

ERNEST A. LACHNER
and ROBERT E. JENKINS

*Systematics, Distribution,
and Evolution of the Chub
Genus *Nocomis* Girard
(Pisces, Cyprinidae) of
Eastern United States, With
Descriptions of New Species*

SERIAL PUBLICATIONS OF THE SMITHSONIAN INSTITUTION

The emphasis upon publications as a means of diffusing knowledge was expressed by the first Secretary of the Smithsonian Institution. In his formal plan for the Institution, Joseph Henry articulated a program that included the following statement: "It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge." This keynote of basic research has been adhered to over the years in the issuance of thousands of titles in serial publications under the Smithsonian imprint, commencing with *Smithsonian Contributions to Knowledge* in 1848 and continuing with the following active series:

Smithsonian Annals of Flight
Smithsonian Contributions to Anthropology
Smithsonian Contributions to Astrophysics
Smithsonian Contributions to Botany
Smithsonian Contributions to the Earth Sciences
Smithsonian Contributions to Paleobiology
Smithsonian Contributions to Zoology
Smithsonian Studies in History and Technology

In these series, the Institution publishes original articles and monographs dealing with the research and collections of its several museums and offices and of professional colleagues at other institutions of learning. These papers report newly acquired facts, synoptic interpretations of data, or original theory in specialized fields. These publications are distributed by mailing lists to libraries, laboratories, and other interested institutions and specialists throughout the world. Individual copies may be obtained from the Smithsonian Institution Press as long as stocks are available.

S. DILLON RIPLEY
Secretary
Smithsonian Institution

SMITHSONIAN CONTRIBUTIONS TO
ZOOLOGY

NUMBER 85

Ernest A. Lachner
and *Robert E. Jenkins*

Systematics, Distribution,
and Evolution of the
Chub Genus *Nocomis*
Girard (Pisces, Cyprinidae)
of Eastern United States,
With Descriptions of
New Species

SMITHSONIAN INSTITUTION PRESS

CITY OF WASHINGTON

1971

ABSTRACT

Lachner, Ernest A., and Robert E. Jenkins. Systematics, Distribution, and Evolution of the Chub Genus *Nocomis* Girard (Pisces, Cyprinidae) of Eastern United States, with Descriptions of New Species. *Smithsonian Contributions to Zoology*, number 85, 97 pages, 1971.—The chub genus *Nocomis* Girard of North America is characterized and relationships among three species groups are discussed. Two new species are described from the central Appalachian region, both in the micropogon species group.

The three species groups are defined and their characters are summarized; namely, the biguttatus group with three species, the micropogon group with three species, and the leptcephalus group with three subspecies. The central Appalachian region is inhabited by four species, *N. micropogon* (river chub), *N. platyrhynchus*, new species, (bigmouth chub) and *N. raneyi*, new species (bull chub) of the micropogon group, all of which are sympatric with *N. leptcephalus* (blue-head chub) in one or more river drainages. A key to these four species and a discussion of the nomenclatural history of the genus and nominal species are included. Important diagnostic characters useful in differentiating among the specific and several infraspecific populations are discussed, evaluated, and summarized in twenty-seven tables. An account of each species includes a synonymy, diagnosis, description, and comparison of meristic and morphometric characters, coloration in life and in preservation, population differentiation, reproduction, growth and size attained, materials studied and geographic distribution. The species are illustrated, special body features are drawn, distributions are plotted, and important character data are shown in thirty figures.

The ecological requirements of the chubs are reviewed and species preferences discussed. Regional ecology is reviewed in respect to occurrence and abundance of the species. Associations, interrelationships and frequency of hybridization are compared among the four species. Differences are observed among the species of the micropogon group in their frequency of hybridization with *N. leptcephalus*.

The biological and geological evidence providing an explanation of the dispersal of the chubs and other species of fishes in various interdrainage exchanges in the central Appalachian region is comprehensively reviewed. Possible routes of entry into the several drainages are proposed. Present, detailed distributional patterns of the chubs and other species are related with geologic events, and present and past ecological conditions in an effort to understand the conditions, barriers, and routes affecting dispersal. Three kinds of geological events that operated in the dispersal of chubs are considered: stream capture, eustatic changes of the Atlantic Coastal Plain, and Pleistocene drainage modifications. The discussion on the evolution of the species of *Nocomis* is based on morphology, coloration, zoogeography, and life history.

Official publication date for each title is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, Smithsonian Year.

UNITED STATES GOVERNMENT PRINTING OFFICE
WASHINGTON : 1971

For sale by the Superintendent of Documents, U. S. Government Printing Office
Washington, D. C. 20402 - Price \$1.25 (paper cover)

Contents

	<i>Page</i>
Preface	1
Introduction	2
Acknowledgments	6
Diagnostic Characters	7
Genus <i>Nocomis</i> Girard	13
Key to the Species of <i>Nocomis</i>	16
The micropogon Group	16
<i>Nocomis raneyi</i> , new species	17
Atypical <i>Nocomis raneyi</i>	32
<i>Nocomis platyrhynchus</i> , new species	37
<i>Nocomis micropogon</i> (Cope)	42
The leptocephalus Group	50
<i>Nocomis leptocephalus</i> (Girard)	50
Ecology, Association, and Frequency of Hybridization	55
Dispersal: The Biological and Geological Evidence	61
Evolution of <i>Nocomis</i>	73
Summary	78
Literature Cited	80
Tables 1–27	85
Index	95

Ernest A. Lachner
and Robert E. Jenkins

Systematics, Distribution, and Evolution of the Chub Genus *Nocomis* Girard (Pisces, Cyprinidae) of Eastern United States, With Descriptions of New Species

Preface

The first author of this series of studies became interested in the systematics and life history of the North American barbeled cyprinids, Genus *Nocomis*, more than twenty years ago. A new species was discovered from the Roanoke River in 1946 based on one large adult male. Shortly thereafter, a new form was found in the New-Kanawha River drainage. At that time three highly differentiated and widely distributed species in the genus were recognized, *N. biguttatus*, *N. leptocephalus*, and *N. micropogon*. Additional collections of the new forms from the central Appalachians and adequate collections of the described species accumulated slowly at first, and little progress was made toward an understanding of the systematics of the group. Relationships among the species were not clear because the primary diagnostic characters showed allometric development and they were also sexually dimorphic. In addition, some species showed considerable populational divergence in certain river systems on a subspecific or racial level. It became apparent from preliminary exploratory studies that new forms were also present in the Cumberland and Green River drainages, the

Arkansas River drainage, and in rivers of the southern Appalachian slope.

Solution of the systematic problems necessitated large series of adults from the major drainages of eastern United States, westward to the Ozarks and the Missouri River basin. In recent years extensive collections became available through the cooperation of many institutional and state workers. Many tuberculate adult male specimens, which are of greatest importance for systematic study, were obtained mainly by electro-seining and angling. These collections and those housed in other American museums, numbering more than 100,000 specimens, coupled with recent field work brought the study to fruition.

The systematic studies revealed that the three recognized species were members of separate groups, each group containing three forms. New insight was obtained on generic relationships among the American cyprinid genera *Hybopsis*, *Nocomis*, and *Notropis* and of the evolution of the nest building chubs, *Nocomis*. Field studies contributed comparative data on the ecology, distribution, and dispersal of the species. Intensive appraisal of important diagnostic characters showed that certain specimens, identified as "variants" in the early stages of the study, represented natural interspecific hybrids. Five interspecific *Nocomis* hybrid combinations were discovered and seventeen intergeneric combinations in-

Ernest A. Lachner, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560. Robert E. Jenkins, Roanoke College, Salem, Virginia 24153.

volving *Nocomis* with other cyprinid genera were described. A population of *N. micropogon*, inhabiting the Potomac River, approaches characters of the new species in the New River drainage and may have resulted from introgressive hybridization from early and limited dispersal through the headwaters of the Monongahela River at times when these waterways (Greenbrier, Monongahela, Potomac) were variously connected.

It was known that the males of the three previously established species (*N. biguttatus*, *N. micropogon*, and *N. leptocephalus*) build and guard large gravel nests during the spring reproductive period. The reproductive behavior of *N. biguttatus* and *N. micropogon* was reported by several authors as well as the utilization of the nests of these three species by other fishes as reproductive sites. Since the morphology (the number and distribution of nuptial tubercles on the head and body and the development of nuptial head crests) differs among *Nocomis* species, it was pertinent to investigate whether all species of *Nocomis* construct nests, and to determine possible differences in their breeding behaviors related to the specific nuptial characters. It was discovered that the males of all species of *Nocomis* build a nest which is guarded by a solitary male. The interactions between interspecific and intergeneric breeding populations over the nest were studied in respect to agonistic and compatible associations, particularly involving the breeding male *Nocomis*. The extent and significance of the utilization of the nests of *Nocomis* by other fishes, especially the cyprinids, were comprehensively evaluated. Since the reproductive activities of chubs necessitates relatively large amounts of water with moderate to fast flow, beds of small gravel and comparatively large areas (the small creeks are not inhabited by *Nocomis*, and fighting occurs when the males have limited nesting space), it is not possible to experimentally breed the species without elaborate and extensive habitat construction, using large artificial riffle-pool complexes; consequently stream sites were sought and selected where observation and study under natural conditions could be done for all the species of *Nocomis*. The various breeding behavioral patterns and associations of species were thus evaluated in regard to their functional and/or evolutionary significance. The impact of these associations in the production of natural hybrids was

appraised. Thus, a study of the evolutionary biology of the chubs emerged.

Two individuals participated in various portions of the overall study during their doctoral programs, Martin L. Wiley and Robert E. Jenkins. One study in this series was recently published (Lachner and Jenkins, 1967). A related study was completed by Wiley (1969) on the comparative morphology and histology of nuptial tubercles in fishes.

Six parts will complete this series of studies, all to be published shortly in the *Smithsonian Contributions to Zoology*:

1. "Systematics, Distribution and Evolution of the Chub Genus *Nocomis* (Pisces, Cyprinidae) of Eastern United States, with Descriptions of New Species," by Ernest A. Lachner and Robert E. Jenkins. [Number 85]
2. "Populations of the Polytypic Species *Nocomis leptocephalus* (Girard) with a Description of a New Subspecies," by Ernest A. Lachner and Martin L. Wiley. [Number 92]
3. "Systematics, Distribution, and Evolution of the *Nocomis biguttatus* species group (Family Cyprinidae: Pisces) with a Description of a New Species from the Ozark Upland," by Ernest A. Lachner and Robert E. Jenkins. [Number 91]
4. "Criteria for Analysis and Interpretation of the American Fish Genera *Nocomis* Girard and *Hybopsis* Agassiz," by Robert E. Jenkins and Ernest A. Lachner. [Number 90]
5. "Natural Interspecific and Intergeneric Cyprinid Hybrids Involving the Chub Genus *Nocomis*," by Ernest A. Lachner, Robert E. Jenkins, and Martin L. Wiley. [In preparation]
6. "Reproduction, Behavior, Nest Associations, Hybridization, and Interrelationships Between the Chub Genus *Nocomis* and Other North American Cyprinid Fishes," by Ernest A. Lachner. [In preparation]

Introduction

During a spring collecting trip in 1946 to the central Appalachian region of Virginia, Edward C. Raney, Robert D. Ross, and Ernest A. Lachner examined the catch of a lone angler on the Roanoke River at Salem, Virginia. A large cyprinid on his stringer appeared distinctive from the known members of the nest-building chubs, genus *Nocomis*. Subsequent exploration and study revealed that this specimen

represented a new species confined to several drainages of the central Atlantic slope and that a related undescribed form occurred in the New River drainage. Both forms are closely related to the river chub, *N. micropogon*, a species widely distributed over northeastern United States. Another species, *N. leptocephalus*, sympatric with both species in the area, was also treated. The large amount of study material obtained in recent years made it possible to consider the geographic distribution and dispersal of the species in detail which proved relevant to the interpretation of their evolution.

The objectives of this paper are to (1) describe two new species of American barbeled cyprinids from the central Appalachian region; (2) to discuss their relationships within the micropogon species-group and to describe the species-groups in the genus; (3) to summarize the pertinent information on the ecology of the four species of the central Appalachian region; and (4) to describe the geographic distributions of the species and to postulate their dispersal, based on current distribution, ecology, and the geological history of the region.

METHODS.—The methods of counting meristic characters and measuring body proportions were taken as outlined by Hubbs and Lagler (1958: 19-26) in most instances. Other methods were used when the conventional procedures proved unsatisfactory or when a character was specialized to necessitate exploratory study before a satisfactory procedure was selected. The terminology used is explained below.

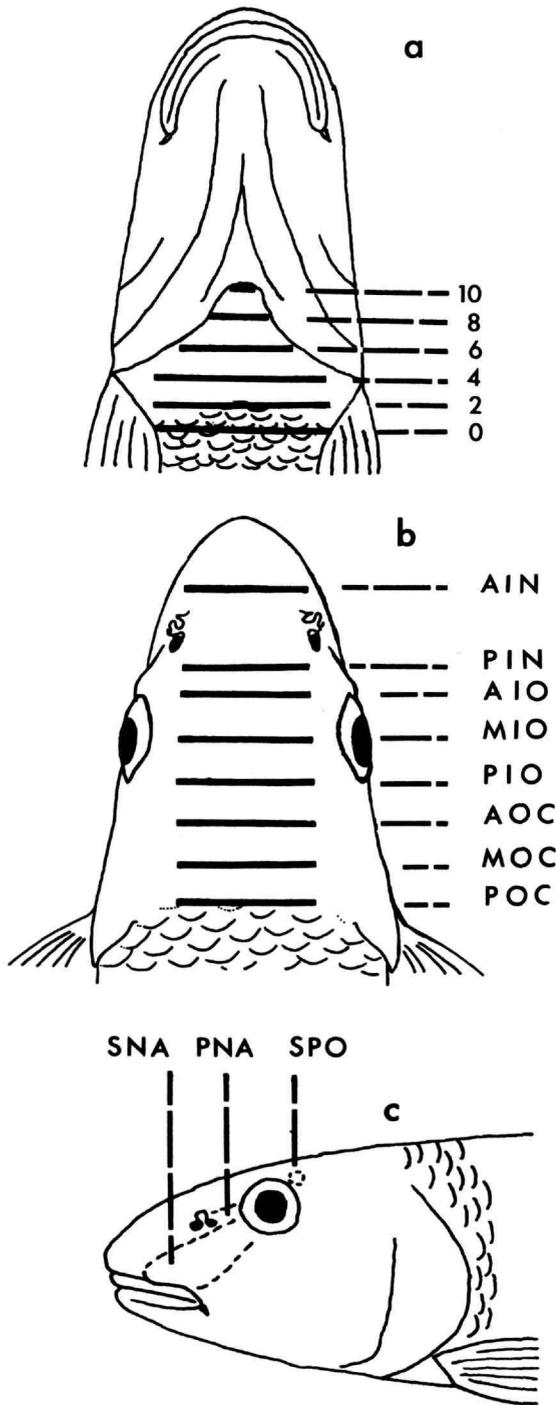
All measurements of length refer to the standard length (SL) in millimeters (mm) unless otherwise stated. The width of the gape was measured as the least distance between the angles of the lips with the mouth in a normal, closed position. The length of the head was taken as the greatest distance from the tip of the snout to the posterior margin of the bony opercle. The postorbital length is the longest measure from the bony orbit to the posterior margin of the bony opercle. The total vertebral count includes the vertebrae in the Weberian complex, presumably four, and the hypural plate as one. The caudal vertebrae count started with the first, elongate haemal spine. This distinction was not possible in the small specimens. The sexes were determined by gonadal inspection. A binocular microscope was used for sexing, determining tubercle and scale development

and counting meristic characters in small specimens.

Our tabular data, particularly that referring to meristic characters, was largely taken from samples of seven to ten specimens each spread over the range of a species within the various river systems as the material permitted. The tabular data is arranged by drainages and, when possible, in geographical sequence.

The breast is considered to be the area bounded by the isthmus, opercular membranes, pectoral fin bases and a line connecting the posterior pectoral fin bases. The degree of breast squamation was quantified by employing the lines shown in Figure 1a and odd-numbered lines between these (not shown). To evaluate the degree of squamation (Table 18), a line was first determined at which the most anterior scales were located. If the breast was fully scaled up to a certain line, the degree of squamation was regarded as the number of the line. When the breast was only partially scaled in areas behind the most anterior scale, it was given an averaged but lower rating. For example, the squamation in Figure 1a is rated as 1. The most anterior scale is at line 2 but only about one half of the area between lines 0 and 2 is scaled. Specimens with both an unscaled breast and an unscaled portion of the area posterior to line 0 were rated as 0.

It was necessary to describe the extent of development of head tubercles as well as their distribution and numbers. For convenience, four stages were recognized in tubercle development, the spot, bud, nuptial tubercle, and scar. Spots (tubercle "anlagen") appear as small, round, light to gray areas in the deeper epidermis. Spots appear first in juveniles and with further development they increase in diameter, become lighter with a darkened center and approach the epidermal surface. Tubercle buds arise in the center as small pimples, having rounded or pointed tips. Nuptial tubercles represent the completed growth stage following budding (Figure 2, see also Wiley, 1969, and Wiley and Collette, 1970). They are hard, cornified structures that attain their greatest development more or less synchronously with the spring reproductive period of the mature males. In life the nuptial tubercles reflect a pearlescent hue particularly at the peak of the reproductive cycle. Tubercle scars are shallow to moderately deep, discolored cavities resulting from the loss of the nuptial tubercles. Unless specifically indicated, data refer-



ring to the numbers and distribution of tubercles may represent any of these four stages.

Tubercle numbers refer, unless otherwise stated, to the total number of tubercles or their counterparts developed on the head. Recently developed spots often contrast poorly with the head coloration and may often be difficult to observe. A film of water applied to the head while counting appreciably aided in discerning the spots. The absence of an opening in the spots distinguishes them from cephalic pores which are often superficially similar in appearance. Tubercles, scars, and buds are easily observed.

Difficulty was encountered in obtaining accurate counts on specimens with high numbers of crowded tubercles. Counting particular tubercles twice or skipping some was avoided by subdividing the head into small quadrants. The quadrants were gently lined with a draftsman pen using a solution of alizarine in ethyl alcohol after the head was dried of excess moisture. This stain dissolved from specimens within about one week.

The areas and lines of the head referred to in discussions of development and distribution of tubercles are indicated in Figure 1b, c. The interorbital and occipital areas are subdivided in order to adequately describe details of tuberculation. The following areas are designated: snout, anterior to line AIN; internasal, between lines AIN and PIN; pre-interorbital, between lines PIN and AIO; anterior interorbital, between lines AIO and MIO; posterior interorbital, between lines MIO and PIO; anterior occipital, between lines PIO and AOC; mid-occipital, between lines AOC and MOC; posterior occipital, between lines MOC and POC. The subnasal area is over the lachrymal bone.

The posterior distribution of tubercles was designated as the line nearest to the most posterior tubercle along the midline area of the head. The absence of tubercles from the snout in the approxi-

FIGURE 1.—Heads of *Nocomis* showing areas and lines pertaining to breast squamation and tuberculation of head: a, degrees of breast squamation (see page 3, methods); b, head tuberculation, dorsal areas; c, head tuberculation, lateral areas. AIN—anterior internasal line; PIN—posterior internasal line; AIO, MIO, PIO—anterior, mid and posterior interorbital lines, respectively; AOC, MOC, POC—anterior, mid and posterior occipital lines. SNA—subnasal [=lachrymal] region; PNA—posterior nasal region; SPO—suprapostorbital position.

mate area from the AIN line to slightly anterior to this line is regarded as a hiatus.

The terminology "nuptial crest" and "swelling" is one of degree. A nuptial crest is a large swelling on the head extending from the internasal area to the nape, where it often descends abruptly, and resembles a "cocks comb" in profile (Figures 23a,c, 25). A "swelling" may represent the early stages of a crest (Figures 10b, 23b) or it may remain a slightly swollen area on the dorsal part of the head. The swelling generally begins its development between the internasal and interorbital area.

Life colors were observed in the field from living specimens and/or from color photographs taken from freshly killed specimens. These colors are distinguished in the text from colors recorded from freshly preserved specimens.

The synonymy pertains to those references dealing with the species of *Nocomis* from the central Appalachian region and where it is pertinent to an understanding of the species. A complete synonymy is not possible, for much of the nomenclature in the early literature of the area refers to *Nocomis* (or *Hybopsis*) *kentuckiensis*, an unidentified nominal form. No specific allocation can be made without the original material because the descriptions are not adequate and illustrations are wanting.

The distribution maps (Figures 19, 20, 28, 29), show all localities involving the new species. Only those localities of *N. micropogon* and *N. leptocephalus* occurring in the drainages with the new species or in adjacent drainages were plotted. These localities are pertinent to an understanding of the geographic distributions and stream captures, and ecological relationships among populations between and within respective species. When more than one collection was taken from a specific locality, only one was indicated on the map.

Distances pertaining to localities are given in air-miles (airmi) or roadmiles (rdmi), but where it was not stated by a collector the most likely measure was determined from maps and/or by some indication of the collector's field route, activities, and notes. The geographic locations of collections plotted on distribution maps were checked with the United States Geological Survey topographic and state maps and route maps of states and counties. A map tracer was used whenever needed for deter-

mining localities given in roadmiles and for measuring stream length.

Descriptive accounts of particular specimens or populations are included in the text, as necessary for an understanding of certain special aspects of

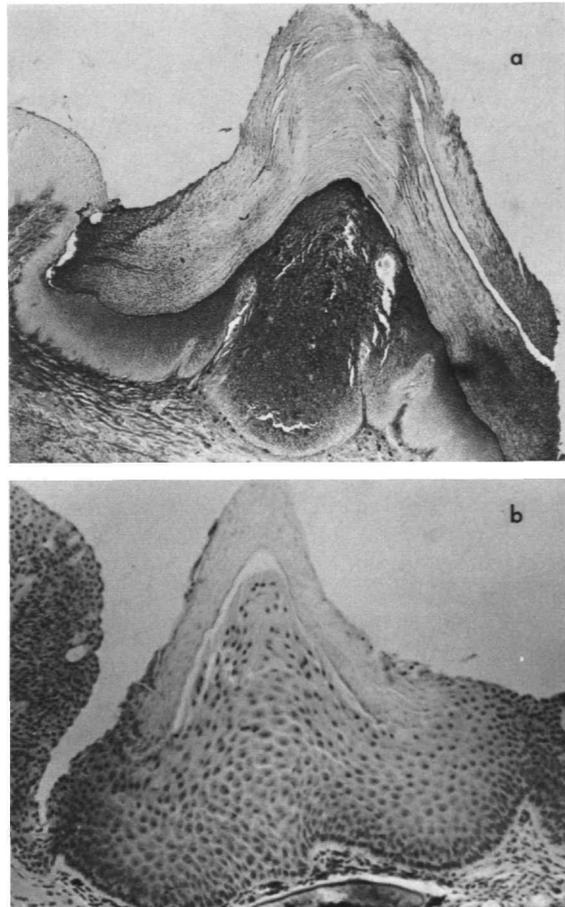


FIGURE 2.—a, Section of a large tubercle from the nuptial crest of *N. leptocephalus*, 147 mm, from the South Fork, Roanoke River, Montgomery County, Virginia, captured in May 1964. The section is 2 mm high from basement membrane to tip, and 2.3 mm wide. The conical keratinized cap is composed of flattened cells forming laminae that separate in preparation. The epidermal core of epithelial cells is penetrated by a series of vascularized dermal papillae. The longer papillae have a series of whorled, spiraling capillaries supported by collagenous tissue and some germinal epithelial cells. Parts of several loops are visible in the section. (Section prepared in Mallory's triple stain.) b, Section of a tubercle from the pectoral fin of a nuptial *N. biguttatus*, KU 7295, 122 mm, collected 14 June 1962 from the Pecatorica River. (Both photographs taken by Martin L. Wiley).

the distribution, dispersal, ecology, or sympatric occurrence of the species. Detailed accounts are given of variation in morphology and of the coloration of all size stages, for this information is necessary for proper identification of living specimens that are observed in the field in studies of reproduction and behavior, nest associations and interrelationships, and of hybridization.

MATERIALS.—A great portion of the material examined from the critical area of western Virginia was taken in recent years during survey studies of several major drainages by Robert D. Ross, his associates, and students of the Virginia Polytechnic Institute, Blacksburg, Virginia. Most of these collections were made using an alternate polarity electroseine with about thirty feet of wire between terminals and with a 115-230 volt AC 2500 Watt generator. This device is effective in obtaining large series of chubs, including the adults from the deeper waters and beneath boulders and banks, and in obtaining a more qualitative and quantitative estimate of local populations. Most of our material from West Virginia was collected or acquired by Frank J. Schwartz, Institute of Marine Sciences, University of North Carolina, Morehead City, North Carolina, and Robert Sumner, Fish Division, Department of Natural Resources, Lewisburg, West Virginia. The several thousand specimens of *Nocomis* taken by these individuals in their surveys are now housed largely at the National Museum of Natural History.

Other collections in the following institutions taken mainly over the past half-century by individuals or survey parties using various sized nets, electric shocking devices, poisons particularly at pre-impoundment stations, angling, traps, etc., have been examined: Auburn University; Field Museum of Natural History, Chicago (CNHM); Cornell University (CU); Duke University (DU); Indiana University (Ind. U.); Kentucky Department of Fish and Wildlife (KFW); University of Louisville; University of Michigan Museum of Zoology (UMMZ); University of Minnesota; National Museum of Natural History (USNM); Oklahoma State University Museum of Zoology (OSUMZ); University of Richmond (UR); Stanford University, Division of Systematic Biology (SU), recently transferred to the California Academy of Sciences.

It is estimated that more than 50,000 specimens

have been examined from these institutions, contributing either directly or indirectly to this study. Locality data for collections pertaining to the new species are listed in the materials section of the respective species. Only the institutions and number of collections from which morphological data were taken are listed for *N. micropogon* and *N. leptcephalus*. Many other collections of these two species examined in the above institutions provided an enormous amount of distributional data. These collections are not listed, but the localities are plotted on the distribution maps when they occur within the treated area.

Acknowledgments

It would be difficult to list the many individuals who have contributed to this study through their field observations, collecting efforts, and museum aid. We are grateful for this cooperation and we wish to acknowledge the special effort made by the following individuals for their prompt assistance in the loan and exchange of collections or in providing pertinent information: Joseph R. Bailey, Duke University; Walter R. Courtenay, Jr., Florida Atlantic University; Reeve M. Bailey and Robert Rush Miller, Museum of Zoology, University of Michigan; James E. Böhlke, Academy of Natural Sciences, Philadelphia; William M. Clay, University of Louisville; Daniel M. Cohen and Bruce B. Collette, Systematics Laboratory, U. S. Fish and Wildlife Service, Washington, D. C.; Royal D. Suttkus and Glenn H. Clemmer, Tulane University; Edward C. Raney, Cornell University; John Ramsey, Fisheries Research Unit, Auburn University; Robert D. Ross, Virginia Polytechnic Institute; Frank J. Schwartz and Robert Sumner.

The following present and former staff contributed most of the illustrative material: Carolyn Bartlett Gast and A. M. Awl, detailed drawings of specimens; Fanny Phillips, diagrammatic figures and graph; Janet L. Robinson, two scatter diagrams; Jack Scott and James Griffen, photographs. Douglass M. Payne, Cornell University, took certain photographs. Glenn H. Clemmer drafted the base map of the Blackwater River. Other drawings and photographs were made by Martin L. Wiley and the authors. Martin L. Wiley read the manuscript and provided valuable suggestions for its improvement.

The second author was able to pursue these studies, including field work, in the fall of 1964 and through July of 1965 with aid from National Science Foundation Grant No. 23395 to Dr. Edward C. Raney, Cornell University. Ernest A. Lachner received support from the Smithsonian Institution Research Awards, Nos. 3316 and 3347, and the Office of Environmental Sciences, Smithsonian Institution.

Diagnostic Characters

The important characters useful in differentiating among the several specific or infraspecific populations are discussed below. Group characters are largely omitted from this discussion.

HEAD TUBERCULATION, HEAD CRESTS, AND SWELLINGS.—The distribution, number, size, and developmental patterns of the head tubercles represent the most critical characters in the separation of the species, and they also represent important evolutionary characters.

Two developmental stages, as defined in the Methods section (p. 3), precede the attainment of enlarged head tubercles. The first stage is the tubercle spot. These first appear, depending on the species, in juveniles of both sexes from between 30 to 80 mm SL. At first they are barely discernible and

remain so in juvenile males and juvenile to adult females of some species, while in other species they become conspicuously enlarged. The second stage is the tubercle bud, a raised area in the center of a tubercle spot which occurs in males of all species and sometimes in females of certain species. The buds vary in texture and size from relatively small and moderately soft to large and well cornified, the latter advanced stage approaching the definitive adult tubercle in development. Individual specimens are often found with both spots and buds, and in these cases the buds apparently grow from the earlier developed spots. Some species develop nearly their adult complement of tubercle spots or buds when juveniles. Other species show a progressive increase in tubercle numbers and distribution over the head with increase in growth throughout life. The number and growth patterns of tubercles are shown in Tables 1-7, 9, 10, 13, 19 and Figure 4. The incipient species differences in adult tubercle number and distribution are evident from the early developmental stages in juveniles (Figure 3). Many specimens of both sexes are specifically identifiable at these stages by their spots and/or buds. Differences also occur in the relative frequency of occurrence of tubercle buds in size classes among the species (Table 4).

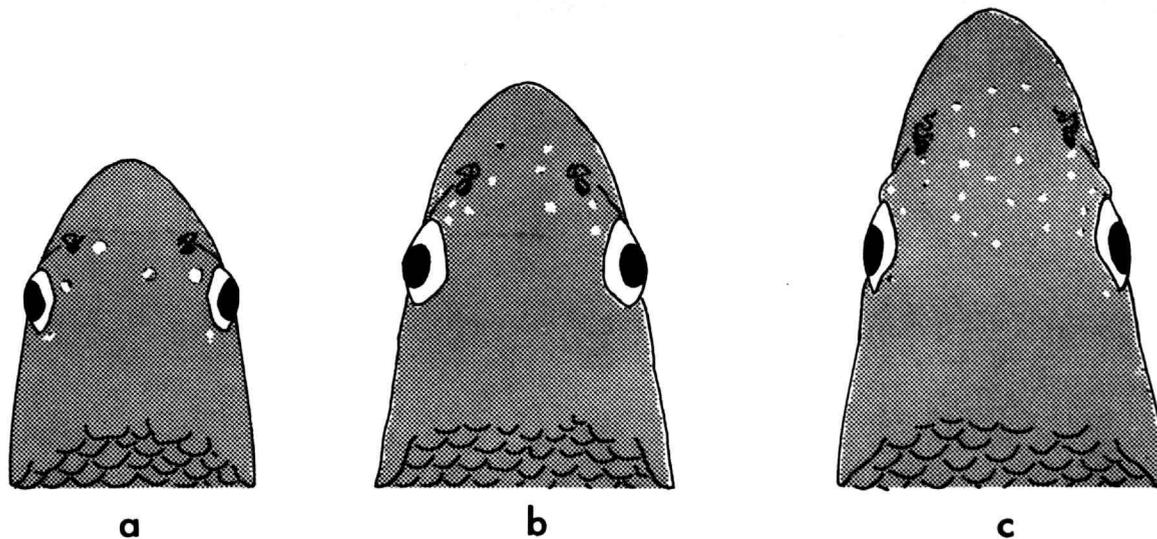


FIGURE 3.—Typical early patterns in the development of tubercles and their size in three species of *Nocomis*. a, *N. leptocephalus*, 66 mm female, James drainage; b, *N. micropogon*, 85 mm female, Tennessee drainage; c, *N. raneyi*, 99 mm male, Roanoke drainage.

Breeding tubercles develop on the head and the dorsal surface of the pectoral fin in nuptial males (Figures 9, 10, 11, 16, 22–27). They attain the height of their development during or slightly before the spring spawning period, coincident with the development of nuptial coloration and head crests or swellings. It is not known if the tubercle "anlagen" increase in number and size at different rates during certain seasons in the females and immature males. They probably do not increase in number in mature males during the reproductive season since spots were never seen on tuberculate males or on post-nuptial males soon after the reproductive season. Tubercle size is related to age or maturity since tubercles average larger in larger males. In *N. micropogon* some overlap occurs between the size of small tubercles of breeding males and large buds of nonbreeding males. There is a consistent difference in size of tubercles between the species although considerable variation exists within species.

Tubercles were never found to be fully developed in females. The female *Nocomis* is not known to participate in nest-building nor to share any of the reproductive activities of the male that may necessitate highly developed tubercles. Ramaswami and Hasler (1955:65-66) induced growth of tubercles in females of *N. biguttatus* to well-developed stages by testosterone injection.

Tubercles in *Nocomis* possibly serve several functions. Since these white to gray-colored epidermal structures are highly conspicuous, they may act as a warning mechanism to individuals of the same and other species, including potential egg predators, that infringe upon the active, nest-building male. Tubercles provide a formidable armament for the male in his defense of the nest, accomplished by butting an intruder with the head. Many breeding males with well-developed tubercles are found with fresh, moderately deep cavities on the head, indicating that tubercles were lost by force. In this respect, the large, nuptial crest or swelling, which is generally best developed in the largest males, may serve to cushion the brain from such impact. This is the best use we can presently conceive of as a possible function of the crest or swelling. The shining tubercles may attract females to the nest, and, since the patterns in which they develop differ among the species, they may also function as an aid in species recognition. The tubercles on the side of the

head, generally all of which are supported beneath by the lachrymal bone, and possibly those dorso-laterally on the head, may aid in maintaining some contact with the female during the spawning act, as do the pectoral fin tubercles. Evidence that male head tubercles function in the stimulation of the female through contact was given for a species of *Notropis* by Koehn (1965:466) and a species of *Etheostoma* (Percidae) by Braasch and Smith (1967: 7, fig. 3). There is no evidence for this function in *Nocomis*.

The head tubercles are deciduous on postnuptial males. Those that are not lost from agonistic behavior apparently fall off shortly after the spawning period. Some tubercles in preserved specimens appear as if they had crumbled apart. Sites once covered by tubercles are scarred and, being evident, are of taxonomic importance as are the other stages of tubercle development. Many of the largest and oldest males die soon after spawning. These specimens are sometimes seen drifting slowly downstream before death or are found dead on the stream bottom, with the previously tuberculated areas and other injuries infected with water fungus, *Saprolegnia*. Tubercle scars of surviving males apparently heal during the summer. Some scars may have a central "core," a remnant of the lost tubercle, or, sometimes a bud may be present. By late summer, the larger adults of certain species usually have buds in varying growth stages and all species show no evidence of fresh scars.

MERISTIC CHARACTERS.—The following meristic characters are tabulated in Tables 8, 11, 12, 14–16: lateral-line scales, body circumferential scale rows, rows of scales above and below the lateral line, caudal peduncle scale rows, pectoral fin rays, and vertebral numbers.

The species differ little in the above meristic characters although certain average values and ranges of counts are particularly useful in distinguishing and relating various populations. The most useful characters are the circumferential scale rows around the body, and vertebral numbers. Scale counts above and below the lateral line and along the lateral line correlate in numbers within species with the circumferential count, but the differences are of somewhat lesser magnitude.

Geographic variation in these meristic characters is apparent and, in a few cases, we have found

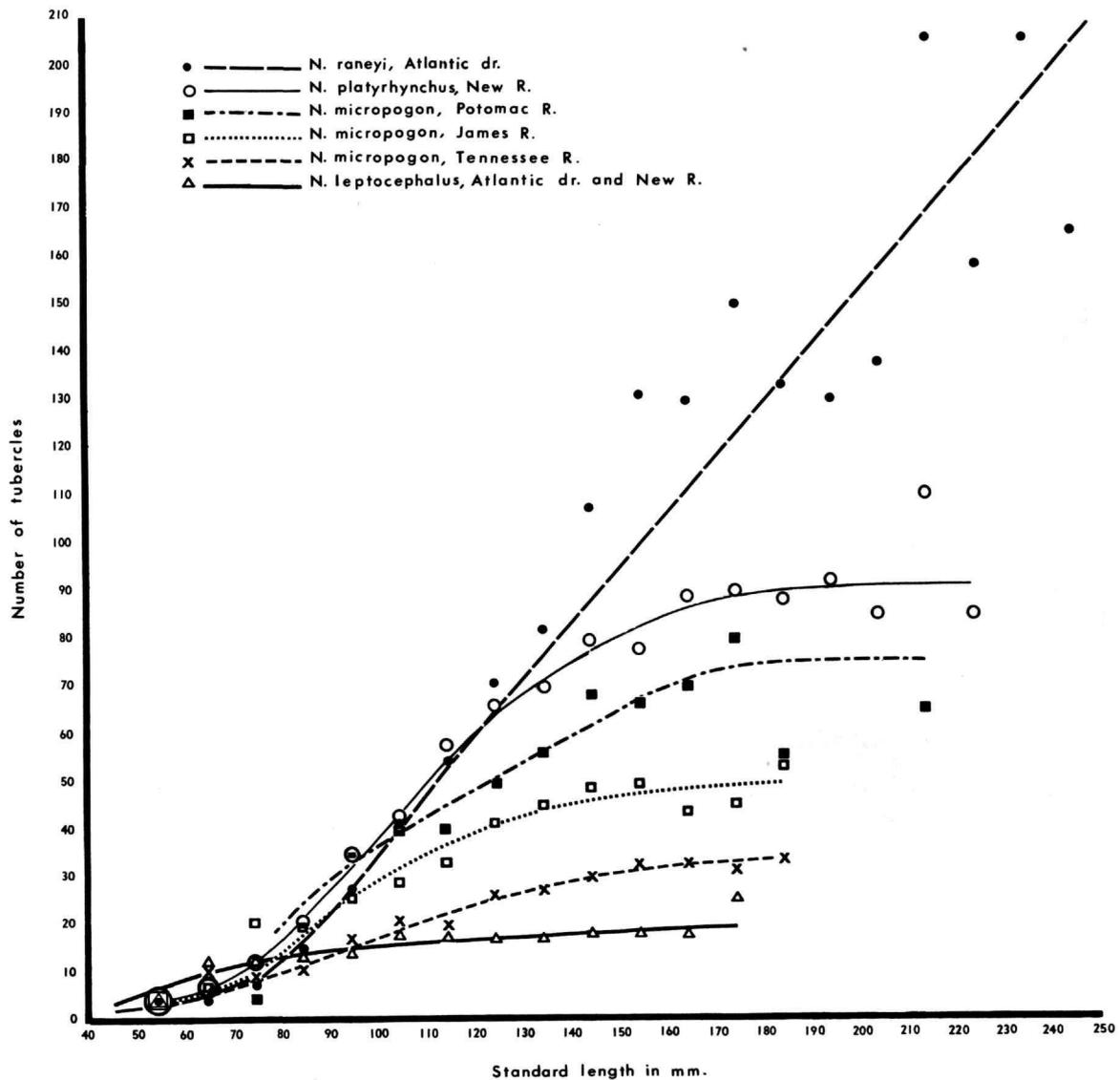


FIGURE 4.—The relationship between body length and number of head tubercles in four species of *Nocomis* of the central Appalachian region. Three populations of the river chub, *N. micropogon*, are compared from the Potomac, James, and Tennessee Rivers. The curves were fitted to mean values by inspection. The data for both sexes were combined. The mean values were plotted from data in Tables 5-7, 9, 10, 13, based on a total of 1712 specimens.

differences among populations within a single drainage. Intraspecific differentiation is discussed in each species following the descriptive data.

MORPHOMETRIC CHARACTERS—Lachner's (1946:

207-208) key to three species of *Nocomis* contained morphometric characters. Raney (1950:161), Moore (1957:109), and Ross (1959:12) and others employed a modification of this key. We have reevaluated the

characters used by these authors and surveyed additional ones with respect to possible allometric growth.

Many morphological characteristics of the head

and body among the species were compared in a preliminary manner. While notable differences were observed, it soon became apparent that there were considerable allometric growth changes extending

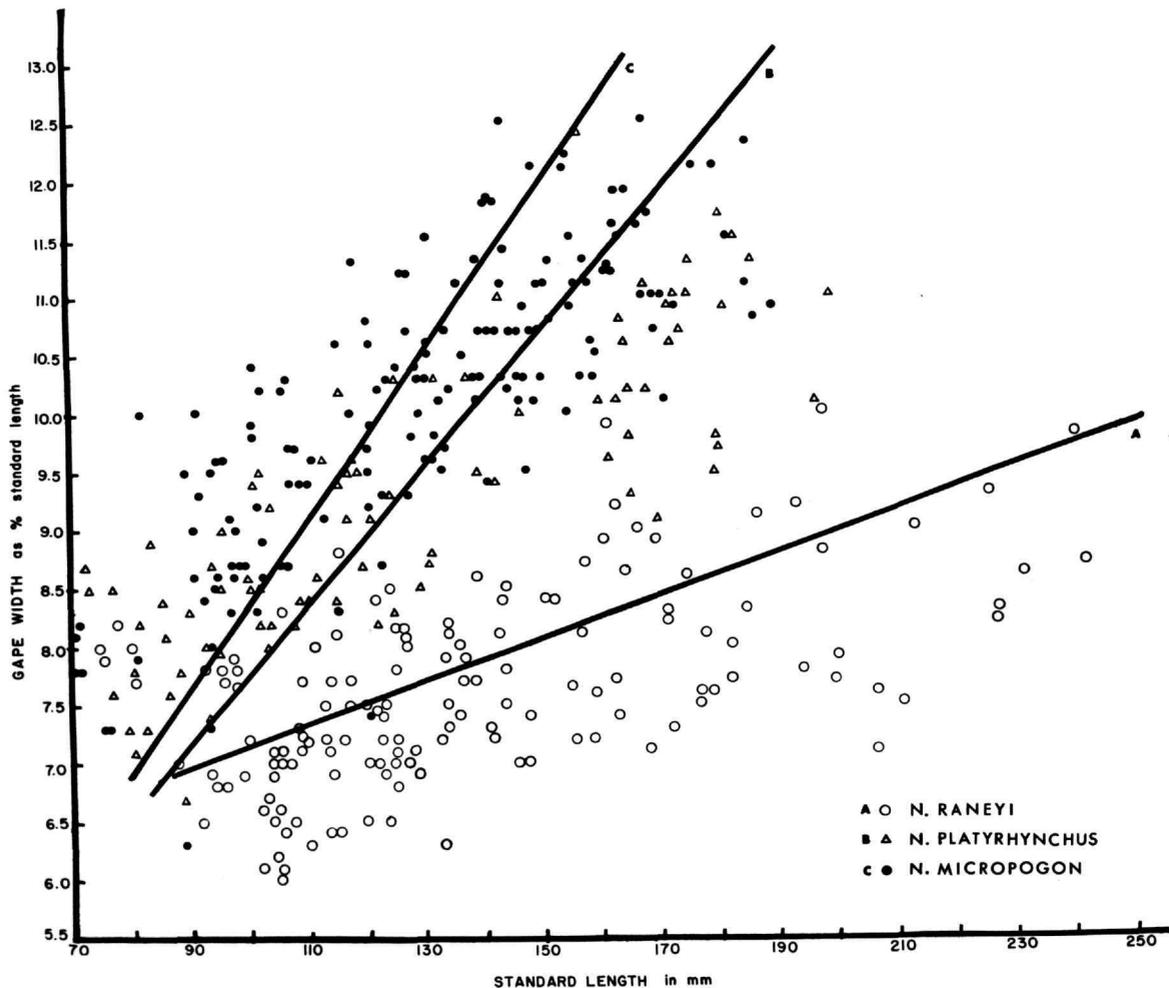


FIGURE 5.—The relationship between standard length and gape width in three species of *Nocomis*. The plots are based on 146 *N. raneyi*, 88 *N. platyrhynchus* and 151 *N. micropogon* taken from specimens sampled over the ranges of the species. The regression equations are: *N. micropogon*, $y = .0294X + 6.24$, $n = 92$; *N. platyrhynchus*, $y = .0247X + 6.07$, $n = 103$; *N. raneyi*, $y = .0075X + 6.68$, $n = 96$.

Tests of difference of slopes and heights (intercepts) of pairs of regression lines were performed by analysis of covariance (Snedecor, 1956:394-399). F values yielding probabilities greater than .95 were considered significant. The slope of the regression of gape width (as % of SL) on standard length of *N. raneyi* is significantly different from *N. platyrhynchus* ($F = 64.18$) and *N. micropogon* ($F = 60.51$). The slope of the regression lines for *N. micropogon* and *N. platyrhynchus* do not differ significantly ($F = 2.97$) but the heights are different ($F = 42.19$).

in sizes among the young, juveniles, subadults, and mature adult males. The range of a character over these growth stages was so great that they proved to be of little immediate systematic value. Exceptions were found, such as the width of gape and length of snout (Tables 17, 20, 21; Figures 5, 6, 7). These two characters proved useful in distinguishing the two new allopatric forms when each character was related with body size and with each other.

Thirteen additional proportional characters are presented for adult males in Table 25. Most of these characters showed allometric growth but the average values, when based only on adults, provide useful indices that differ among the species.

INTESTINE.—Raney (1947:129) and Moore (1957:108-109) reported that the leptocephalus group has

a looped intestine. This feature constitutes a principle diagnostic group character. Miller (1963:19-20) cited several studies indicating that the Cyprinidae do not possess a true stomach. We refer to the often somewhat swollen anterior portion of the digestive tract (from the posterior end of the esophagus to the first intestinal bend) as an intestinal bulb. The leptocephalus group has the ascending and descending portions of the intestine looped or whorled just posterior to the second intestinal bend and ventral to the intestinal bulb (Figure 8b). Other species of *Nocomis* sometimes have a small to moderate lateral loop but it is never extensively developed (Figure 8a). Specimens of the leptocephalus complex sometimes lack the looped intestine, particularly in certain southern races, and they thus may resemble the micropogon group in this character.

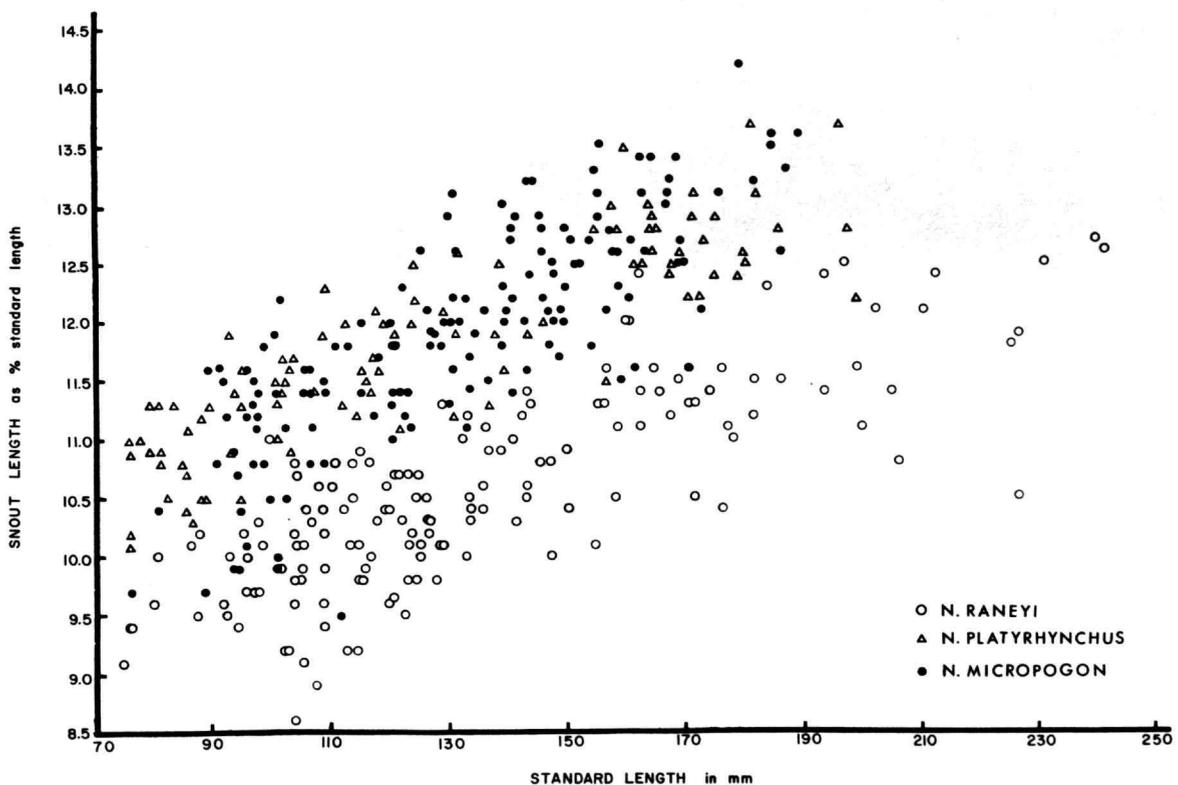


FIGURE 6.—The relationship between standard length and snout length in three species of *Nocomis*. The plots are based on 151 *N. raneyi*, 92 *N. platyrhynchus*, and 159 *N. micropogon* taken from specimens sampled over the ranges of the species.

BREAST SQUAMATION.—A summary of the degree of breast squamation is given in Table 18 with the data segregated by species and drainages. This character showed differences among the species, among some drainage populations within a species, and within species from various geographical areas.

COLORATION.—Life and alcoholic color patterns

showed important interspecific differences and relationships among the groups of *Nocomis*. Sexual dichromatism and color changes associated with growth and season, and local and geographic variation were studied for each species. Certain color differences were evident; other color differences were more subtly developed and noticed only after handling a large number of specimens.

The brilliant nuptial coloration of the male, strikingly different from that of females and nonbreeding males, is very similar among the species of the micropogon group. Differences were found between the micropogon group and the leptocephalus group. Individual differences in breeding color within each species, other than that due to geographic variation, appear to be related to proximity to the peak of reproductive activities and to age or size. Differences also occur in coloration of females and nonbreeding males, particularly between the species groups. The color changes with growth are slight in juveniles, adult females and nonbreeding males of each species. Geographic variation occurs in nup-

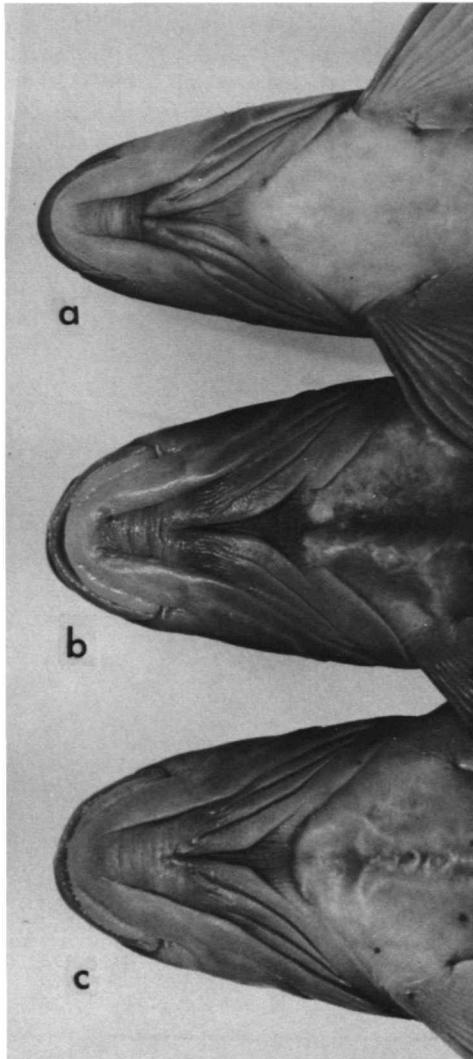


FIGURE 7.—The width of gape and contour of lower jaw in three species of *Nocomis*: a, *N. raneyi*, 181 mm, James River drainage; b, *N. platyrhynchus*, 183 mm, New River drainage; c, *N. micropogon*, 185 mm, James River drainage.

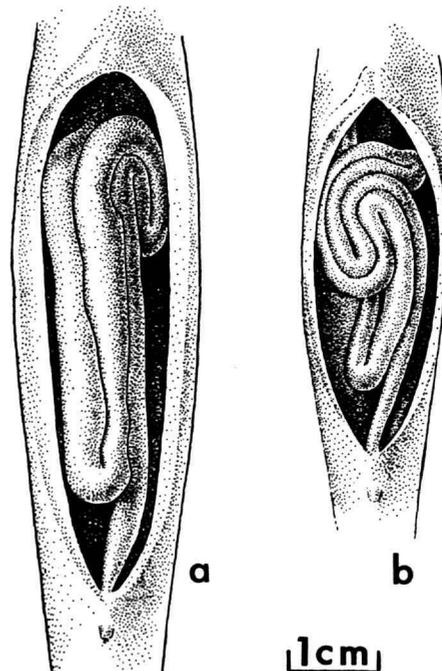


FIGURE 8.—Comparison of intestinal looping: a, *Nocomis raneyi*, female, 113 mm; b, *N. leptocephalus*, female, 86 mm.

tial coloration of *N. leptcephalus* and perhaps in fin coloration of *N. micropogon*.

Sexual dimorphism is pronounced in all species of *Nocomis*. The males at maturity, which may be coincident with the breeding season, or several months before, develop bright colors on the body and fins. The young, juveniles, immature adults, and adult females remain characteristically pale colored. The nuptial males develop enlarged tubercles on the head and pectoral fins, and laterally on the body in two species of the biguttatus group. The adult females develop head spots approaching the full complement of tubercles of the males. Nuptial males develop large head crests or swellings (except the biguttatus group) whereas the females show no trace of tissue enlargement. Adult males acquire rounded head contours contrasting greatly with the sharper lines of the young, juveniles, immature adults, and adult females. The solitary nuptial male constructs a mound nest of gravel that he transports in his mouth.

Genus *Nocomis* Girard

Nocomis Girard, 1856:190 (type species: *Nocomis nebrascensis* Girard = *Semotilus biguttatus* Kirkland by monotypy).

DIAGNOSIS.—Barbled cyprinids, the nuptial males having the following characters: large breeding tubercles on the head (and on body in two species of the biguttatus group), that show a phylogeny among the species in their number, distribution and size; expansive crest or swelling on head (crests absent in biguttatus species group); elaborate breeding coloration on body of pink-rosy, orange and/or blue. Nuptial males construct a mound-nest by carrying stones in mouth. Body bicolored, dark above, light below, with heavy dark scale margins and a dark postopercular bar. Body size large, adult males 100 to 250 mm SL. Mouth normal, moderate to large in size, with one terminal maxillary barbel. Scales large, lateral line almost always fewer than 44, body circumferential scales less than 37. Pharyngeal teeth 1,4-4,1 to 3-3. Scale radii in posterior field only, total number in adults 23-54. Total vertebrae number 38 to 43, precaudal vertebrae 21 to 24.

DESCRIPTION.—Body robust to moderately elongate or compressed. Morphometric growth rate generally moderately to markedly allometric. Head moderate, 25-29 percent of SL, slightly rounded to

flattish above. Snout short to long, 8-14 percent of SL, acutely pointed to well-rounded or blunt and declivous. Mouth subterminal, moderately oblique to nearly horizontal; frenum absent; lower jaw included; gape and upper jaw moderate to large, 7-12 and 7-11 percent of SL, respectively. Lips moderately thick. Single pair of small barbels occasionally absent; origin on flesh over posterior ventral edge of maxilla and sometimes slightly attached to basal portion of lip angle. Orbit small to moderate, 4-8 percent of SL; position lateral to slightly dorso-lateral.

Fins moderate in length; dorsal origin about midlength of body, over or, usually, slightly posterior to pelvic origin; fin margins on dorsal and anal straight, pectoral and pelvic moderately to well rounded, caudal deeply to slightly forked. Caudal fin lobes equal to moderately subequal, upper lobe generally longest and more pointed. Dorsal fin rays 8, and 7, pelvic 8, pectoral 15-19.

Pharyngeal teeth, 1,4-4,1 to 3-3, stout, tooth I or I-III usually with small hook, grinding surface usually developed; tooth arch moderate to stout, pitted surface well sculptured. Gill rakers usually 5-10, short to moderate in length, very rarely with bifurcate tips. Pseudobranchiae well developed. Intestine simple (S-shaped), or an accessory loop on left side, or a single but much convoluted ventral whorl. Peritoneum lightly to heavily pigmented with melanophores.

Lateral line on body complete, almost straight and horizontal to moderately curved; cephalic canals complete, canaliculi well developed (Reno, 1967, 1969b, gives pore counts). Cutaneous taste buds moderate in size, not densely concentrated, present on lower head, snout, lips and barbel; compound buds on first pectoral fin membrane.

Scales with sub-basal focus; eccentric circuli sharply angulate in antero-lateral field; radii numerous limited to posterior field; primary and secondary radii present.

Scales moderately large, the ranges in several characters follow: lateral line 37-43, body circumference 27-38, caudal peduncle 16-20. Breast completely scaled to naked. Vertebrae 38-42.

Color (in alcohol) dark above, light to colorless below; midlateral to dorsal scales with posterior and anterior (scale pockets) margins dark; dark lateral band and dark caudal spot well developed to absent.

Body color (in life) dorsally blackish, olive or tannish; laterally olive greenish, light tannish or light yellowish. Fins olivaceous to reddish orange or color almost entirely absent. Iris partially golden to red-orange.

Sexual dimorphism and dichromatism highly developed in adult males; nuptial tubercles moderate to large, erect, antrorse or curve laterad; tubercles distributed on dorsal and lateral head, nape and sometimes on lateral body; tubercles on pectoral fin rays, 2-9, uniserial, retrorse.

Habitat is streams of sand, gravel, and rocky beds, living near bottom.

Distribution primarily eastern and central United States.

Three species groups, seven species, nine forms.

NOMENCLATURE HISTORY.—The presence of a barbel at, or very close to, the angle of the lip (and other gross similarities) was the principle character involved in the confusion of interpreting several nominal American cyprinid genera. The taxonomic rank of *Nocomis* vacillated between genus, subgenus, and group or section for over 100 years. *Nocomis* was recently resubmerged into the synonymy of *Hybopsis* Agassiz (Bailey, 1951:192) with seven other nominal genera: *Yuriria* Jordan and Evermann, *Erimystax* Jordan, *Platygobio* Gill, *Macrhybopsis* Cockerell and Allison, *Extrarius* Jordan, *Oregonichthys* Hubbs, and *Couesius* Jordan. The weakness of this arrangement became evident when it was learned that the barbel may be a weak, variable systematic character and that other strong group characters had been overlooked. Entire populations of the barbeled species *Hybopsis* (*Hybopsis*) *amblops* and *Hybopsis* (*Erimystax*) *harperi* may lack barbels. Species with barbels also have been recently assigned to *Notropis* (*N. boucardi* for one), a characteristically nonbarbeled American cyprinid genus. In barbeled genera not allocated to *Hybopsis*, the barbel sometimes may be absent or reduced. Current studies based on other characters have also shown a close relationship between *Hybopsis amblops winchelli*, usually having barbels, and *Notropis amnis*, lacking barbels. As a consequence, a number of workers have recently attacked these generic problems by investigating new character systems such as tuberculation, pigmentation, brain patterns, cephalic lateral line sensory canals, and various osteological features. A review of the nomen-

clature history of *Hybopsis* is given by Reno (1969a). A critique of the genus *Nocomis* with a discussion of other North American barbeled cyprinids, particularly *Hybopsis*, will be presented in part 4 of these studies (*Smithsonian Contributions to Zoology*, Number 90).

The species of *Nocomis*, other than our new forms, were all described by 1864. Species were referred by early workers to the genera *Semotilus* Rafinesque, *Hybopsis* Agassiz, *Leuciscus* Klein, *Leucosomus* Heckel, *Nocomis* Girard, and *Ceratichthys* Baird.

The genus *Hybopsis* and type species *Hybopsis gracilis* (= *amblops* Rafinesque, 1820) were described by Agassiz (1854) but the presence or absence of a barbel was not mentioned. For this reason and because the descriptions were brief, the identifications of these taxa were long uncertain. Girard (1856:210-211, 1858:255) recognized *Hybopsis* and mentioned barbels in his accounts, but based his generic description on species other than the type of *Hybopsis*. Subsequently, such authors as Cope (1864:279, 1868:230, 1869:379, 1870:460), Gunther (1868:211), Jordan (1875:38, 1876:94, 1877a:45, 1877b:333, 1877c:27, 1877d:57) and Jordan and Copeland (1876:150) referred certain nonbarbeled cyprinids to *Hybopsis*. On occasion, the barbeled species *H. storerianus* Kirtland was included. Later, however, Jordan (1878b:426) and Jordan and Gilbert (1833:212) aligned *Hybopsis* with barbeled minnows, although they questioned their assignment and recognized the junior name *Ceratichthys*. Either *Ceratichthys* or *Nocomis* were used rather than *Hybopsis* in Jordan (1878a:305, 1879:108, 1880:290, 1882:859, 1884:287) and C. H. Gilbert (1884:203). *Ceratichthys* Baird and Girard (1853, type species *C. vigilax*) was based on a North American cyprinid currently placed in the genus *Pimephales* Rafinesque, 1820. The taxonomic and nomenclature histories of *Ceratichthys* and *Pimephales* were reviewed by Hubbs and Ortenburger (1929:35-38), Hubbs and Black (1947), and Cross (1953).

Close relationships among the forms of *Nocomis* were recognized by Cope (1869:364) and Jordan (1878b:426-427) who were first to place the nominal forms together and exclude all other groups and species from one section of their expanded genus of barbeled minnows. While the forms of

Nocomis were long thereafter included under a broadened *Nocomis*, *Ceratichthys*, or *Hybopsis*, the species of *Nocomis* apparently were considered to constitute a distinct group of subgenus. The first formal opinions that *Nocomis* is not congeneric with these groups was based on scale studies by Cockerell and Allison (1909:159, 161–163), Cockerell and Callaway (1909:189), and Cockerell (1913:130). These authors apparently examined scales from only *N. effusus* (called *kentuckiensis*) and were not generally followed by subsequent writers. We do, however, agree that the scales of *Nocomis* are distinctive from those species once thought to be close relatives. *Nocomis* and other groups with which it was regarded as congeneric were elevated to separate generic status by Jordan (1924) when *Hybopsis* was (temporarily) reidentified with species of *Notropis*. Hubbs (1926:27) and others also recognized *Nocomis* as a genus. *Nocomis* held generic status until Bailey (1951:192) grouped it, with the nominal genera listed above, under *Hybopsis*. *Platygobio* and *Couesius* had not been previously associated with the other seven taxa. There was discontent with this arrangement and since 1966 at least six publications include *Nocomis* at the generic level.

The taxonomic and nomenclatural confusion in the early history of the species of *Nocomis* was largely a result of the very close species relationships, their relatively similar general morphology, and the failure by systematists to recognize the value of certain secondary sexual characters, such as the development of tubercles.

Although seven specific names were proposed clearly for *Nocomis* by the end of 1864, three of which are now applied to species and one to a subspecies, only one, *Luxilus kentuckiensis* Rafinesque, 1820, was generally recognized up until 1926, as a senior synonym for all species of *Nocomis*. The earliest alignments of *kentuckiensis* were with species of the subgenus *Cyprinella* of *Notropis* (*analostanus*, see Gibbs, 1963:521) and at least one other species, *Semotilus biguttatus* Kirtland (1840a, b). Jordan (1876) identified it with *Notropis cornutus* but later (1877c, 1882) stated that it was still not satisfactorily identified. Soon after, Jordan (1885b: 185) curiously stated in his Errata section that (*N.*) *biguttatus* "seems to be the *Luxilus kentuckiensis* Raf." Thereafter, *kentuckiensis* was used

for species of *Nocomis* until Hubbs (1926:28) considered it to be unidentifiable. Both Hubbs (loc. cit.) and Lachner and Jenkins (1967:558) gave reasons for regarding *kentuckiensis* as unrecognizable. Hubbs (1926:27–29) recognized *Nocomis* as a complex of three species, *biguttatus*, *leptocephalus* and *micropogon*, illustrated each, including features of the nuptial males, and clarified their synonymy. *Semotilus biguttatus* Kirtland (1840a,b) was described and figured from nuptial males, leaving no doubt as to its identity. Its synonyms are *Ceratichthys nebracensis* Girard (1856), *Ceratichthys stigmaticus* Cope (1864), and *Ceratichthys cyclotis* Cope (1864). The species *leptocephalus* and one of its subspecies, *bellicus*, were described by Girard in 1856 under *Ceratichthys* and *Nocomis* respectively. *Ceratichthys micropogon* dates from Cope (1864). It is interesting to note that the supposed single species of *Nocomis* (*kentuckiensis*) was frequently stated to be the, or one of the, most widely distributed of North American cyprinids.

Catostomus melanotus Rafinesque (1820:302) as with *Luxilus kentuckiensis* was briefly and poorly described, based apparently on specimens from the Ohio River basin. It was referred to *Nocomis* with uncertainty, or in part, by Jordan (1876, 1877c, 1882, 1885a, 1885b), Jordan and Copeland (1876), Jordan and Evermann (1896), and others. Hubbs (1926:28) regarded *melanotus* as unidentifiable and as likely a catostomid as a cyprinid. We concur with Hubbs' decision. We have also examined the unpublished rough sketch of *melanotus* by Rafinesque (Smithsonian Institution Library) but this afforded no additional clue.

Recently, additional species and forms have been discovered or recognized, and considerable information on the evolution and interrelationships with the genus is known. Our studies indicate that *Nocomis* is clearly divisible into three species groups, each partly comprised of one of the species recognized by Hubbs (1926). The differences among the species groups are compared in Table 22. Some characters in which they differ only slightly are included since these appear to have some biological significance. The major group differences and aspects of their evolution are discussed by Lachner and Jenkins (1967) and herein in the section on evolution.

Key to the Species of *Nocomis* of the Central Appalachian Region

1. Tubercles present on snout anterior to internasal area and on subnasal area in one to three rows in adults and larger juveniles; many tubercles on head, numbering more than 25 in adults; intestine not whorled, occasionally with, at most, a small dorsad or laterad loop along the anterior half of descending portion; scales on body smaller, circumferential scale rows number 30 or more in about 94 percent of specimens sampled 2
 Tubercles always absent on snout anterior to internasal area and always absent on subnasal area; head tubercles greatly reduced in numbers, almost always fewer than 25; intestine usually whorled or with an anterior loop extending to right side covering part of alimentary tract; scales on body larger, circumferential scale rows number less than 30 in 72 percent of specimens sampled. Bluehead chub, *N. leptocephalus* (Girard)
2. Adults typically with smaller and more numerous head tubercles extending in a relatively uniform pattern from the snout along the midline to the occipital area; head tubercles extend posteriorly on midline beyond the anterior interorbital area (AIO) in almost all specimens over 100 mm; hiatus in tuberculation on snout in adults only occasionally present; tubercles number about 60 to 200 in subadults to adults; scales smaller, average values of circumferential scale rows segregated by drainage populations are higher than 32.6 and for lateral line scale rows higher than 40.1; more vertebrae, average values for drainage populations range from 40.5 to 41.6 3
 Adults typically with larger and fewer head tubercles, grouped in the area from the snout to the interorbital area; head tubercles do not extend posteriorly on midline beyond the anterior interorbital area (except some Potomac and Monongahela drainage specimens in which a few tubercles extend to the posterior interorbital area) and almost always occur in a V-shaped, anteriorly directed pattern; a hiatus in tuberculation almost always occurring along midline of snout leaving a small isolated patch near tip of snout; tubercles number fewer than 60 in almost all specimens, and appreciably fewer in the subadults (except the Potomac River population, where slightly higher numbers occur); scales larger, averages for circumferential scale rows range below 32.3 and for lateral line scale rows from 39.9 or lower, when segregated by drainage populations; fewer vertebrae, average values for drainage populations range from 39.3 to 40.4 River chub, *N. micropogon* (Cope)
3. Mouth narrow (Figure 5), gape width almost always less than 9.5 percent of standard length; snout short (Figure 6); body more compressed and deeper in the adults; dark lateral band on body inconspicuous in preserved specimens of juveniles and absent in adults; breast usually naked, or partially scaled; tubercles on forehead crowded, those posterior to midinterorbital line equally or slightly more widely spaced than those anterior to line; pharyngeal arch stout, the limbs short and broad Bull chub, *N. raneyi*, new species
 Mouth wide, gape width almost always greater than 9.5 percent of standard length in adults and subadults larger than 130 mm; snout long; body not compressed and deep in the adults; dark lateral band on body moderately or well developed in preserved specimens of juveniles and adults; breast almost always well scaled; tubercles posterior to midinterorbital line comparatively more widely spaced than those anterior to line; pharyngeal arch weaker, the limbs longer and narrower Bigmouth chub, *N. platyrhynchus*, new species

The micropogon Group

DESCRIPTION.—Nuptial males develop a moderate to large number of tubercles (Figure 4) on head, dorsally, from tip of snout to midoccipital area; tubercles erect or directed laterad, and moderate to large in size; tubercles present over lachrymal in one to three rows; a large more posterior nuptial crest developed by older (larger) males; breeding coloration of nuptial male rosy pink on lower head

and lower body, olive-greenish on upper body; a wide, dark anterior and posterior scale border in adults; dark caudal spot in juveniles small, indistinct; intestine almost always S-shaped; dentition 4-4; scale size intermediate, body circumferential scales range from 28 to 39; body more elongate; snout more pointed; posterior edge of preopercle usually slanted anteriorly below; males attain largest maximum sizes of all *Nocomis*; males of all

three species in group construct large mound-nests, the largest in genus, using small to large size gravel. The species include: *N. micropogon*, widely ranging over much of northeastern United States, from New York and the James River, Virginia, westward, not reaching the Mississippi River; *N. raneyi*, of five central Atlantic slope drainages, and *N. platyrhynchus* of the New River drainage.

Nocomis raneyi, new species

BULL CHUB

FIGURES 7, 9, 10-17

Hybopsis kentuckiensis.—Jordan, 1889:123 (Roanoke dr. [in part], 126 (Tar dr.), 129 (Neuse dr. [part]).

Hybopsis species.—Robins and Raney, 1956:31.

Hybopsis (*Nocomis*) species 2.—Reno, 1969b:739.

Nocomis micropogon.—Burton and Odum, 1945:186 [part].

Nocomis species.—Raney, 1950:184.

DIAGNOSIS.—Differs from the other micropogon group members in: mouth small (Figure 5); snout short (Figure 6, Tables 17, 20, 21); body deep, more compressed laterally in adult males; head tubercles in adults often more than 100 (Table 5) and densely developed from tip of snout to interorbital area; caudal fin more sharply forked; pharyngeal tooth arch stout with short limbs (Figure 18).

DESCRIPTION.—*Morphometry*: Proportional measurements expressed in thousandths of the standard length are given in Table 23 for the holotype, 5 male paratypes, 53 to 227 mm, and 5 female paratypes, 68 to 180 mm. Because of the allometric growth, additional proportional data are given in Table 25 for 13 characters of 24 mature males having a mean length of 200 mm and ranging from 172 to 242 mm. *N. raneyi* is compared in these characters with the adults of the three other chub species from the study area. Many proportions increase with increase in body length. The diameter of the orbit is an exception, decreasing with increase in body length, a characteristic of all known species of *Nocomis*. A number of morphometric values may appear higher in males than in females, but when plotted against body length there are no appreciable differences. The higher values in the males relate only to the larger body size attained by them.

The head is pointy and the body slender in the young and juveniles of *N. raneyi*, resembling *N.*

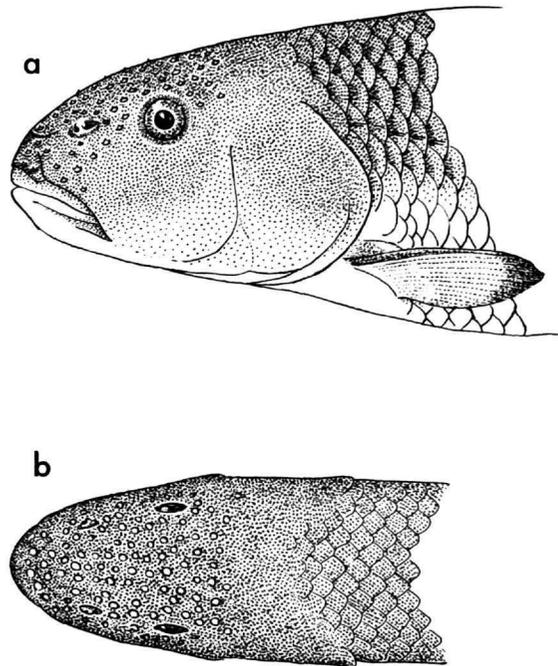


FIGURE 9.—Head of male *Nocomis raneyi* showing distribution of tubercles, tubercle scars, and contour. Paratype, USNM 166404, 229 mm, captured in Roanoke River at Salem, Virginia on 21 June 1946: a, lateral view; b, dorsal view. (Drawn by A. M. Awl.)

platyrhynchus and unlike the more robust body and deeper head of *N. leptocephalus* (Figure 17). As the males approach maturity the facial features become greatly modified, the forehead becomes deep and rounded and the body somewhat slab sided (compare Figure 17, juveniles; Figure 16, tubercle-bud stage in male; Plate 14, adult female in tubercle-spot stage; Figures 10, 12, 15, nuptial tubercle stage of breeding male). In the development of the facial features at maturity *N. raneyi* resembles *N. platyrhynchus* more closely than *N. micropogon* or *N. leptocephalus*.

Two morphometric characters, although showing allometric growth, proved significant in segregating a majority of specimens of *N. raneyi* from its two species cognates in the micropogon group: these were gape width (Figures 5, 7) and snout length (Figure 6), when related to body length. The relationships of gape width plotted against standard

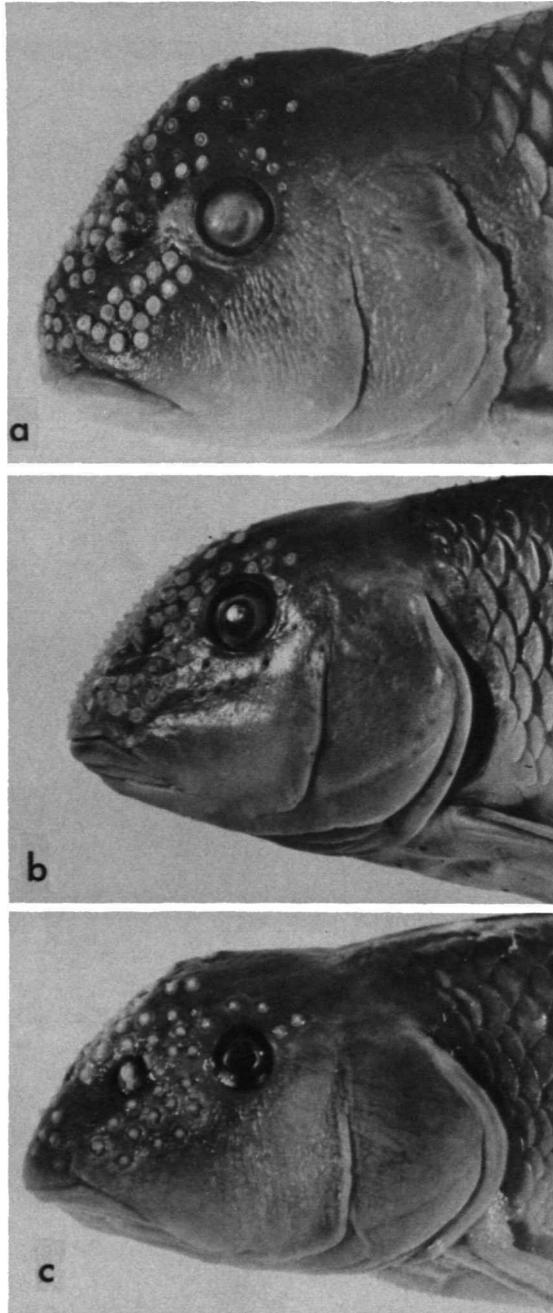
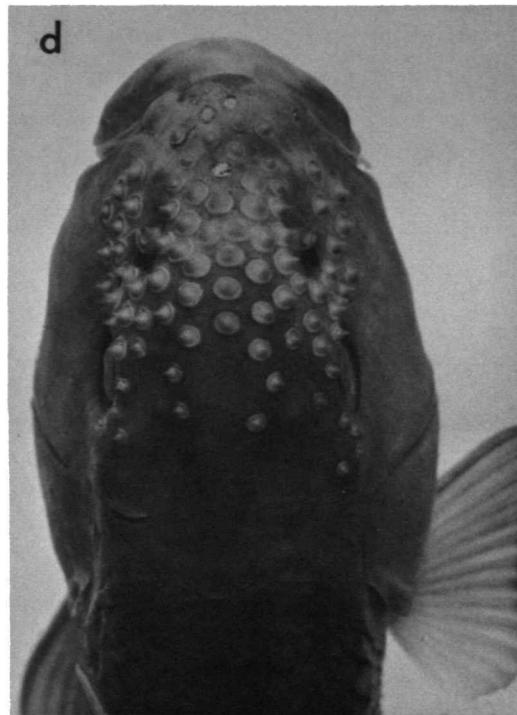
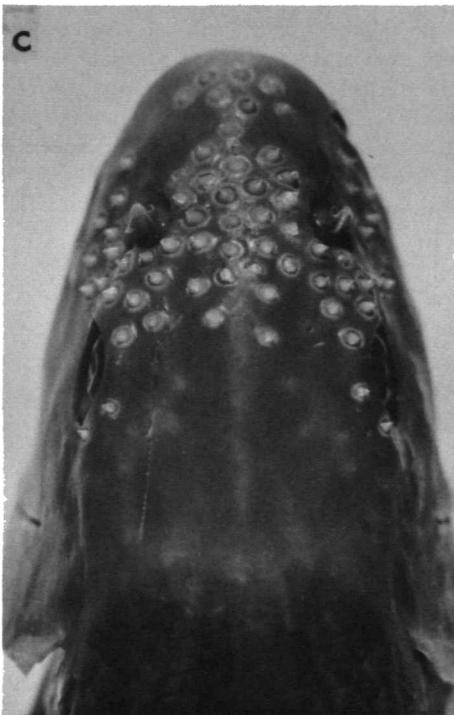
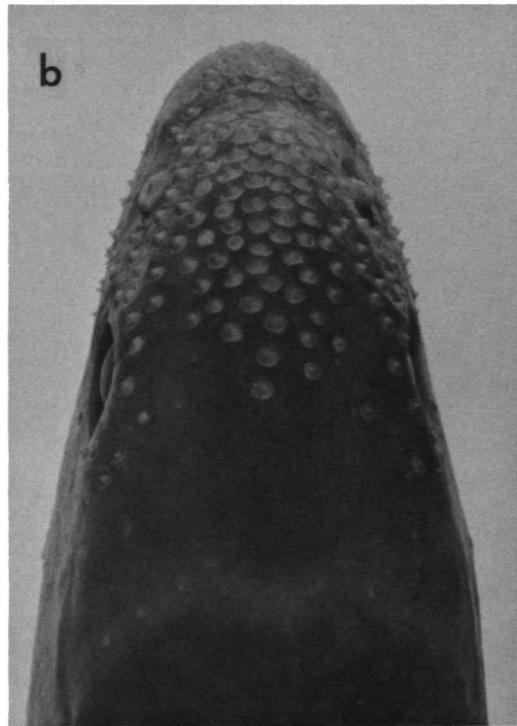
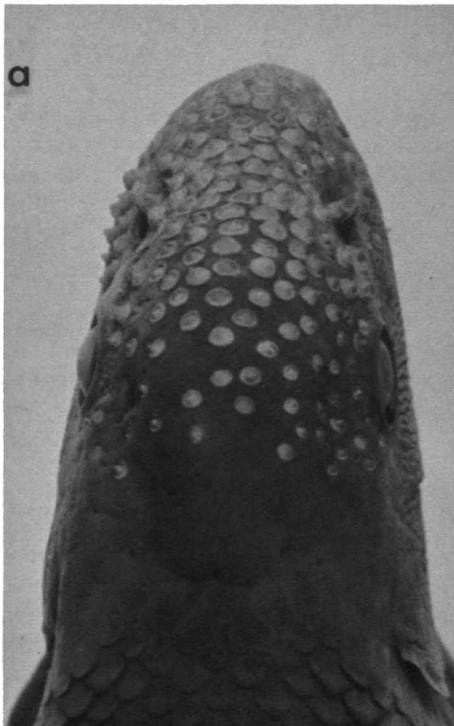


FIGURE 10.—Lateral view of heads of two species of *Nocomis*. Note uniform size of tubercles and their presence on snout and subnasal areas. Nuptial crests are in different stages of development. *a*, *N. raneyi*, USNM 194625, 232 mm, taken 23 May 1964, Craig Creek, James drainage, Virginia; *b*, *N. raneyi*, USNM 197684, 198 mm, taken 28 June 1963, Roanoke River, Virginia; *c*, *N. platyrhynchus*, TU 25902, 195 mm, taken 19 June 1962, South Fork New River, North Carolina.

the ranges of the species. The tests of difference of slopes and heights (intercepts) of pairs of regression lines were performed by analysis of covariance (Snedecor, 1956:394–399). F values yielding probabilities greater than .95 were considered significant. The slope of the regression of gape width (as percent of SL) on standard length of *N. raneyi* is significantly different from *N. platyrhynchus* ($F=64.18$) and *N. micropogon* ($F=60.51$). The slope of the regression lines for *N. micropogon* and *N. platyrhynchus* do not differ significantly ($F=2.97$) but the heights are different ($F=42.19$). The regression equations are *N. micropogon*, $y = .0294X + 6.24$, $n=92$; *N. platyrhynchus*, $y = .0247X + 6.07$, $n=103$; *N. raneyi*, $y = .0075X + 6.68$, $n=96$. The same collections were used, as above in plotting snout length against standard length for the same three species (Figure 6). The consistently shorter snout (average) is shown for any respective body length in *N. raneyi*, although the differences are not of the same magnitude as in the gape width. The influence of increase in body length on the gape width and snout length is shown in Tables 17, 20 and 21 for *N. raneyi* and *N. platyrhynchus*, the

FIGURE 11.—Variation in tubercle development in *Nocomis raneyi* and *N. platyrhynchus*: *a*, *N. raneyi*, USNM 194625, 232 mm, taken 23 May 1964, Craig Creek, James drainage. Tubercles widespread in interorbital and anterior occipital areas and crowded on snout. *b*, *N. raneyi*, USNM 194606, 211 mm, taken 5 July 1961, Blackwater River, Roanoke drainage. Slightly reduced tuberculation is shown in interorbital area compared to specimen on left. Tubercle size smaller than in most *N. raneyi*. *c*, *N. platyrhynchus*, CU 47590, 198 mm, taken 3 May 1964, Toms Creek, New drainage. Only a few tubercles are present in the interorbital area and a hiatus is nearly present on snout. *d*, *N. platyrhynchus*, USNM 194819, 200 mm, taken 10 May 1964, New River, Virginia. A slightly greater number of tubercles is shown in the interorbital and snout areas compared to specimen on left.

length (Figure 5) is based on 146 *N. raneyi*, 88 *N. platyrhynchus*, and 151 *N. micropogon* from specimens of all sizes, sexes combined, and sampled over



specimens divided into three size groups, 50 to 99 mm SL, 100 to 149 mm SL and 150 mm SL and larger. When gape width is plotted against snout length for each specimen, only 60 percent separation occurred in the smaller sized group and about 88 percent in the two larger groups.

The preopercle-opercle suture, as it approaches the angle on lower head, is directed forward in almost all specimens of *N. raneyi*. In a sample of 400 specimens from three drainages, the James, Roanoke, and Chowan, the suture was considerably directed forward (an angle of 10 to 20 degrees) in 75 percent of the sample; 20 percent with suture slightly directly forward; and 5 percent with suture perpendicular or posteriorly directed in respect to the horizontal axis of body.

The fin shapes among the species of the micro-pogon group are relatively similar (Figures 12, 13, 14, 17, 25) except the caudal fin in *N. raneyi*, which is more deeply forked, especially noticeable in the subadults and adult females.

The intestine is simple, elongate and S-shaped, frequently with an accessory loop (47 of 49 specimens from over its range). This organ differs greatly from that of *N. leptocephalus*, in which it is whorled and extends under the intestinal bulb (Figure 8).

The following are other general features of head and body. The dorsal contour of the head on specimens without cephalic swelling is almost straight to gently curved and slopes slightly to moderately downward from the occiput to the internasal region,

more so in the anterior portion. A slight to moderate dip in contour, sometimes causing a small hump, is usually present in the internasal region, except on some of the large males. The snout anteriorly is rather short and subconical or moderately rounded. On some specimens the tip of the snout appears more elongate and/or acuminate. The head ventrally is almost straight and slightly less oblique to the horizontal axis than the dorsal contour of the head.

The mouth is small in the young to moderate in size in adult males; it is oblique and subterminal, being slightly to moderately overhung by the snout tip. The lower jaw is included. The jaw angle is positioned at or slightly posterior to a line ventrad from the posterior nostril. In lateral view the upper lip is generally oblique, being slightly to moderately slanted downward; however, in some specimens the anterior half of the upper lip is directed slightly above the horizontal, the posterior half directed below. The lower lip is straight and directed somewhat downward. In ventral view the lips are semi-circular or they are round anteriorly, the sides diverging, straight, or curving medially. The lateral portion of the upper lip extends to the ventral head margin except at the jaw angle where it is slightly less than the head width at that point. The premaxilla is protractile and a deep groove is present around the entire lips except along the anterior portion of the lower lip where it is absent. The lips are fleshy, appearing more enlarged in nuptial males. The single pair of terminal maxillary barbels

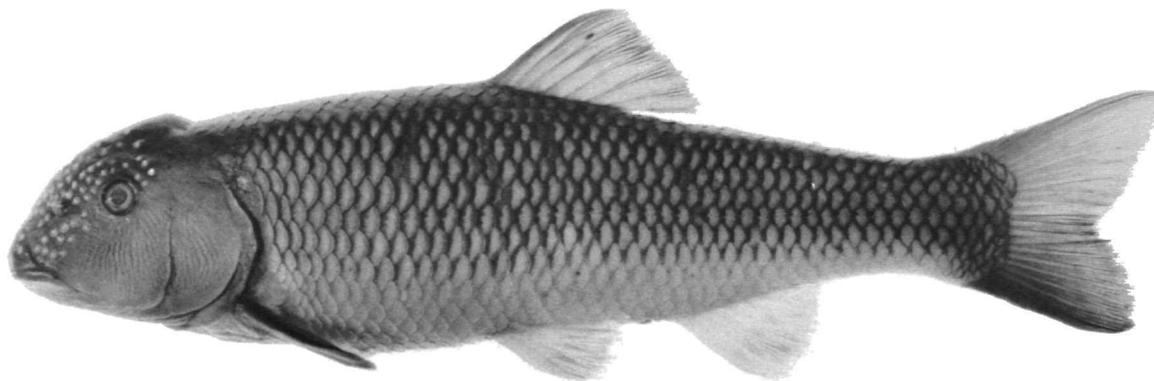


FIGURE 12.—Crested, nuptial male of *Nocomis raneyi*, USNM 194633, holotype, 242 mm, taken 29 May 1964 from Craig Creek, James River, Virginia.

are short and sometimes not excised from the deep groove behind the jaw angle, and are abundantly supplied with taste buds.

The eye is small, the fleshy orbit is round or slightly obliquely or horizontally elongate. The lachrymal bone is oblique to the horizontal, especially in adult males, and reaches the upper lip just above which an obvious crease in the skin is present along its anterior end. The branchiostegal membranes are united to the posterior isthmus, the distance between the points of insertion of the membrane are about half the gape width. The epidermis in the interbranchial isthmus area is longitudinally folded; below the mouth it is folded at right angles to the longitudinal axis.

The body is elongate and subterete, slightly compressed in subadults to moderately compressed in nuptial males, widest and deepest midway between occiput and origin of dorsal fin. The back is slightly to moderately elevated above the occiput level, highest at the dorsal fin origin or just anterior to this. The predorsal body contour is straight or slightly convex, somewhat oblique to the horizontal axis, and is continuous with the posterior head dorsum contour, or a slight abrupt rise to the body level is sometimes present at the occiput. The postdorsal contour is straight and slopes slightly more downwardly than the predorsal contour; it is upturned beginning just anterior to the procurvent

caudal fin rays. The dorsal fin base is straight but usually more oblique to the horizontal axis than the postdorsal contour. The ventral body contour is gently rounded, generally not deep, from the isthmus to the anal fin origin, straight and moderately directed upward at the anal fin base, and then almost straight and sloping slightly upward to a point just anterior to the procurvent caudal fin rays where it is downwardly curved. The caudal peduncle is moderate in length and depth, rather narrow in width.

The lateral line is complete, slightly downwardly curved anteriorly, and straight posteriorly. The line begins on the body at the posterior opercle insertion, slopes quite obliquely downward for a short distance over the cleithrum to a point slightly above the midlateral level, then slopes slightly downward through the first seven to nine vertical scale rows to the midlateral level or to a point slightly below this; in the latter case it slopes gently back upwards and attains the midlateral level at a point usually just posterior to a vertical line from the dorsal fin origin. Upon attaining the midlateral level it is rather straight and horizontal to the posteriormost scale overlying the bases of the midcaudal fin rays.

The urogenital papilla in both sexes is fleshy and moderate to rather large in size, the length about 1 to 1.5 times the greatest width. It changes in shape from bulbous to subconical with a small ori-

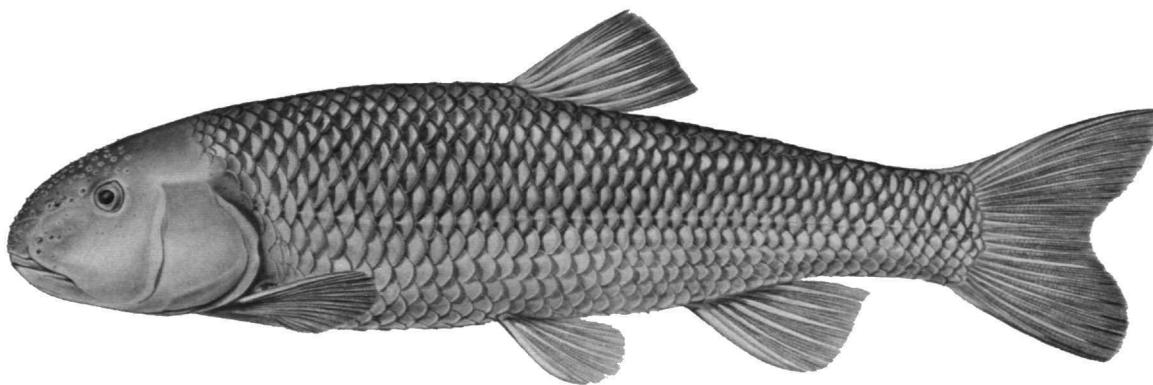


FIGURE 13.—A postnuptial male *Nocomis raneyi* (Paratype, USNM 166404, 229 mm), with tubercles and tubercle scars on head, captured in the Roanoke River at Salem, Virginia on 21 June 1946 [hypoid area somewhat downflexed due to specimen previously being on stringer]. (Drawn by Carolyn Bartlett Gast.)

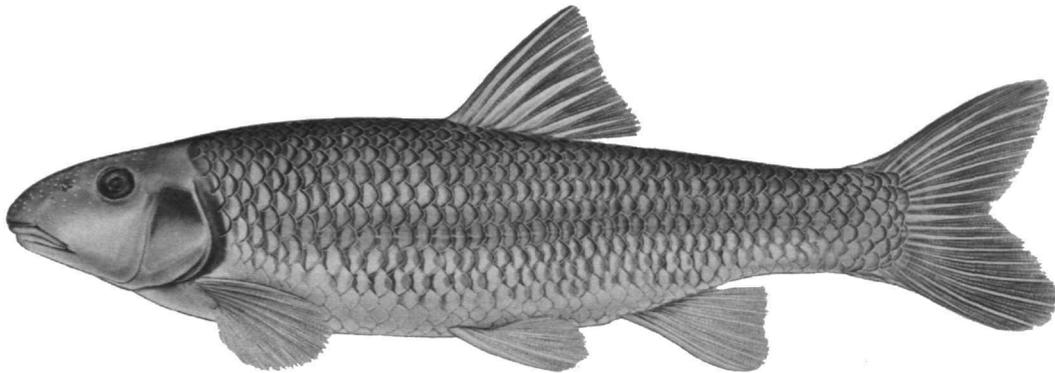


FIGURE 14.—An adult female *Nocomis raneyi*, USNM 191036, 179 mm, captured on 18 September 1959 from Contentnea Creek, Neuse drainage. The tubercle "spots" are evident in specimens of this size. The pointy snout is characteristic of the adult females and of both sexes when juveniles. (Drawn by Carolyn Bartlett Gast.)

face in the adults. Much of the papilla rests in a depression before the origin of the anal fin, being more excised from this in larger specimens.

The entire body, except the breast, is scaled. Laterally, the exposed portion of the anterior scales is higher than long, especially just behind the cleithrum where they appear diamond shaped, although the posterior margin is somewhat rounded. The exposed portion of the lateral caudal peduncle scales is about equal in height and length, appearing square. The posterior margin of lateral line scales is usually slightly to moderately indented. The dorsal and ventral scales are quite variable in size and shape; anteriorly they tend to be smaller and imbedded.

Cutaneous sense organs are present over the entire head, laterally and dorsally on the scales of the first one or two vertical scale rows, ventrally back to about the anal area, and on the upper and lower surfaces of the interradiial membranes of the pectoral fin. They are largest on the head ventrally, especially on the lips.

The alimentary tract is a simple loop, the longitudinal lengths of the tract are straight or slightly curved. The intestinal bulb extends posteriad on the right side to just before the vent and, unless full of food, is only slightly wider than the intestine. The intestine then bends sharply mediad and anteriorly to just behind the pericardium (the ascending intestine), and it sometimes bends sharply to

the left side and posteriad to the vent (the descending intestine). Usually, instead of the ascending portion bending directly into the descending portion, an additional short loop, about 10 to 30 percent (sometimes to 50 percent) the length of the descending portion, occurs on the left side at the end of the ascending intestine and laterad or dorsad to the descending portion into which it leads. Sometimes a short anterior length of the ascending and descending portions is "kinked" laterad to the right side.

The fins are moderate in length except the slightly elongate caudal. The margin of the pectoral fin is moderately angulate to round. The free margin is angulate from the tip of rays 1 to 10 (the apex at ray 4, the longest ray) or moderately rounded between these rays; it is then broadly rounded along the tips of the much shorter posterior rays to the posterior base. The margin of the pelvic fin is broadly rounded or almost straight with rounded corners, ray 3 or 4 being the longest. When appressed, the pelvic fin may reach or is quite short of the urogenital papilla base. The tip of the anal fin, anteriorly, is slightly or well rounded to its longest ray (ray 2 or 3), then straight or slightly incurved to the last ray. The origin of the dorsal fin is positioned well anterior to the midbody point and usually over the origin of the pelvic fin, sometimes slightly posterior to the latter. The anterior tip is pointed or slightly round; ray 1 or 2 is longest and falls short of the

posterior rays when appressed. The margin of the dorsal fin is usually straight, sometimes slightly incurved. The caudal fin is well forked, the fork apex is broadly rounded or very obtusely angulate. The lobes are always subequal in length; the upper lobe always longer and its tip usually narrower. The tip of the upper lobe in young and juveniles is pointed or round, in adults it is acuminate. The lower lobe is broadly rounded in young and usually quite pointed in adults. The well-developed procurrent caudal rays form a distinct middorsal and mid-ventral ridge on the posterior caudal peduncle.

Meristic characters: Values for squamation counts for *N. raneyi* are close to *N. platyrhynchus* and they are somewhat intermediate between the lower values usually for *N. micropogon* and *N. leptocephalus* and higher values of *N. effusus* (Lachner and Jenkins, 1967). The range of the mean values for *N. raneyi* taken usually from five drainages, with the count of the holotype in parentheses, follow: circumferential scale rows (Table 12), 32.9 to 33.4 (35); lateral line scale rows (Table 8), 41.0 to 41.6 (41); scale rows above lateral line (Table 11), 7.3 to 7.7 (8); scale rows below lateral line (Table 11), 6.1 to 6.4 (7); caudal peduncle scale rows (Table 14), 16.1 to 16.7 (17); pectoral fin rays (Table 16), 16.8 to 17.1; total vertebral numbers (Table 15), 40.9 to 41.6.

Assigning numerical values for the degree of breast squamation (Table 18) was useful in demonstrating specific differences in the micropogon group as well as showing certain racial differences. *N. raneyi* almost always has a scaleless breast in the James, Chowan, and Roanoke Rivers, whereas it is about 50 percent scaled in the Tar and Neuse Rivers.

Tuberculation: Data pertaining to tubercle development, distribution, and numbers is summarized in Tables 1, 3, 4, 5. Early tubercle development is shown in Figure 3c. The relationship between increase in tubercle numbers with increase in standard length is shown in Figure 4. The distribution of head tubercles is illustrated in Figures 9, 10, 11, 12 (holotype), and 16 for immature specimens and nuptial adults.

The tubercle pattern and the relationship between increase in tubercle numbers with increase in body length is similar in both sexes. At first inspection this sex similarity may not appear correct be-

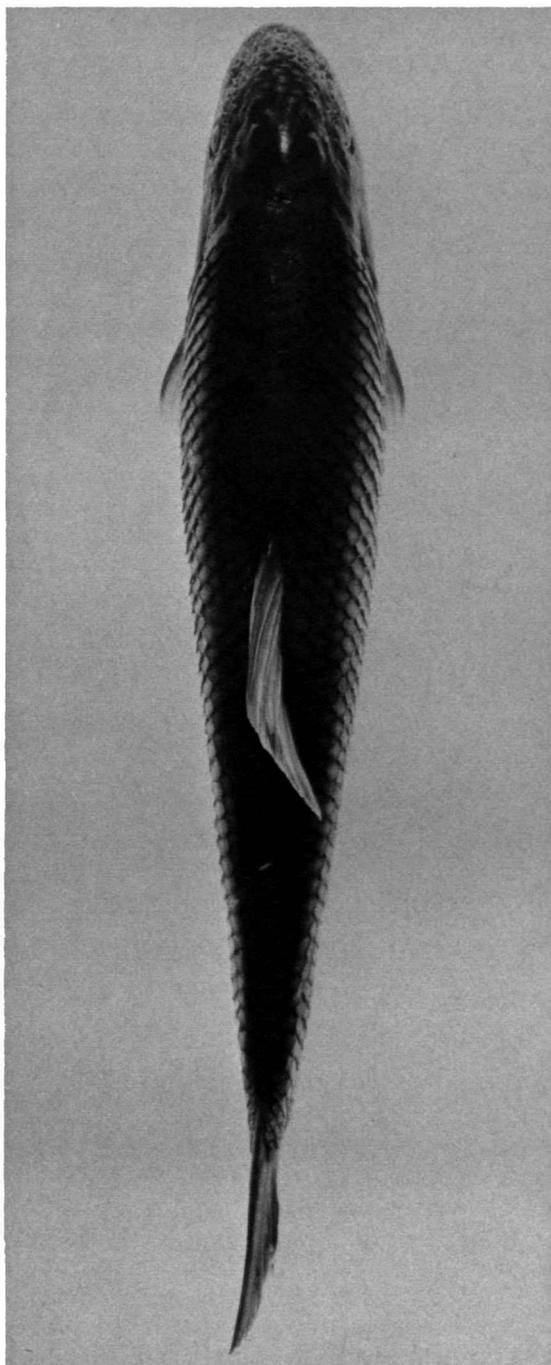
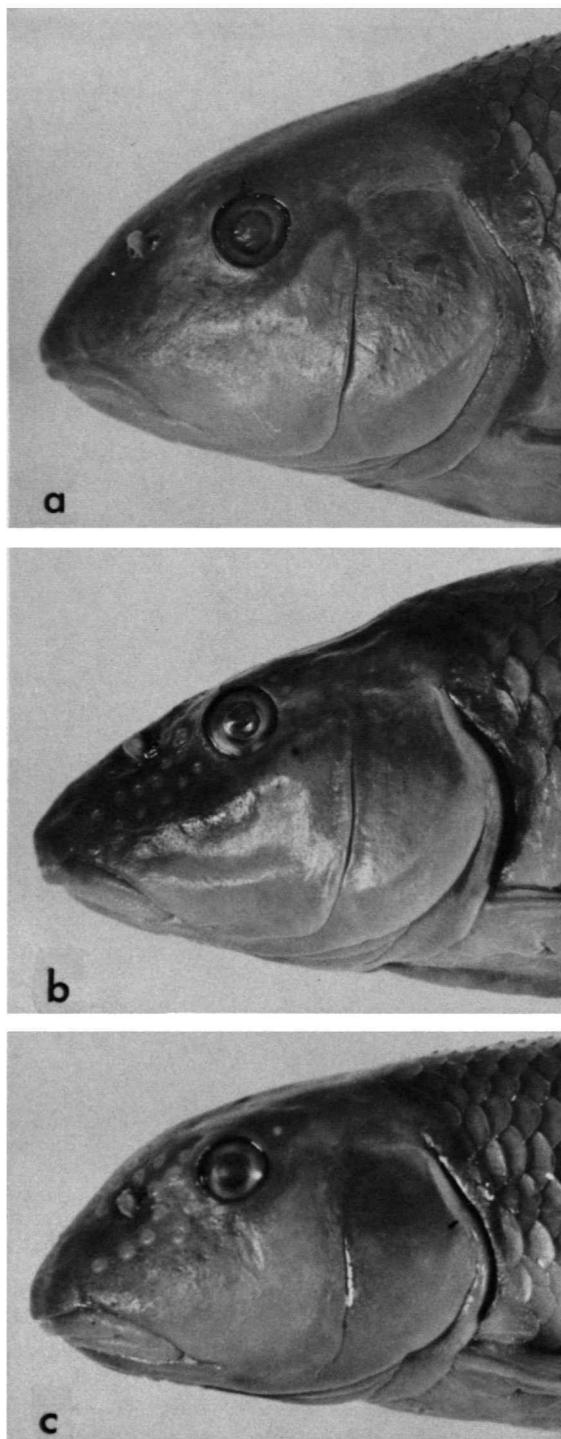


FIGURE 15.—Dorsal profile of *Nocomis raneyi*, holotype, USNM 194633.



cause the tubercle spots are difficult to discern in the females (at most, they develop only to a fine bud stage), except in the largest specimens, and initial trials at counting will give lower improper values. Also, the males attain a larger size and a greater average number of tubercles. The tubercles first appear in *N. raneyi* as small, light spots, often 15 or more, and extend from the anterior internasal line to the midinterorbital line (Figure 3c). They rarely commence development in specimens under 60 mm SL, and they are often not discernible at lengths of 60 to 85 mm SL. With increase in body length, the tubercles develop posteriorly on the head, but almost always stop development at the posterior interorbital line (Table 1). The snout and subnasal tubercles are last to develop in *N. raneyi*. The full complement of tubercles, which may exceed 200 in nuptial males, extends from the tip of snout (Figure 9) to the posterior interorbital area, and includes a supra-orbital ring and two or three irregular rows on the lachrymal area. The tubercles are closely spaced from the anterior interorbital to the tip of snout. *N. raneyi* differs in the latter character from *N. platyrhynchus*, which sometimes shows reduced tuberculation before the anterior internasal area, and differs considerably from *N. micropogon*, which usually has a hiatus of tubercles in this area. A character exclusive to *N. raneyi* is the continued increase in numbers with increase in body length (Table 5; Figure 4). No other species of *Nocomis* has this characteristic. The head tubercles of *N. raneyi* are relatively uniform in size, but they are somewhat larger in the area extending from the internasal to the interorbital. The largest tubercles are about 1.8 to 1.9 mm in diameter. The smallest tubercles occur on the snout. Tubercles average somewhat larger in *N. platyrhynchus*. They are large in *N. micropogon* and very large in *N. leptocephalus*. All of our data on size of tuberculate or scarred adult specimens (Table 3) and the body

FIGURE 16.—The spot or bud stage in tubercle development of three species of *Nocomis*. Note the sharper snout configuration of these non-nuptial males compared with the specimens in Figure 10. *a*, *N. raneyi*, USNM 194627, 194 mm, taken 6 June 1963, Craig Creek, James drainage, Virginia; *b*, *N. platyrhynchus*, USNM 194877, 183 mm, taken 6 July 1963, Big Walker Creek, New drainage, Virginia; *c*, *N. micropogon*, USNM 166482, 173 mm, taken 17 October 1947, Susquehanna River drainage, Pennsylvania.

FIGURE 17.—Juvenile stages of three species of *Nocomis*: a, *N. raneyi*, 83 mm, James drainage; b, *N. micropogon*, 87 mm, Potomac drainage; c, *N. leptcephalus*, 81 mm, James drainage.

length when tubercle buds first appear (Table 4) indicates that *N. raneyi* matures at an appreciably larger size than *N. micropogon* or *N. platyrhynchus*. Observations of nuptial males of *N. raneyi* attending their mound-nests corroborates this point.

Small tubercles are present on the dorsal portion of the rays of the pectoral fin, in a single row per ray, and they occur modally on rays 2 to 5 or 6, rarely on rays 2 to 7 and 8.

Nuptial crest: Because of the difficulty in capturing the adult males, which are secretive, solitary, and prefer the deeper waters, complete sequential development of the nuptial crest with maturity is not determinable from our material. The swelling first appears in the internasal to snout area and enlarges to a rounded "cocks comb" that extends to the occiput (Figure 12). An immature male specimen, 194 mm SL, (Figure 16a) taken 6 June 1963 from Craig Creek, has the typical sharp snout of

smaller immature males or mature females but has a very slight internasal-interorbital swelling. Three later stages in the development of the nuptial crest are seen on the following specimens of *N. raneyi*: 198 mm SL, captured 28 June 1963 with moderately swollen area from snout to occiput (Figure 10b); 232 mm SL, captured 23 May 1964 with large crest (Figure 10a); and 242 mm SL, taken 29 May 1964 with very large crest (Figure 12). Many very large nuptial *N. raneyi* have been observed during the reproductive period in Craig and Catawba Creeks, James drainage over the past several years by the first author and all specimens had large crests. A postnuptial male, 229 mm SL (Figure 13), taken 21 June 1946 from the Roanoke River, has a moderate head swelling, but whether this was its maximum development during spawning or it had since receded somewhat was not determined.

The crest in *N. raneyi* is shaped and located dif-

ferently than in *N. micropogon* and *N. leptocephalus*. Both of the latter species develop higher, more dome-like crests, that are more forward on the head, particularly in *N. leptocephalus*.

Pharyngeal dentition: The pharyngeal tooth count is 4–4 in 21 pairs of arches in specimens from the James, Roanoke, Tar, and Neuse River drainages. The teeth are very stout and moderate in length. The arch is stout, broad, with short upper and lower limbs. In the large *N. raneyi* (Figure 18) the arch is massive, and probably stoutest of all *Nocomis*. The pitted surface is deeply sculptured, but the pits are not usually as extensively developed as in other species of *Nocomis*.

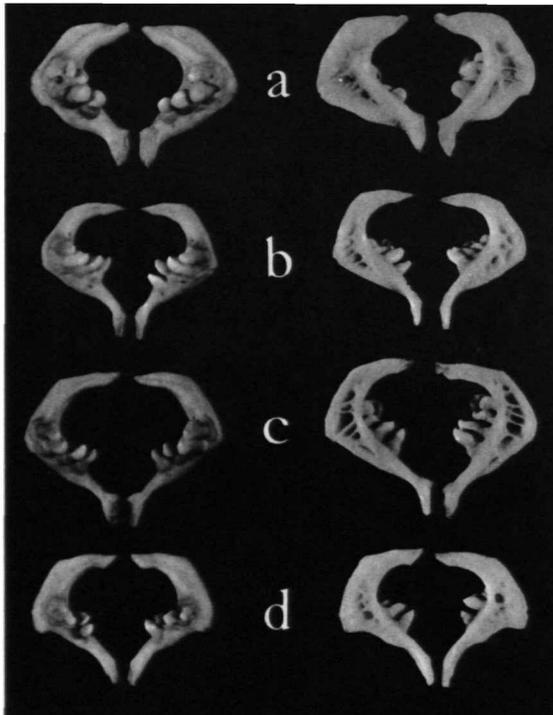


FIGURE 18.—The pharyngeal arches of four species of *Nocomis*: a, *N. raneyi*, 186 mm SL; b, *N. platyrhynchus*, 203 mm; c, *N. micropogon*, 219 mm; d, *N. leptocephalus*, Savannah River, 206 mm.

Coloration: Juveniles, adult females and subadult males from the James and Roanoke River drainages show no significant local or geographic color difference in life or in preservation, or among these size stages.

The characteristic scale color pattern on the body, dorsally and laterally, ventrad to 1–3 scale-rows above the pelvic fin base, has two basic aspects, the dark scale margins and the light median scale color. In the lateral line area the exposed portions of the scales are sharply bicolored. The dark anterior margin (the excised scale pocket membrane) and the posterior margin meet at the dorsal and ventral edge of the scales, thus surrounding the light median area. The inner edge of the anterior margin is vertically straight or slightly curved except in the lateral line scale-row where it is indented at the level of the lateral line canal pores. The inner edge of the posterior margin follows the curve of the actual scale margin; its outer edge extends to and is darkest at the scale edge. The anterior margin is generally slightly wider than the posterior margin. The scale margins are slightly wider on the anterior body scales than those on the posterior body. A reduction in scale bicolouration occurs ventrad and dorsad; the margin decreases in width and intensity ventrad until absent, and increases in width and intensity dorsad, where, on the dorsum, the dark margin nearly or entirely fills in the light median area. Smaller juveniles generally have narrower margins than the larger adults; thus they have average lighter colors. The colors of the margins are, on the dorsum, usually black-olive, some brown-olive, and grade from dark olive dorsolaterally, olive or yellow-olive in the lateral line area to pale olive or pale yellow-olive below. Some tints of green iridescence also appear on the margins. In some specimens there is a sharp body bicolouration, effected by appreciable lighter colors in the lateral line area.

The medians of the lateral body scales are iridescent silver with a cast of yellow to olive in most specimens. Iridescent violet and green hues are also present in the lateral region of many specimens, and these colors are particularly evident in sunlight. The silver color is almost entirely replaced dorsad by the dark scale margins. The belly is pearly white whereas the breast, where scales are absent, is less lustrous or gray-white. An iridescent

silver-yellow to silver-olive middorsal stripe about one scale in width is developed from the occiput to the dorsal fin and on the anterior half to the entire postdorsum of specimens up to 120–160 mm SL.

A horizontal lateral band occurs in most smaller juveniles and in a few specimens up to about 130 mm SL, including some adult females. When fully developed, it extends from the tip of the lachrymal bone (interrupted by the orbit) through the lateral line area to the area over the caudal base, and ranges 1.5–2.5 scales in width, narrowing just before the caudal base area and then widening slightly. The intensity is variable, generally being darkest, but rarely blackish, in smaller juveniles. It is generally darkest over the caudal peduncle and, when faint, it is usually present only in this area. The lateral band is effected by a relative darkening beneath the medians of the scales and lighter medians 1–2 scale rows above.

The basicaudal spot is small, generally amorphous, confluent or slightly separated from and usually darker than the end of the lateral band. It is almost always absent from specimens larger than 120 mm SL, and often in many smaller ones.

A black or blue-black, slightly curving bar occurs from the pectoral fin base to the dorsum behind the opercular opening, entirely over the cleithrum or extending slightly posterior to it.

The head, dorsally, to the snout tip is black, brown, or dark olive. The occipital line is slightly lighter than the head dorsum. In some large adult males a dark blue cast occurs on the head and anterior dorsal part of the body. The head, laterally, over the upper operculum, below the orbit and over the lachrymal is largely yellow-olive to dark olive with iridescent silver, gold and green sometimes masking the olive; the iridescence is most intense along the upper edge of the operculum. The outer, upper lip is a lighter olive than the snout, dorsally. The ventro-lateral head is silvery with some golden reflections. The head ventrally, including the lower jaw, is white to gray-white. The opercular membrane is olive laterally, and pale olive ventrally. The inner iris in almost all specimens is narrowly bordered by iridescent yellow, gold, orange, or combinations of these colors. This iris ring is sometimes interrupted by the black to light olive areas of the outer iris, or it is absent.

Fin coloration is variable in its intensity and areas of development. The pale yellow to reddish colors are almost entirely confined to the inter-radial membranes and the membranes between ray branches; sometimes they shade into the rays of juveniles. Membranes lacking these colors are hyaline to dusky gray, sometimes dusky olive in the larger specimens. Portions of the fin rays appear blackish since melanophores occur along the rays and ray joints, generally being heaviest on the dorsal fin and lightest, or sometimes absent, on the anal and pelvic fins; a greater deposition occurs in larger specimens. Color is almost always lacking along the fin margins, the margin being hyaline to dull white, generally widest on the anal and narrowest on the caudal.

The typical caudal fin coloration is a light red in the distal $\frac{1}{3}$ – $\frac{1}{2}$ of the fin membrane, deepest in the distal portion of the lobes and usually extending basally from these. In a number of specimens the basal portion of the medial membranes is suffused with pale red. The reddish shade is generally deeper in larger specimens. In some juveniles it is orangish red; in an immature female 110 mm SL, it was orange. In a few specimens the membrane color is very weak or absent. A recently preserved, large adult female from the Neuse River drainage had a light red outer caudal. The rays are yellowish olive to dark olive, tending to be colorless and clear in small specimens. In larger specimens, the thick skin over the outer edge of the most ventral ray is light gray.

The distal half of the dorsal fin membrane is usually light red to orangish red; sometimes this color is suffused through the entire membrane. The red is deepest in the distal portion of the anterior membrane. The rays are yellow-olive to olive, or colorless in smaller specimens.

The pectoral fin rays are dusky yellow to pale olive, being the most colorful distally. The membrane is gray-white, often with an orange suffusion distally. The thick skin over the first ray is very dark except for the gray-white anterior edge.

The distal pelvic fin ray is light or moderate yellow to yellow-olive, and grades basally to light olive or colorless; the medial and distal rays often have a tinge of light orange. Most of the first ray and the distal portion of rays 2 and 3 are milky white or yellow-white. The membrane is clear to light gray.

The anal fin is the least colorful. The rays are pale yellow to pale olive over $\frac{1}{2}$ - $\frac{2}{3}$ of their length. The first ray is white or yellow-white. The membrane is clear to dull white.

The striking color features of the nuptial male in life are a pink or rosy on the head, body and fins and the accentuation of certain other body colors over those of nonbreeding adult males. The most highly colored male we examined (USNM 194625, 237 mm SL) had well-developed tubercles and a large crest, captured in the James drainage, 23 May 1964, probably in the midst of breeding activities for many fresh nests were about. The most intense nuptial color was rosy, located from the posterior end of the postopercular bar, in the level from one scale-row below the lateral line to the upper pectoral fin base, posterior to the pelvic fin base. The color was deepest in the anterior portion of this area. It extended as light pink to the area over the anterior anal fin base, where it ended. The color graded to faint pink on the belly and was absent from the scaleless breast area.

The lower head, laterally, below a line from about the jaw angle obliquely to midheight of the opercle, was pink to light pink with some portions of this area being suffused with olive. The upper opercular area was olive. The head, ventrally, including the lower jaw (but not the upper jaw) was pink, deepest over the distal portion of the branchiostegal area.

A heavy silver-bronze iridescence colored the medians of the scales of the body, laterally, above the lateral line and it was present in the medians of only the lightest dorsal scales. A faint pink suffused the medians of the third to fourth scale-rows above the lateral line between the postopercular bar and pelvic fin levels.

The dorsal fin membranes were light pink (with some dusky olive in the basal third). In addition to the yellow, olive, and orange colors of nonbreeding specimens, the pectoral and pelvic fins had a suffuse pink, slightly lighter than that of the dorsal fin. There was only a very slight pink suffusion in the distal anterior membranes of the otherwise typically colored anal fin. The caudal fin lacked pink coloration. A milky-white color occurred along the tips of the dorsal, pectoral, pelvic, and anal fin rays.

Three highly tuberculate (one with many tubercle scars) males, 197, 212 and 242 mm (holotype) SL

with small to large crests, were captured on 28 June 1963, 15 May 1963, and 29 May 1964, respectively, from the upper Roanoke drainage (first specimen) and the James drainage. These and many observations by Lachner of spawning males provided additional data on life coloration. The significant feature of the breeding *N. raneyi* (and other *Nocomis*) is to "turn on" his colors to high intensities just prior to or during the spawning acts.

Only slight color differences were found among these males and the male described (USNM 194625, 237 mm SL) but the intensities differed appreciably. The intensity and area of development of the pink-rosy coloration was about the same as described above but it could be more or less intense depending on the spawning "peak" of the male. Pink color was usually absent from the fins. In some males in the "peak" of spawning all fins had a lemon-yellow margin. The lateral body medians of the scales above the lateral line in the holotype were iridescent silver-bronze. In some, it was iridescent olive-yellow, a slightly brighter yellow than that seen in any other specimens of *N. raneyi*.

The light red caudal fin coloration occupied the distal half of all membranes in most of the males, but it was confined to the distal half of the upper lobe in the holotype. In some active, spawning males the caudal fin is dusky-olive. Melanophore deposition along the rays and ray joints was heaviest in the largest nuptial males, particularly in the distal half of the dorsal fin, but in the smaller males it was no heavier than that in large nonbreeding adult males. The same is true of the dark scale margins. No trace of a dark lateral band was observed.

After chubs are placed in preservative (10% formalin and alcohol), the iridescent colors are rapidly lost. A few days thereafter all that remain are the dark colors of the scale margins, fin rays, lateral band and caudal spot and various tones of black-gray to light gray.

Melanophores underlie the dark scale margin and dark head coloration seen in life. Their patterns in alcohol are about the same as the overlying life colors and are shown in the illustrations.

With the fading of the iridescent median scale colors, certain patterns appear and some become more pronounced on the body. These are produced by the "subscale" melanophores which are located

on the undersides of scales and on the musculature. The dark horizontal midlateral band on the body seems to remain in well-preserved specimens that possessed it in life. The band is produced largely or entirely by a heavier concentration of subscale melanophores. Other shades of lighter lateral and blackish dorsal medians of scales are also due mainly to subscale melanophores. The light middorsal stripe of living specimens turns darker than the adjacent dorsum color in preservative. In many specimens, slightly dark horizontal lines, running nearly or entirely the length of the body, occur on the body laterally, above the lateral line, and sometimes to 3 to 4 scale-rows below the lateral line. The lines are produced by the slightly heavier deposition of subscale melanophores in the areas beneath the dorsal and ventral edges of the scales rather than beneath the medians of the scales.

A slight average difference in coloration exists in the lateral margins of the scales between the sexes, this being noticed only in preserved specimens. Many adult females have slightly wider anterior and posterior scale margins than those of males of similar size.

POPULATIONS.—The drainage populations of *N. raneyi* are similar. Only two characters show distinctive interdrainage divergence, the degree of breast squamation (Table 18) and the number of vertebrae (Table 15). Both characters partially differentiate the populations in the James, Chowan and Roanoke drainages from those in the Tar and Neuse. Breast scales in the James, Chowan and Roanoke drainages are almost always absent (93% of 138 specimens) and the breast was never half scaled. The Tar-Neuse populations had only one of 41 specimens naked and about 80 percent had the breast scaled about one third or more. The mean values for total vertebral numbers were practically the same for the Tar and the Neuse drainages (40.9 and 41.0) and lower than in the three more northern drainages (41.4, 41.6, and 41.4).

REPRODUCTION AND GROWTH.—The male of *N. raneyi* constructs a mound-nest (as in all species of *Nocomis*) of gravel that he transports in his mouth. The completed nest may exceed three to four feet in diameter. (The reproductive behavior of the species of *Nocomis*, including *N. raneyi* will be treated in part 6, see p. 2). *N. raneyi* attains the largest size of all the species in the genus, the largest

male examined was 266 mm SL and the largest female, 180 mm SL, both from the Neuse drainage. All nuptial males exceeded in length the largest female captured. Several large males over 200 mm SL aged by scale analysis were in their fourth and fifth year of life.

ETYMOLOGY.—This species is named after Edward C. Raney, scientist and teacher, Cornell University, Ithaca, New York, whose enthusiasm and guidance placed many American students on the professional pathway to ichthyology.

The vernacular name, bull chub, was composed by us because of the large size and aggressive habits of the crested nuptial males during the spawning period. The nuptial *N. raneyi* sometimes engages in lengthy battles with other nuptial males of his own kind when nesting territories overlap. The native people in southwestern Virginia refer to *N. raneyi* as a chub, pinkbelly chub, hornyhead or nestmaker, but they generally do not differentiate among the four species in the area.

MATERIALS EXAMINED.—A total of 106 collections from 84 localities in five drainages were examined.

Holotype: USNM 194633, a nuptial male 242 mm in standard length, captured in Craig Creek, Craig County, Virginia, 2.2 road miles on Rt. 311 southwest (upstream) from Newcastle, at first bridge from Newcastle, 29 May 1964 with shocker by Robert E. Jenkins and Robert L. Miles. Five paratypes, USNM 194266, were taken with the holotype.

The Craig Creek system of James drainage and the Roanoke drainage materials are designated as paratypes.

The collections are listed below by drainages and major tributaries in progressive upstream order; following the collection date is the number of specimens captured (in parentheses). Designations given as "same locality" or "same collection" refer to the immediately preceding locality or collection.

James River Drainage, Virginia

Craig Creek, Botetourt County.—USNM 194624: at 1 mi above mouth, second bridge over Craig from Eagle Rock, 23 May 1964 (3). USNM 177397: at 2.5 mi above mouth, 3 airmi SW Gala, 3 July 1958 (26). USNM 194625; jct. Rtes. 615-683 (at suspension bridge) 3.3 rdmi NE (downstream) Oriskany, 15.4 rdmi NE Newcastle on Rte. 615-42, 23 May 1964 (3).

Craig Creek, Craig County.—USNM 194626: bridge on Rte. 606 leading to Camp Easter Seal (Rte. 606 turns off Rte. 615

at 9.2 rdmi NE Newcastle), 24 May 1964 (2). USNM 194627: at 2.3 airimi NE Newcastle, 6 June 1963 (29). USNM 194628: Pinetop, 2 airimi NE Newcastle, 11 May 1963 (15). USNM 194629: Rte. 616 ford, 1.2 airimi NE Newcastle, 16 August 1957 (133). USNM 194630: same locality, 12 October 1960 (71). USNM 194631: same locality, 15 May 1963 (172). USNM 194632: holotype locality, 16 May 1957 (16). USNM 194634: Rte. 311 bridge, 3 rdmi SW Newcastle, 19 August 1958 (4). UR 1538: Rte. 311 bridge, 5.6 rdmi SSW Newcastle, just N Abbott, 27 June 1963 (2).

Johns Creek, Craig County.—CU 20356: along Rte. 42 in Newcastle, about 0.5 mi above mouth, 5 June 1951 (15). CU 24859: same locality, 7 July 1952 (13). USNM 194635: same locality, 3 October 1953 (12). USNM 194637: at 1.8 mi W (upstream from) Newcastle in Nutter Mountain gorge, 16 August 1957 (4). USNM 194638: at 4.8 mi W Newcastle, 16 August 1957 (25). UMMZ 181830: at 7 mi above Newcastle, 27 August 1941 (1). CU 48564: at 4.35 rdmi W jct. Rtes. 311–658 on Rte. 658, 7.75 airimi W Newcastle, 10 May 1965 (8). CU 48445: at 1.3 rdmi SW jct. Rtes. 632–635 on Rte. 632, 10.8 airimi WSW Newcastle, 27 March 1965 (2). USNM 194639: most downstream Rte. 632 bridge, 12 airimi WSW Newcastle, 4.75 airimi NE (downstream) Maggie, 1 October 1957 (2). USNM 194640: second Rte. 632 bridge upstream from Newcastle, 2.8 airimi NE Maggie, 30 May 1964 (7). UR 1796: first Rte. 632 bridge 2 rdmi NE jct. Rtes. 632–658 at Maggie, 27 June 1963 (24). CU 47594: at 1 rdmi NE jct. Rtes. 632–656 at Maggie, along field off Rte. 632, 29 May 1964 (27).

Chowan River Drainage, Virginia

Sappony Creek, Sussex County.—CU 16911: Rte. 40 bridge, 2.2 mi W town of Stony Creek, 27 March 1949 (3).

Stony Creek, Dinwiddie County.—CU 47335: at 1.2 mi S Dinwiddie on Rte. 1, 21 March 1948 (18).

Nottoway River, Brunswick-Dinwiddie County line.—USNM 177357: Rte. 1 bridge, 29 July 1958 (8).

Meherrin River, Lunenburg-Mecklenburg County line.—USNM 194642 (2 collections lumped): (a) Rte. 138 bridge, Union Mill, 5.1 airimi NNE South Hill, 29 July 1958; and (b) bridge just N Ogburn, 7 airimi NW South Hill, 3 September 1958 (42). CU 43628: same collection as (b) (1). USNM 194258: Rte. 49 bridge, 31 July 1958 (2).

Roanoke River Drainage, Virginia and North Carolina

DAN RIVER SYSTEM

North Carolina, Rockingham County.—USNM 171727: Leaksville, 6 April 1947 (10).

Virginia, Henry County.—USNM 171593: Beaver Cr., 1.5 mi NW Martinsville, 22 June 1946 (1). USNM 194261: Town Cr., trib. Smith R., Rte. 604 bridge, 1.75 mi SW Henry, near railroad bridge, 6 August 1958 (1).

ROANOKE RIVER SYSTEM, VIRGINIA

Otter River, Bedford County.—USNM 171595: at 4 mi NNE Bedford, 21 June 1946 (13). USNM 166406: at 4 mi NNW

Bedford on Rte. 43, 5 September 1947 (4). USNM 166405: at 5 mi NW Bedford on Rte. 43, 9 June 1947 (11).

Otter River, Campbell County.—UMMZ 181434: Rte. 682, S of Evington, 12 June 1956 (3).

Pigg River, Franklin County.—USNM 163436: Rte. 220 bridge, 1 mi S Rocky Mount, 3 April 1948 (106). USNM 194601: same locality, 19 June 1962 (2).

Blackwater River, Franklin County.—USNM 194602: Rte. 616 low-water bridge, 3.7 airimi SE Scruggs, 7.8 airimi SSE Haleford, 11 August 1958 (49). USNM 194605: same locality, 5 July 1961 (28). USNM 194606: at 0.75 mi downstream from Rte. 670 bridge and gauging station, 3.1 airimi SSW Scruggs, 4.6 airimi W Bedford-Franklin-Pittsylvania Co. line, 5 July 1961 (1). USNM 194603: Rte. 670 bridge by gauging station, 2.7 rivermi upstream from mouth Gills Cr., 7.2 mi S Haleford, 11 July 1958 (3). OSUMZ 5991: same locality, 5 July 1961 (68). USNM 194609: at 4.8 airimi SW Scruggs, 8.6 airimi SSW Haleford, 11 August 1958 (18). USNM 194610: near Crafts Church, 7.8 airimi W Bedford-Franklin-Pittsylvania Co. line, 6 July 1961 (62). USNM 177395: at 3.8 airimi NE Redwood, 8.2 airimi ENE Rocky Mount, 5 July 1956 (19). USNM 177376: Rte. 122 bridge 4 airimi NE Rocky Mount, 5 July 1956 (6). USNM 194611: same locality, 7 July 1958 (7). USNM 194612: at Blaine in rocket fuel plant area just E of Rte. 220 bridge, 3 airimi NNE Rocky Mount, 22 August 1957 (11). USNM 194613: same locality, 4 July 1961 (109). USNM 194614: same locality, 6 April 1963 (69). USNM 194615: Rte. 220 bridge, 2.8 mi NNE Rocky Mount, 21 August 1957 (3). CU 25032: Rte. 919 (old Rte. 220) bridge, 2.5 airimi NW Rocky Mount, 22 June 1946 (1). CU 47595: same locality, 5 July 1956 (21). UMMZ 181433: same locality, 17 May 1931 (3). USNM 194617: jct. Rtes. 643–732–737, 4.75 airimi WNW Rocky Mount, 15 October 1961 (41). USNM 194618: Rte. 740 bridge, 1.8 airimi NE Calloway, 15 October 1961 (9). USNM 194619: North Fork Blackwater along Rte. 641, 2 airimi NE Calloway, 14 October 1961 (14).

Blackwater System, Gills Creek, Franklin County.—USNM 194607: about 4.5 rivermi above mouth in Blackwater, 5 airimi SE Hales Fort Church, 2.1 airimi SW Scruggs, 6 July 1961 (2). USNM 194604: 2.5 mi SW Scruggs, 5.9 airimi SSW Haleford, 7 August 1958 (1).

Back Creek, Roanoke County.—USNM 194620: Rte. 657 bridge, 0.5 mi from Rte. 220 intersection, 4.5 airimi S Roanoke, 3 July 1961 (7).

Roanoke River, Roanoke County.—USNM 40240: at or near Roanoke, 31 July–2 August 1888 (1). USNM 166404: Salem, 21 June 1946 (1). UMMZ 181431: at 2 mi above Salem, 13 June 1956 (3). CU 20769: Glenvar, 6 June 1951 (1). CU 24771: same locality, 30 June 1952 (2). UR 2025: same locality (at RR station just off Rte. 11), 11 July 1963. (11). USNM 197684: first Rte. 639 bridge from Rte. 11, 1.5 airimi ESE Riverside, 3.5 airimi ENE Lafayette, 28 June 1963 (19). TU 25885: at 8 mi SW Salem on Rte. 11, 18 June 1962 (3). USNM 194255: Roanoke-Montgomery Co. line, Rt. 11 bridge, 11 September 1956 (7).

South Fork, Roanoke River, Montgomery County.—USNM 194621: bridge off Rte. 11, 1 mi S Elliston, 2.3 mi N Shawsville, near Bench Mark 1282, 12 August 1958 (1). CU 24788: Rte. 11 bridge, 2.4 mi S Elliston, 9 July 1952 (3). CU 24728:

about 1 airmi SE Shawsville along Rte. 609. [Figured in detail in Schwartz and Dutcher (1962: 370)], 9 July 1952 (2). USNM 194265: same locality, 13 September 1954 (1). USNM 194254: same locality, 2 July 1956 (2). USNM 194622: same locality, 12 August 1958 (1). USNM 177283: same locality, 31 August 1958 (2). USNM 171594: at 2 mi N Alleghany Springs, 22 June 1946 (1). USNM 194623: at 0.75 mi N Alleghany Springs, 2 mi S Shawsville, 16 October 1951 (2).

Tar River Drainage, North Carolina

Tar River or Fishing Creek, Edgecombe County.—USNM 191108: Rte. 1500 bridge about 4.5 mi SW Lawrence, 5.5 mi NNE Tarboro, 19 September 1959 (10). TU 34466: Rte. 44 bridge, 1.9 mi NW Tarboro, 6 September 1964 (8). USNM 40324: at 2 mi below Rocky Mount, 29 August 1888 (2).

Tar River, Nash County.—USNM 191049: railroad bridge just N Rocky Mount, 19 September 1959 (10). TU 34508: Rte. 64 bridge, 7.7 mi NE Pilot, 6 September 1964 (96).

Tar River, Granville County.—UMMZ 181832: Rte. 15 bridge, 7 mi SSW Oxford, 4.5 mi NNE Hester, 30 August 1946 (3). UMMZ 181432: 0.5 mi W Providence, 26 Novem-

ber 1953 (23). CU 19505: at 1 mi SW Providence (presumed same locality as UMMZ 181432), 30 March 1951 (9).

Neuse River Drainage, North Carolina

Nahunta Swamp Creek, Wayne County.—CU 11892: at 1.2 mi N Pikeville, 27 June 1946 (1).

Contentnea Creek, Wilson County.—USNM 191036: about 3 mi SW Wilson, golf club below Rte. 301, 18 September 1959 (25). DU F-122: 4 August 1961 (1).

Falling Creek, Lenoir County.—TU 34439: Rte. 70 bridge, 8.2 mi W Kinston, 5 September 1964 (1).

Little River, Wayne County.—USNM 40386: just W of Goldsboro, 29 August 1888 (6).

Crabtree Creek, Wake County.—UMMZ 161963: Raleigh, 11 October 1929 (2). UMMZ 181430: same locality, 9 May 1930 (3).

Neuse River, Wake County.—USNM 194272: Raleigh, 1890 (2). USNM 40462: below dam at Milburnie, near Raleigh, 27 August 1888 (16). USNM 190975: same locality, 16 September 1959 (4). TU 34532: Rte. 64 bridge at Milburnie, 7 September 1964 (5). USNM 190997: Falls, below bridge, 17 September 1959 (8).

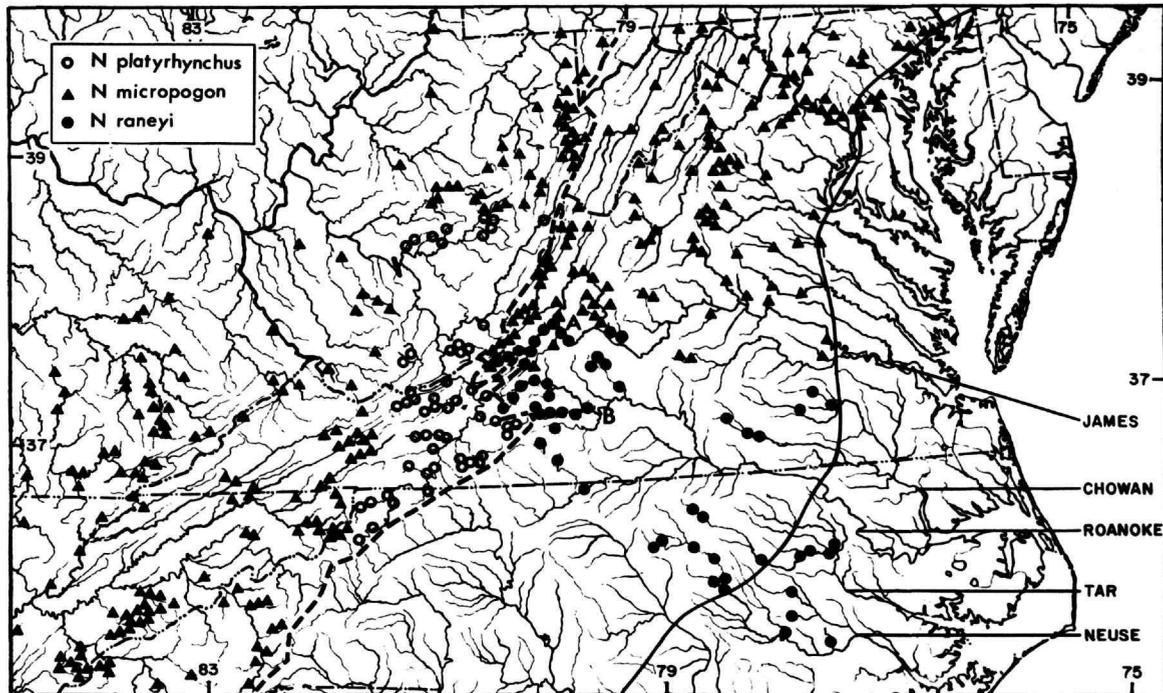


FIGURE 19.—Distribution of *Nocomis platyrhynchus*, *N. micropogon* and *N. raneyi* in the central eastern region. The Atlantic-Gulf drainage divide is indicated by the heavy, broken line; the Fall Line by the North-South solid line. The Kanawha Falls, West Virginia, is marked by a heavy bar just downstream from the Gauley River (the last river tributary to the New River downstream inhabited by *N. platyrhynchus*). The areas west of letter A and B are enlarged in Figures 20 and 29. The names of important rivers west of the divide are labeled in Figure 28.

Neuse River, Durham County.—UMMZ 181429: Rte. 15 bridge, 9 mi NE Durham, 29 August 1946 (23).

Eno River, Orange County.—USNM 188555: 1.6 mi NE Rte. 70 on Rte. 1567, and 1.1 mi NW on Rte. 1569, 10 May 1964 (30). USNM 188736: same locality, 25 May 1964 (12). DU (unnumbered): below Hillsboro, 18 November 1941 (2).

DISTRIBUTION.—*N. raneyi* is a central Appalachian, Atlantic slope species with its center of distribution in Virginia. It occurs in the James, Chowan, and Roanoke drainages of Virginia and in the Tar and Neuse drainages of eastern North Carolina (Figure 19). We examined 116 collections from 84 localities in the five drainages. Ecological distribution is discussed in the Ecology section.

It apparently is restricted in the James drainage to a small portion of the upper basin, in Craig and Botetourt counties (Figure 20), and was found downstream on only one occasion. We had extensive collections (182) from the James drainage, in which at least one species of *Nocomis* was taken from 141 localities scattered throughout the drainage, the majority from the upper half of the basin; more than 3400 *Nocomis* specimens are involved.

This species probably is continuously distributed, or nearly so, in the 116 rivermile length of the Craig-Johns Creek system (except for its headwaters) since it was taken in 34 collections from 23 localities and was represented in almost every collection made within the middle and lower system; 742 specimens were taken. One collection of four specimens (CU 48533) is from Catawba Creek at 0.4 rivermiles above its mouth where breeding males have also been regularly observed recently. One hybrid *N. micropogon* × *N. raneyi* was found in middle Catawba Creek (UMMZ 174826) and another (USNM 194636) in Johns Creek at Newcastle. One specimen (CU 48491) was collected in Pedlar River, Amherst County, 4 rivermiles above its mouth, which is 52 rivermiles downstream from the Catawba Creek mouth. (See discussion of atypical specimens of *N. raneyi*, pp. 32–36).

The bull chub occurs in the Virginia portion of the Chowan drainage (only six collections) in two of its three main tributary systems, the Nottoway and Meherrin Rivers.

It is widely distributed in the upper montane and upper Piedmont portion of the middle Roanoke drainage. Fifty-one collections from 37 localities were examined. All localities in the upper Roanoke

are along the South Fork and upper main channel except for one that is in Back Creek. In the middle basin, populations are present in the Blackwater (Figure 29), Pigg, and Otter Rivers. Its apparent absence from other upper and middle Roanoke tributaries, some rather well collected, is noted in the Ecology section. It has been taken on only three occasions in the Dan River system, the largest southern montane and Piedmont Roanoke tributary.

N. raneyi is widespread in the Tar and Neuse drainages; 24 collections from 21 localities were examined.

Atypical *Nocomis raneyi*

Specimens that generally agree with our concept of *N. raneyi*, but which are divergent in certain characters have been collected from the James drainage and are referred to herein as atypical *N. raneyi*. Atypical specimens were collected mainly between the ranges of two apparently disjunct populations of typical *N. raneyi* and partially within the interrupted range of *N. micropogon* in the James (Figure 20). The 13 collections of atypical specimens are from the main James channel and lower portion of all except one of its major tributaries from Craig Creek to 47 miles downriver. The specific localities are given at the end of this discussion. The most upstream locality, in Craig Creek, is 17.5 rivermiles above its mouth, where one atypical tuberculate male, in spawning or just entering postnuptial condition, was captured in 1967 with a typical nuptial male. Sixteen days earlier an apparently eggbound, atypical female was picked up dead at the same locality. Three collections, totaling 47 typical specimens only, were taken in a four year period earlier at the same locality. Typical and atypical specimens were also collected together at the mouth of Craig Creek. In three collections from Craig Creek within 0.5 to 3 miles from its mouth, 32 typical specimens only were taken. The two forms were collected together in one lower Catawba Creek collection and the atypical form was collected alone on three occasions from this stretch of stream including James River about 100 feet above the Catawba mouth. Typical specimens captured outnumbered atypical ones in lower Craig while the opposite was true in lower Catawba. Recent breeding behavioral observations in lower Catawba, however, involve several

typical nuptial males and only one atypical (or hybrid?) specimen. The main James has yielded only atypical specimens. The most downstream locality for an atypical specimen is the mouth of Rocky Row Run, which is 11 rivermiles above the mouth of Pedlar River within which a typical specimen of *N. raneyi* was found. *N. micropogon* is widespread in the large Maury River system, which enters the James four miles above the Rocky Row Run mouth; *N. raneyi* is not known from this system.

There are 79 atypical specimens which range from 42 to 229 mm SL, including several prenuptial and postnuptial males and a tuberculate male. Two or three small specimens could not be classified with certainty as atypical or typical *N. raneyi*.

There are no apparent differences between atypical and typical *N. raneyi* in the following characters in which typical *N. raneyi* differs significantly from *N. micropogon*; circumferential and lateral line

scales, vertebral numbers (Table 27), breast squamation, all aspects of body morphometry, size attained, coloration in life and in preservative, and the pharyngeal arches.

Some features in the atypical series generally are somewhat intermediate between typical *N. raneyi* and *N. micropogon*. Other characters in which the atypical form differs from *N. raneyi* are also unlike those of *N. micropogon* and they are not intermediate between the two species. The main differences between atypical and typical *N. raneyi* are in certain aspects of tuberculation, involving tubercle numbers, posterior distribution, early development, and size.

In larger juveniles and adults, the numbers are generally intermediate between typical *N. raneyi* and *N. micropogon* (Figure 21). The most posterior distribution also is somewhat intermediate between these two forms, ranging in adults from the P10 to A0C lines, more often ending at the A10 line; when

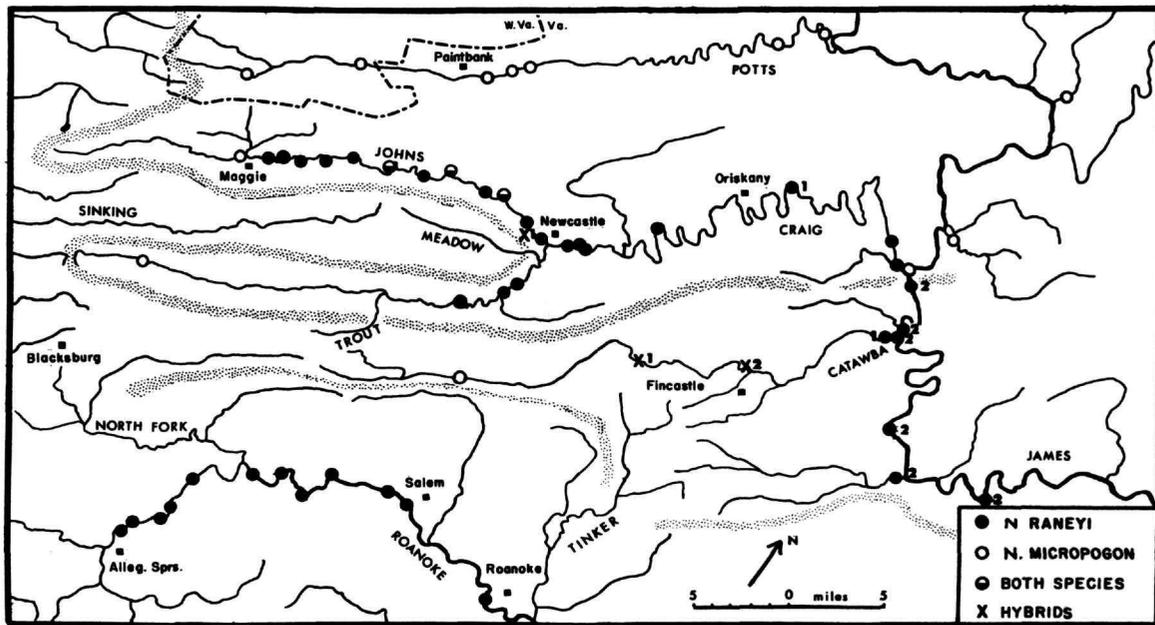


FIGURE 20.—Distribution of *Nocomis raneyi* and *N. micropogon* in the upper James and Roanoke drainages (see letter A of Figure 19). The common occurrence of *N. leptocephalus* in the area was omitted to avoid confusion in symbols. Hybrid combinations are indicated: X¹ = *N. micropogon* × *N. raneyi*; X² = *N. leptocephalus* × *N. micropogon*, in Catawba River. Solid dot¹ = atypical and typical *N. raneyi*; solid dot² = atypical *N. raneyi* only. Sinking Creek and other headwater tributaries of the New drainage are shown in the upper left part of the map; certain main mountain ridges are indicated by stippling.

extending into and beyond the interorbital area, the tubercles usually are more scattered than in typical *N. raneyi*. The most posterior tubercles are on or near the dorsal midline, as in typical *N. raneyi*, rather than dorso-laterally as in *N. micropogon*. The reduction and scattering of posterior tubercles in the atypical form results in lower tubercle numbers compared with typical *N. raneyi*. Almost all atypical specimens have tubercle spots and/or buds that are larger than the maximum size of spots and

buds in typical *N. raneyi* and, in many of the former, these structures exceed even the maximum size of those in *N. micropogon* of similar body length. The spots first appear in smaller atypical specimens than in any species of the micropogon group. The spots of most of the smallest atypical specimens have buds. All young or small juveniles, including females, from 42–62 mm SL, have 7–18 spots or buds. Thus, in small atypical specimens, the pattern of tubercle appearance and their increase is most simi-

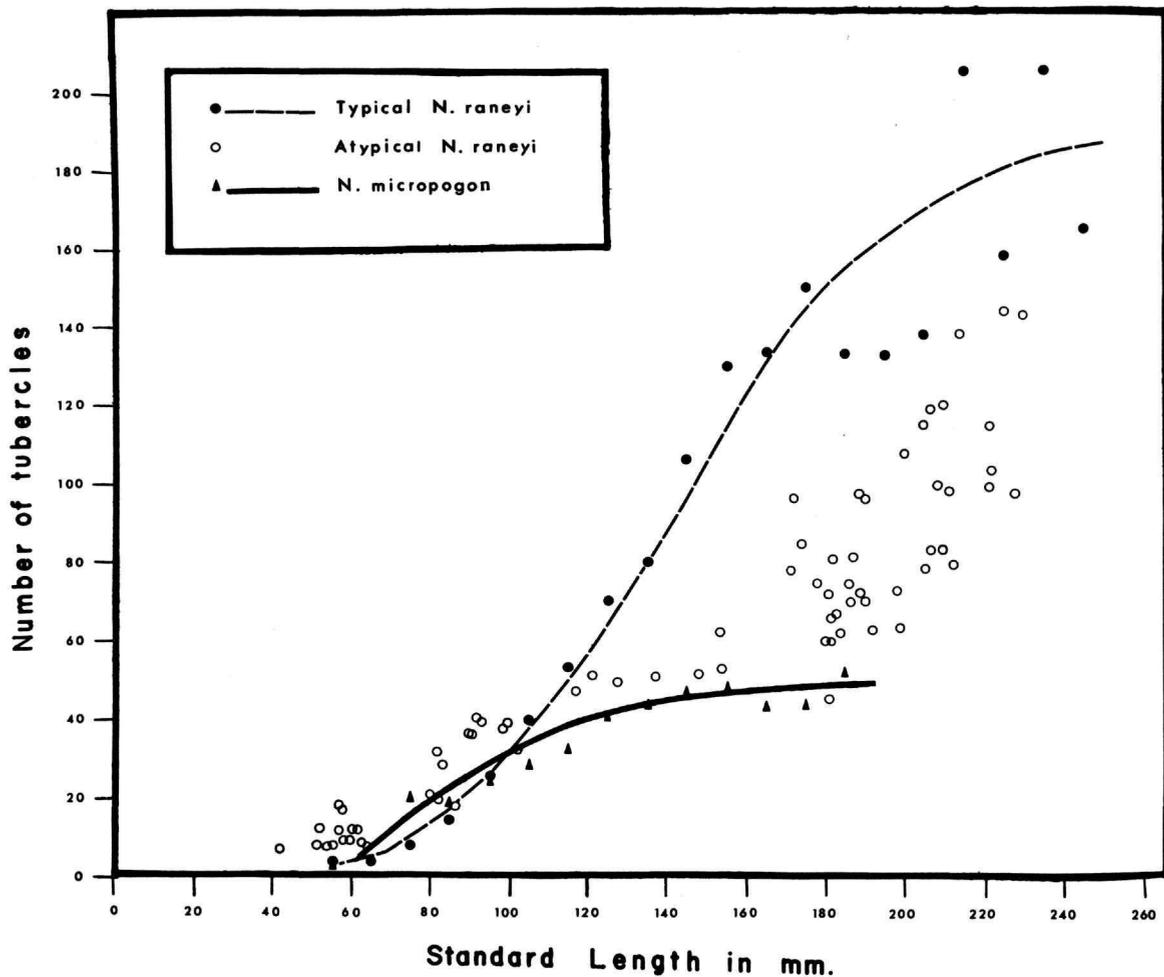


FIGURE 21.—The relationship between number of tubercles and standard length in typical *N. raneyi* (all drainages; data from Table 5), atypical *N. raneyi* (James drainage) and *N. micropogon* (James drainage; see Table 10). The curves for typical *N. raneyi* and *N. micropogon* were fitted to the mean values of the 10 mm size groups. Data for atypical *N. raneyi* are plotted from individual specimens.

lar to *N. micropogon*, but at larger sizes it conforms better to the *N. raneyi* pattern. Although there is a tubercle reduction in the atypical form, there is no trend toward development of a hiatus between the snout and internasal tubercles, which agrees with *N. raneyi* and not *N. micropogon*.

Other characters in which the atypical specimens differ from the species of the micropogon group are discussed below. The snout profile of most young and small juveniles is usually quite rounded, appearing somewhat swollen. The lower caudal fin lobe is considerably shortened and more rounded. The anterior rays of the anal fin are often reduced in length, resulting in a smaller fin with a broadly convex margin. The paired fins are frequently shorter and more broadly rounded.

The following factors are considered in an attempt to determine the origin and significance of the atypical specimens: (1) distribution and relative abundance with regard to opportunity for intergradation or interspecific hybridization between *N. micropogon* and *N. raneyi*; (2) atypical *N. raneyi* morphology in relation to that of *Nocomis* intergrades and hybrids; and (3) possible influence(s) by environmental disturbance.

Almost all atypical specimens were taken from an area connecting the two main populations of *N. micropogon* (one above Craig system, one from Maury system downstream) and the main typical *N. raneyi* population (Craig Creek area). The range of the atypical specimens may thus be one in which the forms met and freely interbred in the past. However, the presence of typical *N. raneyi* below the atypical area (known from one specimen from Pedlar River), and the occurrence of *N. micropogon* with typical *N. raneyi* in the Craig and Catawba systems are difficult to explain by intergradation, particularly since *N. raneyi* probably entered the James drainage in the Craig Creek area (see Dispersal section, p. 70). Relative rarity of one parental species is frequently cited as an important factor in production of hybrids. Although *N. micropogon* is unknown from the James River section with atypical *N. raneyi* and the lower portion of most tributaries of this section, these larger waters have not been well collected. Even if *N. micropogon* is present but rare in this section, the abundance of atypical specimens and small numbers of typical *N. raneyi*

(only in a small portion of the section) is not explained by hybridization within the section.

The atypical specimens conform to *N. raneyi* in most diagnostic characters; in the others they are roughly intermediate between *N. micropogon* and typical *N. raneyi* or differ from both species. The atypical form does not agree with the concept of an intergrade population, variably intermediate in most or all diagnostic characters (as we have found in subspecific intergrades of *N. leptcephalus* and populations of *N. micropogon* that show effects of apparent introgressive hybridization with *N. platyrhynchus*). Interspecific hybrids are generally intermediate but may deviate to the extent that they are extreme in certain characters, thus not excluding atypical *N. raneyi* from this category.

James River water is very darkly colored, due to the effluent from a large pulp mill at Covington, Virginia, downstream through the upper half or more of the atypical *N. raneyi* section. The peculiar morphology of the atypical *N. raneyi* may be induced by pollution. Indirect evidence from local anglers indicates that *N. raneyi* spawn in the main channel of the James. It would then be in direct contact with pollution beginning at early developmental stages. Lindsey (1956:770) gave evidence that fin shape in certain Canadian populations of *Couesius plumbeus* may be influenced by environmental conditions. De Sylva, Kalber, and Shuster (1962:29) noted deformed fins in striped bass collected in proximity to a chemical plant. Many cyprinid fishes with malformed mouths and fins were found by Larimore and Smith (1963:353) near a pollution source in an Illinois stream. Beadles (1966) concluded that industrial and domestic effluents could have produced variations in meristic and morphometric characteristics of subpopulations of three cyprinid species in an Oklahoma stream. Additional literature treating morphological variations caused by environmental conditions in fishes was summarized by Barlow (1961).

It is more probable that the atypical condition of *N. raneyi* is due to its development in polluted waters rather than to other alternatives treated. Solution of this problem must include additional collections, observations, and experimental work.

MATERIAL EXAMINED.—Atypical *N. raneyi* from the James drainage, Virginia. Included are museum numbers and number of specimens of typical *N.*

raneyi taken with three of these series. Collections are listed in progressive downstream order; following the collection date is the number of specimens captured (in parentheses).

Botetourt County.—USNM 201895: Craig Cr. at jct. Rtes. 614-683, 7.5 airmi W. Eagle Rock, 20 May 1967 (1). USNM 201898: same locality at USNM 201895, 6 June 1967 (1); taken with one typical specimen, USNM 201897. CU 50596: Craig Cr. at mouth, James River, 30 and 31 March 1965 (3); taken with two typical specimens, CU 48427. CU 52208: James R. at Eagle Rock, about 0.5 mi downstream Craig Cr. mouth, 1966 after 1 June (14). CU 47586: James R. about 100-200 ft. above mouth Catawba Cr., 24 October 1964 (15). CU 47568: Catawba Cr. 0.2 mi above mouth, 24 October 1964 (3). CU 52597: Catawba Cr. 0.4 mi above mouth, 10 May 1965 (6) taken with four typical specimens, CU 48533. CU 50820: same locality as CU 52597 (1). TU 25858: James R. at Springwood, 18 June 1962 (10). CU 47587: same locality as TU 25858, 23 October 1964 (10). CU 48438: Looney Cr. 0.3 mi above mouth, 30 March 1965 (3). CU 48426: James R. at mouth Jennings Cr., 29 March 1965 (11).

Amherst County.—CU 48549: Rocky Row Run at mouth, James R., at Snowden, 10 airmi S Buena Vista, 9 May 1965 (1).

PROBLEMATIC SPECIMENS FROM THE CRAIG CREEK AREA.—Craig Creek, Catawba Creek, and the James River near their mouths, all part of the James drainage, is one of the most critical areas in this study, for conclusions on the status of the forms of the micropogon group have been based on specimens found in this drainage area. Since some of the series from this area include small, poorly preserved, and difficult to identify specimens of apparent hybrids, and typical and atypical specimens, a discussion of our methods (some subjective) used to identify these and other series is warranted. These collections also assume considerable importance due to a recent impoundment of a section of the Johns Creek system, the proposed impoundment of much of Craig Creek (Mussey, 1948:20), and channelization of the lower 17 miles of Johns Creek. This is the only area in which three species of *Nocomis* have been collected together.

No adult *N. micropogon* were available from the Craig area. However, juvenile *N. micropogon* were taken from upper Johns Creek (TU 25469, 6 specimens), upper Craig Creek (UMMZ 135413, 2 specimens), and upper Catawba Creek (CU 50610, 1 specimen). These have the tubercle pattern of adult *N. micropogon* well developed or incipient and their meristic (Table 27) and morphometric values are well within the ranges of *N. micropogon*. Also clear-

ly determined are three specimens (UMMZ 135401) taken with one *N. raneyi* (UMMZ 181830) from middle Johns Creek. The three range from 60-80 mm SL and have the juvenile tubercle pattern, low meristic values, long snout and larger mouth of *N. micropogon*. The specimen identified as *N. raneyi* lacks tubercle spots (as expected for this species at 60 mm SL but not for *N. micropogon*), has 35 circumferential scales, 41 vertebrae, and, in coloration and morphometry, resembles *N. raneyi*.

The species were taken together on two other occasions from the lower half of Johns Creek. The most upstream collection, was 1.5 miles east of Craig Healing Springs and consisted of two specimens (CU 50340, 36 mm SL; and CU 52598, 42 mm SL). Both are too small to be identified by tubercle spots and morphometry, although CU 52598 has a rather long snout, like *N. micropogon*. The snout of the other specimen is more like *N. raneyi*. The apparent *N. micropogon* specimen has 30 circumferential scales; no *N. raneyi* was found with 30 circumferential scales and a 31 count is rare. Its vertebrae number 41, which is occasional for *N. micropogon* but typical for *N. raneyi*; the lateral line count of 40 applies to both species. Thus CU 52598 is identified as, probably, *N. micropogon*. CU 50340 is identified as, probably, *N. raneyi* from its appearance and vertebral count of 42; we have not found a vertebral count of 42 in *N. micropogon* over its range. The circumferential count of 32 and lateral line of 40 are common to both species.

The other collection from Johns Creek, at 4.2 roadmiles on Rte. 311 from Newcastle, includes seven *N. raneyi* (CU 50422), 37-116 mm SL, one *N. micropogon* (CU 50423), 39 mm SL, and several *N. leptcephalus*. The 39 mm specimen has more heavily pigmented scale margins, a longer snout than the other young specimens, 30 circumferential scales, and 40 vertebrae, thus apparently representing *N. micropogon*. One specimen with tubercle development, 116 mm SL, shows the typical juvenile pattern of *N. raneyi*. The other six specimens apparently are young *N. raneyi* based on scale counts, and vertebrae of 41 (2), 42 (3), and 43 (1).

All except one specimen from Craig Creek, near its mouth, and the James River in the immediate vicinity are typical or atypical *N. raneyi*. The exception, a specimen (CU 47584), 65 mm SL, lacks tubercle spots, has 41 vertebrae, 40 lateral line scales,

and 30 circumferential scales. The circumferential count falls out of the range of *N. raneyi*. The gape width of 6.8 percent SL and snout length of 8.5 percent SL is intermediate between *N. micropogon* and *N. raneyi*. It is tentatively identified as *N. micropogon*.

The nearest locality upriver (USNM 132064 taken around 1880) is in lower Mill Creek, a James River tributary about five miles above the mouth of Craig Creek. The 14 specimens are very poorly preserved and small, 45–80 mm SL. The unscaled breasts and the unwhorled intestines exclude these being *N. leptocephalus*. They are identified as *N. micropogon* mainly by the meristic values: circumferential scales 29 (1), 30 (5), 31 (5), 32 (2); lateral line scales 38 (3), 39 (8), 40 (2); total vertebrae 39 (6), 40 (7), 41 (1). The tubercle spot pattern, typical of juvenile *N. micropogon*, was discernible only in the largest specimen.

The characters of atypical specimens, but basically *N. raneyi*, from lower Craig and Catawba Creeks and the James River are given above. We found two specimens from the Craig Creek area, one from lower Johns Creek and one from middle Catawba Creek, that do not fit our concept of the atypical specimens, but rather, are intermediate between *N. micropogon* and *N. raneyi* in most of the diagnostic characters. These have been determined as hybrids between the two species. We have not found atypical specimens from the vicinities in which these specimens were taken. They will be described in paper 5 on hybridization (p. 2).

Nocomis platyrhynchus, new species

BIGMOUTH CHUB

FIGURES 7, 10, 11, 16

Ceratichthys biguttatus.—Cope, 1868: 226, 240 [(ANSP) Walker Creek].

Hybopsis kentuckyensis.—Goldsborough and Clark, 1908:36 [New River drainage, West Virginia].

Hybopsis kentuckyensis.—Breder and Breder, 1923: 11 [South Fork New River].

Hybopsis micropogon.—Raney, 1941:3 [New River].—Ross and Perkins, 1959 [(part) New drainage records].

Hybopsis species.—Robins and Raney, 1956:31 [New River].—Ross, 1959: 12, 16, 25 [New River above Kanawha Falls].—Ross and Perkins, 1959:12, 19, 24, 27 [(part) New drainage records].

Hybopsis leptocephala.—Ross and Perkins, 1959 [(part) New drainage records].

Hybopsis (Nocomis) species 1.—Reno, 1969b, p. 739.

DIAGNOSIS.—A species resembling *N. micropogon* in body features and approaching *N. raneyi* in certain aspects of head tuberculation and squamation; mouth wide (Figure 5); snout long (Figure 6, Tables 17, 20, 21); body subterete; maximum number of head tubercles in largest specimens approaching average values of about 100 or less (Table 6); tubercles not densely developed on snout in adults; tubercles characteristically present in the occipital area in most adult specimens, sometimes extending to the posterior occipital line (Table 2); breast typically scaled, usually from 50 to 100 percent in all river populations (Table 18); caudal fin olive-orange in subadults and moderately forked; pharyngeal arch of moderate proportions, the edentulous processes longer than in *N. raneyi* (Figure 18).

DESCRIPTION.—*Morphometry*: Proportional measurements, expressed in thousandths of the standard length, are given for the holotype, 5 male paratypes, 57 to 195 mm SL and 5 female paratypes, 65 to 142 mm SL in Table 24. Additional proportional data are given in Table 25 for 13 characters of 31 adult males having a mean length of 178 mm and ranging from 159 to 214 mm SL. The general growth pattern is similar to that described for *N. raneyi*. In the young and smaller juveniles, all three species of the micropogon group are very similar in their body features. At about 70 mm SL (Figures 5, 6) the gape width and snout length begin to show different developments in *N. platyrhynchus* (and *N. micropogon*) compared with that of *N. raneyi*. The wide mouth, longer snout, and more rounded, subterete, body of the adults, particularly the nuptial males, give the former two species a stouter, more robust appearance. The systematic significance of the gape width and snout length in the micropogon group was treated under *N. raneyi* (p. 18).

The preopercle-opercle suture is most often perpendicular in relation to horizontal body axis, or the lower portion is slightly posteriorly directed. In a sample of 100 specimens, 5 had suture line directed forward at an angle of about 10° to 20°; 22 specimens had suture very slightly directed forward; 73 specimens had suture perpendicular or it was slightly posteriorly directed, in relation to horizontal body axis.

The intestine is simple, elongate, and S-shaped (84%) or with a very short anterior bend (16% of 44 specimens).

Other general features of the head and body are very close to those of *N. micropogon*: Head moderately elongate and wide, but not deep; head widest at posterior part of opercle and deepest at the occiput. Dorsal and ventral body contours, excluding nuptial males, as in *N. raneyi*, except snout only moderately elongate and pointed to slightly or moderately rounded as in *N. micropogon*; mouth moderate in size in young to large in adult males; mouth slightly oblique, subterminal and slightly to moderately overhung by the tip of snout; angle of jaw at or slightly posterior to vertical from posterior nostril; shape and position of lips, barbel, eye and lachrymal bone is in *N. raneyi*.

The body is elongate and subterete, only slightly compressed in adult males compared to *N. raneyi*; body deepest and widest midway between occiput and origin of dorsal fin; predorsal body contour slightly convex; postdorsal body contour is straight and slopes downward; ventral body contour gently rounded from head to origin of anal fin; lateral line, urogenital papilla, scale pattern except breast, and cutaneous sense organs as in *N. raneyi*; shape and size of fins are much like those of *N. raneyi*, except caudal fin is more shallowly forked, the notch more broadly rounded, than in *N. raneyi*, particularly in adult males (resembling caudal of *N. micropogon*); lobes of caudal fin sometimes slightly subequal, upper lobe a little longer in young and juveniles, and the lower lobe slightly longer in adult males.

Meristic characters: Squamation values are close to those of *N. raneyi*. The range of mean values of specimens from the main channel of the New River and its major tributaries follow, with holotype data in parentheses: Circumferential scale rows, 32.7 to 34.2 (34) (Table 12); lateral line scale rows, 39.6 to 40.3 (41) (Table 8); scale rows above lateral line, 6.6 (8) (Table 11); caudal peduncle scale rows, 16.8 (17) (Table 14); pectoral fin rays, 17.5 (Table 16); total vertebral numbers, 40.5 to 40.6 (Table 15).

The breast (Table 18) is one half to fully scaled in most specimens, the modal values for the main New River and its major tributaries show about a three fourths scaled condition. In breast squamation, *N. platyrhynchus* is unlike the James, Chowan, and Roanoke River populations of *N. raneyi*, but it is close to the Tar and Neuse populations of *N. raneyi*, certain drainage populations of *N. micro-*

pogon and to the consistently high values for *N. leptcephalus*.

Tuberculation: Data pertaining to tubercle development, distribution and numbers are summarized in Tables 2, 3, 4, and 6. The relationship between increase in tubercle numbers with increase in standard length is shown in Figure 4. The distribution of head tubercles is illustrated in Figures 10, 11, and 16. Tubercle pattern and increase in tubercle numbers with increase in body length is fairly similar in the sexes. The males attain a larger size than the females (Table 6) and thus a greater average number of tubercles. *N. platyrhynchus* is characterized as having fewer tubercles than *N. raneyi* but more than *N. micropogon*; their distribution on the head extends, dorsally, over a greater area than in both of the latter species; the increase in tubercle numbers slopes off at about 150 mm SL (Figure 4). The tubercles first appear as small, light spots in the internasal area, intermediate in numbers between *N. raneyi* and *N. micropogon* (Figure 3). The tubercles rarely can be seen at body lengths up to 60 mm SL. Both males and females may have no visible tubercle spots at 70 mm SL in some specimens. With increase in body length the tubercles develop posteriorly on the head, the complete tubercle pattern being developed in some specimens about 100 mm SL. (Table 2). The snout and subnasal tubercles develop more slowly than those on the top of the head. Up to three rows of tubercles may be present in the lachrymal area of the larger males. Tubercles on the snout of *N. platyrhynchus* are more abundant than in *N. micropogon* and do not form a hiatus in the adults as in the latter species, but some specimens may show a tendency towards a hiatus in having reduced tuberculation between tip of snout and the internasal area. Average tubercle size is approximately intermediate between that of *N. micropogon* and *N. raneyi*; the largest tubercles occur in the internasal area or just behind. The tubercle bud stage first appears at about 80 mm SL (Table 4) at a size similar to the first development in *N. micropogon*, and appears in both species at a much smaller size than in *N. raneyi*.

Small tubercles are present on the pectoral fin rays as in *N. raneyi*, but they are most often present on rays 2 to 6.

Nuptial crest: Small or moderate nuptial crests

are present on tuberculate specimens 195 to 200 mm SL. A large male, 195 mm SL, taken 19 June 1962 (Figure 10) has a moderate crest. A specimen 183 mm SL captured 6 July 1963 (Figure 16) has no trace of head swelling and has the typical sharp, pointy subadult snout. Two specimens, 198 mm SL taken on 3 May 1964 and 200 mm taken on 10 May 1964, have moderate to large crests. The crest is highest just posterior to the interorbital area. No male *N. platyrhynchus* in the "peak" of crest development, which occurs in other *Nocomis* during spawning or just before, has been captured or observed in life.

Pharyngeal dentition: The tooth count is 4-4 (12 pairs of arches), the teeth being moderate in length and width. The arch is only moderately broad, the edentulous processes comparatively long and slender (Figure 18). The pitted surface is sculptured more extensively than in *N. raneyi*. The arch in *N. platyrhynchus* is very similar to that of *N. micropogon*.

Coloration: The coloration of *N. platyrhynchus* is similar to that of *N. raneyi* except that the former retains the dark, lateral body stripe in the adults of both sexes (as in *N. micropogon*) and the caudal fin is more olive-orange (as in certain populations of *N. micropogon*) rather than the reddish color of *N. raneyi*. Some adult males of *N. platyrhynchus* have lemon-yellow pelvic fins, not noted in any other species of *Nocomis*.

The dark horizontal midlateral stripe is retained in large adult females, nonbreeding and tuberculate adult males. In both sexes of *N. raneyi*, however, the stripe is lost before these stages of maturity. In life, the holotype and topoparatypes of adult females, subadults or nonbreeding adult males and juveniles of *N. platyrhynchus* captured elsewhere have the median scale color along the lateral band area light to moderate pale green. The color appeared to be deep-lying. The scale edges were rather sharply defined from the iridescent scale medians dorsad and ventrad. Almost immediately upon placing each specimen in formalin, the green disappeared and was replaced by dark gray. The occurrence, area of development, and intensity of the lateral stripe are variable. The stripe is present in most size classes of both sexes including the three available tuberculate males. The stripe is sometimes absent from juveniles, subadults, and adults

in the same collections containing similar specimens with a stripe. It is absent most often from poorly preserved or faded specimens. In most specimens with a stripe, it is developed mainly on the posterior half of the body, but it is developed in many specimens the entire body length. The dark scale margins on the lateral body are slightly wider in *N. platyrhynchus* than in *N. raneyi* and slightly narrower than in *N. micropogon*.

The caudal fins of many juveniles and subadults observed in life and fresh specimens captured by the use of fish poisons were olive-orange. Some postnuptial and nonbreeding adult males had reddish colors on the outer membranes of the caudal and dorsal fins. The pelvic fins of recently preserved, large specimens (USNM 194870) were yellow over most of their length, but this color was absent in many other specimens captured and observed before preservation.

We have not seen a living, nuptial male in close-up or a freshly captured specimen. A large, crested tuberculate male, 200 mm SL (USNM 194816) captured and observed on 10 May 1964 by James E. Carico, Lynchburg College, had the "ventral part of the head and belly pink to the anus."

REPRODUCTION AND GROWTH.—Over the past several years large nests of the bigmouth chub were observed in the Greenbrier River system during May. The nests, often, were over three feet in diameter and always in the deeper, swifter channels of the stream where it was particularly difficult to carry on observations. The length-frequencies for 255 males and females is summarized in Table 6. The largest specimen was a male, 222 mm SL. As in *N. raneyi*, the males attain a much larger size than the females, only a few females exceeding 120 mm.

ETYMOLOGY.—The specific name, *platyrhynchus*, and the vernacular name, bigmouth chub, is in reference to the large gape width.

MATERIALS EXAMINED.—Holotype: USNM 194817, a nontuberculate male 163 mm in standard length, captured in Big Walker Creek, Bland County, Virginia, 0.25 roadmiles west of Bland-Giles county line on Rte. 670 on 6 July 1963 with shocker by Robert E. Jenkins, Robert L. Miles, and Fred D. Hinson. Seven paratypes, USNM 194877, were taken with the holotype.

Only materials from Virginia and North Carolina are designated as paratypes.

The collections are listed below by drainages and major tributaries in progressive upstream order; following the collection date is the number of specimens captured (in parentheses).

New River Drainage, Virginia and North Carolina

VIRGINIA COLLECTIONS

Main Channel, New River, Montgomery-Pulaski line.—USNM 194870: about 0.5 mi downstream McCoy, 3-5 July 1964 (13).

Main Channel, New River, Grayson County.—USNM 194819: at 1 mi upstream Rte. 58-221 bridge, 4 mi W Galax, 10 May 1964 (1).

East River, Giles County.—UMMZ 95253: Glenlyn, 11 September 1928 (1).

Wolf Creek, Bland County.—USNM 56871: Rocky Gap, 23 July 1900 (4). USNM 177380: at 1.5 rdmi E. Grapefield, 5 August 1957 (21). USNM 194812: Clear Fork, at 1.5 airmi SW Rocky Gap, 7 August 1957 (3). USNM 194815: at Camp Roland, 3.1 airmi W Bastian, 6.75 airmi SW Rocky Gap, 6 August 1957 (8). UMMZ 139446: between Bastian and Norris, 22 August 1936 (3).

Big Walker Creek, Bland County.—CU 47593: at 1 mi SE Crandon, 11 July 1957 (23). USNM 177353: same locality, 12 July 1957 (4).

Little Walker Creek, Pulaski County.—USNM 194822: at 6.8 rdmi above mouth, 29 August 1957 (2). USNM 194257: on Rte. 601, 3.5 mi W jct. Rtes. 100-601, 7.1 airmi NW Dublin, 1 July 1957 (10).

No Business Creek, Bland County.—USNM 194805: first Rte. 608 bridge, about 1 mi. N. of its mouth, 3 July 1957 (6).

Toms Creek, Montgomery County.—CU 47590: bridge just downstream from mouth Poverty Creek, 6.5 mi W Blacksburg, 3 May 1964 (1).

Little River, Floyd County.—CU 24833: Rte. 8 bridge, 4.6 mi S Riner, 2 July 1952 (14). UR 887: same locality, 2 July 1958 (13). CU 41815: Rte. 221 bridge, 6.2 mi. NE Floyd, 31 March 1962 (6). USNM 194810: Graystown, Rte. 699 bridge, 7 airmi S Radford, 23 August 1957 (8).

West Fork, Little River, Floyd County.—CU 24801: Rte. 8 bridge, 2.5 mi ENE Floyd, 2 July 1952 (5). CU 47592: (no specific data) 28 April 1962 (6).

Big Reed Island Creek, Carroll County.—USNM 194808: Rte. 654 bridge, 2 mi S. jct. Rte. 654-58, 9.7 airmi ESE Hillsville, 15 July 1957 (3). USNM 177400, New R. drainage (no specific data) (29).

Snake Creek, Carroll County.—USNM 177381: Rte. 58 bridge, 6 airmi ESE Hillsville, 16 July 1957 (27).

Little Reed Island Creek, Carroll County.—USNM 194813: at 0.5 mi N jct. Rtes. 52-769 on 769, 20 August 1957 (7). USNM 194816: bridge at jct. Rtes. 769-771, 20 August 1957 (9).

Reed Creek, Wythe County.—USNM 89439: about 4 mi E Wytheville, 6 August 1888 (1). USNM 194251: at 1.4 rivermi from mouth, 6.8 airmi ESE Max Meadows, 12 August 1957 (5). USNM 194807: Max Meadows, 0.4 mi SW of town, 12 August 1957 (6). USNM 177403: at 1 mi above Rte. 11

bridge, 3.5 airmi W jct. Rtes. 11-52 in Wytheville, 13 August 1957 (34).

Cripple Creek, Wythe County.—USNM 194809: at 3.8 rivermi above mouth, 1.8 mi NW Ivanhoe, 13 August 1957 (7).

Elk Creek, Grayson County.—USNM 194260: Comers Rock, 10.8 airmi NNW Independence, 25 July 1957 (35). CU 25812: mouth 7 mi W Galax on Rte. 58, 28 August 1953 (140).

Fox Creek, Grayson County.—USNM 194814: mouth Middle Fox Creek, jct. Rtes. 678-711, 9.5 airmi NW Independence, 13 July 1963 (2). USNM 194821: just below mouth Little Fox Creek, 1.2 mi NW on Rte. 711 from jct. Rtes. 58-711, 8.75 airmi W. Independence, 23 July 1957 (1). USNM 194811: (no specific date) May 1964 (2).

NORTH CAROLINA COLLECTIONS

Little River, Allegheny County.—UMMZ 147552: Rte. 21 bridge, 1 mi SE Sparta, 27 August 1946 (11). UMMZ 165439: at 7 mi NE Sparta, 23 July 1953 (34).

North Fork, New River, Ashe County.—USNM 171737: at 1 mi NNE Warrentonville, 1 April 1940 (25). DU (unnumbered): near Bina, 100 yds above mouth Big Horse Creek, 25 July 1941 (2). DU (unnumbered): 2.5 mi above mouth, 26 July 1941 (2).

South Fork, New River, Ashe County.—DU (unnumbered): at 3.5 mi NW Scottsville, 28 June 1949 (5). TU 25902: at 4 mi SW Scottsville, 19 June 1962 (17).

South Fork, New River, Watauga County.—CU 47591: Rte. 221 bridge, 1.6 mi E Boone, 8 September 1947 (33). USNM 166408: at 0.5 mi below Todd, 24 August 1941 (4). CU 21865: Rte. 221 bridge between Boone and Deep Gap, 22 July 1952 (43). DU (unnumbered: mouth Fighting Creek, 27 August 1949 (4).

Material not designated as paratypes.

NEW RIVER TRIBUTARIES, VIRGINIA

West Fork, Little River, Floyd County.—USNM 194252: Rte. 720 bridge 0.5 mi from jct. Rtes. 720-729, 30 July 1957 (1).

Dismal Creek, Bland-Giles County line.—USNM 194820: the "Cascades," about 6.8 airmi NW White Gate, 10 October 1956 (2).

Wolf Creek, Bland County.—USNM 56666: Rocky Gap, 23 July 1900 (1).

NEW RIVER AND TRIBUTARIES, WEST VIRGINIA

Main channel, New River, Raleigh County.—USNM 203916: 8.2 mi below Hinton, 1 September 1966 (87).

Main channel, New River, Fayette County.—USNM 204451: at Power Dam pool upstream from Rte. 21; just below Hawks Nest State Park above Kanawha Falls, 18 September 1968 (1).

Indian Creek, Monroe County.—CU 25772: at 1.8 mi SE Monroe line on Rte. 12, 25 August 1953 (5). UMMZ 118782: midway between Red Sulphur Spring and Greenville, 15 July 1933 (3). UMMZ 118793: Greenville, 15 July 1933 (22).

Turkey Creek of Indian Creek, Monroe County.—UMMZ 119163: 28 August 1933 (8).

Bluestone River.—USNM 56828: Abbs Valley W. P. Hay, collector (4). USNM 56982: Abbs Valley, 29 July 1900 (7).

Camp Creek, Mercer County.—UMMZ 95272: 11 September 1928 (19).

Rock Creek, Mercer County.—UMMZ 118737: 9 July 1933 (7). UMMZ 95261: along hwy. N of Princeton, 11 September 1928 (10).

Rich Creek, Mercer County.—UMMZ 118745: 2 mi above Spanishburg, 9 August 1933 (3).

Second Creek, Greenbrier River, Greenbrier-Monroe County line.—UMMZ 95230: S of Ronceverte, 10 September 1928 (3). UMMZ 118855: at Nickells Mill, 5 mi from mouth, 18 July 1933 (2).

Greenbrier River, Greenbrier County.—USNM 203917: first riffle area below bridge at Anthony downstream to just below mouth of Anthony Creek, 31 August 1966 (220).

Muddy Creek, Greenbrier River, Greenbrier County.—USNM 203915: 1 mi above Alderson, 11 August 1966 (18).

Second Creek, Greenbrier River, Greenbrier County.—USNM 171697: 30 July 1931 (5). UMMZ 118842: near Greenbrier-Monroe Co. line, 17 July 1933 (11).

Ozle Creek, Greenbrier River, Greenbrier County.—USNM 194824: on Rte. 60, 3 mi E White Sulphur Springs, 28 June 1955 (1).

Howards Creek, Greenbrier River, Greenbrier County.—USNM 194825: W of White Sulphur Springs, 13 October 1956 (1). UMMZ 95222: south edge of White Sulphur Springs and 2 mi below, 10 September 1928 (27).

Greenbrier River, Pocahontas County.—USNM 56560: Durbin, 21 July 1899 (2). CU 20673: Durbin, 5 June 1951 (9). USNM 171610: near Bartow, 27 June 1935 (4). CU 23859: just E. Bartow, 5 June 1951 (9).

East Fork, Greenbrier River, Pocahontas County.—USNM 194826: at 1 mi E Bartow, jct. Rtes. 28–250, 14 October 1956 (11).

Deer Creek, Greenbrier River, Pocahontas County.—USNM 194823: on Rte. 28, 4 mi E Cass near jct. Rtes. 8–28, 1 mi SW Greenbank (5). UMMZ 118886: Boyer, 21 July 1933 (1).

North Fork, Greenbrier River, and Deer Creek.—UMMZ 118899: Greenbank, 18 July 1933 (1).

Gauley River, Nicholas County.—CU 20866: Rte. 41, 3 mi S Summersville, 4 October 1951 (47).

Twenty-mile Creek, Gauley River, Nicholas County.—UMMZ 95281: mouth about 6 mi above Gauley Bridge, 12 September 1928 (7). UMMZ 119065: Dixie, 15 August 1933 (5). Peters Creek, Gauley River, Nicholas County.—UMMZ 119029: at 3 mi W Summersville, 7 July 1933 (4).

Muddlety Creek, Gauley River, Nicholas County.—UMMZ 108168: 1 May 1932 (5).

Gauley River, Webster County.—UMMZ 119008: above Bolair, 7 August 1933 (1). UMMZ 165755: at 5 mi above Bolair, 8 August 1953 (28).

Cranberry River, Gauley River, Webster County.—UMMZ 165699: at mouth of Dogway, 4 August 1953 (5).

Williams River, Gauley River, Webster County.—UMMZ

165706: at mouth of Three Forks, 6 August 1953 (17). UMMZ 118951: by a beaver dammed trib. to Gauley, 3 August 1933 (25).

DISTRIBUTION.—*N. platyrhynchus* is a western Appalachian slope species (Figure 19), confined to, and widely distributed in, the New River drainage of West Virginia, Virginia, and North Carolina. Kanawha Falls, located at the town of Glen Ferris, Fayette County, West Virginia, is herein regarded as the geologic and faunistic divide of the New-Kanawha River system into two major portions. The New River drainage is that portion above this barrier (including Sandstone Falls) to its headwaters, the North and South Forks in northwestern North Carolina. The Kanawha River drainage is the shorter portion below the Falls to its mouth in the Ohio River. The division between the upper and lower New drainage is recognized as the boundary of the Ridge and Valley province and the interior Allegheny Plateau. The New River leaves the Ridge and Valley province at approximately the Virginia-West Virginia state line (Dietrich, 1959: 12).

N. platyrhynchus occurs throughout the upper New drainage. Fifty records from 48 localities are from almost all major tributaries and the main channel. Within the lower New, this species is known from four major tributaries. Four records are from Indian Creek, which enters the New just downstream from the upper-lower New drainage boundary, and ten records are from Gauley River, which flows into the New about one mile above Kanawha Falls. Entering the New between these tributaries are the Greenbrier and Bluestone rivers, from which we have 23 collections. One collection of 87 specimens was taken in the lower main channel of the New River, (USNM 203916) 8.2 miles below Hinton, resulting from a poison station to survey the large river fauna by the West Virginia Department of Natural Resources. The bigmouth chub was the most common fish species encountered. Many juveniles were not picked up. *N. platyrhynchus* is also abundant in the Greenbrier River. The collection of 220 specimens (USNM 203917), taken just below Anthony, of juveniles to subadults represent only a sample from a poison station also by the West Virginia Department of Natural Resources. The bigmouth chub was also the most common species observed at this locality.

***Nocomis micropogon* (Cope)**

RIVER CHUB

FIGURES 16, 17, 22-25

Ceratichthys micropogon Cope, 1864: 277 [type, ANSP 5061, Conestoga River, Pennsylvania]; 1869: 366, pl. 12: fig. 2 [redescription].—Fowler, 1909: 550, pl. 27.

Hybopsis kentuckiensis.—Jordan, 1889a: 110 [part]; 1889b: 9, pl. 3: figs. 10, 11.—Goldsborough and Clark, 1908: 36 [part].

NOMENCLATURE.—*N. micropogon* was briefly described by Cope (1864:277) from a single specimen from the Conestoga River, a tributary of the Susquehanna River, Pennsylvania, collected by a member of the Linnaean Society of Lancaster probably around 1863. Cope (1869:366), when redescribing the specimen, stated that it might be a hybrid *Ceratichthys* [= *Nocomis*] × *Hypsilepis* [= *Notropis (Luxilus)*] *cornutus*. Thereafter specific status of *micropogon* was questioned or it was synonymized with other species of *Nocomis*, until Hubbs (1926: 27-29) used *micropogon* as the name for a valid species of *Nocomis*. Hubbs apparently based his decision on earlier descriptions of it by Cope (1864; 1869:366, pl. 12: fig. 2) and Fowler (1909:550-552) and because only one species was known to occur in the Susquehanna drainage.

Examination of the type (ANSP 5061, 67 mm SL) shows that it apparently is a hybrid *Nocomis micropogon* × *Notropis cornutus*. Cope (1869) correctly recognized that, in particular, its head resembles that of *Notropis cornutus*. Its anterior lateral scales are more elevated and the lateral line is more down-curved than in *Nocomis* and thus indicates *Notropis (Luxilus)* parentage. Mouth position and angle, very small size of the two barbels, and moderately large eye size are approximately intermediate between these two stocks. The breast is considerably more scaled than the Susquehanna population of *N. micropogon*. The holotype resembles other hybrid specimens of *N. micropogon* × *N. cornutus*, which is a common combination in our hybrid studies.

The presence of a tooth in the minor row of the type would also tend to confirm its hybrid origin. The pharyngeal teeth in *N. micropogon* are always 4-4, in *N. cornutus* 2,4-4,2. Cope (1869) reported the type to have 4-4 teeth but Fowler (1909:550) gave 1?,4-4,1?. It is not clear, but probably the arches have at least one minor tooth row; the numbers could be interpreted as 4-4 to 1,4-4,2 depend-

ing upon whether the cavities anterior to the major tooth row are regarded as tooth scars or foramina. Based upon our examination of many other *Nocomis* arches, at least one tooth in the minor row was present but lost when dissected by Cope. The parentage of *N. cornutus* is also indicated by the long and well-hooked lowermost tooth of each arch; the lowermost one in *Nocomis* is relatively short with a conic, lesser hook on the head.

Other characters of the type are lateral line scales about 39, caudal peduncle scales 16, anal rays 7, pectoral rays 18. Other scale counts could not be made since some scales are missing. Color pattern is not obvious since the specimen is faded.

Article 17(2) of the International Code of Zoological Nomenclature (1961:17) states that a name is or remains available even though "in the case of a species-group name, it is found that the original description relates to . . . an animal or animals later found to be hybrid; . . ." In accordance with the Code, we restrict the name *Ceratichthys micropogon* Cope to that presumed parent of the type specimen.

Only a few particular references pertaining to the central Appalachian area are considered in the synonymy of this wide-ranging, frequently encountered species.

DIAGNOSIS.—A species most closely related to *N. platyrhynchus* but differs in having fewer tubercles, reduced tubercle pattern, and larger scales. The head tubercles in adults are grouped from the snout to the interorbital area and do not extend posteriorly on the midline beyond the anterior interorbital area, forming a V-shaped pattern. Snout tubercles almost always not forming a confluent pattern with those at anterior internasal area thus causing a hiatus in tuberculation. Tubercles number fewer than 60 in almost all adults. The means for total tubercle numbers for the various river populations range from about 30 to 65. Scales larger, the mean values for circumferential scale rows and lateral line scales (Tables 8, 12) are all lower in *N. micropogon* than in *N. platyrhynchus*.

DESCRIPTION.—*Morphometry*: Proportional data is given in Table 25 for 51 specimens, 29 of which were grouped from the Potomac, Rappahannock, and James River drainages, with a mean length of 165 mm SL and ranging from 142 to 189 mm and 22 specimens from the Tennessee River drainage with a mean length of 161 mm and ranging from

141 to 188 mm. Although the Tennessee population shows the greatest reduction in tubercle numbers, the morphometric data agrees with that of other *N. micropogon* drainage populations. The head length of the Tennessee population may be somewhat shorter (mean, 27.2% of body length) than the Potomac-James group (mean, 28.4%).

The proportional features of *N. micropogon* are generally similar to those of *N. platyrhynchus*. There is some difference in the gape width between these species (Figure 5; see *N. raneyi*, p. 18), the heights of the regression lines are statistically different. This difference is of a subtle nature (Figure 7) and often when disassociated with body size, it was of no systematic use. A juvenile *N. micropogon* is shown on Figure 17.

The slope of the preopercle-opercle suture is similar to that of *N. platyrhynchus*; the lower portion is most often perpendicular to the horizontal body axis or it is slightly posteriorly directed (70% of 200 specimens), 24 percent with suture line very slightly directed forward, and 6 percent with suture line directed forward at an angle of about 10° to 20°.

The intestine is simple, elongate and S-shaped (39% in a sample of 75 specimens), or with a very short kink (45%) or moderate kink (16%, see Figure 8a for *N. raneyi*).

Meristic characters: Many of the meristic characters were segregated by drainages in order to compare populations of this wide-ranging species, and possibly to associate related populations with early dispersal and stream capture. Most of the mean values for the meristic characters in *N. micropogon* are lowest for its species group, but are higher than those for *N. leptocephalus*. The range and mean values are given for as many as 19 drainages or regions for circumferential scale rows (Table 12), lateral line scales (Table 8), scale rows above and below the lateral line (Table 11), rows of scales around the caudal peduncle (Table 14), number of pectoral fin rays (Table 16) and vertebral numbers (Table 15). The higher means for the circumferential scale rows in the Monongahela, Youghiogheny, and Potomac drainages may have been influenced by relatively recent gene interchange. The higher values in the Tennessee and Cumberland drainages contrast with the low values in nearby Kentucky, Big Sandy, and Kanawha populations. These differ-

ences also may be linked with recent drainage exchanges of *N. micropogon* stocks.

The breast squamation (Table 18) differs among populations from those having scaleless or only slightly scaled breasts to those completely scaled or nearly so. There is also great variation in this character within some drainages. For example, the Tennessee and Cumberland drainages contain specimens with breasts ranging from scaleless to fully scaled. The Atlantic slope drainages from the Susquehanna southward to the James consistently have few or no scales on the breast. The major drainages west of the divide, such as the Tennessee, Cumberland, Kentucky, Kanawha tributaries, Monongahela and Allegheny, show consistently higher values for the degree of breast squamation.

Tuberculation: The development, distributional pattern, and numbers of tubercles for *N. micro-*

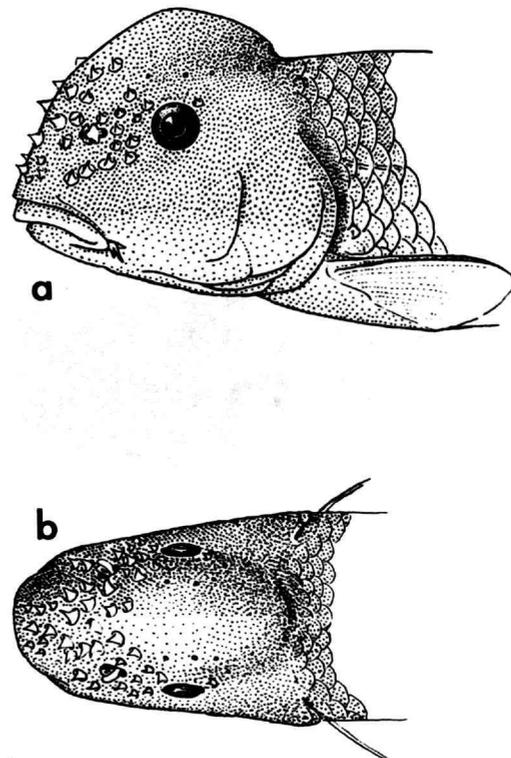
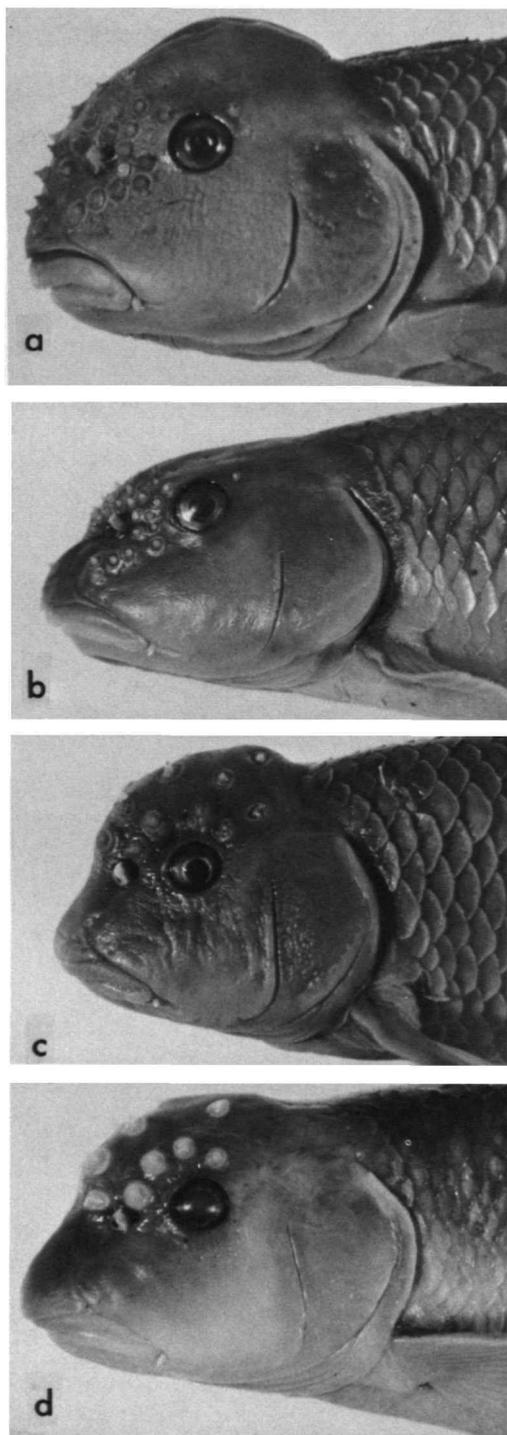


FIGURE 22.—Head of nuptial male *Nocomis micropogon*, USNM 166416, 165 mm, captured in Stone Creek, Juniata River, Susquehanna drainage, Pennsylvania, 3 June 1948: a, lateral view; b, dorsal view. (Drawn by A. M. Awl.)



pogon is summarized in Tables 3, 4, 7, 9, 10, and 13. The relationship between increase in tubercle numbers with increase in body length for three important drainage populations of *N. micropogon*, and compared with *N. leptocephalus*, *N. platyrhynchus*, and *N. raneyi*, is shown in Figure 4. Early development and pattern of tubercle spots is illustrated in Figure 3. The distribution of head tubercles in non-breeding males and nuptial males is shown in Figures 16, 23–25. The tuberculation in *N. micropogon* is characterized as having fewer tubercle numbers than *N. platyrhynchus* (and much fewer than *N. raneyi*) but appreciably more than *N. leptocephalus* (Figure 4). The tubercles average slightly larger than those of *N. platyrhynchus* but much smaller than in *N. leptocephalus* (Figure 24). The tubercles are distributed from the snout to the anterior interorbital area, with a hiatus almost always present between the snout and the anterior internasal area.

The tubercles first appear as light spots in the internasal area (Figure 3). They first appear in specimens 50 to 60 mm SL of both sexes, but they are sometimes not developed at sizes ranging from 60 to 75 mm SL. With increase in body length the tubercles develop on the tip of the snout and also spread posteriorly to the anterior interorbital area, where a V-pattern is formed by the absence of tubercles along the midline. The increment in tubercle numbers with increase in body length is considerably reduced at about 120 mm SL for all the river populations except the Potomac, in which reduction occurs at about 150 mm SL. The lachrymal tubercles are slowest in developing. There is usually only one or two rows of lachrymal tubercles in *N. micropogon*.

Tubercles are present on pectoral fin rays 2 to 4 (2 specimens); 2 to 5 (5); 2 to 6 (37), and 2 to 7 (10).

Significant aspects of the tuberculation in *N. micropogon* in the Potomac and Monongahela drain-

FIGURE 23.—The distribution and number of head tubercles and crests of nuptial males of *Nocomis micropogon* and *Nocomis leptocephalus*. Observe absence of snout and subnasal tubercles in *N. leptocephalus*: a, *N. micropogon*, USNM 166485, 166 mm, collected 3 June 1948, Juniata River, Susquehanna drainage; b, *N. micropogon*, CU 41642, 168 mm, collected 24 May 1961, Tioughnioga River, Susquehanna drainage; c, *N. leptocephalus*, Duke University Collection, 145 mm, Eno River, Neuse drainage; d, *N. leptocephalus*, USNM 194715, 157 mm, collected in May 1964, Roanoke drainage.

ages are the higher numbers of tubercles and a more posterior distribution, sometimes extending to the posterior interorbital area. In tuberculation, and in

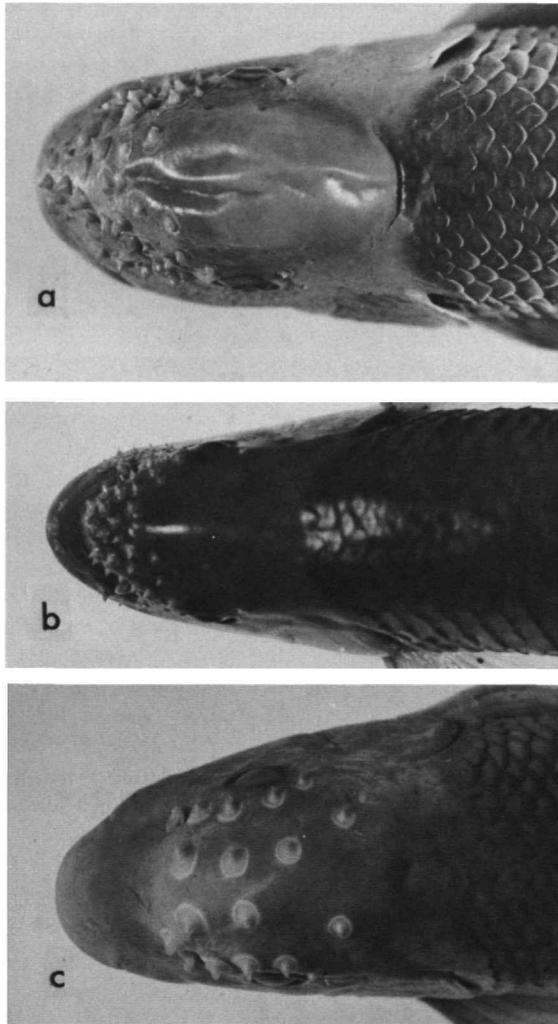


FIGURE 24.—Dorsal views of heads of *Nocomis micropogon* and *N. leptcephalus* showing size and distribution of tubercle development. *a*, *N. micropogon*, USNM 166485, 168 mm, taken 3 June 1948, Juniata River, Susquehanna drainage. *b*, *N. micropogon*, CU 41642, 168 mm, taken 24 May 1961, Tioughnioga River, Susquehanna drainage. A hiatus, typical for *N. micropogon*, is present between tubercles on snout and internasal areas. The hiatus is absent in the specimen above. *c*, *N. leptcephalus*, USNM 194715, 159 mm, taken May 1964, Roanoke drainage, Virginia. Large tubercles develop in the internasal-interorbital area and never on the snout in this species.

some meristic characters, *N. micropogon* of these drainages closely approaches character values of *N. platyrhynchus*. Possible introgressive hybridization of these two species resulting from exchanges of stocks via the Greenbrier-Monongahela-Potomac drainages is discussed in the section on dispersal (p. 66). The Potomac and Monongahela populations are very similar in respect to total number of tubercles, increase in numbers with increase in body length and the relative variation of tubercle numbers by size groups (Table 7). The James drainage population (Table 10), which is to the south of the Potomac, and the Susquehanna population, which is to the north (Table 13), have similar numbers of tubercles and appreciably fewer than the Potomac population. *N. micropogon* from the Tennessee drainage has the lowest number of tubercles (Table 9) for the species. The average values for tubercle numbers of mature males of varying body lengths were: Potomac-Monongahela population, about 50 to 65; James, Susquehanna, and west of Allegheny Mountains, about 40 to 50; Tennessee drainage, about 30.

Nuptial crest: Nuptial crests or swellings were observed on specimens of various sizes. Some swelling and moderate to large crests were found on specimens in the following standard length size-groups: 100–119, 2 specimens; 120–139, 2 (4 with crests); 140–159, 5 (19); 160–179, 6 (10); 180–199, 3 (5); 200–219, 1 (1). These data, as with that pertaining to the development of tubercle buds (Table 4) and the presence of tubercles or scars (Table 3), suggest that different males mature at different sizes or ages, or that they mature and spawn more than once. Since tubercle scars are present on nonbreeding males that are developing tubercle buds, it is assumed that some males spawn more than one season.

Pharyngeal dentition: The tooth count is 4–4 (Figure 18) in 34 pairs of arches in which the specimens were sampled over the range of the species. The teeth and arch are like that of *N. platyrhynchus*.

Coloration: Only particular aspects of the coloration of *N. micropogon* will be discussed because much of the salient color and pattern has been treated above under the two other group members. Lachner (1952: 437–439) described the coloration of *N. micropogon*, chiefly from specimens from the northeastern portion of its range, the Allegheny, upper and middle Susquehanna and Lake Ontario drainages. It was noted that a dark horizontal mid-

lateral stripe is prominent in the young and juveniles of *N. micropogon* while only faintly visible in formalin preserved specimens of adult males. In the large number of preserved adults now available, we find that a majority of specimens have a dark lateral stripe, but it may be faded or absent in preservation. The lateral stripe is present in specimens over the geographic range of the species. Its relative frequency of occurrence, portions of the body on which it is developed and the intensity in adult males and females agree with that of *N. platyrhynchus*.

Reighard (1943:400) observed that living young males of *N. micropogon* with tuberculate heads have a well-marked lateral stripe. He did not state this for the large nuptial males engaged in reproductive activities. Lachner (1952:438) stated that nuptial male *N. micropogon* do not show a conspicuous dark lateral stripe in life as was observed in *N. biguttatus*. Our recent observations on nest-building males from the upper Susquehanna drainage show that a light stripe is effected by light green medians of the scales, or a moderate to heavy dark stripe by the blackish scale margins on the midlateral level; the intensity of the stripe can change rapidly. The light green medians of the scales were also seen in living juvenile and adult males and females from the James, Potomac, and upper Tennessee drainages. Upon preservation, the medians of the scales turn light to dark slate color. The lateral stripe was similar to that of living *N. platyrhynchus*.

The pink-rosy nuptial coloration of the male is developed in the same area of the body as in *N. raneyi* and *N. platyrhynchus*. It has been observed in males from Lake Ontario, upper and middle Susquehanna, Rappahannock, James, upper Tennessee, and Allegheny drainages. Reighard (1943:400) reported it from Michigan. The most intensely colored male we have seen, 160 mm SL (CU 48579), was captured in the upper Susquehanna on 30 May 1965 during the spawning period. Its rosy color was developed dorsad to three scale-rows above the lateral line. The medians of the scales in the lateral stripe area were very light pink, lighter than those above and below, with the light green color barely present.

The olive-yellow middorsal stripe described for juveniles of both sexes and smaller adult females of *N. raneyi* is generally present in the same life stages and sexes of *N. micropogon* as well as in *N. platy-*

rhynchus. It was also present, but faint, on the largely blackish dorsum of a captured living nuptial male *N. micropogon* of 150 mm SL.

The coloration of the paired and anal fins of *N. micropogon* is similar to that of both *N. raneyi* and *N. platyrhynchus*. The yellow pelvic fin coloration of a nuptial male after one week in preservative approached that of the specimens of *N. platyrhynchus* (USNM 194870). Lachner (1952:438) noted white coloration on the tips of the rays of the paired and anal fins of nuptial males and we have observed it on the tips of the anterior dorsal fin rays of a nuptial male.

Caudal and dorsal fin coloration may show some geographic differentiation. There appear to be two types of caudal color pattern, an orange-reddish one in populations from the southern part of the range, and an olive, olive-orange, or olive-yellow one in northern populations. The distinctiveness of these color differences is not clear and little data are available on variation in shades. The caudal fin in juveniles to adults of the southern populations is fairly reddish in color, approaching that of *N. raneyi*, and much like that of *N. platyrhynchus*. The distal caudal and dorsal membranes were light orange-red, the basal membranes being olive in several post-nuptial males and females and nonbreeding adult males collected in the upper James drainage during late July 1963. A highly tuberculate crested male with nuptial color from the Rappahannock drainage had an orange-reddish outer caudal. The most striking caudal coloration yet seen in *N. micropogon* was that of five postnuptial males (USNM 194689) having tubercles or tubercle scars, crests, and pink lower coloration, taken in the upper North Fork of Holston River, Tennessee drainage on 2 July 1963. The caudal fin color, a bright orange-red, was developed over most of the fin which was largely olive basally.

The orange-red caudal fin (color over half of entire fin and, in some, over anterior distal dorsal fin) has been observed by us in living or freshly preserved specimens of the following growth stages: lower Potomac, living juveniles; Shenandoah of Potomac, preserved adult males; upper Rappahannock, preserved juveniles and an adult male; upper James, living juveniles and adults; Powell, Clinch, and North Fork Holston of upper Tennessee, living juveniles and adults. Carter R. Gilbert (personal

communication) has observed *N. micropogon* with reddish caudals in the upper Cumberland drainage. The "olive" caudal fin appears to be characteristic of northern populations. In Catatank Creek, upper Susquehanna drainage, juvenile and adult females and nonbreeding males generally have yellow-olive rays, sometimes appearing amber. Distally the membranes are translucent grayish olive; basally they are more grayish, tending to be clear. All specimens from Catatank, except one nuptial male captured in May 1965 lacked reddish or orangish coloration. The exception, a highly rosy-colored male *N. micropogon* had a faint yellow-orange in the distal one half to two thirds of the membranes of the caudal lobes and a tinge of this color in the distal portion of the medial membranes. Lachner (1952:438) stated that the dorsal and caudal fins of *N. micropogon* were yellowish with some red near the tips of the rays; his specimens were from Lake Ontario tributaries, upper and middle Susquehanna, and the Allegheny drainages. Hubbs and Lagler (1958:69) state that the caudal fin of *N. micropogon* is not red, in contrast to the red caudal fin of young *N. biguttatus* in life. Trautman (1957:86, 295) stated that *N. micropogon* in Ohio (Great Lakes and Ohio River basins) has a slate-colored caudal that is never flushed with red, that it may be a faint orange in some young and that it may have a reddish or orange tinge in specimens only from polluted waters. Information is lacking on details of caudal fin coloration

in the Ohio basin of Indiana and much of Kentucky and West Virginia. Most of the freshly preserved juveniles and a ripe female in two series from Deer Creek, Susquehanna River, near its mouth, taken during the 1965 spawning season, had faint tinges of reddish orange on the distal membranes of the caudal.

In summary, there appears to be some evidence that two caudal fin color forms exist. The difficulty in evaluating the significance of these color forms is that we lack comparative data. We have observed the two forms from different geographical areas, but we know little of the exact areas or drainages each occupies, and of the intermediate areas or regions in which both forms may occur. We know that some colors can be intensely developed, or "turned on," in *Nocomis* within a few seconds, but this was not noted for caudal color. We have resorted to color guides only in the laboratory; none were used in the field other than, occasionally, colored objects, such as differently colored plastic chips. The shades of red, reddish orange or olive-orange, and the reflections from these colors, in free-living and freshly captured specimens may be variously interpreted by different individuals at different times. Specimens were seen, or available for observation, one at a time, spread out over years of observations by any one individual, and thus comparative, objective data were not obtained.

POPULATIONS.—The northern drainage popula-

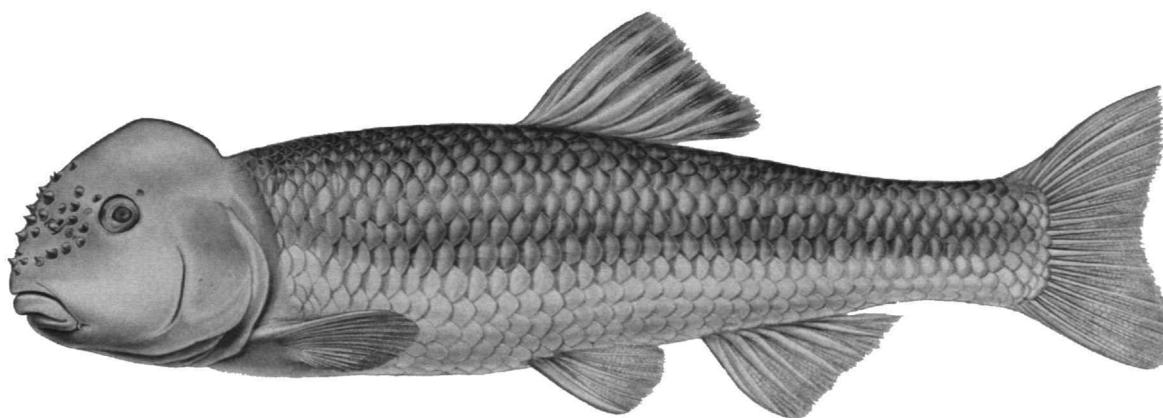


FIGURE 25.—Crested, nuptial male *Nocomis micropogon*, USNM 166416, 165 mm, captured in Stone Creek, Juniata River, Susquehanna drainage, Pennsylvania, 3 June 1948. (Drawn by Carolyn Bartlett Gast.)

tions of the river chub, from Michigan to New York, are very much alike. The principle area of differentiation, excluding the caudal fin color forms discussed above, is in the drainages of the central Appalachian region. Here the interesting divergence is in the Potomac and upper Monongahela drainage populations, both having finer scales, higher tubercle numbers, and more extensive distribution of tubercles than in river chubs of adjacent drainages. The Tennessee drainage population has a notable reduction in numbers of head tubercles, as well as having shorter heads. The most southern population of the Atlantic slope, in the James drainage, resembles the northern populations in respect to tubercle numbers and distribution. Populations in the Kentucky drainage and in tributaries of the Kanawha drainage are fine-scaled compared to Cumberland and Tennessee drainage stocks. *N. micropogon* of the Atlantic slope streams typically have reduced squamation on the breast or have the naked condition.

We find no significant differentiation over the range of the river chub to merit recognition of subspecific populations. The similarities in some of the drainage populations may be related to stream capture and early dispersal of stocks.

REPRODUCTION AND GROWTH.—The nest-building, reproduction, age and growth of *N. micropogon* is discussed by Lachner (1952) and compared with *N. biguttatus* and *N. leptocephalus*. Of the thousands of specimens recently examined, one specimen of *N. micropogon* (Table 7) from the Potomac drainage just exceeded 200 mm SL and another, by far the largest specimen known, measured about 270 mm SL. This large crested nuptial male (TU 8928) is recorded from Lake Pontchartrain, Mandeville, Louisiana, May 1877, "collection of G. Kohn, New Orleans, La." A few tubercles are intact and these plus the tubercle scars total 60, a typical number for the species. The tubercle pattern is also normal for the species. The locality is completely out of the known range for *N. micropogon*. The specimen consists of the head and entire skin of the body attached to the head, including the fins. It probably was an item of curiosity and could have been hand-transported down the Mississippi by the river traffic of the time.

MATERIALS EXAMINED.—Data were taken from 395 collections. The total number of collections studied

from each of 18 drainages is given and these are further subdivided by the institution and number of collections housed.

Susquehanna 24: CU 8, UMMZ 2, USNM 14. Chesapeake Bay tribs. 10: CU 3, UMMZ 7. Potomac 30: CU 8, UMMZ 2, USNM 20. Rappahannock 19: CU 8, UMMZ 3, UR 1, USNM 7. York 3: UR 1, USNM 2. James 54: ANSP 1, CU 11, UMMZ 7, USNM 34. Savannah 4: CU 1, TU 2, USNM 1. Tennessee 77: CU 3, DU 1, UMMZ 39, USNM 34. Cumberland 27: CNHM 1, CU 5, Ind. U. 1, SU 1, TU 2, UMMZ 13, USNM 4. Kentucky 21: CNHM 1, KFW 2, UMMZ 5, USNM 13. Big Sandy 8: CU 1, UMMZ 1, USNM 6. Guyandot 5: CU 1, UMMZ 1, USNM 3. Coal, Kanawha 10: CU 1, UMMZ 1, USNM 8. Elk, Kanawha 10: CU 5, UMMZ 5. Ohio tribs., W. Va. 5: CU 3, USNM 2. Monongahela 52: CU 6, USNM 46. Allegheny 20: CU 1, UMMZ 4, USNM 15. Lake Erie-Ontario, N. Y. 23: CU 7, USNM 16.

DISTRIBUTION.—*N. micropogon* is native to a large portion of northeastern United States and does not occur west of the Mississippi River. Its range on the Atlantic slope is southward from the Susquehanna drainage in New York to the James drainage in Virginia, absent southward except for a population in the upper Savannah drainage. The only known population on the Gulf of Mexico slope occurs in one river system of the upper Mobile Bay drainage. West of the Appalachian divide it occurs from the Tennessee drainage tributaries of northern Alabama and southwestern Tennessee, and from the Wabash drainage of Illinois (P. W. Smith, 1965:7), up (eastward) throughout most of the Ohio River basin. It is found in the Great Lakes drainage of the Lower Peninsula of Michigan eastward to Lake Ontario tributaries in New York and Ontario. The river chub is apparently absent from significant portions of some drainages, and the entire length of other drainages, mainly within the southwestern lowland portion of this general range.

N. micropogon occurs in all major drainages tributary to the western shore of Chesapeake Bay, from the Susquehanna to the James (Figure 19). Records are available from throughout most of the Susquehanna drainage of New York and Pennsylvania (except from some large, poorly collected, and polluted areas), to near its mouth in Maryland. It occurs in all minor Chesapeake Bay drainages of sufficient size from Swan Creek to Patuxent River, Maryland. Most Potomac drainage records are from throughout the upper and lower main basin in Maryland and Virginia including its large tributary, the Shenan-

doah River system of Virginia. This species may be rare in the North and South Forks and North and South Branches of the Potomac River, largely in West Virginia and western Maryland. Relatively few specimens were seen from this montane region, but it has been poorly collected. The river chub occurs in all major upper Rappahannock drainage tributaries, Virginia, and has been taken from its lower freshwater portion just above the Fall Zone. Six locality records of *N. micropogon* from the York drainage, Virginia, indicate that it is widespread therein.

N. micropogon occurs throughout most of the James drainage of Virginia and West Virginia. The river chub was taken in 68 collections from 63 localities of the 182 James drainage collections that include *Nocomis*. The majority of the collections are from major upper tributaries, such as the Jackson River, Back, Dunlap, and Potts Creeks and, in the middle portion, the James, Maury (North) River and its tributaries. Three collections are from the Piedmont-based Appomattox River, the longest James tributary; two are from its headwaters, the other in Swift Creek, a tributary entering the Appomattox near its mouth in the James River estuary.

The river chub occurs commonly above and below the restricted range of *N. raneyi* in the James but is rare within the range of *N. raneyi* (Figure 20). Only 13 or 14 specimens of the river chub were captured in the Craig Creek system compared to 742 specimens of *N. raneyi*. Six specimens of *N. micropogon* (TU 25469) were taken with one specimen of *N. leptocephalus* and three hybrid *N. leptocephalus* × *N. micropogon* from upper Johns Creek, near Maggie. *N. micropogon* and *N. raneyi* are known to have been collected together only three times, all from the lower half of Johns Creek. The upstream and downstream localities are believed to be accurate but the location of the middle station is approximate. Specimens UMMZ 135401 and 181830 were from the latter station, which was reported by G. W. Burton to be "seven miles above Newcastle." It was plotted by measuring seven miles above (upstream from) Newcastle along State Route 311 and County Route 658. Two specimens of *N. micropogon* (UMMZ 135413) are from Craig Creek, and were collected by Burton, supposedly 25 miles west of Newcastle. No point on Craig Creek is 25 air- or roadmiles west of Newcastle. The collection is lo-

cated as 25 roadmiles on Route 311 and County Route 621 southwest (upstream from) Newcastle. This probably is still erroneous since the locality would be in the extreme headwaters. Craig Creek, from this locality to four miles downstream, is quite small, about 4–10 feet in width, smaller than streams typically inhabited by the river chub. Presumably, the specimens are from Craig Creek, although probably from somewhat below the given locality. From correspondence of Burton it is indicated that he collected only in the Craig system, James drainage. Our numerous attempts to find a river chub in the Craig system were unsuccessful although one juvenile specimen (CU 47584), tentatively identified as this species, was collected at the mouth of Craig Creek.

Only one specimen of *N. micropogon* (CU 50610) from Catawba Creek was found, this being from the headwaters. Hybrid *N. leptocephalus* × *N. micropogon* (USNM 171685) and *N. micropogon* × *N. raneyi* are known from the middle Catawba. *N. leptocephalus* is common throughout Catawba Creek.

N. micropogon apparently is common in sizable streams surrounding the Craig and Catawba Creek areas. Upriver, nearest to the range of *N. raneyi*, the river chub (USNM 132064) was collected from Mill Creek in 1885, near its mouth in the James River at Gala, approximately five rivermiles upstream from the mouth of Craig Creek, and in other streams shown in Figure 19. It is widely distributed in the Maury River whose mouth is 16 rivermiles above that of the Pedlar River system, from which a specimen of *N. raneyi* was taken.

The five specimens upon which Fowler (1945:77) based his record of *N. micropogon* from the Roanoke drainage were found to be *N. leptocephalus*.

The ten records (CU, TU, USNM) of *N. micropogon* from the Chatooga and Keowee River systems, upper Savannah drainage, South Carolina and Georgia, indicate widespread occurrence therein. Another locality is in the Savannah River, Abbeville County, South Carolina. Most of these localities were plotted by Lachner and Jenkins (1967:fig. 7). *N. leptocephalus* was taken in only one of the eleven collections.

Our only records of *N. micropogon* on the Gulf slope (TU, 5 collections) are from the Coosawattee system (upper Coosa) of the Mobile Bay drainage in Gilmer County, northwestern Georgia. These col-

lections were noted by Suttkus and Ramsey (1967: 139–140).

Within the New-Kanawha system, *N. micropogon* is known only below Kanawha Falls, from Coal and Elk Rivers, the two largest tributaries of the Kanawha drainage. Specimens were taken from upper and lower Coal River; those from Elk River are all from the upper portion. No specimens of chubs were available from other Kanawha tributaries. The fauna here and elsewhere in West Virginia has been largely extirpated by mining (Goldsborough and Clark, 1908: 31–32; Kinney, 1964: 22–24) and industrial pollution.

The wide occurrence of *N. micropogon* in the southwestern Ohio River basin was discussed and illustrated by Lachner and Jenkins (1967). Its distribution north of the Ohio River, in Indiana and Ohio, was analyzed and mapped respectively by Gerking (1945:48–49, map 25) and Trautman (1957: 296, map 61). The river chub is also widely distributed in most of the remainder of the Ohio basin of West Virginia, Pennsylvania, and New York.

Within the Great Lakes drainage, *N. micropogon* occupies streams of the entire lower Peninsula of Michigan (Hubbs and Lagler, 1958:78), thence eastward, within Ontario Province streams of the Lake Huron basin south of Georgian Bay and the northern Lake Erie basin, to approximately the midlength of the northern Lake Ontario basin (Radforth, 1944: 59–60, fig. 22). It ranges eastward, from the southeastern corner of Michigan, in streams of southern Lake Erie, including the Maumee River drainage of Ohio (Trautman, 1957:296–297, map 61), and Lake Ontario basins to the Finger Lakes drainage of New York. However, within the southern Lake Ontario basin, this species is apparently absent from the entire Genesee River drainage, since it was not reported by Greeley (1927) and later collectors. It is common in Salmon Creek which enters Lake Ontario six miles west of the Genesee mouth. East of the Salmon Creek mouth there is a 52 mile gap in its distribution, ending at Blind Sodus Creek, whose mouth is 16 miles west of the mouth of Oswego River, the Finger Lakes outlet. Within the Finger Lakes drainage, *N. micropogon* is known from Catherine Creek, which enters the south end of Seneca Lake, the Cayuga Lake basin and one record is from a Seneca River tributary downstream from Cayuga Lake.

The leptocephalus Group

DESCRIPTION.—Nuptial males develop few tubercles (Figure 4) on head, numbering fewer than 30 and often less than 20 (Table 19). In populations of the south Atlantic and Gulf slope drainages the nuptial males have even fewer tubercles, in some, averaging about 6. Tubercles extend from internasal area to occiput, depending on subspecies. Tubercles absent on snout and lachrymal areas. A large, nuptial crest developed by larger males positioned more anteriorly than in the micropogon group. Breeding coloration of nuptial male bluish on head and body or, body with orange, brassy or tan lateral stripe. Dark marking on anterior portion of scale in adults narrower than micropogon group. Caudal spot dark, small, indistinct in juveniles (compared to large, distinct spot in biguttatus group). Intestine almost always with a ventral whorl (except in some collections from southeastern United States). Dentition 4–4 to 3–3. Scales large, body circumferential scales range from 26 to 33. Body comparatively short and stocky; snout blunt; posterior edge of preopercle usually vertical or sloped posteriorly below. Males attain an intermediate size for genus except one southeastern population which is larger. Males of the three subspecies construct small to moderately sized mound-nests of fine to small gravel. The three subspecies include *Nocomis l. leptocephalus* of the Atlantic slope from the Potomac and New drainages southward to the Savannah River; a new subspecies (see paper 2, p. 2) of the southeast Appalachian slope in the Savannah, Altamaha and Apalachicola drainages; and *Nocomis l. bellicus* of the southern Gulf slope in the Mobile drainage westward to certain eastern tributaries of the Mississippi River.

Nocomis leptocephalus (Girard)

BLUEHEAD CHUB

FIGURES 17, 23, 24, 26, 27

Ceraticthys leptocephalus Girard, 1856: 213 [type locality, Salem, North Carolina; Yakin River system].

Hybopsis kentuckiensis.—Jordan, 1889a: 123 [(part) Roanoke drainage].

Hybopsis leptocephala.—Ross, 1959: 12, 16, 25 [New drainage].—Ross and Perkins, 1959 [(part) New drainage].

Hybopsis micropogon.—Ross, 1959: 12–13 [(part) Potomac drainage].—Ross and Perkins, 1959: 16 [(part) New drainage].

Hybopsis species.—Ross and Perkins, 1959: 12, 19, 24, 27 [(part) New drainage].

Nocomis leptocephalus.—Jackson and Henderson, 1942: 95 [(part) Roanoke River].—Burton and Odum, 1945 [(part) James drainage].

Nocomis micropogon.—Fowler, 1945: 77 (Roanoke drainage).—Burton and Odum, 1945 [(part) New drainage].

DIAGNOSIS.—A stout bodied species differing from all other *Nocomis* in the reduced numbers of head tubercles, almost always fewer than 25 in the typical subspecies of the central Atlantic slope and reduced to 6 for nuptial adults in the southern, Gulf slope form; tubercles absent on snout, subnasal, and lachrymal areas; intestine whorled in almost all drainage populations, in all from the central Atlantic slope; scales large, mean values for circumferential scales for drainage populations less than 30; values for most meristic characters are lower than in all other species of *Nocomis*.

DESCRIPTION.—*Morphometry*: Table 25 contains proportional data for 13 characters of 47 specimens from the James, Roanoke, and New drainages. The body features are fairly constant within size-groups among the drainage populations of the Atlantic slope as well as among the three subspecies over the entire range of the species. Most of the variation in characters is associated with changes related to allometric growth.

Compared to other species of *Nocomis*, the body is short, stout, and comparatively deep. The snout is short (averages 11.6% SL), the interorbital wide (9.3% SL), and the lachrymal short (6.9% SL). The dorsal and anal fins in the adults have a rounded contour; the pectoral and pelvic fins are short and rounded. Compare the deeper and more blunt head and deeper body of the juvenile with *N. micropogon* and *N. raneyi* in Figure 17.

The intestine is unlike any other *Nocomis*, having a pronounced whorl or anterior loop extending to the right side and covering part of the anterior alimentary tract (Figure 8), except in certain collections of the southeastern Atlantic slope subspecies. All populations of the typical subspecies ranging north of the Savannah drainage show constant and relatively uniform development of the intestine. It is typically coiled in small juveniles at 25 to 30 mm SL. Its dark, coiled outline may be seen through the pale belly tissue in these small sizes without cutting open the abdominal cavity.

The slope of the preopercle-opercle suture is directed forward at the angle only slightly in 43 specimens measured and either perpendicular or posteriorly directed in 157 specimens.

Meristic characters: Summaries of meristic characters, usually for five drainage populations of the central Atlantic area, including the range for mean values, are as follows: circumferential scale-rows, 28.1 to 29.4 (Table 12); scale-rows along the lateral line, 38.1 to 39.9 (Table 8); scale-rows above lateral line, 6.1 to 6.8, and scale-rows below lateral line, 4.8 to 5.4 (Table 11); caudal peduncle scale-rows, 16.0 to 16.3 (Table 14); number of pectoral fin rays, 16.5 to 16.9 (Table 16); total number of vertebrae, 38.9 to 39.8 (Table 15). Most of the meristic characters have lower values than for all other species of *Nocomis*, but they were homogeneous, and showed little divergence and were of little value in solving the systematic boundaries of the infraspecific populations. Specimens from certain tributaries of the New drainage, such as Fox Creek, had higher circumferential and lateral line counts compared with those in other New drainage localities or those of the James and Roanoke drainages. The same characters for specimens in the Tar and Neuse Rivers had somewhat lower values compared with those of the James and Roanoke. We cannot attach any particular significance to these differences.

The breast is almost always fully scaled (Table 18). In a sample of 107 specimens from several drainages, the breast was about one half scaled in 4, three quarters scaled in 69, and fully scaled or nearly so in 34 specimens. *N. leptocephalus* differs from the micropogon group in the constantly high degree of breast squamation.

Tuberculation: The number of head tubercles in specimens from the James, Roanoke, and upper New drainages, segregated by sex and size groups is summarized in Table 19. A comparison of tubercle numbers by size-groups with the species of the micropogon group is shown in Figure 4. The typical, early tubercle development and pattern is illustrated in Figure 3. The distribution of head tubercles in nuptial males is shown in Figures 23, 24, 26, 27. Tuberculation in *N. leptocephalus* is characterized by a great reduction in numbers, the lowest for any species of *Nocomis*; by an enlargement of the tubercle size, the largest for any species of *Nocomis*; and by the absence of tubercles from the snout, subnasal,

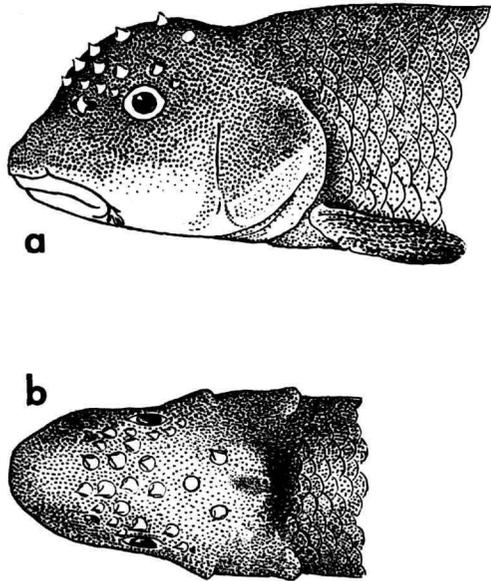


FIGURE 26.—Head of male *Nocomis leptocephalus*, CU 10542, 153 mm, showing nuptial crest and tubercle development, taken 23 June 1946 from a tributary of the Ararat River, Yadkin River system: a, lateral view; b, dorsal view. (Drawn by A. M. Awl.)

and lachrymal areas. The tubercles first appear as large, light spots in the internasal-anterior inter-orbital area, at about 30 to 40 mm SL. With increase in body length the tubercles increase in numbers and spread to the posterior occipital line in the adults. Some specimens of both sexes may not have visible spots at body lengths of 35 to 45 mm SL. The distribution and numbers of tubercles is the primary character in the separation of the three subspecies of *N. leptocephalus*. The data on tubercle numbers and distribution above (Table 19) pertains to the typical subspecies, in which the numbers are highest and the adult pattern most extensively developed. Analysis of the subspecific populations of *N. leptocephalus* will be treated in a separate paper. Tubercle numbers for *N. l. leptocephalus* are almost always fewer than 25. *N. l. bellicus* has the lowest number, 7 or fewer in the adults. The early tubercle pattern for *N. l. leptocephalus*, as shown for small juveniles in Figure 3, is actually the definitive adult pattern in *N. l. bellicus*.

N. leptocephalus has more tubercles on the pectoral fin rays than species of the micropogon group.

Tubercles are present on pectoral fin rays 2 to 6 (8 specimens), 2 to 7 (18), 2 to 8 (23), 2 to 9 (1), and 2 to 10 (2).

Nuptial crests: The development of the crest in *N. leptocephalus* is similar to its development in the micropogon group. In *N. leptocephalus* large crests develop on smaller size specimens than in the micropogon group. Its development is undoubtedly associated with age and maturity. The crests of *N. leptocephalus* become more greatly developed at a position somewhat more forward on the head than in the micropogon group, the swelling is often very large just posterior to the internasal area. Crests, moderate to large, were present on the following size-groups (in mm): 110–119 (1 specimen), 120–129 (4), 130–139 (5), 140–149 (10), 150–159 (5), 160–169 (4).

Pharyngeal dentition: Tooth numbers were 4–4 in 90 percent of 92 specimens sampled over the range of all three subspecies. Counts of less than 4–4 comprised the other 10 percent of the sample, these being 3–4 or 4–3, 3–3, and 2–4. The structure of the arch and the pitted surface is similar to the arch of *N. micropogon*.

Coloration: Two different primary color forms exist in living nuptial males of *N. leptocephalus*. *N. l. leptocephalus* has both forms as described by Lachner (1952:439). Those in the Roanoke and Neuse drainages have blue on the head laterally, an orangish lateral stripe, and variable amounts of shades of orange in the fins while in the Pee Dee drainage the body laterally is bluish instead of orange. Further observations by the authors and others have shown that the orange-sided form is also in the New and James drainages in the northern part of the range while the blue-sided form also exists in the Santee drainage south of the Pee Dee drainage. Additionally, males of the northern color form, at the height of nuptial coloration, have the lateral stripe abruptly changing from orange to olive-yellow, caudally, from about the vertical from middle of the dorsal fin. Both forms at the peak of color intensity have a tan to brown nuchal crest and the dorsum above the lateral stripe is colored brown to bluish black.

Nuptial males develop a light to moderate blue on the lateral and ventral head, deepest on the opercle and on the cheek, faintest on the lower jaw and branchiostegal regions. The tubercle region is dark

tan to brown in living, large males; the tan turns to dark olive after several hours in formalin. Of ten tuberculate males captured in the upper James drainage during 10–30 May 1963–1965, the deepest shade developed on the lateral head was moderate blue in one specimen, a light blue in five specimens (faint blue-gray or blue color absent on the ventral head) and the blue was not detectable in four specimens. In one specimen the light blue color turned noticeably darker while being examined out of water. The color also turned darker in all specimens with blue upon being in formalin for about fifteen minutes; those without the color developed a light or moderate blue. A postnuptial male with *Saprolegnia* over its tubercle scars was observed in the stream to have a fairly dark blue head. The blue head color of living and preserved *N. leptocephalus* is lighter than the bluish black color that sometimes develops on the head of recently preserved nuptial male specimens of *N. raneyi* and *N. micropogon*. The coloration of the head of the latter species is unlike the nuptial head color of *N. leptocephalus* in life.

The other nuptial color component in the northern male *N. leptocephalus*, radically different from the pink-rosy lower sides of the micropogon group, is the horizontal stripe of faint to dark, coppery to rusty-orange. This is developed in the scale medians from the postopercular bar to about the dorsal fin base level, within 3.5 scale-rows above to 1 scale-row below the lateral line at its widest point (anteriorly)

and tapering slightly to the dorsal fin level. The edge of this stripe is fairly sharply delimited below by the whitish lower sides, somewhat less above since the dorso-lateral scale medians have brassy iridescence. The stripe then grades posteriad to the level above the anal fin base into a bright olivish yellow, this shade being more yellowish than the dorso-lateral region just above it, and then grades over the caudal peduncle to a less bright, light yellow-olive, about the shade of the dorso-lateral scale medians.

A deviation from the typical orange stripe was seen in nuptial males from Craig Creek, captured on 15 May 1963 where many fresh nests were present. In three of the five nuptial males taken, the scale medians were pink in the anterior lateral stripe area from the postopercular bar posteriad to the level of the anterior base of the dorsal fin; the most ventral row of scale medians in that area had a suffuse yellow added. The posterior portion of the midlateral stripe was typical olive-yellow. Many nuptial males more recently taken or observed in the upper James, several of which were from Craig Creek, had an orange area or stripe anteriorly on the side of the body.

The head coloration of all sizes except the nuptial males and some postnuptial males is very similar to that of the members of the micropogon group; it differs in that the dorsum is slightly lighter, ranging from tan-olive to dark olive. The inner "color ring" of the iris is wide, often occupying half of its

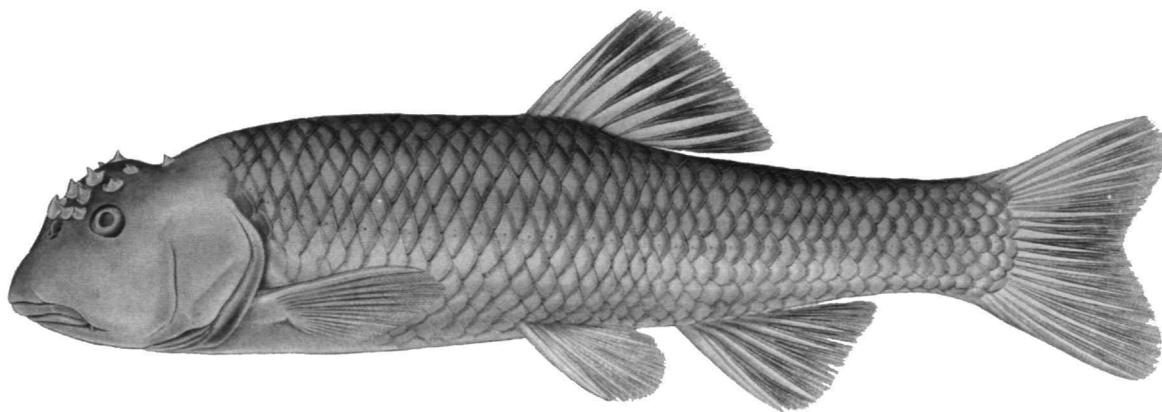


FIGURE 27.—Crested, tuberculate male of *Nocomis leptocephalus*, USNM 166392, 165 mm, from the Dan River, Roanoke drainage, collected 8 June 1947. (Drawn by Carolyn Bartlett Gast.)

width, and is colored bright orange, red-orange, or red. It is very rarely interrupted by the blackish outer iris color. Most specimens of *N. leptocephalus* can be separated in the field from the micropogon group by this character alone.

The body color grades from dark above to white on the belly. The color of the median of the scales, laterally on the body, tends to be lighter in some specimens, being more of an iridescent yellow-green than yellow-olive and often with brassy iridescence.

The dark midlateral stripe and basicaudal spot is often absent but prominent in some living and preserved juvenile and adult females and juvenile males. Preserved adult males rarely have a well-developed stripe and, when present, it is usually only on the caudal peduncle. An iridescent yellow-olive, mid-dorsal stripe is generally present in all but the larger adult males; this soon turns darker than the adjacent dorsal area in formalin. A moderately dark lateral stripe and light middorsal stripe were seen in a highly tuberculate male of about 130 mm SL that was building a nest in the upper James drainage. No specimens were observed in life with a light greenish lateral band as seen in *N. micropogon* and *N. platyrhynchus*.

The fins are colored yellow-olive, usually with small to large areas of orange or, infrequently, slightly reddish orange. These colors are generally restricted to the rays but in some specimens they extend slightly into the membranes. The membranes are clear to clouded with white and some olive. An accentuation of the fin colors has not been noted in nuptial males. One nuptial male with intense body color had pale dorsal and caudal fins, lacking the yellow and orange, and it had only slight shades of these colors in the other fins. The pelvic fin rays were milky white along the branches. The fins of *N. l. leptocephalus* have a heavier deposition of melanophores along the rays and ray joints than in the micropogon group; it is heaviest in the dorsal fin, the rays appearing almost entirely black in larger nuptial males.

Some slight but rather consistent differences from the micropogon group are seen in the melanophore pigmentation of alcoholic specimens. The anterior margins of the scales are narrower, sometimes absent (when the scale just anterior entirely covers the scale pocket below), while the posterior margins of the scales are wider and do not have a sharply de-

fined inner edge. Frequently the posterior margins do not extend to the actual posterior edge of the scales. Adult females have wider scale margins than adult males.

REPRODUCTION AND GROWTH.—The nest building, spawning, and reproductive behavior of this species is now well known, based on recent studies by Lachner, which will appear in the sixth paper of this series (p. 2), in which the reproductive behavior of all species of *Nocomis* will be treated. The age and growth of *N. leptocephalus* was treated by Lachner (1952); the largest specimen studied was a male in the 115–120 mm SL size class. In Table 19 we report on one male specimen in the 170–179 mm SL size class. After having examined about 30,000 specimens from over its range we encountered one collection of 11 tuberculate males that dwarfed all others known. This collection (TU 29534) was taken in Toxaway River, above Lake Toxaway, Transylvania County, North Carolina, on 14 July 1962. Ten of the specimens ranged from 192 to 214 mm SL, and the smallest was 172 mm SL.

MATERIALS EXAMINED.—The 124 collections from five drainages are given followed by the institution and number of collections housed.

James 25: CU 11, UMMZ 5, USNM 9. Roanoke 45: CU 6, UMMZ 1, USNM 38. Tar 10: CU 9, USNM 1. Neuse 12: CU 4, USNM 8. New 32: CU 11, UMMZ 1, USNM 17, DU 3.

DISTRIBUTION.—*Nocomis l. leptocephalus* is distributed on the Atlantic slope from the Potomac drainage in Virginia southward to the Santee drainage and west of the Appalachian Divide in the upper New drainage (partly shown in Figure 28).

The only known collections of *N. leptocephalus* from the Potomac drainage were taken in 1956 and 1958 by R. D. Ross and his associates from Back Creek and Middle River, tributaries of the upper South Fork of Shenandoah River, Augusta County, Virginia (all USNM collections). The single specimen known from the Rappahannock drainage was captured in South River, a tributary of upper Rappahannock River, Greene County, Virginia, in 1951 by E. C. Raney and C. R. Robins (CU 46283). The York drainage was first included within the range of *N. leptocephalus* by Raney (1950:161). Six collections were available, all from tributaries of the Pamunkey River, one of the two major tributaries of the York estuary.

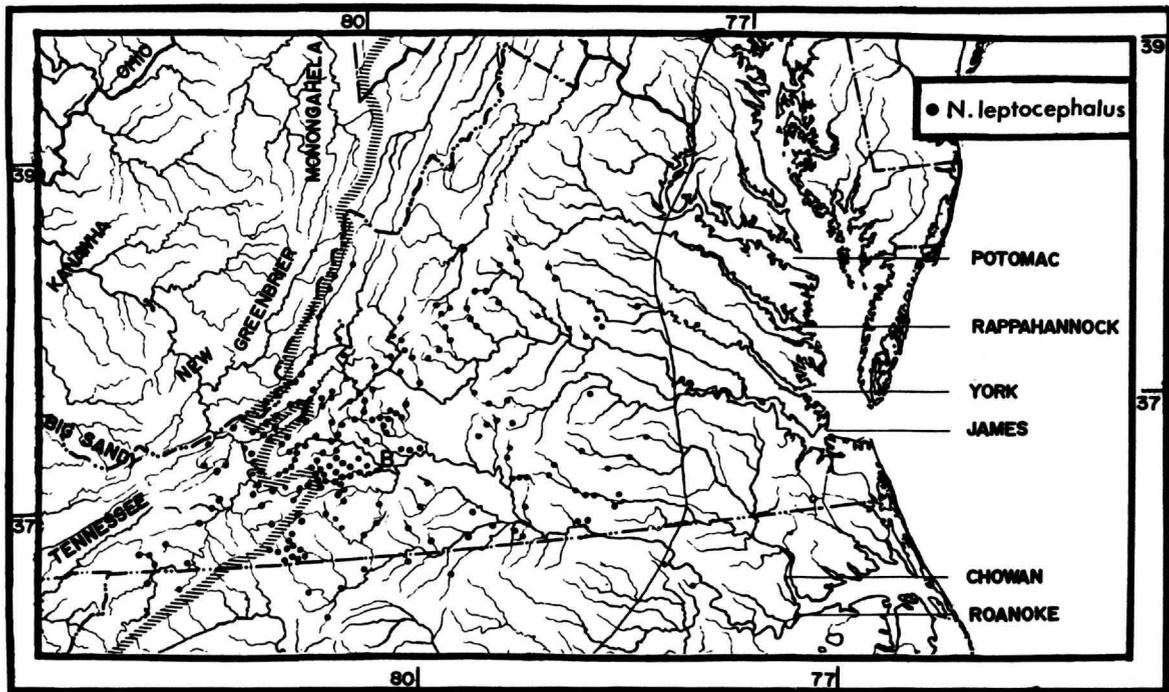


FIGURE 28.—Distribution of *Nocomis leptocephalus* in the northern portion of its range, on the Atlantic slope from the Potomac drainage to the Roanoke drainage and west of the divide in the New drainage. Its distribution within the Blackwater River system (directly west of Letter B) is shown in detail in Figure 29. The horizontal bars represent the drainage divide line and the solid line the Fall Line.

N. leptocephalus occurs widely within the James, Chowan, Roanoke, Tar, and Neuse drainages.

This species also has a wide distribution within the upper New drainage of Virginia but, apparently, it does not occur in its headwaters or the lower New. The farthest downstream record is one specimen taken in 1885 from Wolf Creek, Giles County, which enters the New just upstream from the Virginia-West Virginia state line. As known from collections and angling, this species is common in much of Big Stony Creek, the first major tributary just upstream from the mouth of Wolf Creek. Fox Creek is the uppermost tributary known to be inhabited, whose mouth is just downstream from the Virginia-North Carolina state line, where it was taken commonly in 8 collections from 6 well-spaced localities.

Ecology, Association, and Frequency of Hybridization

REGIONAL ECOLOGY.—The habitats of the four species of chubs are basically similar although there is some ecological variation within their geographic ranges. Generally, the species of *Nocomis* prefer clear, moderate to warm water streams of intermediate gradients. They are carnivorous fishes common over bottoms composed of gravel, rubble, and boulders, and usually with scant or no higher aquatic vegetation.

The primary ecological distinction between the species groups is their preference for different size streams. The three species of the micropogon group generally inhabit larger streams, becoming the dominant chub in streams averaging wider than 40–60

feet. This preference has been noted throughout most of the range of *N. micropogon* (Lachner, 1952: 434-435 and included references; Gerking, 1945:15, 48; Trautman, 1957:297) and is likewise true for *N. raneyi* and *N. platyrhynchus*.

There may be limited upstream movement correlated with the breeding season. Miller (1964:316) noted that sometimes mature *N. micropogon* did not appear in certain breeding areas until early May in Catatank Creek, Susquehanna drainage, New York. Raney (1950:161) mentioned an upstream movement of this species to spawning areas in April and May. We note that nuptial males, ripe females, and juveniles of *N. raneyi* were seen or commonly captured on 29-30 May 1964 in an upstream portion of Johns Creek averaging 15-25 feet in width. Whether the adults remain upstream after spawning in this relatively narrow section is unknown. A number of older adult males die soon after spawning.

Less information is available concerning the distribution and abundance of river chubs in the large river channels. They occur locally in certain rivers where adequate sampling was made. The James River where (atypical) *N. raneyi* was taken fairly commonly is 60 to 150 yards in width. *N. raneyi* was also captured in the larger sections of the Tar and Neuse rivers. Several adult *N. platyrhynchus* were caught by sport fishermen at localities in the main channel of the New River in Virginia where large nests, obviously of this species, were seen. Large nests have also been observed in the deeper waters of the Greenbrier River and the Knapp Creek tributary, West Virginia, over the past several years. Several records are available of *N. micropogon* from the lower Potomac River down to Great Falls just above tide level. Lachner (1952:434) mentioned that larger adults of this species are taken from deep river holes by fishermen; these and more recent observations were made in western Pennsylvania. H. M. Smith (1907:104) stated that in North Carolina *N. kentuckiensis* (Rafinesque) shows a preference for larger streams. His records are probably based on specimens of *N. raneyi* in the east and *N. micropogon* from the Tennessee drainage.

N. leptocephalus generally is most abundant in small streams, although there is usually much overlap with species of the micropogon group in intermediate stretches. This species is common to abundant in streams averaging from 10 to 50 feet in

width, but it rarely occurs in extreme headwaters.

The juvenile and adult chubs commonly occupy both the riffle and pool habitats. These life stages were collected in about equal numbers in moderate to rapid riffles and short to moderate length pools of the upper James, Roanoke, and New drainages. They seldom occur in the long stretches of slack water. *N. leptocephalus* is frequently common in rapid, small mountain streams that are stocked with trout.

A stream bottom composition partly of gravel and rubble is an important factor in the maintenance of a sizeable population of *Nocomis*, especially since these materials are essential for nest building. Other bottom types in various combinations are occupied. The largest populations of the four species in Virginia and of *N. micropogon* in Ohio (Trautman, 1957:297), Indiana (Gerking, 1945:15, 48), and elsewhere are most commonly found where current-swept gravel, rubble, and boulders predominate. The decline or disappearance of populations of the widely distributed *N. micropogon* with increased turbidity and siltation is generally observed. *N. raneyi* populations apparently have also declined in more silted sections of the Roanoke drainage.

The well-established populations of *N. raneyi*, *N. micropogon*, and *N. leptocephalus* in typical Piedmont streams indicate their adaptiveness to this type of habitat. Lower gradients, sandy bottoms and somewhat greater turbidity generally characterize streams of this province but gravel, rubble, and sometimes boulder riffles occur. *N. raneyi* and *N. micropogon* do not tolerate sandy bottom conditions as extreme as those where *N. leptocephalus* is sometimes common; this may account for the apparent absence of *N. raneyi* from several Piedmont tributaries of the Roanoke and its rarity in others such as the middle Dan River.

The rarity of chubs in streams of the Coastal Plain province is probably related to the general absence of riffles, exposed gravel and rubble. The courses of the eastern rivers through the Fall Zone, the transitional belt of varying width (whose eastern limit is the Fall Line) between the Piedmont and Coastal Plain, are generally marked by a series of rapids and cascades which provide some habitat. From the James northward the Coastal Plain rivers and most of the generally small tributaries are tidal or brackish up to the Fall Line. However, the rivers

south of the James do not drop to sea level so quickly, and their channels are on crystalline rock with rapids occurring for about 20 miles after entering the Coastal Plain (Fenneman, 1938:13, 129). The presence of riffles in some upper Coastal Plain tributaries may be accredited to drainage of higher terraces during which time some have cut deposits to the crystalline rocks of the Piedmont (Clark, et al., 1912:26). Headward extension with exposure of gravel and rock by erosion, beginning with the post-Pleistocene elevation of the Coastal Plain (Clark and Miller, 1912:200), seems to be still in effect.

N. raneyi and *N. micropogon* occur in the Fall Zone and sparingly in the upper Coastal Plain province. Jordan (1889a:109–110) noted that a rapid and rocky portion of Swift Creek, James drainage, just below the Fall Zone has a fauna “essentially that of the upland streams.” The southeastern limit of *N. micropogon* (excluding the upper Savannah drainage population) is the James drainage, and for reasons stated above, its distribution terminates at or near the Fall Zone. *N. raneyi* has available a rather wide lowland region in southeastern Virginia and northeastern North Carolina but few streams are probably suitable. It is not known from the Coastal Plain portion of the Chowan and Roanoke drainages although one collection from the Chowan is in or near the Fall Zone. Of the 24 collections of *N. raneyi* from the Tar and Neuse drainages seven were taken from the Fall Zone and nine below. Of the latter, some were from moderate to rather large streams with riffles, bordered at least in part by swampland, and with lightly brown-colored water. One stream, Nahunta Swamp Creek, Neuse drainage, averages only 10 feet in width. No species of *Nocomis* is known to inhabit the predominantly slow blackwater type of stream or inner portions of swamps.

N. leptcephalus was taken in the Fall Zone from the York and the Chowan drainage southward to the Neuse and in most cases with *N. raneyi*. The former species apparently avoids Coastal Plain streams in the central Atlantic region, for we know of only one collection from this area in a Roanoke tributary.

N. micropogon, the only member of the species group inhabiting central United States, shows a distinct preference for recently glaciated regions within the northern and middle, lowland portions of its

range in the Ohio River drainage basin. It is absent from the region covered by the Illinoian glacier south of the Wisconsin glacier limit in Indiana (largely the lower Wabash drainage) except for a borderline record (Gerking, 1945:15, 48–49, map 25). The habitat here is generally unsuitable, prevailing conditions being similar to or more limiting than those on the Atlantic Coastal Plain. Jordan (1889a:160) stated that the lower Wabash tributaries “are mostly sluggish and yellow with clay and mud”. Gerking (1945:17) indicated the same for the lower Wabash flood plain. Trautman (1957:11) noted that most unglaciated and hence undisturbed and almost base-level streams of southeastern Ohio have no well-developed riffles while the glacial streams in this region have relatively high gradients. Some of the latter streams are inhabited by the river chub (Trautman, 1957:296–297, map 61). Its absence from other Ohio River tributaries in Kentucky may be related to similar sluggish conditions.

Higher aquatic vegetation is not common in most areas inhabited by the micropogon group and *N. leptcephalus*. Generally, habitats suitable for good plant growth are borderline situations for these species. An exception is the well-established growth of water willow, *Justicia*, in portions of the upper James and New drainages supporting a thriving chub population, and similarly reported in Ohio by Trautman (1957:297). This stout emergent herb often grows in dense stands along the shore and in shallow pools and riffles. Shockley (1949:259–261) found stream areas supporting a growth of *Justicia* to be more productive than those where it was absent. Submerged portions of water willow usually show retention of much organic detritus and an abundance of aquatic insects. Chubs also are found in streams with good growths of the algae *Cladophora* and the vascular riverweed, *Podostemum*. Lachner (1950:230; 1952:434) found a large population of *N. micropogon* in streams with an abundance of algae, chiefly *Cladophora*, and vascular plants (several species of *Potamogeton*), in Lake Ontario tributaries of New York. Smith and Bean (1899:183) reported this species as common over grassy bottoms of the Potomac River.

Lachner (1950) found the food of *N. micropogon* in western New York to be largely aquatic insect larvae with lesser percentages of Crustacea and Mollusca. In many instances, algae, chiefly *Cladophora*,

and vascular plants were taken in large quantities. Much of the plant material is probably ingested incidentally with animal food since it appears to be undigested. Fishes are rarely included in the diet of chubs. Differences in food ingested by *N. micropogon* were found among young, juveniles, and adults and, within the juvenile stage, among certain seasons (Lachner, 1950). Comparative food studies of the species of chubs occurring sympatrically might reveal differences, especially since *N. leptocephalus* has a long, whorled intestine, differing from all other *Nocomis*. Flemer and Woolcott (1966:83-84) analyzed food intake of 249 specimens of *N. leptocephalus* from a typical, lower piedmont tributary of the James River just above the Fall Line. They found a great preference for plant food by this species, forming a high percent of total items eaten. They concluded that the plant material was specifically selected by *N. leptocephalus*.

ASSOCIATION AND FREQUENCY OF HYBRIDIZATION.—The following discussions refer to the extent that the species of chubs occur syntopically (occupy the same macrohabitat) or together (Rivas, 1964). All species occurring in the same drainage have been collected together. However, differences among the species of the micropogon group in their frequency of occurrence with *N. leptocephalus* are revealed and the apparent noncompatibility between *N. raneyi* and *N. micropogon* is discussed. The data support our preceding statements concerning stream size preferences. The relative frequencies of hybridization between certain of the species are reported below. Factors involved in hybrid formation will be discussed in papers 5 and 6 on the study of *Nocomis* hybrids and reproduction.

The data summarized in Table 26 are derived largely from intensively sampled tributary systems of the James, Roanoke, and New drainages. In order to eliminate bias from small collections and those taken by selective angling, the data indicating syntopy or allotopy (Rivas, 1964) are from collections in which a minimum of ten specimens were taken. The sampling intensity for the four species in intermediate size streams was about the same.

In the James drainage, *N. leptocephalus* was taken with *N. raneyi* in 89 percent of the collections (Table 26) from the Craig Creek system (Figure 20). In approximately the center of this system, in five collections from three localities in lower Craig Creek

just below Newcastle, *N. raneyi* was always found to be the more abundant species, appreciably outnumbering *N. leptocephalus* (429 to 239 specimens). In upper Craig Creek within a radius of about 3.5 miles above Newcastle, *N. raneyi* was taken in three collections from two localities, but in less numbers than *N. leptocephalus* (26 to 52 specimens). Two juvenile *N. raneyi* were taken about 5.5 miles above Newcastle, but none have been found above this area. *N. raneyi* was found to extend well up Johns Creek to within 0.75 mile of Maggie, the latter being where *N. micropogon* and hybrids of *N. leptocephalus* × *N. micropogon* were taken. In three large collections, two in spring and one in summer, from within 3 miles of Maggie, 58 *N. raneyi* and 92 *N. leptocephalus* were taken, the latter species being more numerous in each. The stream in this area averages about 15 to 25 feet wide. *N. leptocephalus* apparently becomes progressively less numerous below the Newcastle area. A sparse spawning population occurs down into the middle section of lower Craig Creek. Only *N. raneyi* was taken in four collections from the lower 3 miles of Craig Creek.

The Blackwater River of the Roanoke drainage in Franklin County, Virginia, is a well-surveyed stream in which similar distributional relationships were found between *N. raneyi* and *N. leptocephalus* as observed in Craig Creek (Figure 29). The Blackwater is a typical Piedmont river; its lower portion is about equal in size to lower Craig Creek. Of the 22 collections (15 localities) in which *N. raneyi* was taken, all but two are in the main channel from lower North Fork near its mouth in Roanoke River. *N. leptocephalus* was taken at all but one location. A progressive upstream decrease in the relative numbers of *N. raneyi* is indicated when the main channel is divided into three sections of approximately equal lengths and by calculating the percentage composition of each species per section. *N. raneyi* comprised 93 percent of the 246 chubs taken in the downstream section; in the middle section, 76 percent of 296 specimens; and upstream, 21 percent of 505 specimens. The progressive change in relative numbers is also indicated in almost all individual collections. In the two collections from the lower portion of the most downstream, and major, tributary of the Blackwater, *N. raneyi* comprised only three of the 49 chubs taken. *N. leptocephalus* is

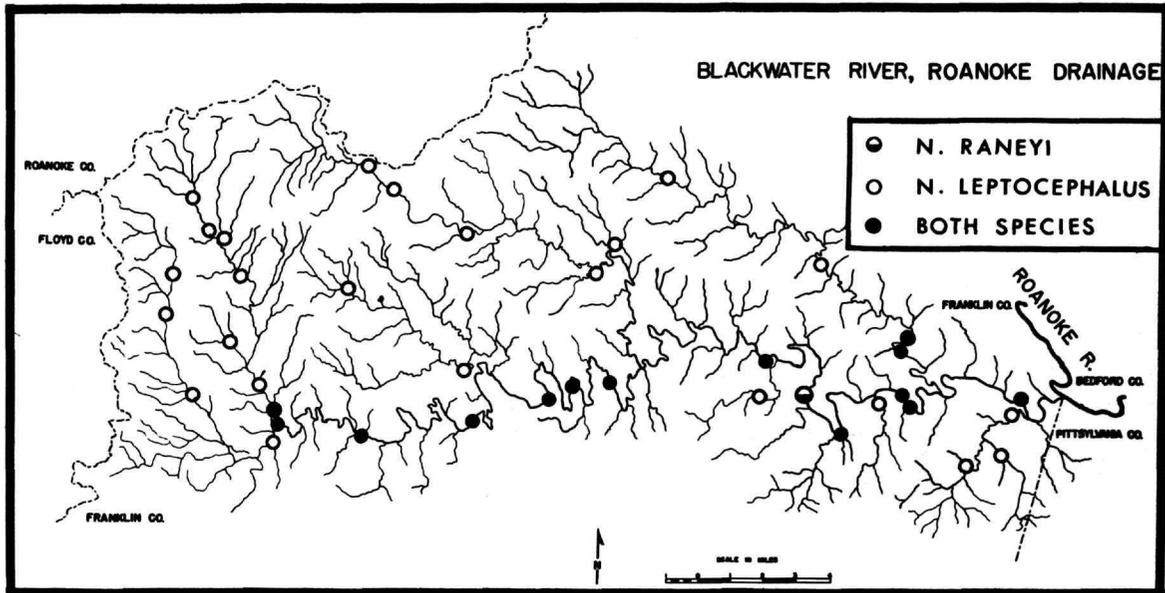


FIGURE 29.—Distributinal relationships to stream size of *Nocomis raneyi* and *N. leptocephalus* within the Blackwater River system of the Roanoke drainage. The most important ecological difference between these species over the ranges was the preference by *N. raneyi* for the larger and deeper streams and a partial preference for the smaller tributaries by *N. leptocephalus*; the latter habitat was almost entirely avoided by *N. raneyi*. The map is an enlarged portion of the Roanoke drainage directly west of the letter B in Figures 19 and 28.

common to abundant in the remainder of the tributary system in which *N. raneyi* is absent or rare.

The distributinal relationships in the intensively collected lower South Fork and upper main channel of the Roanoke River, Montgomery and Roanoke counties (Figure 20) are somewhat different. Although within the Appalachian province, the bottom of these streams is generally much more silted than that of Craig Creek to the north, even though riffles are more frequent in the Roanoke River than in Craig Creek. The Roanoke River at the city of Salem, Virginia, averages about the same in width as lowermost Craig Creek. *N. leptocephalus* was captured in all nine lower South Fork collections (five localities) in which *N. raneyi* was taken. The uppermost locality is near the town of Alleghany Springs, where the stream averages about 30 to 40 feet in width. *N. raneyi* comprised only 3 percent of 510 chubs captured. Only *N. leptocephalus* was taken in numerous additional collections from lower South Fork and farther upstream. Although *N. raneyi*

showed an expected increase in relative numbers in the downstream direction, it was taken from the upper main channel only at seven localities in ten collections, in which it accounted for 29 percent of the 228 total chub catch. The large majority of the recent collections (through 1970) from the main Roanoke from Salem upstream did not include *N. raneyi*, although *N. leptocephalus* was, at least, common. The only collection (USNM 197684) in which *N. raneyi* was common was from a bottom area with less silt than at all other main Roanoke localities. The upper Roanoke record from below Salem was made in 1888. The Roanoke River from the city of Roanoke downstream is now badly polluted.

The known case of hybridization between these species occurred in the upper Roanoke. Ten specimens of *N. leptocephalus*, one of *N. raneyi*, and two hybrids were taken.

Elsewhere in the Roanoke and in the Chowan, Tar, and Neuse drainages about the same distributinal relations prevail between *N. raneyi* and *N.*

leptocephalus as that in the James and Roanoke drainages.

In contrast to *N. raneyi*, *N. micropogon* was found less frequently with *N. leptocephalus* in the James drainage (61% of the comparable collections, Table 26). Included in this percentage are six collections with hybrids of *N. leptocephalus* × *N. micropogon* taken with nonhybrid specimens of only one or the other species. The occurrence of one or more hybrid specimens was relatively high, hybrids being taken in 60 percent of 25 collections. Only three of the 15 hybrid collections contained less than ten specimens; thus it appears that this hybrid combination may occur fairly frequently (87 specimens examined). Hybridization occurred in almost all tributaries in which the two species were taken together and, within each tributary, in a frequency ratio about equal to the relative number of collections from that tributary.

Ecological conditions in the upper New River basin of the Blue Ridge and Appalachian provinces are varied but generally montane. Individual tributary systems in Virginia are described by Ross and Perkins (1959), Shoup (1948), and Burton and Odum (1945). In the Virginia portion of the upper New the relations between *N. platyrhynchus* and *N. leptocephalus* are rather similar to those between the latter species and *N. micropogon* in the James drainage. *N. leptocephalus* was absent from the West Virginia portion of the New River drainage; collections of *N. platyrhynchus* from this area are not included in the following comparison. The two species were syntopic in 63 percent of 16 comparable collections. Hybrids were taken in three (20% of 15 samples), each from a different tributary system.

The distributional relationships between *N. raneyi* and *N. micropogon* in the James drainage have ecological and zoogeographical significance. *N. micropogon* has been taken about as commonly and in equal numbers throughout the James, exclusive of the Craig Creek system, as *N. raneyi* has been taken in the Craig system (excluding the stream section a short distance below Newcastle that is eutrophically enriched). *N. micropogon*, however, is rare within the Craig system, being taken in only four or five collections and in small numbers (see p. 49). Two of the collections are from the headwaters, a habitat marginal for the micropogon group because of the small stream size. *N. raneyi* is generally distributed

downstream and one of the most dominant members of the fauna. As might be expected to occur between closely related ecological homologues, this pattern of distribution and relative abundance suggests that *N. micropogon* is being largely displaced from the Craig Creek system (as well as the lower Catawba) by competition with the apparently better adapted *N. raneyi*. *N. micropogon* may be the more successful of the two species in tributaries upriver from Craig Creek and downriver in the Maury River system. Perhaps here the period of their contact, if any, has been of such short duration that changes in distribution have not occurred. One hybrid *N. micropogon* × *N. raneyi* was taken in lower Johns Creek and one was taken in lower Catawba Creek (see p. 49), where observations in the last several years have revealed only high breeding populations of *N. leptocephalus* and constant breeding numbers of *N. raneyi*.

SUMMARY.—On the basis of similar ecological preferences, and apparent competition in the Craig Creek system, the three species of the micropogon group are regarded as ecological homologues. *N. raneyi* almost always coexists with *N. leptocephalus* in moderate-size streams. There is a definite tendency for *N. leptocephalus* to occur less frequently with *N. micropogon* and *N. platyrhynchus*. The greater frequency of occurrence of *N. raneyi* with *N. leptocephalus* suggests that competition is somewhat more intense between the latter species and *N. micropogon* and *N. platyrhynchus*.

There are differences among the species of the micropogon group in their frequency of hybridization with *N. leptocephalus*, this being inversely proportional to the frequency of syntopic occurrence. Hybridization between *N. raneyi* and *N. leptocephalus* is rare, only two specimens are known from a habitat more disturbed than that of the other streams which were intensively sampled. *N. micropogon* and *N. leptocephalus* hybridize comparatively commonly (87 specimens known). Although the number of collections in which *N. platyrhynchus* and *N. leptocephalus* were taken together, and the number of specimens involved, is less than those of the other two combinations of chubs, the frequency of hybridization is appreciably (5 specimens are known to us) less than that of the *N. leptocephalus* × *N. micropogon* combination.

Dispersal: Biological and Geological Evidence

The ichthyofauna of central eastern United States presents many stimulating zoogeographical problems, such as the dispersal of the species of the micropogon group, the leptocephalus group and of several of their associates. Possible routes of entry into various drainages have been recognized. These are often indicated by biological evidence of present distributional patterns and relationships and past geological events. In some cases, however, routes have been conjectured only from biological evidence since complementary geological information is meager or nonexistent. While this procedure may not be justifiable since distribution patterns are known to change, the fact remains that populations have crossed drainage divides in some manner. Therefore, attempts are made herein to offer explanations of how dispersal may have occurred. Past and present ecological conditions are considered.

Three kinds of geological events have operated in the dispersal of chubs. These are stream captures, eustatic changes of the Atlantic Coastal Plain, and Pleistocene drainage modifications. An obvious fourth means of dispersal is movement from one drainage system to another through past and existing interconnecting main rivers.

STREAM CAPTURE.—The geological literature on the occurrence of and evidence for captures in western Virginia and adjacent portions of West Virginia is extensive. It appears that numerous captures have occurred which made it possible for stocks of fishes to spread among several drainages. Major papers treating this subject are by Wright (1931, 1934, 1936), Thompson (1939), and Dietrich (1959), and numerous additional references are in their bibliographies. It is interesting to note that Dietrich (1959:30), a geologist, invoked biological evidence from fishes in support of a geological hypothesis. A century ago, Cope (1869) concluded that the faunal similarities among opposing drainages in western Virginia may have resulted in part from headwater transfers. Recently Ross and Carico (1963:7–12) documented two stream captures to support hypotheses on the dispersal of certain fishes between the New and Tennessee drainages. Other authors (Robins and Raney, 1956:31; C. R. Gilbert, 1961:456; 1964:106) mention possible use of stream captures by fishes in western Virginia. Other instances

of isolation, subsequent differentiation, and present distributional patterns of fishes in this region can be accounted for primarily by these events.

When invoking stream capture as an agent of dispersal, the biology of the fishes, ecology of the region, and nature of stream capture are factors that should be considered. Some factors are species abundance, interspecific competition, habitual movement and migration of species, size and flow of streams, and other ecological expedients or barriers. Some important geological factors are the magnitude of the theater of stream capture, the duration of the water connection between opposing drainages and the numbers and sequence of captures that occurred in a region. The absence of certain species today from a drainage from which its associated species have successfully entered is perplexing and may be explained by subsequent change in stream conditions, competition, and extirpation.

Another problem in correlating dispersal with stream capture is the uncertainty or lack of information concerning the dates of occurrence. Thompson's statement (1939:1353) that "captures that can now be definitely recognized belong to comparatively recent geologic times" provides a positive argument for adopting the concept of capture. Many captures described can probably be assigned to post-Harrisburg time, a period of stream rejuvenation which began in the late Tertiary (Wright, 1934:38). In addition, since Wright (1931:246) pointed out that evidence of capture soon disappears with active dissection of the capture area, we may safely assume that many more captures occurred than are presently detectable [see also Ross (1969) and Jenkins, Lachner, and Schwartz (ms)].

EUSTATIC CHANGES OF THE ATLANTIC COASTAL PLAIN.—Dispersal can be equated with eustatic changes of the Atlantic Coastal Plain during or somewhat after Pleistocene time. During such times the several drainages now entering the western shore of Chesapeake Bay, from south of the present Susquehanna River mouth to the James drainage, were sometimes tributary to the extended freshwater Susquehanna, hereafter called the Greater Susquehanna River (Shattuck, 1906:134, pl. 31). This resulted from a general increase in elevation of the central Atlantic Coastal Plain and/or a lowering of sea level (Flint, 1957:270). Lougee (1953:264–265) stated that sea level was at or near its lowest level

during the last glacial climax. It is also possible that a drainage similar to the Greater Susquehanna was in existence during earlier periods of Pleistocene glaciation (Flint, 1957:270).

At the same time it is likely that similar events occurred in North Carolina, in present Albemarle

Sound where the Chowan drainage would have been a tributary of the Greater Roanoke River, and in Pamlico Sound where the Tar and Neuse drainages would have been conjoined to form the Greater Pamlico River. Some authors consider the Chowan to be a present Roanoke tributary, but this is not

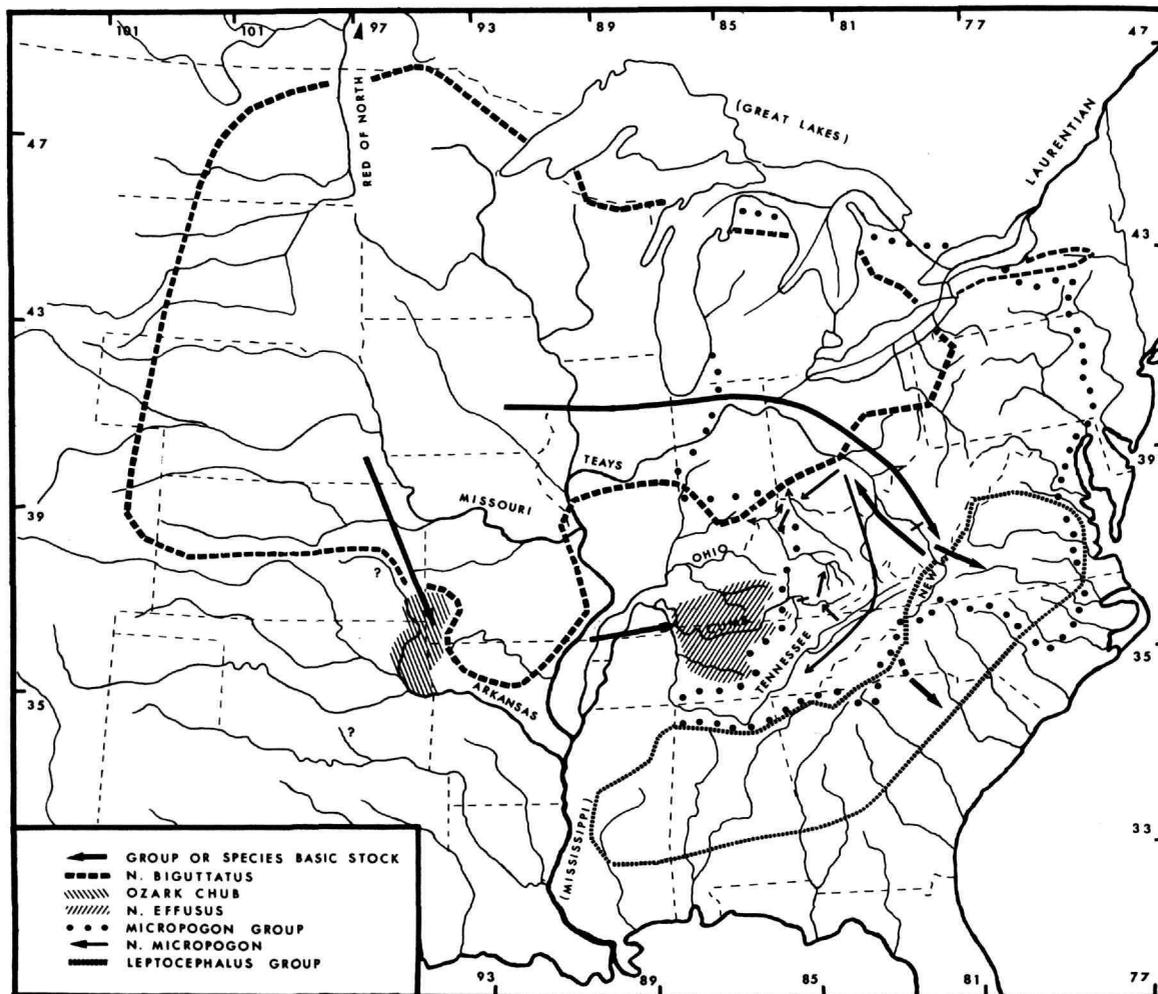


FIGURE 30.—The present distribution of certain species and species groups of *Nocomis* superimposed over stages in drainage development. The probable principal dispersal routes of basic *Nocomis* stocks are indicated by wide and narrow arrows. Stages of formation of the Mississippi and Great Lakes drainage basins are only approximations, probably present during the late pre-Pleistocene and/or Pleistocene periods. The Laurentian River is shown to occupy the present Great Lakes basin. The distributions of the species or species groups, in shaded areas or outlined by dotted lines, represent total ranges; some areas within these ranges may be uninhabited. Drainage patterns adapted from Leverett (1902), Tight (1903), Fenneman (1938), and Janssen (1953).

likely since the large lower channels of these drainages are separated by tidal flats (Hubbs and Raney, 1944:5), thus largely or entirely preventing dispersal of most freshwater species between them. Opportunity for dispersal of species considered herein through extended channels is thought not to have occurred earlier than the Pleistocene since there was a Pliocene submergence of the Coastal Plain (Clark and Miller, 1912:215).

PLEISTOCENE DRAINAGE MODIFICATIONS NORTHWARD.—Several means of late Pleistocene dispersal in the Great Lakes and adjacent regions are discussed under the following species accounts.

The vast preglacial Teays River system (Figure 30) served as a reservoir for a large portion of the North American ichthyofauna and provided an early means of dispersal. Its upper and middle portions are of much importance in this study. The upper Teays, approximately, is regarded as the New-Kanawha River system after the occlusion of the middle Teays and formation of the present Ohio River during Pleistocene glaciation; however, some drainage relationships of the Teays with the earlier Ohio, Tennessee and Cumberland drainages are uncertain. Detailed discussion of the history of the Teays system is presented by Leverett (1902), Tight (1903), and others and, of a more general nature, Janssen (1953) and Flint (1957:170–171).

Nocomis platyrhynchus: The basic stock of the micropogon group probably occupied the middle and upper Teays River system (Figure 30), perhaps during late Pliocene and certainly part of Pleistocene times.

The bigmouth chub may represent the form closest to the basic stock of this group and probably evolved in the New River drainage (upper Teays) where it is presently confined. Kanawha Falls, approximately 24 feet in height, and Sandstone Falls just upstream, apparently served as an effective barrier for isolation of the segment of its ancestral stock from that below. The period of inception of Kanawha Falls is not dated, however; it may have been during pre-Pleistocene times. If the ancestor of *N. platyrhynchus* was below the Falls and was prevented from directly entering the New, it may have made its entry through stream capture between Elk River of the Kanawha drainage and Gauley River of the New, an event for which there is geological evidence (Campbell, 1896:669–670).

The New drainage has a unique fauna, partly characterized by several endemic forms and further marked by the absence of a large fraction of the fauna of the Ohio basin. Ross (1959) listed and discussed the members of this fauna. Forms, in addition to *N. platyrhynchus* that most likely evolved in the New are the cyprinids *Notropis scabriceps* and *Phenacobius teretulus*, and the percids *Etheostoma osburni* and *Etheostoma kanawhae*. Most of these species occur widely within the New, from its headwaters to Gauley River, but none are known below Kanawha Falls. It therefore seems that Kanawha Falls has been the major impediment to their establishment in the Kanawha drainage. The several tumultuous rapids, cascades, and low falls in the New River gorge of West Virginia (Campbell and Mendenhall, 1896; Reger, 1926:3, 90) also may limit downstream dispersal.

Despite its endemics, the New drainage has a depauperate fauna in relation to the size of the basin. There is evidence to suspect that the earlier New drainage fauna was similar to that of the Ohio basin and that its depauperate nature probably resulted from extirpation. The Kanawha drainage fauna is essentially that of the middle Ohio basin. Particular examples of probable extirpated forms are species of redhorse suckers (genus *Moxostoma*, subgenus *Moxostoma*). The occurrence today of some species of this group in Atlantic slope drainages from the James southward may be best explained as their having crossed the Appalachian divide from the New drainage. Ross and Perkins (1959) discuss factors that possibly combined to limit this fauna. Some of the ecological factors mentioned (*ibid.*:10) were "the general absence of aquatic plant life, the narrow poorly developed flood plains, the hard bottom, steep gradient and high velocity which by abrasion kept the stream bottom well scoured." Speciation in the New also may have been in response to some of these conditions.

N. micropogon: Certain stages in the dispersal of *N. micropogon* can be readily postulated whereas others are not clear. The present range of *N. micropogon* south of the Great Lakes drainage may reflect much of its early distribution. A population of the ancestral stock of the micropogon group remaining below Kanawha Falls in the Teays system probably speciated to *N. micropogon*. Subsequently this species may have occupied the middle Teays

drainage of West Virginia, Kentucky, Ohio, and Indiana including the future upper Wabash drainage (Figure 30). Alternatives available for its ingress to the Tennessee and Cumberland drainages are discussed on page 50. *N. micropogon* probably never occurred west of the Mississippi, even if it once did reach the extreme lower Ohio basin. This would attend the possibility that the lower Teays (early Mississippi) and Ohio were separate systems (Feneman, 1938:89-90). On the other hand, these large rivers conjoined in the extensive lowland region would still have been more of a barrier than an agent of dispersal.

More than one region may have served as a refugium from which the river chub spread northward during inter- and postglacial times, to repopulate northern Ohio River tributaries and enter the Great Lakes drainage. Evidence does not favor the lower Wabash drainage as having been a refugium for a Teays stock. This drainage was almost entirely overwhelmed by the Illinoian glacier (Gerking, 1945). During glaciation the nonglaciated lower Wabash, although certainly of a character different from that today, probably was adversely affected. Seasonal and diurnal variations of proglacial discharge, sometimes perhaps catastrophic in proportion, combined with sediment and ice loads (Dyson, 1962:77-80; Flint, 1957:174-175) would have greatly restricted fish inhabitants.

Ancestors of populations now occupying drainages of unglaciated Kentucky and West Virginia are likely to have moved northward after glacial recession into northern Ohio River tributaries.

Perhaps the most important center of dispersal for river chub populations now occupying the Ohio, Great Lakes, and Atlantic slope drainages was a southern portion of the Old Allegheny River system, probably the Old Lower Allegheny. The three separate preglacial component drainages of the Old Allegheny system flowed northward to the present Lake Erie basin (Leverett, 1902:129-138). *N. micropogon* presumably entered the Old Allegheny through stream capture with the Teays. Following interconnection of the Allegheny components with the Ohio River due to glacial advance, the river chub may have spread downriver into Ohio drainage tributaries when uncovered from the ice sheets. Deglaciation of the northern portion of the Allegheny basin would have permitted influx to glacial

Lake Maumee (Lake Erie basin), through Conneaut Creek, a present Lake Erie tributary in Pennsylvania whose upper portion was involved in a drainage reversal with the Allegheny in an area of the Old Middle Allegheny (Leverett, 1902:214). Its presence in the lower Allegheny during glacial times would enhance the probability of its reaching the vicinity of Conneaut Creek before its diversion. Dispersal to the upper Allegheny probably postdated the Cuba Outlet connection between the Allegheny and Genesee drainages since *N. micropogon* is not known from the latter. Ross (1958a:17-18) discusses a complex distribution problem in this region involving subspecies of *Campostoma anomalum*.

Once *N. micropogon* entered the developing Great Lakes basin in the Lake Maumee area, it could have entered future Lake Erie tributaries in Ohio and Ontario and the Maumee drainage of northeastern Indiana. Passage to the Wabash drainage from the Maumee through the Fort Wayne Outlet would follow if this outlet remained open sufficiently long after the Conneaut Creek diversion and/or if ample water connection through the low divide in the Fort Wayne region existed during more recent periods of high water (Gerking, 1945:8).

Dispersal northward could have ensued into the developing Lake Huron basin including its tributaries in Ontario south of Georgian Bay and those of the eastern shore of the Lower Peninsula of Michigan. Some movement to the western shore of the Lower Peninsula may have been around its northern end, but this is unlikely since the river chub apparently did not reach (or has not persisted in) streams of the Upper Peninsula. The eastern shore of Lake Michigan was probably populated after movement across the Lower Peninsula through a later stage of the Grand River connection. Since *N. micropogon* has not appeared in the Illinois drainage, it probably did not reach the region just north of the upper Illinois until after the Chicago outlet was closed.

Dispersal northeastward from Conneaut Creek could have followed the development of Lake Erie and thence entry of streams of the present western Lake Ontario basin, probably during the Lake Lundy stage. Entrance to the Lake Ontario basin at a later stage would apparently necessitate passage

over and establishment below newly created Niagara Falls (Fenneman, 1938:495, 499).

Natural occupation of Lake Ontario streams may have progressed slowly. A notable (52 mile) break occurs in the river chub's distribution in the southern Lake Ontario drainage, from just west of the mouth of the Genesee River to 16 miles west of the mouth of Oswego River. Two records break the distributional gap, both from the same area and constitute the only occurrence in a tributary of the eastern lakeshore (excepting those from the Finger Lakes drainage). Dispersal along the lakeshore may involve a relatively long period of time for the river chub, especially since for long distances only small streams enter the lake and unsuitable habitats are present (these conditions not permitting establishment of large populations for continuing outward dispersal). Since the New York lakeshore tributaries have been, comparatively, thoroughly collected (Greeley, 1940:42), the easternmost records may indicate local extirpation or unsuitable habitat in the gap area, bait-minnow introduction, or dispersal by natural means. All four alternatives are feasible. Some of the streams do not provide the larger water type of habitat for the river chub; however, this species is common in a relatively short, western Lake Ontario streams and in Salmon Creek, its easternmost stream before the gap. The lower Genesee drainage, whose mouth is just east of Salmon Creek, would provide a large area of apparently suitable habitat. The area is heavily fished by sportsmen. The hardy chubs, frequently used as bait, could have been discharged from a bait pail. Natural means of dispersal would entail the river chub moving northward from the Susquehanna drainage, via the Horseheads Outlet during the Lake Newberry stage (Fairchild, 1934:1097, fig. 8, 1099), through the Finger Lakes drainage to the lakeshore. A problem with the latter hypothesis is that *N. micropogon* is relatively rare, and the recent records are widely scattered in the Finger Lakes basin, while it is common throughout the adjacent upper Susquehanna. Greeley (1928:84, 97) stated that the Finger Lakes drainage was extensively collected, and reported only a single collection of the river chub from Catharine Creek, the Seneca Lake inlet. He attributed its presence there to a canal connection with the Susquehanna drainage. Although this is possible, it is now known to have a wider, although local-

ized, distribution in the Finger Lakes drainage which may have resulted from the same factors considered for the Lake Ontario shore area.

The river chub probably occupied at least some of the Atlantic slope drainages during glacial times and it had a history somewhat different from that which occurred northward and westward. Evidence for a relatively long eastern occurrence is that its spread throughout all the drainages of its central, eastern range probably required considerable time, and its movement throughout most of the James should predate the entry of *N. raneyi* into this drainage. Populations south of the Susquehanna may be derived from stocks older than the northern forms. C. R. Gilbert (1964:109) has given biological support in suggesting that *Notropis cornutus* entered this area at an early time.

N. micropogon possibly entered the Susquehanna by stream capture from the Allegheny drainage. This view conflicts with Bailey's statement (1945:125) that "some Great Lakes forms found in the Susquehanna system are absent from the upper Ohio basin; thus, stream capture from that [latter] source fails to supply a tenable explanation" for dispersal to the Susquehanna.

N. micropogon probably first gained the central Atlantic slope by entering the Potomac drainage through stream captures from either or both Youghiohony and Cheat River tributaries, Monongahela drainage (once part of Old Allegheny system). Biological and/or geological evidence for these captures is cited by Ross (1958b:5-6), Gibbs (1957:205), and Schwartz (1965). Dispersal to the James and Rappahannock was possible during a stage in the development of the Shenandoah River of the Potomac, during the period the Shenandoah attained its drainage by a series of piracies (Stose, 1922:7; Watson and Cline, 1913).

The Greater Susquehanna River may have been an ample means of faunal exchange among all Chesapeake Bay tributary drainages, thus accounting for the presence of the river chub in the York drainage, the minor Chesapeake drainages, and the Appomattox River which now enters the James River estuary. Certain factors, however, militate against assumption that the Greater Susquehanna was the major means of dispersal among its tributaries. This obviously was a large river, certainly so during late Pleistocene periods of precipitation,

in which smaller stream and some large stream fishes would not have found suitable conditions. Lower Potomac species such as *Ericymba buccata*, *Percopsis omiscomaycus*, and *Percina caprodes semifasciata* might be expected to have spread more widely through the Greater Susquehanna but are not known south of the Potomac on the Atlantic slope. The presence of *Notropis s. spilopterus* in this region, only in the Susquehanna and Potomac including their lower portions, is good reason to believe it entered the latter by headland stream capture (Gibbs, 1957:194–205, fig. 3) and not through the Greater Susquehanna. Other factors may confuse this issue. Some species may have entered the upper portions of larger Chesapeake drainages at a relatively recent period and sufficient time for spread through the Greater Susquehanna may not have been available.

Our interpretation of the relationships of the species of river chubs and their populations in the lower New, upper Monongahela, and Potomac drainages is given further credence by consulting the stream history of the area. We have discussed certain morphological similarities that suggest an exchange of river chub forms occurred between the New and Monongahela. A likely avenue of exchange would be a capture that occurred between the upper Greenbrier River of the New and upper Cheat River of the Monongahela. This is supported from geological evidence by Fridley (1933) and Wright (1934: 55). Additional biological evidence for a capture in this area is the distribution of *Percina oxyrhyncha*. This species is widespread in the New-Kanawha system but the only known population in the Ohio system above the Kanawha River mouth occurs in the upper Monongahela (Hubbs and Raney, 1939: 1–3). (Additional possible agencies of ingress of *N. micropogon* into the New drainage are the piracies of Greenbrier River tributaries by three tributaries of Back Creek of the upper James drainage (Thompson, 1939:1352–1353) and the two captures documented by Ross and Carico (1963:7–12) involving Holston River tributaries of the upper Tennessee drainage, and tributaries of the upper New drainage). We have also indicated a relationship between the Potomac and Monongahela populations of *N. micropogon*. A stock of the Monongahela form of *N. micropogon* could possibly have entered the Potomac drainage through the capture discussed by

Schwartz (1965) for *Etheostoma blennioides*, and subsequently spread throughout the latter drainage.

The entrance of *N. micropogon* into, and spread within, the southwestern Ohio basin includes several complex facets. (See Figure 7 in Lachner and Jenkins, 1967, for the distribution of *N. micropogon* and other *Nocomis* in this region.) The middle Teays is shown (Figure 30) as it flowed in pre-Pleistocene times (through Ohio, Indiana, and Illinois); this portion may have reformed during Pleistocene interglacial periods (Janssen, 1953). The latter possibility is discussed below since *N. micropogon* may have evolved during the Pleistocene. It is not known whether the Kentucky and Licking drainages emptied directly into the middle Teays or into the early Ohio River.

We presume that *N. micropogon* evolved from a stock of the bigmouth chub, *N. platyrhynchus* of the New River, the latter believed to be the most primitive form in the micropogon group. The early range of *N. micropogon* within the region of the present southwestern Ohio basin possibly included only the Big Sandy drainage, shown to be a Teays tributary (Leverett, 1902), and perhaps the Licking and Kentucky drainages. Another alternative, its having evolved in the most southwestern parts of the Ohio basin (Cumberland and Tennessee drainages), is unlikely since it would have needed considerable time to attain its wide range in nonglaciated regions east of the Ohio basin, and since much of its range in the southwestern Ohio basin appears to be recently acquired.

The two alternatives available for the spread of *N. micropogon* deep into the present southwestern Ohio basin are through possible main river connections with the lower Teays or lower Ohio River, and/or through stream captures with upper or middle Teays tributaries (present middle Ohio basin) in the region about southwestern Virginia and eastern Tennessee and Kentucky. Some of the evidence against the first alternative is the lowland and large river conditions the species would have to traverse in the long bend of the middle and lower Teays. It could have used the more recent and shorter Ohio River after the present course of the Ohio was determined by glacial advance but this route is also unlikely due to river conditions similar to the Teays. If *N. micropogon* did use a large river pathway downstream to the Green, Cumberland, and Ten-

nessee, upon entering these drainages it could have encountered competition from *N. effusus*, a species more adapted to the lower gradients. Their distributional relationships in the Cumberland (Lachner and Jenkins, 1967) support the latter hypothesis. These species are allopatric except for being collected together on one possible occasion near a fringe of their ranges. Even if the latter record is valid, this does not mean that close competition is lacking. The absence of *N. micropogon* from the Green drainage is evidence that it did not use a downriver course to the Cumberland and Tennessee or, if it did, that this species and *N. effusus* were incompatible in the Green, the latter being dominant.

Ingresses of *N. micropogon* into the Tennessee and Cumberland drainages were most likely through stream capture since there is considerable biological evidence for this, some geologic evidence, and a bulk of evidence against lower main river entry. The favored sequence of entrance may have been from Big Sandy to Tennessee, then into the Cumberland, and then the first (or another) entrance into the Kentucky drainage. It could have been attained the Kentucky and Licking drainages if these were middle Teays tributaries and probably entered them once they were connected to the Ohio River.

Evidence is given above that the early range of *N. micropogon* included the Big Sandy drainage, a tributary of the middle Teays and presently a middle Ohio basin tributary. Much of the upper Tennessee drainage of Virginia is adjacent to the upper Big Sandy. An unknown capture(s) is invoked to account for transferal of *N. micropogon* from the Big Sandy to the Tennessee. This species would not have entered the Tennessee from the adjacent portion of the upper Teays (present New drainage) since its cognate, *N. platyrhynchus*, occurs therein. *N. micropogon* has spread throughout most of the middle and upper Tennessee, but is apparently absent from most of its lower portion. Since the habitat in some lower Tennessee tributaries appears quite suitable, its absence may be related to a somewhat slow downriver dispersal rate, large stream size and/or lower stream gradients. The many uninhabited streams are additional evidence that *N. micropogon* entered the Tennessee from the northeast and not through the lower Teays or Ohio Rivers.

Stream capture involving the Tennessee and upper Cumberland is most likely. Even if *N. micropogon*

had dispersed upriver in the Cumberland through the large area occupied by *N. effusus*, the former species would have had to surmount Cumberland River Falls—an impossibility—in order to attain its distribution throughout the upper Cumberland. The upper Cumberland has a depauperate fauna (Kuehne and Bailey, 1961) compared to those of the middle Cumberland and upper Tennessee. *N. micropogon* was either one of the relatively few species to make the crossing, or to survive thereafter.

The well-established population of *N. micropogon* in the middle Cumberland was probably derived from washing over the falls and/or from stream capture between Big South Fork of the Cumberland and the Tennessee or between Rockcastle River, or surrounding tributaries of the Cumberland and the Kentucky drainage. Explanation of the presence of the population in the Caney Fork system, middle Cumberland, presents greater difficulties. *N. micropogon* may have entered Caney Fork directly through stream capture with the middle Tennessee drainage. Possibly, it is a relict population predating farther upriver movement of *N. effusus*, and now cut off from the main population by *N. effusus* (and impoundments). It probably is not the result of human introduction since one specimen was collected in 1917, earlier than times of considerable trucking about of bait minnows. The use of minnows as bait in the recently created southwestern Ohio basin impoundments is now heavy.

The Cumberland-Kentucky drainage divide was very likely crossed through stream capture, with the direction of movement largely into the Kentucky. Kuehne and Bailey (1961) give good geological evidence for capture between these drainages and biological evidence for movement in the same direction.

The differentiation of *N. micropogon* observed in eastern Kentucky has zoogeographic implications. The largest differences in mean values of body circumferential scales are among adjacent drainage populations sampled (Table 12) in the Cumberland (grand mean 32.1), Kentucky (29.9), and Big Sandy (31.9). The differences between the Kentucky and the former and latter are, respectively, 2.2 and 2.0. The next greatest differences from Atlantic slope drainage populations are 1.3 and 1.2; all others are less, usually considerably less than 1.0. *N. micropogon* is thus relatively consistent in circumferential scale numbers over most of its range, except in

eastern Kentucky. A distinct bimodality exists in the frequency distribution of the scale counts from the Kentucky drainage. We have not found a bimodal distribution of meristic characters from any other drainage population of *Nocomis*. Population differences in other characters are present but less marked. Lateral line differences approach those of the circumferential scales. The Tennessee drainage population has the most reduced tuberculation and smallest head parts within the species. Too few large specimens are available from eastern Kentucky to determine relationships by these morphometric characters.

Additional differences became evident after segregating the eastern Kentucky circumferential scale counts by tributary systems or areas within the Cumberland and Kentucky drainages (Lachner and Jenkins, 1967, Table 3). The difference (1.3) between the means in scales between the middle and upper Cumberland populations, separated by the Falls, indicates their partial isolation; some individuals may still go over the Falls.

Within the Kentucky drainage, 86 specimens from the South and Middle Fork systems (the two more westerly of the three Forks of the upper Kentucky drainage) have a mean of 30.2. There are no significant differences or trends among the individual samples from the two systems. Thus the western upper Kentucky drainage mean of 30.2 and upper Cumberland mean of 32.7 are appreciably different and represent the greatest scale difference among adjacent populations of *N. micropogon* and within all other species of *Nocomis*. The upper Cumberland and Kentucky are in the same or similar physiographic areas; thus these differences probably are genetically based. The same was concluded by Kuehne and Bailey (1961:4) for a species of darter (Percidae) with two subspecies that have similar differences and distributions. It would be difficult to think, because of this difference, that the South and Middle Fork populations are derived from the upper Cumberland population through relatively recent stream capture, were it not for the fact that the populations of the North Fork and Red River systems, Kentucky drainage, also are apparently different from the South and Middle Fork populations. The mean circumferential scale values from the Red River (29.3, 20 specimens), a mid-drainage tributary, and the North Fork tributaries (29.0, 26

specimens) are lower than those from the South and Middle Forks, and also lower than in any other population of *N. micropogon* (Table 12). The strongly asymmetrical frequency distributions (Lachner and Jenkins, 1967, table 3) for both the North Fork and Red River samples suggest that selection is operating strongly against individuals with scales larger than those found in these populations.

Several implications are derived from the Kentucky drainage data. It appears that a trend toward a large-scaled form began in the Kentucky, probably prior to the entrance into the upper Kentucky of a finer scaled population from the upper Cumberland. The stream capture described by Kuehne and Bailey (1961) occurred between the upper Cumberland and a tributary of South Fork of the Kentucky. Such a capture would interject the finer scaled Cumberland form within the range of a larger scaled differentiate of the Kentucky. Downstream movement within the South Fork and then through the main Kentucky River would lead a fine-scaled form first to the Middle Fork. Two aspects of the number of circumferential scales for the South Fork-Middle Fork sample are notable: (1) The mean is somewhat intermediate between those for the upper Cumberland drainage and the North Fork-Red River samples although much closer to the latter. (2) A distinct bimodality exists for the South Fork-Middle Fork sample. An intermediate mean may be expected with either occurrence or absence of interbreeding between a fine-scaled upper Cumberland form and a large-scaled North Fork-Red River form. The bimodality may indicate divergence of these forms to a level higher than that of a race. The *Nocomis* of the Kentucky, upper Cumberland, and adjacent drainages warrant further study, particularly to determine if possible differences in fin coloration (see p. 46) correlate with scale differences.

The question of dispersal from the Kentucky River of the large-scaled form cannot be adequately appraised at present since we have little data on adjacent populations. Drainages of nonglaciated Kentucky and West Virginia are believed to have served as refugia for *N. micropogon* during glacial times. Study of Ohio and Indiana populations may yield clues to the determination of which refugia held their ancestors.

The 15 specimens of *N. micropogon* from the Licking drainage, between the Kentucky and Big

Sandy drainages, have a mean value of 30.7 circumferential scales, distributed as 28 (in 1 specimen), 30 (3), 31 (10), 32 (1). Four specimens (CU 25595) from the Little Sandy River, northeastern Kentucky, have counts of 29 (1 specimen), 30 (1), 31 (2). The mean for 56 specimens from the Big Sandy drainage is 31.9. The means are similar or somewhat lower from southern Ohio River populations farther upriver from the Big Sandy, in West Virginia. These data indicate that the large-scale Kentucky drainage population may not have spread widely south of the Ohio River.

Why *N. biguttatus* is not at least moderately distributed in the southwestern Ohio basin is a perplexing question. *N. biguttatus* generally inhabits streams of lower gradient than does *N. micropogon* (Lachner and Jenkins, 1967:573). The latter apparently is absent from most of northern Kentucky, a region partly suitable for occupancy by *N. biguttatus*, and thus it would not be a competitor. One reason may be that the eastward extension of *N. biguttatus* is probably largely or solely related to postglacial drainage events north of the Ohio River and its habit of keeping within glaciated regions in the East. Its entire range north of the Ohio River is Recent and is almost entirely within or peripheral to regions of Illinoian glaciation; it is thus absent from the major portion of southern Ohio and Indiana (and Illinois). With its current absence from these areas, it is somewhat unlikely that it crossed the Ohio River even though it occurs in the northern Ohio basin. The single southeastern population, known in Elkhorn Creek, lower Kentucky drainage, in all probability stems from bait bucket escapees. The Elkhorn has been a popular smallmouth bass fishing stream for the last century (Towles and McClane, 1965:446), and chubs are favored bait.

The upper Savannah drainage population of *N. micropogon* was probably derived from the Little Tennessee River of Tennessee drainage by stream capture. Capture here is well documented by geological and additional biological evidence (Ramsey and Woolcott, ms).

The presence of *N. micropogon* in the Coosawattee system of the Mobile drainage may be attributed to stream capture with the Hiwassee system of the Tennessee. We have not further examined this or considered other possibilities.

N. raneyi: This species probably evolved in the

Roanoke drainage from an ancestral stock of *N. platyrhynchus* after its transfer by stream capture from the New drainage. Ample opportunity for passage to the Roanoke seems to have been available. Wright (1934:61-72), Thompson (1939), and Dietrich (1959) argued that drainage loss by Little River and other adjacent New River tributaries was effected by headward erosion of the lower elevated upper Roanoke in the region of present North and South Forks of the Roanoke River. Wright (1934:61) believed the Roanoke captured an area of approximately 200 square miles formerly drained by the New since the close of the Harrisburg cycle (late Tertiary). Dietrich (1959:29-32) also supported a hypothesis that the headwaters of the Dan River, Roanoke drainage, have captured portions of Big Reed Island Creek of New drainage. *N. raneyi* is a member of the rich and distinctive Roanoke fauna composed of several endemic and semi-endemic forms, many of which have their heritage to the west.

With the Roanoke drainage as its center of dispersal, *N. raneyi* spread northward and southward. Ingress to the Chowan drainage may, in part, have been during the Pleistocene when the latter was tributary to the Greater Roanoke. Some events have certainly facilitated dispersal between these drainages since recent collecting has shown the Chowan fauna to be very similar to that of the Roanoke. A major problem lies in how *N. raneyi* and several other species, now common to the Roanoke, Tar, and Neuse, entered one of the latter two from the Roanoke.

Although specific geological evidence is lacking for stream captures between the Chowan, Roanoke, Tar, and Neuse drainages, apparently because the evidence would be obliterated on the easily eroded Piedmont and Coastal Plain cover, captures may be inferred to have occurred during late Pliocene to Recent times. Clark and Miller (1912:215) stated that coincident with the Pliocene submergence of the Coastal Plain there seems to have been a slight elevation and tilting of the Piedmont west of the shoreline, and that (op. cit.:200) successive uplifts of the Coastal Plain occurred during the late Pleistocene period of shore terracing. Accompanying rejuvenation and subsequent headward erosion, with lack of structural control in these provinces, may well have resulted in captures. The lower Roanoke presently has no large tributaries entering from the

north or south; these were probably lost by capture to the Chowan, Tar, and Neuse. Further, as the Coastal Plain emerged from inundations, swampy conditions must have once been more continuous than at present. Some swamps are not yet discontinuous, but are now becoming so (R. D. Ross, personal communication).

Biological evidence confirms these hypotheses. A large number of species is shared by the four drainages, some of which are small stream forms that are less likely to have utilized river-mouth connections. In addition to transfer with Piedmont captures, the occurrence of common upland species in Coastal Plain streams, such as *N. raneyi*, suggests the possibility that they may at times have gotten through some swamp connections to adjacent drainages. Members of the more typical Coastal Plain fauna probably attained part of their wide ranges in similar manner.

The entry of *N. raneyi* into the James drainage from the upper Roanoke is an interesting problem with several aspects, best treated after establishing some pertinent distributional facts. Its limited range in the James is roughly paralleled by that of three additional species of the upper Roanoke drainage that are not known from north of the James drainage or the New drainage. These are a sucker *Moxostoma cervinum*, a madtom catfish *Noturus gilberti*, and a darter *Percina crassa roanoka*. Of the three, *M. cervinum* appears to have spread farthest within the James, perhaps due to greater vagility. This species is known from the middle and lower Craig Creek system and only downriver, in lower Catawba and Jennings Creeks, and in lower Buffalo Creek of the lower Maury River system. The known range within the James of *N. gilberti* and *P. crassa roanoka* is entirely within the Craig Creek system. These three species are taken in about equal abundance in the Craig Creek system and the upper Roanoke drainage. These peculiar distribution patterns stand out after consideration of the entire James and Roanoke fauna. These two drainages share numerous other species, some of which range widely or are more or less restricted to the central Appalachians; all, however, range throughout most of the James and Roanoke drainages or generally occur where their preferred conditions exist. (The single exception is *Pimephales notatus*, a popular bait and farm pond culture species, widely distributed in the New

drainage, whose small range within the upper Roanoke appears to have resulted from introductions.) In order to have achieved their wider distributions these species probably were exchanged at a date earlier than that of the first-mentioned four species and/or at more than one locality. In addition, isolation of some geminate pairs has been sufficiently long for differentiation to the specific or subspecific level (see C. R. Gilbert, 1961:455-456; 1964:107, for discussion of these cases).

The similar and limited ranges of the four species strongly suggest that they entered the Craig Creek area of the James from the upper Roanoke through a relatively recent connection. They do not appear to be restricted by lack of suitable stream conditions elsewhere in the James since their preferred habitat, although unoccupied, is readily accessible. No distinct ecological differences are apparent between the Craig Creek system and other upper and many middle James tributaries. Some evidence (p. 49) indicates that *N. micropogon* probably occupied the Craig Creek system prior to the entry of *N. raneyi* into the James. Competition with *N. micropogon* may be one factor limiting the further dispersal of *N. raneyi* within the James. As evidenced by the limited distributions of the three other species, however, which do not appear to be restricted by competition, their entrance to the James was probably of such recent date that sufficient time to achieve wide distributions has not elapsed.

Robins and Raney (1956:31) suggested that the populations of *M. cervinum* and *N. gilberti* in the Craig Creek system were derived from the Roanoke drainage through stream capture, but that *Hybopsis* "sp" (= *N. raneyi*) could have come from the Roanoke or New drainages. Present morphological knowledge of the chubs excludes the latter alternative.

Connections between the Roanoke and James drainages (Figure 20) were probably available. There appears to have been a complex of recent captures in the present valleys of North Fork of Roanoke River and Catawba Creek, involving these streams, a Craig Creek and a New drainage tributary (Wright, 1934:68). Trout Creek, a small upper Craig Creek tributary that heads against upper North Fork and flows through a gap in the Craig Creek-North Fork divide, probably captured a portion of North Fork. This seems to be the only possible route through

which fishes could have entered Craig Creek directly from the Roanoke since they are separated elsewhere by relatively unbroken mountain ridges. Another possible capture is one between North Fork and Catawba Creek. Although fishes might cross the existing low divide as it is flooded during a period of excessive rain, the divide may not have shifted much at the expense of either stream (R. D. Ross, personal communication). A third alternative may be connection in Fincastle Valley between Catawba Creek and upper Tinker Creek, the major Roanoke River tributary at Roanoke. Evidence for this capture is given by Wright (1934:62-63).

The distributions of these four species have some significance, bearing on which of these possible routes may have been used. Although *N. raneyi* is not known from North Fork of Roanoke (not taken in five collections containing *N. leptocephalus*), it may be in its lower portion. At least two of the three other species were taken from North Fork. All four probably occurred in lower Tinker Creek which now suffers from pollution. *N. raneyi* and *M. cervinum* occur in lower Catawba Creek, but the two other species are absent or rare therein since they were not taken in the eight known collections from lower and middle Catawba. Thus, although *N. gilberti* and *P. crassa roanoka* may have entered the James from either the North Fork or Tinker Creek, their apparent restriction to the Craig Creek system suggests that they entered via a North Fork-Trout Creek capture. This cannot be said for *N. raneyi* and *M. cervinum* since they range more widely. Further complexity results from the existence of the atypical population of *N. raneyi* in the main James, between the Craig and Catawba Creek populations and the Pedlar River population. Whatever factors have affected this population, they probably operated subsequent to the spread of the typical form from Craig or Catawba Creeks to Pedlar River. The bull chub and sucker apparently have not dispersed to James tributaries upriver from Craig Creek. The main channel and tributaries between Craig and (upstream to) Potts Creek, however, are poorly sampled or they have not been collected.

We have considered that perhaps the four species were introduced by man into the James from the Roanoke. This may be suspected owing to the limited ranges and only recent records of the species. Our records of *N. raneyi* in the James date from

1941, when G. W. Burton (Burton and Odum, 1945) collected a single specimen. The three other species were not reported from the Craig Creek system by Burton and Odum (1945) and our records of these date from 1951. Apparently the only fish collection made in this system before Burton's was by Cope in 1867 (Cope, 1868). None of Cope's material has been labeled as from Craig Creek, and none of it represents any of the four species. Very few specimens from Burton's work are at the University of Michigan Museum of Zoology, probably since only the "necessary specimens [were] preserved" (Burton and Odum, 1945:183). Recent collecting in the Craig system above Newcastle yielded ten native species, in addition to those discussed above, that are relatively common but were not listed by Burton and Odum. Other species taken at only a few stations by Burton were found to be comparatively widespread. The lack of early records of the four species is probably related to insufficient collecting and loss of collections.

There is evidence that the four species were not introduced by man. Since *N. gilberti* is generally an uncommon species in the Roanoke there is slight chance of it being captured and introduced by fishermen. The chances are also slight that the common but relatively delicate darter would survive an extended period in a bait bucket. Few bait collectors really get into riffles, which are the preferred habitat of these two species. The hardy *N. raneyi* are more easily taken by bait collectors, but this species is generally uncommon in the upper Roanoke. The establishment of the Craig Creek and atypical populations of *N. raneyi* downstream almost certainly predates any recent introduction. The five spillway-type dams across the James River between Jennings Creek and Pedlar River have probably been in effect since the latter part of the last century. Their height, from 8-25 feet, would impede movement.

A final and important point is to reexamine the historical and problematical status of *M. cervinum* in the James drainage in light of recent data. The probable absence of *M. cervinum* in the James drainage and its early confusion with *Moxostoma (Thoburnia) rhothoecum*, widely distributed in the James, was discussed by Hubbs (1930:43-44), Raney and Lachner (1946b:218), and Raney (1950:159). Soon afterward, Robins and Raney (1956:31) report-

ed the capture of *M. cervinum* from Johns Creek at Newcastle and later it was found to range an appreciable distance downstream. The two suckers occur syntopically in the Craig Creek system. Cope (1868:236) described and gave the type locality of *M. cervinum* as the headwaters of the Roanoke and James Rivers, Virginia. From Cope's paper it is clear that he collected in the Craig Creek system and he mentioned no other upper James tributary. *M. rhothoecum* was not recognized by Cope. Robins and Raney (1956:25-26) found that Cope's James drainage specimens, designated by Fowler as cotypes of *M. cervinum*, were *M. rhothoecum*. It appears then, that Cope's color plate clearly depicting the diagnostic coloration of *M. cervinum*, was based on specimens from the Roanoke drainage where he also collected, and where this species is common. The possibility remains, though, that Cope saw *M. cervinum* from the Craig Creek system but, as was sometimes the case, the specimens were not saved or were subsequently lost.

It should be noted that most of the more downstream records of *Thoburnia rhothoeca* listed by Burton and Odum (1945:186-187, tables 4 and 5) probably were, in part or entirely, *M. cervinum* since this species replaces the former in larger streams and is the more abundant of the two in the Newcastle area today. Jordan (1889a:109), prior to the description of a *Thoburnia*, reported *M. cervinum* from Elk Creek, a short, direct tributary of the James River about eight river miles upstream from the mouth of Maury River, and from lower Buffalo Creek, apparently just upstream from the locality at which *M. cervinum* was recently taken. For several reasons, one being Jordan's color description of his specimens, Raney and Lachner (1946b:218) concluded that "they were largely *Thoburnia*" (*M. rhothoecum*). Hubbs (1930:43) found at the Museum of Comparative Zoology one of Jordan's specimens of "*cervinum*" from Buffalo Creek to be *M. rhothoecum* and we located three of the same among the old Indiana University collection now at the Museum of Zoology, University of Michigan and six at the National Museum of Natural History. It still appears, however, that characters of both suckers were included in Jordan's description and that at least some of his "older" specimens were *M. cervinum*. After leaving the James drainage, Jordan collected in the upper Roanoke where he may have

taken *M. cervinum* and then compounded the colors of at least two species of suckers under his account of *M. cervinum* from the James. It is strongly indicated that *M. cervinum* and the other three species were in the James drainage long before fishermen with minnow buckets became common and transportation easy.

N. leptocephalus: The origin of the leptocephalus group is not clear, but after differentiation of the more northern form, *N. l. leptocephalus*, considerable dispersal occurred that included entry into several drainages. Its further advance northward along the Atlantic slope and westward may have been through some of the same connections utilized by *N. raneyi*. *N. leptocephalus* typically inhabits smaller streams than the members of the micropogon group. It would thus be suspected, more than the latter group, to cross drainage divides with greater frequency through small headwater captures. The dispersal of *N. leptocephalus* raises the possibility that there may have been many undetected or geologically unconfirmed captures in the central Appalachians. Once *N. leptocephalus* entered a drainage, a wide distribution within the drainage would probably have taken longer than for a large stream inhabitant.

We have no data that indicate whether *N. leptocephalus* occupied the Neuse, Tar, Roanoke, and Chowan before *N. raneyi*. Its entry into the James probably predates that of *N. raneyi* because it is widespread in the James and it occurs farther northward. The bluehead chub may have entered the James drainage by captures along the broad front of adjacency of the Roanoke and Chowan to the James. The Greater Susquehanna River is invoked to account for the presence of *N. leptocephalus* in the York drainage.

The occurrence of *N. leptocephalus* within single stream systems of both the Rappahannock and Potomac drainages suggests it got into these by stream captures from the adjacent James drainage. There is no evidence for or against the possibility that these may be due to introductions. A third alternative, through the Greater Susquehanna, is quite unlikely, particularly in the Potomac case, since the streams where *N. leptocephalus* is known in the two drainages are headwaters, appreciable distances from the drainage mouths. Inspection of topographic maps of the upper Piedmont in the region of tribu-

taries of the Rapidan River, Rappahannock drainage, and those of the Rivanna River of the James, show that headwaters of these streams are opposed to each other although no definite elbow of capture is evident. Clear geological evidence is given by Thompson (1939:1350-1351) for a capture of the Potomac by a Rivanna River tributary in the Blue Ridge near the Albemarle-Augusta County line. If *N. leptocephalus* used this connection it would have entered South River of the Potomac at a point approximately midway between the two nearby Potomac streams in which it was taken.

Entry of *N. leptocephalus* into the New drainage was probably through one or more of the recent captures by the Roanoke. This species is known only from Virginia tributaries of the New. Three additional species, *Chrosomus oreas*, *Notropis albeolus*, and *Notropis cerasinus*, are also known in the New almost exclusively from the Virginia portion and may also be recent arrivals. The most upstream tributaries where these four species were taken are Fox and Wilson Creeks, Grayson County, which enter the New just downstream from the Virginia-North Carolina state line. Geological barriers to further dispersal up the New are not known to have existed in the past.

Downstream in Virginia near the Virginia-West Virginia line, *C. oreas* is known from Big Stony Creek, Giles County (Ross and Perkins, 1959:27). Ross and Perkins (1959:27) and C. R. Gilbert (1964: 139, map 3) gave records of *N. cerasinus* from Big Stony. The range of *N. albeolus* extends farthest downstream of the four species. C. R. Gilbert (1964: 156) reported a collection from the lower Greenbrier River and believed its presence there was due to very recent dispersal or introduction, as it was not collected earlier from this stream and in streams somewhat farther upriver in West Virginia and Virginia just across the state line. The Bluestone Dam, completed in 1949, on the New River one mile above the mouth of the Greenbrier, and its impounded waters extending up to the state line, obstructed recent dispersal. The presence of *N. albeolus* in the Greenbrier may be related to earlier dispersal or introduction.

Evolution of *Nocomis*

Our interpretation of the phylogeny of the species of *Nocomis* is based on morphology, coloration,

zoogeography, and life history. The most primitive *Nocomis* is probably the biguttatus group (Lachner and Jenkins, 1967). The tubercles in the species of this group are rather evenly spaced dorsally over the head. They are absent on the snout. The tubercles are small to moderate in size (but large compared to almost all American cyprinids). The general pattern appears to be the basic one that has become modified in various manners within the micropogon and leptocephalus groups. Generally, the cyprinids with unspecialized breeding habits tend to have small tubercles distributed over the head in no outstanding pattern, although some differences in the patterns usually exist among the species. Development of particular tubercle patterns and larger tubercle size correlate in many of the North American cyprinids known to have specialized reproductive behaviors, such as nest building, special mode of spawning and highly developed territorialities. Examples of these specialized forms, in addition to *Nocomis*, include *Camptostoma*, *Semotilus*, *Pimephales*, and certain *Notropis*. The two related, nest-building species of *Exoglossum* are notable exceptions.

The tubercles are slightly to considerably larger in all members of the micropogon and leptocephalus groups compared with those of the biguttatus group. A probable specialization of tubercle distribution, shown only by the micropogon group, is their development on the anterior snout and lachrymal areas. A trend toward this condition is actually seen in the biguttatus group since the dorsal tubercles are developed slightly anterior to the anterior internasal line and, in adults, there are 1-3 tubercles located in the subnasal area but not over the lachrymal bone.

Large body size would be of selective advantage for nest construction and defense. *N. biguttatus* is, over its range, the smallest species and it may follow that the larger size of all of the other species is the derived condition.

Another important phylogenetic character is the pharyngeal dentition. The general trend in North American cyprinids is probably toward loss of teeth in the major and minor rows and a subsequent loss of the minor row. The dentition of *N. biguttatus* and the Redspot chub, an undescribed species (part 3) in the Arkansas and Red River drainages, is almost always 1,4-4,1, sometimes 1,4-4,0; loss of the minor tooth row would result in the dental formula

of an early stock of the micropogon and leptocephalus groups. *N. effusus*, considered an advanced form in the biguttatus group (Lachner and Jenkins, 1967) also lost the minor tooth row.

Linear (rowed) arrangement of head tubercles does not appear to be a primitive condition in *Nocomis*. The head tubercles in the biguttatus group do not align in definite rows when the adult complement is approached or fully developed. Occasionally several tubercles form a longitudinal line over a portion of the head but this appears to be the result of chance. We do not know how Branson (1962:536) construed that most head tubercles occur in rows on the nuptial male of *N. biguttatus*. The pattern of early tubercle development in juveniles of the biguttatus group also does not indicate a rowed condition since the first several tubercle spots that appear in the many juveniles examined are widely scattered. Only occasionally in small juveniles of *N. platyrhynchus* and *N. raneyi* do some of the tubercle spots tend to align into longitudinal rows through the internasal and anterior interorbital areas; in such cases several randomly located tubercle spots are also present. With growth in all of these species, rows are not evident.

In apparently advanced species of *Nocomis* in which a moderate to low number of tubercles occur, there is a trend for individual tubercles to develop consistently in specific locations and, in some cases, they appear to be arranged linearly. In *N. micropogon* the tubercles in the anterior middorsal region often develop in four rows, two curving posterolaterad on each side from the anterior internasal area to the anterior edge of the orbits. This trend is most evident in the Tennessee drainage population of *N. micropogon* which averages the lowest total tubercle numbers within the species. The first tubercle spots that develop in juveniles of this species are included in the internasal rows.

A similar situation but more extreme than in *N. micropogon* occurs in the leptocephalus group. These forms have the largest tubercles (the largest of North American cyprinids) and the lowest number in *Nocomis*, and the tubercles generally develop more constantly in specific areas of the head than in *N. micropogon*. This is particularly shown by the southern form, *N. leptocephalus bellicus*, adult males of which almost always have only six tubercles and which develop in nearly the same places on all

specimens. The posterior internasal and anterior interorbital tubercles of the leptocephalus group are those that particularly develop in the same location of the head. A row typically curves just above the dorsal half of the orbits.

In the micropogon and leptocephalus groups the tubercles are always largest where tubercle spots first develop, in the internasal and interorbital areas. The tubercles in the biguttatus group are largest in the occipital areas; spots first develop in the internasal and interorbital areas, but before many appear in these areas they also develop in the occipital region.

Developmental patterns parallel to those in *Nocomis* occur in other species of North American cyprinids. The large majority of those species with high tubercle numbers on the head dorsally do not have rowed tubercles. When rows are present, they often occur over rather narrow bones and other supporting structures. An example is the distinct tubercle rows over the mandible in species of the subgenus *Pteronotropis*, genus *Notropis* (Bailey and Suttkus, 1952, pl. 2). The rows over the lachrymal bone in all species of the micropogon group is another example. When present on the fins, tubercles occur on the rays. Tubercles often tend to have a linear development near edges or folds of skin such as around the orbits and above the lips. When present on scales, the tubercles are usually at the free, posterior margin, forming a row. All species of *Pimephales* have a low number of tubercles and they are large in size, comparable to the leptocephalus group. Also in *Pimephales*, the tubercles develop in rather definite locations and form rows (Hubbs and Black, 1947:13-17). From developmental patterns of tubercles, other morphological aspects and zoogeography, Gibbs (1957:187, 189-192) postulated that the occurrence in rows of head tubercles is primitive within the subgenus *Cyprinella*, genus *Notropis*, and that the scattered tubercle condition is derived. Results of a detailed study of tubercle development (Koehn, 1965) in one of the presumably derived species of *Cyprinella* indicate that its early tubercle pattern is similar to the adult pattern of primitive species. Examination of many nuptial males of *Cyprinella* indicates that dorsal head tubercles tend to be more linearly arranged in the species with fewer and larger tubercles, which may also be the primitive condition within *Cyprinella*.

Synthesis of these comments on tubercle development is difficult since there appear to be several factors involved. Limited area for basal attachment would be a simple reason for linear development of tubercles over narrow supporting structures. Tubercle rows about the orbit and other structures could be a protective mechanism during agonistic behavior and nest-building activities. Tubercles developed along the edge of scales would come into more use than if they were more basal, near the imbricated scale base. Genetic fixity for confinement of few tubercles to discrete areas may be associated with specific behavior patterns. Tubercles that develop in rows, such as on the snout of *Pimephales* and the dorsal part of the head of species of *Cyprinella*, may serve more efficiently in special breeding behaviors.

The biguttatus group is most closely related to the micropogon group; neither is particularly closely related to the leptocephalus group. The nuptial male coloration, consisting in the biguttatus and micropogon groups of pink and reddish over the lower head and body, is quite unlike the blues and oranges in the leptocephalus group. The whorled intestine of the latter group, readily derived from the simple S-shape intestine of the two other groups, is also unique within *Nocomis*.

The nuptial crest appears to be a functional and adaptive character. It is prominently developed in the micropogon and leptocephalus groups. Some nuptial male specimens of *N. effusus* have a very slight head swelling which has not been observed in *N. biguttatus*; this may be a lesser development of the crest. Possibly the crest arose independently within the micropogon and leptocephalus groups. The fact that the crest is alike in development and general form in these two groups, and that it is unknown in other cyprinid fishes, suggests common ancestry among the two groups and that it was not derived independently.

Crest development, lateral curving of the tips of tubercles and loss of the minor tooth rows relate early stocks of the micropogon and leptocephalus groups. The leptocephalus group would be regarded as the most divergent from a common biguttatus stock.

The crest is perhaps an adaptation for lessening the effects of head impact from certain agonistic behavior. The moderate enlargement of tubercles in

two of the three species of the micropogon group and the considerable enlargement of tubercles in the leptocephalus group may correlate with the development of large crests in these groups. A large, hard (cornified) tubercle pressing into the cephalic region upon impact would give more severe shock than smaller tubercles. *N. l. bellicus* and an undescribed subspecies (part 2) are apparently derived from *N. l. leptocephalus* by loss of the occipital and medial interorbital tubercles and show a trend toward reduction of the crest posteriorly. However, *N. micropogon* lacks tubercles in the interorbital and occipital areas where the crest is often well formed.

The direction in which the tips of tubercles point is different in the groups. The head tubercles of most cyprinid species have erect or antrorse tips. The tubercles or their tips in *N. biguttatus* are mainly antrorse, but a few are more or less erect. The tips of most tubercles in the other two groups of *Nocomis* are erect or curved laterally.

The development of a hiatus (absence of tubercles) between the anterior snout and internasal tubercles occurs in the micropogon group. The absence of tubercles may have a functional basis, for the development of tubercles, especially large ones, would inhibit the protractility of the upper jaw. A complete absence, or but a few tubercles, occurs between the anterior snout and internasal areas in *N. micropogon*; tubercles are usually present in this area in *N. platyrhynchus* and are always present in *N. raneyi*. The absence of tubercles at the hiatus is correlated with tubercle size in these three species, *N. micropogon* developing the largest tubercles and *N. raneyi* the smallest. Within the subgenus *Cyprinella*, 14 of 16 included species also develop a hiatus in tubercle distribution (Gibbs, 1957:187), in the same region as in the micropogon group. The hiatus is absent in two species that have small tubercles and, for additional reasons, are regarded as a distinct species group within *Cyprinella* (Gibbs, 1961). The hiatus occurs over the areas where the vertex of an angle is produced when the mouth is opened and the upper jaw is protracted, or the skin in this area during protraction is stretched to a greater extent than in adjacent areas. Some specimens have wrinkles or folds of skin in the hiatus area, apparently the result of upper jaw movement. The bases of large *Nocomis* tubercles developed in the hiatus area would tend to impede jaw action or be eroded

off from such action. This is particularly apt to occur during nest building in *Nocomis*, as the males very often open the mouth to about its full extent when picking up large gravel. Small-based tubercles in the hiatus area probably do not produce such an effect and/or may not be as readily shed from the skin stretching beneath them.

A red postocular spot occurs only in the biguttatus group. It probably arose in the biguttatus group after the origin of the other groups. The postocular area in all species of *Nocomis* is usually lighter in shade than the immediate surrounding area. Genetic fixity for retention of a red blush color by the nuptial male may have occurred since this could be an effective species-recognition mark. Its variable development among the species of the biguttatus group is discussed by Lachner and Jenkins (1967).

SUMMARY.—The basic stock of the micropogon group, after some differentiation from its precursor (biguttatus line), may be characterized as having tubercles completely distributed over the head and lachrymal bone; tubercles small to moderate in size with many tips directed laterad; rosy nuptial body color; nuptial crest present, perhaps small, in breeding males; pharyngeal tooth arch structurally moderate to heavy; teeth 4–4; body size moderate to large. The form presently closest to this prototype is *N. platyrhynchus*. The head tubercles in *N. platyrhynchus* are widely distributed, often posterior to the midoccipital or posterior occipital lines as in the biguttatus group. They are more widespread than in *N. raneyi*, and tubercles never occur in the occipital, and rarely in the interorbital areas in *N. micropogon*. Adults of *N. biguttatus* generally have a fairly sharp downward break of the contour of the nape at the occiput, down to a somewhat flat head dorsum. Such contours are best developed in *N. platyrhynchus*, less often and not as well developed in *N. micropogon* and *N. raneyi*.

The area of origin of *N. platyrhynchus* was probably the upper Teays River system. Its prototype, derived from a stock of the biguttatus group, moved into the lower and/or middle Teays. Kanawha Falls on the New-Kanawha River provided opportunity for differentiation of *N. platyrhynchus* stock in the New drainage above. Geographically, the upper Teays is central to the present ranges of the two species derived from *N. platyrhynchus* stock, *N. micropogon* and *N. raneyi*.

Stream capture between the Roanoke and New River drainages permitted transfer of a *N. platyrhynchus* stock into the Roanoke drainage and could have led to the origin of *N. raneyi* in the Roanoke through subsequent isolation and differentiation.

N. raneyi is the most divergent species in the micropogon group and relatively unique within *Nocomis* in some of its diagnostic characters. The head and its parts have small features, particularly the mouth. The body is moderately deep and compressed in adult males. Juveniles have the most streamlined body form in *Nocomis*. The caudal fin area is large, the lobes varying in larger specimens from subequal to considerably unequal, the upper lobe always longer. This unequal condition of the caudal fin lobes was thought by Uyeno and Miller (1965:38) to be unique among North American cyprinids to *Pogonichthys*, a monotypic western genus. *N. raneyi* is the largest species in the genus and in this respect rivals the fallfish, *Semotilus corporalis*, the largest cyprinid in eastern United States.

The tubercle distribution in *N. raneyi* approaches the primitive condition and it is not greatly different from *N. platyrhynchus* (or the basic group stock). The most posterior tubercles in adult males generally occur in the P10 and A0C areas. The small tubercles are rather closely spaced dorsally over most of the head, extremely so on the snout and internasal areas. Two other probable primitive conditions in *Nocomis* are seen in characters of *N. raneyi*. The pharyngeal arches are heavy and their anterior edentulous processes are short, as in the biguttatus group. The scales are relatively small in size, though somewhat larger than in *N. biguttatus*.

N. micropogon probably arose from *N. platyrhynchus* or a stock common to both in a portion of the middle Teays system, below Kanawha Falls, or in a drainage that was involved in stream capture with the upper Teays. *N. micropogon* has the most reduced tuberculation of the micropogon group, having the least number and most restricted distribution, but has the largest tubercles.

N. micropogon and *N. platyrhynchus* differ from *N. raneyi* (as reviewed above) and, in some characters, from all other *Nocomis* in the development of the tubercle pattern, tubercle numbers, broad head, slender pharyngeal arch, dark lateral body stripe,

size of intestinal loop, and nature of caudal fin. In the two characters which best separate *N. micropogon* from *N. platyrhynchus*, the latter is more similar to but still different from *N. raneyi*. One is the occurrence of tubercles in the interorbital and occipital areas. This is probably the primitive condition within the group, best retained in *N. platyrhynchus*. The small scales in the circumferential series of *N. platyrhynchus* may indicate inheritance from the primitive micropogon group stock, or adaptation to ecological conditions in the somewhat higher altitudes of the New River drainage as compared to most or all other regions inhabited by group members.

Several conditions indicate that introgressive hybridization may have occurred in the past between *N. micropogon* and *N. platyrhynchus*. The overall similarity of these species is part of the evidence. Tuberculation in *N. platyrhynchus* is extreme for the micropogon group in their posterior distribution, since these sometimes occur in the POC area (probably a primitive condition); however, it is also the most variable species in this respect. A good proportion of large juveniles and adults have tubercles only as far posterior as the A10 and M10 lines. In addition, all specimens with tubercles developed into the more posterior head areas have them widely scattered, much more so than in *N. raneyi*. Thus, although in some specimens tubercles occur in the occipital area, the total tubercle number is not increased (Table 2). The expression of other characters in *N. platyrhynchus* may also be due to hybridization with *N. micropogon*. The similarity of populations of *N. micropogon* in the Monongahela and Potomac River drainages, described above, support a hybridization hypothesis. From the Monongahela-Potomac populations we obtain the highest tubercle counts. This is effected by an extreme crowding of internasal tubercles and increased posterior distribution. Stream capture apparently has occurred between the New and Monongahela and between the Monongahela and the Potomac drainages (see Dispersal, p. 66).

An interesting aspect of hybridization is the relatively common occurrence of the hybrid combination *N. leptocephalus* × *N. micropogon* in the James River drainage where these species are sympatric over a great area of the river system and are often captured together. Eighty-seven specimens have been

examined of this hybrid combination. The hybrid specimens have been taken in many tributaries and their occurrence does not reflect any particular geographical area. The James River drainage is the only one in which these two species are known to occur together abundantly. *N. micropogon's* close relative in the New River system, *N. platyrhynchus*, is sympatric also with *N. leptocephalus* over a large area of the system; however, we have found only five specimens of *N. leptocephalus* × *N. platyrhynchus*. The relatively uncommon production of hybrids may be associated with different specific reproductive ecologies, or it may be related to genetic incompatibility. We know that *N. leptocephalus* prefers smaller streams and occupies the swifter waters (sometimes riffles) of these streams for its nest sites. *N. platyrhynchus* prefers larger streams and nests in the deeper pool areas, out of the riffles. *N. micropogon* and *N. platyrhynchus* are not known to be sympatric in any portion of their range and thus we cannot evaluate their genetic compatibility. We also have the following interspecific hybrid combinations of *Nocomis*: *N. micropogon* × *N. raneyi*, 2 specimens; *N. leptocephalus* × *N. raneyi*, 2 specimens; *N. biguttatus* × *N. micropogon*, 1 specimen. Incompatibility between the latter two species is suggested for they are sympathetic over most of northeastern United States, they have been collected together abundantly (*N. micropogon* and *N. raneyi* rarely), in many intermediate streams they occur together commonly and in approximately equal numbers, both species build nests and have similar spawning habits, both forms have spawning periods that overlap, and both forms hybridize fairly commonly with members of other cyprinid genera. We have placed these species in separate groups on the basis of morphological characters, and we have done likewise with the parental stocks of the common hybrid *N. leptocephalus* × *N. micropogon*. Intergeneric hybrids involving *Nocomis* and other cyprinids most frequently involve *N. biguttatus*, *N. micropogon*, and *N. leptocephalus*. This hybridization may be most facilitated by the great geographical distributions and abundance of these species and in their choice of wider reproductive ecological sites.

The unknown precursor of *Nocomis* was probably not an elaborate nest builder and probably had fewer sexually dimorphic features. The trend for selection to act more on sexually dimorphic charac-

ters is characteristic of *Nocomis*, probably related to the functional aspects of nest construction, nest guarding and territorial maintenance by the male, and the need, particularly by the females, to recognize the males. We thus find in the evolution of the chubs, elaboration or adaptive reduction of important diagnostic characters as the extent of tuberculation, development of nuptial crests and development of particular reproductive colorations among the three recognized groups and among the species or forms within the groups. The immediate precursor of *N. biguttatus* probably was highly tuberculate. The dorsal head tuberculation is well developed and similar in the three living species of the biguttatus group. Evolution in the group involved the tuberculation of the lateral body scales, degree of squamation, reduction in dentition and, to a lesser degree, the development of the postocular spot.

The primitive stock of the micropogon group, best exemplified by *N. platyrhynchus*, shows relationships with biguttatus stock in the widely distributed, cephalic tuberculation, smaller tubercles, finer squamation, and stouter pharyngeal arch. Evolution within the micropogon group involved, mainly: the reduction in tubercle numbers; reduction in cephalic tubercle distribution; increase in tubercle size; crest development; and in the differentiation of the pharyngeal arch, size of scales, special features of the head (as mouth size) and the caudal fin. The leptocephalus group shows a greater reduction in tubercle numbers compared with the micropogon group, a reduction in cephalic tubercle distribution, great increase in tubercle size, specific reproductive coloration, stouter body, and coarser scales. Evolution within the forms of the leptocephalus group also involved further reduction of cephalic tubercle numbers and distribution, and in the differentiation of special reproductive color patterns.

Summary

The chub genus *Nocomis* Girard of North America has been characterized and relationships among three species groups in *Nocomis* were discussed. Two new species were described from the central Appalachian region, both in the micropogon species group. Characters separating *Nocomis* from other barbeled cyprinids are that the nuptial males have

large breeding tubercles on the head that show a phylogeny among the species in their number, distribution, and size; have expansive crests or swellings on the head in two species groups that develop coincidentally with the spawning period; develop elaborate breeding coloration; construct large mound-nests of gravel which they transport in their mouths. The genus has large scales, the body circumferential scales are fewer than 37; the pharyngeal teeth number 1,4-4,1 to 3-3; the scale radii are present only in the posterior field and the total number of radii in the adults ranges from 23 to 54; the total number of vertebrae ranges from 38 to 43; and a single, terminal maxillary barbel.

The three species groups were defined and their characters summarized, namely, the biguttatus group with three species, the micropogon group with three species, and the leptocephalus group with three subspecies. The central Appalachian region is inhabited by four species, *N. micropogon* (river chub), *N. platyrhynchus*, new species (bigmouth chub), and *N. raneyi*, new species (bull chub), of the micropogon group, all of which are sympatric with *N. leptocephalus* (bluehead chub) in one or more river drainages. A discussion of the nomenclatural history of the genus and nominal species was given and important diagnostic characters useful in differentiating among the specific and several infraspecific populations were discussed, evaluated, and summarized. The critical specific and subspecific characters, such as cephalic tuberculation involving the distribution, number, size and developmental patterns of tubercles, cephalic crests or swellings and nuptial body coloration are sexually dimorphic, developing elaborately in the males. Many morphometric characters, as well as tubercle numbers and distribution, show an allometric relationship with body size. An account of each species has included a synonymy, diagnosis, description and comparison of meristic and morphometric characters, coloration in life and in preservation, populational differentiation, reproduction, growth and size attained, materials studied and geographic distribution. The species are illustrated, special body features are drawn, distributions are plotted, and important character data are shown in text figures.

N. micropogon and *N. leptocephalus* are widely distributed, the former occurring over most of north-eastern United States and the latter is found chiefly

on the Atlantic and Gulf slopes. In the study area, *N. leptocephalus* is found east of the Atlantic drainage divide north to the Potomac River and west of the divide in the upper New River (New-Kanawha River system). *N. micropogon* occurs east of the Appalachian divide from the James drainage northward and throughout the western slope including the Kanawha River system (below the Falls). Both of these species are common and are widely distributed in the James River drainage. *N. raneyi* is an Atlantic slope form, occurring in the James, Chowan, Roanoke, Tar and Neuse drainages, where it is found commonly and is widely sympatric with *N. leptocephalus*. These two species and *N. micropogon* occur together in limited areas of the James drainage. *N. platyrhynchus* is found throughout the New River system, where part of its range overlaps that of *N. leptocephalus*.

The ecological requirements of the chubs were reviewed and species preferences discussed. The primary ecological distinction among the species is stream size. Regional ecology was reviewed in respect to occurrence and abundance of the species. Generally, the species of *Nocomis* prefer clear, moderate to warm water streams of intermediate gradients. They are chiefly carnivorous, common over stream beds of gravel, rubble, and boulders. Well-established populations of three species in typical Piedmont streams indicate an adaptiveness to this shifting, sandy habitat. All species of chubs are rare below the Fall Line in the upper Coastal Plain province.

Associations, interrelationships and frequency of hybridization were compared among the four species. The three species of the micropogon group were regarded as ecological homologues. *N. leptocephalus* almost always coexists with *N. raneyi* in moderate-sized streams, where they occur sympatrically, and it occurs less frequently with *N. micropogon* and *N. platyrhynchus*. Differences are observed among the species of the micropogon group in their frequency of hybridization with *N. leptocephalus*. Hybridization is somewhat inversely proportional to the frequency of syntopic occurrence. Only two natural hybrids *N. raneyi* × *N. leptocephalus* were found, whereas *N. micropogon* × *N. leptocephalus* hybrids are comparatively common (87 specimens known). A population of *N. raneyi* in a limited area of the James River is considered atypical. The

meristic and morphometrical data of this atypical population were compared with typical *N. raneyi* and *N. micropogon* from the James drainage. Introgressive hybridization may have occurred between *N. micropogon* and *N. platyrhynchus* because it best explains the similarity of populations of the former in the Monongahela and Potomac River drainages with the latter species in the New River system.

The biological and geological evidence providing an explanation of the dispersal of the chubs and other species of fishes in various interdrainage exchanges in the central Appalachian region was comprehensively reviewed. Possible routes of entry into the several drainages were proposed. Present, detailed distributional patterns of the chubs and other species were related with geologic events, and present and past ecological conditions, in an effort to understand the conditions, barriers, and routes affecting dispersal. Three kinds of geological events that operated in the dispersal of chubs are considered: stream capture, eustatic changes of the Atlantic Coastal Plain, and Pleistocene drainage modifications.

The interpretation of evolution in *Nocomis* is based on morphology, coloration, zoogeography, and life history. The unknown precursor of *Nocomis* was probably not an elaborate nest builder and probably had fewer sexually dimorphic features. The trend for selection to act more on sexually dimorphic features is characteristic of *Nocomis*, probably related mainly to the functional aspects of nest construction, nest guarding and territorial maintenance by the male. *Nocomis* shows an elaboration or adaptive reduction of important diagnostic characters as the extent of tuberculation, development of nuptial crests, and development of particular reproductive colorations. The most primitive *Nocomis* are probably of the biguttatus group, based on, among other characters, the general pattern, small size and relatively large numbers of cephalic tubercles. This general tubercle pattern appears to be the basic one that has become modified in various manners within the micropogon and leptocephalus groups. The primitive stock of the micropogon group, best exemplified by *N. platyrhynchus*, shows relationships with biguttatus stock in the widely distributed cephalic tuberculation, small tubercles, fine squamation, and stout pharyngeal arch. Evolution within the micropogon group involved, mainly: the reduction in

tubercle numbers; reduction in cephalic tubercle distribution; increase in tubercle size; development of the nuptial crest; and in the differentiation of the pharyngeal arch, size of scales, and certain head and body features. The leptocephalus group, the most advanced, shows a greater reduction in tubercle numbers compared with the micropogon group, a reduction in cephalic tubercle distribution, great increase in tubercle size, development of specific reproductive coloration, stouter body and coarser scales. The forms of the leptocephalus group evolved further in the greater reduction of cephalic tubercle numbers and distribution, and in the differentiation of special reproductive body colorations.

Literature Cited

- Agassiz, L.
1854. Notice of a Collection of Fishes from the Southern Bend of the Tennessee River, in the State of Alabama. *American Journal of Science and Arts*, 17:297-308 and 353-365.
- Bailey, R. M.
1945. [Review] Some Considerations on the Distribution of Fishes in Ontario, by I. Radforth, 1944. *Copeia*, 2:125-126.
1951. A Check List of the Fishes of Iowa with Keys for Identification. J. R. Harlow and E. B. Speaker, In *Iowa Fish and Fishing*, Pages 187-238. Des Moines, Iowa: Iowa State Conservation Commission.
- Bailey, R. M., and R. D. Suttkus
1952. *Notropis signipinnis*, a New Cyprinid Fish from Southeastern United States. *Occasional Papers Museum of Zoology, University of Michigan*, 542:1-15.
- Baird, S. F., and C. Girard
1853. Description of New Species of Fishes, Collected by Captains R. B. Marcy and G. B. McClellan, in Arkansas. *Proceedings of the Academy of Natural Science* (Philadelphia), 6:390-392.
- Barlow, G. W.
1961. Causes and Significance of Morphological Variation in Fishes. *Systematic Zoology*, 10 (3):105-117.
- Beadles, J. K.
1966. The Effect of Domestic and Oil Refinery Effluents on Meristic and Morphometric Characteristics of Three Cyprinid Fishes. Ph.D. Dissertation, Oklahoma State University, 85 pages.
- Braasch, M. E., and P. W. Smith
1967. The Life History of the Slough Darter, *Etheostoma gracile* (Pisces, Percidae). *Illinois Natural History Survey, Biological Notes*, number 58:1-12, 7 figures.
- Branson, B. A.
1962. Observations on the Breeding Tubercles of Some Ozarkian Minnows with Notes on the Barbels of *Hybopsis*. *Copeia*, (3):532-539.
- Breder, C. M. and R. B. Breder
1923. A List of Fishes, Amphibians and Reptiles Collected in Ashe County, North Carolina. *Zoologica*, 4(1):1-23.
- Burton, G. W. and E. P. Odum
1945. The Distribution of Stream Fish in the Vicinity of Mountain Lake, Virginia. *Ecology*, 26 (2):182-194.
- Campbell, M. R.
1896. Drainage Modifications and Their Interpretations. *Journal of Geology*, 4:567-581, 657-678.
- Campbell, M. R. and W. C. Mendenhall
1896. Geologic Section Along the New and Kanawha Rivers in West Virginia. *17th Annual Report of the U. S. Geological Survey*, part 2:479-511.
- Clark, W. B. and B. L. Miller
1912. The Physiography and Geology of the Coastal Plain Province of Virginia. *Virginia Geological Survey Bulletin*, 4:1-274.
- Clark, W. B., B. L. Miller, L. W. Stephenson, B. L. Johnson and H. N. Parker
1912. The Coastal Plain of North Carolina. *North Carolina Geological and Economical Survey*, 3:1-552.
- Cockerell, T. D. A.
1913. Observations on Fish Scales. *Bulletin of the Bureau of Fisheries*, 32:117-174.
- Cockerell, T. D. A. and E. M. Allison
1909. The Scales of Some American Cyprinidae. *Proceedings of the Biological Society of Washington*, 22:157-163.
- Cockerell, T. D. A. and O. Callaway
1909. Observations on the Fishes of the Genus *Notropis*. *Proceedings of the Biological Society of Washington*, 22:189-196.
- Cope, E. D.
1864. Partial Catalogue of the Cold-Blooded Vertebrata of Michigan, Part I. *Proceedings of the Academy of Natural Science* (Philadelphia), 16:276-285.
1868. On the Distribution of Fresh-Water Fishes in the Allegheny Region of Southwestern Virginia. *Journal of the Academy of Natural Science* (Philadelphia), series 2, 6 (5):207-247.
1869. Synopsis of the Cyprinidae of Pennsylvania. *Transactions of the American Philosophical Society*. 13 (new series, part 3):351-410, plates 10-13.
1870. Partial Synopsis of the Fishes of the Fresh Waters of North Carolina. *Proceedings of the American Philosophical Society*, 1870:448-495.
- Cross, F. B.
1953. Nomenclature in the Pimephalinae, with Special Reference to the Bullhead Minnow, *Pimephales vigilax perspicuus* (Girard). *Transactions of the Kansas Academy of Science*, 56 (1):92-96.
- de Sylva, D. P., F. A. Kalber, and C. N. Shuster
1962. Fishes and Ecological Conditions in the Shore Zone of the Delaware River Estuary, with Notes on Other Species Collected in Deeper Water. *University of Delaware Marine Laboratory, Information Service*, 5:1-164.
- Dietrich, R. V.
1959. Geology and Mineral Resources of Floyd County of the Blue Ridge Upland, Southwestern Virginia. *Bulletin of the Virginia Polytechnical Institute Engi-*

- neering Experimental Station, series 134, 52 (12):1-160, 48 plates.
- Dyson, J. L.
1962. *The World of Ice*. 292 pages. New York: Alfred A. Knopf.
- Fairchild, H. L.
1934. Seneca Valley Physiographic and Glacial History. *Bulletin of the Geological Society of America*, 45: 1073-1109, plate 131, 9 figures.
- Fenneman, N. M.
1938. *Physiography of Eastern United States*. 714 pages. New York: McGraw-Hill.
- Flemer, D. A. and W. S. Woolcott
1966. Food Habits and Distribution of the Fishes of Tuckahoe Creek, Virginia, with Special Emphasis on the Bluegill, *Lepomis m. macrochirus* Rafinesque. *Chesapeake Science*, 7(2):75-89.
- Flint, R. F.
1957. *Glacial and Pleistocene Geology*. 553 pages. New York: John Wiley and Sons.
- Fowler, H. W.
1909. A Synopsis of the Cyprinidae of Pennsylvania. *Proceedings of the Academy of Natural Sciences, Philadelphia*, 60(1908):517-553, plate 27.
1945. A Study of the Fishes of the Southern Piedmont and Coastal Plain. *Monographs of the Academy of Natural Sciences, Philadelphia*, 7:1-408, figures 1-313.
- Fridley, H. M.
1933. Drainage Diversions of the Cheat River. *Proceedings of the West Virginia Academy of Science* 6:85-88.
- Gerking, S. D.
1945. The Distribution of the Fishes of Indiana. *Investigations Indiana Lakes and Streams, Indiana Department of Conservation*, 3(1):1-137, maps 1-113.
- Gibbs, R. H., Jr.
1957. 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.
1961. Cyprinid Fishes of the Subgenus *Cyprinella* of *Notropis*, IV: The *Notropis galacturus-camurus* Complex. *The American Midland Naturalist*, 66 (2):337-354.
1963. Cyprinid Fishes of the Subgenus *Cyprinella* of *Notropis*: The *Notropis whipplei-analostanus-chloristrus* complex. *Copeia*, (3):511-528.
- Gilbert, C. H.
1884. A List of Fishes Collected in the East Fork of White River, Indiana, with Descriptions of Two New Species. *Proceedings of the United States National Museum*, 7:199-205.
- Gilbert, C. R.
1961. *Notropis semperasper*, a New Cyprinid Fish From the Upper James River System, Virginia. *Copeia*, 4:450-456.
1964. The American Cyprinid Fishes of the Subgenus *Luxilus* (Genus *Notropis*). *Bulletin of the Florida State Museum*, 8 (2):95-194.
- Giles, A. W.
1918. The Country About Camp Lee, Virginia. *Virginia Geological Survey Bulletin*, 16:1-40.
- Girard, C.
1856. Researches Upon the Cyprinoid Fishes Inhabiting the Fresh Waters of the United States of America, West of the Mississippi Valley, from Specimens in the Museum of the Smithsonian Institution. *Proceedings of the Academy of Natural Sciences, Philadelphia*, 8:165-213.
1858. Fishes, Part 4. In *General Report upon the Zoology of the Several Pacific Railroad Routes*. United States Senate Miscellaneous Documents, Number 78, 33rd Congress, 2nd Session, 400 pages.
- Goldsborough, E. L. and H. W. Clark
1908. Fishes of West Virginia. *Bureau of Fisheries Bulletin*, (1907)27:29-39, 1 illustration.
- Greeley, J. R.
1927. Fishes of the Genesee Region with an Annotated List. In *A Biological Survey of the Genesee River System. 16th Annual Report of the New York State Conservation Department (1926)*, supplement, 47-66.
1928. Fishes of the Oswego Watershed. In *A Biological Survey of the Oswego River System. 17th Annual Report, New York State Conservation Department (1927)*, Supplement, 84-107.
1940. Fishes of the Watershed with Annotated List. In *A Biological Survey of the Lake Ontario Watershed. 29th Annual Report, New York State Conservation Department (1939)*, Supplement, 42-81.
- Gunther, A.
1868. Catalogue of the Physostomi, Containing the Families Heteropygii, Cyprinidae, Gonorrhynchidae, Hyodontidae, Osteoglossidae, Clupeidae, Chirocentridae, Alepocephalidae, Notopteridae, Halosauridae, in the Collection of the British Museum. *Catalogue of Fishes British Museum, Taylor and Francis, London*, 7:1-512.
- Hubbs, C. L.
1926. A Check-list of the Fishes of the Great Lakes and Tributary Waters, with Nomenclatorial Notes and Analytical Keys. *Miscellaneous Publications of the Museum of Zoology, University of Michigan*, 15:1-77.
1930. Materials for a Revision of the Catostomid Fishes of Eastern North America. *Miscellaneous Publications of the Museum of Zoology, University of Michigan*, 20:1-47.
- Hubbs, C. L. and J. D. Black
1947. Revision of *Ceratichthys*, a Genus of American Cyprinid Fishes. *Miscellaneous Publications of the Museum of Zoology, University of Michigan*, Number 66: 56 Pages.
- Hubbs, C. L. and K. F. Lagler
1958. Fishes of the Great Lakes Region. *Cranbrook Institute of Science Bulletin*, 26:1-213.
- Hubbs, C. L. and A. I. Ortenburger
1929. Further Notes on the Fishes of Oklahoma with Descriptions of New Species of Cyprinidae. *Publica-*

- tions of the University of Oklahoma Biological Survey, 1(2):17-43.
- Hubbs, C. L. and E. C. Raney
 1939. *Hadropterus oxyrhynchus*, a New Percid Fish from Virginia and West Virginia. *Occasional Papers of the Museum of Zoology, University of Michigan*, 396:1-9, 1 plate.
1944. Systematic Notes on North American Siluroid Fishes of the Genus *Schilbeodes*. *Occasional Papers of the Museum of Zoology, University of Michigan*, 487:1-36.
- Jackson, H. W. and C. Henderson
 1942. A Study of the Stream Pollution Problem in the Roanoke, Virginia, Metropolitan District, Part II: Macroscopic Invertebrate and Vertebrate Faunae, The Toxicity of Viscose Wastes to Fishes. *Virginia Polytechnic Institute Engineering Experimental Station Bulletin, series 51*, 35(10):91-120.
- Janssen, R. E.
 1953. The Teays River, Ancient Precursor of the East. *Science Monthly*, 77:306-314.
- Jenkins, R. E., E. A. Lachner, and F. J. Schwartz
 ms. Fishes of the Central Appalachian Drainages: Their Distribution and Dispersal. In A Distributional History of the Biota of the Southern Appalachians, Part III: Vertebrates. *Research Division Monograph, Virginia Polytechnic Institute* (Blacksburg).
- Jordan, D. S.
 1875. Synopsis of the Genera of Fishes to be Looked for in Indiana. *6th Annual Report Geological Survey Indiana*, 11-42.
1876. Concerning the Fishes of the Ichthyologia Ohiensis. *Buffalo Society of the Natural Science Bulletin*, 3:91-97.
- 1877a. On the Fishes of Northern Indiana. *Proceedings of the Academy of Natural Sciences, Philadelphia*, 29:42-82.
- 1877b. A partial Synopsis of the Fishes of Upper Georgia; with Supplementary Papers on Fishes of Tennessee, Kentucky, and Indiana. *Annales of the New York Lyceum of Natural History*, 11:307-377.
- 1877c. Contributions to North American Ichthyology . . . I: Review of Rafinesque's Memoirs on North American Fishes. *United States National Museum Bulletin*, 9:1-53.
- 1877d. Contributions to North American Ichthyology. 2A. Notes on Cottidae, Etheostomatidae, Percidae, Centrarchidae, Aphododeridae, Dorysomatidae, and Cyprinidae, with Revisions of the Genera and Descriptions of New and Little Known Species. *United States National Museum Bulletin*, 10:1-68.
- 1878a. *Manual of the Vertebrates of the Northern United States*. Edition 2. Chicago: Jansen, McClurg and Company.
- 1878b. A Catalogue of the Fishes of the Fresh Waters of North America. *United States Geological and Geographical Survey Territories Bulletin*, 4:407-442.
1879. On the Distribution of Fresh-Water Fishes of the United States. *Annales of the New York Academy Science* 1:92-120.
1880. *Manual of the Vertebrates of the Northern United States*. Edition 3. Chicago: Jansen, McClurg and Company.
1882. Report on the Fishes of Ohio. Section IV. *Report Geological Survey Ohio* 4(Zoology and Botany, Part I): 737-1002.
1884. *A Manual of the Vertebrates of the Northern United States*. Edition 4. Chicago: Jansen, McClurg and Company.
- 1885a. Identification of the Species of Cyprinidae and Catostomidae, Described by Dr. Charles Girard, in the Proceedings of the Academy of Natural Sciences of Philadelphia for 1856. *Proceedings of the United States National Museum*, 8(500):118-127.
- 1885b. A Catalogue of the Fishes Known to Inhabit The Waters of North America, North of the Tropic of Cancer, with Notes on the Species Discovered in 1883 and 1884. *Annual Report of the Commission of Fish and Fisheries*, 1885:787-973[1-185].
- 1889a. Report of Explorations Made During 1888 in the Allegheny Region of Virginia, North Carolina, and Tennessee, and in Western Indiana, with an Account of the Fishes Found in Each of the River Basins of Those Regions. *United States Fisheries Commission Bulletin*, 8(1888):97-173.
- 1889b. Six Species of North American Fresh-Water Fishes. Natural History Illustrations. 672. Prepared Under the Direction of Louis Agassiz and Spencer F. Baird, 1849. Smithsonian Institution, 12 pages, 6 plates.
1924. Concerning the Genus *Hybopsis* of Agassiz. *Copeia*, 126:51-52.
- Jordan, D. S. and H. E. Copeland
 1876. Check List of the Fishes of the Fresh Waters of North America. *Buffalo Society Natural Science Bulletin*, 3:133-164.
- Jordan, D. S. and B. W. Evermann
 1896. The Fishes of North and Middle America, Part I. *United States National Museum Bulletin*, 47:1-954.
- Jordan, D. S. and C. H. Gilbert
 1883. Synopsis of the Fishes of North America. *United States National Museum Bulletin*, 16:1-1018.
- Kinney, E. C.
 1964. Extent of Acid Mine Pollution in the United States Affecting Fish and Wildlife. *United States Department of Interior Fish and Wildlife Circular*, 191: 1-27.
- Kirtland, J. P.
 1840a. Descriptions of Fifteen New Species of Fishes. *American Journal of Science*, 38:392.
- 1840b. Descriptions of the Fishes of the Ohio River and its Tributaries. *Boston Journal Natural History*, 3:338-352.
- Koehn, R. K.
 1965. Development and Ecological Significance of Nuptial

- Tubercles of the Red Shiner, *Notropis lutrensis*. *Copeia* (4):462-467.
- Kuehne, R. A., and R. M. Bailey
1961. Stream Capture and Distribution of the Percid Fish *Etheostoma sagitta*, with Geologic and Taxonomic Notes. *Copeia*, (1):1-8.
- Lachner, E. A.
1946. Studies on the Biology of the Chubs (Genus *Nocomis*, Family Cyprinidae) of Northeastern United States. *Cornell University Thesis Abstracts*, 207-210.
1950. The Comparative Food Habits of the Cyprinid Fishes *Nocomis biguttatus* and *Nocomis micropogon* in Western New York. *Journal of the Washington Academy of Science*, 40(7):229-236.
1952. Studies of the Biology of the Cyprinid Fishes of the Chub Genus *Nocomis* of Northeastern United States. *American Midland Naturalist*, 48(2):433-466.
- 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* (3):557-580, figures 1-7.
- Larimore, R. W. and P. W. Smith
1963. The Fishes of Champaign County, Illinois, as Affected by 60 Years of Stream Changes. *Illinois Natural History Survey Bulletin*, 28(2):299-382.
- Leverett, F.
1902. Glacial Formations and Drainage Features of the Erie and Ohio Basins. *United States Geological Survey Monographs*, 41(1901):1-802.
- Lindsey, C. C.
1956. Distribution and Taxonomy of Fishes in the Mackenzie Drainage of British Columbia. *Journal of the Fisheries Research Board of Canada*, 13(6):759-789.
- Lougee, R. J.
1953. A Chronology of Postglacial Time in Eastern North America. *Science Monthly*, 76(5):259-276.
- Miller, R. J.
1963. Comparative Morphology of Three Cyprinid Fishes: *Notropis cornutus*, *Notropis rubellus*, and the Hybrid, *Notropis cornutus* × *Notropis rubellus*. *American Midland Naturalist*, 69(1):1-33.
1964. Behavior and Ecology of Some North American Cyprinid Fishes. *American Midland Naturalist*, 72(2):313-357.
- Moore, G. A.
1957. Fishes. In Blair, et al., *Vertebrates of the United States*. Pages 31-210. New York: McGraw-Hill Book Company.
- Mussey, O. D.
1948. Major Storage Reservoirs of Virginia. *Virginia Conservation Commission, Division of Water Resources and Power Bulletin*, 9:1-23.
- Radforth, I.
1944. Some Considerations on the Distribution of Fishes in Ontario. *Contributions of the Royal Ontario Museum of Zoology*, 25:1-116, 32 figures.
- Rafinesque, C. S.
1820. Fishes of the River Ohio. *The Western Review and Miscellaneous Magazine* (Lexington, Kentucky), (4):235-242; 2(5):299-307 (not numbered consecutively).
- Ramaswami, L. S. and A. D. Hasler
1955. Hormones and Secondary Sex Characters in the Minnow, *Hyborhynchus*. *Physiological Zoology*, 28(1):62-68.
- Ramsey, J. S. and W. S. Woolcott
ms. Zoogeography of the Fish Fauna of the Upper Savannah River System, North Carolina, South Carolina, and Georgia.
- Raney E. C.
1941. *Poecilichthys kanawhae*, a New Darter from the Upper New River System in North Carolina and Virginia. *Occasional Papers of the Museum of Zoology, University of Michigan*, 434:1-16.
1947. *Nocomis* Nests Used by Other Breeding Cyprinid Fishes in Virginia. *Zoologica*, 32(3):125-132, 1 plate.
1950. Freshwater Fishes, Pages 151-194. In *The James River Basin Past, Present and Future*. Richmond: Virginia Academy of Science.
- Raney, E. C. and E. A. Lachner
1946a. Age and Growth of the Rustyside sucker, *Thoburnia rhotroeca* (Thoburn). *American Midland Naturalist*, 36(3):675-681.
1946b. *Thoburnia hamiltoni*, a New Sucker From the Upper Roanoke River System in Virginia. *Copeia*, (4):218-226.
- Reger, D. B.
1926. Mercer, Monroe, and Summers Counties. *West Virginia Geological Survey*, 1-963.
- Reighard, J.
1943. The Breeding Habits of the River Chub, *Nocomis micropogon* (Cope). *Papers of the Michigan Academy of Science, Arts and Letters*, 28:397-423.
- Reno, H. W.
1967. Descriptions and Analyses of the Cephalic Lateral-line Systems of the Cyprinid Genus *Hybopsis*. *Thesis, Oklahoma State University, Stillwater, Oklahoma*: 1-121.
1969a. A Partial Nomenclatural Review of *Hybopsis* (Pisces: Cyprinidae). *Proceedings Oklahoma Academy Science* 48:65-71.
1969b. Cephalic Lateral-Line Systems of the Cyprinid Genus *Hybopsis*. *Copeia*, 4:736-773.
- Rivas, L. R.
1964. A Reinterpretation of the Concepts "Sympatric" and "Allopatric" with Proposal of the Additional Terms "Syntopic" and "Allotopic". *Systematic Zoology* 13 (1):42-43.
- Robins, C. R. and E. C. Raney
1956. Studies of the Catostomid Fishes of the Genus *Moxostoma*, With Descriptions of Two New Species. *Cornell University Agriculture Experimental Station, Memoir* 343, Ithaca, New York, 56 Pages.
- Ross, R. D.
1958a. Races of the Cyprinid Fish *Camptostoma anomalum pullum* (Agassiz) in Eastern United States. *Virginia*

- Agriculture Experimental Station, Technical Bulletin* 136:1-20.
- 1958b Some Taxonomic Problems of Shenandoah River Fishes. *Virginia Agriculture Experimental Station, Technical Bulletin* 137:1-10.
1959. Drainage Evolution and Distribution Problems of the Fishes of the New (Upper Kanawha) River System in Virginia; Part 4. Key to the Identification of Fishes. *Virginia Agriculture Experimental Station, Technical Bulletin* 146:1-27.
1969. Drainage Evolution and Fish Distribution Problems in the Southern Appalachians of Virginia. Pages 277-292, text-figures 1-5, in A Distributional History of the Biotā of the Southern Appalachians, Part I: Invertebrates. *Research Division Monograph 1, Virginia Polytechnic Institute* (Blacksburg).
- Ross, R. D. and J. E. Carico
1963. Records and Distribution Problems of Fishes of the North, Middle, and South Forks of the Holston River, Virginia. *Virginia Agriculture Experimental Station Technical Bulletin*, 161:1-23.
- Ross, R. D. and B. D. Perkins
1959. Drainage Evolution and Distribution Problems of the Fishes of the New (Upper Kanawha) River System in Virginia, Part 3: Records of Fishes of the New River. *Virginia Agriculture Experimental Station Technical Bulletin*, 145:1-35.
- Schwartz, F. J.
1965. The Distribution and Probable Postglacial Dispersal of the Percid Fish, *Etheostoma b. blennioides*, in the Potomac River. *Copeia*, (3):285-290, figures 1-2.
- Schwartz, F. J. and B. W. Dutcher
1962. Tooth Replacement and Food of the Cyprinid *Notropis cerasinus* from the Roanoke River, Virginia. *American Midland Naturalist*, 68(2):369-375.
- Shattuck, G. B.
1906. The Pliocene and Pleistocene Deposits of Maryland. Pages 23-137, plates 1-31. In *Maryland Geological Survey, Pliocene and Pleistocene*. Baltimore: Johns Hopkins Press.
- Shockley, C. H.
1949. Fish and Invertebrate Populations of an Indiana Bass Stream. *Investigations Indiana Lakes and Streams*, 3(5):247-270.
- Shoup, C. S.
1948. Limnological Observations on Some Streams of the New River Watershed in the Vicinity of Mountain Lake, Virginia. *Journal Elisha Mitchell Science Society*, 64(1):1-12.
- Smith, H. M.
1907. *The Fishes of North Carolina*. 453 pages. volume 2. Raleigh: North Carolina Geological and Economic Survey.
- Smith, H. M. and B. A. Bean
1899. List of Fishes Known to Inhabit the Waters of the District of Columbia and Vicinity. *United States Fisheries Commission Bulletin*, 1898:179-187.
- Smith, P. W.
1965. A Preliminary List of the Lampreys and Fishes of Illinois. *Illinois Natural History Survey, Biological Notes* number 54:1-12.
- Snedecor, G. W.
1956. *Statistical Methods*. 5th Edition. 534 Pages. Ames, Iowa: Iowa State College Press.
- Stose, G. W.
1922. Geography, Geology. In Stose, G. W. and H. D. Miser, Manganese Deposits of Western Virginia. *Virginia Geological Survey Bulletin*, 23:5-42, plates 2-8, Figure 1.
- Suttkus, R. D. and J. S. Ramsey
1967. *Percina aurolineata*, a New Percid Fish from the Alabama River System and a Discussion of Ecology, Distribution, and Hybridization of Darters of the Subgenus *Hadropterus*. *Tulane Studies in Zoology*, 13:129-145.
- Thompson, H. D.
1939. Drainage Evolution in the Southern Appalachians. *Geological Society of America Bulletin*, 50:1323-1356.
- Tight, W. G.
1903. Drainage Modification in Southeastern Ohio and Adjacent Parts of West Virginia and Kentucky. *United States Geological Survey Professional Paper*, 13 (series B, 26):1-111.
- Towles, H. and A. J. McClane
1965. Kentucky. In A. J. McClane, editor, *McClane's Standard Fishing Encyclopedia*. Pages 446-448. New York: Holt, Rinehart and Winston.
- Trautman, M. B.
1957. *The Fishes of Ohio*. 683 pages, 172 figures, 7 plates, 172 maps. Columbus: Ohio State University Press.
- Uyeno, T. and R. R. Miller
1965. Middle Pliocene Cyprinid Fishes From the Bidahochi Formation, Arizona. *Copeia*, 1:28-41.
- Watson, T. L. and J. H. Cline
1913. Drainage Changes in the Shenandoah Valley Region of Virginia. *University of Virginia Philosophical Society Science Bulletin, series 1*(17):349-368.
- Wiley, M. L.
1969. Comparative Morphology and Histology of Nuptial Tubercles in Fishes. *The George Washington University Thesis Abstract*, 2 pages.
- Wiley, M. L. and B. B. Collette
1970. Breeding Tubercles and Contact Organs in Fishes: Their Occurrence, Structure, and Significance. *American Museum Natural History Bulletin*, 143 (3):145-216, figures 1-13.
- Wright, F. J.
1931. The Older Appalachians of the South. *Dennison University Bulletin*, vol. 31, *Journal of Scientific Laboratories* 26:145-246, 38 plates.
1934. The Newer Appalachians of the South, Part 1: Between the Potomac and New Rivers. *Dennison University Bulletin*, vol. 34, *Journal of Scientific Laboratories* 29:1-105, 28 plates, 3 figures.
1936. The Newer Appalachians of the South, Part 2: South of the New River. *Dennison University Bulletin*, vol. 36, *Journal of Scientific Laboratories* 31:93-142, plates 27-58, figures 1-6.

Tables

TABLE 1.—The progressive development of tubercles posteriorly on the head with increase in body length in *Nocomis raneyi* taken from Atlantic drainages. (Data for sexes combined; see text for explanation of symbols.)

Standard length (in mm)	PIN	AIO	MIO	FIO	AOC	MOC	POC
60-69	1	1					
70-79	3	5	1				
80-89	6	4	2				
90-99	5	12	9				
100-109	3	17	18	5		1	
110-119	2	18	24	14	1	1	
120-129	-	13	21	17	-	-	
130-139	-	4	10	13	-	-	
140-149	1	1	5	16	2	-	
150-159		2	3	4	2	-	
160-169		1	4	7	1	2	
170-179		-	-	3	-	1	
180-189		-	1	2	1	-	1
190-199	1	1	5	-	-	-	
200-209				2	1		
210-219				2	-		
220-229				2	1		
230-239				-	1		
240-249				1	1		

TABLE 2.—The progressive development of tubercles posteriorly on the head with increase in body length in *Nocomis platyrhynchus* taken from the upper New drainage. (Data for sexes combined; see text for explanation of symbols.)

Standard length (in mm)	PIN	AIO	MIO	FIO	AOC	MOC	POC
50-59	1						
60-69	8	3					
70-79	9	9	1				
80-89	6	17	2	-	1		1
90-99	2	20	7	-	-		1
100-109	1	14	10	1	-	1	
110-119	-	7	6	5	2	-	1
120-129	1	3	7	5	1	1	3
130-139		1	4	4	2	1	-
140-149		1	3	3	2	1	-
150-159		1	4	3	1	-	-
160-169		1	1	6	-	2	5
170-179		-	4	2	1	1	3
180-189		1	1	2	1	1	1
190-199		1	2	2		1	
200-209			-	2			
210-219			1	1			
220-229			1				

TABLE 3.—The presence of tubercles or scars on mature male specimens, by size categories, of four species of *Nocomis*.

Species	Drainage	Standard length													
		100-109	110-119	120-129	130-139	140-149	150-159	160-169	170-179	180-189	190-199	200-209	210-219	220-229	230-239
<i>N. raneyi</i>									1	2	2	2	1	1	1
<i>N. platyrhynchus</i>					1	-	1	1	3	3	2	1	1		
<i>N. micropogon</i>	Susquehanna			1	2	8	8	7							
	Potomac				2	2	3	4	3	1	-	-	1		
	Rappahannock			1	1	-	1	1							
	James	1	-	-	-	-	-	1	-	4					
	Tennessee		2	2	1	4	7	6	4	3					
	Allegheny					3	4	2	1						
	Other northern drainages	1	-	3	3	7	3	2	-	1					
<i>N. leptocephalus</i>		1	7	14	14	18	11	4	1						

TABLE 4.—The relative size at which tubercle buds develop in several species of chubs (*Nocomis*) segregated by sex. (Specimens of *N. micropogon* from several northern, eastern, and central drainages.)

Species	Sex	Standard length													
		70-79	80-89	90-99	100-109	110-119	120-129	130-139	140-149	150-159	160-169	170-179	180-189	190-199	200-209
<i>N. raneyi</i>	♂									1	3	2	1	2	
<i>N. platyrhynchus</i>	♂		2	4	6	4	9	6	4	6	12	10	4	2	-
	♀			4	2	3	1	-	1						1
<i>N. micropogon</i>	♂	3	6	9	13	9	24	28	19	16	13	1	1		
	♀	1	4	4	5	12	8	4	2						

TABLE 7.—The number of head tubercles, sexes combined, in Nocomis micropogon from the Potomac drainage and the Cheat and Tygart rivers of the upper Monongahela drainage. (Data for the Monongahela specimens in parentheses.)

Standard length in mm	Number of tubercles on head										N ₁	N ₂	X̄
	0-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99			
210-219						1					1		64.5
200-209											-		-
190-199											-		-
180-189					1						1		54.5
170-179							1	1			2		79.5
160-169					2	2	3	-	1	8			69.5
150-159					1	3	5	5	1	15	1		65.8
140-149					1	2	2	3	2	10	2		67.8
130-139			1	7	5	4	1	1		19	5		54.5
120-129		1	-	8	3	3				15	4		49.2
110-119		1	7	3	1	1				13	-		39.9
100-109			2	10	8	1	1			22	7		39.5
90-99			(2)	(3)	(2)	(2)				9	7		34.5
80-89			(2)	(2)						-	4		-
70-79		1	(3)	(4)						1	7		4.5
60-69			(2)								2		
50-59											1		

N₁ - Potomac drainage

N₂ - Cheat and Tygart rivers

X̄ - Includes only the Potomac drainage specimens

TABLE 8.—The number of rows of scales along the lateral line in four species of Nocomis.

Species	Lateral line scale rows										N	X̄		
	36	37	38	39	40	41	42	43	44	45				
raneyi														
James					3	31	45	47	13				139	41.3
Chowan							15	16	3				34	41.6
Roanoke							16	38	38	6	2	2	102	41.5
Tar							2	10	23	8	5		48	41.1
Neuse							1	15	33	14	2		65	41.0
platyrhynchus														
New, Va.- N. C.						23	61	44	9	2			139	40.3
Indian						1	9	13	2				25	39.6
Bluestone							9	11	8				28	40.0
Greenbrier							4	19	7	1			31	40.2
Gauley							5	21	7	1			34	40.1
micropogon														
Susquehanna					1	14	27	20	3				65	39.2
Chesapeake tribs., Md.					3	11	9	4					27	38.5
Potomac					1	16	41	31	5	1	1		95	39.3
Rappahannock					1	25	20	6	1				53	38.6
York						10	-	4					14	38.6
James					4	31	64	46	9	2			156	39.2
Savannah						2	19	11	1				33	39.3
Tennessee						8	40	47	18	4	1		118	39.8
Cumberland						1	22	31	9	4	1		68	39.9
Kentucky						19	59	24	2				104	39.1
Big Sandy						6	16	19	3				44	39.4
Guyandot						1	9	4					14	39.2
Coal, Kanawha						5	15	9	1				30	39.2
Elk, Kanawha						2	9	16	6	1			34	39.9
Ohio tribs., W. Va.					1	3	10	9	1				24	39.3
Monongahela					1	4	20	23	7				55	39.6
Allegheny						6	31	22	4				63	39.4
Lake Erie, Ontario, N.Y.						3	37	26	5				71	39.5
leptocephalus														
James					2	46	18	18	7	4			95	38.9
Roanoke					7	26	50	42	10	1			136	39.2
Tar					2	4	16	14	4	1			41	38.4
Neuse						9	21	6	3				39	38.1
New						13	27	31	16	11	2		100	39.9

TABLE 9.—The number of head tubercles, segregated by sex, in Nocomis micropogon taken from the upper Tennessee drainage. (Females in parentheses.)

Standard length in mm	Number of tubercles on head						N	N	X̄
	0-9	10-19	20-29	30-39	40-49	50-59			
180-189				3	6		9	-	31.6
170-179				3	2	1	6	-	31.2
160-169				5	8	1	14	-	31.6
150-159				8	8	1	18	-	31.7
140-149				16	10	1	27	1	29.1
130-139			1	10	2		13	3	26.4
120-129				(1)	(2)		17	5	25.4
110-119				(2)	(3)		8	6	19.5
100-109		(1)	(4)	(1)	7		11	17	18.8
90-99		(1)	(10)	(6)	5		10	10	15.0
80-89		(4)	(6)	1	6		8	7	10.5
70-79		1	(6)	6	11		17	7	7.4
60-69		(6)	(1)	6	25		25	3	4.5

X̄ Sexes combined.

TABLE 10.—The number of head tubercles, segregated by sex, in *Nocomis micropogon* taken from the James drainage. (Females in parentheses.)

Standard length in mm	Number of tubercles on head							N ♂	N ♀	\bar{x}
	0-9	10-19	20-29	30-39	40-49	50-59	60-69			
180-189					2	2	1	5	-	52.5
170-179					1			1	-	44.5
160-169				3	2	-	1	6	-	42.8
150-159				1	1	3		5	-	48.5
140-149			(1)	-	4	2	2	8	3	48.1
130-139				2	3	2		7	2	44.5
120-129			(1)	4	(2)	3	2	9	5	40.9
110-119		(1)	(4)	1	1	1		3	13	32.6
100-109		(4)	(8)	3	2	1		6	14	28.5
90-99	(2)	1	5	(2)	10			17	16	25.4
80-89	(1)	(6)	(6)	(2)	3			10	15	19.3
70-79	3	(12)	(2)					11		20.1
60-69	(13)	6	2					24	21	5.0
50-59	(14)	3						3	14	4.5
	(2)								2	

 \bar{x} Sexes combined.TABLE 11.—The number of rows of scales above and below the lateral line in four species of *Nocomis*.

Species	Scale rows above lateral line						Scale rows below lateral line						
	6	7	8	9	N	\bar{x}	4	5	6	7	8	N	\bar{x}
<u>ranevi</u>													
James		28	54	1	83	7.7	1	45	33			79	6.4
Chowan		7	8		15	7.5		15	1			16	6.1
Rosnoke	1	37	24	1	63	7.4	2	49	12			63	6.2
Tar		4	2		6	7.3		5	1			6	6.2
Neuse		7	13		20	7.7		16	3			19	6.2
<u>platyrhynchus</u>													
New, Va.-N. C.		25	42		67	7.6	26	38	2			66	6.6
<u>micropogon</u>													
Potomac		39	7		46	7.2		44	2			46	6.0
Rappahannock		17	5		22	7.2	1	16	4			21	6.1
York	1	3	1		5	7.0	3	3				6	5.5
James	2	57	3		62	7.0	8	59	5			72	6.0
Tennessee	1	35	7		43	7.1	1	38	4			43	6.1
Cumberland		12	19	1	32	7.7	4	32	4			31	6.0
Kentucky		24	1		25	7.0	12	12				24	5.5
Guyandot		3	1		4	7.3	1	3				4	5.8
Kanawha	1	2			3	6.7	1	2				3	5.7
Monongahela		12			12	7.0	4	8				12	5.7
Lake Ontario	5	20			25	6.8	7	18				25	5.7
<u>leptocephalus</u>													
James		4	14		18	6.8	5	7	6			18	5.1
Rosnoke		79	54		133	6.4	3	114	16			133	5.1
Tar		12	1		13	6.1	2	11				13	4.9
Neuse		26	5		31	6.2	5	26				31	4.8
New		26	34	1	61	6.6	2	34	25	1		62	5.4

TABLE 12.—The circumferential scale rows in four species of *Nocomis*.

Species	Circumferential scale rows														N	\bar{X}	
	26	27	28	29	30	31	32	33	34	35	36	37	38	39			
raneyi																	
James						1	58	54	28	28	8					177	33.3
Chowan							9	14	9	3	3					38	33.4
Roanoke						7	28	26	12	13	3	1				90	33.1
Tar						2	17	16	11	2	1					49	32.9
Neuse						5	18	19	16	6						64	33.0
platyrhynchus																	
New, Va.-N. C.						2	14	39	63	49	30	1	1	1		200	34.2
Indian							6	13	8	1						28	33.1
Bluestone			1	-	2	8	15	7								33	32.7
Greenbrier			2	5	7	21	20	2	1							58	33.2
Gauley						7	20	21	3	2	1					54	33.6
micropogon																	
Susquehanna			1	8	26	24	4	3								66	30.5
Chesapeake tribs., Md.			1	5	7	11	5	1	-	2						32	31.8
Potomac				7	16	32	33	14	3	1						106	32.4
Rappahannock				3	10	18	10	8								49	31.2
York			1	-	1	5	4	2	1							14	31.5
James			2	9	51	65	41	11	4	1						184	31.0
Savannah				1	10	13	7	4								35	31.1
Tennessee				7	14	43	29	23	13	2	1					132	31.8
Cumberland			1	2	6	14	23	22	6	2						76	32.1
Kentucky			16	35	20	37	7	1								116	29.9
Big Sandy			1	3	6	10	13	18	5							56	31.9
Guyandot				2	3	4	4	1								14	30.9
Coal-Kanawha				7	14	11	2	1								35	30.3
Elk-Kanawha			1	2	11	33	12	4								63	31.0
Ohio tribs., W. Va.				1	8	7	7	-	1							24	31.0
Monongahela				1	14	29	24	12	4	1						85	31.6
Youghiogheny					6	4	6	2								18	32.2
Allegheny				4	13	12	14	10	3	-	1					57	31.5
Lake Erie, Ontario, N. Y.			2	2	13	23	28	3	2	1	1					75	31.3
leptocephalus																	
James	1	1	36	18	21	13	3									93	29.2
Roanoke		6	61	57	30	5										159	28.8
Tar	1	-	39	3	2											45	28.1
Neuse	1	5	33	1	4	-	1									45	28.1
New			32	34	34	16	3	1								120	29.4

TABLE 13.—The number of head tubercles in *Nocomis micropogon* taken from the Susquehanna drainage and localities over most of the range of the species west of the Allegheny Mountains.

S. L. in mm	Number of tubercles on head							N
	0-9	10-19	20-29	30-39	40-49	50-59	60-69	
180-189				1				1
170-179				-	2			2
160-169		1	3	8	3			15
150-159		1	10	5	3	1		20
140-149		3	11	12	4	1		31
130-139		3	8	10	4			25
120-129		2	7	7	6	2		24
110-119		1	5	4	5	3		18
100-109		1	4	4	3	2	1	15
90-99	1	3	3	1	4			12
80-89	1	4	-	3				8
70-79	1	1	-	1				3
60-69	1							1
50-59	1							1

TABLE 14.—The number of rows of scales around the caudal peduncle in four species of *Nocomis*.

Species	Caudal peduncle scale rows							N	\bar{x}	
	14	15	16	17	18	19	20			
raneyi										
James			50	21					71	16.3
Chowan			1	13	1	1			16	16.1
Roanoke			1	44	16	3			64	16.3
Tar				10	7	-	2		19	16.7
Neuse				20	4	-	1		25	16.3
platyrhynchus										
New, Va.-N. C.				36	28	16	1	1	82	16.8
micropogon										
Susquehanna			1	28					29	16.0
Potomac			1	40	4				45	16.1
Rappahannock				26					26	16.0
York			1	7	1	2	1		12	16.6
James	1		1	60	7				69	16.1
Tennessee				35	5	3	1		44	16.3
Cumberland			1	49	15	8	3		77	16.5
Kentucky			1	2	84	2	1		90	16.0
Kanawha				7					7	16.0
Monongahela				22	2	1			25	16.2
Allegheny			1	31	5	1			38	16.2
Lake Erie, Ontario, N. Y.				32	2				34	16.1
leptocephalus										
James				15	1	1			17	16.2
Roanoke				38	7	2			47	16.2
Tar				8					8	16.0
Neuse				17					17	16.0
New				47	11	4			62	16.3

TABLE 18.—The degree of breast squamation in four species of *Nocomis*.

Species	Squamation ratings					
	0	1-2	3-4	5-6	7-8	9-10
<i>raneyi</i>						
James	58	6	1			
Chowan	20					
Roanoke	50	3				
Tar	1	3	2	5	2	
Neuse		4	8	10	6	
<i>platyrhynchus</i>						
New, Va.-N. C.	2	16	26	47	45	4
Indian				4	10	1
Bluestone		1	-	1	4	1
Greenbrier				2	20	5
Gauley	1	-	3	13	17	1
<i>micropogon</i>						
Susquehanna	20	18	5	1		
Chesapeake tribe., Md.	18	8	1			
Potomac	31	25				
Rappahannock	20	12	2			
York	3	5				
James	30	41	1			
Savannah	17	7	2	1		
Tennessee	3	9	10	15	26	4
Cumberland	6	18	6	9	6	1
Kentucky		9	12	14	37	2
Big Sandy		5	2	4	2	
Guyandot		4	2	3	1	
Coal, Kanawha	4	3	1	10	1	1
Elk, Kanawha	1	18	5	8	4	
Ohio tribe., W. Va.		6	3	3	2	
Monongahela	16	22	8	2	3	1
Allegheny	1	8	8	6	6	
Lake Erie, Ontario-N. Y.	3	5	9			
<i>leptocephalus</i>						
James, to Neuse and New				4	69	34

TABLE 20.—The relationship between snout length and gape width in 121 juvenile and subadult specimens of two species of *Nocomis* ranging in size from 100 to 149 mm in standard length. The higher values, in parentheses, refer to *N. platyrhynchus*, the others to *N. raneyi* of the Atlantic slope. An overlap of about 12 percent occurred in this sample.

Gape width in per cent of S. L.	Snout length in per cent of S. L.									
	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	
11.0							(1)			
10.5										
10.0						(2)	(1)	(2)		
9.5						(3)	(1)	(2)		
9.0					(1)	(5)	(1)			
8.5					(4)	(2)	(2)			
8.0			1	1	(1)	(3)	(2)	(2)		
7.5				7	5	1				
7.0			2	5	6	2	1			
6.5	1	2	7	13	7	3				
6.0	1	2	4	3	2					
		2	2	3	2					

TABLE 19.—The number of head tubercles, segregated by sex, in *Nocomis leptocephalus* taken from the James, Roanoke, and upper New drainages. (Females in parentheses.)

Standard length in mm	Number of tubercles on head					
	0-9	10-19	20-29	N ♂	N ♀	\bar{x}
170-179			1	1	-	24.5
160-169		3	1	4	-	17.0
150-159		8	3	11	-	17.2
140-149		16	6	22	-	17.2
130-139		23	6	29	-	16.6
120-129		18	4	22	-	16.3
110-119		24	8	32	-	16.7
100-109		(5)	18	10	5	17.3
90-99		(8)	13		8	13.4
80-89	(5)	(28)	23	2	33	14.5
70-79	(3)	(13)	(1)	1	17	12.7
60-69	(6)	(18)	9	1	24	8.3
50-59	(9)	(16)	3		44	5.2
40-49	(17)	(22)	3		17	4.5
30-39	(11)	(10)			10	4.5
	(1)				1	

\bar{x} - Sexes combined.

TABLE 21.—The relationship between snout length and gape width in 70 adults, chiefly males, of two species of *Nocomis* ranging in size above 149 mm in standard length. The higher values in parentheses refer to *N. platyrhynchus*, the lower values to *N. raneyi*. An overlap of 12.9 percent occurred in this sample.

Gape width in per cent of S. L.	Snout length in per cent of S. L.							
	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5
11.5						(2)	(1)	
11.0					(3)	(2)		
10.5						(4)	(2)	(1)
10.0					(2)	(2)	-	(2)
9.5					(1)	(3)		
9.0					1	(2)		
8.5			2	2	2			
8.0			1	3	2	2		
7.5	2	2	4	1	1			
7.0	2	1	3	3	2			
	1	-	4					

TABLE 22.—Comparison of the three species groups of *Nocomis*.

Character	Species-groups		
	<u>biguttatus</u>	<u>micropogon</u>	<u>leptocephalus</u>
Nuptial tubercles	moderate, many	moderate to large, many	very large, few
Size, number			
Distribution, head dorsum	mid-snout to occiput	tip of snout to mid-occiput	internasal to occiput
lacrimal body	absent	present	absent
pectoral fin rays	present or absent	absent	absent
direction	2 to 5 or 6	2 to 5 or 6	2 to 8 or 9
Nuptial crest	almost always antrorse	erect, some laterad	erect and laterad
Coloration	absent or slight swelling	large, more posterior	large to moderate, more anterior
nuptial	pink-rosy, lower head and body	pink-rosy, lower head and body	head and body bluish or body with orange stripe and pink belly
caudal spot, yg. & jwv.	large, round, distinct	small, indistinct	small, indistinct
anal fin (life)	orangish, brightest fin	light orange to pale	pale or light olive
upper body (life)	olive-greenish	olive-greenish	olive-tannish
scale (dark anterior)	wider	wider	narrower
red postocular spot	present	absent	absent
Intestine	S-shape	S-shape or small accessory loop on left side	one ventral whorl
Pharyngeal teeth	1,4-4,1 to 4-4	4-4	4-4 to 3-3
Scalcs, size	smaller	intermediate	larger
body, circumferential	31 to 38	28 to 39	26 to 33
Vertebrae	38 to 42	38 to 44	38 to 41
Body form	stocky to somewhat elongate	more elongate	more stocky
Mouth	more terminal, oblique	more inferior, horizontal	more inferior, horizontal
Snout, shape	rounded to pointed	more pointed	more blunt, declivous
internasal hump	usually absent	usually present	usually absent
Preopercle, posterior edge	intermediate	usually slanted anterior, below, except large males	vertical or slanted posterior, below
Caudal fin lobes	usually equal	upper lobe usually longer	lower lobe often slightly longer
Lateral line curvature	straighter, passing through lateral stripe	straighter, passing through lateral stripe	more down-curved passing through lower lateral stripe or below
Size attained	smaller to moderate	larger	moderate
Distribution	Mississippi, southern Great Lakes, upper Red River of North basins	Ohio R. and southern Great Lakes basins, central Atlantic slope	central and south Atlantic slope, west to southeast Mississippi R. tributaries
Species and subspecies	<u>biguttatus</u> <u>effusus</u> Ozark chub, n. sp.	<u>micropogon</u> <u>platyrhynchus</u> , n. sp. <u>raneyi</u> , n. sp.	<u>l. leptocephalus</u> <u>l. bellieus</u> <u>l. n. subsp.</u> (southeast)

TABLE 23.—Proportional measurements of *Nocomis raneyi* expressed in thousandths of standard length.

Measurements	Males						Females				
	Holotype 194633	194626	194684	194617	194603	194614	191036	194631	194602	194614	194614
Standard length, mm	242	227	198	150	96	53	180	142	121	93	68
Head length	260	258	261	252	254	253	244	246	245	254	260
Snout length	126	119	121	109	97	95	109	103	99	95	105
Postorbital length	112	118	119	103	109	95	107	106	104	99	99
Lacrimal, greatest length	81	81	82	80	70	61	73	68	66	66	65
Orbit length	46	46	47	55	64	72	51	54	58	58	74
Interorbital, bony width	92	84	90	80	74	72	84	73	74	75	78
Gape width	89	83	92	84	68	76	74	72	74	78	80
Upper jaw length	89	87	87	81	72	72	77	75	70	72	75
Predorsal length	562	530	552	541	548	548	523	532	546	530	555
Caudal peduncle length	209	225	215	212	226	215	198	217	211	217	212
Caudal peduncle depth	116	110	116	111	118	110	119	110	113	109	111
Body, greatest depth	267	259	280	244	259	232	264	247	276	241	238
Body, greatest width	172	153	176	165	161	147	169	174	168	165	155

TABLE 24.—Proportional measurements of *Nocomis platyrhynchus* expressed in thousandths of standard length.

Measurements	Holotype USNM 194817	Males					Females				
		TU 194817	USNM 194804	USNM 194812	USNM 194817	USNM 194804	USNM 194257	USNM 194811	TU 25902	USNM 194816	USNM 194257
Standard length, mm.	163	195	159	133	82	57	142	123	109	86	65
Head length	285	292	289	274	268	283	279	281	275	284	268
Snout length	125	135	128	123	108	108	117	122	117	112	107
Postorbital length	126	137	131	114	104	115	121	120	117	119	109
Lachrymal, greatest length	89	96	87	83	74	66	79	77	77	76	71
Orbit length	54	48	50	53	69	84	57	58	61	69	65
Interorbital, bony width	83	96	84	77	67	75	70	72	78	68	71
Gape width	102	100	106	93	82	84	80	88	87	78	84
Upper jaw length	92	98	99	90	85	87	92	91	90	93	76
Predorsal length	551	517	550	538	520	581	543	559	561	549	546
Caudal peduncle length	230	234	225	229	235	213	212	208	219	210	219
Caudal peduncle depth	114	115	116	115	113	119	110	113	111	114	116
Body, greatest depth	252	256	241	226	224	234	230	274	271	248	223
Body, greatest width	172	151	177	159	150	154	151	191	180	159	140

TABLE 25.—Comparison of morphometric characters in adult males of four species of *Nocomis*. Measurements are expressed in thousandths of standard length.

Species	<i>raneyi</i>	<i>platyrhynchus</i>	<i>micropogon</i>	<i>leptocephalus</i>
Total sample	24	31	51	47
Drainage and subsample	James 12 Roanoke 11 Neuse 1	New	Potomac 13 Rappahannock 2 James 14	Tennessee 22 Roanoke 9 New 6
Standard length, mm : mean	200	178	165	161
range	172-242	159-214	142-189	141-188
Head length	260	278	284	272
Snout length	244-275 116	260-292 126	272-300 131	262-285 125
Postorbital length	104-126 117	119-137 123	121-148 126	114-135 121
Lachrymal, greatest length	110-131 81	112-137 87	114-136 87	111-130 82
Orbit, bony length	71-88 49	79-96 50	80-99 53	75-91 52
Interorbital, bony width	45-54 86	45-56 85	49-58 88	47-59 82
Gape width	78-95 83	75-103 104	77-94 108	66-92 104
Upper jaw length	71-103 85	91-115 98	88-123 102	94-130 100
Predorsal length	79-98 542	89-106 542	91-113 546	92-115 533
Caudal peduncle length	517-567 211	517-576 226	529-565 215	516-558 226
Caudal peduncle depth	193-225 115	210-243 118	201-231 116	211-240 116
Body, greatest depth	106-123 263	108-126 249	106-130 252	108-125 238
Body, greatest width	226-287 158	224-278 165	220-288 169	218-263 168
	131-189	134-190	149-203	151-190
				148-205

TABLE 26.—Association and frequency of hybridization of *Nocomis leptocephalus* with three related species of river chubs.

Species	Number of collections 1/	Number of collections in column I in which <i>leptocephalus</i> occurred	Percent occurrence with <i>leptocephalus</i>	Number of collections 2/ with <i>leptocephalus</i> and		Total number of specimens involved in columns IV and V
				hybrids	excluding hybrids	
<i>raneyi</i>						
James 2/	18	16	89	-	16	940
Chowan	4	4	100	-	4	189
Roanoke	41	39	95	1	45	2098
Tar	4	3	75	-	3	64
Neuse	7	7	100	-	8	205
TOTAL	-	-	-	-	-	3496
<i>platyrhynchus</i>						
New, Va.	16	10	63	3	12	328
<i>micropogon</i>						
James	23	14	61	15 4/	10	478

1/ Only collections with a minimum of 10 specimens were considered in columns I-III.

2/ Includes only the collections from the Craig-Johns Creek system.

3/ Includes collections with two or more specimens.

4/ Includes three collections lacking typical *N. micropogon* and three lacking typical *N. leptocephalus*.TABLE 27.—Comparison of certain meristic characters of *Nocomis raneyi*, atypical *N. raneyi*, and *N. micropogon* from the James drainage.

	CIRCUMFERENTIAL SCALES								N	\bar{X}	
	28	29	30	31	32	33	34	35			36
<i>raneyi</i>											
Craig				1	57	53	27	27	7	172	33.3
Catawba					1	1	1	1		4	34.5
TOTAL ¹				1	58	54	28	28	8	177	33.3
atypical <i>raneyi</i>				1	11	17	20	13	9	71	33.8
<i>micropogon</i>											
Above Craig ²		6	15	28	16	5	3	1		74	31.2
Craig area		1	8	10	4	2				25	30.9
Below Craig	2	2	28	27	21	4	1			85	30.9
	LATERAL LINE SCALES										
	37	38	39	40	41	42	43				
<i>raneyi</i>											
Craig				3	31	43	44	13		134	41.2
Catawba						1	3			4	41.8
TOTAL ¹				3	31	45	47	13		139	41.3
atypical <i>raneyi</i>					8	40	19	3		70	41.2
<i>micropogon</i>											
Above Craig ²		4	25	25	5	2				61	39.6
Craig area		5	14	6						25	39.0
Below Craig	4	22	25	15	4					70	38.9
	TOTAL VERTEBRAE										
	39	40	41	42	43	44					
<i>raneyi</i>											
Craig		10	64	47	4	1				126	41.4
Catawba			2	2						4	41.5
TOTAL ¹		10	66	50	4	1				131	41.4
atypical <i>raneyi</i>		3	23	22	2	1				51	41.5
<i>micropogon</i>											
Above Craig ²		20	25	6						51	39.7
Craig area		7	12	1						20	39.7
Below Craig		8	9	2						19	39.7

1 - includes one specimen from Pedlar River

2 - Mill, Craig, Johns and Catawba Creeks

Index

- albeolus*, *Notropis*, 73
amblops winchelli, *Hybopsis*, 14
amnis, *Notropis*, 14
anomalum, *Campostoma*, 64
Association, 58-60
Atypical *Nocomis raneyi*, 32-36, 56
Bigmouth chub, 16, 37
biguttatus, *Ceratichthys*, 37
 Nocomis, 15, 69, 78
 Semotilus, 13, 15
blennioides, *Etheostoma*, 66
Bluehead chub, 16, 50
boucardi, *Notropis*, 14
Breeding tubercles, 7, 8
Brest squamation, 12
buccata, *Ericymba*, 66
Bull chub, 16, 17
Campostoma, 73
 anomalum, 64
caprodes semifasciata, *Percina*, 66
Catostomus melanotus, 15
cerasinus, *Notropis*, 73
Ceratichthys, 14-15
 biguttatus, 37
 cyclotis, 15
 leptocephalus, 50
 micropogon, 15, 42
 nebrascensis, 15
 stigmaticus, 15
 vigilax, 14
Ceratichthys × *Hypsilepis*, 42
cervinum, *Moxostoma*, 70
Chrosomus oreas, 73
Cladophora, 57
Coastal Plain province, 56, 57
 Eustatic changes, 61-63
 Pliocene submergence, 69
Coloration, 12
 Nocomis leptocephalus, 51
 Nocomis micropogon, 45-57
 Nocomis platyrhynchus, 39
 Nocomis raneyi, 26-29
Color forms, 47
cornutus, *Notropis*, 65
corporalis, *Semotilus*, 76
Couesius, 15
 plumbeus, 35
crassa roanoka, *Percina*, 70
Crests (See Nuptial crests)
Cuba Outlet, 64
Cumberland River Falls, 67
cyclotis, *Ceratichthys*, 15
Cyprinella, 74, 75
darter, 70
Dentition (See Pharyngeal dentition)
Diagnostic characters, 7-13
Dispersal, 61-73
 Kanawha Falls, 63
 Nocomis leptocephalus, 72-73
 Nocomis micropogon, 63
 Nocomis platyrhynchus, 63
 Nocomis raneyi, 69-72
Distribution
 Nocomis leptocephalus, 54-55
 Nocomis micropogon, 48-50
 Nocomis platyrhynchus, 41
 Nocomis raneyi, 32
Ecology (See Regional ecology)
effusus, *Nocomis*, 67, 74
Ericymba buccata, 66
Erimystax, 14
Etheostoma blennioides, 66
 kanawhae, 63
 osburni, 63
Etymology
 Nocomis platyrhynchus, 37
 Nocomis raneyi, 29
Evolution, 73-78
 Summary, 76-78
Exoglossum, 73
Extrarius, 14
Fall Line (See Fall Zone)
Fall Zone, 56-57
Falls
 Cumberland River, 67
 Kanawha, 63
Geological events, 61
 Eustatic changes, 61-63
 Pleistocene drainage modifications, 63
 Stream capture, 61
gilberti, *Noturus*, 70
glacier, Illinoian, 64
Greater Susquehanna River, 61, 65
harperi, *Hybopsis*, 14
Head crests, 7 (See also Nuptial crests)
Head tuberculation, 7 (See also Tuberculation)
hiatus, 75
Hybopsis, 14-15
 amblops winchelli, 14
 harperi, 14
 kentuckiensis, 17, 37 42 50
 kentuckyensis, 37

Hybopsis—Cont.

- leptocephala*, 37, 50
- micropogon*, 37, 50

Hybridization

- Frequency, 58-60
- Introgressive, 35, 45
- Summary, 60, 77, 79

Hybrids

- Ceratichthys* × *Hypsilepis*, 42
- Nocomis biguttatus* × *Nocomis micropogon*, 77
- Nocomis leptocephalus* × *Nocomis micropogon*, 49, 58, 60, 77
- Nocomis leptocephalus* × *Nocomis platyrhynchus*, 60
- Nocomis leptocephalus* × *Nocomis raneyi*, 59
- Nocomis micropogon* × *Nocomis raneyi*, 49, 60
- Nocomis micropogon* × *Notropis cornutus*, 42

Illinoian glacier, 64

Intestine, 11

Introgressive hybridization, 35, 45

Justicia, 57*kanawhae*, *Etheostoma*, 63*kentuckiensis*, *Luxilus*, 15

- Hybopsis*, 17, 37, 50

kentuckyensis, *Hybopsis*, 37

Key, 16

Lake Maumee, 64

leptocephala, *Hybopsis*, 37, 50*leptocephalus*, *Ceratichthys*, 50*leptocephalus* group, 50*leptocephalus*, *Nocomis*, 50

- Coloration, 51
- Description, 50-54
- Diagnosis, 51
- Dispersal, 72-73
- Distribution, 54-55
- Growth, 54
- Key, 16
- Materials, 54
- Nuptial crest, 51
- Reproduction, 54
- Tuberculation, 51

Leuciscus, 14*Leucosomus*, 14*Luxilus kentuckiensis*, 15*Macrhybopsis*, 14

Madtom catfish, 70

Materials, 6

- Nocomis leptocephalus*, 54
- Nocomis micropogon*, 48
- Nocomis platyrhynchus*, 39-41
- Nocomis raneyi*, 29-32

melanotus, *Catostomus*, 15

Meristic characters, 8

- Nocomis leptocephalus*, 51
- Nocomis micropogon*, 43
- Nocomis platyrhynchus*, 38
- Nocomis raneyi*, 23

Methods, 3

micropogon, *Nocomis*

Coloration, 45-47

Color forms, 47

Description, 42-47

Diagnosis, 42

Dispersal, 63-69

Distribution, 48-50

Evolution, 76-78

Growth, 48

Key, 16

Materials, 48

Nomenclature, 42

Nuptial crest, 45

Populations, 47-48

Reproduction, 48

Tuberculation, 43-45

micropogon, *Ceratichthys*, 15, 42

group, 17

Hybopsis, 37, 50

Morphometric characters, 9, 17-23, 37-38, 42-43, 51

Moxostoma, 63*cervinum*, 70*rhothoecum*, 71*nebrascensis*, *Ceratichthys*, 15*Nocomis*, 13*Nocomis**biguttatus*, 15, 69, 78

Description, 13

Diagnosis, 13

Dispersal, 61-73

Evolution, 73-78

Key, 16

leptocephalus, 15, 37, 50-55, 72-73*leptocephalus bellicus*, 50*micropogon*, 15, 16, 42-50, 63-69, 76-78*nebrascensis*, 13

Nomenclatural history, 14

platyrhynchus (new species), 16, 37-41, 63, 76-79*raneyi* (new species), 16, 17-37, 69-72, 76-78*Nocomis biguttatus* × *Nocomis micropogon*, 77*effusus*, 67, 74*leptocephalus* × *Nocomis micropogon*, 49, 58, 60, 77*leptocephalus* × *Nocomis platyrhynchus*, 60*leptocephalus* × *Nocomis raneyi*, 59, 60, 77*micropogon* × *Nocomis raneyi*, 49, 60*micropogon* × *Notropis cornutus*, 42*notatus*, *Pimephales*, 70*Notropis*, 73*albeolus*, 73*amnis*, 14*boucardi*, 14*cerasinus*, 73*cornutus*, 65*scabriceps*, 63*spilopterus*, 66*Noturus gilberti*, 70

Nuptial coloration, 12, 26-29, 39, 45-47, 51

Nuptial crests, 5, 25-26, 38-39, 45, 51

Old Allegheny River, 64

- omiscomaycus*, *Percopsis*, 66
oreas, *Chrosomus*, 73
Oregonichthys, 14
osburni, *Etheostoma*, 63
oxyrhyncha, *Percina*, 66
Percina caprodes semifasciata, 66
 crassa roanoka, 70
 oxyrhyncha, 66
Percopsis omiscomaycus, 66
 Pharyngeal dentition, 26, 39, 45, 51
Phenacobius teretulus, 63
 Piedmont, 69
 streams, 56
Pimephales, 14, 73, 74, 75
Pimephales notatus, 70
Platyobio, 14
platyrhynchus, *Nocomis* (new species), 37
 Coloration, 39
 Description, 37-39
 Diagnosis, 37
 Dispersal, 63
 Distribution, 41
 Etymology, 37
 Evolution, 76-78
 Growth, 39
 Key, 16
 Materials, 39-41
 Nuptial crest, 38-39
 Reproduction, 39
 Tuberculation, 38
 Pleistocene
 Drainage modifications, 62, 63
 Glaciation, 62
plumbeus, *Couesius*, 35
Podostemum, 57
Pogonichthys, 76
 Populations
 micropogon, 47-48
 raneyi, 29
Potamogeton, 57
 Problematic specimens, 36-37
Pteronotropis, 74
raneyi, *Nocomis* (new species), 17
 Atypical, 32-36
 Coloration, 26-29
 Description, 17-29
 Diagnosis, 17
 Dispersal, 69-72
 Distribution, 32
 Etymology, 29
 Evolution, 76-78
 Growth, 29
 Key, 16
 Materials, 29-32
 Nuptial crest, 25-26
 Populations, 29
 Problematical specimens, 36-37
 Reproduction, 29
 Tuberculation, 23-25
 Redspot chub, 73
 Regional ecology, 55-58
 Reproduction, 29, 39, 48, 54
rhothoecum, *Moxostoma*, 71
 River chub, 16, 42
Saprolegnia, 8
scabriceps, *Notropis*, 63
Semotilus, 14, 73
Semotilus biguttatus, 13, 15
Semotilus corporalis, 76
spilopterus, *Notropis*, 66
stigmaticus, *Ceratichthys*, 15
 Stream capture, 61
 Sucker, 70
 Swellings, 5, 7
 Teays River, 62, 63, 64, 67, 76
teretulus, *Phenacobius*, 63
Thoburnia (See *rhothoecum*)
 Tubercle, 5, 7
 anlagen, 3, 8
 bud, 3, 7
 evolution, 74, 75
 function, 8
 hiatus, 75
 scar, 3, 8
 spot, 3, 7
 Tuberculation
 evolution, 74, 75
 Nocomis leptocephalus, 51
 Nocomis micropogon, 43-45
 Nocomis platyrhynchus, 38
 Nocomis raneyi, 23-25
vigilax, *Ceratichthys*, 14
Yuriria, 14

Publication in Smithsonian Contributions to Zoology

Manuscripts for serial publications are accepted by the Smithsonian Institution Press subject to substantive review, only through departments of the various Smithsonian museums. Non-Smithsonian authors should address inquiries to the appropriate department. If submission is invited, the following format requirements of the Press should govern the preparation of copy.

Copy must be typewritten, double-spaced, on one side of standard white bond paper, with 1½" top and left margins, submitted in ribbon copy with a carbon or duplicate, and accompanied by the original artwork. Duplicate copies of all material, including illustrations, should be retained by the author. There may be several paragraphs to a page, but each page should begin with a new paragraph. Number all pages consecutively, including title page, abstract, text, literature cited, legends, and tables. A manuscript should consist of at least thirty pages, including typescript and illustrations.

The *title* should be complete and clear for easy indexing by abstracting services. Taxonomic titles will carry a final line indicating the higher categories to which the taxon is referable: "(Hymenoptera: Sphecidae)." Include an *abstract* as an introductory part of the text. Identify the *author* on the first page of text with an unnumbered footnote that includes his professional mailing address. A *table of contents* is optional. An *index*, if required, may be supplied by the author when he returns page proof.

Two *headings* are used: (1) text heads (boldface in print) for major sections and chapters and (2) paragraph sideheads (caps and small caps in print) for subdivisions. Further headings may be worked out with the editor.

In *taxonomic keys*, number only the first item of each couplet; if there is only one couplet, omit the number. For easy reference, number also the taxa and their corresponding headings throughout the text; do not incorporate page references in the key.

In *synonymy*, use the short form (taxon, author, date, page) with a full reference at the end of the paper under "Literature Cited." Begin each taxon at the left margin with subsequent lines indented about three spaces. Within a taxon, use a period-dash (.—) to separate each entry. Enclose with square brackets any annotation in or at the end of the taxon. For *synonymy* and *references within the text*, use the author-date system: "(Jones 1910)." Use the colon system for page references: "(Jones 1910:122)," and abbreviate further data: "(Jones 1910:122, fig. 3, pl. 5: fig. 1)."

Simple *tabulations* in the text (e.g., columns of data) may carry headings or not, but they should not contain rules. Formal *tables* must be submitted as pages separate from the text, and each table, no matter how large, should be pasted up as a single sheet of copy.

Use the *metric system* instead of (or in addition to) the English system.

Illustrations (line drawings, maps, photographs, shaded drawings) usually can be intermixed throughout the printed text. They will be termed *Figures* and should be numbered consecutively; however, if a group of figures is treated as a single figure, the individual components should be indicated by lowercase italic letters on the illustration, in the legend, and in text references: "Figure 9*b*." Submit all legends on pages separate from the text and not attached to the artwork. An instruction sheet for the preparation of illustrations is available from the Press on request.

In the *bibliography* (usually called "Literature Cited"), spell out book, journal, and article titles, using initial caps with all words except minor terms such as "and, of, the." (For capitalization of titles in foreign languages, follow the national practice of each language.) Under-score (for italics) book and journal titles. Use the colon-parentheses system for volume number and page citations: "10(2):5-9." Spell out such words as "figures," "plates," "pages."

For *free copies* of his own paper, a Smithsonian author should indicate his requirements on "Form 36" (submitted to the Press with the manuscript). A non-Smithsonian author will receive fifty free copies; order forms for quantities above this amount, with instructions for payment, will be supplied when page proof is forwarded.

