of N. atrapiculus.

DISTRIBUTION AND VARIATION.—Intergrades are found in the North River and Hurricane Creek systems, western and eastern tributaries respectively of the Black Warrior River at Tuscaloosa (Fig. 7). Both of these stream systems lie almost precisely on the Fall Line. A single poorly preserved juvenile (CU 46500) from Yellow Creek, the next major Black Warrior tributary upstream from Hurricane Creek, is tentatively considered an intergrade, primarily on its geographical provenance.

The characters of N. b. bellus are relatively constant as far up the Black Warrior drainage as the Cypress Creek system, just southwest of Tuscaloosa, Alabama (UAIC uncat.). The next known upstream population of the species inhabits the North River. Carroll Creek, the lower-most tributary of the North River, has yielded specimens grading from almost pure N. b. bellus into typical intergrades, determined primarily on the basis of fin pigmentation. Otherwise the North River system appears

to be inhabited only by intergrades and their characters vary little from one creek to another.

The Hurricane Creek system lies northeast of Tuscaloosa and enters the Black Warrior almost opposite North River. As mentioned above, one collection of typical N. b. bellus (UAIC 326) purported to be from this creek is assumed to be the result of a data mixup. Specimens collected from this same locality both before and after UAIC 326 seem to be typical intergrades. Because of inadequate material, no comments can be made on the possibility of variation within Hurricane Creek.

ORIGIN OF INTERCRADES AND TAXONOMIC STATUS OF N. b. alegnotus. -The taxonomic status accorded N. b. alegnotus is dependent upon one's interpretation of the populations herein called intergrades. I have assumed that the approximate morphological intermediacy of these populations is the result of past gene exchange between two divergent subspecies along a zone of sharp ecological and geographic separation, the Fall Line. However, at present the most downstream locality for N. b. alegnotus (Valley Creek) is roughly 36 river miles upstream from the mouth of Hurricane Creek. Thus available knowledge suggests that N. b. alegnotus is not now in direct genetic contact with intergrades. probably explains why the characters of the intergrades are skewed toward N. b. bellus. It also leaves open the possibility that years of evolution in genetic isolation have reduced or perhaps destroyed the reproductive compatability of N. b. alegnotus with intergrades and/or N. b. The apparent recent establishment of N. b. bellus within the tentative range of N. b. alegnotus, while otherwise unfortunate, may eventually shed some light on this possibility.

The highly divergent nature of N. b. alegnotus and the distributional pattern involved suggest an alternative interpretation. The Fall Line populations are peripheral to the range of N. b. bellus and they exist in an ecological situation atypical for that form. Perhaps these populations have behaved as classical peripheral isolates (Mayr, 1963:386-93) and have diverged from the central populations because of different selective pressures, genetic drift, or for some other reason unrelated to past gene exchange with N. b. alegnotus. Perhaps the over-all intermediacy of the "intergrades" is only coincidental. If this were the case, alegnotus would merit specific rank. Although tenable, this hypothesis involves several more assumptions than does the more conservative approach taken herein.

The distribution and variation of *N. bellus* in the Black Warrior system are complex and partially analyzed at present, and the situation is likely to become more confused with time. Alterations of native distributions probably started long ago with the building of navigational locks

on the river and the initiation of strip mining. The latter is continuing at a fast pace in the Black Warrior basin, and its effects apparently extirpated one population of N. b. alegnotus in the late 1960's. A major reservoir is now being developed on the North River and others are planned for the area. Many of the streams populated by N. bellus are threatened by the inevitable alteration and pollution accompanying the encroachment of nearby cities. It is hoped that the description of N. b. alegnotus and the concomitant unsolved problems will emphasize the urgent need for more (preferably breeding) material from throughout the upper Black Warrior system.

MATERIAL EXAMINED

MOBILE BAY DRAINAGE, BLACK WARRIOR RIVER SYSTEM.

Yellow Creek.—Alabama, Tuscaloosa Co.: CU 46500 (Yellow Cr., 10 mi. S Oakman, Hwy. 69).

Hurricane Creek and tributaries.—Alabama, Tuscaloosa Co.: CU 19258, 19277, 42318, UAIC 56, 58, 59, 805, 1765, 1792, USNM 166016.

North River and tributaries.—Alabama, Fayette Co.: UAIC 1178, 1179, 1183, 1187, 1190. Tuscaloosa Co.: CU 53164, 53352, TU 27546, 30188, UAIC 168, 170, 1081, 1152, 3037.

Notropis roseipinnis Hay in Jordan 1885

CHERRYFIN SHINER

Figure 3D, E

Minnilus rubripinnis Hay, 1881:509-11 (original description; in synopsis and key to subgenus Lythrurus). Hay, 1883:71, 74 (color notes; range). Jordan and Gilbert, 1883:198-9 (in key; description). Preoccupied.

Notropis roseipinnis Hay in Jordan, 1885b:27 (replacement name for Minnilus rubri-

pinnis Hay). Jordan, 1885b:27 (listed; range). Jordan and Evermann, 1896a: 260 (listed; range based in part on N. atrapiculus). Jordan and Evermann, 1896b:258, 298 (in key; description; range based in part on N. atrapiculus). Pratt, 1923:84 (characters; range based in part on N. atrapiculus). Fowler, 1945:30 (listed, Alabama dr.; Escambia dr. occurrence based on N. atrapiculus). Bailey, Winn, and Smith, 1954:156 (range, in part). Carr and Goin, 1955:54 (range, in part). Eddy, 1957:126 (in key; characters; range in part based on N. atapiculus). Howell, 1957:237, 245-52, map 32 (in key; description; Ala. records, in part based on N. atrapiculus). Briggs, 1958:261 (range, in part). Cook, 1959:33, 38, 107, 121-2 (in key; spawn April to June; description; Mississippi distribution). Schrenkeisen, 1963:124 (range, in part; characters). Cliburn, 1965:264 (Pascagoula dr. records). Martin, 1965:299 (occurrence and frequency in Tallahala Cr., Pascagoula dr.). Ramsey, 1965:94 (listed, Alabama dr.). Caldwell, 1966:219, 226 (Biloxi and St. Louis Bay dr. records). Douglas and Davis, 1967:15 (listed from La.). Tucker, 1967:88-9, 192, map 51 (par-

tial synonymy; records from Mobile Bay basin; habitat; distribution; possible competitive exclusion with *N. bellus*). Moore, 1968:73, 80 (in key; characters; range in part based on *N. atrapiculus*). Smith-Vaniz, 1968:36, 49, 125-6, 131, fig. 76 (in key; partial synonymy; Alabama range, based in part on *N. atrapicu*-

lus; zoogeography).

Jordan, Evermann, and Clark, 1930:126 (listed; synonymy; Lythrurus roseipinnis. range, in part based on N. atrapiculus). Pratt, 1935:80 (characters; range based

in part on N. atrapiculus). Driver, 1942:275 (in key; range).

Types.—The types of Minnilus rubripinnis Hay (1881) must serve also as the types of the replacement name Notropis roseipinnis Hay (in Jordan, 1885b) (Article 72d, International Code of Zoological Nomenclature). The type series by original designation is USNM 27420, consisting of 17 specimens (one specimen of unidentified Notropis removed to USNM 203324) collected in the Chickasawha(y) River and tributaries near Enterprise, Clarke County, Mississippi (Pascagoula drainage), in March or April 1880, by O. P. Hay (Hay, 1881:488-9, 510). The specimens are poorly preserved and scaleless, but important features of fin pigmentation are still evident. A specimen about 45 mm SL is chosen as lectotype and retains the original This specimen exhibits typical fin pigmentation (fin pigmentation index 3+0=3) and has 12 anal rays and about 42 lateral line scales. The 16 other syntypes are recataloged as lectoparatypes, USNM 203325.

Jordan and Evermann (1896b:298) indicated that USNM 32302 was also part of the type series. This series of two specimens bears appropriate locality data, but labels in the jar indicate that the specimens were probably in Jordan's hands when Hay wrote his description. If such is the case, they apparently do not qualify as par-The name roseipinnis was proposed as a substitute for rubripinnis by Hay (in Jordan, 1885b:27) when the latter was found to be preoccupied in the genus by Argureus rubripinnis Heckel [= Notropis cornutus (Mitchill) according to Gilbert

(1964)].

DIAGNOSIS.—See Tables 16 and 17 and the Comparisons section of the species account.

DESCRIPTION.—Certain counts are presented in Tables 4-10. Measurements are presented in Tables 14 and 15. General physiognomy and pigmentation are shown in Figs. 3D-E. Details of chin and fin pigmentation are illustrated in Figs. 2B and 4A-D.

Body circumference scales (16) 17-20 (22), modally 19, above lateral line and (9) 11-13 (16), modally 11, below. Caudal peduncle scales 5-9 above lateral line and 3-7 below, with usual count (85 percent) 7-2-5=14. Pharyngeal tooth counts from throughout range as follows in 71 specimens: 1,4-4,1 (3 specimens); 1,4-4,2

(5); 2,4-4,1 (7); 2,4-3,2 (2); and 2,4-4,2 (54).

Scales moderately imbricate over most of body. Extent of reduction in predorsal squamation quite variable. At one extreme predorsal and anterior dorsolateral scales only slightly reduced in size and imbrication, and naked interspaces, when present, very narrow. At other extreme large section of anterior dorsolateral part of body devoid of scales. Occasionally apex of this subtriangular naked area extends Various intermediate conditions exist, with scales in this back to dorsal fin origin. area, especially near head, reduced in size, partially embedded, and separated from one another by naked interspaces of varying widths. Reduction of squamation on anterior dorsolateral area of body does not necessarily affect squamation of predorsal midline; typically it is complete from dorsal fin to head. Mean index of anterior dorsolateral scale reduction varies between 1.28 and 3.47 (Table 11).

Lower jaw occasionally included with upper (76 specimens) but usually terminates equal with (291 specimens) or projects slightly beyond (156 specimens) it. Chin rarely (31 specimens) protrudes strongly. Fleshy orbit length averages slightly

longer than snout. Body compressed, varying from slender to deep.

Lateral line on body complete and decurved, reaching lowest point over or slightly in advance of pelvic fin base. Supratemporal canal broadly interrupted at dorsal midline, and often with secondary interruptions. Most frequent ST pore count formulas 2,2 (225 specimens); 1+2,2+1 (58); 1+2,2 (12); 2,3 (10); 3,2 (10); 2,1 (10); 1,2 (9); and 2,2+1 (8). Supraorbital canal incomplete (not joining postocular commissure) but uninterrupted along its length; pore counts for 350 specimens 7 (37 specimens), 8 (255), 9 (53), and 10 (5), x=8.1. Preoperculomandibular canal only rarely (16 of 738 specimens) interrupted along its length; pore counts given in Table 10. Dermosphenotic bone reduced, either absent or present but weakly ossified in adults. Infraorbital canal varies from incomplete to complete at juncture with postocular commissure over position of bone. In 133 specimens with complete IO canals, pore counts 11 (10 specimens), 12 (48), 13 (45), 14 (22), 15 (6), and 16 (2); $\bar{x} = 12.8$. Most frequent pore count formulas for specimens with dermosphenotic interruption 11+2 (86 specimens), 10+2 (76), 11+3 (46), 10+3 (44), 12+2 (24), 9+2 (16), and 12+3 (13). Number of IO pores before dermosphenotic disjuncture (when present) 9 (22 specimens), 10 (125), 11 (136), 12 (43), 13 (5), and 14 (3); $\bar{x} = 10.7$.

Lips and preorbital blotch occasionally prominently black but usually little or no darker than adjacent snout and chin. Chin pigmentation typical of Gulf Coast populations illustrated in Fig. 2B. Heavy pigment extending posteriorly on mandibles to near angle of mouth; gular pigment extending posteriorly to or occasionally beyond limit of mandibular pigment. This pattern of chin pigmentation not consistently developed in Mississippi Valley populations. Superficial pigmentation of head dorsum, snout, and temporal-upper opercular areas rather uniformly dark and scattered. Development of melanin along posterior margin of cleithrum variable. If present, pigment usually weak but occasionally forming poorly defined bar.

Middorsal stripe well developed before dorsal fin but less so posteriorly, not surrounding dorsal fin base. Scales on upper half of sides occasionally margined with melanin, producing faint crosshatched pattern. More often, pigment in this area more uniformly dispersed, and crosshatching obscured or obliterated. In specimens with high index of scale reduction, anterior dorsolateral scales lighter than intervening naked spaces, standing out as pale spots (see Smith-Vaniz, 1968:fig. 76). Darkened scales absent from flanks. Pigment over anterior dorsolateral myosepta formed faint chevrons in about 14 percent of breeding males and 9 percent of breeding females examined. Bar markings absent from sides. Body of breeding males not melanistic.

Dusky lateral stripe originating at base of caudal fin. On caudal peduncle it is about one scale row wide, with ill-defined borders. Stripe broadens and fades anterior to anal fin. Midlateral body sometimes slightly more dusky than upper sides, but lateral stripe rarely continuing forward to head. Pigment on upper half of opercle usually not forming band, and poorly defined band passing around snout tip rarely present. No discrete caudal spot, but lateral stripe may broaden slightly over hypural plate. At midbody, pigment may extend one-half to two scale rows below lateral line, primarily along scale borders. Dark punctulations usually lacking above and below lateral line pores. Dark pigment usually weakly to moderately developed about anus, along anal fin base, and along ventral margin of caudal peduncle. Anterior basidorsal spot absent.

FIN PIGMENTATION.—N. roseipinnis has the most specific pattern of fin pigmentation in the roseipinnis complex. Though fin pigment intensifies slightly during the reproductive season, the basic pattern is conspicuous in both sexes throughout the year. The following description is based on spawning adults.

In both sexes apex of dorsal fin marked by two lanceolate black spots formed by heavy melanin deposits on distal fourth of first two interradial membranes (Figs. 3D-E, 4A). Concentrations of pigment often present in and about branches of rays 3 through 8, but seldom heavy enough to form secondary spots. In males basal and posterior portions of dorsal fin liberally dusted with melanophores. In females these areas of fin more sparsely pigmented. In both sexes fin has narrow, clear border.

Anal fin dominated by black, lanceolate- or slash-shaped spot at apex (Figs. 3D-E, 4B). Primary spot located subterminally in distal third of first interradial membrane. In males entire membrane may be black, but in females pigment adheres closely to first (unbranched) ray, not extending entirely across membrane to second ray. Pigment concentrations in and around branches of second ray usually heavy, and secondary dark slash often present on membrane along posterior border

of ray 2. In East a few scattered melanophores may be present on basal portions of interradial membranes 1 through about 3, on membranes between branches of third ray, and along borders of rays 3 through 5 or 6. In western part of range anal fin pigment more extensive. Secondary slashes and/or isolated melanophores may occur posteriorly to eighth interradial membrane (in males) and often all rays bordered by pigment. Intensity of these markings progressively decreases posteriorly. Males usually have heavier and more extensive anal fin pigment than do females.

All caudal fin rays bordered by melanin. In breeding males, pigment often scattered over interradial membranes, especially near tips of lobes. Females usually

lack caudal interradial pigment.

First ray of pectoral fin bordered by melanophores along margins. Rays 2 through about 6 variously bordered, primarily along basal portions (Fig. 4C). The seven are similar

Pelvic fin pigmentation exhibits sexual and geographic variation. Males usually have more extensive pelvic fin pigment than females. In eastern part of range fin usually immaculate. At most, narrow fringe of pigment trails first one or two rays; but these streaks usually invisible to unaided eye (Figs. 3D, 4D). In west pelvic fin pigment better developed. Dark streaks or lanceolate spots developed on membranes along posterior border of rays as far back as the fourth (Fig. 3E). Occasionally all pelvic rays with narrow black borders, progressively decreasing in intensity posteriorly.

N. roseipinnis exhibits geographic variation in the fin pigmentation index (Tables 12 and 13). Low values in the east correspond to populations with reduced anal and pelvic fin pigment. High values in the west reflect more extensive fin pigment. Lower values for breeding females correspond to less extensive fin pigment in that sex. Most Gulf Coast populations show relatively little ontogenetic change in the fin pigmentation index (Figs. 5, 6). Only the Mississippi Valley population show note-

worthy addition of melanin with size.

BREEDING COLORATION

Males.—Except for a narrow, colorless marginal band, dorsal fin membranes of breeding males washed with bright orange-red. The few observations available indicate that the presence of erythrophores on the anal and pelvic fins may be related to the presence of melanophores. In a Pascagoula drainage collection melanin was absent from the pelvic fins and present in only the first 2 or 3 anal fin membranes. Close examination revealed that red pigment was absent from the pelvic fins and present only at the apex of the anal fin, limited to those membranes that bore melanin. In a Pearl drainage collection, by contrast, the breeding males had melanin in the first 1 to 3 pelvic membranes and first 3 to 6 anal membranes; and red color was present in every membrane that was darkened. In breeding males, interradial membranes of caudal fin lightly washed with pinkish-orange. Two semicircular, colorless spots over bases of upper and lower caudal rays contrast with dusky body and colored caudal fin. Pectoral fin may bear light red streak in first few membranes.

Iris faint orange-red, and occasionally a faint orange wash visible around nostrils and in gular area. In life venter is white, dorsum olive-tan. Lateral body dominated by a broad silvery band that often reflects metallic blue. In sexually advanced males pale rosy band parallels upper margin of silvery band; this color best developed anteriorly.

FEMALES.—Breeding females are colored like males in most respects but are

generally less vivid.

BREEDING TUBERCULATION

MALES.—Pectoral fin tuberculation of N. roseipinnis is like that of N. b. bellus, with these exceptions: (1) A few weak tubercles may or may not be present along

the midlength of the first ray. (2) Tubercles on the dorsal surface of rays 2 through about 8 average slightly smaller and more crowded. In extreme cases a coarse shagreen is formed, with up to about 20 tubercles per fin ray segment arranged in 3 or 4 irregular rows or randomly scattered over each ray. Except occasionally for a few small tubercles on the second rudimentary ray of the dorsal fin, the dorsal, caudal, anal, and pelvic fins usually are devoid of tubercles.

Head tuberculation of *N. roseipinnis* is like that described for *N. b. bellus* except as follows: (1) Only the Bayou Pierre and Big Black populations approach *N. b. bellus* in the development of opercular and postorbital tubercles. (2) The interopercle and branchiostegal rays are less consistently tuberculate; and tubercles on

these areas, when present, are fewer and more scattered.

Body tuberculation is similar to that described for N. b. bellus with the following exceptions: (1) Breast and prepelvic tubercles are usually present, but the belly between these two areas is usually nontuberculate. (2) Tubercles anteriorly on the sides average fewer, usually 3 to 6 along the posterior margin of each scale. They usually are erect but may occasionally vary from slightly antrorse to slightly retrorse in the same collection. (3) Body tubercles normally form only where a scale is present to act as a substrate. Thus extent of tuberculation on the anterior dorsolateral area of the body varies with degree of scale reduction. When scales are large and naked spaces small or absent, tuberculation is developed as in N. b. bellus. When scales are reduced in size, the number of tubercles per scale is reduced; the extreme condition is one centrally located tubercle per scale. No tubercles appear in naked spaces between scales and tubercles fail to develop on the anterior dorsolateral part of the body when that area is scaleless.

Qualitative observations suggest slight average differences between Gulf Coast and Mississippi Valley populations in the tubercule features noted below. Mississippi Valley populations have (1) tubercles on the lower opercle and postorbital area with greater frequency, (2) interopercular and branchiostegal tubercles slightly stronger and more consistently developed, (3) tubercles in the prepelvic area fewer and weaker, and (4) predorsal and nape tubercles more consistently antrorse. (5) Except as noted above, Mississippi Valley populations have slightly smaller and more numerous tubercles on most areas of the head and body.

FEMALES.—The tuberculation of female N. roseipinnis is like that previously described for female N. b. bellus.

Comparisons.—The important differentiating characters between N. roseipinnis and N. b. bellus are pointed out in Tables 16 and 17. The extensive geographic variation in N. roseipinnis masks the sharp distinctions between these two forms. Where they come into proximity in the Mobile Bay basin, the degree of separation is very high in body depth, caudal peduncle depth, dorsal fin length (Tables 14 and 15), fin pigmentation index (Tables 12 and 13), and anterior dorsolateral scale reduction (Table 11). In the western part of its range, however, N. roseipinnis becomes similar to, equal to, or even more extreme than N. b. bellus in all these characters.

The most trenchant differences between *N. roseipinnis* and *N. b. bellus* are details of fin pigmentation. In addition to the features pointed out above and shown in Figs. 3 and 4, there are cryptic developmental differences. In *N. roseipinnis* anal and pelvic fin patterns develop through an intensification of pigment along the posterior borders

of the rays. In early stages dark streaks are present on the membrane along the posterior margin of the first several rays. With advanced development (either increasing size, increasing sexual development, or moving west in the range) these streaks darken; and in the anal fin they broaden to form lanceolate apical spots. In N. b. bellus, by contrast, incipient anal and pelvic fin bands begin development as isolated melanophores scattered randomly on the membranes at the margin of the fins. The number and density of these melanophores increases with advanced development.

N. roseipinnis is compared with N. atrapiculus in Tables 16 and 17 and in the Comparisons section under the latter species. N. roseipinnis is sympatric, occasionally syntopic, with N. umbratilis and N. fumeus in the Bayou Pierre, Big Black, and Yazoo drainages in western Mississippi and with the latter species in some tributaries of Lake Pontchartrain. It is readily distinguished from both by its fin pigmentation. N. fumeus has no interradial fin pigment. The fins of male N. umbratilis become dusky only during the breeding season, and pigment is uniformly dispersed and forms no specific pattern. N. roseipinnis differs further from N. umbratilis in lacking an anterior basidorsal spot.

SEXUAL DIMORPHISM.—Sexual dimorphism in tuberculation, breeding coloration, and fin pigmentation have been discussed above. No sexual dimorphism in meristic characters was noted.

Sexual dimorphism in morphometric characters is summarized in Table 2. A sample of 43 breeding males and 25 breeding females from the Pascagoula River drainage was used for statistical comparison with Student's t-test. All specimens measured were 40-50 mm SL. SL for both males and females was 44.16 mm. Levels of probability greater than 0.1 were considered not significant (ns). Following each character is given (first) the range and mean for males (second) the range and mean for females, and (third) the probability that the two means are significantly different. Predorsal length: 535-573, 554.4; 532-578, 558.4; ns. Postdorsal length: 461-502, 475.9; 454-483, 468.1; < 0.001. Prepelvic length: 459-497, 478.9; 474-509, 492.8; <0.001. Preanal length: 603-653, 634.6; 630-667, 645.8; <0.001: Head length: 224-251, 237.2; 223-261, 239.4; ns. Head depth: 154-174, 164.8; 150-179, 164.3; ns. Postorbital head length: 90-112, 98.5; 92-105, 98.6; ns. Snout length: 63-77, 71.2; 66-78, 71.6; ns. Upper jaw length: 75-94, 85.1; 78-95, 86.1; ns. Gape width: 50-68, 58.3; 51-68, 57.2; ns. Fleshy orbit length: 67-80, 73.5; 66-83, 75.8; <0.01. Fleshy interorbital width: 80-94, 88.3; 80-94, 86.8; ns. Body depth: 201-251, 224.4; 192-274, 227.2; ns. Body width: 112-138, 127.6; 119-164, 139.6; < 0.001. Caudal peduncle length: 193-237, 213.8; 183-225, 210.4; ns. Caudal peduncle depth: 90-109, 97.0; 79-100,

92.8; <0.001. Dorsal fin length: 188-227, 205.7; 186-213, 199.4; <0.005. Anal fin length: 203-240, 223.7; 190-228, 214.3; <0.001. Pectoral fin length: 157-182, 168.6; 160-183, 168.6; ns. Pelvic fin length: 128-148, 137.5; 123-146, 131.7; <0.001. The wider body of females is due in part to ovarian enlargement. Despite sharp average differences in measurements between drainages (Table 15), relative sexual differences exhibit inconsequential interdrainage variation (Snelson, 1970:163-4).

Throughout most of the warmer months females may be recognized by their enlarged urogenital papilla, which extends posteriorly to about the anal fin origin. The papilla of males is not enlarged.

N. roseipinnis shows significant sexual dimorphism in adult size. Of 112 collections, a male was the largest specimen in 91, a female in 21. This deviates from a hypothesized ratio of 50:50 by a Chi-square value of 43.75, which is highly significant at much less than 0.005. The largest male examined was 53.0 mm SL; the largest female was 50.0 mm SL.

Geographic Variation.—Data available from the three known collections of *N. roseipinnis* from the Yazoo drainage are entered in the Tables. The paucity of material and the widely disjunct nature of the samples preclude any meaningful characterization of the populations in this drainage. Thus the Yazoo population is not considered in the following discussion. In all respects except perhaps body circumference scales and predorsal scale rows (Tables 6 and 7), Yazoo specimens show satisfactory tentative agreement with the Bayou Pierre and Big Black populations.

N. roseipinnis shows more geographic variation than any other member of the roseipinnis complex. The bulk of this variation fits into one of three patterns: (1) variation slight and random; (2) Mississippi Valley populations differ on average from combined Gulf slope populations, but variation irregular along Gulf slope; (3) variation clinal, with varying degrees of regularity, from east (Mobile Bay) to west (Lake Pontchartrain) to northwest (Bayou Pierre and Big Black).

The following characters fall into pattern 1 above: lateral line scales (Table 5), pectoral fin rays (Table 9), gill rakers (Table 10), predorsal length, prepelvic length, preanal length, head length, postorbital head length, upper jaw length, fleshy orbit length, and anal fin length (overall values shown in Table 14; see Snelson, 1970:table 32 for individual drainage values). Several characters fit into pattern 2; but Mississippi Valley populations average lower than those along the Gulf Coast in only one case, predorsal scale rows (Table 7). In the following characters Mississippi Valley samples average higher than the combined Gulf Coast samples: body circumference scales (Table 6), caudal peduncle scales (Table 8), head depth, snout length, gape width, fleshy interorbital

width, body width, caudal peduncle length, and pectoral fin length (Table 15).

Of the characters that exhibit clinal variation (pattern 3 above), only two, anal rays (Table 9) and index of anterior dorsolateral scale reduction (Table 11), decrease in value from east to west to northwest. In both these characters the Mobile Bay and Biloxi-St. Louis Bays populations, although not adjacent, are similar, and they differ from surrounding drainages. The other characters fitting pattern 3 tend to increase in value toward the west. These characters are preoperculomandibular canal pores (Table 10), postdorsal length, pelvic fin length, body depth, caudal peduncle depth, and dorsal fin length (Table 15). In the latter three there is an unusually large "step" in the cline between the Lake Pontchartrain and Mississippi Valley populations.

North-south or upstream-downstream clinal variation usually is assumed to be a phenotypic and/or genetic response to ecological factors, usually temperature, occasionally light, which vary clinally in the same direction. East-west clinal variation along the Gulf slope does not fit neatly into any such scheme. This is especially true for N. roseipinnis; the linear extent of its range covers no more than 250 miles in regions of three states with presumably similar meteorological conditions. Bailey and Suttkus (1952:11-12) reported an irregular east-west gradient in the anal ray count of Notropis signipinnis, though in their example the number increased toward the west. Thomerson (1966) also noted east-west clinal variation in Gulf slope populations of Fundulus olivaceus (Storer). Taylor (1969) reported clinal west to east increases along the Gulf Coast in number of pectoral rays in Noturus leptacanthus Jordan and in number of anal rays and vertebrae in Noturus funebris Gilbert and Swain.

Variation in the total index of fin pigmentation (Tables 12 and 13) is complicated and does not fit any of the patterns discussed above. The three eastern drainages have low values and are similar, but in all cases except breeding males below 40 mm SL, the Mobile Bay population averages the lowest. The amount of fin pigment is greatly increased in the Pearl drainage as shown by its high index values. The index drops off abruptly to intermediate values in the Lake Pontchartrain drainage. In the Mississippi basin the index is high in the Big Black and very high in the Bayou Pierre. In most cases an increase in index value is accompanied and partially explained by a stronger tendency for the amount of fin pigment to increase with size (Figs. 5, 6).

It is generally recognized that deposition of melanin can be affected by ecological factors. Specimens from dark-stained water are often unusually dusky, whereas the same species from white (colorless) or turbid

water may be more pallid. Thus it is tempting to speculate that graphic variation in the amount of fin pigment is genetically or phenotypically related to water color. I have tried to clarify this question by comparing water colors of 85 Pearl drainage collections of N. roseipinnis with that of 38 Mobile Bay and Pascagoula collections. To minimize variation water color information was extracted only from the field notes of R. D. Suttkus and J. S. Ramsey. These two men have worked together extensively in the field, and I assume that they judge and record water color similarly. Three classes of water color were recognized, white (=colorless), light brown (=slightly brown), and brown (=dark brown). For the combined Mobile Bay and Pascagoula drainages, the water colors for collections of N. roseipinnis were characterized as follows: 14 (37%) white, 8 (21%) light brown, and 16 (42%) brown. For the Pearl drainage, the values were 43 collections (50%) white, 9 (11%) light brown, and 33 (39%) brown. In spite of the limitations of such data, apparently Pearl drainage streams inhabited by N. roseipinnis do not have darker water than those streams in the Mobile Bay and Pascagoula drainages. On the contrary, Pearl drainage streams perhaps average lighter in color. Thus water color differences do not seem to explain the high fin pigmentation index of Pearl drainage N. roseipinnis as compared with Mobile Bay and Pascagoula populations.

As pointed out in the Description, the chin pigmentation of *N. rosei-pinnis* shows minor geographic variation. Minor geographic variation in tuberculation is also suggested in the Breeding Tuberculation section.

Arguments, some substantial, might be made for the recognition of subspecies in N. roseipinnis. In totality of meristic and morphometric characters, the Mississippi Valley populations differ decidedly from Gulf slope populations. However when considered individually, most of the differences are minor and overlap is broad. The most salient differences are in those three measurements that exhibit a "step" in the cline between the Lake Pontchartrain and Bayou Pierre systems (Table 15). For a point of separation between 245 and 246, the average divergence (Ginsburg, 1954) between the combined Mississippi Valley and combined Gulf slope populations in body depth is 94 percent. Average divergence for caudal peduncle depth is 91 percent for separation anywhere between 101 and 103. Average divergence for dorsal fin length is 83 percent anywhere between 219 and 222. (The data suggest that body depth and caudal peduncle depth are positively correlated, so that they are not properly considered as two independent characters. There is no apparent correlation between dorsal fin length and either depth measurement.) Although the northwestern populations act as the terminal element in clinal variation of these three characters, the magnitude of the

"step" between the Gulf Coast and Mississippi Valley is rather imposing. This is especially true when the three differences are considered along with the several minor distinctions of the Mississippi Valley populations.

Confusion is introduced by variation in fin pigmentation (Tables 12 and 13), a character of primary systematic importance in this species complex. Subspecies defined on the basis of fin pigmentation would not correspond to those based primarily on measurements. most similar western drainages are not the Bayou Pierre and Big Black, but the Bayou Pierre and Pearl. The Big Black averages somewhat lower than the latter two, but could arbitrarily be included with them without undue stress. This would raise the question of how to treat the Lake Pontchartrain population. Its geographic position makes it illogical to consider it comprised of intergrades between an eastern and western subspecies. To make the eastern subspecies polytopic by including the Pontchartrain population would be equally untenable. If the limits of the western group were again expanded, Lake Pontchartrain might also be included. This would move the dividing line between the eastern and western groups back to St. Louis Bay, two drainages east of where measurements would place it.

Combination of the two character complexes conceivably might produce a western subspecies in the Mississippi Valley and an eastern subspecies in St. Louis Bay through Mobile Bay. The hypothetical intergrades, from the Pearl and Lake Pontchartrain systems, would then be like the western subspecies in fin pigment but would be the terminal elements of an east-west cline in the three differentiating measurements.

Recognition of subspecies hardly seems justified from a pragmatic viewpoint if it does not result in some significant categorization and ordering of variation within the species. This is difficult to accomplish objectively when several important characters vary discordantly. The complications discussed above emphasize that subspecific partitioning of *N. roseipinnis* not only would be an arbitrary process, but also would obscure rather than clarify the interesting east-west clines involved.

DISTRIBUTION AND HABITAT.—Distributional records of *N. roseipinnis* are plotted in Fig. 7. This is a common species in Gulf Coast drainages from Mobile Bay west through Lake Pontchartrain. All previous records of *N. roseipinnis* from drainages east of Mobile Bay were based on *N. atrapiculus*. Howell's (1957) single record of *N. bellus* from the Perdido River system (UAIC 122, 2 juveniles; Ala., Escambia Co., stream 1 mi. from Baldwin Co. line on Rt. 31; 6 June 1951) probably was based on *N. roseipinnis* or *N. atrapiculus*. The specimens apparently are lost. This record probably formed the evidence for the inclusion of *N. roseipinnis* in the Perdido fauna by Smith-Vaniz (1968:131). Otherwise no

species of *Lythrurus* has been found in the drainage, despite substantial collecting. No specimens have been examined from the Wolf or Tchoutacabouffa River systems, two minor basins in Hancock, Harrison, and Pearl River counties, Mississippi; but Cook (1959:122) records the species from both drainages.

In the Mississippi Valley, *N. roseipinnis* inhabits the Bayou Pierre, Big Black, and Yazoo drainages in Mississippi. Only three widely separated records are known from the latter system. I have recently been informed (R. C. Cashner, pers. comm.) that *N. roseipinnis* also is found in Coles Creek (Jefferson Co., Miss.), but I have not examined specimens.

Speculation on how this species gained entrance into Mississippi River tributaries must center around either stream capture or lowland transfer. Stream capture, if it has taken place, probably has been between the Pearl and the Bayou Pierre and/or Big Black drainages. This is suggested by the close approximation of these systems and the low relief of the divides between them. The fact that the Mississippi Valley range of the species is limited to three adjacent drainage systems also favors transfer by relatively localized stream capture somewhere in western Mississippi.

The Mississippi River has followed varying courses in its lower reaches as it deposited its extensive delta. The entire New Orleans-Lake Pontchartrain-Lake Borgne area is of recent origin, resulting from the settling and compacting of alluvium deposited when the River did not follow its present course. The Metairie-Mississippi River departed from its existing channel at about the town of Kenner (Jefferson Parish) and flowed east through what is now New Orleans toward Lake Borgne (Russell, 1936, 1940).

At this stage the mouth of the Mississippi River was very near the present mouth of the Pearl River. It seems probable that two such closely approximated rivers would have been interconnected from time to time by an ever-changing system of anastomosing tributaries, distributaries, and cut-off channels so characteristic of active deltas. Even if they were not directly connected, the water from the Metairie-Mississippi would have created a low-salinity bridge in the present-day Lake Pontchartrain-Lake Borgne area. These circumstances should have afforded ample opportunity for *N. roseipinnis* to move from the Pearl drainage into the Mississippi drainage via a lowland route.

The major difficulty with this hypothesis is the present-day distribution of *N. roseipinnis* in the Mississippi basin. If this species moved up the Mississippi, why is it now limited to three adjacent tributaries on one side of the river? Why is it absent from the Homochitto system in south-

western Mississippi and from streams west of the river? Perhaps the species was once more widespread in the Mississippi Valley but has been extirpated from all but the most favorable habitats. The three widely disjunct records from the Yazoo basin suggest that populations remaining in that drainage are relicts of a once more-extensive distribution.

The contiguous distributions of *N. roseipinnis* and *N. b. bellus* in the lower Mobile basin are shown in Fig. 8, and the possibility of a competitive interaction is considered in the Habitat and Distribution section under the latter form.

N. roseipinnis is restricted to Coastal Plain streams, usually of small (5 ft. wide) to moderate (35 ft. wide) size. Dr. R. D. Suttkus, who has done much year-round collecting in the main Pearl River, informs me that N. roseipinnis is found in the river primarily during winter, and then only in small numbers (pers. comm.). The inhabited streams usually are characterized as follows: water ranging from white to brown stained, from clear to (probably temporarily) turbid; vegetation absent to present and abundant; bottoms basically sand or small gravel, occasionally some hardpan clay or bedrock, with varying overlays of silt and detritus; riffle- and/or run-pool type habitat with moderate gradient. My limited observations indicate that N. roseipinnis, like all other members of the roseipinnis complex, prefers slow, deep pools and the slower parts of runs, distinctly avoiding fast, shallow water.

MATERIAL EXAMINED

MOBILE BAY DRAINAGE.

ALABAMA.—Baldwin Co.: UAIC 2335 (Pine Log Cr., Ala. Rt. 59, ca. 2 mi. S. Tensaw, T2N, R3E, Sec. 7), 2336 (Holley Cr., Ala. Hwy. 59, ca. 5 mi. N. Tensaw, T3N, R3E, Sec. 34), 2337 (Turkey Cr., Ala. Hwy. 59, T3N, R3E, Sec. 24). Baldwin-Monroe Co. line: TU 32555, 44396, 44424, UAIC 2338 (all same locality: Little R., at Chrysler, Ala. Hwy. 59, T4N, R4E, Sec. 25). Clarke Co.: TU 32544, 38768, 40415, UAIC 2314 (all same locality: trib. Hals Lake, 1.6 mi. E. Carlton, Hwy. 19, T4N, R2E, Sec. 1), TU 34025, 41451 (both same locality: Sand Hill Cr., trib. Alabama R., 1.1 mi. W Choctaw Bluff), TU 38758 (Sand Hill Cr., 3 mi. NW Choctaw Bluff), 32514, UAIC 2316 (both same locality: Big Reedy Cr., trib. Alabama R., 7 mi. NE Carlton, T5N, R3E, Sec. 22), UAIC 2317 (Little Reedy Cr., T5N, R3E, Sec. 15), 2318 (Sizemore Cr., T5N, R4E, Sec. 7), 2319 (2.7 mi. E Gainstown, T6N, R4E, Sec. 34). Mobile Co.: CU 12633 (trib. Chickasaw Cr., 5.2 mi. E Semmes, Rt. 42), 16656 (Clear Cr., 4.7 mi. E Semmes), TU 1642 (Cedar Cr., trib. Tombigbee R., 8.7 mi. W Mt. Vernon), 2600 (Sand Hill Cr., trib. Chickasaw Cr., 6.7 mi. S Citronelle, Hwy. 45), 16361 (trib. Mobile Bay, 3.5 mi. SE Semmes, Hwy. 98), 32398 (Sandy Hill Cr., trib. Chickasaw Cr., 7.9 mi. S Citronelle, Hwy. 45), UAIC 134 B (Cold Cr., 7.25 mi. S Mt. Vernon, U. S. Hwy. 43), 156 (1 mi. N Theodore, U. S. Hwy. 90), 440 (Beaver Pond Cr., N of Chunchula, Hwy. 45). Monroe Co.: TU 32580 (Limestone Cr., trib. Alabama R., 3.3 mi. NW Monroeville, Hwy. 41), 43249 (trib. Alabama R., 5.7 mi. E Eureka Landing), UAIC 522 (Limestone Cr. backwater, 4 mi. NE Monroeville, Ala. Rt. 47), 2354 (Baileys Cr., Homewood, T5N, R5E, Sec. 29), 2355 (Shomo Cr., Mt._Pleasant, T4N, R4E), 2370 (unnamed trib. Limestone Cr., Co. Rt. 20, 2 mi. E Monroeville). Washington Co.: CU 16168 (Gaines Cr., trib. Bassett Cr., 2.8 mi. S Leroy).

PASCAGOULA DRAINAGE.

Alabama.—Mobile Co.: CU 12464, TU 57, 1129, 21166, UAIC 504, 2462, 2463, 2481, 2483, 2488, 2490, 2492, 2495. Mississippi, Clarke Co.: CU 13960, 15605, 15702, TU 3909, 37485, 48733, UAIC 1583. Covington Co.: CU 12582, 16260, NLU 8498, 8538, TU 26578, 28609. Forrest Co.: CU 15661, NLU 5603, 5812, 6027, 7033, 7709, TU 1567, 45468, USNM 128859, 128892, 128906, 128908. George Co.: CU 12474, 12524, TU 1122, 16353. Greene Co.: TU 28457. Jackson Co.: TU 28074, UAIC 875, 892. Jones Co.: TU 28638, 30054, 39393, 48714. Lamar Co.: CU 15622, NLU 5601, 5922, TU 1615, 45459, 51439, UAIC 2681. Lauderdale Co.: TU 7481. Smith Co.: TU 48682. Stone Co.: NLU 9076, 9155, TU 16344, 28106, 45472, UAIC 894. Wayne Co.: CU 16180, 16188, 16240, 16256, TU 8033, 8050, 8055.

BILOXI BAY DRAINAGE

Mississippi.—Harrison Co.: TU 9720, UAIC 876, 877, 1708, 1720, 1736. Pearl River Co.: TU 45234. Stone Co.: CU 16634, UAIC 1737.

St. Louis Bay Drainage

Mississippi.—Hancock Co.: UAIC 1734. Harrison Co.: UAIC 1722, 1728, 1735. Pearl River Co.: UAIC 1738, 1739, 1740.

PEARL DRAINAGE.

Mississippi.—Copiah Co.: TU 23858, 26732, 28859, 33927, 36555. Hancock Co.: CU 31724. Hinds Co.: UMMZ 161129. Jefferson Davis Co.: CU 12495, TU 17627. Kemper Co.: TU 29011. Lawrence Co.: TU 14097, 26898, 28710. Leake Co.: TU 17668, 26567, 26594, USNM 128858, 128907. Lincoln Co.: CU 16274, TU 26629, 27277, 46464. Marion Co.: CU 14309, 16617, 37419, TU 25, 61, 88, 176, 4867, 4917, 15661, 17704, 17945, 23498, 26546, 28738, 36091. Neshoba Co.: TU 28991. Pearl River Co.: CU 31907, TU 1630, 1649, 5122, 5807, 23442, 23479, 23552, 45953. Pike Co.: TU 27478, 46843. Rankin Co.: TU 28966. Simpson Co.: TU 17736, 23447, 23581, 26776, 26796, 26816, 28946, 39830. Walthall Co.: TU 13994, 26826. Winston Co.: TU 28692. Louisiana, St. Tammany Par.: CU 53273, TU 742, 1675, 8353, 12643, 15453, 18626, 23390, 25833, 34742, 36049, 46078, 69503. Washington Par.: CU 16326, NLU 1501, 4335, 4351, 4366, 6436, 6581, TU 982, 1556, 3418, 3601, 4810, 7199, 7237, 23360, 27181, 42981.

LAKE PONTCHARTRAIN DRAINAGE

MISSISSIPPI.—Amite Co.: UAIC 1275, 1576, 1925, UMMZ 154361. Wilkinson Co.: UAIC 1577, UMMZ 146605. Louisiana, East Feliciana Par.: CU 16311, FSU 9334, NLU 1235, 1327, 1328, 1330, 1331, 1332, 1386, 2411, 2431, TU 4664, 4711, 6150, 7875, 32333. St. Helena Par.: NLU 1621, 2106, 2107, 3976, 4380, TU 5220. St. Tammany Par.: NLU 3793, 6385, 7095, 8148, TU 4445, 5898, 7991. Tangipahoa Par.: CU 16322, NLU 1232, 1314, 1320, 1369, 1518, 1696, 2470, 2479, 2502, 3232, 4316, 6485, TU 3745, 9879, 45545, 48456. Washington Par.: NLU 6449, 7480.

BAYOU PIERRE DRAINAGE

MISSISSIPPI.—Claiborne Co.: NLU 8309, 9190, TU 32941. Copiah Co.: FSU 10730, 15421, NLU 5222, 5416, 9167, TU 31716, 37466, 40377, 46477, 46506, 46741. Hinds Co.: FSU 15432, NLU 3623, 3763, 3886, 4020, 4063, 5253, 5329, 8062, TU 31792. Lincoln Co.: UAIC 1268.

BIG BLACK DRAINAGE

MISSISSIPPI.—Attala Co.: FSU 10786. Carroll Co.: UMMZ 161098. Choctaw Co.: FSU 10396, 10546, UAIC 1344. Hinds Co.: FSU 9246. Holmes Co.: FSU 9415, 10709, TU 3691, 33032. Madison Co.: UAIC 1084, 1701, 1702, USNM 128905. Montgomery Co.: FSU 9417, 10538, USNM 165975. Warren Co.: CU 37186, UAIC 244, 245, 246, 252, 253, 399. Webster Co.: FSU 9180, 10525, UAIC 1643, USNM 165969.

YAZOO DRAINAGE

Mississippi.—Pontotoc Co.: UMMZ 113450 (Cane Cr., 3 mi. NE Thaxton). Warren Co.: UAIC 250 (Glass Bayou, 0.7 mi. E Yazoo Diversion Canal, 0.6 mi. SSE Ft. Nogalee in city of Vicksburg). Webster Co.: FSU 15408 (Saboughla Cr., 0.5 mi. W Bellefountaine, St. Hwy. 404).

Notropis atrapiculus, new species

BLACKTIP SHINER

Figure 3C

Notropis roseipinnis. Gilbert, 1891:158 (Escambia dr. records). Jordan and Evermann, 1896a:260 (range, in part). Jordan and Evermann, 1896b:258, 298 (range, in part). Pratt, 1923:84 (range, in part). Fowler, 1945:30 (listed, Escambia dr.). Bailey, Winn, and Smith, 1954:125, 156 (partial synonymy; Escambia dr. records; habitat; range, based in part on N. roseipinnis). Carr and Goin, 1955:20, 54 (in key; description; range based in part on N. roseipinnis). Eddy, 1957:126 (range, in part). Howell, 1957:249-50, map 32 (Escambia, Choctawhatchee, and Chattahoochee dr. records). Briggs, 1958: 261 (listed from Fla.; range based in part on N. roseipinnis). Williams, 1965: 23, 82-3, 85 (records and distribution in Tallapoosa R. system; transfer over Conecuh Falls). Moore, 1968:80 (range, in part). Smith-Vaniz, 1968:49, 125-6, 131 (references to populations in drainages east of Mobile Bay).

Lythrurus roseipinnis. Jordan, Evermann, and Clark, 1930:126 (range, in part).

Pratt, 1935:80 (range, in part).

Notropis bellus. Howell, 1957:242-3, map 31 (Yellow, Choctawhatchee, and Chattahoochee dr. records). Ramsey, 1965:24, 27, 93 (listed, Apalachicola dr.). Smith-Vaniz, 1968:44, 125 (undescribed form from Apalachicola dr.).

TYPES.—Holotype: CU 53343, a tuberculate adult male 47.7 mm SL; Choctaw-hatchee dr., Ala., Barbour Co., Sikes Creek, trib. West Fork Choctawhatchee R., on unnumbered Co. Hwy., 3.5 airmi. ENE center of Clio; T9N, R25E, Sec. 33; 21 May 1969; Franklin F. Snelson, Jr. and Bruce W. Menzel (FFS-69-18).

PARATYPES.—CU 53351, 20 specimens collected with the holotype. A series I collected at the type locality 24 May 1968, cataloged as CU 53142 (26) and USNM 204314 (8). TU 2509 (36), Choctawhatchee dr., Ala., Houston Co., Panther Cr., on Hwy. 84, 3 mi. W jct. Pinehard Farm Rd., 11.5 airmi. W center Dothan, T3N, R25E, Sec. 7; 29 May 1951; R. D. Suttkus and Hancock.

Important counts of the holotype are as follows: anal rays 11; pectoral rays 13; lateral line scales 41; body circumference scales 19-2-11=32; predorsal scale rows 23; caudal peduncle scales 7-2-5=14; IO canal incomplete at dermosphenotic bone, with pores 11+2; POM canal pores 11; index of anterior dorsolateral scale reduction 3; index of fin pigmentation 9+4=13. Measurements of the holotype, expressed as thousandths of SL, are as follows: predorsal length 538, postdorsal length 490, prepelvic length 483, preanal length 642, head length 239, head depth 168, postorbital head length 94, snout length 70, upper jaw length 86, gape width 60, fleshy orbit

length 78, fleshy interorbital width 91, body depth 232, body width 131, caudal peduncle length 217, caudal peduncle depth 101, dorsal fin length 218, anal fin length 222, pectoral fin length 167, and pelvic fin length 145.

DIAGNOSIS.—See Tables 16 and 17 and the Comparisons section of the species account.

Description.—Certain counts are presented in Tables 4-10. Measurements are presented in Table 14. General physiognomy and pigmentation are shown in Fig. 3C. Details of fin pigmentation are illustrated in Figs. 4E-H.

Body circumference scales 17-21 (23), modally 19, above lateral line and (10) 11-13 (18), modally 12 or 13, below. Caudal peduncle scales 5-9 above lateral line and 4-7 below, with typical counts of 7 and 5 respectively. Pharyngeal tooth counts from throughout range as follows in 39 specimens: 1,4-4,1 (in 2 specimens); 1,4-4,2 (1); 2,4-4,1 (2); 1,5-4,2 (1); and 2,4-4,2 (33).

Scales moderately imbricate over most of body. Scales smaller predorsally and imbrication slightly to strongly reduced. In latter case, anterior dorsolateral part of body bears only few small, partially embedded scales, isolated from one another by large naked spaces. In extreme instances this area, especially near head, scaleless. Mean index of anterior dorsolateral scale reduction varies between 1.77 and 2.46 (Table 11).

Lower jaw usually included within (78 specimens) or terminating equal with (137 specimens) upper jaw. Chin occasionally protrudes slightly beyond upper jaw (32 specimens) but only rarely projects strongly (4 specimens). Fleshy orbit length averages slightly longer than snout. Body moderately deep and compressed.

Lateral line on body complete and decurved, reaching lowest point over or slightly before pelvic fin base. Supratemporal canal broadly interrupted at dorsal midline but seldom with secondary interruptions. In order of their frequency, pore count formulas for ST canal 2,2 (96 specimens); 2,1 (28); 1,1 (18); 1,2 (17); 3,2 (5); 2,2+1 (5); 2,3 (3); 1+2,1 (2); 1+2,2 (2), 3,3 (1); 1,3 (1); 1,0 (1); and 1,2+1 (1). Supraorbital canal incomplete (not joining postocular commissure) but uninterrupted along its course; pore counts for 173 specimens 6 (2 specimens), 7 (14), 8 (124), 9 (30), and 10 (3); $\bar{x} = 8.1$. Preoperculomandibular canal rarely (6) of 284 specimens) interrupted along its length; pore counts presented in Table 10. Dermosphenotic bone usually either poorly ossified or absent. Infraorbital canal ranging from incomplete to complete at juncture with postocular commissure over position of this bone. Pore counts for 63 adults with complete IO canals 11 (4 specimens), 12 (15), 13 (21), 14 (20), and 15 (3); $\bar{x} = 13.0$. Most frequent pore count formulas for 154 adults with IO canal partially or fully incomplete were 11+2 (40 specimens), 10+2 (21), 11+3 (18), 12+2 (17), 10+3 (13), 12+3 (4), 13+3(4), and 13+2 (3). Number of IO pores in advance of dermosphenotic disjuncture (when present) 9 (6 specimens), 10 (37), 11 (60), 12 (24), 13 (8), and 14 (2); $\bar{x} = 10.8$.

Lips usually only slightly darker than adjacent snout and chin. Chin pigmentation highly variable, ranging from like that of $N.\ b.\ bellus$ (Fig. 2A) to like that of $N.\ roseipinnis$ (Fig. 2B). Usually no darkened preorbital blotch and no suggestion of dark band passing around snout. Superficial pigmentation of snout, head dorsum, and temporal-upper opercular areas uniformly dark and scattered. Scapular pigment usually absent in females; usually weak or absent in males but occasionally minor concentration of melanophores along posterior margin of cleithrum forms poorly defined bar.

Dark middorsal stripe moderately developed anterior to dorsal fin, more weakly developed posteriorly, not surrounding dorsal fin base. On anterior dorsolateral area of body, pigment under anterior half of each scale slightly weaker than that under posterior half; and weak concentration of melanin margins each scale. Crosshatched pattern, if produced, vague and variable, better developed in females than in males. In specimens with high index of scale reduction, anterior dorsolateral body scales,

being somewhat lighter than dusky intervening naked speces, appear as light spots. Neither darkened scales nor chevron-shaped markings along myosepta developed in

either sex. Bar markings absent and breeding males not melanistic.

Poorly defined dusky stripe present midlaterally on caudal peduncle. Stripe about one scale row wide posteriorly, weak to moderate in intensity, with ill-defined borders. Over and anterior to anal fin stripe broadens and fades abruptly. Occasionally midlateral trunk slightly more dusky than upper sides, but this rarely gives impression that lateral stripe extends forward to head. Usually no band across upper half of opercle. No discrete caudal spot present, though lateral stripe may broaden slightly over hypural plate. At midbody pigment usually extends one-half to two scale rows below lateral line, primarily along scale margins. Discrete punctulations above and below each lateral line pore usually absent. Melanophores weakly to moderately developed along anal fin base and in double row along ventral margin of caudal peduncle. Anterior basidorsal spot absent.

FIN PIGMENTATION.—Breeding adults form the basis of the following description. In non-breeding adults, and especially juveniles, the intensity and amount of fin pigment is reduced, but the basic patterns of deposition usually are discernible

throughout most of the year.

Pigmentation of dorsal fin intermediate in most respects between that of N.b. bellus and N. roseipinnis. In breeding males, narrow, clear border along margin of fin. Broad, black, subtriangular band located immediately proximal. Melanin darkest and most extensive near apex of fin, in first two to three interradial membranes. Pigment weaker posteriorly, primarily developed in and about ray branches (Figs. 3C, 4E). Consequently, band narrows and fades posteriorly. Proximal to this band, interradial membranes lightly sprinkled with melanophores. In females, pattern of dorsal fin like that of males, but uniformly lighter.

Dark subtriangular blotch located subterminally at apex of anal fin of breeding males (Figs. 3C, 4F). It is broadest and darkest at tip of fin, formed by pigment on interradial membranes in and about ray branches. Blotch fades and narrows as interradial pigment is progressively reduced posteriorly. Posterior extent of pigment dependent on size; in small males, restricted primarily to apex of fin, extending posteriorly only to the second or third interradial membrane. Pattern in these cases superficially similar to that of *N. roseipinnis*. In large males interradial melanophores extend more posteriad, occasionally to last membrane. Consequently apical blotch drawn out into subtriangular band lying subterminally along fin margin; such specimens superficially resemble *N. b. bellus*. Both Figs. 3C and 4F represent condition in moderately large males. Apical blotch or tapering band contrasts sharply with basal portion of fin, which may have few melanophores scattered along ray borders but usually lacks interradial pigment.

Anal fin pigment more weakly developed in females, occasionally invisible to unaided eye. Pattern like that of males, and extent of pigment varies with size. In small breeding females, melanophores present only at apex of fin in membranes 1 or 2, and occasionally interradial pigment entirely absent. Pigment spreads posteriorly

with increasing size, occasionally to eighth interradial membrane.

All principal caudal rays bordered by melanophores in both sexes. In breeding males, some or all caudal interradial membranes may be dusted with pigment, especially near tips of lobes and at fork of fin. Rarely entire posterior margin of fin fringed by dusky band. Females may be like males but usually have interradial pigment reduced or absent.

In breeding males first ray of pectoral fin bordered along both edges by melanophores, and occasionally few scattered melanophores on first interradial membrane. Rays 2 through about 5 more weakly bordered, primarily along basal portions. Dark spot developed at apex of fin, formed by pigment concentrated primarily in membrane between primary branches of second (first branched) ray (Fig. 4G). In females apical spot may be absent or present but very weak (visible only with magnification).

Apex of pelvic fin of breeding males usually marked by dark subtriangular blotch that originates in first interradial membrane and tapers and fades posteriorly (Figs. 3C, 4H). Pigment deposited on membranes in and about ray branches. Posterior extent of pigment dependent on size. Small males may have no interradial pigment, or only first one or two membranes may bear melanophores; in large males interradial pigment may extend back to sixth membrane. Thus, small males superficially similar to N. roseipinnis, large males approaching N. b. bellus. Both Figs. 3C and 4H illustrate condition in moderately large male. Basal portion of fin usually without interradial pigment, but few melanophores may border some or all rays.

Females often lack pelvic interradial pigment. When developed, pigment weak, rarely extending farther back than second membrane. Pattern of deposition like that

of males.

The extent of anal and pelvic fin pigment in N. atrapiculus tends to increase with size. Consequently the total index of fin pigmentation shows strong ontogenetic increase. Both sexes start out at similar values, but large females lag considerably behind males (Figs. 5, 6). Index values for N. atrapiculus lie interjacent between those of N. b. bellus and eastern populations of N. roseipinnis (Tables 12 and 13).

BREEDING COLORATION

MALES.—Bright red distributed throughout dorsal fin membranes proximal to black subterminal band. Fin margined by narrow, colorless band. Limited information suggests that presence of color in the anal and pelvic fins is more variable, perhaps in a geographic sense. Color slides of two breeding males from the Chattahoochee drainage (CU 15810) show the first four to five anal interradial membranes bright red basally. Both these males also exhibit a faint wash of red at the apex of the pelvic fins, in the first two to three interradial membranes. Observations and/or color slides of breeding males from all other drainages occupied by the species have not shown red in the pelvic fin and only occasionally have revealed a few erythrophores among the melanophores at the apex of the anal fin. (If consistent, this would counter the situation in N. roseipinnis, where observations suggest that the presence of erythrophores is correlated with the presence of melanophores in the anal and pelvic fins.) Caudal fin lightly washed with orange-red, primarily on interradial membranes. Two semicircular colorless spots over bases of upper and lower caudal fin rays contrast sharply with dusky body and colored caudal fin. Pectoral fin normally colorless but occasionally with faint streak of red in first interradial membrane.

Iris of breeding males washed with orange-red; rarely a light orange spot on body at base of pectoral fin. In life venter is white, dorsum olive green. Side of body dominated by broad silvery band that often reflects steel-blue iridescence. In sexually advanced males pale pinkish-orange band parallels upper margin of silvery lateral band. This deep-lying color best developed on (occasionally restricted to) anterior part of body and most obvious in life or after some of the silvery overlay has faded in preservation.

FEMALES.—Dorsal and caudal fins of breeding females colored similarly to those of males but not so bright. Apparently females normally lack red on other areas of fins and body.

BREEDING TUBERCULATION

MALES.—Pectoral fin tuberculation of N. atrapiculus is like that of N. b. bellus with two exceptions. N. atrapiculus agrees better with N. roseipinnis in that (1) the first ray may or may not bear a few, scattered tubercles; and (2) the tubercles on rays 2 through about 8 average slightly smaller and more close-set, occasionally forming a coarse shagreen.

The previous description of head tuberculation of N. b. bellus applies equally well to N. atrapiculus with the following exceptions: (1) Head dorsum tubercles

occasionally are slightly antrorse. Like N. roseipinnis, (2) tubercles rarely develop on the postorbital and lower opercular areas, and (3) tubercles average fewer and more scattered and are less consistently present on the interopercle and branchiostegal rays.

Body tuberculation of *N. atrapiculus* is similar to that described for *N. b. bellus* with two principal exceptions, in which it is more like *N. roseipinnis*. (1) There are about 3-6 usually erect tubercles along the posterior margins of the scales on the side of the body. (2) The degree of tuberculation on the anterior dorsolateral area of the body is contingent upon the reduction of squamation in that area, as explained above for *N. roseipinnis*.

FEMALES.—The tubercle description given previously for females of N. b. bellus applies equally well to N. atrapiculus females.

COMPARISONS.—The summaries of diagnostic features in Tables 16 and 17 emphasize the subtle differentiation and perplexing intermediacy of N. atrapiculus as compared with N. b. bellus and N. roseipinnis. (This discussion considers only eastern populations of N. roseipinnis, as these are in closest geographic proximity to N. atrapiculus and N. b. bellus.) N. atrapiculus is interjacent between, and overlaps significantly with, N. b. bellus and N. roseipinnis in eight quantitative characters (anal rays, scale reduction index, fin pigment index, predorsal length, body depth, caudal peduncle length, caudal peduncle depth, dorsal fin length) important in the differentiation of the last two forms. Although it may be closer to one form or the other in some of these characters, the calculation of a character (=hybrid) index gives an overall value of 45, surprisingly close to exact intermediacy (50) (Snelson, 1970: Table 40). Other diagnostic characters noted in Tables 16 and 17 do nothing to nullify the over-all intermediacy of N. atrapiculus. It is like N. b. bellus in number of preoperculomandibular canal pores but like N. roseipinnis in number of predorsal scale rows, gill rakers, and fleshy orbit length. It averages higher than both other species in head length, snout length, and body circumference scales. In the latter character N. atrapiculus, though extreme, is closer to N. roseipinnis than to N. b. bellus. Although it averages extreme in these three characters, N. atrapiculus is not strongly differentiated because of broad overlap with its two relatives.

N. atrapiculus is approximately intermediate between N. b. bellus and N. roseipinnis in features of fin pigmentation, but in this case the degree of differentiation between the three forms is high. Strong separation in the total index of fin pigmentation is partly obscured by the presentation of the data in Tables 12 and 13. Males of N. b. bellus and eastern N. roseipinnis show relatively little ontogenetic change in the index value, whereas N. atrapiculus exhibits a strong ontogenetic increase (Fig. 5). The same is true for females, except that the index of N. b. bellus increases asymptotically with size (Fig. 6). Consequently, small specimens of N. atrapiculus have index values overlapping those of N.

roseipinnis; whereas large specimens, primarily males, have values approaching and overlapping those of N. b. bellus. Nevertheless, the degree of overlap is low at most sizes; and most specimens of these three forms can be identified on this count alone. The greatest overlap (the poorest separation) is between small females of N. atrapiculus and N. roseipinnis.

Though they overlap somewhat in the quantitative index, breeding specimens of this trio are completely separable on qualitative aspects of pattern and development of fin pigment. The differences are illustrated in Figs. 3 and 4, and details are noted in the appropriate descriptive sections. To summarize briefly, the dorsal, anal, pectoral, and pelvic fins in breeding males of N. b. bellus are margined by dark bands of uniform width and intensity. Eastern N. roseipinnis are characterized by dark lanceolate spots at the apexes of the dorsal and anal fins. pelvic fin may be without pigment or may have a faint black streak near the tip. The pectoral fin is without any special pigmentary feature. N. atrapiculus, the dark band bordering the dorsal fin is wide and intense anteriorly, but it tapers and fades posteriorly. The anal and pelvic fins usually are marked by a dark apical blotch that tapers and fades posteriorly. In large specimens the apex of this subtriangular blotch may extend far posteriorly along the border of the fin, tending to form an uneven band. Such bands are readily distinguished from those of N. b. bellus by their lack of uniform width and intensity. The pectoral fin in breeding males of N. atrapiculus is marked by a small dark spot at its apex.

Differences between N. b. bellus and N. roseipinnis in the development of fin pigment are pointed out in the Comparisons section of the latter species. N. atrapiculus contrasts with N. b. bellus in that anal and pelvic fin pigment first develops only at the apex of the fin. Unlike N. roseipinnis, pigment does not form as a dark streak along the posterior margin of a ray; instead the pattern originates from a few melanophores scattered over the first few interradial membranes. The first place melanophores concentrate is in the crotch of the first branched ray.

SEXUAL DIMORPHISM.—Sexual differences in tuberculation, breeding coloration, and fin pigmentation have been pointed out above. No sexual dimorphism in meristic characters was noted.

Sexual dimorphism in morphometric characters is summarized in Table 2. A sample of 39 breeding males and 30 breeding females from the Choctawhatchee and Escambia River drainages was used for statistical comparison with Student's *t*-test. All specimens measured were 40-50 mm SL. Mean SL for males was 43.49 mm; mean SL for females was 43.78. Levels of probability greater than 0.1 were considered not sig-

nificant (ns). Following each character is given (first) the range and mean for males, (second) the range and mean for females, and (third) the probability that the two means are significantly different. Predorsal length: 534-562, 547.6; 533-569, 550.2; ns. Postdorsal length: 464-495, 481.5; 460-494, 477.9; <0.1. Prepelvic length: 473-497, 486.3; 475-511, 496.2; <0.001. Preanal length: 619-659, 640.9; 629-669, 650.1; <0.001. Head length: 234-259, 244.1; 232-257, 245.1; ns. Head depth: 161-176, 169.6; 161-184, 173.5; <0.001. Postorbital head length: 93-106, 99.8; 92-106, 99.8; ns. Snout length: 68-80, 74.4; 65-80, 74.4; ns. Upper jaw length: 81-95, 87.0; 84-95, 88.8; <0.025. Gape width: 54-66, 59.6; 53-67, 59.9; ns. Fleshy orbit length: 72-84, 77.7; 74-85, 79.3; <0.025. Fleshy interorbital width: 86-96, 92.1; 85-102, 92.5; ns. Body depth: 224-263, 238.5; 228-265, 246.6; < 0.001. Body width: 118-145, 131.0; 126-156, 138.2; <0.001. Caudal peduncle length: 205-228, 216.4; 193-238, 213.4; ns. Caudal peduncle depth: 97-110, 102.5; 92-103, 98.8; <0.001. Dorsal fin length: 205-243, 224.3; 194-233, 218.7; < 0.025. Anal fin length: 213-243, 226.3; 203-233, 216.7; <0.001. Pectoral fin length: 160-192, 174.9; 166-188, 177.2; ns. Pelvic fin length: 142-160, 149.2; 129-150, 143.2; < 0.001. Body depth and width and to some extent head depth were influenced by the distended abdomens of the gravid females.

The urogenital papilla of breeding females is enlarged and protrudes posteriorly to about the anal fin origin. In males the papilla is not enlarged. This difference is manifest to some degree throughout most of the year and facilitates external sexing.

Of 37 collections containing mature specimens of both sexes, a male was the largest specimen in 22, a female the largest in 15. This deviates from a hypothesized ratio of 50:50 by a Chi-square value of 1.32, which is significant at an unacceptably low level of 0.25. Thus *N. atrapiculus* may contrast with its two close relatives by lacking sexual dimorphism in maximum adult size. The largest male examined was 52.5 mm SL; the largest female was 51.0 mm SL.

Geographic Variation.—The samples of *N. atrapiculus* from the Yellow River drainage average higher than populations from neighboring drainages in body circumference scales (Table 6), predorsal scale rows (Table 7), anal rays (Table 9), and index of anterior dorsolateral scale reduction (Table 11). Otherwise the only trenchant patterns of geographic variation are in POM canal pores, which show a clinal decrease from east to west (Table 10), and in the index of anterior dorsolateral scale reduction, which is high in the Yellow River drainage and decreases both east and west (Table 11). The data available reveal no noteworthy interdrainage variation in fin pigmentation or in morphometric characters.

DISTRIBUTION AND HABITAT.—N. atrapiculus is found along the eastern Gulf slope in the Escambia, Yellow, Choctawhatchee, and Apalachicola drainages of Alabama, Florida, and Georgia (Fig. 7). Within the Apalachicola drainage the species is widespread in the Chattahoochee system, but it is known from only a few geographically restricted localities in the upper Flint system. There are no records from the Chipola River system. Smith-Vaniz (1968:131) included N. atrapiculus (his N. roseipinnis, in part) in the fauna of the Blackwater River drainage. I have examined no specimens from that drainage, and a recent survey, now totaling more than 50 collections, has failed to disclose its presence there (J. D. Williams, pers. comm.). The two juveniles from the Perdido River system, reported as N. bellus by Howell (1957), probably were this species or N. roseipinnis. The specimens apparently are lost, and reasonable collecting effort in the Perdido has not otherwise yielded a species of Lythrurus.

The spurious Conecuh-Tallapoosa connection originated through the diversion of the upper Conecuh River, originally of the Escambia drainage, into the Tallapoosa River system of the Alabama drainage. The man-made diversion canal at the eastern edge of Union Springs (Bullock Co., Ala.) shunts water from the Conecuh River across a 35 ft. high waterfall (locally known as Conecuh Falls) into Old Town Creek of the Tallapoosa system (Monroe, 1941; Williams, 1965). The falls have been an effective barrier to upstream dispersal; but *N. atrapiculus*, native to the upper Conecuh River, has descended the falls and established a population in the plunge pool at its base (Williams, 1965; Smith-Vaniz, 1968: 125). Downstream movement beyond this point is blocked by severe pollution. Fishes reappear in Old Town Creek approximately 9 stream miles below the plunge pool. From this point downstream the creek is inhabited by *N. b. bellus*, which is native to the Tallapoosa system (Williams, 1965, and pers. comm.).

N. atrapiculus is obligatorily limited to the Coastal Plain province in the Escambia, Yellow, and Choctawhatchee drainages, but it exists both above and below the Fall Line in the Apalachicola drainage. It normally is found in small (5 ft. wide) to moderate-sized (35 ft. wide) streams usually composed of pools alternating with shorter stretches of riffles or runs. Stream gradients are moderate. Bottom materials are principally sand, occasionally with some silt, clay, or gravel also present. Water ranges from colorless to brown stained. The species probably is not tolerant of continuous turbidity, but it is often collected in streams temporarily roiled by recent rains. Vegetation may be present or absent.

N. atrapiculus, like its close relatives, is primarily an inhabitant of

deep pools with little or no current. It is not unusual to fail to locate the species in extensive stretches of stream and then to find many individuals concentrated in one long, deep pool.

Taxonomic Status.—As pointed out above, the ranges of N. b. bellus and N. roseipinnis interdigitate in the lower Mobile Bay basin (Fig. 8). The two forms never have been collected together; and it is hypothesized that allopatry is maintained by strong habitat selection, interspecific competition, or some combination of these. Where their ranges abut, they are strongly differentiated in several characters, and apparently no significant gene exchange takes place between them. Thus available evidence strongly indicates that N. b. bellus and N. roseipinnis are valid biological species. This fact is basic to the consideration of the status of N. atrapiculus. Tempting though it might be, the taxonomic positions of these three closely related forms cannot be resolved by reducing them all to subspecies.

Should the pollution block in Old Town Creek (see above under Distribution and Habitat) ever be removed, *N. atrapiculus* and *N. b. bellus* would probably come into contact. The degree of reproductive isolation they would exhibit in sympatry would be an objective measure of their taxonomic status. For the present they apparently are maintained in allopatry by an uninhabitable section of stream, and the taxonomic and evolutionary position of *N. atrapiculus* must be judged on a subjective basis.

The difficulties of classifying N. atrapiculus relative to N. b. bellus and N. roseipinnis may be summarized as follows: (1) N. atrapiculus is allopatric from its two close relatives. (2) It is intermediate between and strongly differentiated from them in only one character complex, fin pigmentation. (3) In other characters it averages extreme in three, interjacent in eight, like N. b. bellus in one, and like N. roseipinnis in three. It is not strongly differentiated from the other two forms in any of these supplemental characteristics. (4) The overall aspect of N. atrapiculus is intermediacy between N. b. bellus and N. roseipinnis.

It has been suggested that allopatric populations of dubious status be classified as subspecies (Mayr, 1969). Within this philosophical framework *N. atrapiculus* would appear to be a logical candidate for subspecific treatment. However, the decision of whether to ally *N. atrapiculus* with *N. b. bellus* or with *N. roseipinnis* would have to be made arbitrarily. By emphasizing various combinations of characters, arguments might be made for associating it with either. But when all characters are considered, neither treatment could be objective or convincing.

The two remaining alternatives are to accord this form specific rank

or to leave it unnamed and *incertae sedis*. For practical and heuristic reasons I prefer specific recognition of *N. atrapiculus*.

ETYMOLOGY.—The name atrapiculus is a compound of the Latin atra (black) and apiculus, the diminutive of apex (tip, point). The name refers to the usual confinement of interradial pigment to the apex of the anal and pelvic fins.

MATERIAL EXAMINED

None of the material listed below is designated as paratypes.

ESCAMBIA DRAINAGE

Alabama.—Butler Co.: TU 3103 (trib. Pigeon Cr., 9.4 mi. W Rutledge, Hwy. 10), UAIC 358 (trib. Persimmon Cr., 2 mi. W Greenville, Hwy. 10), UMMZ 88727 (Persimmon Cr., 0.5 mi. E Greenville), 88744 (trib. Persimmon Cr., 1 mi. W Greenville, Rt. 10), 124084 (Rocky Cr., S of Greenville), 124122 (Hawkins Cr., 3 mi. S Greenville), 139143 (Rocky Cr., trib. Persimmon Cr., 1 mi. N Georgiana, 2.75 mi. S Chapman). Conecuh Co.: CU 16144 (Jay Branch of Mill Cr., 2.4 mi E Evergreen), 16214 (Boggy Branch, trib. Sepulga R., 4.8 mi. SW McKenzie, Rt. 84), UAIC 128 (1 mi. E on U. S. Hwy. 31 from jct. Ala. Hwy. 3), 146 (trib. Sepulga R., 2.5 mi. N Sepulga R. bridge, U. S. Hwy. 31), 412 (Cane Cr., 2.1 mi. N Evergreen, Hwy. 83), UMMZ 124070 (Mills Cr., 1 mi. E Evergreen), 155514 (Bear Cr., U. S. Hwy. 31, 2 mi. S Castleberry), 165977 (Murder Cr., Castleberry). Crenshaw Co.: CU 14021 (Dry Cr., trib. Coneuh R., 3.6 mi. N Brantley), TU 2593 (trib. Patsaliga R., 2.0 mi. W Luverne, Rt. 10), UAIC 1043 (2 mi. N of Hwy. 29 on farm rd. from Lapine and Petrey to Luverne), UMMZ 88712 (Little Rattlesnake Cr., 7 mi. W Luverne). Pike Co.: UAIC 360 (9.5 mi. W Troy, Hwy. 10). Precise locality uncertain. Butler Co.: USNM 43481, 43543 (both same locality: Greenville).

YELLOW DRAINAGE

ALABAMA.—Covington Co.: CU 16215, 53355, UAIC 1825 (all same locality: Five Runs Cr., ca. 2 mi. E Andalusia, U. S. Hwy. 84, T4N, R16E, Sec. 15), UAIC 141 (4 mi. E Andalusia, U. S. Hwy. 84), 1827 (trib. Yellow R., ca. 12 mi. W Lockhart, Lockhart-Wing Rd., T1N, R15E), 372, 3552 (both same locality: Yellow R., 5 mi. W Opp, U. S. Hwy. 84, T4N, R17E, Sec. 33), UAIC 3569 (Big Creek, 10 mi. E Wing, Co. Hwy. 4, T1N, R16E, Sec. 28), 3570 (Hogfoot Cr., ca. 7 airmi. S Andalusia, T2N, R15E, Sec. 2). FLORIDA.—Okaloosa Co.: UAIC 3554 (Big Horse Cr., 3 mi. E Blackman, Fla. Hwy. 2, T5N, R24W, Sec. 24.)

CHOCTAWHATCHEE DRAINAGE

ALABAMA.—Barbour Co.: CU 53151 (Pea Cr., Co. Hwy. 27, 1.6 rdmi. NW jct. Hwy. 51, 2.75 airmi. NNW center Louisville, T10N, R25E, Sec. 29), UAIC 2891 (Sikes Cr., 3.75 mi. NW Blue Springs). Bullock Co.: UAIC 2887 (Indian Cr., 10 mi. SSE Union Springs, dirt rd.). Coffee Co.: CU 16229 (trib. Claybank Cr.), 53344, UAIC 3505 (both same locality: Little Double Bridges Cr., Co. Hwy. 14, 7.1 airmi. SW center Enterprise, T3N, R21E, Secs. 4,9), TU 37396 (Cripple Cr., trib. Pea R., 1.1 mi. N Kinston, Hwy. 189), UAIC 1203 (Pages Cr., ca. 6.5 mi. N Kinston, Hwy. 189), 3501 (Hays Cr., Hwy. 189, 10 mi. SW Elba, T4N, R19E, Sec. 15), 3502 (Whitewater Cr., unnumbered Hwy. 4.5 mi. NE Elba, T6N, R20E, Sec. 10), 3503 (Whitewater Cr., 12 mi. NE Elba, T7N, R21E, Sec. 16). Dale Co.: CU 16116 (trib. Claybank Cr., 2.0 mi. W Ozark, Rt. 27), 21168 (trib. Choctawhatchee R., 8.2 mi. W Dothan), TU 3707 (7.2 mi. NNW) jct. Echo Farm Rd. and Hwy. 136),

UAIC 369 (Judy Cr., 5.5 mi. E Ozark, Hwy. 27), 370 (Claybank Cr., 3.5 mi. SW Ozark, nr. jct. Hwys. 27 and 231, T6N, R23E, Sec. 36), UMMZ 88693 (Choctawhatchee R., 9 mi. S Ozark). Geneva Co.: TU 2385 (trib. Choctawhatchee R., 2.8 mi. N Hartford, Hwy. 66), 2430 (trib. Choctawhatchee R., 1.8 mi. N Black), 2498 (trib. Choctawhatchee R., 5.5 mi. N Hartford, Hwy. 66), UAIC 1893 (Spring Cr., 2.5 mi. NE Black, Black-Hartford Hwy., T1N, R23E, Sec. 27), 3506 (Tight Eye Cr., off Hwy. 87, 4.5 mi. NE Samson, T2N, R21E, Sec. 11). Henry Co.: CU 17152 (Choctawhatchee R., 5 mi. W Graball, Rt. 10), TU 3905 (Blackwood Cr., 3.0 mi. NW jct. Echo Farm Rd. and Hwy. 136), UAIC 368 (10 mi. SW Abbeville, 0.5 mi. from Miller's Fish Camp). Houston Co.: CU 53304 (trib. Choctawhatchee R., 5.7 mi. W Dothan). Pike Co.: CU 14319, 53127, UAIC 362 (all same locality: Buckhorn Cr., Hwy. 29, 4.1 rdmi. S Bullock-Pike Co. line, 5.25 airmi. ENE Banks, T10N, R23E, Sec. 17), TU 3216 (trib. Buckhorn Cr., 7.1 mi. S Perote, Hwy. 29). Florida.—Holmes Co.: ESU 4412, TU 20681 (both same locality: East Pittman Cr., 0.8 mi. N East Pittman), TU 186 (trib. Choctawhatchee R., 4.7 mi. SSW Geneva), UAIC 1205 (trib. Chesnut Cr., Hwy. 2A, Sweet Gum Head), UMMZ 166314 (Parrot Cr., 6 mi. SW Geneva, Ala., T6N, R16W, Sec. 31). Walton Co.: FSU 5416 (Crooked Cr., 3.8 airmi. NW Red Bay, Rt. 183).

APALACHICOLA DRAINAGE

CHATTAHOOCHEE RIVER SYSTEM.—GEORGIA. Chattahoochee Co.: AU 572, CU 17158 (both same locality: Hichitee Cr., 4.1 mi. S Cusseta, Rt. 27). Stewart Co.: AU 1060, CU 17783 (both same locality: Hannahatchee Cr., 6.0 mi. S Stewart-Chattahoochee Co. line, Hwy. 27), CU 17501 (trib. Hannahatchee Cr., 4.1 mi. N Lumpkin, Rt. 27), 15876, TU 17281 (both same locality: Hodchodkee Cr., trib. Pataula Cr., 1.4 mi. S Lumpkin, Rt. 27). Talbot Co.: CU 15810, FSU 7053, TU 7648 (all same locality: S. Fk. Upatoi Cr., 7.0 mi. S Talbotton, Rt. 80). ALABAMA. Barbour Co.: AU 461 (Leak Cr., R27E, T11N, Sec. 16), 1061 (trib. Leak Cr., R27E, T11N, Sec. 14), UAIC 366 (10 mi. S Eufaula, Hwy. 241). Chambers Co.: AU 418 (Osanippa Cr., trib. Chattahoochee R., 1.4 mi. N Cusseta, Co. Rt. 55), CU 53332 (Osanippa Cr., Hwy. 29, S of Fairfax). Henry Co.: AU 1062 (McRae Cr., 11.8 mi. E Abbeville, Ala. Hwy. 10), CU 17485 (trib. Abbie Cr., 1.2 mi. E Abbeville, Rt. 10), 17758 (trib. Abbie Cr., 2.6 mi. S Abbeville, Rt. 241). Houston Co.: AU 607 (3.6 mi. S Columbia, Hwy. 95). Lee Co.: UMMZ 123972 (Uchee Cr., Marvyn), 12411 (Doodle Cr., nr. Marvyn), 124080, 128754 (both same locality: Watoolee Cr., trib. Uchee Cr., S of Marvyn). Russell Co.: AU 1059 (trib. Hatchechubbee Cr., 0.15 mi. S Pittsview, Hwy. 431), CU 13979 (trib. Uchee Cr., 3.1 mi. W Marvyn, Rt. 80), 53182 (Adams Branch, 3.0 rdmi. WSW jct. Co. Hwy. 32 and Rt. 80 on 32, 4.75 airmi. WSW Crawford, T17N, R28E, Sec. 32), TU 10704 (trib. Little Uchee Cr., 1.1 mi. E Crawford, Hwy. 80), 12152 (trib. Little Uchee Cr., 7.9 mi. W Chattahoochee R., Phenix City), UMMZ 124075 (Uchee Cr.), 128746 (Brush Cr., trib. Uchee Cr.).

FLINT RIVER SYSTEM.—GEORGIA. Clayton—Fayette Co.: AU 1420 (trib. Flint R., 4.2 mi. S Riverdale, Hwy. 85). Meriwether Co.: CU 50696 (Cane Cr., 5 mi. N Warm Springs, Hwy. 85W). Pike Co.: CU 17463 (Elkins Cr., trib. Flint R., 5.4 mi. E Concord, Rt. 18). Talbot Co.: CU 21136 (trib. Lazer Cr., 2.9 mi. W Talbotton, Ga. Rt. 208).

CONECUH-TALLAPOOSA DRAINAGE

ALABAMA.—Bullock Co.: CU 53157, UAIC 1561, 1562 (all same locality: Old Town Cr., Hwy. 40, 0.4 rdmi. ENE jct. Hwy. 82, E city limit Union Springs, T14N, R23E, Sec. 35), UAIC 1564 (Conecuh R., nr. Chunnenugee).

EVOLUTION OF THE roseipinnis Species Complex

The closest relatives of the *roseipinnis* complex appear to be forms of the *umbratilis* complex, specifically *N. umbratilis cyanocephalus*. These two groups are similar in tuberculation, number of vertebrae, general physiognomy, the presence of fin interradial pigment, breeding colors, and other secondary sexual features (Table 3). The primary features distinguishing the *roseipinnis* complex from the *umbratilis* complex are lack of the anterior basidorsal spot, larger scales, and more specific and seasonally constant patterns of fin pigmentation. In all these differentiating characters, the character states of the *umbratilis* complex are assumed to be primitive, those of the *roseipinnis* complex derived.

These two groups have undergone their evolution allopatrically, the *umbratilis* complex in the Mississippi Valley, the *roseipinnis* complex in Gulf Coastal streams east of the Mississippi River. Thus, the *roseipinnis* complex probably arose after a stock similar to *N. u. cyanocephalus* invaded the eastern Gulf slope, possibly through a Tennessee-Alabama River connection.

In many respects—fin pigmentation, physiognomy, secondary sexual characters, and anterior dorsolateral scale reduction—N. b. bellus has diverged the least from N. u. cyanocephalus and is assumed to be the most primitive member of the roseipinnis complex. Perhaps the habit of spawning over the nests of sunfish (Lepomis) also was acquired from its ancestor.

During the course of its evolution in the Mobile Bay basin, a stock of N. b. bellus gave rise to N. b. alegnotus above the Fall Line in the Black Warrior system. Some of the characters (e.g., reduced lateral line system and reduced fin pigmentation) of N. b. alegnotus could be accounted for by neoteny, but others (e.g., pigment characters, proportional characters, and meristic characters) probably could not. On the whole, N. b. alegnotus is the most divergent member of the roseipinnis complex. Although its present taxonomic position is questionable, it is assumed to have interbred with N. b. bellus at some time past to produce intermediate populations at the Fall Line. Other possibilities are considered above under the account of Intergrades.

Nothing concrete can be said about the evolution of *N. roseipinnis* and *N. atrapiculus* because of their uncertain phylogenetic relationships to one another and to *N. b. bellus*. The reduced and highly specific fin pigmentation of *N. roseipinnis* is clearly an advanced condition; but the species varies so much in other characters (e.g., body shape and anterior dorsolateral body squamation) that its overall divergence is difficult to assess. In morphology, *N. atrapiculus* is intermediate between eastern

populations of *N. roseipinnis* and *N. b. bellus*. If only eastern populations of *N. roseipinnis* are considered, these three species align from most primitive to most advanced as follows: *N. b. bellus*, *N. atrapiculus*, *N. roseipinnis*.

The interrelationships of these three forms may be explained by any of five plausible hypotheses. Additional information will be required to decide which of these is most likely to be correct:

- (1) In view of the morphological sequence noted above, perhaps the most logical hypothesis is that N. b. bellus gave rise to N. atrapiculus on the eastern Gulf slope, and the latter gave rise to N. roseipinnis through subsequent westward expansion.
- (2) Stocks of N. b. bellus, isolated in appropriate Gulf Coastal streams east and west of the Mobile Basin, may have independently given rise to both N. atrapiculus and N. roseipinnis.
- (3) Perhaps a stock of N. b. bellus, isolated in a Gulf Coastal stream of Mississippi or Louisiana, gave rise to N. roseipinnis; and the latter gave rise to N. atrapiculus through subsequent eastward expansion. The morphological intermediacy of N. atrapiculus makes this perhaps the least attractive of these first three possibilities.
- (4) Because of its morphological intermediacy, one is forced to entertain the hypothesis that *N. atrapiculus* arose through hybridization between *N. b. bellus* and *N. roseipinnis*. This hybridization might have taken place in the lower Mobile Basin as *N. roseipinnis*, expanding eastward, established sympatry with its ancestor *N. b. bellus*. Further eastward expansion and subsequent evolution of a hybrid stock may have given rise to *N. atrapiculus*.
- (5) Because of its morphological intermediacy, it might be suggested that *N. atrapiculus* is the ancestor of both *N. b. bellus* and *N. roseipinnis*, but its geographic location makes this possibility rather unlikely.

Other hypotheses might be invoked to explain the evolution of this trio, but most would be considerably more complex and less realistic than those noted above. This is not to say that the above models are without difficulties. The nature of the Mississippi Valley populations of *N. roseipinnis* is particularly difficult to reconcile. In having less reduced fin pigment, these appear to be among the most primitive populations of the species. Furthermore they are the least divergent in terms of reduction in squamation and in body form. None of the hypotheses advanced

above can easily account for the most primitive populations of *N. rosei-pinnis* being found in the Mississippi Valley.

Some of the divergent characters of the Mobile Bay populations of *N. roseipinnis* may be accounted for by character displacement (Brown and Wilson, 1956), in which *N. roseipinnis* diverged from *N. b. bellus* through the reinforcement of reproductive isolating mechanisms. Character displacement will not account for the generally advanced nature of Gulf slope populations of *N. roseipinnis* as compared with Mississippi Valley populations, nor will it explain the strong east-west clinal variation exhibited by the species. There appears to be no way in which characters built up in sympatry can disperse back through allopatric populations of the species involved (see discussion following Sibley, 1961). Furthermore, Biloxi and St. Louis Bays populations of *N. roseipinnis* are nearly as extreme as the Mobile Bay stock in several characters (e.g., anal rays, anterior dorsolateral scale reduction); and there is no evidence that the former populations have ever been in contact with *N. b. bellus*.

LITERATURE CITED

- Bailey, R. M. et al. 1970. A list of common and scientific names of fishes from the United States and Canada. Amer. Fish. Soc., Spec. Pub. No. 6 (third ed.).
- ——, and R. D. Suttkus. 1952. Notropis signipinnis, a new cyprinid fish from southeastern United States. Occ. Pap. Mus. Zool. Univ. Michigan 542:1-15.
- , H. E. Winn, and C. L. Smith. 1954. Fishes from the Escambia River, Alabama and Florida, with ecologic and taxonomic notes. Proc. Acad. Natur. Sci. Philadelphia 106:109-164.
- Böhlke, J. E. 1953. A catalogue of the type specimens of recent fishes in the Natural History Museum of Stanford University. Stanford Ichthyological Bull. 5: 1-168.
- Boschung, H. T., Jr. 1961. An annotated list of fishes from the Coosa River system of Alabama. Amer. Midl. Natur. 66(2):257-285.
- Branson, B. A. 1962. Observations on the breeding tubercles of some Ozarkian minnows, with notes on the barbels of *Hybopsis*. Copeia 1962(3):532-539.
- Briggs, J. C. 1958. A list of Florida fishes and their distribution. Bull. Florida State Mus. 2(8):223-318.
- Brown, W. L., Jr., and E. O. Wilson. 1956. Character displacement. Syst. Zool. 5:49-64.
- Caldwell, R. D. 1966. Fishes from the freshwater streams of the Biloxi Bay and St. Louis Bay drainage systems of Mississippi. J. Mississippi Acad. Sci. 12:213-231.
- Carr, Archie and C. J. Goin. 1955. Guide to the reptiles, amphibians, and freshwater fishes of Florida. Univ. Florida Press, Gainesville, Fla. 341 p.
- Cliburn, J. W. 1965. Fishes of four stream systems of the Pascagoula River basin. J. Mississippi Acad. Sci. 11:247-268.
- Collette, B. B. 1965. Systematic significance of breeding tubercles in fishes of the family Percidae. Proc. U. S. Nat. Mus. 117:567-614.
- Cook, F. A. 1959. Freshwater fishes in Mississippi. Mississippi Game and Fish Comm., Jackson, Miss. 239 p.
- Deubler, E. E. 1955. A taxonomic study of the cyprinid fish Clinostomus vandoisulus (Valenciennes) in the eastern United States. Unpublished Ph. D. thesis, Cornell Univ., Ithaca, N. Y. 167 p.

- Douglas, N. H. and J. T. Davis. 1967. Checklist of the freshwater fishes of Louisiana. Louisiana Wild Life and Fish. Comm., Baton Rouge, La. 29 p.
- Driver, E. C. 1942. Name that animal. Kraushar Press, Northampton, Mass. 527 p.
- Eddy, S. 1957. How to know the freshwater fishes. Wm. C. Brown Co., Dubuque, Iowa. 253 p.
- Fowler, H. W. 1945. A study of the fishes of the southern Piedmont and Coastal Plain. Acad. Natur. Sci. Philadelphia Monogr. No. 7:1-408.
- Gibbs, R. H., Jr. 1957a. 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.
- ——. 1957b. Cyprinid fishes of the subgenus Cyprinella of Notropis. II. Distribution and variation of Notropis spilopterus, with the description of a new subspecies. Lloydia 20(3):186-211.
- Gilbert, C. H. 1884. A list of fishes collected in the East Fork of White River, Indiana, with descriptions of two new species. Proc. U. S. Nat. Mus. 7:199-205.
- Gilbert, C. R. 1961. Hybridization versus intergradation: An inquiry into the relationship of two cyprinid fishes. Copeia 1961(2):181-192.
- ----. 1964. The American cyprinid fishes of the subgenus Luxilus (genus Notropis). Bull. Florida State Mus., Biol. Sci. 8(2):95-194.
- Ginsburg, Isaac. 1954. Certain measures of intergradation and divergence. Zoologica 39(1):31-35.
- Harrington, R. W., Jr. 1955. The osteogranium of the American cyprinid fish, Notropis bifrenatus, with an annotated synonymy of teleost skull bones. Copeia 1955(4):267-290.
- Hay, O. P. 1881. On a collection of fishes from eastern Mississippi. Proc. U. S. Nat. Mus. 3:488-515.
- ——. 1883. On a collection of fishes from the lower Mississippi Valley. Bull. U. S. Fish Comm. 2:57-75.
- Howell, H. H. 1957. A taxonomic and distributional study of the genus *Notropis* in Alabama. Unpublished Ph. D. thesis, Univ. Alabama, University, Ala. 288 p.
- Howell, W. M. and J. D. Williams. 1971. Notropis gibbsi, a new cyprinid fish from the Tallapoosa River system in Alabama and Georgia. Copeia 1971(1):55-64.
- Hubbs, C. L. and J. D. Black. 1940. Notropis perpallidus, a new minnow from Arkansas. Copeia 1940(1):46-49.
- ——, and K. F. Lagler. 1958. Fishes of the Great Lakes region. Rev. ed. Bull. Cranbrook Inst. Sci. No. 26, 213 p.
- ——, and A. I. Ortenburger. 1929. Fishes collected in Oklahoma and Arkansas in 1927. Pub. Univ. Oklahoma Biol. Surv. 1(3):47-112.
- Hunter, J. R. and A. D. Hasler. 1965. Spawning association of the redfin shiner, Notropis umbratilis, and the green sunfish, Lepomis cyanellus. Copeia 1965(3):265-281.
- Huntsman, G. R. 1967. Nuptial tubercles in carpsuckers (Carpiodes). Copeia 1967(2):457-458.
- Illick, H. J. 1956. A comparative study of the cephalic lateral-line system of North American Cyprinidae. Amer. Midl. Natur. 56(1):204-223.
- International Congress of Zoology. 1961. International Code of Zoological Nomenclature, adopted by the XV International Congress of Zoology. Int. Trust for Zool. Nomenclature, London, England. 176 p.
- Jenkins, R. E. and Timothy Zorach. 1970. Zoogeography and characters of the American cyprinid fish Notropis bifrenatus. Chesapeake Sci. 11(3):174-182.

- Jordan, D. S. 1876. Manual of the vertebrates of the northern United States. . . . 1st ed. Jansen, McClurg and Co., Chicago, Ill. 342 p.
- ————. 1877a. On the fishes of northern Indiana. Proc. Acad. Natur. Sci. Philadelphia, 29:42-82.
- ----. 1877b. 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 Illinois. Bull. Illinois State Lab. Natur. Hist. 2:37-70.
- ----- 1882. Report on the fishes of Ohio. Rep. Ohio Geol. Surv. 4:735-1002.
- —. 1885a. Supplementary notes on North American fishes. Proc. U. S. Nat. Mus. 7:545-548.
- America north of the Tropic of Cancer, with notes on species discovered in 1883 and 1884. Extracted from Annu. Rep. Comm. Fish and Fisheries 1884: 1-185 (separate).
- ——.. 1919. The genera of fishes, part III, from Guenther to Gill, 1859-1880, twenty-two years, with the accepted type of each. Leland Stanford Junior Univ. Pub., Univ. Ser., pp. 285-410.
- ——. 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. 446 p.
- ——, and H. E. Copeland. 1877. Check list of the fishes of the fresh waters of North America. Bull. Buffalo Soc. Natur. Sci. 3:133-164.
- ——, and B. W. Evermann. 1896a. A check-list of the fishes and fish-like vertebrates of North and Middle America. Rep. U. S. Comm. Fish and Fisheries 21:207-584.
- ----, and ----. 1896b. The fishes of North and Middle America. Bull. U. S. Nat. Mus. 47(1):1-1240.
- ———, and H. W. Clark. 1930. Check list of the fishes and fishlike vertebrates of North and Middle America north of the northern boundary of Venezuela and Colombia. Rep. U. S. Comm. Fish. 1928, App. 10:1-670.
- ----, and C. H. Gilbert. 1877. On the genera of North American fresh-water fishes. Proc. Acad. Natur. Sci. Philadelphia. 29:83-104.
- ——, and ——. 1883. Synopsis of the fishes of North America. Bull. U. S. Nat. Mus. 16:1-1018.
- , and S. E. Meek. 1884. Description of four new species of Cyprinidae in the United States National Museum. Proc. U. S. Nat. Mus. 7:474-477.
- Koehn, R. K. 1965. Development and ecological significance of nuptial tubercules of the red shiner, *Notropis lutrensis*. Copeia 1965(4):462-467.
- Lachner, E. A. and R. E. Jenkins. 1967. Systematics, distribution, and evolution of the chub genus *Nocomis* (Cyprinidae) in the southwestern Ohio River basin, with the description of a new species. Copeia 1967(3):557-580.
- ——, and ——. 1971. Systematics, distribution, and evolution of the chub genus *Nocomis* Girard (Pisces, Cyprinidae) of eastern United States, with descriptions of new species. Smithsonian Contrib. Zool. 85:1-97.
- Lekander, Bertil. 1949. The sensory line system and the canal bones in the head of some Ostariophysi. Acta Zoologica 30:1-131.
- Martin, B. J. 1965. The fishes of the Tallahala Creek drainage system (Jasper, Jones, and Perry Counties, Mississippi). J. Mississippi Acad. Sci. 11:295-305.
- Mayr, Ernst. 1963. Animal species and evolution. The Belknap Press of Harvard Univ. Press, Cambridge, Mass. 797 p.
- 1969. Principles of systematic zoology. McGraw-Hill Book Co., New York, N. Y. 428 p.
- Miller, R. R. 1963. Synonymy, characters, and variation of *Gila crassicauda*, a rare Californian minnow, with an account of its hybridization with *Lavinia exilicauda*. California Fish and Game 49(1):20-29.

- Monroe, W. H. 1941. Notes on deposits of Selma and Ripley age in Alabama. Bull. Alabama Geol. Surv. 48:1-138.
- Moore, G. A. 1968. Fishes, p. 22-165. In W. F. Blair, A. P. Blair, P. Brodkorb, F. R. Cagle, and G. A. Moore; Vertebrates of the United States, 2nd ed. McGraw-Hill Book Co., New York, N. Y. 616 p.
- Ortenburger, A. I. and C. L. Hubbs. 1926. A report on the fishes of Oklahoma, with descriptions of new genera and species. Proc. Oklahoma Acad. Sci. 6: 123-141.
- Pratt, H. S. 1923. A manual of land and fresh water vertebrate animals of the United States. P. Blakiston's Son and Co., Philadelphia, Pa. 422 p.
- Rafinesque, C. S. 1820. Ichthyologia Ohiensis. Reprinted with biographic and other notes by R. E. Call, 1899. Burrows Brothers, Cleveland, Ohio. 175 p.
- Ramsey, J. S. 1965. Zoogeographic studies on the freshwater fish fauna of rivers draining the southern Appalachian region. Unpublished Ph. D. thesis, Tulane Univ., New Orleans, La. 130 p.
- Reno, H. W. 1966. The infraorbital canal, its lateral-line ossicles and neuromasts in the minnows *Notropis volucellus* and *N. buchanani*. Copeia 1966(3):403-413.
- Russell, R. J. 1936. Physiography of lower Mississippi River delta. In Reports on the geology of Plaquemines and St. Bernard Parishes. Bull. Louisiana Geol. Surv. 8:3-199.
- ——. 1940. Quaternary history of Louisiana. Bull. Geol. Soc. Amer. 51:1199-1234.
- Schrenkeisen, Ray. 1963. Field book of fresh-water fishes of North America. G. P. Putnam's Sons, New York, N. Y. 312 p.
- Sibley, C. G. 1961. Hybridization and isolating mechanisms (and discussion), p. 69-88. In W. F. Blair, ed., Vertebrate Speciation. Univ. Texas Press, Austin, Texas.
- Smith-Vaniz, W. F. 1968. Freshwater fishes of Alabama. Auburn Univ. Agr. Exp. Sta., Auburn, Ala. 211 p.
- Snedecor, G. W. and W. G. Cochran.
 1967. Statistical methods applied to experiments in agriculture and biology.
 6th ed. Iowa State Univ. Press, Ames, Iowa.
 593 p.
- Snelson, F. F., Jr. 1968. Systematics of the cyprinid fish Notropis amoenus, with comments on the subgenus Notropis. Copeia 1968(4):776-802.
- ----. 1970. Systematics of some minnows of the subgenus Lythrurus, genus Notropis (Pisces: Cyprinidae). Unpublished Ph. D. thesis, Cornell Univ., Ithaca, N. Y. 310 p.
- ——. 1971. Notropis mekistocholas, a new herbivorous cyprinid fish endemic to the Cape Fear River basin, North Carolina. Copeia 1971(3):449-462.
- Suttkus, R. D. 1955. Notropis euryzonus, a new cyprinid fish from the Chatta-hoochee River system of Georgia and Alabama. Tulane Stud. Zool. 3(5):85-100.
- ——, and G. H. Clemmer. 1968. Notropis edwardraneyi, a new cyprinid fish from the Alabama and Tombigbee River systems and a discussion of related species. Tulane Stud. Zool. and Bot. 15(1):18-39.
- ——, and E. C. Raney. 1955a. Notropis baileyi, a new cyprinid fish from the Pascagoula and Mobile Bay drainages of Mississippi and Alabama. Tulane Stud. Zool. 2(5):71-86.
- ______, and ______. 1955b. Notropis hypsilepis, a new cyprinid fish from the Apalachicola River system of Georgia and Alabama. Tulane Stud. Zool. 2(7): 161-170.

- Mobile Bay drainage of Alabama and Georgia, with studies of related species. Tulane Stud. Zool. 3(1):3-33.
- Swift, C. C. 1970. A review of the eastern North American cyprinid fishes of the Notropis texanus species group (subgenus Alburnops), with a definition of the subgenus Hydrophlox, and materials for a revision of the subgenus Alburnops. Unpublished Ph. D. thesis, Florida State Univ., Tallahassee, Fla. 474 p.
- Taylor, W. R. 1967. An enzyme method of clearing and staining small vertebrates. Proc. U. S. Nat. Mus. 122 (3596):1-17.
- ——. 1969. A revision of the catfish genus *Noturus* Rafinesque with an analysis of higher groups in the Ictaluridae. Bull. U. S. Nat. Mus. 282:1-315.
- Thomerson, J. E. 1966. A comparative biosystematic study of *Fundulus notatus* and *Fundulus olivaceus* (Pisces: Cyprinodontidae). Tulane Stud. Zool. 13(1): 29-47.
- Tucker, C. E. 1967. A study of the fishes of the eastern Mobile Basin. Unpublished Ph. D. thesis, Univ. Alabama, University, Ala. 245 p.
- Vladykov, V. D. 1963. A review of salmonid genera and their broad geographical distribution. Trans. Roy. Soc. Canada Ser. IV, 1(3):459-504.
- Wall, B. R., Jr. 1968. Studies on the fishes of the Bear Creek drainage of the Tennessee River system. Unpublished M. S. thesis, Univ. Alabama, University, Ala. 93 p.
- Williams, J. D. 1965. Studies on the fishes of the Tallapoosa River system in Alabama and Georgia. Unpublished M. S. thesis, Univ. Alabama, University, Ala. 135 p.

TABLE 1. CONDITION OF THE INFRAORBITAL LATEROSENSORY CANAL AT THE POSITION OF THE DERMOSPHENOTIC BONE IN A COMPOSITE SAMPLE OF N. b.bellus.1

Size Class (in mm SL)	Incomplete ²	Partially Interrupted	Complete
<39.9	19 (56%)	7 (21%)	8 (23%)
40.0 = 44.9	74 (57%)	30 (23%)	26 (20%)
45.0 - 49.9	68 (40%)	41 (24%)	62 (36%)
50.0 - 54.9	12 (19%)	8 (13%)	43 (68%)
> 55.0	4 (18%)	3 (14%)	15 (68%)

- All drainages and both sexes combined.
 Under each column heading is given the number of specimens in a particular size class exhibiting that condition followed by the percentage of the size class which that condition constitutes.

TABLE 2. SUMMARY OF SEXUAL DIMORPHISM IN MEASUREMENTS OF SOME MEMBERS OF THE SUBGENUS Lythrurus.1

Character	fu²	um	ba	bb	at	ro	ar	li
Predorsal length	F	_	F		_	_	F	F
Postdorsal length	_	M	M	M	M	M	M	_
Prepelvic length	F	F	\mathbf{F}	F	F	\mathbf{F}	\mathbf{F}	\mathbf{F}
Preanal length	F	F	\mathbf{F}	F	F	F	\mathbf{F}	F
Head length	F	M	_	_	_	_	_	_
Head depth	F	M	_	_	F	_	_	_
Postorbital head length	_	M	-	-	-	_	-	M
Snout length	_	M	_	M	_	_	_	_
Upper jaw length	F	_	_	_	F	_	F	_
Gape width	_	M	_	_	_	_	M	_
Fleshy orbit length	\mathbf{F}	F	F	F	F	F	F	F
Fleshy interorbital width	~	M	_	_		_	M	M
Body depth	F	_	F	_	F	_	\mathbf{F}	F
Body width	F	F	F	F	F	F	F	F
Caudal peduncle length	M	M	M	_	_	_	M	M
Caudal peduncle depth	-	M	M	M	M	M	M	M
Dorsal fin length	\mathbf{F}	M	_	M	M	M	M	_
Anal fin length	-	M	M	M	M	M	M	M
Pectoral fin length	\mathbf{F}	M	_	_	_	_	M	_
Pelvic fin length	-	M	M	M	M	M	M	M

^{1. &}quot;F" indicates that females have significantly larger means than males, "M" indicates the reverse, and a dash indicates no significant difference between the means. Student's t statistic was used for comparing means. Levels of probability

greater than 0.1 were considered not significant.

2. fu=fumeus; um=umbratilis; ba=bellus alegnotus; bb=b. bellus; at=atrapiculus; ro = roseipinnis; ar = ardens; li = lirus.

Table 3. Summary of Diagnostic Characters of the Four Species Complexes Within the Subgenus Lythrurus.

Character	fumeus complex	umbratilis complex	ardens complex	roseipinnis complex
Members	N. fumeus	N. umbratilis	N. ardens, N. lirus	N. roseipinnis, N. b. bellus, N. b. alegnotus, N. atrapiculus
Vertebrae	Usually 35–37	Usually 36–38	Usually 37–40	Usually 35–37
Head tubercles ¹ Dorsal	Geographically variable; small, scattered, and erect when developed	Moderate in size, scattered and erect	Moderately large, con- centrated, and antrorse	Moderately small, scat- tered, and erect
Lateral and ventral	Geographically variable; absent or present	Present	Usually absent	Present
Lower jaw	Geographically variable; one or two weak rows (occasionally absent) or two well-developed rows	Usually two well- developed rows	Absent, few restricted to chin tip, or one variable row (rarely two variable rows)	Two well-developed rows
Anterior basidorsal spot	Absent	Present but variable	Present or absent	Absent
Melanin deposits in fin membranes	Absent	Present, weak to strong; not deposited in any specific pattern; usually present only in breeding males	Absent	Present, weak to strong (secondarily reduced in N. b. alegnotus); deposited in specific patterns; present in both sexes year round
Breeding colors ¹	Yellow	Usually red	Bright red (ardens) to weak, variable orange, red, or gold, or absent (lirus)	Red

^{1.} Breeding males.

Table 4. Numbers of Vertebrae (Including the Weberian Apparatus as four and the Urostylar Vertebra as one) in Members of the Subgenus Lythrurus. Except for Members of the roseipinnis Complex, Counts from Throughout the Range of the Species are Condensed to a Single Frequency Distribution.

			Prec	auda	ıl				Ca	udal							-	Γotal				
Form and Drainage	16	17	18	19	20	x	17	18	19	20	21	x	34	35	36	37	38	39	40	41	N	x
N. fumeus	2	74	29			17.3		29	68	7	1	18.8		14	71	17	3				105	36.1
N. umbratilis		27	96	11		17.9		36	87	11		18.8		2	48	73	11				134	36.7
N. bellus alegnotus																						
Black Warrior		17	18			17.4	1	12	13	2		18.6		9	11	8					28	36.0
N. bellus: bellus x alegnotus																						
North R.	1	12	6	1		17.3		6	14			18.7	1	1	14	4					20	36.1
N. bellus bellus	_																					
Tennessee		11	20	2		17.7	2	9	22			18.6		2	19	11	1				33	36.3
Tombigbee	3	29	2			17.0		8	24	2		18.8		9	23	2					34	35.8
Alabama	1	13	1			17.0			12	3		19.2			12	3					15	36.2
Tallapoosa		12	2			17.1		1	11	2		19.1			11	3					14	36.2
N. atrapiculus																						
Apalachicola		13	2			17.1		4	10	1		18.8		2	12	1					15	35.9
Choctawhatchee		24	6			17.2		7	20	3		18.9		3	23	3	1				30	36.1
Escambia		5	10			17.7		7	7	1		18.6			11	4					15	36.3
N. roseipinnis																						
Mobile Bay		9	16			17.6		4	11	10		19.2			6	16	3				25	36.9
Pascagoula		4	27			17.9		7	19	5		18.9			8	21	2				31	36.8
Pearl		11	18			17.6		7	17	5		18.9			14	13	2				29	36.6
Lake Pontchartrai	n	12	11			17.5		8	14	1		18.7		1	17	5					2 3	36.2
Bayou Pierre	1	25	5			17.1		15	15	1		18.5		12	17	2					31	35.7
Big Black	2	25	6			17.1	1	13	16	3		18.6		11	19	3					33	35.8
N. adens			17	95	12	19.0		1	26	79	18	19.9				1	30	77	15	1	124	38.9
N. lirus			12	48		18.8		22	27	10	1	18.8				26	30	4			60	37.6

Table 5. Number of Lateral Line Scales in Members of the roseipinnis Complex.

Form and Drainage	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	N	$\overline{\mathbf{x}}$
N. bellus alegnotus			_								_	-					
Black Warrior		1	14	14	24	27	10	11	2							103	39.4
N. bellus: bellus x alegnotus																	
North R.	1	2	6	17	15	18	16	2	1	_	1					79	39.3
N. bellus bellus																	
Tennessee			4	13	6	18	16	9	2	1						69	40.0
Tombigbee		5	10	38	24	45	18	11	7							158	39.4
Black Warrior		4	16	27	18	16	16	4	4	1						106	39.1
Alabama		2	8	15	30	16	25	20	18	4	2	1				141	40.4
Tallapoosa				12	11	23	29	16	9	4	2 3	_	1			108	40.8
N. atrapiculus																	
Apalachicola		3	11	12	14	29	13	9	3	1	1					96	39.6
Choctawhatchee		1	7	10	29	30	22	16	7	3	1					126	40:1
Yellow				4	15	12	12	9	5	1						58	40.4
Escambia			2	3	12	19	15	7	3	$\bar{3}$						64	40.4
Conecuh-Tallapoosa				2	4	5	9	2	1							23	40.3
N. roseipinnis																	
Mobile Bay				11	10	26	29	14	7	7	2	1				107	40.8
Pascagoula		1	1	8	25	30	35	22	14	3	2 3	$\overline{4}$			•	146	40.8
Biloxi-St. Louis Bays			2	8	6	15	5	4	1	1						42	39.8
Pearl		1	4	11	20	30	20	19	16	4	4					129	40.7
Lake Pontchartrain		1	7	24	27	25	27	13	13	2	1					140	40.0
Bayou Pierre		4	4	25	18	25	20	13	11	1	1					122	39.9
Big Black		1	1	4	10	18	24	27	15	4	5	3	1	_	1	114	41.5
Yazoo	9			2	1	5	2	_	_	_	1	_	_		-	11	40.2

Table 6. Number of Body Circumference Scales in Members of the roseipinnis Complex.

Form and Drainage	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	N	x
N. bellus alegnotus		•															
Black Warrior		4	13	19	22	21	12	7	4							102	30.2
N. bellus: bellus x alegnotus																	
North R.	2	_	5	8	22	16	15	5	1	1	2	_	_	1		78	30.8
N. bellus bellus																	
Tennessee		2	5	11	20	17	4	6	1	2 5	2					70	30.6
Tombigbee		2	3	11	37	38	29	23	11	5	2 1					160	31.4
Black Warrior	1	2	8	13	40	19	12	8	5							108	30.4
Alabama		3	4	16	41	39	15	12	11	4						145	30.9
Tallapoosa		1	5	18	21	25	24	11	4	4 5	2					116	31.1
N. atrapiculus																	
Apalachicola					6	17	20	19	22	14	8	5	1	_	1	113	33.3
Choctawhatchee					3	8	24	28	32	19	16	1	1			132	33.6
Yellow					i	_	4	11	16	9	12	6	3	_	1	63	34.7
Escambia					3	10	9	24	7	9	3	6 1	3	1	-	70	33.3
Conecuh-Tallapoosa					ī	2	4	6	4	4	4	ī	•	_		26	33.7
N. roseipinnis					_	_	_		-	_	-	_					00
Mobile Bay			2	12	20	15	26	16	4	6	_	1				102	31.5
Pascagoula			_	1	8	16	33	42	22	8	12	2				144	32.9
Biloxi-St. Louis Bays				ī	8	14	10	5	4	ī	3	_				46	31.9
Pearl				2	10	18	29	29	28	7	ī	4				128	32.7
Lake Pontchartrain				7	20	21	35	19	28	8	5	_	1			144	32.3
Bayou Pierre				-	4	10	13	32	32	19	9	4	_	1		124	33.6
Big Black				1	10	14	23	16	27	12	9	3	2	i		118	33.2
Yazoo				-	2	2	4	1	2.		Ü	1	_	-		12	32.3

Table 7. Number of Predorsal Scale Rows in Members of the roseipinnis Complex.

Form and Drainage	16	17	18	19	20	21	22	23	24	25	26	27	28	29	N	x
N. bellus alegnotus						•										
Black Warrior			2	5	28	27	22	8	8	2	1				103	21.3
N. bellus: bellus x alegnotus																
North R.			2	6	12	19	21	11	3	2	_	2			78	21.5
V. bellus bellus																
Tennessee		1	_	6	14	22	13	10	5	_	1	_	1		73	21.4
Tombigbee	1	_	5	17	42	36	30	21	6	3	ī				162	21.1
Black Warrior			9	14	31	26	21	6	6	•	_				113	20.7
Alabama		1	2	13	33	28	37	25	7	_	1				147	21.3
Tallapoosa		_	4	6	24	23	29	19	10	1	_				116	21.5
V. atrapiculus			_	-				20		-					110	
Apalachicola			1	1	10	20	28	23	15	12	4	3			117	22,6
Choctawhatchee			_	-	5	19	28	40	24	8	6	•			130	22.8
Yellow					•	1	10	13	19	13	5	2			63	23.9
Escambia					4	$\tilde{7}$	21	24	9	4	3	_			72	22.7
Conecuh-Tallapoosa					ī	2	7	7	$\overset{\circ}{4}$	3	ì				25	23.0
I. roseipinnis					-	_	•		_	•	-				20	20.0
Mobile Bay				1	_	8	32	34	19	12		7			107	23.0
Pascagoula					4	18	27	41	30	20	6	1 3	1	1	151	23.2
Biloxi-St. Louis Bays				1	4	8	9	11	7	5	U	3	1	1		
Pearl				1	3	14	22	39	31	18	4		,		45	22.5
Lake Pontchartrain				3	10	21	29	43	18	16	4 3	-	1		132	23.2
Bayou Pierre				5	11	36	29 26	31	10		J	_	1		144	22.7
Big Black				1	15	18	20 29	31	11 15	5 8	,				125	22.0
Yazoo				1	15	6	29 2			8	1				118	22.3
1 4 2 0 0					1	О	z	1	1						12	21.3

TABLE 8. NUMBER OF CAUDAL PEDUNCLE SCALES IN MEMBERS OF THE roseipinnis Complex.

Form and Drainage	10	11	12	13	14	15	16	17	18	N	
N. bellus alegnotus			_	_		<u>_</u>					
Black Warrior		18	45	49	19					131	12.5
N. bellus: bellus x alegnotus										101	12.0
North R.			7	27	35	9	1	1		80	13.7
N. bellus bellus					-	•	•	•		00	10.1
Tennessee			5	16	39	4	3			67	13.8
Tombigbee			2	15	86	34	15	2		154	14.3
Black Warrior			10	22	54	14	9	-		109	13.9
Alabama				16	56	45	20	5		142	14.6
Tallapoosa			2	18	52	25	10	ĩ		108	14.2
N. atrapiculus								-		100	1 1
Apalachicola			3	9	79	9	1	1		102	14.0
Choctawhatchee			4	16	105	3				128	13.8
Yellow				1	59	3	1			64	14.1
Escambia			1	6	51	2	2			62	14.0
Conecuh-Tallapoosa				1	15	2 5	2 3			24	14.4
N. roseipinnis											~
Mobile Bay	1	1	4	20	79	2	1			108	13.7
Pascagoula				6	128	7	9	_	2	152	14.2
Biloxi-St. Louis Bays				8	34	2			_	44	13.9
Pearl			1	9	102	12	6	2		132	14.1
Lake Pontchartrain			1	25	98	$\overline{13}$	2	2		141	14.0
Bayou Pierre				3	82	19	12	ī	1	118	14.4
Big Black			1	1	69	22	14	8	2	117	14.7
Yazoo					7	2		ĭ	-	10	14.7

Table 9. Number of Anal and Pectoral Fin Rays in Members of the roseipinnis Complex.

				Anal 1	Fin R	ays					Pe	ctora	l Fir	Ray	s	
Form and Drainage	9	10	11	12	13	14	N	x	11	12	13	14	15	16	N	<u>x</u>
N. bellus alegnotus		_	-													
Black Warrior	11	120	35	1			167	10.2		14	35	6			55	12.9
N. bellus: bellus x alegnotus																
North R.	1	79	93	5			178	10.6		5	31	20	1		57	13.3
N. bellus bellus																
Tennessee	2	35	37	4			78	10.6			8	10	10		28	14.1
Tombigbee	4	149	158	7			318	10.5		1	23	77	24		125	14.0
Black Warrior	4	71	69	3			147	10.5		3	22	24	6		55	13.6
Alabama	4	134	124	3			265	10.5		2	33	63	15	1	114	13.8
Tallapoosa	3	101	58	2			164	10.4			16	58	24	1	99	14.
N. atrapiculus														-	•	
Apalachicola		42	90	6			138	10.7	1	8	38	40	4		91	13.4
Choctawhatchee		48	237	18	1		304	10.9		2	27	55	14		98	13.8
Yellow		3	31	8	1		43	11.2		2	8	9			19	13.4
Escambia		23	76	11	_	1	111	10.9		4	15	33	3	1	56	13.7
Conecuh-Tallapoosa		9	21	2		•	32	10.8				4	1	_	5	14.2
N. roseipinnis												_	_		•	
Mobile Bay		2	34	144	57	4	241	12.1		1	14	46	12		73	13.9
Pascagoula	2	7	104	160	22		295	11.7		_	21	68	24	1	114	14.0
Biloxi-St. Louis Bays			22	52	26	2	102	12.1		2	-6	11	1	-	20	13.6
Pearl		8	125	183	26	1	343	11.7		3	38	65	21		127	13.8
Lake Pontchartrain		10	138	110	11	ĩ	270	11.5		6	40	59	17		122	13.
Bayou Pierre		21	166	78	2	_	267	11.2		_	32	41	5		78	13.
Big Black	1	50	268	74	3		396	11.1		1	18	$\hat{47}$	11	1	78	13.9
Yazoo		1	8	1	_		10	11.0		_	8	3		•	11	13.3

Table 10. Number of Preoperculomandibular Canal Pores and Gill Rakers on Lower Limb of First Arch in Members of the roseipinnis Complex.

		I	reop	ercul	omar	ndibu	lar (Canal	Pores					Gill	Rak	ers		
Form and Drainage	8	9	10	11	12	13	14	15	N	$\overline{\mathbf{x}}$	4	. 5	6	7	8	9	N	- x
N. bellus alegnotus																		
Black Warrior		1	7	22	34	19	9		92	12.0			4	26	14	2	46	7.3
N. bellus: bellus x alegnotus													_					
North R.		3	14	21	16	5			59	11.1		1	2	16	1		20	6.9
N. bellus bellus																		
Tennessee		2	10	15	10	6	1		44	11.2		2		11	5	1	23	7.0
Tombigbee		2	7	30	16	14	5		74	11.6			12	39	16		67	7.1
Black Warrior	1	9	25	35	17	6	2	1	96	10.9		1	_	9	1		13	6.8
Alabama			17	52	38	10			117	11.4			10	31	12		53	7.0
Tallapoosa			20	40	36	11			107	11.4			4	42	29	3	78	7.4
N. atrapiculus																		
Apalachicola			14	29	25	16	2		86	11.6]	. 5		21	1		56	6.3
Cĥoctawhatchee		6	18	34	31	7	3		99	11.2		10		14			42	6.1
Yellow		2	4	8	4	_	_	I	19	11.0		1	6	3			10	6.2
Escambia		5	10	24	14	5			58	11.1		4	11	16			31	6.4
Conecuh-Tallapoosa		2	4	9	1				16	10.6		1	4	12			17	6.6
N. roseipinnis																		
Mobile Bay	7	26	43	14	3				93	9.8		2		9			21	6.3
Pascagoula	7	21	77	27.	7	1			140	10.1	1	. 4	34	40	6		85	6.5
Biloxi-St. Louis Bays	1	3	20	8	3				35	10.3			6				6	6:0
Pearl	4	19	50	39	7	2			121	10.3]	. 12	52	40	5		110	6.3
Lake Pontchartrain	1	19	68	39	6	1			134	10.2]	. 24	-	10			69	5,8
Bayou Pierre		9	55	35	9	2			110	10.5		9		16	1		63	6.1
Big Black		8	41	32	4	3	1		89	10.5]	. 2		20	1		52	6.3
Yazoo		1	5	3	_	1			10	10.5		1	6	3			10	6.2

Table 11. Index of Anterior Dorsolateral Scale Reduction in Members of the roseipinnis Complex. See Text for Explanation of Index Values.

Form and Drainage	0	1	2	3	4	N	$\overline{\mathbf{x}}$
N. bellus alegnotus			_				
Black Warrior		2	12	9	1	24	2.37
N. bellus: bellus x alegnotus							
North R.		10	28	9	10	57	2.33
N. bellus bellus						•	
Tennessee	4	24	5	3		36	1.19
Tombigbee	23	58	4			85	0.78
Black Warrior	31	36	6	4	2	79	0.86
Alabama	42	49	1			92	0.55
Tallapoosa	16	15	2			33	0.58
N. atrapiculus							
Apalachicola		27	26	5	4	62	1.77
Choctawhatchee	2	32	29	17	10	90	2.01
Yellow		10	18	14	10	52	2.46
Escambia	3	16	23	9	1	52	1.79
Conecuh-Tallapoosa	2	16	4	2		24	1.25
N. roseipinnis							
Mobile Bay	1	5	10	35	89	140	3.47
Pascagoula		6	57	34	52	149	2.89
Biloxi-St. Louis Bays	1	_	8	11	22	42	3.26
Pearl	4	29	66	55	63	217	2.66
Lake Pontchartrain		15	52	54	35	156	2.70
Bayou Pierre	6	57	32	ì	1	97	1.32
Big Black	4	93	22	7	1	127	1.28
Yazoo	1	6	3	1		11	1.36

Table 12. Total Fin Pigmentation Index for Breeding Males of the *roseipinnis* Complex. Data in Upper Half of Table is for Specimens Less than 40 mm SL; Data in Lower Half for Specimens Equal or Greater than 40 mm SL.

	_																				
Form and Drainage	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	N	x
N. bellus alegnotus	31	_	1		_	_														32	0.1
N. bellus: bellus x alegnotus			3	4	3	2	7	7	1	2	5	1	-	1	1					37	6.6
N. bellus bellus											1. 3	_	_	1	4	23	38	16	1	84	15.7
N. atrapiculus		1	2	8	5	4	2	2	8	8	3	3	2	1						49	6.8
N. roseipinnis																					
Mobile Bay		28	24	4	8	3	I	-	1											69	2.2
Pascagoula		13	25	13	3															54	2.1
Biloxi-St. Louis Bays		5	10	11	1	2														29	2.5
Pearl			1	5	22	24	20	17	10	4										103	5.6
Lake Pontchartrain			5	12	32	15	4	1	2											71	4.2
Bayou Pierre		2	-	4	19	24	23	14	5	1										92	5.4
Big Black		2	10	9	20	22	16	14	8											101	4.9
N. bellus alegnotus	22	_	5	2	_	_	1													30	0.7
N. bellus: bellus x alegnotus					1	1	5	3	4	4	10	12	6	5	4	5	2	2		64	10.8
N. bellus bellus															3		127	93	13	259	16.3
N. atrapiculus								3	3	12	12	12	11	5	10	8	7			83	11.7
N. roseipinnis																					
Mobile Bay		14	25	4	1	3	4													51	2.3
Pascagoula		4	36	31	21	9	4	_	2											107	3.2
Biloxi-St. Louis Bays		3	7	8	1	6														25	3.0
Pearl		1	1	1	14	12	24	36	16	7	4	2	1							119	6.6
Lake Pontchartrain		1	4	10	26	13	8	2	3	1	1									69	4.5
Bayou Pierre					1	-	9	5	5	6	3	3								32	7.8
Big Black	1	2	6	8	6	11	12	2 3	13	7	1	-	1							91	5.9

Table 13. Total Fin Pigmentation Index for Breeding Females of the *roseipinnis* Complex. Data in upper Half of Table is for Specimens Less than 40 mm SL; Data in lower Half for Specimens Equal or Greater than 40 mm SL.

													•							
Form and Drainage	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	N	x
N. bellus alegnotus	13																		13	0.0
N. bellus: bellus x alegnotus	14	13	8	1	1	_	_	1		_	_	1							39	1.4
N. bellus bellus		2	_	_	4	1	5	4	11	8	11	13	14	15	15	14	- 5		121	11.1
N. atrapiculus	7	9	38	24	8	4	9	2											101	2.7
N. roseipinnis																				
Mobile Bay		56	18																74	1.2
Pascagoula		29	31	4															64	1.6
Biloxi-St. Louis Bays		16	7	3	1														27	1.6
Pearl		4	16	36	34	5	3												98	3.3
Lake Pontchartrain		7	33	22	9	2													73	2.5
Bayou Pierre		7	18	23	14	6	1												69	3:0
Big Black		31	61	31	16	5	2												146	2.4
N. bellus alegnotus	25					,										-			25	0.0
N. bellus: bellus x alegnotus	1	17	11	8		2	2	2	_	_	1								44	2.5
N. bellus bellus									4	1	6	9	10	16	44	64	78	15	247	14.6
N. atrapiculus		1	6	19	19	12	15	15	6	$\hat{3}$	3	í		-0		01	••	10	100	5.2
N. roseipinnis		_	•					10	•	·	•	-							100	0.2
Mobile Bay		27	14	1															42	1.4
Pascagoula		17	52	8	4														81	2.0
Biloxi-St. Louis Bays		6	15	2	-	2													25	2.0
Pearl		ž	8	$1\overline{7}$	24	14	5	4											74	4.0
Lake Pontchartrain		6	12	16	7	2	2	-											45	2.8
Bayou Pierre		_		2	3	8	14^{-}	4	3										34	5.7
Big Black		5	7	18	16	7	2	2	_	1									58	3.6

Table 14. Proportional Measurements (Expressed in Thousandths of SL) for Breeding Males of Members of the roscipinnis Complex. Mean is GIVEN ABOVE, RANGE BELOW.1

	bellus	bellus X	bellus	atra-	rosei-
Character	alegnotus	alegnotus	bellus	piculus	pinnis
N	24	28	86	55	181
Mean SL (mm)	43.92	44.42	45.52	44.45	44.14
Predorsal length	549	547	536	548	549
· ·	529-564	534–567	518-563	533-562	52 3–573
Postdorsal length	478	479	492	482	_2
Ŭ	465-506	466-488	474–510	464-499	
Prepelvic length	491	486	480	484	479
	471–504	469-500	459-501	459–497	454 -4 99
Preanal length	635	635	638	640	634
Ö	622-644	621–650	615–655	617–659	603–653
Head length	235	234	239	243	237
8	221-249	220-248	224-258	231-259	224–251
Head depth	159	164	174	170	_2
•	151-166	152-178	156-191	160-178	
Postorbital head	97	97	104	100	99
length	90-102	91-104	95–117	93-107	87-112
Snout length	70	72	71	74	_2
	65- 78	66- 78	66- 79	68- 80	
Upper jaw length	81	83	86 .	87	84
offer im render	77- 88	77- 92	78- 96	81- 95	73- 96
Gape width	59	57	61	60	_2
oup o	53- 67	50- 65	52- 71	52- 66	
Fleshy orbit length	71	70	71	76	75
	65- 76	64- 77	65- 79	67- 84	67- 82
Fleshy interorbital	89	91	94	92	_2
width	82- 97	85-101	85-105	86- 98	
Body depth	220	230	250	241	_2
	196-235	209-255	221-282	216-268	
Body width	136	140	139	133	_2
body widen	127-143	115–157	123-158	118–157	
Caudal peduncle	233	225	226	218	_2
length	216-251	205–248	204-248	201–236	
Caudal peduncle	105	101	107	103	_2
depth	94–113	93-109	97–118	96–110	
Dorsal fin length	205	210	233	224	_2
Dorsar in length	194-225	188–225	211–268	205-243	
Anal fin length	198	219	224	225	226
and in length	184-216	200-236	197-246	211-243	199-252
Pectoral fin length	165	166	179	173	_2
rectoral in length	157–182	155–179	165-205	160–192	
Pelvic fin length	143	141	154	148	_2
retate un tengen	131-150	131–150	141–169	138–160	
	101-100	101-100	141-109	100-100	

¹All specimens measured were 40–50 mm SL. ²A variable character; refer to Table 15.

Table 15. Proportional Measurements (Expressed in Thousandths of SL) That show Interdrainage Variation in Breeding Males of N. roseipinis. Mean is given Above, Range Below¹.

Character	Mobile Bay	Pascagoula	Biloxi-St. Louis Bays	Pearl	Lake Pont- chartrain	Bayou Pierre	Big Black
N	28	43	9	31	15	22	33
Mean SL (mm)	44.07	44.16	44.67	44.36	43.83	44.19	43.91
Postdorsal length	472	476	477	483	482	488	488
O .	459-492	461-502	466-490	459-503	450-495	473-500	473-509
Head depth	158	165	162	164	165	175	173
•	149-168	154-174	156-171	155-172	154-176	166-183	162-186
Snout length	70	7 1	71	70	70	73	72
9	65– 77	63- 77	68- 76	65- 76	65- 77	69- 77	67- 77
Gape width	55	58	55	59	57	61	61
	47- 62	50- 68	50 – 61	52- 69	50- 66	55- 70	55- 69
Fleshy interorbital width	86	88	86	87	89	94	93
	83- 91	80 94	80 91	80 92	85- 94	89- 98	88- 98
Body depth	212	224	218	230	230	266	259
	196-229	201-251	212-235	219 - 252	210-255	247-285	239-280
Body width	124	128	124	132	130	146	139
ŕ	113-139	112-138	117-132	117-146	123-140	133-159	128-160
Caudal peduncle length	211	214	212	217	214	221	222
• 9	186-230	193-237	200-224	201 - 229	194-228	207-232	199-248
Caudal peduncle depth	93	97	98	99	99	109	107
	88-101	90-109	91-106	93-109	96-105	102-116	100-113
Dorsal fin length	204	206	213	215	209	230	225
8	193-217	188-227	204-226	198-230	199-226	215-251	206-249
Pectoral fin length	164	169	171	170	169	179	179
<u> </u>	151–176	157-182	164-184	155-184	159-187	167-198	165-196
Pelvic fin length	137	137	140	141	138	148	147
-	127-148	128-148	133-152	125-159	131-149	140164	134-163

¹All specimens measured were 40-50 mm SL.

Table 16. Summary of the Important Quantitative Characters Differentiating Members of the roseipinnis Complex. All Numbers in Parentheses are Means. Measurements (Presented as Thousandths of SL) are for Breeding Males 40–50 mm SL.

Character	N. bellus alegnotus	N. b. bellus	N. atrapiculus	N. roseipinnis
Body circumference scales	Usually 28–32; modally 29–31; (30.2)	Usually 29–33; modally 30–31; (30.4–31.4)	Usually 31–36; modally 33–34; (33.3–34.7)	Usually 30–35; modally 31–34; (31.5 in East— 33.6 in West)
Caudal peduncle scales	Usually $5-2-5=12$ or $6-2-5=13$	Usually $7-2-5=14$, occasionally $7-2-6=15$	Usually $7-2-5 = 14$	Usually $7-2-5=14$
Anal fin rays	Usually 10, occasionally 11; (10.2)	Usually 10 or 11; (10.4–10.6)	Usually 11, occasionally 10; (10.7–11.2)	Usually 12 (in East) to usually 11 (in West); (12.1 in East—11.1 in West)
Pectoral fin rays	Usually 12-14; (12.9)	Usually 13–15; (13.6–14.1)	Usually 13–15; (13.4–14.2)	Usually 13–15; (13.6–14.0)
POM canal pores	Usually 11-13; (12.0)	Usually 10–12; (10.9–11.6)	Usually 10-12; (10.6-11.6)	Usually 9–11; (9.8–10.5)
Gill rakers	Usually 7–8; (7.3)	Usually 6–8; (6.8–7.4)	Usually 5–7; (6.1–6.6)	Usually 5–7; (5.8–6.5)
% occurrence one pharyngeal tooth in minor row, either side	60%	15%	15%	21%

(Table continued on next page)

1972

SNELSON:

NOTROPIS

(LYTHRURUS)

SYSTEMATICS

Table 17. Summary of the Pigmentary Characters Differentiating Members of the roseipinnis Complex.

Character	N. bellus alegnotus	N. b. bellus	N. atrapiculus	N. roseipinnis
Dorsal fin pigment*	Figs. 3A, 9	Figs. 3B, 4I	Figs. 3C, 4E	Figs. 3D-E, 4A
Anal fin pigment*	Interradial pigment usually absent	Figs. 3B, 4]	Figs. 3C, 4F	Figs. 3D-E, 4B
Pectoral fin pigment *	Similar to <i>N. roseipinni</i> s (Fig. 4C)	Fig. 4K	Fig. 4G	Fig. 4C
Pelvic fin pigment*	Interradial pigment usually absent	Figs. 3B, 4L	Figs. 3C, 4H	Figs. 3D–E, 4D
Fin pigmentation index	·			
Breeding males	Total index value usually 0	Total index value usually 15–17; little change with size	Total index value usually 9–15 in large adults; increases linearly with size	Total index value variable; usually 1–4 in East increasing to 4–9 in West; slight to moderate linear increase with size.
Breeding females	Total index value 0	Total index value usually 10–17 in large adults; increases asymptotically with size	Total index value usually 2–8 in large adults; increases linearly with size	Total index value variable; usually 1–3 in East increasing to 3–6 in West; slight linear increase with size
Lateral stripe	Usually present	Usually absent	Usually absent	Usually absent
Preorbital and lip pigment	Usually conspicuously dark	Usually not con- spicuously dark	Usually not con- spicuously dark	Usually not con- spicuously dark
Chin pigment	Variable	Usually as in Fig. 2A	Variable	Usually as in Fig. 2B along Gulf Coast variable in Miss. Valley
Secondary sexual features°	Body not melanistic; no darkened scales or chevrons	Body tending to become melanistic; darkened lateral body scales and chevron markings on upper anterior sides often present	Body not melanistic; no darkened scales or chevrons	Body not melanistic; usually no darkened scales; chevron markings on upper anterior sides occasionally present

^{*}Breeding males

Contributions to the BULLETIN OF THE FLORIDA STATE MUSEUM, Biological Sciences may be in any field of biology. Manuscripts dealing with natural history or systematic problems involving the southeastern United States or the New World tropics are solicited especially. Manuscripts should be of medium length — circa 50 to 200 pages (15,000-60,000) words). 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 the author receives fifty copies free, and he may purchase additional separates at cost if ordered when page proof is returned.

PREPARATION OF MANUSCRIPT

Contributors should consult recent numbers of the BULLETIN for preferred style and format. Highly recommended as a guide is the CBE Style Manual, third edition, 1972 (Washington, D. C., Amer. Inst. Biol. Sci.).

MSS must be submitted in duplicate (please no onionskin) and satisfy the following minimal requirements: They should be typewritten, double-spaced (especially tables, figure captions, and "literature cited"), on one side of numbered sheets of standard (8½ x 11 in.) bond paper, with at least one-inch margins all around. Tables (which should be unruled) and figure legends should be typed on separate sheets. All illustrations are referred to as figures. They must comply with the following standards: Photographs should be sharp, with good contrast, and printed on glossy paper. Drawings should be made with dense black waterproof ink on quality paper or illustration board. All lettering will be medium weight, sans-serif type (e.g. Futura Medium, News Gothic) in cutout, dry transfer, or lettering guide letters. Make allowance so that after reduction no lowercase letter will be less than 1 mm high (2 mm is preferred) nor any capital letter greater than 5 mm high. The maximum size for illustrations is 8½ in. x 14 in. (twice typepage size); illustrations should not be less than typepage width (4 5/16 in.). Designate the top of each illustration and identify on the back with soft pencil by author's name, MS title, and figure number.