ERNEST A. LACHNER
and MARTIN L. WILEY

Populations of the Polytypic Species Nocomis leptocephalus (Girard) with a Description of a New Subspecies

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY NUMBER 92

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ABSTRACT

Lachner, Ernest A., and Martin L. Wiley. Populations of the Polytypic Species *Nocomis leptocephalus* (Girard) with a Description of a New Subspecies. *Smithsonian Contributions to Zoology,* number 92, 34 pages, 1971.—Three subspecies of the bluehead chub, *Nocomis leptocephalus* (Girard), are recognized. Our conclusions are based on the examination of more than 20,000 specimens housed in American institutions. The typical form, *N. l. leptocephalus,* ranges from the Potomac drainage southward on the Atlantic slope to and including the Santee drainage, and across the Appalachian Divide into the New River. The new subspecies, *N. l. interocularis,* occurs in the Savannah, Altamaha, and Chattahoochee rivers and across the divide in a limited area of the Tennessee River in southeast Tennessee. The nominal form, *N. l. bellicus,* extends from the Alabama River westward to streams draining into the Mississippi River from the east in Louisiana and Mississippi, and in a limited area of the Tennessee River across the divide in northern Alabama.

The diagnostic characters differentiating these subspecies are the number and distribution of head tubercles. These three populations have diverged almost to the species level. Intergrades of *N. l. interocularis* × *N. l. leptocephalus* are recognized from the Edisto River, South Carolina. Two basic color forms are described, a blue and a brassy reddish, the evolutionary significance of which is not understood. The distribution of these two color forms does not correspond entirely to the distribution of the described morphological forms. The whorled intestine, a specific character of *N. leptocephalus,* is often straight in specimens from the Chattahoochee River.

We postulate that in *Nocomis,* decrease in tubercle number and increase in tubercle size may represent a specialized condition that is especially demonstrated among the subspecies of *N. leptocephalus.*

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Populations of the Polytypic Species *Nocomis leptocephalus* (Girard) with a Description of a New Subspecies

Introduction

The status and relationships of the nominal species *Nocomis leptocephalus* (Girard) and *N. bellicus* Girard have received little study since they were described (1856:213). They were included in the synonymy of *Hybopsis kentuckiensis* (Rafinesque) for many years until Hubbs (1926) resurrected *N. leptocephalus.* Subsequent listings by Lachner (1946), Moore (1968), and Bailey et al. (1960) have recognized the two forms, but with little clarification of their morphological differences.

Preliminary studies indicated the existence of an abundant, wide-ranging Piedmont species complex whose range extended from the Potomac River drainage southward to the Savannah River drainage and westward to tributaries of the Mississippi River. First inspection of the data suggested that the several river populations might be interrelated under one species, with characters which formed a cline from the northeast to the south and southwest portion of the range. Analysis of many specimens, however, particularly the adult males, revealed characteristic abrupt breaks in character values between certain adjacent populations, and that three highly diverged populations were actually involved. The objectives of this paper are to describe the morphological components of the species complex of *N. leptocephalus,* including a new subspecies, to discuss the interrelationships of the several populations and to discuss the distribution, zoogeography, and evolution of the species complex.

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Acknowledgments

Hundreds of individuals have contributed to this study by their collecting efforts in amassing over 1,300 collections and over 20,000 specimens from southeastern United States. To these individuals, we offer our great appreciation. Other individuals have provided field observations, museum records, have loaned collections, or made available specimens and facilities to the writers. We are especially grateful for this cooperation, and we express our thanks to the following individuals for their special efforts; Joe Bailey, Duke University (DU); Reeve M. Bailey and Robert Rush Miller, Museum of Zoology, University of Michigan(UMMZ); Herbert Boschung, University of Alabama (UAIC); J. H. Elrod, Auburn University (API); Harry Freeman,

College of Charleston; Robert E. Jenkins, Roanoke College; John Ramsey, Cooperative Fisheries Research Unit, Auburn University; Edward C. Raney, Cornell University (CU); Robert D. Ross, Virginia Polytechnic Institute; Frank J. Schwartz, Institute of Marine Sciences, University of North Carolina; Donald C. Scott, University of Georgia (UG); William F. Smith-Vaniz, Institute of Marine and Atmospheric Sciences, University of Miami; Royal D. Suttkus, Tulane University (TU); Benjamin R. Wall, Jr., University of Alabama; and Ralph Yerger, Florida State University (FSU).

Some specimens were also received from, or examined at, the University of Kansas (KU); Academy of Natural Sciences, Philadelphia (ANSP); the University of Minnesota; Oklahoma State University Museum of Zoology (OAM); and the Mississippi Game and Fish Commission (MGFC).

The staff of the National Museum of Natural History (USNM) contributed the following: Dorothy Hubbs made X-ray photographs, summarized various numerical data, and constructed the distribution map; Carolyn Bartlett Gast made a detailed drawing of the new subspecies; A. M. Awl drew the heads of three subspecies; and the Photographic Services Division made all of the photographs except the head view of *N. l. leptocephalus* (Plate 6, upper) which was provided by Edward C. Raney.

Robert E. Jenkins read the manuscript and offered valuable suggestions.

The first writer was partially supported by Smithsonian Research Awards 3316 and 3347; the second writer was assisted by both awards.

Material Studied

Most of the collections are housed at Cornell University, University of Alabama Ichthyological Collection, University of Georgia, University of Michigan Museum of Zoology, National Museum of Natural History, and Tulane University. The number of collections and specimens studied, segregated by drainage, is summarized below. The total number does not include many of the collections containing only young specimens which were too small to provide data on tubercle development, but which were included on the distribution map.

Nocomis l. leptocephalus

Drainage		*Collections*	*Specimens*
New		51	783
Potomac		4	69
Rappahannock		2	2
York		5	159
James		50	1,471
Chowan		13	334
Roanoke		141	4,746
Tar		11	230
Neuse		23	211
Cape Fear		13	70
Pee Dee		54	1,133
Santee		395	5,343
	Subtotal	762	14,551

Nocomis l. interocularis

Savannah		190	2,275
Ogeechee		3	8
Altamaha		56	1,011
Chattahoochee		62	789
	Subtotal	311	4,083

Nocomis leptocephalus intergrade *interocularis* × *leptocephalus*

Edisto		5	155

Nocomis l. bellicus

Mobile Bay		147	1,111
Pascagoula Bay		12	185
Pearl River		48	248
Mississippi River tributaries		33	433
Tennessee River		4	23
	Subtotal	244	2,000
	TOTAL	1,322	20,789

Methods

The methods used in counting meristic characters and measuring structures and body proportions were similar to those discussed by Lachner and Jenkins (1971). All references to body length are to standard length (SL) in millimeters, unless stated otherwise. The preliminary data of various morphometric characters as well as meristic characters were segregated by size, sex, and river system. The initial tabular data for each character were taken from samples of from ten to twenty specimens when available, and the samples were selected over the range of a population within a river system insofar as possible. When preliminary analysis

of the data revealed no major divergence within or among certain river populations, collation was by river drainage or by subspecies.

The cephalic tubercle counts were easily made, almost always without the use of any great magnification, because the developed tubercles, spots, buds, or scars are very large, comparatively few in number, and are readily discernible. There is no difficulty in obtaining accurate counts, unlike the problem in counting the smaller, numerous tubercles of members of the *Nocomis micropogon* group. The areas of the head referred to in tubercle distribution and location are given designations similar to those presented by Lachner and Jenkins (1971), such as: transverse anterior internasal line (AIN); posterior internasal (PIN); anterior interorbital (AIO); mid-interorbital (MIO); posterior interorbital (PIO); anterior occipital (AOC); mid-occipital (MOC); and posterior occipital (POC). The posterior development of tubercles was recorded as the line nearest the most posterior tubercle (or tubercles). The supraorbital tubercles were not considered in the above designations since they have a comparatively similar development in all three forms, and are independent of the progressive development of the principal head tubercles with increase in body length.

The distribution and number of head tubercles are the two main characters involved in the separation of the subspecies of *N. leptocephalus*. These two characters were also of primary importance in the differentiation of the species of the micropogon group. A detailed discussion of tuberculation in *Nocomis* is presented by Lachner and Jenkins (1971). The total number of head tubercles for *N. l. leptocephalus* in the northern part of its range is summarized by size groups in Table 1. Because significant differentiation in the number of head tubercles occurred in each of the two southern river populations of *N. l. leptocephalus* (Pee Dee and Santee), these are summarized separately by size groups in Tables 2 and 3. No notable differences were observed in total number of head tubercles for the new subspecies in the Savannah, Altamaha, and Chattahoochee (Apalachicola) river drainages, and the data in Table 4 were combined and summarized by size groups; the same was done in Table 5 for similar tubercle data for *N. l. bellicus* from the Alabama River westward to tributaries of the Mississippi River. The allometric relationship of increase in tubercle number with increase in body size for these five diverged populations is shown in Figure 1. The curves were drawn to best fit the means of the body-length groups. The data for these curves are based on a sample of 2,467 specimens, including 196 *N. l. bellicus;* 663 *N. l. interocularis;* and 843 Santee, 160 Pee Dee, and 605 northern specimens of *N. l. leptocephalus.*

The total number of cephalic tubercles of specimens ranging in size from juveniles to adults and segregated by subspecies, intergrades, and major river drainages is summarized in Table 6. This summary shows the difficulty in identifying juvenile specimens, particularly those involving the subspecies *N. l. leptocephalus* and *N. l. interocularis.* Because of the allometric growth relationship of the number of tubercles with body length, specimens 90 mm SL and larger are compared by subspecies, intergrades, and river drainages in Table 7. Most specimens of the bluehead chub are mature at about 90 to 100 mm, and at this size the full complement of tubercles is present in all populations except for *N. l. leptocephalus* in the Santee–Pee Dee drainages (see Figure 1). Figure 2 shows the mean (Av.), range, standard deviation (SD), and the mean $\pm$ two standard errors for the total number of tubercles in the five populations. The values are illustrated for two size groups, 70 to 79 mm SL and all specimens 90 mm SL or greater. The statistical data for this graph are given in Table 11. The differences are much less in the smaller size group, and only the adult or subadult specimens are of practical systematic importance in this problem.

In order to demonstrate the sharp breaks in tubercle numbers among the three subspecies, the southern drainage populations of *N. l. leptocephalus* are compared with *N. l. interocularis* and *N. l. bellicus* in specimens greater than 65 mm, but excluding the supraorbital tubercles (Table 8). Supraorbital tubercles vary somewhat by subspecies, averaging notably fewer in *N. l. bellicus.*

Frequency distributions comparing the occurrence of tubercles posteriorly on the head, segregated by subspecies and river drainages, are given in Table 9. The relationship between body length and the extent of posterior development of head

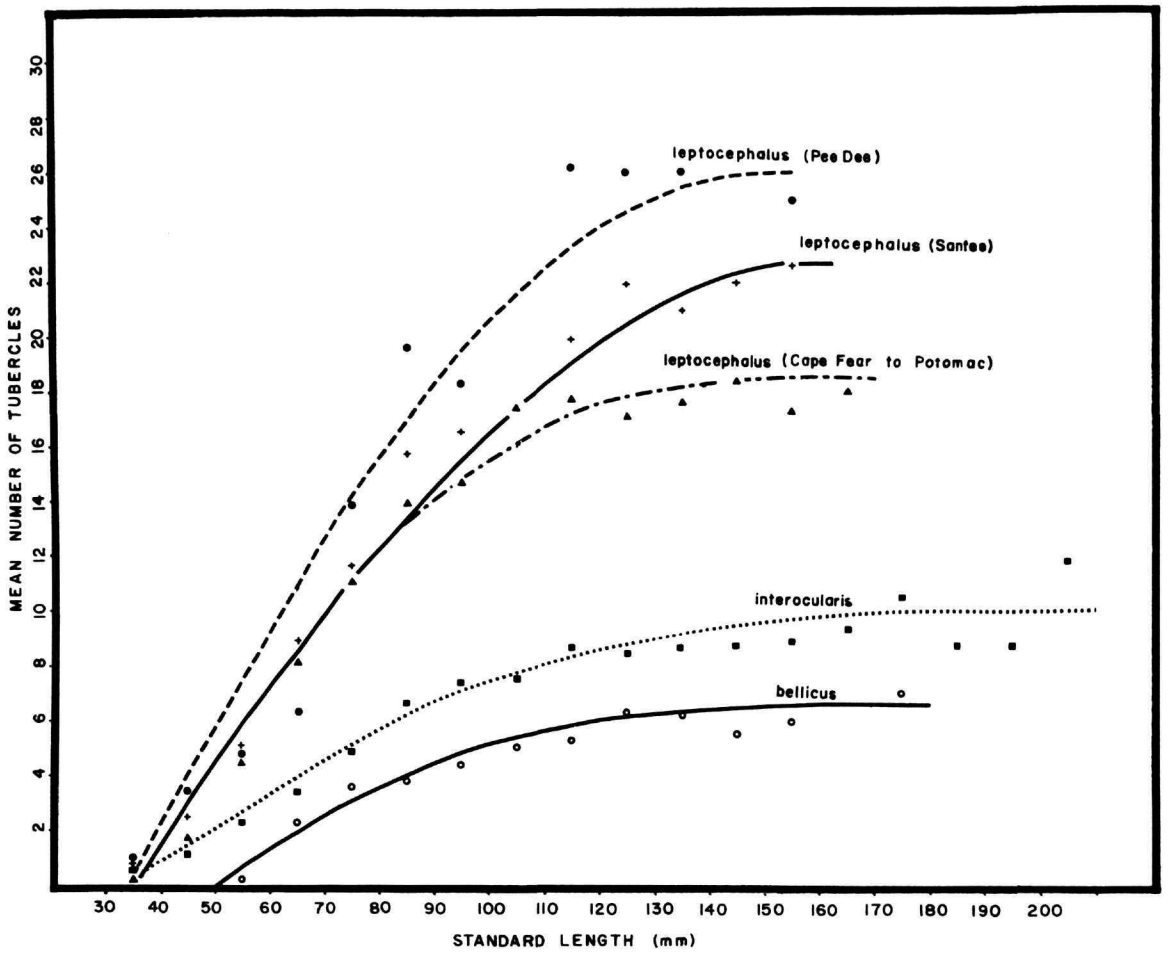

FIGURE 1.—The relationship between body length and number of head tubercles in three subspecies of *N. leptocephalus*. Three populations of *N. l. leptocephalus* are also compared. The curves were fitted to the mean values by inspection. Data for the sexes were combined. The mean values were plotted from data in Tables 1 through 5.

tubercles is summarized by size groups for the Santee River drainage in Table 10.

Vertebral numbers, pharyngeal dentition counts, and circumferential and lateral-line scale numbers are compared by subspecies and by various drainages in Table 12, 13, and 14.

Because of the large number of specimens examined and identified, only the river drainage and the museum catalog number are given in the "Appendix: Specimens Studied" (pages 34–35) for *N. l. leptocephalus* and *N. l. bellicus*. "Appendix: Specimens Studied" (pages 30–34) for *N. l. interocularis* includes the collections for each river system grouped by state and county. Also given are museum catalog number, date of collection, number of specimens (in parentheses), tributary, and locality. Type material is designated only from the Savannah River drainage. Collection data pertaining to the intergrades are listed separately on page 35.

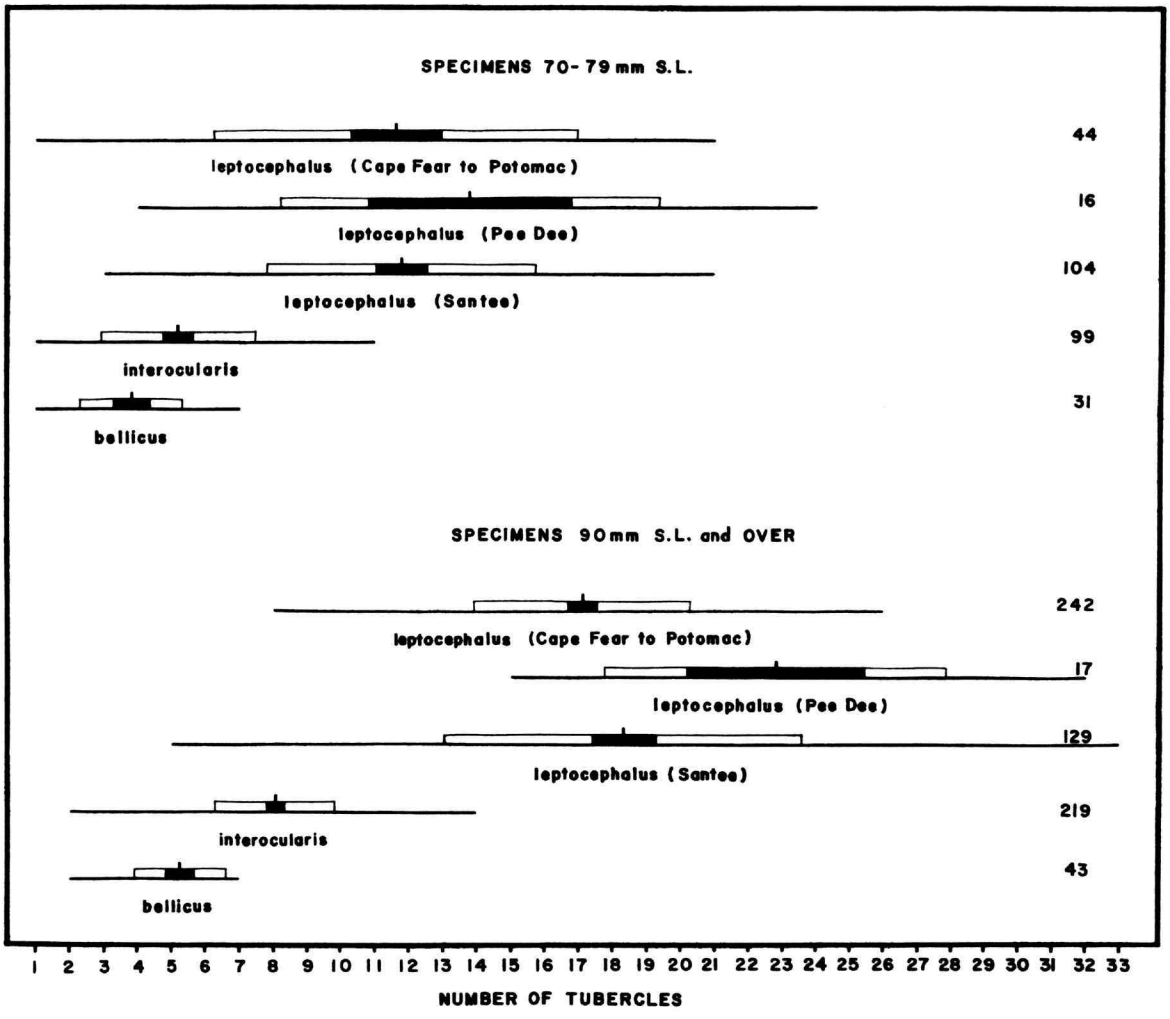

FIGURE 2.—A comparison of the number of cephalic tubercles in two size groups of five populations of *N. leptocephalus*. The graph is based on data presented in Table 11. The following statistics are illustrated: the small vertical line, mean; horizontal line, range; clear bar, mean ± one standard deviation; dark bar, mean ± two standard errors (After Hubbs and Perlmutter, 1942, American Naturalist, volume 76, pages 582–592). The magnitude of difference among the populations is not nearly as great in the 70–79 mm size group as in the size groups 90 mm SL and over.

Nocomis leptocephalus (Girard)

The description, ecology, distribution, dispersal, and evolution of *N. leptocephalus* were treated by Lachner and Jenkins (1971) and compared with the micropogon group, because the several species are sympatric in the central Appalachians. Only the descriptive data which show some measure of divergence and of possible intraspecific systematic value or of evolutionary significance are presented below.

In our preliminary analysis when we had but a

few mature specimens of the *N. l. interocularis–bellicus* forms and when we had not yet examined all museum collections of *N. leptocephalus,* we presumed that the morphological differences were of a clinal nature. The two major characters, number of tubercles and the extent of the posterior distribution on the head, appeared to have higher values and to extend farther back on the head in the northern river populations, while there were progressively lower numbers and a reduction in extent of posterior distribution toward the south and southwestern portion of the range. This concept was abandoned when collections from all the major rivers became available and analysis of the data was made. Two major breaks are discernible in the data of Tables 6 through 9 and 11—one between the Santee and Savannah drainages and the second between the Chattahoochee and the Alabama rivers systems. The three major populations separated by these drainages are within themselves homogeneous in respect to cephalic tubercle numbers and distribution, especially the two southern forms, *N. l. interocularis* and *N. l. bellicus.* The northern form, *N. l. leptocephalus,* diverged significantly in tubercle numbers in both the Pee Dee and Santee drainages, when compared with drainages farther northward and across the Appalachian Divide into the New River system. This divergence was also another factor for dropping the clinal theory, because the higher tubercle values occurred in drainages where lower values would be expected for proper clinal relationships.

The comparatively small population of *N. leptocephalus* in the Edisto River drainage shows intermediacy in characters between *N. l. leptocephalus* and *N. l. interocularis.* This small river, located below the fall line, at one time may have provided a more abundant habitat for the bluehead chub. The number of tubercles of mature Edisto specimens is nearly intermediate between that of specimens of the adjacent Savannah and Santee populations, but the posterior distribution on the head is fairly extensive, approaching that of *N. l. leptocephalus.*

The taxonomic rank that we propose for these populations is influenced by the magnitude of the two major character breaks as well as the intermediate nature of the Edisto population. We recognize three highly diverged subspecies: *N. l. leptocephalus; N. l. interocularis,* new subspecies; and *N. l. bellicus.* The Edisto population is considered to be an intergrade of *N. l. interocularis* × *N. l. leptocephalus.* All nuptial males of *N. l. bellicus* are distinct from *N. l. interocularis.* Only a few nuptial specimens of the latter form show overlap with the typical form; however, since the distinguishing characters are so greatly influenced by allometric growth, it is practically impossible to demonstrate this divergence when attempting to identify a few specimens. The "polytypic species" concept associates evolution with differentiation of these forms. The exact status of *N. leptocephalus* will remain in doubt until we have experimental data. The reproductive behavior involves elaborate nest construction and requires a comparatively spacious reproductive area, thus indoor breeding and rearing studies may be impossible. Since we now have a great amount of information on reproduction, reproductive ecology, breeding behavior, and hybridization in *N. leptocephalus* (as well as most of the other species of *Nocomis*), it would be more feasible to conduct breeding experiments in selected, small natural streams. It would be interesting and easy to place together stocks of the two most divergent forms, *N. l. bellicus* and *N. l. leptocephalus.*

A comparison of the major characters of the three subspecies is given in Table 15.

Nocomis leptocephalus interocularis, new subspecies

PLATES 1, 2, 4, 5; FIGURE 3

Ceratichthys biguttatus.—Jordan and Brayton, 1878: 38, 43.
Nocomis leptocephalus.—Fowler, 1945: 26 [part], 168, 232 [part].

ETYMOLOGY.—The subspecific name, *interocularis,* refers to the characteristic occurrence of tubercles posteriorly to the interorbital area of the head.

HOLOTYPE.—USNM 200757. North Carolina, Transylvania Co., Toxaway R. just below Lake Toxaway Dam. Caught on hook and line. 15 May 1966.

SPECIMENS STUDIED.—A total of 4,083 specimens from 4 drainages, as shown in the tabulation on page 2, were studied. For a listing by localities, see Appendix, pages 30–34.

DIAGNOSIS.—Tuberculation intermediate between *N. l. leptocephalus* and *N. l. bellicus;* total number of head tubercles averages 8, ranges from 7 to 9 in 95 percent of adults and subadults, and does not exceed 14 in study material; tubercle distribution on head not extending posteriorly beyond anterior occipital area, almost always before mid-interorbital area.

DESCRIPTION AND COMPARISON.—*Tuberculation. Body length at first tubercle appearance.* The light tubercle spots are first visible in juvenile specimens of varying sizes. Young-of-year specimens do not show visible spots. A few specimens of *N. l. interocularis* develop one or two spots at 30 to 39 mm. At 40 to 49 mm, 30 of 56 specimens had developed from one to five spots. A few females, 80 to 109 mm, had no visible spots. In the northern population of *N. l. leptocephalus* (Cape Fear River and northward), only a few specimens in the 30 to 39 mm size group had one or two spots, but in the 40 to 49 mm group 67 percent had one to seven spots; almost all specimens above 50 mm had spots. The spots first appear in the Santee and Pee Dee populations at sizes similar to the northern *N. l. leptocephalus.* The spots appear in *N. l. bellicus* at somewhat larger sizes; none were observed in the 30 to 39 mm and 40 to 49 mm size groups. At 50 to 59 mm, only 14 percent had one or two spots; at 60 to 69 mm, 76 percent had one to five spots, nearly the full compliment. All but one specimen examined above 70 mm had spots.

Development of tubercles. The anterior orbital spots usually develop first at about 40 mm in *N. l. interocularis,* followed by the internasal to post-internasal spots at about 50 to 60 mm; the two postorbital spots appear last, at 70 to 80 mm. The development is somewhat similar in the two other subspecies, except that *N. l. leptocephalus* often develops one or two more supraorbital tubercles on each side, and *N. l. bellicus* may lack the posterior supraorbital tubercle. A number of specimens in the Pee Dee population at 70 to 80 mm lack supraorbital tubercles.

Time of budding. Small tubercles or buds may appear in specimens captured in any month of the year, as in the micropogon species group. Development is associated with maturity, and the variable and more rapid rate of growth of some of the males enhances tubercle growth. A few males may have nearly completely developed tubercles in the months of October and November, and slight head swellings may also appear. A 143 mm male from the Santee River drainage had small tubercles when captured in mid-August. No differences in time of budding among the three subspecies was observed, but we lack comparative monthly samples.

Crowding of tubercles at the IN and PIN areas. The tubercles develop very uniformly in the internasal and posterior-internasal area of *N. l. interocularis* (Plate 5, middle, and Figure 3); in *N. l. bellicus* the development is the same except that in almost all specimens the PIN tubercles are absent, leaving only a pair of tubercles in the IN area (Plate 5, lower). There is slight crowding of tubercles in the northern population of *N. l. leptocephalus* (Plate 6, upper), but there is a characteristic and considerable crowding in the Pee Dee and Santee populations (Plate 5, upper, and Plate 6,

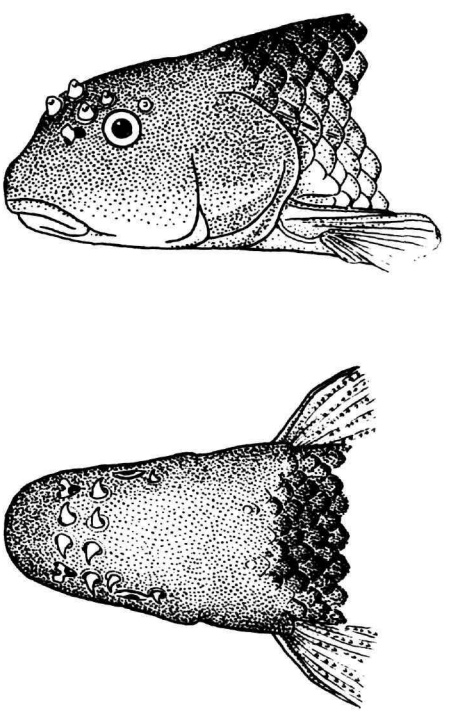

FIGURE 3.—Lateral and dorsal view of tuberculate head of male *N. l. interocularis,* with small crest, 154 mm SL, captured 31 March 1949 from the Altamaha River drainage. (USNM 161701. Drawn by A. M. Awl.)

lower). The increased tuberculation of these populations is not spread uniformly over the head, but occurs in the internasal–interocular area. The occipital tuberculation is less crowded, having only a few tubercles more than the same area in specimens of the northern population. Some tubercles occasionally appear just anterior to the nares in the Pee Dee River population.

Supernumerary nape tubercles. Small spots and, rarely, small buds occur on the nape just before the scaled area; usually a pair is present (Figure 3, bottom), but sometimes there is only one. They occur most often in *N. l. interocularis* (Savannah River, 5 specimens; Altamaha, 1 specimen) and the Santee population (6 specimens) of *N. l. leptocephalus*. Only one specimen in over 9,000 of the northern population of *N. l. leptocephalus* examined had such spots; none were observed in *N. l. bellicus*. These spots may be the remnants of a once fuller and more extensive tuberculation in the precursors of the present *N. leptocephalus*. We have not seen similar spots in other species of *Nocomis* where they could be easily observed, as in the micropogon group.

Rate of increase of tubercles. The general increase in tubercle numbers with increase in body length for five populations of *N. leptocephalus* is illustrated graphically in Figure 1. The slopes of the curves level off at about 100 mm for *N. l. bellicus, N. l. interocularis,* and the northern population of *N. l. leptocephalus*. The curves for the Santee–Pee Dee populations level off at about 120 mm. Neither maximum body size nor growth rate is a factor in tubercle growth rate. The largest bluehead chubs that have been collected are seven male *N. l. interocularis* from the Savannah River drainage (Toxaway River above Lake Toxaway), all of which exceed 200 mm SL and have the normal number of tubercles for that subspecies. At about 50 mm, when *N. l. bellicus* commences to have 1 visible tubercle spot, *N. l. interocularis* averages about 2, and the Pee Dee population of *N. l. leptocephalus* averages about 6. At the 100-mm size group, *N. l. bellicus* averages about 5 tubercles, *N. l. interocularis* about 8, the northern population of *N. l. leptocephalus* about 17, the Santee about 18, and the Pee Dee over 20. The rate of tubercle increase with increase in body length is given for *N. l. interocularis* in Table 4; *N. l. bellicus,* Table 5; the northern race of *N. l. leptocephalus* in Table 1; and the Pee Dee–Santee race in Tables 2 and 3.

Number of tubercles. The total number of cephalic tubercles is a primary character in the separation of the three subspecies. *N. l. interocularis* is the intermediate form, averaging about 8 in the adult–subadult specimens, ranging from about 7 to 9 in 95 percent of the study material and never exceeding 14; *N. l. bellicus* averages about 5, with 4 to 6 in 95 percent of the study sample, and the maximum number does not exceed 7; *N. l. leptocephalus* averages 17 or more in the races, ranging from 16 to 25, and the maximum number was 33. The comparative uniformity in the total number of tubercles present in *N. l. interocularis* and *N. l. bellicus* by river drainages is shown in Tables 6, 7, and 8. The higher maximum numbers in the Pee Dee–Santee race compared to the northern race of *N. l. leptocephalus* is also shown in these Tables. The three subspecies show a significant differentiation in the total tubercle count at the 70 to 79 mm size group and more so at 90 mm and over (see Figure 2 and Table 11). The differences in the means of the Pee Dee and Santee populations may be due to the small Pee Dee sample and, also, that the lower values of the Congaree and Saluda rivers, Santee drainage, were lumped with the Catawba–Broad rivers specimens (Table 6). The data in Table 8 show the high number of tubercles in the internasal–posterior internasal area for the Santee and Pee Dee drainages compared with the lower values for *N. l. interocularis* and *N. l. bellicus*. The crowding is somewhat greater in the Catawba River, Santee drainage, than in the Pee Dee drainage, and more so in the Catawba than the Broad–Congaree–Saluda rivers.

The largest *N. l. interocularis* females were in the 140 to 149 mm and 150 to 159 mm size groups and these three specimens had an average tubercle complement of eight. Some specimens, much smaller than these, in the 70 to 79 mm and 80 to 89 mm groups had more tubercle spots (Table 4). There is considerable variation in tubercle numbers within size groups, the greatest occurring among the juvenile sizes (Tables 1 to 5). Both sexes showed this variation. There were only small tubercle differences between the sexes in most size groups among the three subspecies, the males aver-

aging slightly higher numbers. Greater tubercle differences occurred between the sexes in the Santee population (Table 3). The males in all subspecies attain the larger size, as shown in Tables 1 to 5. This is also true for all other species of *Nocomis*.

Occurrence of head tubercles. The progressive development of tubercles posteriorly on the head is shown in Table 10 for *N. l. leptocephalus* from the Santee River drainage. While the general trend is an increase in posterior occurrence of tubercles with an increase in body size, specimens of both sexes in the juvenile or subadult size group of 70 to 79 mm have the definitive tubercle distribution in the posterior occipital area. All drainage populations of *N. l. leptocephalus* over 60 mm (Table 9) have the majority of specimens with tubercles (buds or spots) already present in the mid-occipital or post-occipital areas. The occurrence of head tubercles in particular areas is one of the best characters for separation of the subspecies (Tables 9 and 15). All nuptial males of the three subspecies can be distinguished by this character, no overlap in tubercle distribution occurring. Specific rank for these populations was not accorded because of the intergrading Edisto population. Table 9 shows that a small juvenile of *N. l. leptocephalus* just showing tubercle spots has a tubercle pattern similar to an adult *N. l. bellicus*. Tubercle distribution, as in tubercle numbers, is comparatively homogeneous within each subspecies. The evolution of the tuberculation has resulted in major character breaks in which three highly differentiated subspecies can be recognized.

Nuptial crests. A discussion of the nuptial crests in *Nocomis* is given by Lachner and Jenkins (1971). The three subspecies of *N. leptocephalus* appear to develop different sized crests (Table 15); *N. l. interocularis* (Plate 2) has a crest intermediate in size between the smaller one of *N. l. bellicus* (Plate 7) and the larger one of *N. l. leptocephalus* (Plate 3). We lack sufficient comparative material to accurately determine this possible differential development.

Vertebral Numbers. The total number of vertebrae ranged from 38 to 41 in the three subspecies (Table 12). *N. l. interocularis* had 40 vertebrae in 86 percent of counts and *N. l. bellicus* had 39 or fewer vertebrae in 88 percent of counts. The northern river drainages of *N. l. leptocephalus* had higher values, approaching 40, compared to those south of the James which had modal values of 39. The Edisto intergrades showed a good intermediate trend (39.4) between those of *N. l. interocularis* (about 40) and those of the southern rivers of *N. l. leptocephalus* (about 39).

Dentition. The number of pharyngeal teeth in all three subspecies (Table 13) is almost always 4–4 (83 specimens); five specimens had 4–3 or 3–4; three had 3–3 ;and one had 2–4. Most of the tooth reduction occurred in *N. l. leptocephalus.* (See Lachner and Jenkins, 1971, for discussion of evolutionary significance of tooth reduction in *Nocomis*).

Squamation. Initial studies suggested possible scale differences among the three subspecies. When samples were increased and selected from many localities within and among river drainages, the results showed only small differences which were of no use in identifying subspecies. Mainly, the mode shifted among the drainages involving one or sometimes two scales in the circumferential count and less in the lateral-line scale count. The difference in the circumferential count is a reflection of the degree of crowding of the belly scales. Lateral-line and circumferential scale counts are summarized in Table 14. In *N. l. interocularis* the Chattahoochee drainage specimens have somewhat lower values than those of the Savannah–Altamaha, and they are very similar to counts for *N. l. bellicus.* The scale counts for *N. l. leptocephalus* were summarized chiefly from data used by Lachner and Jenkins (1971) in comparing scale differences in the four central Appalachian species of *Nocomis.*

Intestine. The whorled intestine characteristic of *N. l. leptocephalus* (for description and illustration, see Lachner and Jenkins 1971) does not hold up as a systematic character, mainly in *N. l. interocularis* of the Chattahoochee River drainage. A highly or moderately whorled intestine is almost always found in *N. leptocephalus* over its range. A slightly whorled intestine is sometimes found in specimens from the Cape Fear, Saluda, and Broad rivers. The typical whorled condition is also found in the Savannah and Altamaha specimens of *N. l. interocularis* and over the range of *N. l. bellicus,* except for one collection. Over 200 specimens of *N. l. interocularis* in eight collections from the Chattahoochee River had straight intestines; other

specimens from these and other collections in the Chattahoochee had whorled intestines. The straight intestine condition resembles that of the micropogon group. The specimens are normal otherwise. One specimen of *N. l. bellicus* from a tributary of the Tallapoosa River, Alabama drainage, had a straight intestine. We associate no systematic trend to the occurrence of the straight intestine among these collections. It is a primitive condition in *Nocomis,* and the Chattahoochee specimens may represent merely reversions.

Nocomis leptocephalus leptocephalus (Girard)

PLATES 3–6

Ceratichthys leptocephalus Girard, 1856: 213 [type locality, Salem, North Carolina, probably Winston-Salem, from a tributary of Yadkin River, Pee Dee River drainage].
Nocomis leptocephalus.—Lachner and Jenkins, 1971: 50.

SPECIMENS STUDIED.—A total of 14,551 specimens from twelve drainages, as shown in the tabulation on page 2, were studied. For a listing by localities, see Appendix, pages 34–35.

Nocomis leptocephalus bellicus Girard

PLATES 4, 5, 7

Nocomis bellicus Girard, 1856, p. 213, [type locality, Black Warrior River, Alabama, Mobile Bay drainage].
Ceratichthys biguttatus.—Hay, 1881:512.
Hybopsis kentuckiensis.—Gilbert, 1891:154.
Hybopsis bellica.—Cook, 1959:132.
Nocomis leptocephalus.—Fowler, 1945:26 [part].
Nocomis leptocephalus bellicus.—Smith-Vaniz, 1968:42.

SPECIMENS STUDIED.—A total of 2,000 specimens from five drainages, as shown in the tabulation on page 2, were studied. For a listing by localities, see localities, see Appendix, page 35.

Nocomis leptocephalus intergrade *interocularis* × *leptocephalus*

SPECIMENS STUDIED.—A total of 155 specimens from the Edisto drainage, as shown in the tabulation on page 2, were studied. For a listing by localities, see Appendix, page 35.

Comparison. The development and occurrence of head tubercles of the Edisto River population is intermediate between *N. l. interocularis* and *N. l. leptocephalus.* The four adult specimens (Table 7) had 16 tubercles, a value higher than the mean (8) and maximum number (14) for *N. l. interocularis* but lower than the mean (17 in northern race, 18 in Santee, 23 in Pee Dee) and much lower than the maximum number (33) in *N. l. leptocephalus.* Further, intermediacy in tubercle numbers of the Edisto population compared with the above two subspecies is shown in a summary of all material that could be counted (Table 6), and in specimens over 65 mm SL, excluding the supraorbital tubercles, in Table 8. The intermediacy of the occurrence of tubercles posteriorly on the head in juveniles and adults (specimens over 60 mm SL) of the Edisto population is compared with the above two subspecies in Table 9. The mode for the Edisto population occurs on the AOC line, a fairly intermediate position between the AIO area, usual for *N. l. interocularis,* and the MOC–POC area, usual for *N. l. leptocephalus.*

The vertebral numbers of 39 (17 specimens), 40 (10), and 41 (1) of the Edisto population are additional intermediate values between the adjacent, southern drainage populations of *N. l. leptocephalus* (about 39 vertebrae) and *N. l. interocularis* (about 40 vertebrae).

The adult and subadult specimens from the Edisto drainage are insufficient to compare this population more precisely with the adjacent populations. The above comparisons of three characters show intermediate values for the Edisto population that are not found among the three drainages (Savannah, Altamaha, and Chattahoochee) in which *N. l. interocularis* occurs nor in drainages from the Santee northward inhabited by *N. l. leptocephalus.* We presume that the Edisto population has received *N. leptocephalus* stocks from both north and south, after these two stocks had diverged into *N. l. leptocephalus* and *N. l. interocularis.* Thus, the last entry of a *N. leptocephalus* stock into the Edisto was probably comparatively recent.

Coloration

The general coloration of *N. l. leptocephalus* is discussed and compared with the other species of *Nocomis* inhabiting the central Appalachian area

by Lachner and Jenkins (1971). Also described are two different primary color forms of *N. l. leptocephalus* among the living nuptial males. A form with a brassy orange-olive coloration on the body laterally and sometimes forming a stripe occurs in the northern race from the Cape Fear drainage northward. Another form with a bluish body occurs in the Pee Dee–Santee drainages.

The blue form also occurs in *N. l. interocularis* of the Savannah River drainage. Following is a description of a prenuptial male, 187 mm SL, collected on 15 May 1966 in Mill Creek, a tributary of Lake Toxaway, Savannah River drainage (USNM 200757). This coloration is characteristic of the Savannah drainage population. The specimen was captured with three females from beneath a cut bank near a nest. Its nuchal crest was not fully developed and the head tubercles were normally distributed, but were not enlarged as in some males. The nuchal crest was brown, the rest of the head slate-blue; eye, yellow-brown; opercular membrane, dark gray; dorsum of the body, brown with a few golden highlights on the postdorsal area; posterior margins of the scales dorsally on the sides above the lateral line, black; lateral band, diffuse, a greenish gray or olivaceous color; belly, bluish white; dorsal fin, slate-blue base with dark gray rays, the posterior having a yellow tinge, and the fin membrane, smoky; pectoral fins, smoky yellow, the rays grayish with the first ray darker; pelvics and anal fins, yellow with a gray cast; caudal fin, a burnt orange, the median rays darkest. A large gravid female in the same collection had the nuchal area and dorsum, brown, with a faint, light, predorsal stripe; lateral band, black with a narrow, diffuse, light brown stripe above and extended anteriorly and prominently onto the postocular area with a faint bar continuing to below the nostrils; opercular membrane, dark gray; body below the lateral band, yellowish; belly, white; dorsal and caudal fins, rust-orange; the other fins, a brownish yellow.

The following coloration was recorded from a living tuberculate, prenuptial male, 144 mm SL, captured in Amy's Creek, Habersham County, Georgia, Chattahoochee River drainage, on 2 April 1970 by Lachner and Wiley: dorsal fin, light pinkish orange, melanophores along base of dorsal fin; caudal fin, olive-orange, lighter near the base with melanophores along basal portion of rays; pectoral fin, deep pink-orange; pelvic fin, deep pink-orange with some white on first ray; anal fin, pink-orange, the outer edge lighter; iris, red; body above lateral line grayish with slight bronze; ventral part of head, light reddish; dorsal part of head, slightly tan to pale olive; belly white to milky. The head tubercles were moderately developed, but the head was only slightly swollen. A gravid female, 119 mm SL, captured with the above male, had the same general color pattern in life except that the fins were very light, showing only traces of color, and the body was pale.

Other color data on adult *N. l. interocularis* are from a color slide of a male, 164 mm SL, collected by E. C. Raney in the Chattahoochee River drainage, Georgia. This tuberculate, prenuptial male had light orange fins, the rays of the dorsal and caudal having a darker burnt orange color. Good comparative color data of nuptial males from the Altamaha drainage are not available.

Observations by the authors and others indicate that the breeding coloration of *N. l. bellicus* in the Alabama River system of the Mobile Bay drainage, Alabama, is essentially the same as the northern color form of *N. l. leptocephalus*, e.g., with the blue head and the lateral orange stripe anteriorly on the body changing to yellow caudally. A color description of a large, prenuptial male *N. l. bellicus* with large tubercles, was recorded from a fresh specimen captured on 16 March 1957 in the Alabama River system, Elmore County, Alabama, by R. D. Suttkus (RDS 2592). The sides of the head were bluish gray; head, dorsally, and entire nape posteriorly to origin of dorsal fin and down on the sides to lateral line, very brassy orange; rest of back and upper sides, bright olive; iris, bright orange-red; caudal fin, olive; leading edge of anal and pelvics, milky; remainder of anal, pelvics and pectorals, olive; dark bar on cleithrum immediately behind opercle. Smaller specimens in same collection have bright orange caudal fin, orangy dorsal fin, and bright orange iris.

A color description of a tuberculate postnuptial male, captured over a nest on 1 July 1965 by R. D. Suttkus (RDS 3717) in the Alabama River system, Clarke County, was recorded in the field as follows: head below lower margin of tubercles, below eye, and below top of opercular opening, pale blue; top

of head, golden brown; iris, bright red-orange; back and upper sides, brown with golden olive overlay; center of scales, golden, especially anteriorly on body and more yellow posteriorly on body; predorsal stripe, golden and broad, one scale row in width; postdorsal stripe tapering posteriorly and more yellowish than predorsal stripe; lower sides of body and belly, pale; pectoral fin, yellowish, the anterior one fourth bright yellow, the color pronounced on anterior rays; pelvic fins, yellowish, more so on anterior rays; dorsal fin, mostly olive, the base bluish, and some yellow on leading edge; caudal fin mostly yellowish olive; and anal fin, yellowish anteriorly, with branching areas of rays also yellowish as in pelvic fins.

A subadult *N. l. bellicus,* 107 mm SL, and a young specimen, 36 mm SL, taken by H. T. Boschung in a tributary of the Cahaba River system, Bibb County, 22 August 1967 (UAIC 2629–1), preserved in 10 percent formalin and ional solution, still retained lifelike colors in January 1968 (H. T. Boschung, personal communication). The larger specimen was colored as follows: body dorsally, dark olive above lateral line, and light olive from lateral line to about two scale rows below; lower body, light to pale; head, dark olive dorsally, light olive laterally, and light blue ventrally; body with no evident lateral band; dorsal fin, bright orange with some olive near base; caudal fin, bright orange; pectoral fins, light olive; pelvic fins, very light olive, with light posterior margins; and anal fin, light olive, with touches of orange along middle portion of rays, and the outer margin, light. The young specimen had the body light brown to dusky above the pronounced dark lateral band and light to dusky below the lateral band; dorsal fin, light orange, the outer margin light to slightly dusky; caudal fin, medium orange, the outer rays light to slightly dusky; and pectorals, pelvics, and anal fins, light to only slightly dusky.

Throughout its range, *N. leptocephalus* is commonly observed to have variable amounts of orange or reddish coloration in the dorsal and caudal fins (and, frequently, in the other fins) in young, juvenile, subadult male and female, and mature female stages.

There is great difficulty in evaluating color differences (aside from those associated with individual variations and populational differences), because of the gradual color changes related to growth and maturity. Also, among the nuptial males, the changes occur throughout the reproductive season and "peak" colors develop immediately at the time of spawning. The characteristic coloration of the nuptial males compared to that of nonnuptial males and all females is discussed by Lachner and Jenkins (1971). The elaborately developed nuptial coloration common to *Nocomis biguttatus, N. effusus, N. micropogon, N. raneyi,* and *N. platyrhynchus* is found in *N. leptocephalus,* except that the problem of interpreting the systematic significance of the coloration is compounded in the latter species by the presence of two basically different nuptial color patterns. The blue body form of *N. l. leptocephalus* of the Pee Dee and Santee river drainages is trenchantly different from the brassy reddish colored northern race of *N. l. leptocephalus* (in all drainages northward from the Cape Fear). These two color forms within *N. l. leptocephalus* correlate with the tubercle differences noted above, i.e., the northern race has fewer tubercles and is brassy reddish while the southern race has more tubercles and is blue. A similar blue color form appears to be typical for *N. l. interocularis.* We are not certain if the nuptial males of the Altamaha drainage develop the blue coloration typical of *N. l. interocularis* of the Savannah drainage. The orange-olive color form reappears in the Alabama drainage and westward in *N. l. bellicus.* In this subspecies, the nuptial males appear to have brighter orange-red colors in the fins than the northern race of *N. l. leptocephalus.* Most significant is the fact that great differentiation in nuptial coloration has occurred within *N. l. leptocephalus,* and probably *N. l. interocularis* and *N. l. bellicus* are also completely different in nuptial coloration.

Geographic Distribution and Ecology

The extensive distribution of *N. leptocephalus* along the Atlantic and Gulf Coast drainages is shown in Figure 4. Collections of the three subspecies and the Edisto intergrades are individually plotted and their distributions are shown in respect to the fall line and the Appalachian Divide. The distribution of *N. l. leptocephalus* is discussed by Lachner and Jenkins (1971) in detail where the northern race occurs sympatrically with three other

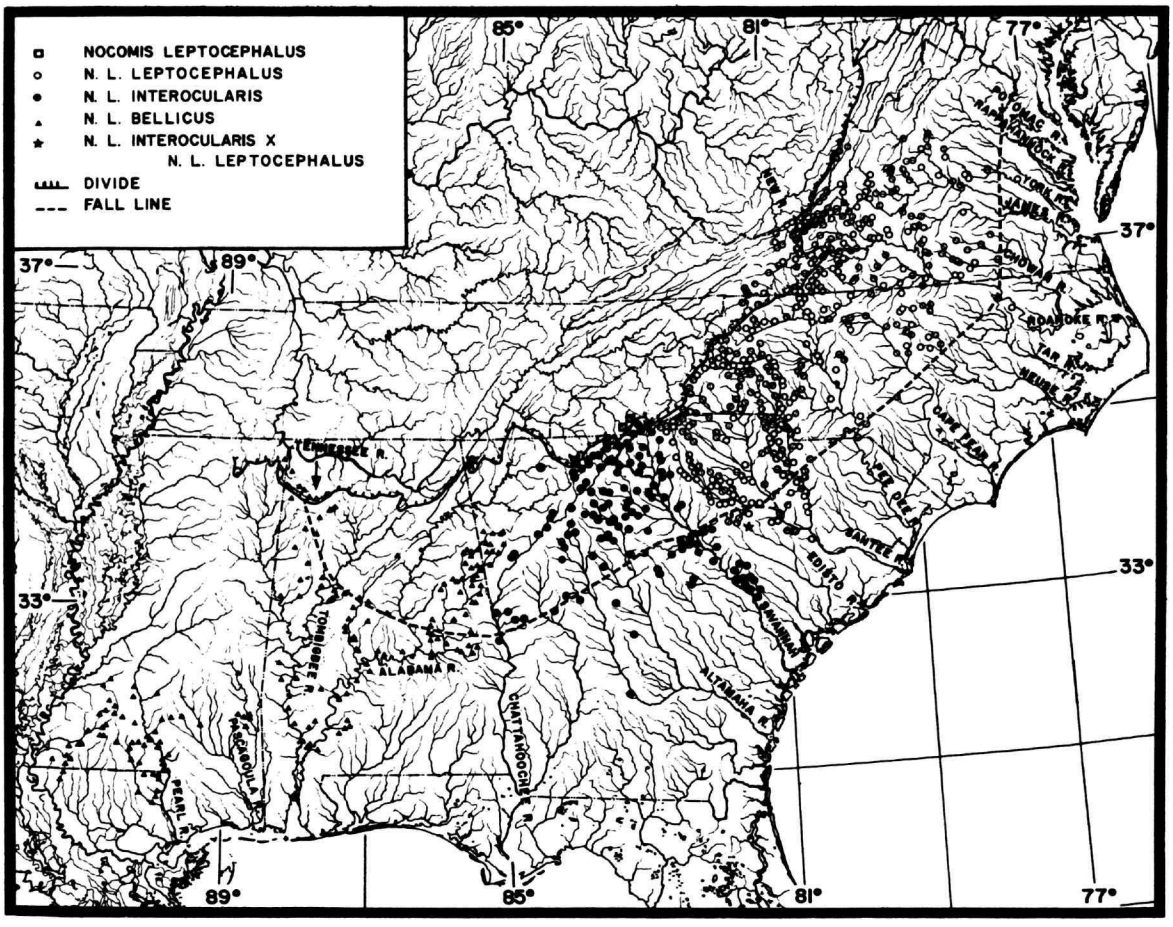

FIGURE 4.— The distribution of *N. leptocephalus*. The three subspecies are plotted with separate symbols. The intergrades, *N. l. interocularis* × *N. l. leptocephalus*, in the Edisto drainage are indicated by a single star, but several collections are actually represented by this plot. When two or more collections were made at (or near) a locality, only one was plotted. The single plot in northern Alabama of *N. l. bellicus* in the Tennessee drainage also represents several collections. The two squares representing *N. leptocephalus* in southeast Tennessee, Tennessee drainage, are based on small specimens and could not be identified to subspecies with assurance. Data for plots are listed in the text, and those that merit special attention are discussed. The Appalachian Divide and the fall line are indicated.

species of *Nocomis* in certain river drainages. *N. l. leptocephalus* is widely distributed in the James drainage, and in limited headwater localities of the Rappahannock and Potomac drainages, where it occurs sympatrically with *N. micropogon*. Across the divide in the middle and upper New River system, its distribution overlaps considerably with *N. platyrhynchus*. In portions of the James, Chowan, Roanoke, Tar, and Neuse drainages, it is more or less commonly associated with *N. raneyi*.

N. l. interocularis is widely distributed in the Savannah and Altamaha drainages, occurring far below the fall line. All of our records occur above the fall line in the Chattahoochee system. *N. mi-*

cropogon is associated with *N. l. interocularis* in the upper Savannah drainage, where the former was probably derived by stream capture from the Little Tennessee River, Tennessee drainage. The presence of *N. leptocephalus* in a restricted area of the Tennessee drainage of North Carolina (probably *N. l. interocularis*) may be associated with stream capture with the Savannah drainage (see discussion by Lachner and Jenkins, 1971). We have examined two collections from this area, totaling eight specimens, all of which were young or juveniles (TU 29663, six specimens, Cedar Creek, tributary to Lake Thorpe, 4.4 mi north of Cashiers, Jackson County; TU 28001, two specimens, Little Tennessee River, Cullasaja River, above Cullasaja Falls, 4.3 mi NW of Highlands, Macon County). Here, *N. leptocephalus* is again sympatric with the widely distributed *N. micropogon* of the Tennessee drainage.

The one plot of *N. l. interocularis* in the upper Coosa River system is based on a typical male specimen, 118 mm SL, captured by R. D. Suttkus in Cartecay River, 7.8 mi SE of Ellijay, Gilmer County, Georgia, on 18 June 1965 (TU 38213). William F. Smith-Vaniz (personal communication) informs us that there is considerable bait fishing in the impounded waters of the area. Populations of *N. l. interocularis* in the nearby Chattahoochee drainage are a ready source of bait. Several species of fishes, including *Nocomis* (Figure 4), are apparently prevented from entry into the Coosa River system by the falls at the Fall Line (Smith-Vaniz, 1968:124, 130).

The southwestern subspecies, *N. l. bellicus*, finding suitable habitat below the fall line, occurs from the Alabama River system westward to certain tributaries flowing into the Mississippi River from the east. It also is common in a restricted area of the Tennessee drainage, where B. R. Wall, Jr., (personal communication) has obtained collections in more than twenty localities of the Bear Creek system (indicated in Figure 4 by one plot mark). Smith-Vaniz (1968:124) cites headwater stream capture in the area involving the Tennessee and the Tombigbee rivers systems and lists four species other than *N. l. bellicus* that also made entry into the Tennessee River from the Tombigbee River system. The presence of *N. micropogon* as well as many other species, in the Coosawatee system, Coosa-Alabama drainage, is probably the result of a stream capture with the Hiwassee system of the Tennessee drainage.

The ecology of *N. leptocephalus* is reviewed by Lachner and Jenkins (1971). Over its large range, the bluehead chub is one of the most abundant species, preferring small stream habitats of about 10 to 50 feet in width and avoiding the larger streams and rivers as well as the extreme headwaters. Clear streams of gravel-rubble bottom composition, particularly current-swept areas, are preferred and necessary for these gravel-mound nest-building chubs (Plate 8). Slack waters are avoided, although the species thrives and is abundant in typical Piedmont streams where lower gradients, sandy bottoms, shifting sands, and some turbidity are characteristic of the habitat, but in these areas some gravel-rubble riffles also occur. The rarity of the bluehead chub along the middle-Atlantic Coastal Plain is probably related to the general absence of riffles or exposed gravel and rubble; however, these ecological conditions also prevail below the fall line of the southern Gulf Coastal area. The widespread distribution of the chub is undoubtedly related to its ability to survive Piedmont and certain Coastal Plain conditions. It probably was able to enter new drainages by way of the mouths of adjacent streams during intermittent periods of sea-level recessions, as well as to enter new drainages by stream capture, because of its ability to survive in relatively small, headwater streams.

Evolution and Dispersal

Lachner and Jenkins (1971) present a detailed account of routes of dispersal in the central Appalachian area.

The enlargement and loss of tubercles probably represents an advanced condition in *Nocomis*. The adaptive significance of large, stout, nuptial tubercles is not known. They would serve as effective weapons in agonistic behavior but nuptial males of *N. leptocephalus*, unlike some other species of *Nocomis* that have smaller, more numerous tubercles on the head, have not been observed to engage in either prolonged or violent fighting or both during the nest-building activities of reproduction. It may be that the large, easily visible tubercles

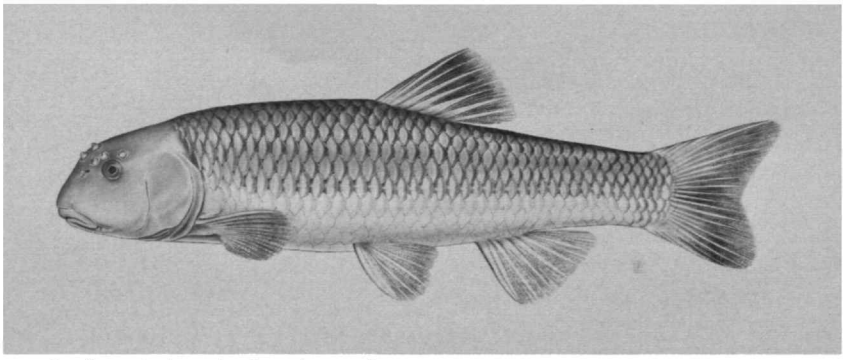

PLATE 1.—Lateral view of tuberculate male *N. l. interocularis*, 154 mm SL, from the Altamaha drainage. (Specimen same as in Figure 3, USNM 161701. Drawn by Carolyn Bartlett Gast.)

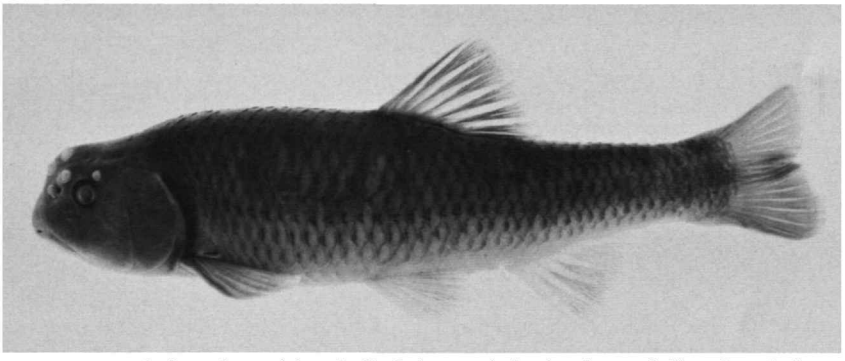

PLATE 2.—Lateral view of nuptial male *N. l. interocularis*, showing cephalic tuberculation and anterior position of moderately developed crest. Photograph of a paratype, USNM 200176, 156 mm SL from the Savannah River drainage, captured 8 July 1957.

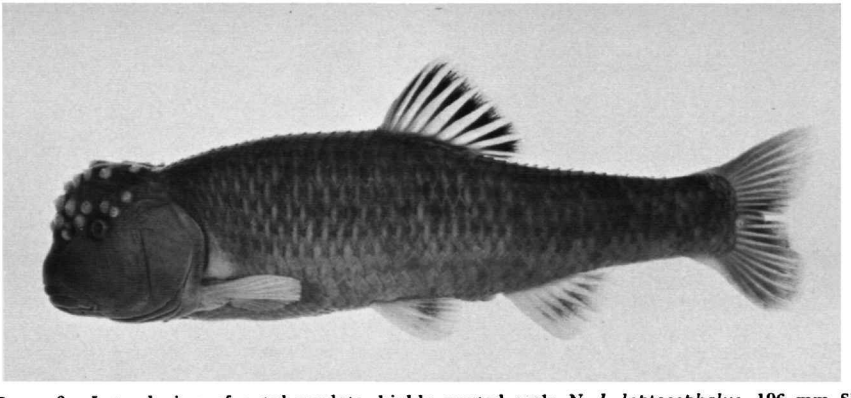

PLATE 3.—Lateral view of a tuberculate, highly crested male *N. l. leptocephalus*, 196 mm SL, captured 16 May 1966, from the Santee River drainage. This specimen (USNM 200758) illustrates the crowding of tubercles (numbering 29) in the Santee–Pee Dee populations.

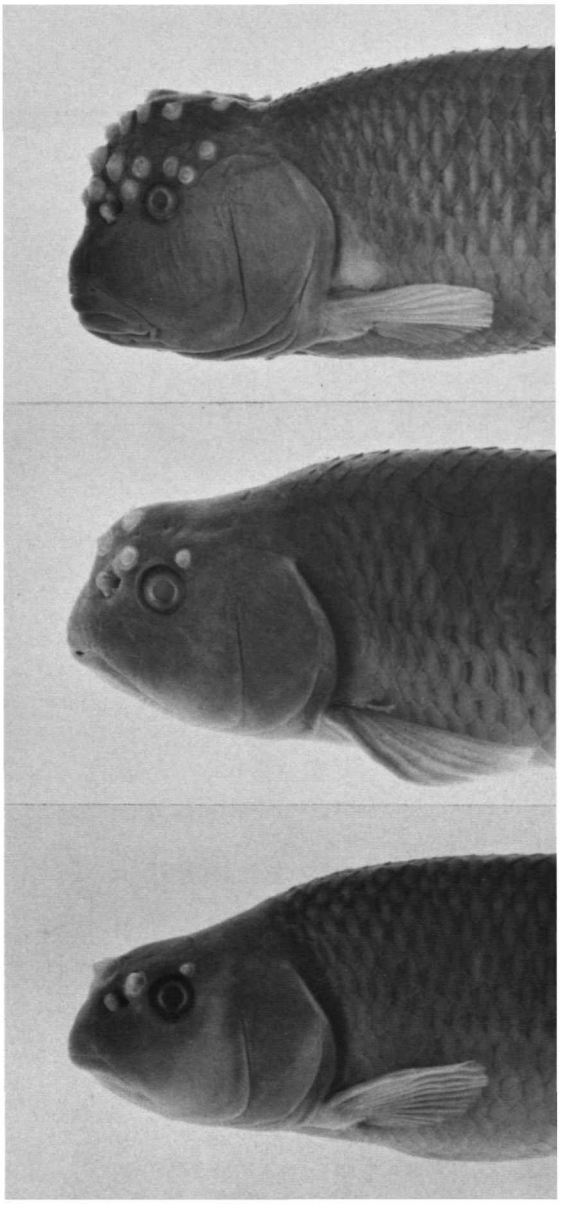

PLATE 4.—Lateral head profiles comparing the tuberculate males of three subspecies of *N. leptocephalus: upper, N. l. leptocephalus,* USNM 200758, Santee drainage, 196 mm SL, captured 16 May 1966 (29 tubercles); middle, *N. l. interocularis,* USNM 200176, Savannah drainage, 156 mm SL, captured 8 July 1957 (8 tubercles); and lower, *N. l. bellicus,* USNM 200756, Mobile Bay drainage, 145 mm SL, captured 3 May 1966 (5 tubercles).

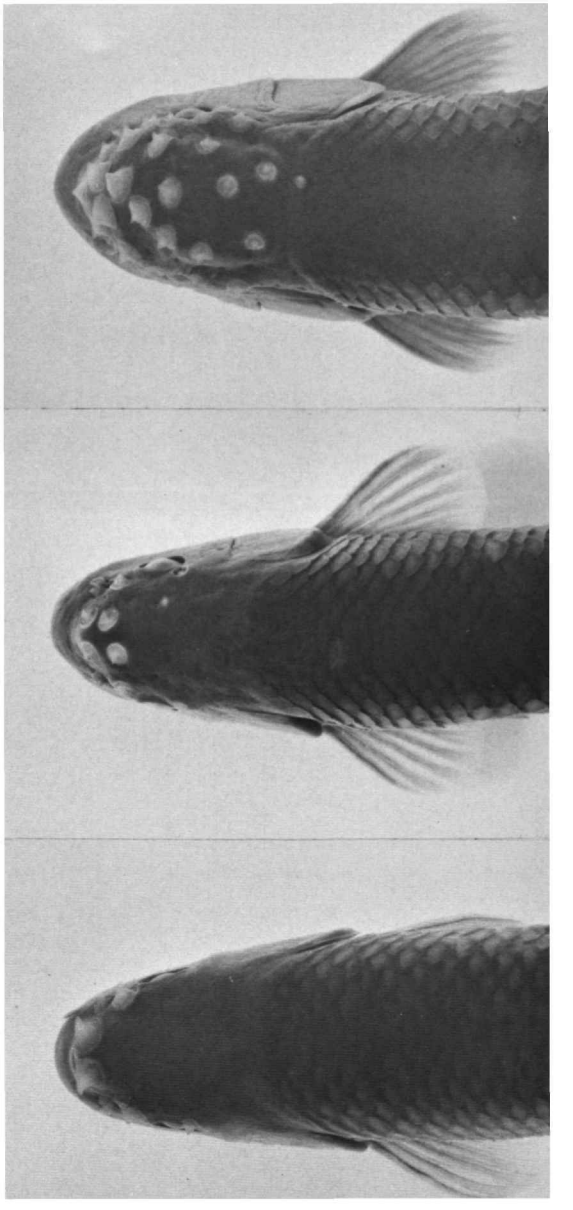

PLATE 5.—Dorsal head profiles comparing the tuberculate males of three subspecies of *N. leptocephalus* (data as in Plate 4): upper, *N. l. leptocephalus;* middle, *N. l. interocularis;* and lower, *N. l. bellicus.*

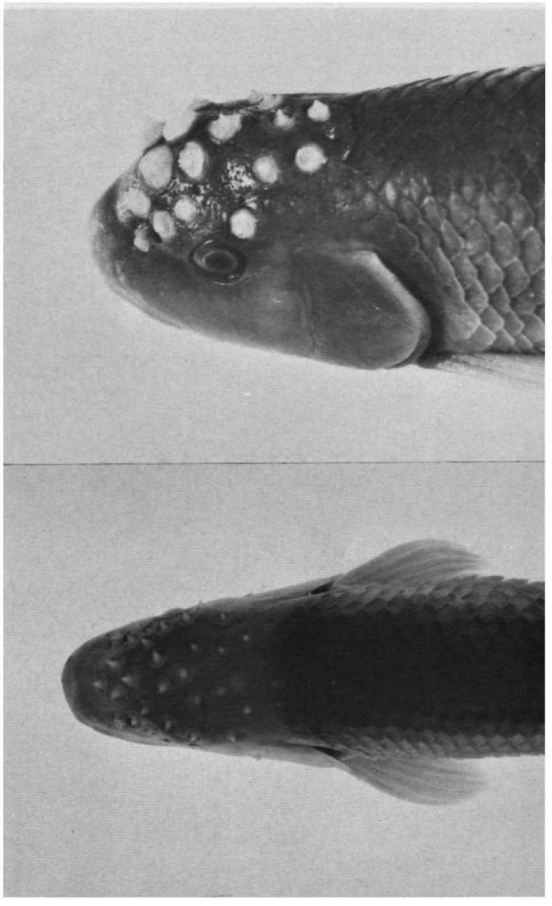

PLATE 6.—Dorso-lateral and dorsal profiles of heads of male *N. l. leptocephalus* representing typical tuberculation patterns of the northern (upper photograph) and southern (lower) races. Upper specimen is from Brush Creek, New River system, Montgomery Co., Virginia, captured June 1951, 140 mm SL with 17 tubercles ((photograph courtesy of Edward C. Raney, field number 2027). Note large tubercles on anterior head and very little crowding compared with specimen shown below. Lower specimen is from a tributary of the Catawba River, Santee drainage, McDowell Co., North Carolina, captured 1 May 1966, 157 mm SL with 31 tubercles.

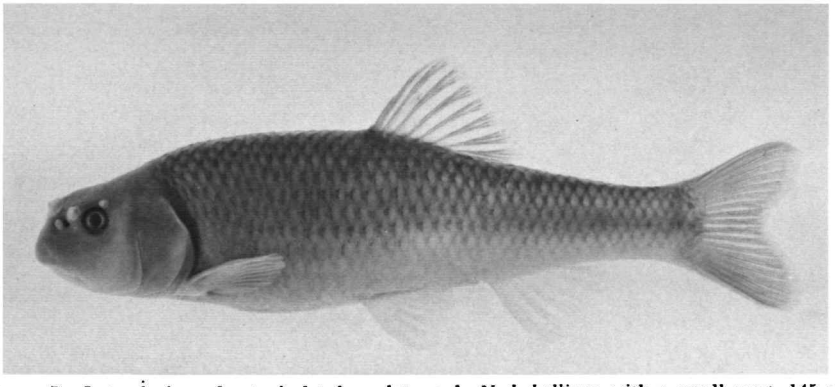

PLATE 7.—Lateral view of a typical tuberculate male *N. l. bellicus*, with a small crest, 145 mm SL, captured 3 May 1966, from a Tallapoosa River tributary, Mobile Bay drainage (USNM 200756).

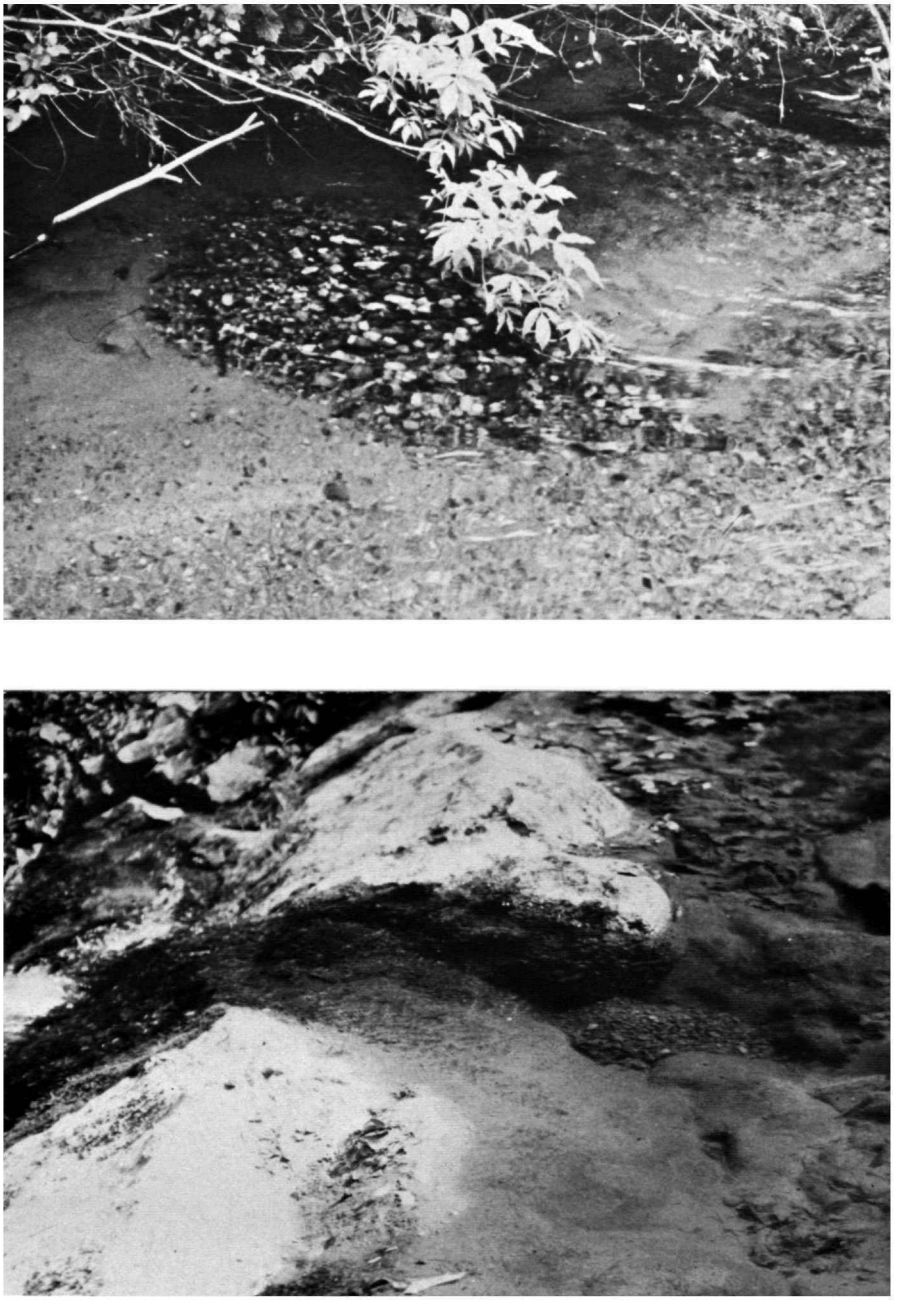

PLATE 8.—Gravel mound-nests of *N. l. leptocephalus:* upper, large nest, over three feet in width, observed in a tributary of the Saluda River, Santee drainage, on 16 May 1966. A large tuberculate male, 196 mm SL (USNM 200758) was captured nearby; and lower, typical, small nest of the bluehead chub in Lapsley Run, James drainage, observed during May and early June 1968 and 1969. The larger males usually build the larger nests.

serve as recognition signals to the female (or they may have some other behavioral significance).

The evolution of the leptocephalus complex is not clear with respect to existing data on morphology and distribution. This species complex, although distinct from the micropogon and biguttatus groups, is most closely related to a *N. micropogon* stock; however, its evolution and dispersal cannot be related to that of the micropogon group. The basic *N. leptocephalus* stock became isolated on the present Atlantic-Gulf slope probably during the Teays Period. It appears most likely that a *N. leptocephalus* stock existed, at first, in the upper Santee–Pee Dee drainage area. This stock could have evolved from a *N. platyrhynchus* type from the Old Teays River (now the upper New River). The high numbers of tubercles, their crowding in the forepart of the head before the eyes, and their occurrence from the internasal to the occipital area are characters of *N. l. leptocephalus* of the Santee–Pee Dee that are also common to *N. platyrhynchus*. This southern *N. l. leptocephalus* stock found dispersal routes to the northeast on the Atlantic slope and westward on the gulf slope at different times and rates via stream capture and by the confluence of fresh waters at the mouths of rivers during Pleistocene sea-level fluctuations.

The westward extension of the *N. leptocephalus* stock ended abruptly at the Mississippi River. It is not known to occur farther westward. Following the dispersal and establishment of *N. leptocephalus* stock on the gulf slope, a considerable period of isolation of the Savannah-Chattahoochee stock from that of the Alabama and more western rivers must have been necessary in order for the divergence of *N. l. bellicus* from *N. l. interocularis* to have reached the present level of differentiation. The distribution of *N. l. bellicus* could have been variously effected during geological times, but its morphological homogeneity suggests considerable gene exchange among the several drainages it now occupies or a recent entrance into the western areas via the upper Mobile drainage.

The old escarpment of the Coosa at about the fall line prevented its entrance into this system. Its limited distribution in the Tennessee River in northern Alabama is a well-documented, recent stream capture involving several Mobile drainage forms. The speciation of other fishes on the gulf slope was reviewed by Smith-Vaniz (1968).

The homogeneity of the characters of *N. l. interocularis* suggests a past history in the Savannah–Chattahoochee area similar in time to that of *N. l. bellicus,* mentioned above. The recent entrance of *N. micropogon* into the upper Savannah via the Tennessee River is also discussed under geographic distribution.

The northward dispersal of *N. leptocephalus* stock from the Santee–Pee Dee area must have occurred during at least two major periods of exchange. The early dispersal of this multituberculate, blue-bodied form could have been northward to the Roanoke–James drainages, and subsequent isolation could have permitted divergence of the northern race toward reduced tuberculation and a brassy orange coloration. The more recent entry of the northern race of *N. l. leptocephalus* across the Appalachian Divide into the New River system and its capture in the James, Rappahannock, and Potomac drainages are discussed by Lachner and Jenkins (1971).

The intermediate population in the Edisto River suggests very recent exchanges of *N. l. interocularis* from the Savannah drainage and *N. l. leptocephalus* from the Santee drainage. The factors related to the development of the blue body coloration in the southern form of *N. l. leptocephalus* and probably all *N. l. interocularis* are not understood. It is of interest that both forms of the leptocephalus complex at opposite ends of the geographic distribution diverged similarly in respect to the basic body coloration of the nuptial male.

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TABLE 1.—*The number of head tubercles in* N. l. leptocephalus *from the New, James, York, Roanoke, Tar, Neuse, and Cape Fear river drainages, segregated by sex (X = not sexed; females in parentheses; mean values with sexes combined).*

SL/mm		NUMBER OF TUBERCLES																									N	N	N	
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	X	♂	♀	X̄
20-29	X	6																											6			0.0
30-39	X	27	1	1																									29			0.1
40-49	X	19	13	10	5	8	1	1	1																				58			1.7
50-59	X	3	3	8	15	12	4	8	6	3	2	2	-	-	1														67			4.4
60-69	X	2	1	2	7	2	5	16	16	3	7	7	3	6	5	6	1	2	2										93			8.2
70-79	♂	2	-	-	-	1	1	-	-	1	1	1	1	1	2	1	-	1	-	2	-	-	1							16		1.1
	♀		(1)	-	-	(1)	-	(3)	(2)	(2)	(1)	(1)	(2)	(3)	(1)	(5)	(4)	(2)	(2)												30	
80-89	♂			1	-	-	-	-	2	-	-	2	3	2	4	3	4	4	3	5	-	1	1	1					36			14.0
	♀						(1)	-	-	(2)	(1)	(1)	(4)	(3)	-	(3)	(3)	(3)	(1)	(4)	-	(2)									28	
90-99	♂													1	2	1	3	3	2	3	5	-	-	-	1				21			14.7
	♀									(1)	(4)	(2)	(4)	(5)	-	(3)	(2)	(2)	(3)	(1)	(1)							(1)			29	
100-109	♂														3	-	1	7	5	4	3	5	3	-	3	1			35			17.5
	♀												(1)	(2)	-	(1)	-	-	(3)	(2)											9	
110-119	♂													1	2	2	2	4	5	5	6	5	3	2	2				39			17.8
	♀												(1)	-	-	-	(1)	(3)	-	-	-	-	-	-	(1)						6	
120-129	♂												1	1	2	-	5	4	5	3	4	2	1	-	-	1	-	1	30			17.1
130-139	♂														3	-	2	5	2	7	4	4	3						30			17.6
140-149	♂															2	2	5	-	2	7	3	1	3	-	1	1		27			18.4
150-159	♂											1	1	-	-	1	-	2	-	2	1	2	1	-	-	1			12			17.3
160-169	♂														1	-	-	1	-	-	1	-	-	-	-	1			4			18.0

TABLE 2.—*The number of head tubercles in* Nocomis l. leptocephalus *from the Pee Dee River drainage, segregated by sex (X = not sexed; females in parentheses; mean values with sexes combined; all specimens, A, under 30 mm had no visable tubercle spots).*

SL/mm		NUMBER OF TUBERCLES																													N	N	N	
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	X	♂	♀	X
20-29	X	A																																	A			0.0
30-39	X		1																															1			1.0
40-49	X		4	1	5	11	1	1	1																									24			3.5
50-59	X		1	4	4	14	12	11	4	1	-	1																						52			4.8
60-69	X			1	2	6	8	11	6	4	2	-	1	3																					44			6.3
70-79	X					1	-	1	-	1	1	1	-	2	-	2	1	-	-	3	1	-	1	-	-	1									16			13.9
80-89	♂										1	-	-	-	-	-	-	-	-	-	-	1	-	1	1	-	-	-	1						5			19.7
	♀																		(1)																	1		
90-99	♂																2	1	-	-	1	1	-	-	-	-	1									6			18.3
	♀																			(1)																	1		
100-109																																						
110-119	♂																							1	-	-	1	2	-	-	-	-	-	1		5		26.2
120-129	♂																											1								1		26.0
130-139	♂																								1	1	-	-	-	-	-	-	1			3		26.0
140-149																																						
150-159	♂																										1									1		25.0

TABLE 3.—*The number of cephalic tubercles with increase in body length in* N. l. leptocephalus *from the Santee River drainage. (Specimens designated by X were not sexed; the sexes were combined for the mean values.)*

SL/mm		NUMBER OF TUBERCLES																																	N	N	N	
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	X	♂	♀	X
20-29	X	4																																		4			0.0
30-39	X	28	10	7	3	1	1																													50			0.9
40-49	X	14	20	45	24	17	12	2	1	-	1																									136			2.5
50-59	X	2	5	22	19	37	33	19	9	13	11	5	4	2	1	-	-	1																		183			5.2
60-69	X			7	9	11	10	8	13	13	11	12	11	12	9	7	4	3	4	5																149			9.0
70-79	♂	1	-	-	-	-	-	-	3	1	-	3	5	6	9	6	4	3	3	2	2	1	1														50		11.7
	♀				(2)	(4)	(3)	(2)	(1)	(3)	(6)	(9)	(5)	(3)	(4)	(3)	(3)	(3)	(2)	(2)																			55	
80-89	♂									1	-	1	2	-	3	6	6	8	7	5	3	4	3	2	2	2	-	1	1							57			15.8
	♀						(1)	(2)	-	(1)	(1)	(2)	(2)	(5)	(3)	(2)	(3)	(1)	(2)	(1)	(2)	(2)																	30	
90-99	♂												2	-	1	4	2	5	4	6	1	4	3	2	2	1	-	1								38			16.6
	♀						(1)	(2)	-	-	(1)	-	(2)	(1)	-	-	-	(1)	(2)	(2)	-	(1)																	13	
100-109	♂												1	-	-	1	2	3	2	-	4	1	4	-	1												19			16.1
	♀								(2)	-	-	(1)	-	(1)	-	(3)	-	-	(1)																					8	
110-119	♂										1	1	-	-	-	-	-	-	-	-	1	2	5	1	2	-	-	-	-	-	1	-	-	1			15			19.9
	♀										(1)	-	-	-	-	-	-	-	-	(1)	-	(1)																	3	
120-129	♂																	1	2	2	4	2	-	-	1	1	-	2	2	1	-	-	-	-	1		19			21.9
130-139	♂																1	-	-	-	1	1	1	-	-	-	-	-	-	-	-	1					5			21.0
140-149	♂																				2	-	-	-	-	-	-	-	-	1							3			22.0
150-159	♂																				2	-	1	-	1	-	-	-	-	-	-	-	1				5			22.6
190-199	♂																														1						1			29.0

TABLE 4.—*The number of head tubercles in* N. l. interocularis *from the Savannah, Altamaha, and Chattahoochee rivers' drainages, segregated by sex (X = not sexed; females in parenthesis; mean values with sexes combined).*

SL/mm		NUMBER OF TUBERCLES															N	N	N	
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	X	♂	♀	$\bar{X}$
20-29	X	4															4			0.0
30-39	X	21	3	3													27			0.3
40-49	X	26	13	8	6	2	1										56			1.1
50-59	X	17	19	21	10	13	8	-	2	-	1						91			2.3
60-69	X	9	4	16	12	11	10	4	4	4	-	-	-	1			75			3.5
70-79	♂	1	1	2	-	4	4	7	6	3	2	-	1					31		5.0
	♀	(3)	(2)	(13)	(7)	(11)	(5)	(9)	(2)	(3)	(1)	(1)							57	
	X				1	1	-	3	3	6	1						15			
80-89	♂				1	2	2	2	5	11	1	-	1					25		6.7
	♀	(2)	-	(1)	(2)	(4)	(2)	(12)	(8)	(6)	-	(1)	-	(1)					39	
	X						2	3	5	13	2						25			
90-99	♂				1	-	1	5	7	7	3							24		7.5
	♀			(1)	-	(2)	(1)	(3)	(1)	(6)	(1)								15	
	X				1	-	-	2	3	17	4	-	1	1	2		31			
100-109	♂					1	1	-	1	9	1	2						15		7.5
	♀	(1)	-	(1)	-	(1)	(1)	(2)	(4)	(7)	(2)								19	
	X							2	-	13	2	3					20			
110-119	♂								2	3	4	6						15		8.7
	♀								(2)	(3)	(2)	-	-	(1)					8	
	X									2							2			
120-129	♂					1	-	1	1	4	1	2	1					11		8.5
	♀								(1)	(1)	(1)								3	
	X									1	-	-	1	1			3			
130-139	♂									4	1	2	1					8		8.7
	♀									(1)	(1)								2	
	X									4	1						5			
140-149	♂								1	1	-	3						5		8.7
	♀									(2)									2	
150-159	♂									4	1	4						9		8.9
	♀									(1)									1	
160-169	♂									1	2	3							6	9.3
170-179	•											1	1						2	10.5
180-189	•								1	-	1	1							3	8.7
190-199	•								1	1	-	2							4	8.8
200-209	•											1	2	1	1	1			6	11.3
210-219	•											1							1	10.0

TABLE 5.—*The number of head tubercles in* N. l. bellicus *from the drainages of Mobile Bay, Pascagoula Bay, Pearl River, and eastern tributaries of the Mississippi River, segregated by sex (X = not sexed; females in parentheses; mean values with sexes combined).*

SL/mm		NUMBER OF TUBERCLES								N	N	N	
		0	1	2	3	4	5	6	7	X	♂	♀	$\bar{X}$
30-39	X	11								11			0.0
40-49	X	23								23			0.0
50-59	X	18	2	1						21			0.2
60-69	X	8	2	4	3	15	2			34			2.6
70-79	♂			3	3	2	1	3	1		13		3.7
	♀	(1)	(2)	(2)	-	(2)						7	
	X					10	-	2		12			
80-89	♂				3	4	-	3			10		3.8
	♀			(4)	(1)	(3)						8	
	X				2	11	-	1		14			
90-99	♂				1	1	1	2			5		4.3
	♀				(1)	(3)						4	
	X			1	-	3	-	2		6			
100-109	♂							2	1		3		5.0
	♀			(1)		(1						2	
110-119	♂					2	-	4			6		5.3
	♀					(2)	-	(1)	(1)			4	
120-129	♂							1	2		3		6.5
	♀							(1)				1	
130-139	♂						1	1	2		4		6.2
	♀							(1)				1	
140-149	♂						1	1			2		5.5
150-159	♂							1			1		6.0
170-179	♂								1		1		7.0

TABLE 6.—*Total number of cephalic tubercles in subspecific populations of* Nocomis leptocephalus *representing all sizes, from juveniles to adults, with sexes combined.*

SUBSPECIES / DRAINAGE	NUMBER OF TUBERCLES PER SPECIMEN																															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
leptocephalus																																	
New	8	8	7	7	5	15	13	4	3	7	10	12	10	13	10	15	8	5	6	4	8	1	3	2	-	2							
James	1	1	3	3	3	7	8	4	6	3	4	5	5	8	5	15	15	11	12	10	4	3	3	3	1	1							
York		3	2	-	-	1	-	-	-	1	-	2	1	1	-	1	1	1															
Roanoke		3	4	4	2	2	4	4	7	5	6	6	8	7	12	21	11	18	18	10	3	-	3	2									
Pamlico (Tar)	3	3	-	1	1	1	-	-	-	-	-	-	1	-	-	1	1	-	1	-	-	1											
Neuse	8	2	6	7	1	2	1	1	1	1	1	1	-	-	1	-	1	-	-	2	-	1											
Cape Fear		1	4	3	1	-	2	-	1	1	-	1	1	1	2	1	1	5	2	1	2	1											
Pee Dee	6	6	11	29	18	22	11	6	3	2	1	5	-	2	3	1	1	4	2	2	1	2	2	2	3	3	1	-	-	-	1	1	
Santee, Catawba, Broad	20	30	32	40	43	15	14	15	11	12	15	14	12	17	7	12	8	12	7	12	8	5	7	4	-	4	3	2	1	1	1	1	1
Congaree	10	38	18	17	22	10	8	10	13	10	12	12	13	12	10	9	10	7	11	2	1	-	1										
Saluda	4	14	6	12	5	11	7	9	8	14	8	4	5	7	9	9	14	5	2	5	8	-	1	-	-	-	-	-	1				
intergrades - Edisto	2	2	5	9	3	9	2	9	3	6	3	2	2	1	3	5																	
interocularis																																	
Savannah	27	34	21	33	25	44	42	112	25	22	5	3	1	1																			
Altamaha	11	27	15	11	5	5	15	16	4	2	2																						
Chattahoochee	6	16	6	9	6	9	3	11	6	10	3	3	2																				
bellicus																																	
Alabama-Tombigbee	2	13	10	29	4	11	4																										
Pascagoula Bay	3	-	1	7	-	5	2																										
Pearl		3	1	6	-	5																											
Mississippi tributaries	2	7	2	25	1	11	3																										

TABLE 7.—*The number of cephalic tubercles in subspecies of* N. leptocephalus, *90 mm and larger in standard length, segregated by river drainages (sexes combined). The intergrades from the Edisto River are* N. l. interocularis × N. l. leptocephalus.

SUBSPECIES / DRAINAGE	NUMBER OF TUBERCLES																															
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
leptocephalus																																		
New											2	3	4	3	4	6	7	6	3	5	5	4	1	1	-	-	2							
James						1	-	-	-	2	1	4	3	4	4	2	11	9	6	11	8	5	3	3	3	1	1							
York																		1	1															
Roanoke										3	1	2	4	4	4	10	19	11	16	17	10	3	-	2	2									
Pamlico (Tar)																	1	1	-	1	-	-	1											
Neuse																		1	-	-	1	-	1											
Cape Fear													1	1	-	-	-	-	3	2	1	2												
Pee Dee																2	1	-	1	1	1	-	1	1	1	3	3	-	-	-	-	1	1	
Santee						1	2	2	-	3	3	5	2	1	9	6	11	14	10	15	12	14	3	7	2	-	3	2	2	2	1	1	-	1
intergrades - Edisto																	4																	
interocularis																																		
Savannah			1	2	3	1	11	19	77	18	23	5	2	1	1																			
Altamaha					1	2	-	5	9	3	2																							
Chattahoochee	1	-	1	-	1	1	5	1	9	5	8	2	2	2																				
bellicus																																		
Alabama-Tombigbee			2	2	8	3	10	3																										
Pascagoula Bay					1	-	1	1																										
Pearl					2	-	3																											
Mississippi tributaries					2	1	6	3																										

TABLE 8.—*The high number of internasal and posterior-internasal tubercles in* N. l. leptocephalus *from the Pee Dee and Santee drainages compared with the lower number in* N. l. interocularis *and* N. l. bellicus *for specimens over 65 mm. (Supraorbital tubercles not counted.)*

SUBSPECIES	NUMBER OF TUBERCLES											
Drainage	0	1	2	3	4	5	6	7	8	9	10	11
leptocephalus												
Pee Dee		1	1	4	7	12	6	4	5	-	2	1
Santee, Catawba	1	2	5	6	32	48	41	18	11	5	5	1
Broad, Congaree		6	12	10	40	27	15	1				
Saluda	2	1	8	7	32	21	21	2	1			
intergrades - Edisto					2	10	3	3	3	-	2	1
interocularis												
Savannah	28	17	63	44	113	6	1					
Altamaha	5	3	11	8	15	3	1					
Chattahoochee	9	5	5	7	17	7	3					
bellicus												
Alabama-Tombigbee	5	4	32	1								
Escatagoula Bay			12	1								
Pearl			10									
Mississippi tributaries	1	2	25									

TABLE 9.—*The extent of tubercle development posteriorly on the head in subspecific populations of* N. leptocephalus *larger than 60 mm.*

SUBSPECIES	AREA OF HEAD							
Drainage	IN	PIN	AIO	MIO	PIO	AOC	MOC	POC
leptocephalus								
New, James, York, Roanoke	1	2	15	8	9	32	86	94
Tar, Neuse, Cape Fear		3	3	2	-	3	18	16
Pee Dee	1	10	4	21	3	12	16	11
Santee, Catawba		8	10	13	12	35	98	31
Broad, Congaree	3	15	14	8	8	21	60	15
Saluda		3	11	10	12	17	49	13
intergrades - Edisto				5	3	13	8	1
interocularis								
Savannah, Altamaha, Chattahoochee	23	136	197	41	5	4		
bellicus								
Alabama to Mississippi	42	68	1					

TABLE 10.—*The relationship between standard length and the extent of posterior development of cephalic tubercles in* N. l. leptocephalus *from the Santee River drainage (size groups marked with an X were not sexed).*

SL/mm	SEX	TN	PTN	ATO	MTO	PTO	AOC	MOC	POC
30–39	X	2	13	5					
40–49	X	5	87	18	6	2	-	1	
50–59	X	5	54	50	35	6	14	10	1
	♂				1	1	1	1	
	♀			(1)					
60–69	X	3	18	22	17	16	27	37	5
	♂						1	1	
	♀							(2)	
70–79	X				3	2	6	6	1
	♂			1	1	2	4	21	5
	♀		(7)	(4)	(5)	(8)	(13)	(16)	(4)
80–89	X			1	-	-	1	3	
	♂						7	33	13
	♀		(1)	(2)	(2)	(1)	(4)	(14)	(3)
90–99	X						1	2	
	♂					1	5	22	7
	♀			(1)	(2)	(1)	(1)	(5)	(3)
100–109	♂						1	12	32
	♀			(1)	-	(1)	(1)	(4)	(1)
110–119	♂			1	-	1	-	10	4
	♀				(1)	-	-	(2)	
120–129	♂						1	9	5
130–139	♂							3	2
140–149	♂							3	
150–159	♂						1	2	2
190–199	♂								1

TABLE 11.—*Statistics comparing the total number of cephalic tubercles of two size groups of five populations of* N. leptocephalus. *These data are shown graphically in Figure 2.*

	90 mm and over size group					70 to 79 mm size group				
SUBSPECIES	No.	$\bar{X}$	SD	SE	$\bar{X} \pm 2$ SE	No.	$\bar{X}$	SD	SE	$\bar{X} \pm 2$ SE
leptocephalus										
Cape Fear, northward	242	17.1	3.42	0.22	16.6–17.5	44	11.6	4.42	0.67	10.3–13.0
Pee Dee	17	22.8	5.08	1.23	20.4–25.3	16	13.9	5.61	1.40	11.1–16.7
Santee	129	18.4	5.33	0.47	17.4–19.3	104	11.9	3.98	0.39	11.1–12.6
interocularis	219	8.2	1.80	0.12	7.9– 8.4	99	5.2	2.31	0.23	4.7– 5.6
bellicus	43	5.2	1.37	0.21	4.8– 5.6	31	3.8	1.53	0.27	3.3– 4.4

TABLE 12.—*The number of vertebrae in three subspecies of* Nocomis leptocephalus *segregated by major river drainages.*

SUBSPECIES - River	VERTEBRAL NUMBERS			
	38	39	40	41
N. l. leptocephalus				
New		24	22	2
Potomac		14	10	2
York		9	12	
James		12	21	3
Chowan	1	11	4	
Roanoke	4	37	11	
Tar	1	2	1	1
Neuse	2	16	1	
Cape Fear		3		
Pee Dee		3	2	
Santee	1	16	6	
Intergrades - Edisto		17	10	1
N. l. interocularis				
Savannah		2	11	
Altamaha		2	12	1
Chattahoochee			14	1
N. l. bellicus				
Mobile Bay		13	3	
Pascagoula Bay		5		
Pearl	2	9	3	
Mississippi tributaries	13	10	1	

TABLE 13.—*The number of pharyngeal teeth in* Nocomis leptocephalus *separated by drainages.*

SUBSPECIES	NUMBER PER RIGHT-LEFT ARCH				
	4 - 4	4 - 3	3 - 4	3 - 3	2 - 4
N. l. leptocephalus					
New	5	-	-	-	-
James	6	-	1	-	-
Roanoke	11	-	-	-	-
Neuse	3	-	1	1	-
Pee Dee	3	-	-	-	-
Santee	14	1	1	1	1
N. l. interocularis					
Savannah	17	-	1	-	-
Altamaha	5	-	-	-	-
Chattahoochee	6	-	-	1	-
N. l. bellicus					
Alabama	5	-	-	-	-
Pascagoula Bay tributaries	2	-	-	-	-
Pearl	2	-	-	-	-
Mississippi River tribs.	4	-	-	-	-
TOTALS	83	1	4	3	1

TABLE 14.—*The number of circumferential and lateral-line scales in* N. leptocephalus. *Data for* N. l. leptocephalus *from the New and James rivers southward to the Santee River were grouped; data for* N. l. bellicus *from the Alabama River westward were grouped.*

SUBSPECIES	CIRCUMFERENTIAL SCALES									LATERAL-LINE SCALES							
Drainage	25	26	27	28	29	30	31	32	33	36	37	38	39	40	41	42	43
leptocephalus		4	27	293	206	131	57	19	4	3	32	173	227	180	62	24	3
intergrades - Edisto				10	12	13	5	1			1	5	21	10	2		
interocularis																	
Savannah			3	22	17	13	8	4	3			6	15	33	14	3	
Altamaha			1	15	10	9	3	2			1	1	8	19	8	2	
Chattahoochee	1	1	4	17	9	3					1	4	20	11	2	1	
bellicus		1	5	13	15	7	5					5	17	15	7	1	

TABLE 15.—*Comparison of the major characters of the subspecies of* N. leptocephalus.

CHARACTER	SUBSPECIES leptocephalus	interocularis	bellicus
Head tubercles			
Total number	Many	Intermediate	Few
Number, 95% of subadults, adults	16-25	7-9	4-6
Mean number	Greater than 17	8	5
Maximum number	33	14	7
Head tubercle distribution	Extensive	Moderate	Restricted
Posterior occurrence	To mid- or postoccipital areas in almost all subadults and adults.	Almost always to anterior or midinterorbital areas.	In internasal or posterior internasal areas.
Maximum posterior occurrence in all specimens examined	POC	AOC	AIO
Nuptial crest	Very large	Large	Moderate
Vertebral number	Modally 39 or 40	40	39
Coloration	Two nuptial male color patterns; blue and brassy-orange	One, blue	One, orange

Appendix: Specimens Studied

Nocomis leptocephalus interocularis, new subspecies (paratypes)

Savannah River system (Georgia)

Burke County.—USNM 161675: Stream from Utley's Cave. 12 October 1951 (14 specimens).

Jefferson County.—USNM 166504: Brushy Cr., tributary of Brier Cr. about 0.4 mi S of Wrens, US 1, 18 September 1947 (2). CU 17377: Brushy Cr., tributary of Brier Cr., 0.9 mi S Wrens, US 1, 24 March 1950 (1). USNM 166503: Reedy Cr., 3.9 mi NE of Wrens, US 1, 18 September 1947 (7).

Richmond County.—TU 38597: Rays Cr., at crossing of Walton Way extension in Augusta, 5 July 1965 (3). TU 38605: Rays Cr., at crossing of Berkman Road in Augusta, 6 July 1965 (2). CU 11980: Rays Cr., 2 mi W of Augusta, 23 March 1948 (8). UMMZ 152758: Small brook in pine woods 2 mi W of Augusta, tributary of Rays Cr., 27 December 1940 (5).

Columbia County.—TU 38588: Little Kiokee Cr., 10.5 mi N of Evans, 27 June 1965 (9). TU 39486: Little Kiokee Cr., 10.5 mi N of Evans on dirt road, 26 October 1965 (2). USNM 161684: Lake Spring Cr., ½ mi from Savannah R., 24 July 1948 (9). USNM 161683: East Fork Cliatt Cr., 24 July 1948 (19). USNM 161682: West Fork Cliatt Cr., 24 July 1948 (13).

McDuffie County.—USNM 161692: Big Cr., 22 July 1948 (22). USNM 161694: Madison Cr., 22 July 1948 (15). USNM 161693: Harts Cr., 20 July 1948 (3).

Columbia–Lincoln County.—USNM 161685: Little R., 23 July 1948 (4).

Lincoln County.—USNM 161690: Cherokee Cr., 23 July 1948 (2). USNM 161689: Gray's Cr., 23 July 1948 (7). USNM 161691: Lloyd's Cr., 23 July 1948 (7).

Oglethorpe County.—UG 283: Buffalo Cr., 6 mi E of Lexington, 29 April 1953 (5). UAIC 1463: Buffalo Cr., about 3 mi E [W?] of Wilkes–Oglethorpe County line, 5 September 1964 (10). USNM 161699: South Fork Broad R., 16 May 1948 (4).

Elbert County.—CU 19719: Morea Cr., 1.3 mi S of Nuberg on Rte. 77, 27 March 1951 (6). UG 636: Little Dove Cr., 0.8 mi E of Deep Creek Baptist Church, 11 April 1959 (20). USNM 161686: Small Cr., 2.5 mi E of Broad R., Georgia Hwy. 72, 15 April 1950 (12).

Madison County.—USNM 161697: Small Cr., 0.5 mi E of Carlton, Georgia Hwy. 72, 15 April 1950 (8). UAIC 1613: Fork Cr., E side of Carlton, Georgia Hwy. 72, 4 June 1965 (5). UG 308: Fork Cr., 2 mi NE Comer, 19 April 1954 (12). UG 22 E: South Fork Broad R., 2 mi S of Carlton, 11 April 1959 (16). TU 26181: South Fork Broad R., 2 mi S of Carlton, 21 April 1962 (19). UG 22 D: South Fork Broad R., 1 mi S of Carlton, 19 April 1954 (7). UG 269: South Fork Broad R., 2 mi W of Comer, 1 November 1952 (3). CU 41277: Stream [South Broad R.?] crossing Rte. 72, 1.8 mi W of Comer, 5 June 1961 (1). TU 26178: South Fork Broad R., 1 mi W of Comer, 21 April 1962 (11). UAIC 1612: South Fork Broad R., about 2 mi E [W?] of Comer, Georgia Hwy. 72, 4 June 1965 (4). USNM 161696: 2.5 mi SE Danielsville, Dewey Powers Farm, 19 June 1950 (1). CU 51112: Tributary of Broad R., 5 mi NE Danielsville on Rte. 29, 27 March 1952 (27). UG 173 A: Small Cr., 3 mi SE Danielsville, 19 April 1954 (4). USNM 166502: Broad R. tributary, 0.7 mi SW of Danielsville, US 29, 10 September 1947 (22). UG 309: Holly Cr., 3 mi N of Carlton, 19 April 1954 (2). USNM 161695: Mason's Cr., 11 mi W of Royston, US 29, 15 April 1950 (16). USNM 165720: Broad R. trib., 10 mi SW of Royston, US 29 (below dam), 5 April 1952 (18). CU 22689: Tributary of the South Fork [of the Broad R.], 2.4 mi NE of Madison County line on Rte. 29, 27 March 1952 (15).

Banks County.—TU 37510: Hudson R., about 2 mi N of Homer, on Hwy. 441, 24 April 1965 (65). CU 21433: Hudson R., 17.6 mi S of Cornelia on Rte. 441, 9 June 1952 (2). CU 21591: Tributary of Hudson R., 1.7 mi N of Homer on Rte. 441, 9 June 1952 (9).

Franklin County.—UG 696: Middle Fork Broad R. NW [SW?] of Carnesville, 23 September 1959 (3). CU 19620: Tributary of Nail Cr., 0.7 mi SW of Ashland, 27 March 1951 (24).

Stephens County.—USNM 161700: Tributary of Broad R., 29 August 1948 (6). UG 637: Carnes Cr., 2 mi S of Toccoa, 11 April 1959 (58). USNM 171671: North Fork Broad R., 3.7 mi W of Toccoa, 9 April 1947 (33). CU 17445: Toccoa Falls, about 2.5 mi from Toccoa, 1 April 1950 (32). CU 21593: Tributary of North Fork of Broad R., 5 mi W of Toccoa on Rte. 123, 8 June 1952 (31). UG 638: Toccoa Cr., just upstream from Georgia Hwy. 17, 11 April 1959 (36).

Hart County.—USNM 161688: Beaver Dam Cr., 3 mi E of Royston at US 29, 15 April 1950 (10). CU 19724: Tributary of Savannah R., 3.3 mi S of Hartwell on Rte. 77, 27 March 1951 (15). UMMZ 94568: Creek S of Hartwell, 12 November 1931 (10). UG 687: Savannah R., 1 mi below Hwy. 29 bridge, 1 September 1959 (37).

Habersham County.—UG 310: Panther Cr., 3 mi S of Tallulah Falls, 23 April 1954 (1). FSU 7418: Panther Cr., 10.2 mi NE of Clarkesville, US Hwy. 441, 16 July 1961 (5). TU 29322: Panther Cr., 3.9 mi SW of Tallulah Falls, US Hwy. 441, 19 June 1962 (9).

Rabun County.—FSU 7422: Tallulah R., 2.2 mi SE of Wiley (about 10 mi S of Clayton), US Hwy. 441, 16 July 1961 (13). TU 29329: Tallulah R., 1.5 mi S of Wiley, US Hwys. 441 and 23, 19 June 1962 (24). UG 492: Bowen Branch (=Boen Creek, Tiger Creek–Tallulah R. tributary just N of Wiley), 14 May 1957 (6). TU 12231: Timpson Cr., 5.4 mi W of Clayton, US Hwy. 76, 8 October 1955 (6). FSU 4078: Timpson Cr., 5.4 mi W of Clayton, Rte. 76, 8 October 1955 (2).. UG 317: Persimmon Cr., tributary, 6 mi WNW of Clayton, 24 April 1954 (9). CU 25174: Tributary of Tallulah R., 6.1 mi W of Clayton on Rte. 76, 3 September 1953 (11). CU 37919: Stream 6 mi N of Wiley on US Hwy. 441 (detour to Clayton), 6 June 1961 (1). UG 711: Persimmon Cr., 2 September 1959 (10). UG 600: Stonewall Cr., on Harley McCall's farm, 16 October 1958 (9). UG 491: Worley Cr., 15 May 1957 (14).

Savannah River system (Georgia–South Carolina state line)

Rabun–Oconee County.—TU 26979: Chattooga R., at Georgia–South Carolina state line on Hwy. 28, just above junction with West Fork, 13 July 1962 (1, cataloged with *N. micropogon* specimens).

Savannah River system (South Carolina)

Allendale County.—USNM 162567: Savannah R., at mi 134.5, just above Ring Jaw Point, 15 May 1952 (1). USNM 200157: East Mill Cr., a branch of Tower Runs [Lower Three Runs?] Cr., 3.0 mi E of Martin, South Carolina Hwy. 37, 12 June 1957 (1). CU 15152: Tributary of Lower Three Runs Creek, 3.6 mi NW of Appleton on Rte. 28, 7 June 1949 (24).

Barnwell County.—USNM 200164: Branch of Three Runs Cr., 1.5 mi S of Donora, 2.5 mi E of Dunbarton, 20 August 1951 (1). USNM 200186: Branch of Lower Three Runs Cr., slightly NE of South Carolina Hwy. 40, SE of Donora, 2–3 mi E of Dunbarton, 8 October 1951 (1). USNM 200151: Branch of Lower Three Runs Cr., 3.5 mi S of Donora, 1 mi N of South Carolina 40, 1 October 1951 (2). USNM 200176: Branch of Lower Three Runs Cr., 1–1.5 mi S of Donora, 2–3 mi E of Dunbarton, 8 July 1957 (1). USNM 192858: Branch of Lower Three Runs Cr., 3–4 mi S of Donora, 8 July 1957 (6). USNM 200144: Poplar Br. of Lower Three Runs Cr., 0.75 mi W of South Carolina Hwy. 39, 0.6 mi N of R.R. crossing, 1.5–2 mi N of Dunbarton, 12 June 1957 (1). USNM 200171: Fork of Lower Three Runs Cr., 5–6 mi NW Snelling, on South Carolina Hwy. 53, 1–1.5 mi E of South Carolina Hwy. 39 just E of Joyce Branch, 11 June 1957 (1). USNM 200179: Joyce Branch of Lower Three Runs Cr., 4–5 mi N of Dunbarton, 1 mi W of South Carolina Hwy. 39, 11 June 1957 (3). USNM 200187: Joyce Branch, 1 mi W of Hwy. 39, 4.5 mi N of Dunbarton, 9 June 1952 (4). USNM 200145: Hattie Cr., 3.5 mi S of Meyer's Mill, at South Carolina Hwy. 28, 13 August 1951 (19). USNM 200159: Hattie Cr., 3.5–4 mi S of Meyer's Mill, 1.5 mi NE Hattieville, South Carolina Hwy. 28, 13 August 1952 (2). USNM 200172: Same locality as USNM 200159, 12 August 1958 (2). USNM 200182: Steel Cr., 3.5 mi W of Dunbarton, Hwy. 64, 8 August 1951 (8). USNM 200158: Branch of Steel Cr., 1.5 mi NE of Meyer's Mill, South Carolina 122, 8 August 1951 (3). USNM 200181: Branch of Steel Cr., 1 mi E of Meyer's Mill, South Carolina 55, 8 August 1951 (5). USNM 200184: Steel Cr., 2 mi W of Meyer's Mill, South Carolina 56, 10 August 1951 (9). USNM 192856: Steel Cr., 2.5 mi W of Meyer's Mill, South Carolina Hwy. 56, 7 July 1952 (4). USNM 200141: Same locality as USNM 192856, 5 August 1958 (7). USNM 200178: Spring Branch, 0.5 mi W of Meyer's Mill, South Carolina 56, 13 August 1951 (1). USNM 200166: Upper East Branch of Steel Cr. about 0.5 mi W of Meyer's Mill, South Carolina 56, 7 July 1952 (1). USNM 200183: Same locality as USNM 200166: 5 August 1958 (4). USNM 200175: Branch of Steel Cr., just S of Meyer's Mill, South Carolina 28, 13 August 1951 (1). USNM 200142: Same locality as USNM 200175, 5 August 1958 (4). USNM 200156: Branch of Steel Cr., 0.5 mi SW of South Carolina Hwy. 28, 3 mi SSW of Meyer's Mill, 17 September 1951 (4). USNM 200168: Same locality as USNM 200156, 12 August 1958 (3). USNM 200177: Pen Creek, 5 mi SE of Ellenton at South Carolina Hwy. 28, 26 July 1951 (1). USNM 200146: Pen Cr., at intersection with C. & W.C. R.R., 5 mi SE of Ellenton, 6 August 1951 (2). USNM 200174: Pen Cr., about 6.5 mi SE of Ellenton, 2 mi SW of South Carolina 28, 3.5 mi NE of Savannah R., 14 July 1952 (4). USNM 200160: Indian Grave Cr., 3.5 mi SE of Ellenton, South Carolina Hwy. 64, 3 August 1951 (4). USNM 200173: Pen Cr., 5 mi SE of Ellenton, South Carolina 64, 3 August 1951 (4). USNM 200185: Pen Cr., 5 mi W of Dunbarton, about 1.5 mi N of South Carolina Hwy. 64, 12 August 1958 (1). USNM 161674: Pen Cr., 10 October 1951 (3). USNM 200165: Upper Four Mile Cr., 2 mi E of Ellenton, at South Carolina 48, 19 May 1952 (1). USNM 161673: Four Mile Cr., 10 October 1951 (1).

Aiken County.—USNM 200154: Upper Four Mile Cr., 5.4 mi E of Ellenton, 0.5 mi NE South Carolina 149, 25 July 1951 (6). USNM 162551: Upper Three Runs Cr., at South Carolina Hwy. 28, 3 May 1952 (4). USNM 192854: Upper Three Runs Cr., Tims Branch, 1 July 1958 (19). USNM 200167: Tims Branch, 2 mi E South Carolina Hwy. 19, on South Carolina 148, 25 July 1951 (1). USNM 200161: Branch of Tinker Cr., 1 mi W of Kennedy's Lake, 1 October 1951 (2). USNM 200180: In Pond at grist mill on Reedy Branch of Tinker Cr., a branch of Upper Three Runs Cr., 8 mi SW of White Pond, 13 June 1957 (3). USNM 200150: Mossy Branch of Tinker Cr., 0.1 mi SW of Mossy School, 10 mi NNW of Dunbarton, South Carolina Hwy. 124, 7 July 1952 (1). USNM 200143: Same locality as 200150, 28 June 1957 (4). USNM 200149: Tinker Cr., a branch of Upper Three Runs Cr., 2.5 to 3 mi downstream from Kennedy's Lake, 26 June 1957 (2). USNM 200162: Upper Three Runs Cr., 9 mi W of White Pond, 4 mi E of Talatha, South Carolina Hwy. 781, 27 June 1952 (1). USNM 200163: Henry's Pond and stream behind pond, on Beulah Fork of Upper Three Runs Cr., 0.5 mi N of South Carolina Hwy. 781, 7 November 1952 (1). USNM 200148: Same locality as 200163, 14 June 1957 (1). USNM 200169: Turner Branch, 1.5 mi SE of Hawthorne, 13 July 1951 (1). USNM 200202: Same locality as 200169, 16 July 1951 (4). USNM 200152: Same locality as 200169, 30 June 1952 (2). USNM 200147: Same locality as 200169, 27 July 1958 (8). CU 24384: Turner Branch of Upper Three Runs Cr., 1.5 mi SE of Hawthorne, 30 June 1952 (4). USNM 200153: Turner's Pond, below the dam at headwater of Turner Branch of Upper Three Runs Cr., 1 to 1.5 mi SE of Hawthorne, 1.5 mi E of South Carolina Hwy. 19, 27 June 1958 (5). USNM 200155: Beulah Branch of Upper Three Runs Cr., 0.8 mi W of South Carolina Hwy. 781, 14 June 1957 (4). USNM 200170: Upper Three Runs Cr., 3.8 mi E of South Carolina Hwy. 19 on road 10A to Aiken, 25 July 1958 (1). UG 364: Pond, AEC Savannah River Plant, 15 June 1954 (22).

Edgefield County.—USNM 86190: Sweetwater Cr., 24 August 1922 (5). TU 38623: Stevens Cr. tributary, 4.6 mi E of

Parksville, county Rte. 533–138, 7 July 1965 (4). TU 39477: Log Cr., at US 25 crossing 4 mi N of 25–25A intersection just N of Edgefield, 25 October 1965 (9).

Edgefield–McCormick County line.—TU 38613: Stevens Cr., 1.4 mi N of Parksville, county Rte. 533–21, 7 July 1965 (15).

Abbeville County.—CU 19593: Calhoun Cr., 7.6 mi E of Calhoun Falls on Rte. 72, 27 March 1951 (25). CU 19648: Little R., 5.6 mi E of Calhoun Falls, 27 March 1951 (4).

Anderson County.—CU 19668: Beaver Dam Cr., 2.5 mi E of Anderson on Rte. 29, 25 March 1951 (1). TU 26190. Tributary of Savannah R., [Little Generostee Cr.?] 5 mi W of Iva, South Carolina Hwy. 184, 21 April 1962 (30). USNM 162959: Tributary 6 mi SW of Anderson, US 29, 4 April 1952 (27). CU 11446: Tributary of Generostee Cr., 5 mi W of Anderson, 9 April 1947 (31). CU 19602: Twenty-three Mile Cr., 0.9 mi NW of Sandy Springs, 11.1 mi NW of Anderson on Rte. 76, 25 March 1951 (1). CU 19749: Eighteen Mile Cr., 1 mi NW of Pendleton on Rte. 76, 25 March 1951 (5). USNM 166501: Seneca R. tributary, 0.9 mi NW of Pendleton, 10 September 1947 (66). CU 37916: Hurricane Cr., Rte. 28 bridge, 0.9 mi NW of junction of Rte. 28 and bypass 28, 3 June 1961 (3).

Oconee County.—CU 19752: Cane Cr., 3 mi SW [SE?] of Walhalla on [off?] South Carolina Rte. 28, 25 March 1951 (21). USNM 94577: Little Cane Cr., Walhalla, 28 March 1930 (39). USNM 94578: Cane Cr., Walhalla, 28 March 1930 (6). USNM 94579: Pond, 8 mi NE of Walhalla, 31 March 1930 (15). TU 26955: Little R., 8 mi NE of Walhalla, South Carolina Rte. 11, 5 July 1962 (12). TU 26971: Thompson R., Whitewater R. tributary, 1.4 mi S of North Carolina–South Carolina state line in Sumter National Forest, 10 July 1962 (5). TU 29461: Bearcamp Cr., near junction with Horsepasture R., 0.5 mi SE of North Carolina state line, 10 July 1962 (2). USNM 168102: Chauga Cr., 3 mi NE of South Carolina–Georgia state line, US 123, 12 September 1954 (2). USNM 171628: Coneross Cr. tributary, 5.3 mi S of Seneca, 9 April 1947 (4). CU 11448: Tributary of Coneross Cr., 5.3 mi S of Seneca, 9 April 1947 (4). CU 17365: Tributary of Tugaloo R., 4.7 mi N of Fair Play on Rte. 59, 1 April 1950 (6). CU 17307: Tributary of Tugaloo R., 2.4 mi W of Fair Play on Rte. 59, 0.9 mi E of Tugaloo R, 1 April 1950 (1). USNM 171690: East Village Cr., Chattooga R. tributary just S of Mountain Rest on Rte. 28, 30 August 1946 (13). TU 26974: Chauga R., 15.9 mi S of Georgia–South Carolina state line on Hwy. 28, 13 July 1962 (5). UMMZ 165635: Cedar Cr., Chauga R. tributary 9 mi NW of Walhalla, 31 October 1940 (11). UMMZ 165544: Bonecamp Cr., 10 mi NW of Walhalla, 31 October 1940 (77). UMMZ 165610: Chauga R., 2 mi SE of Mountain Rest, 4 November 1940 (57).

Pickens County.—CU 19795: Tributary of Twelve Mile Cr., 3 mi NNW of Pickens on Rte. 178, 24 March 1951 (25). CU 38134: Tributary of Keowee R., 8.4 mi E of Oconee–Pickens County line on Rte. 11, 3 June 1961 (6). USNM 171733: Keowee R. tributary, just E of Keowee R.R. crossing about 10 mi S of North Carolina state line, Rte. 288, 30 August 1946 (14).

Oconee–Pickens County line.—TU 26996: Confluence of Horsepasture and Toxaway rivers, 1.5 mi S of North Carolina–South Carolina state line, 1 July 1962 (6). TU 29585: Toxaway R., 0.25 mi S of junction with North Carolina state line, elev. 1,060 ft, 23 July 1962 (13).

North Carolina

Transylvania County.—TU 29420: Bearcamp Cr., Horsepasture R. tributary, 0.2 mi N of South Carolina state line, 28 June 1962 (8). TU 29391: Bearcamp Cr., 4 mi S of Oakland, 25 June 1962 (12). TU 27001: Same locality as TU 29391, 24 July 1962 (34). TU 29784: Same locality as TU 29391, 27 August 1962 (12). TU 28023: Horsepasture R., 0.5 mi N of North Carolina–South Carolina state line, 6 June 1962 (15). TU 29319: Horsepasture R., at bridge 3 mi S Oakland on gravel road, 18 June 1962 (7). TU 29314: Horsepasture R., 2.5 mi S of Sapphire–Oakland on Whitewater road, 18 June 1962 (10). TU 29303: Horsepasture R., 1.1 mi S of Oakland on Sapphire road, 14 June 1962 (5). TU 29436: Horsepasture R., between Drift Fall and Rainbow Falls, 2.6 mi SW of Oakland, 3 July 1962 (3). TU 29599: Toxaway Cr., Toxaway R. tributary, 3 mi SW of Rosman, 31 July 1962 (27). TU 29422: Bearwallow Cr., about 1.7 mi N of North Carolina–South Carolina state line, 29 June 1962 (2). TU 29261: Bearwallow Cr., 1.9 mi due N of South Carolina state line, elev. 1,410 ft, 7 June 1962 (5). TU 29288: Bearwallow Cr., at junction with Toxaway R. 2.0 mi N of South Carolina state line, 10 June 1962 (11). TU 29449: Toxaway R., just below Toxaway Falls, 2 July 1962 (344). USNM 200757: Mill Cr. where it begins to back up at entrance into Lake Toxaway, about 50 yds below bridge. Also in Toxaway R. just below Lake Toxaway Dam. 15 May 1966 (6). TU 29309: Toxaway R., above Lake Toxaway, 2.6 mi W of town of Lake Toxaway, 15 June 1962 (21). TU 29450: Same locality as TU 29309, [probably 2 July 1962] (1). TU 29534: Same locality as TU 29309, 14 July 1962 (11).

Jackson County.—TU 28017: Chattooga R. tributary [Fowler Cr.?], 1.7 mi S of Cashiers, South Carolina Hwy. 107, 4 June 1962 (2). TU 29652: Chattooga R., 2.7 mi S of Cashiers, 7 August 1962 (5). UMMZ 156134: Horsepasture R., S of Lake Fairfield, 2 July 1947 (32).

Nocomis leptocephalus interocularis, new subspecies (non-paratypes)

Ogeechee River system (Georgia)

Warren–Hancock County line.—TU 39498: Ogeechee R., at Jewell, 26 October 1965 (6). OAM [no number]: Ogeechee R., below dam at Mayfield, 30 August 1964.

Taliaferro County.—UMMZ 158016: Ogeechee R., 0.75 mi S of Robinson, 27 August 1939 (2).

Altamaha River system (Georgia)

Wilcox County.—USNM 166508: Ocmulgee R. tributary, at Oscewichee Springs, 14 mi N of Fitzgerald, 17 September

1947 (1).

Monroe County.—UMMZ 88309: Tobesofkee Cr. tributary, 0.5 mi W of Forsyth, 3 September 1929 (4).

Lamar County.—UMMZ 88302: Little Towaliga Cr., near Barnesville, 3 September 1929 (86).

Henry County.—CU 17524: Walnut Cr., 1.5 mi N of McDonough, 29 March 1950 (9).

Dekalb County.—CU 51015: South R., 4.9 mi SE of junction of Rtes. 12–78 on Rte. 12, SE of Atlanta, 7 September 1953 (3). UAIC 1447: Ocmulgee R. tributary, about 2 mi W of Georgia R.R., SE of Stone Mountain, 30 August 1964 (39).

Gwinnett County.—USNM 165731: Ocmulgee R. tributary, 5.5 mi W of Loganville, 5 April 1952 (10). UAIC 1449: Ocmulgee R. tributary, 4 mi W Loganville, about 5 mi W of Gwinnett–Walton County line, 30 August 1964 (5). USNM 165736: Tributary, 9 mi WSW of Snellville, 5 April 1952 (6). UAIC 1448: Yellow R., about 2 mi E of Dekalb–Gwinnett County line near Snellville, 30 August 1964 (2). TU 26140: Yellow R., 7 mi E of Duluth, 20 April 1962 (13).

Laurens County.—UMMZ 88372: Rocky Cr., near Dudley on Georgia state road 26, 2 mi from Beckley County line, 5 September 1929 (10). UMMZ 88388: Hunger and Hardship Cr., 5 mi SW of Dublin, 5 September 1929 (13).

Jones County.—TU 12050: Commissioners Cr., 2.4 mi E of James, 16 September 1955 (4).

Jasper County.—TU 37507: Little R. tributary, 12.1 mi NE of Monticello, 24 April 1965 (20).

Newton County.—TU 26161: Little R. tributary, 2 mi N of Newborn, 20 April 1962 (47).

Greene County.—UAIC 1620: Richland Cr., about 2 mi W of Greensboro, 5 June 1965 (1). UMMZ 158005: Richland Cr., 1.5 mi W of Greensboro, 27 August 1939 (14).

Walton County.—USNM 161703: Jack's Cr., at bridge at High Shoals, on Goodhope Rd., 31 March 1949 (2). USNM 161702: Jack's Cr., below Mill dam, 1 mi E of Goodhope, 31 March 1949 (11). USNM 165730: Tributary, 1 mi NE of of Monroe, 5 April 1952 (21). USNM 161701: Apalachee R., Mill Race at High Shoals, 31 March 1949 (2).

Oconee County.—CU 37846: West Branch Oconee R. [Apalachee R.?], at Morgan–Oconee County line on Rte. 129, 4 June 1961 (4). USNM 161698: Apalachee R., at High Shoals, 9 August 1950 (4). CU 51049: Barbers Cr., Hope Mill near Princeton, 3 September 1950 (8).

Oglethorpe County.—UAIC 1465: Creek on US 78 about 9 mi E of Athens airport, 5 September 1964 (7).

Clarke County.—UG 3: South Prong, 3 mi SE of Athens, 19 October 1947 (3). USNM 161678: McNutt's Cr., 14 May 1948 (8). USNM 161676: McNutt's Cr., at YWCA camp, 4 November 1947 (62). USNM 161677: McNutt's Cr., at YWCA camp, 18 February 1950 (7). USNM 161680: Middle Oconee R., at Princeton, 14 April 1950 (1). UG 340: Middle Oconee R., 0.5 mi below dam at Princeton, 30 April 1954 (1) UG 265: Oconee R., 3 mi W of Athens, 2 October 1952 (2). USNM 161679: Middle Oconee R., 5 October 1947 (3). UG 420: Middle Fork Oconee R., 26 October 1954 (4). USNM 161671: Small tributary, Middle Oconee R., 29 April 1951 (7). USNM 161670: Oconee R., at Athens, 3 March 1951 (2). UMMZ 87059: Athens, 1853 (5). UMMZ 94578: Biggers Cr., NW Athens, 12 November 1931 (3). USNM 161681: Bobbin Mill Cr., 20 September 1947 (34).

Barrow County.—USNM 161669: Beechwood Cr., 22 April 1951 (1). CU 21438: Tributary of Mulberry Fork, 1.2 mi NW of junction of Rte. 124 and Rte. 211, 9 June 1952 (22). USNM 166507: Tributary of North [Middle?] Oconee R., 2.5 mi N of Winder, 11 September 1947 (238).

Jackson County.—UMMZ 94529: Allens Cr., N of Talmo, 12 November 1931 (103). CU 21444: Curry Cr., just inside Jefferson city limit, 9 June 1952 (27). CU 21397: Tributary of Oconee R., 3.3 mi SW of Commerce, 9 June 1952 (2).

Hall County.—CU 17341: Mulberry Fork, tributary of Middle Fork of Oconee R., 13.8 mi S of Gainesville, 31 March 1950 (24). CU 21437: Tributary of Mulberry Fork, 4.1 mi NW of junction of Rte. 124 and Rte. 211, 9 June 1952 (7). CU 11203: Tributary of Oconee R., 2 mi NW of Gillsville, 9 April 1947 (2). CU 17427: Same locality as CU 11203, 1 April 1950 (9). CU 19809: Same locality as CU 11203, 26 March 1951 (28). CU 43581: East Branch [North Fork] of Oconee R., W of Gillsville, 11 September 1962 (30). TU 30496: East Fork [tributary of North Fork] of Oconee R., about 2 mi N of Gillsville, 22 September 1963 (3). USNM 171734: [tributary of] Oconee R., 2 mi NW of Gillsville, 9 April 1947 (20). TU 30484: North Oconee R., 5.9 mi NE of Gainesville, 22 September 1963 (5).

Chattahoochee River system (Alabama)

Lee County.—UAIC 1233: Wacoochee Cr T 19 N, R 29 E, Sec. 23, 4 April 1964 (4).

Chattahoochee River system (Georgia)

Upson County.—TU 27525: Potato Cr., Flint R. tributary, 5 mi SW of Thomaston, 23 April 1962 (5).

Harris County.—FSU 6688: Mulberry Cr. tributary, 7.9 mi E of Hamilton, 17 August 1960 (11). CU 17514: Tributary of Mulberry Cr., 7.7 mi E of Hamilton, 29 March 1950 (5). UMMZ 157884: Mountain Cr., 2.5 mi SE of Chipley, 23 August 1939 (3).

Troup County.—UMMZ 157892: Flat Shoal Cr., 7.2 mi NW of Chipley, 23 August 1939 (2). TU 7527: Tributary of Chattahoochee R., 5.8 mi SW of La Grange, 8 October 1953 (21).

Meriweather County.—FSU 7040: Sulpher Cr. tributary, 2 mi NE of Pine Mountain, 16 August 1960 (40).

Carroll County.—UAIC 1095: Wolf Cr., 5 mi NE of Whitesburg, 8 December 1963 (1).

Douglas County.—UAIC 1093: 0.9 mi S of McWhorter, 7 December 1963 (31).

Cobb County.—USNM 161672: Nickajack Cr., at Camp Highlands, 4, 11 March 1951 (14).

Fulton County.—UMMZ 88296: Nancy Cr., about 10 mi N of Atlanta, 2 August 1929 (11). CU 51023: Nancy Cr., 9.7 mi S of Roswell, 6 September 1953 (5). CU 17136: Vickery Cr., at junction with Chattahoochee R. at limits of Roswell, 30 March 1950 (1). TU 12131: Vickery Cr., 0.6 mi E of Ros-

well, 6 October 1955 (1). TU 26128: Vickery Cr. tributary, 4 mi NE of Roswell, 20 April 1962 (20).

Gwinnett County.—UG 819: Richland Cr., 1 mi from Chattahoochee R., 20 October 1962 (13).

Hall County.—USNM 93201: 7 mi NW of Gainesville, 1933 (4). CU 21445: Tributary of Chattahoochee R. 1 mi N of junction of Rte. 52 and Rte. 129, 10 June 1952 (5). USNM 166505: Chestatee R. tributary, 12.4 mi N of Gainesville, 11 September 1947 (135). CU 19819: Tributary of Chestatee R. 1 mi SE of Murraysville, 26 March 1951 (19).

Lumpkin County.—USNM 166506: Chestatee R. tributary, 1.3 mi WSW of Dahlonega, 11 September 1947 (9). CU 21418: Cane Cr., 1.5 mi SW Dahlonega, 10 June 1952 (1). CU 10990: Cane Cr., 1.6 mi WSW of Dahlonega, 10 April 1947 (1). TU 38362: Cane Cr., 2 mi W of Dahlonega, 21 June 1965 (4). UG 604: Cane Cr., at first bridge N of Dahlonega, 20 October 1958 (7). FSU 7523: Chestatee R., at mouth of Yahoola Cr., 2.1 mi SE of Dahlonega, 17 July 1961 (3). UG 607: Yahoola Cr., at bridge behind Yahoola Church, 21 October 1958 (10). TU 30448: Chestatee R., 4 mi SE of Dahlonega, 14 April 1963 (6). TU 29773: Chestatee R., 10.7 mi NW of Cleveland, 17 August 1962 (2). TU 30423: Chestatee R., about 10 mi NW of Cleveland, 14 April 1963 (64). UG 593: Dick's Cr., 0.8 mi above junction with Water's Creek, 9 October 1958 (20). UMMZ 165559: Dick's Cr., tributary of Chestatee R., 15 mi W of Cleveland, 17 October 1940 (15).

White County.—TU 29764: Little Tesnatee Cr., 1.4 mi NW of Cleveland, 17 August 1962 (14). USNM 161704: Little Tesnatee Cr. tributary, 1 mi W of Cleveland, 3 April 1949 (1). TU 38325: Tesnatee Cr. tributary, 1.8 mi NW of Cleveland, 21 June 1965 (67). TU 30437: Tesnatee Cr. tributary, 2 mi NW of Cleveland, 14 April 1963 (23). UMMZ 94590: Turner Cr., N of Cleveland, 13 November 1931 (2). UG 592: Spoilcane Cr., 0.75 mi above its mouth, 8 October 1958 (1). UG 591: Spoilcane Cr., 1 mi above Chattahoochee Management Area, 8 October 1958 (10). UMMZ 165618: Chattahoochee R., 4 mi above Helen, 21 October 1940 (4).

Habersham County.—CU21404: Tributary, Chattahoochee R. 2.9 mi SW of Cornelia, 8 June 1952 (2). CU 50304: Tenner Branch near Cornelia, late spring 1951 (15). CU 18109: Grant Cr., tributary of Soque R. near its junction with Chattahoochee R. near Cornelia, June 1949 (15). CU 17431: Tributary of Chattahoochee R., 2.7 mi E of Chattahoochee R. on Rte. 115, 1 April 1950 (11). CU 17439: Tributary of Soque R., 1 mi W Soque R. on Rte. 115, 1 April 1950 (1). FSU 5717: Soque R. tributary, 1.5 mi W of Clarkesville, 16 July 1961 (5). USNM 168091: Tributary below dam, 2.4 mi WNW of Clarkesville, 11 September 1954 (9). USNM 171663: Soque R. tributary, 5 mi NE of Clarkesville, 9 April 1947 (4). USNM 161687: Soque R., at Watt's Mill, 9 mi N of Clarkesville, 3 April 1949 (2). UG 606: Soque R., 0.75 mi upstream from Watt's Mill, 21 October 1958 (2). UG 597: Raper Cr., at Wickle's store, 13 October 1958 (2). UG 598: Raper Cr., (at the mines), 13 October 1958 (4). UG 588: Soque R. near Chimney Mountain Farm, 30 October 1958 (5). UG 587: Soque R., 0.25 mi above the last bridge upstream, 30 September 1958 (13).

White County.—UG 622: Chickamauga Cr., 1 mi above Hwy. 255, 22 October 1958 (6). UG 621: Sautee Cr., at bridge off Hwy. 256, 22 October 1958 (9). UG 623: McClure Cr., 0.25 mi above "lower" bridge, 22 October 1958 (20). TU 29758: Dukes Cr., 1 mi SW of Nacoochee, 16 August 1962 (30).

White–Habersham County line.—UG 838: Chattahoochee R. 24 October 1958 (9).

Nocomis leptocephalus leptocephalus (Girard)

New River: USNM 103979, 171707, 177352, 177356, 177359, 177378, 177379, 177382, 177390, 177394, 177402, 177407, 194273, 194701–194710, 194806, 199736, 199738, 199740. CU 19415, 19456, 20452, 20940, 23848, 24749, 24968, 25318, 25352, 25787, 38202, 42132. TU 25496, 25531, 25597, 28001, 29663. UMMZ 126229, 136636, 137969, 147651. DU F–110, F–113, F–116.

Potomac River: USNM 177355, 194659–194661.

Rappahannock River: CU 46283, 52054.

York River: USNM 100224, 107725, 107739, 171617, 194277.

James River: USNM 100186, 100196, 100218, 103991, 105083, 107503, 163435, 166490, 171632, 171633, 171659, 171730, 194263, 194626, 194633, 194669, 194693–194697, 194699, 194700, 194731, 194732, 194735–194737, 199697, 199701, 199708, 199711, 199713, 199715 199717. CU 11358, 11595, 12222, 20949, 23828, 23875, 24162, 24167, 29156. UMMZ 171383, 174486, 174679, 174721, 174827, 175113.

Chowan River: USNM 101342, 171619, 177383, 194744, 194745, 194759–194761. CU 11883, 18603, 33164, 50437, 50981.

Roanoke River: USNM 100168, 100177, 101329, 101332, 102059, 102060, 103976, 104007, 104012, 104017, 104028, 105071, 107591, 107595, 107604, 107616, 107634, 107651, 116564, 132024, 162826–162830, 162882, 162883, 166388–166399, 166491, 168143, 171618, 171621–171623, 171626, 171636, 171637, 171639, 171649, 171652, 171655, 171656, 171658, 171661, 171676, 171678. 171683, 171684, 171694, 171696, 171702, 171704–171706, 171708, 171709, 171724–171726, 171731, 171736, 171738, 171742, 177374, 177377, 177390, 177399, 177405, 177406, 194256, 194264, 194711–194730, 194754–194758, 194762–194771, 199870, 199963, 199980, 200017, 200089. CU 11497, 11914, 11959, 13875, 14001, 16833, 50402, 50824, 50960, 50971. KU 3284. TU 25887. UMMZ 137586, 171360, 174707, 175141. ANSP 1857–70, 75732. DU F–129.

Tar River: USNM 171657, 171660. CU 19432, 19475, 19504, 19521, 25881, 25908, 26024, 31739. UMMZ 147581.

Neuse River: USNM 69799, 171605, 171616, 171634, 171635, 171650, 171653, 171667, 171729, 188554, 188737, 194269, 194270. CU 9535, 19842, 25868, 31686, 34483. DU F–107, F–126, F–128, F–130.

Cape Fear River: USNM 40289, 93222, 166492, 171609, 171624, 171625, 188571. CU 31676, 31752. DU F–115, F–117, F–125, F–127.

Pee Dee River: USNM 104002, 105048, 105069, 105073, 105078, 105081, 162925–162927, 162947, 164309, 166493, 171607, 171608, 171638, 171668–171670, 171677, 171682,

171695, 171703, 171712. CU 3501, 10981, 11212, 11342, 11423, 11434, 11490, 11527, 14278, 17177, 19559, 19634, 19727, 21323, 21358, 25380, 29831, 29841, 30036, 31665, 31821, 37701, 37942, 38176. KU 8879. TU 29835. ANSP 1850–56. UMMZ 139432, 147635.

Santee River: USNM 40515, 87164, 92448, 92476, 93211, 100655, 100661, 119086, 119291, 162898, 162903–162905, 162939, 162953, 166403, 166427, 166494, 166496, 166498–166500, 168130, 171604, 171606, 171627, 171640, 171648, 171651, 171654, 171672, 171674, 171675, 171679, 171686, 171710, 171711, 171728, 171740, 171741, 171743, 192852, 192855, 192857, 199758–199768, 199771–199797, 199799, 199801, 199803–199811, 199813–199815, 199840, 199841, 199858–199869, 199871–199898, 199900–199902, 199904–199928, 199930–199936, 199944, 199946–199952, 199954–199962, 199964–199968, 199970–199979, 199982–199984, 199992–200013, 200015, 200016, 200018–200024, 200026–200029, 200031–200037, 200051–200088, 200090–200098, 200127–200132, 200134–200140, 200188–200200, 200755, 200758. TU 16498, 25939, 26199, 27485, 27492, 27494, 27513, 28231, 28234, 29445. ANSP 1826–40. KU 5270, 5272, 8890. CU 9935, 10064, 10123, 10535, 11756, 11938, 11962, 17070, 17074, 17091, 17114, 17201, 17305, 17540, 17722, 19225, 19288, 19331, 19340, 19399, 19552, 19659, 19674, 19688, 19690, 19704, 19711, 19714, 19716, 19741, 19788, 21243, 21371, 21382, 21386, 21394, 25167, 25859, 25972, 25978, 26060, 28359, 31857, 37841, 38063, 38076, 38108, 46430, 50883. UMMZ 163859, 165641. DU F-118. Univ. Minn. 17673.

Nocomis leptocephalus bellicus Girard

Mobile Bay drainage (Alabama–Tombigbee rivers)

UAIC 58, 59, 427, 432, 435, 492, 523, 532, 533, 678, 680, 685, 814, 819, 822, 829, 888, 928, 934, 959, 960, 961, 963, 965, 966, 971, 972, 1036, 1038, 1039, 1064, 1066–1069, 1098, 1102, 1232, 1241, 1249, 1250, 1282, 1284, 1307–1310, 1312, 1315, 1317–1319, 1354, 1359–1363, 1375, 1376, 1378, 1379, 1381, 1382, 1387, 1479, 1496, 1497, 1500, 1504, 1514, 1593, 1668, 1771, 1829, 1863, 1864, 1876, 1891, 1892, 2005.

TU 2628, 3421, 9932, 12083, 15282, 18702, 24555, 25992, 27340, 27551, 27555, 29903, 30187, 30227, 30950, 32434, 32490, 32510, 32527, 32539, 32581, 32599, 32656, 32673, 32690, 32694, 32740, 34405, 35071, 35161, 35174, 35319, 35324, 35373, 38749, 38771, 40595, 40650, 40664.

UMMZ 113917, 124065, 124100, 146514, 146530, 166359, 166379, 168662, 168667, 168761, 175830, 177740, 177752.

CU 13781, 13997, 16021, 19256, 40212, 42314, 42357.

USNM 161705, 166009, 199543, 200756.

API 404–2, 501–1, 714.

Pascagoula Bay drainage

TU 8032, 8041, 8053, 8065, 9899, 15439, 39390.

UMMZ 157784.

CU 11618, 12581, 16252, 16257.

Pearl River drainage

TU 980, 1545, 3605, 3845, 7505, 7600, 13998, 14100, 15151, 15203, 15524, 16736, 17525, 17943, 19806, 23385, 23423, 23500, 23748, 26837, 26869, 26683, 26886, 27182, 27280, 27336, 27481, 28703, 28780, 28830, 28869, 30130, 31672, 31686, 36090, 40101.

CU 11859, 12487, 15684, 16266, 16613, 37393, 46419.

UMMZ 113775, 155350, 161151, 175388.

USNM 131905.

Eastern Mississippi River tributaries

UAIC 1268, 1269, 1587.

FSU 9186, 10727.

TU 2925, 7214, 7897, 11998, 15130, 16621, 19776, 19843, 23889, 23953, 28896, 30154, 30888, 30897, 31790, 32343, 32923, 40281, 40370.

UMMZ 161199, 161208.

USNM 172027, 172034.

CU 37581.

MGFC 4468, 4520, 5754, 5755.

Tennessee River drainage

UAIC 1760, 1776, 1886.

TU 40533.

Nocomis leptocephalus intergrade *interocularis* × *leptocephalus*

Edisto River drainage (South Carolina)

Aiken County.—USNM 200201: Chinguapin Cr., 6.4 mi SSW of Leesville at South Carolina Hwy. 391 crossing, 5 July 1956 (50). CU 29851: Chinguapin Cr. tributary, 6.7 mi S of Batesburg, Rte. 391, 28 March 1956 (28). USNM 203918: Chinguapin Cr., about 4 mi S of Batesburg, 0.25 mi W of Rte. 391, 20 April 1967 (40). USNM 203920: Chinguapin Cr., about 6 mi S of Batesburg, 20 April 1967 (10). USNM 203919: Chinguapin Cr., about 3.5 mi SSW of Batesburg, 21 April 1967 (27).

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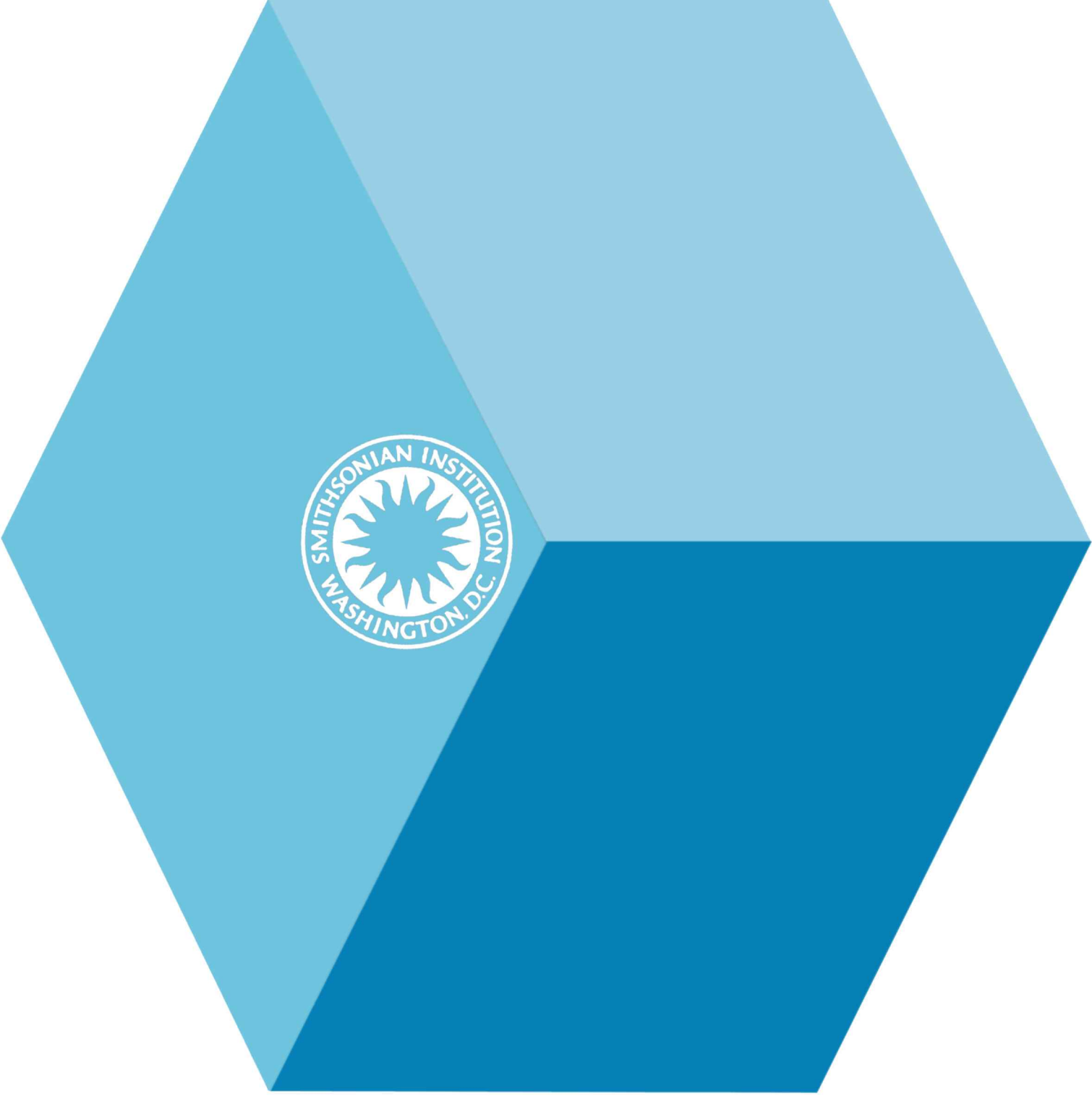
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