

ERNEST A. LACHNER  
and ROBERT E. JENKINS

*Systematics, Distribution,  
and Evolution of the  
Nocomis biguttatus  
Species Group (Family  
Cyprinidae: Pisces) with  
a Description of a  
New Species from  
the Ozark Upland*

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SMITHSONIAN CONTRIBUTIONS TO  
ZOOLOGY

NUMBER 91

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SMITHSONIAN INSTITUTION PRESS  
CITY OF WASHINGTON

1971

## ABSTRACT

Lachner, Ernest A., and Robert E. Jenkins. Systematics, Distribution, and Evolution of the *Nocomis biguttatus* Species Group (Family Cyprinidae: Pisces), with a Description of a New Species from the Ozark Upland. *Smithsonian Contributions to Zoology*, number 91, 28 pages, 1971.—This study treats the three allopatric species of the *Nocomis biguttatus* group: *N. biguttatus*, *N. effusus*, and *N. asper*, a new species. The systematics, distribution, ecology, evolution, and zoogeography of the species are compared. The region of the Ozark upland is emphasized because it is inhabited by the new species. *N. asper* is distinguished from *N. biguttatus* mainly in having a characteristic tuberculation pattern present on the body of the adults which never appears on the latter species. *N. asper* differs from *N. effusus* primarily in having two rows of pharyngeal teeth compared to one row in the latter, and in having about one fourth of its tuberculate body scales bearing two or more tubercles compared with only 3 percent bearing two tubercles in the latter species. The coloration of the nuptial males of the three species differs.

*Nocomis biguttatus* is a wide-ranging form found naturally in the Missouri, upper Mississippi, northern Ohio, and the Great Lakes drainages. It avoids the nonglaciated regions of the upper Mississippi and Ohio drainages. This species is restricted to a few scattered populations in the middle and lower Missouri drainage—evidence of a once more widely distributed species that has been largely extirpated from this drainage mainly by the erosional history of the area, increased agricultural practices, and by droughts. *N. asper* and *N. effusus* have restricted distributions on opposite sides of the Mississippi Valley. *N. asper* is contained chiefly in the Ozark upland of the Arkansas River drainage of the tri-state area of Arkansas, Oklahoma, and Missouri, with probable isolated populations in the upper Neosho system of Kansas and in the Arkansas drainage of central Oklahoma, and a well-established population in the Blue River system, Red drainage, of south-central Oklahoma. Such isolated populations also are regarded as evidence of a wider distribution of these species in these drainages in the past. The disjunct populations of *N. asper* are paralleled closely by the occurrence of isolated populations of *Notropis pilsbryi* in the Arkansas River and Red River drainages. *N. effusus* is confined in the southwestern Ohio River basin to the Duck River system of the lower Tennessee drainage, the lower and middle Cumberland River drainage below its falls, and in the upper Green River drainage.

The species of the biguttatus group chiefly inhabit tributaries and avoid the main rivers. Clear-water streams, small-to-moderate in size, with low-to-moderate gradients, and with clean substrates of gravel, rubble, and some sand, provide the preferred ecological requirements. Generally, the preferred streams have a moderate balance of riffles and pools. Turbid or silt-laden waters are avoided.

The *Nocomis biguttatus* species group is considered to be the most primitive group within the genus; this assumption is based mainly on the generalized pattern of tuberculation on the head and on the presence of two rows of pharyngeal teeth. The primitive condition persists in *N. biguttatus*. The body tuberculation in *N. asper* and *N. effusus* (absent in *N. biguttatus*) demonstrates evolution of another type of tubercle pattern in *Nocomis*. The reduction in the number of tubercles per scale, the reduction in the distribution of tuberculate body scales, and the increase in the size of tubercles on the scales of the body of *N. effusus* are regarded as specialized conditions and correlate with the evolutionary trends of head tubercle development in the two other species groups of *Nocomis*.

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

UNITED STATES GOVERNMENT PRINTING OFFICE  
WASHINGTON : 1971

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For sale by the Superintendent of Documents, U.S. Government Printing Office  
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Ernest A. Lachner  
and Robert E. Jenkins

# Systematics, Distribution, and Evolution of the *Nocomis biguttatus* Species Group (Family Cyprinidae: Pisces) with a Description of a New Species from the Ozark Upland

## Introduction

Studies over the past several years have revealed a new species of the *Nocomis biguttatus* species group in the Arkansas River drainage. The new species is related to *N. effusus* Lachner and Jenkins (1967) in body tuberculation, and to *N. biguttatus* (Kirtland) in its pharyngeal dentition. One problem of concern to us was the possibility of the existence of intergrading populations in adjacent drainages north of the Arkansas River drainage, such as the White River. We attempted to obtain representative series of chubs from drainages where existing museum collections were inadequate. A survey of systematic characters in the wide-ranging *N. biguttatus* was initiated. A factor complicating the study was the need for nuptial male specimens in order to ascertain the extent of body tubercle development—a critical diagnostic character. Body tuberculation is completely developed only in the mature males. The large chubs are difficult to capture with conventional small seines. They are captured best by angling and by using an electric shocker.

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In the *Nocomis biguttatus* species group, as with all other species of *Nocomis*, tuberculation is an important evolutionary character. In two species of the *N. biguttatus* species group, however, nuptial tubercles not only develop on the head but are uniquely present on the body. The head tuberculation, in regard to tubercle numbers, size, and occurrence, is similar in all three species of the biguttatus group (in contrast to a great amount of interspecific differentiation in the *N. micropogon* species group and the *N. leptocephalus* species group).

The *Nocomis biguttatus* species group was described and compared with the two other *Nocomis* species groups by Lachner and Jenkins (1967; 1971). The objectives of this paper are to describe a new species of *Nocomis* and to compare the three species of the biguttatus group in respect to their systematics, distribution, ecology, and evolution.

The nominal species *Nocomis biguttatus* (Kirtland) was described briefly in 1840 from Yellow Creek, Mahoning River, Ohio. Lachner and Jenkins (1967) described the second member of the species group, *N. effusus*, from the Cumberland, Green, and lower Tennessee drainages. The systematic characters of these two species were treated in detail by Lachner and Jenkins, and their distribution and evolution were dis-

cussed with particular emphasis on the occurrence of members of the genus in the southwestern Ohio River basin.

### Acknowledgments

We are deeply appreciative of the efforts of many individuals who freely loaned collections in their care, provided data concerning the collections, and made space and facilities available to us. Our special thanks go to George A. Moore, Oklahoma State University (OSUMZ) for providing the holotype and life-color observations of the new species, and to Kirk Strawn, Texas A. and M. University, for providing an excellent series of tuberculate adult paratypes and other specimens, some of which he hand carried to Washington from Arkansas after several successful attempts at pole fishing.

Material was examined or data received from the following individuals or institutions: Edward C. Raney, Cornell University (CU); Frank B. Cross, University of Kansas (KU); William L. Pflieger, Missouri Conservation Department; William M. Palmer, North Carolina State Museum (NCSM); Royal D. Suttkus, Tulane University (TU); Carter R. Gilbert, University of Florida (UF); William M. Clay, University of Louisville (UL); Reeve M. Bailey and Robert Rush Miller, University of Michigan (UMMZ); Old Indiana University Collection at University of Michigan, UMMZ (IU); Carl D. Riggs and L. C. Hill, University of Oklahoma (UOMZ); National Museum of Natural History, Washington, D.C. (USNM); James E. Bohlke, Academy of Natural Sciences, Philadelphia (ANSP); George C. Becker, Wisconsin State University (WSU); D. E. McAllister, National Museum of Canada (NMC); W. B. Scott, Royal Ontario Museum (ROM).

The illustrative materials were done by supported individuals or divisions of the Smithsonian Institution, as follows: Carolyn Bartlett Gast and A. M. Awl, detailed drawings; Gertrude H. Nicholson, scatter diagrams; Dorothy L. Hubbs and Martin L. Wiley, maps, X-rays, and technical assistance; Richard H. Goodyear, computer operation and analysis; and the Photographic Services Division.

The first author received support from the Smithsonian Institution Research Foundation; the second

author received support from National Science Foundation Grant No. 23395 to Edward C. Raney, Cornell University.

### Methods and Materials

The methods and techniques employed in this study are the same as those given by Lachner and Jenkins (1967; 1971). All body length measurements refer to standard length (SL) in millimeters (mm) unless stated otherwise. Abbreviations are spelled out when used for the first time in the text. The institutional abbreviations used in the sections on "specimens studied" are defined in the section "Acknowledgments"; for example, National Museum of Natural History, Washington, D.C. (USNM).

The number of body scales bearing tubercles were counted on the left side from tuberculate or tubercle-scarred males. The body tubercles are discernible as spots on larger females and nonbreeding males, but tubercles in this state of development are difficult to see and to count accurately. Many of our specimens had some discernible body tubercle-spot development, but these data were not used in our tabular comparisons.

Only collections containing tuberculate specimens from the Arkansas River drainage are designated as type materials. The number of specimens (in parentheses) and their size range is listed in the data for the type material. The number of specimens only is given for the nontype materials. The collections are arranged and grouped by basin, drainage, and state.

The collections plotted on the distribution map for *Nocomis biguttatus* include all material examined and data from reliable published accounts of major state or regional surveys. Collections occurring together or in nearby areas were indicated by one plot on the distribution map. The primary synonymy is listed; also included are those references where examination was made of the authors' original material and of material that had some particular bearing on this study.

### *Nocomis biguttatus* Species Group

The following characters best describe this group: head with many moderate-size, nuptial tubercles extending from mid-snout to occiput; tubercles absent on lachrymal; tubercles present laterally on body in two



species, and arranged in rows; head tubercles usually antrorse; nuptial crest absent; red postocular spot present in life; dark caudal spot in young and in juveniles

large, round, and distinct; pharyngeal dentition 1,4-4,1 to 4-4; scales small, about 31 to 38 in circumferential series.

### Key to the Species of the *Nocomis biguttatus* Species Group

1. Nuptial tubercles or tubercle spots absent on body; pharyngeal teeth number 1,4-4,1, occasionally lacking a tooth on minor row of one side. North-central United States, from Missouri River and Mississippi River drainages to northern Ohio River and Great Lakes drainages.....Hornyhead chub, *Nocomis biguttatus* (Kirtland)
- Nuptial tubercles or tubercle spots present laterally on body of adults, visible in both sexes; pharyngeal teeth in one or two rows, numbering almost always 1,4-4,1 or 1,4-4,0, and 4-4.....2
2. Pharyngeal teeth in one row, 4-4 (only one specimen known with 0,4-4,1); lateral body scales when tuberculate almost always with one tubercle per scale (97 percent), rarely with two tubercles per scale and never three or more; body tubercles large, about the size of the average head tubercles, or larger; tubercles commonly on one or two rows of scales below lateral line. In life, red postocular spot weakly developed, and only noticeable in large males; pectoral and pelvic fins reddish orange; caudal fin reddish. Southwestern Ohio River basin in the Green and Cumberland drainages and Duck system of Tennessee drainage.....Redtail chub, *Nocomis effusus* Lachner and Jenkins
- Pharyngeal teeth in two rows, 1,4-4,1, rarely 1,4-4,0 (only one specimen with 1,4-4,2); lateral body scales, when tuberculate, frequently with two tubercles per scale (about 23 percent), sometimes three tubercles per scale (maximum of four observed); body tubercles small, much smaller than head tubercles; tubercles seldom occurring on second scale row below lateral line. In life, red postocular spot well developed, observed in both sexes at sizes as small as 100 mm SL; pectoral and pelvic fins pinkish yellow; caudal fin pinkish olive. Red and Arkansas drainages.....Redspot chub, *Nocomis asper*, new species

#### *Nocomis asper*, new species

Redspot chub  
FIGURES 1, 2

*Hybopsis biguttatus*.—Branson 1962:535, fig. 9; 1967:133.—Hall 1952:57.—Linder 1955:175 [Red drainage].—Reno 1969:739 [in part, Arkansas drainage].

*Hybopsis (Nocomis) biguttata*.—Davis and Miller 1967:5 [in part].

*Hybopsis kentuckiensis*.—Meek 1891:126; 1894:85 [Neosho system].—Evermann and Kendall 1895:471 [in part].

*Nocomis biguttatus*.—Hubbs and Ortenburger 1929:65 [Arkansas drainage].

*Nocomis* sp.—Lachner and Jenkins 1967:577 [evolution].

SPECIMENS STUDIED.—HOLOTYPE: USNM 204851: Arkansas drainage, Oklahoma, Mayes County, Big Spring Creek at Camp Gailand, 5 mi S. Locust Grove, 7 May 1949, G. A. Moore and class, male, 178.5 mm.

PARATYPES: ARKANSAS DRAINAGE. USNM 204852: Same data as for holotype. (15 specimens) 30 to 90 mm SL.

OSUMZ 5159: Oklahoma, Cherokee County, Barren Fork River, Muskogee, Boy Scout Camp, (3) 131-165.

OSUMZ 5722: Oklahoma, Cherokee County, Bar-

ren Fork Creek, tributary to Illinois River at Camp Egan. 2 May 1959, G. A. Moore, M. R. Curd, (2) 136-145.

OSUMZ 5106: Oklahoma, Delaware County, Spavinaw Creek, 5.2 mi N. Colcord. 25 June 1955, Linder, Branson, Greer, and Sutton, (4) 41-143.

TU 48547: Arkansas, Benton County, Spavinaw Creek, (Hole #3). 10 June 1966, graduate students, University of Arkansas, (9) 49-175.

TU 48613: Arkansas, Benton County, Spavinaw Creek, (Hole #2). 10 June 1966, graduate students, University of Arkansas, (28) 39-182.

TU 48658: Arkansas, Benton County, Spavinaw Creek (Hole #4). 10 June 1967, graduate students, University of Arkansas, (14) 43-177.

USNM 193358: Arkansas, Washington County, Clear Creek, tributary to upper Illinois River. 5 June 1962, K. Strawn and others, (9) 72-176.

OTHER COLLECTIONS (listed by states): ARKANSAS DRAINAGE. Arkansas: TU 48645 (7), 59138 (2), UMMZ 80913 (2), 97774 (3), 103176 (3), 108906-7 (2), 122948 (1), 123465 (1), 123712 (1), 128351 (4), 170912 (1), 175440 (2), USNM 163278 (5).

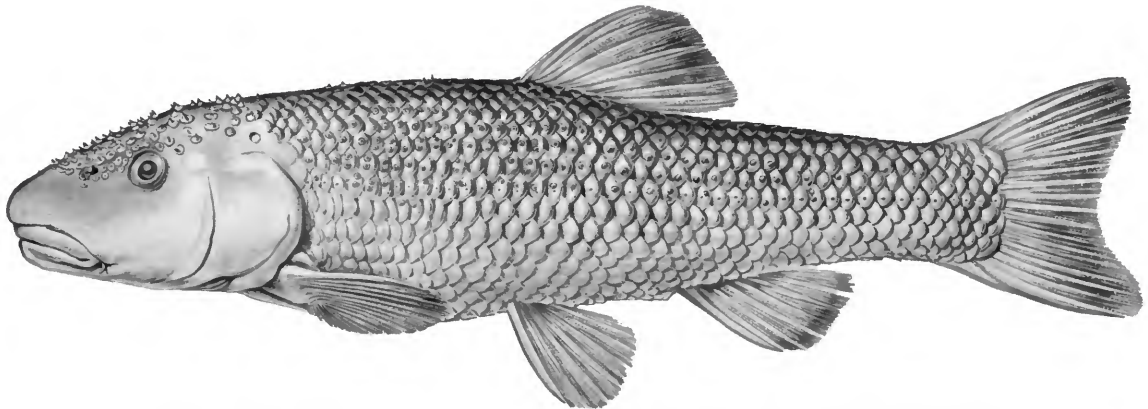


FIGURE 1.—Lateral view of *Nocomis asper*, holotype, USNM 204851, a nuptial male, 179 mm SL, taken 7 May 1949 from Big Spring Creek, Arkansas River drainage. Drawn by C. B. Gast. (Light postocular spot omitted in Figure 2.)

Missouri: UMMZ 103208 (19), 119995 (1), 151498 (1), 151569 (1), USNM 42855 (1), 63229 (1).

Oklahoma: OSUMZ 103 (2), 132 (1), 428 (2), 528 (1), 2388 (1), 2409 (6), 2410 (2), 2412 (6), 2418 (1), 4828 (1), TU 16585 (5), UMMZ 80915 (2), 116770 (7), 116796 (16), UOMZ 7584 (4),

15473 (2), 29504 (1), 29665 (1), USNM 62055 (7), 204854 (8).

RED DRAINAGE. Oklahoma: Johnston County, Blue River. CU 52267 (12), near Connerville, July 1966. CU 52401 (15), Connerville, 4 June 1967. NCSM 4733 (3), 1 mi E. Connerville, May 1967. OSUMZ 1499 (2), 10 mi W. Wapanuka, 3 mi S. Route 7 at Hughes Crossing, 6 April 1947. OSUMZ 2091 (1), at bridge on Route 99, 5 April 1947. UOMZ 30442 (2), Connerville, 29 July 1960. UOMZ 31134 (16), Connerville, Route 99 bridge, 1 July 1959.

DIAGNOSIS.—A species of the biguttatus group, most closely related to *Nocomis effusus*, but differing from it in having two rows of pharyngeal teeth, tuberculate lateral body scales often having two or three tubercles, pinkish-yellow pectoral and pelvic fins, and a well-developed red postocular spot present in both sexes of subadults and adults.

DESCRIPTION: MORPHOMETRY.—The body proportions of *Nocomis asper*, general shape and contour, are close to those described for *N. effusus* (Lachner and Jenkins 1967:563). Proportional measurements for five large males (including the holotype) and five large females are given in Table 1. In *N. asper*, as is true for all species of *Nocomis*, characters involving allometric growth have values for males exceeding those of females (except orbit), because the males attain an average larger size than the females. The relative increase of two characters—head length and snout length—with increase in body length for *N. asper* is shown in Figures 3 and 4.

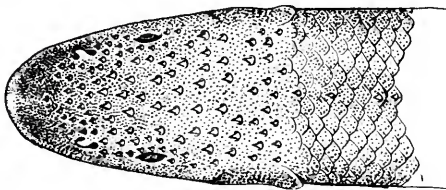
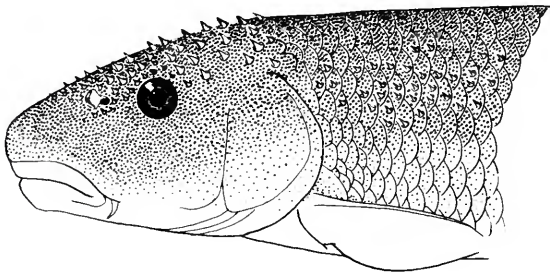


FIGURE 2.—Dorsal and lateral view of the head of *Nocomis asper*, holotype. Drawn by A. M. Awl.

TABLE 1.—Proportional measurements of 5 adult male (including the holotype) and 5 female *Nocomis asper* from the Arkansas River drainage (expressed in thousandths of the standard length)

Character	Holotype ♂	♂		♀	
		$\bar{X}$	Range	$\bar{X}$	Range
SL in mm	178.5	(174)	161-181	(150)	139-166
Head length	292	(287)	274-293	(278)	268-287
Snout length	135	(130)	120-135	(115)	112-119
Postorbital length	126	(121)	119-126	(121)	111-128
Upper lip, length	109	(115)	105-128	(99)	93-113
Gape width	114	(108)	105-114	(92)	89-94
Orbit, bony length	47	(46)	43-48	(49)	46-53
Interorbit, bony width	92	(95)	89-101	(79)	74-84
Predorsal length	551	(536)	520-551	(551)	540-572
Caudal peduncle length	216	(221)	211-230	(208)	196-215
Caudal peduncle depth	107	(108)	104-111	(99)	92-107
Body, greatest depth	244	(235)	227-244	(252)	244-262
Body, greatest width	164	(160)	151-168	(172)	155-182
Pectoral fin length	184	(178)	168-184	(163)	158-168
Pelvic fin length	151	(158)	151-167	(139)	132-146

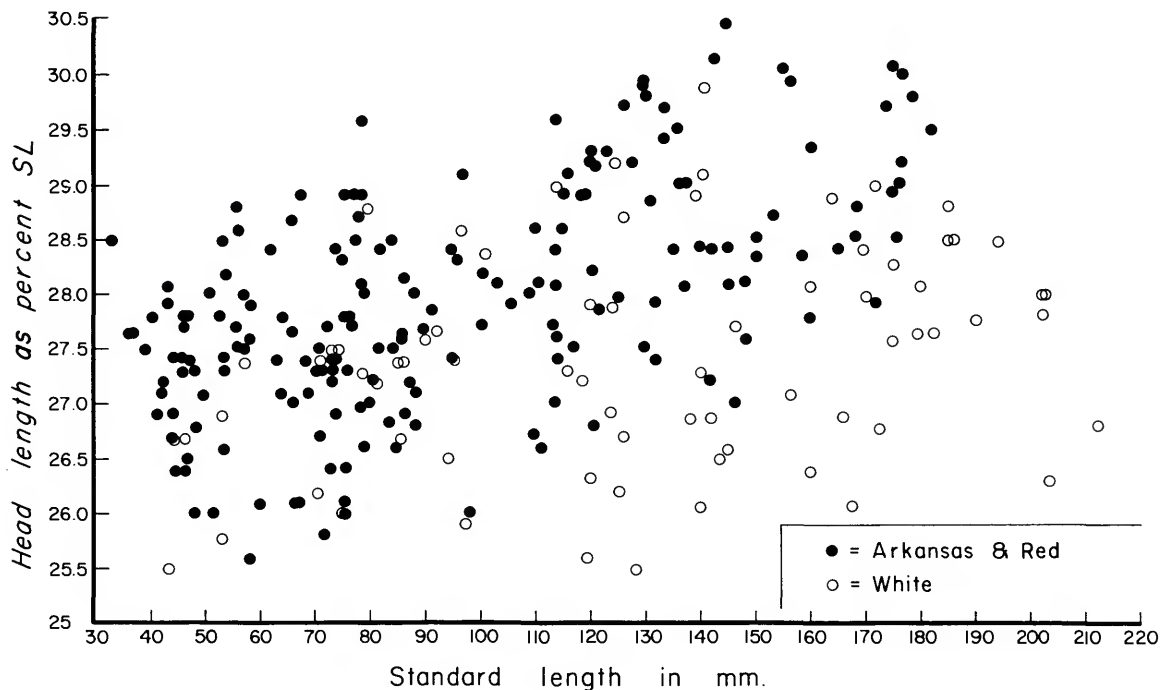


FIGURE 3.—Comparison of head length as percent of standard length, plotted against standard length in *Nocomis asper* from the Arkansas River and Red River drainages and *N. biguttatus* from the White River drainage. The head lengths were statistically different in these two populations.

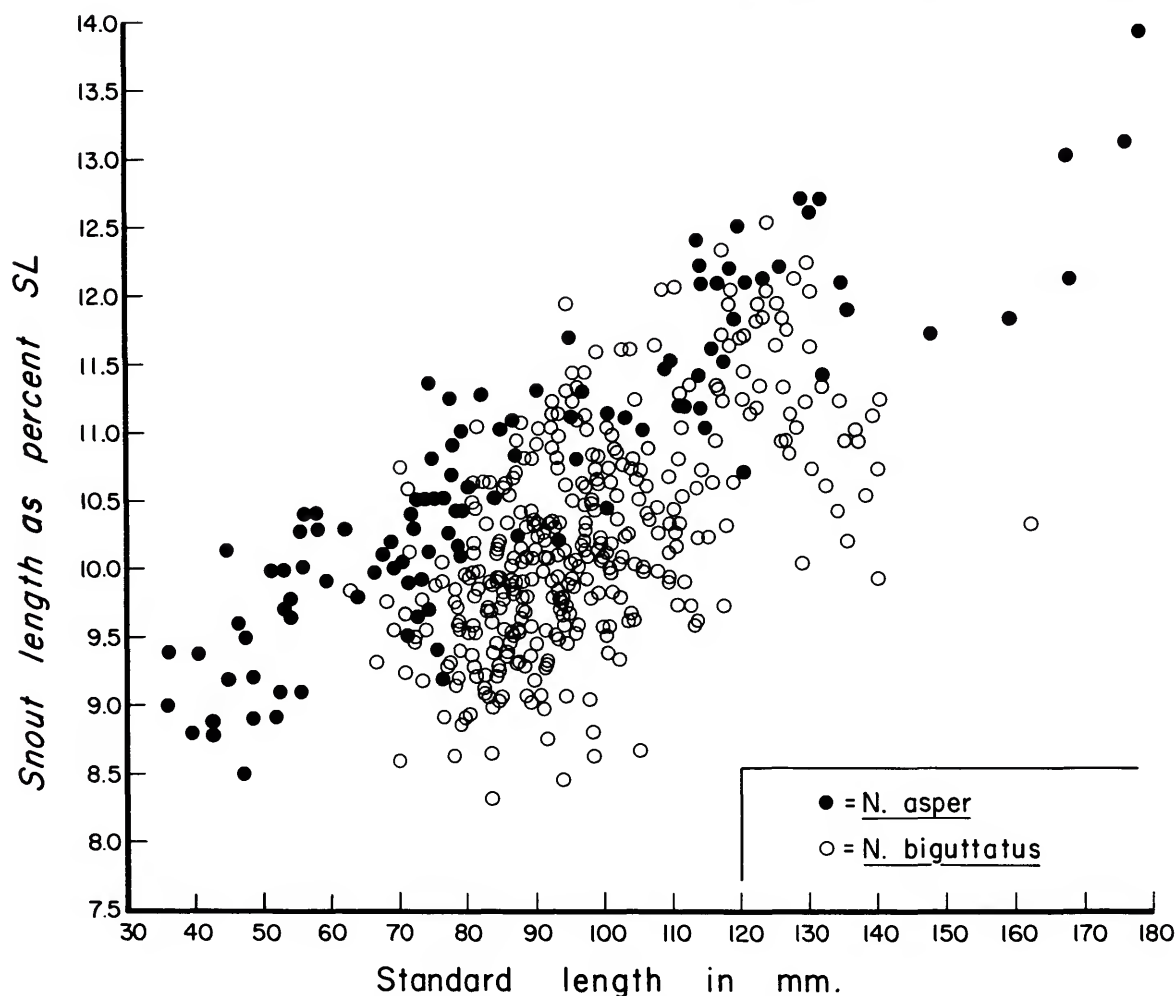


FIGURE 4.—Comparison of snout length as percent of standard length, plotted against standard length in *Nocomis asper* from the Arkansas and Red River drainages and *N. biguttatus* from the Great Lakes, Mississippi River and lower Ohio River drainages.

**MERISTIC CHARACTERS.**—*Nocomis asper* is a comparatively coarse-scaled member of the species group, the circumferential scales average about 34 (Table 2), caudal peduncle scales about 18, and the lateral line scales about 41.

Vertebrae, counting the hypural plate as one and the vertebrae included in the Weberian apparatus as four, average 40.1 (Table 2) from the Red and Arkansas drainages and range from 39 to 41.

**TUBERCULATION.**—The discussion of tubercles concerns the nuptial males, on which the tubercles become enlarged. The tubercle numbers and distribution are

similar in individuals of similar sizes of both sexes, except that the tubercles in the females appear as light spots, not readily discernible.

The head tubercles are distributed from about the midportion of the snout to the occiput (Figures 1 and 2). There is no hiatus in the tubercle distribution on the snout. A row of several tubercles occurs just below the nares in the larger nuptial males. The head tubercles of *Nocomis asper* compare closely with those of *N. biguttatus* and *N. effusus* in number, size, and distribution (Tables 3, 4, and 5). The tubercles are larger posteriorly on the head and smaller on the forehead

TABLE 2.—The number of scales and vertebrae in species of the *Nocomis biguttatus* group (Great Lakes sample includes Ohio and upper Mississippi specimens)

Species and locality	Lateral line											Caudal peduncle								
	38	39	40	41	42	43	44	45	46	N	$\bar{X}$	16	17	18	19	20	21	N	$\bar{X}$	
<i>biguttatus</i>																				
Great Lakes, etc.	9	29	21	6	4	1					70	39.6	51	15	4	3	1		74	16.5
Missouri		1	4	7	4	3	4	1	1		25	42.0	2	4	8	3	5		22	18.2
Lower Mississippi			1	3	5	1	1				11	41.8	2	2	4	3			11	17.7
White			8	3	6	14	10	2			43	42.5		1	8	15	17		41	19.2
<i>asper</i>																				
Arkansas		5	15	28	25	9	4				86	41.3	4	22	23	16	21		86	18.3
Red	1	1	10	9	1	3	2	1			28	41.0	3	9	11	6			29	17.7
<i>effusus</i>																				
All drainages		2	18	37	57	20	3				137	41.6		4	9	22	111	1	147	19.7
	Circumferential											Vertebrae								
	30	31	32	33	34	35	36	37	38	39	N	$\bar{X}$	38	39	40	41	42	N	$\bar{X}$	
<i>biguttatus</i>																				
Great Lakes, etc.	1	5	11	23	20	12	1				73	33.3	1	42	83	4		130	39.7	
Missouri				2	1	5	5	6	4	2	1	26	35.8		1	7	5		13	40.3
Lower Mississippi					1	1	4	5	2			13	35.5		2	2			4	39.5
White					1	13	16	9	2			41	35.0		1	32	10		43	40.2
<i>asper</i>																				
Arkansas		2	8	22	27	17	10	2				88	34.0		1	12	3		16	40.1
Red				2	5	12	7	2				28	34.1		2	10	3		15	40.1
<i>effusus</i>																				
All drainages					9	42	39	40	13	2	145	36.1			10	47	1	58	40.8	

and snout. The tubercles are mainly antrorse posteriorly on the head; those on the snout may be antrorse or erect. A few tubercles near the side of the head are directed laterally.

The tubercles on the nape and body are located centrally or subcentrally on the exposed portion of the scales. The body tubercles are considerably smaller than those on the head. The tuberculation of the nape is variable. In some specimens the nape is profusely tuberculate from the head to the origin of the dorsal fin, some specimens have the nape only moderately tuberculate, and in others there are only a few nape tubercles anteriorly, just posterior to the head. Usually more tubercles are on the nape near the occiput.

The first and second scale rows above the lateral line bear the greatest number of tubercles on the body, laterally; well over one half of the scales are tuber-

culate. Tubercles occur on scales of the third row above the lateral line and on the lateral line row, but the frequency of occurrence is about one half that of rows one and two above the lateral line. Some tubercles are on the first scale row below the lateral line, but the number varies from none to twenty nine tuberculate scales in seventeen nuptial males. In some specimens a few scales with tubercles are present on the fourth row above the lateral line and to a lesser extent on the second row below the lateral line. The tubercle-bearing scales are mainly on the anterior half of the body. Scales at the end of the caudal peduncle are free of tubercles.

Tubercle-bearing scales often have more than one tubercle; in our sample of seventeen nuptial males, 74.9 percent of tuberculate scales had one tubercle, 22.8 percent had two tubercles, and 2.3 percent



TABLE 3.—The number of cephalic tubercles in *Nocomis asper* from the Arkansas and Red River drainages (data for the sexes were combined)

SL in mm	Number of cephalic tubercles															Total number	
	0	1-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99	100-109	110-119	120-129	130-139		140-149
50-59	4	4	2														10
60-69		2	3	3	—	1											9
70-79			1	4	4	1	1										11
80-89			1	—	3	3	1										8
90-99			1	—	—	2	—	1									4
100-109						2											2
110-119							2	2	—	2							6
120-129								3	3								6
130-139								1	3	1	3	2					10
140-149									2	1	4	2					9
150-159										2	3	2	—	1			8
160-169										2	—	2	1				5
170-179								1	—	1	3	3	1				9
180-189																1	1

had three tubercles per scale (Tables 6, 7, 8, and 9). The larger nuptial males averaged more tuberculated scales than the smaller specimens, when the sample of seventeen males was divided into five 10-mm-size groups (Table 7).

The head tubercles develop before the body tubercles, appearing first within the area between the posterior internasal line and the midinterorbital line in juvenile specimens about 50-79 mm SL. There is a progressive tubercle development posteriorly on the head with increase in body size. The full head tubercle pattern is attained in juvenile sizes. As in *Nocomis biguttatus* and *N. effusus*, the tubercles on the snout and on the subnasal area are the last of the head tubercles to develop. After the complete pattern of tubercles on the head appears, there is a progressive increase in tubercle numbers with increase in body length (Table 3) through maturity and, apparently, through successive reproductive seasons. Some males and females in the group 50-59-mm-size SL had tubercle spots appearing on the head. The largest nuptial male examined, 182 mm SL, had about 145 head tubercles.

Almost all specimens under 100 mm SL had no body tubercle spots, although head tuberculation was well developed. A few males in the size group 90 to 99 mm SL had a few body tubercles. Gravid females, 120 to 129 mm SL, showed development of some body tubercle spots. Well-developed tubercles are present

on the dorsal portion of pectoral fin rays 2 to 5 or 6 and sometimes on ray 7.

**NUPTIAL CREST OR SWELLING.**—No specimen of *Nocomis asper* shows evidence of the small swellings observed in some specimens of *N. effusus* (Lachner and Jenkins 1967:562). In all nuptial males of *N. asper* and *N. biguttatus*, as well as almost all *N. effusus* observed, the head is free of any development of a crest; the typical nuptial crests are restricted to the species of the *N. micropogon* and *N. leptocephalus* species groups (Lachner and Jenkins 1971).

**PHARYNGEAL TEETH.**—The pharyngeal tooth count is 1,4-4,1 in 22 pairs of arches from the Arkansas and Red drainages, 0,4-4-,1 in one specimen and 1,4-4,2 in one. The tooth count is similar to that of *Nocomis biguttatus*. In a sample of 52 *N. biguttatus* from the Great Lakes, Ohio, Mississippi, and Missouri drainages 47 pairs of arches had a pharyngeal tooth count of 1,4-4,1, five had 1,4-4,0 or 0,4-4,1, and one specimen was questionably 4-4. In size and shape the arch is similar to that described for *N. effusus*. (Lachner and Jenkins 1967:564). The stout teeth and arches of the three members of the *biguttatus* group are probably indistinguishable.

**COLORATION.**—The following observations were taken from the holotype by George A. Moore on 7 May 1949 at the time of capture: a red postocular spot; pectorals and pelvics pink on outer two thirds, yellow on inner one third, the fin rays darkened with melanin

TABLE 4.—The number of cephalic tubercles in *Nocomis biguttatus* from the White River drainage (data for the sexes were combined)

SL in mm	Number of cephalic tubercles															Total number	
	1-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99	100-109	110-119	120-129	130-139	140-149		150-159
50-59	1																1
60-69		1															1
70-79			1	2													3
80-89			1	2	1												4
90-99			1	—	2	1											4
100-109							1										1
110-119							1	1	—	1							3
120-129								2	5								7
130-139											1						1
140-149							2	1	1	3							7
150-159								1	—	—	1						2
160-169									2	1	1	—	2				6
170-179								1	1	—	2	1	1				6
180-189								1	1	—	—	—	2	1			5
190-199									1	—	1	—	—	—	1		3
200-209										1	—	—	2	—	—	1	4
210-219												1					1

on the distal one fourth; anal fin pale; belly slightly washed with pink; caudal fin with some pink; dorsal fin rays outlined in black, the interradial membranes clear.

Other life colors of nuptial males and females observed over the nests and spawning were recorded by the authors on 7 and 12 June 1967, in Spavinaw and Flint Creeks, Delaware County, Oklahoma. The nuptial males have a faint dark midlateral band on body. The body is olivaceous, laterally. The belly, chin, and branchiostegals are light rosy to pinkish. The postocular spot is red or reddish orange, prominent, sharply outlined, almost circular, and seen on subadults and adults, and also on mature females at 100 mm SL; some smaller juveniles have a pale, brassy postocular spot. The tuberculated area of the head is smoky blue; the tubercles are whitish. The pectoral fin is olive to pinkish on the outer half, and light orange to pinkish yellow basally. The dorsal fin is olive, the rays dark. The pelvics and anal fins are somewhat dark basally, the first ray milky orange, and the distal half light pinkish orange. The lobes of the caudal fin are light pinkish orange, the color becoming light olive basally on the fin. The caudal fin is noticeably pale in life compared with the brilliant orange-red caudal fin of *Nocomis effusus*. The middorsal light stripe was faint in adults of both sexes.

The large females are colored pale olive to greenish olive dorsolaterally. The outer portion of the caudal fin is very light orange, the basal portion pale. The other fins are pale with a light orange tinge.

In preservation, the nuptial males lack the dark lateral band on the body as well as the basicaudal spot, or they are very faint. Some of the adult females and larger juveniles of both sexes have a moderately developed dark, lateral body band and a conspicuous round basicaudal spot. The color pattern of *Nocomis asper* in preservation in respect to size and sex of specimens is similar to the pattern of *N. biguttatus* (Lachner 1952; Lachner and Jenkins 1967).

ETYMOLOGY.—The specific name, *asper*, refers to the rough head and body of the nuptial male caused by the development of many tubercles; the common name, redspot chub, is in reference to the bright red, postocular spot present on the adults and subadults of both sexes.

REPRODUCTION AND GROWTH.—*Nocomis asper*, as in all other species of *Nocomis*, is a nest builder. Nest construction, spawning, reproductive and other behavior were observed by the authors on 7 and 12 June, 1967. These studies will appear in a separate paper on reproductive behavior in the genus *Nocomis*.

The largest male examined was 182 mm SL. Seventeen nuptial males ranging from 143 to 182 mm in

TABLE 5.—The number of cephalic tubercles in *Nocomis biguttatus* from the Missouri, Mississippi, Ohio, and Great Lakes drainages (data for the sexes were combined)

SL in mm	Number of cephalic tubercles														Total number
	0	1-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99	100-109	110-119		
40-49		1													1
50-59	1	4	3	—	1										9
60-69				4	2	1									7
70-79			1	7	12	8	2								30
80-89				12	31	40	15	4	1						103
90-99				4	21	51	28	6	—	1					111
100-109					7	17	25	8	6	2					65
110-119						6	13	10	7	2	1	—	1		47
120-129						4	9	11	4	2	—	1			31
130-139						1	2	1	8	3	1				16
140-149								1	2						3
150-159															—
160-169										1					1

length averaged 167.2 mm. The largest female *asper* examined was 168 mm SL. Also, as in other species of *Nocomis*, the males of *N. asper* attain the larger size. Some females are mature, having enlarged ovaries, at 100 to 110 mm SL.

### *Nocomis biguttatus* (Kirtland)

Hornyhead chub  
FIGURES 5, 6, and 7

*Semotilus biguttatus* Kirtland, 1840:344, pl. 5, fig. 1 [type locality: Yellow Creek, Mahoning River, Ohio River system, Ohio].

*Ceratichthys cyclotis* Cope, 1864:277 [lectotype, ANSP 2113; type locality: Michigan, herein designated].

*Ceratichthys stigmaticus* Cope, 1864:278 [type locality: Michigan].

*Hybopsis kentuckiensis*.—Fowler 1918:33, plate VIII [redescription].

*Nocomis biguttatus*.—Hubbs 1926:28, pl. I, fig. 1; pl. II, fig. 3.

*Nocomis nebrascensis* Girard, 1856:190 [type locality: Sweet Water River, Platte River system].

**NOMENCLATURE.**—Certain nomenclatural problems involving *Nocomis biguttatus* commenced when Rafinesque (1820:48) described *Luxilus kentuckiensis*, which was a composite account, probably involving species of *Nocomis* and perhaps species of *Notropis*. This early history is briefly reviewed by Lachner and

Jenkins (1967:558-559). The next available name for a species of *Nocomis* was Kirtland's description of *Semotilus biguttatus* (1840:344). His specimens were taken in Yellow Creek, a tributary of the Mahoning River, Ohio. His description and illustration of the nuptial male (Plate 5, Figure 1) and coloration easily identify the above synonyms with the species of *Nocomis* that Kirtland had found. One problem remains which could involve the security of the entrenched name *Nocomis micropogon* (Cope). Cope (1864) described two species of *Nocomis* on page 277, *Ceratichthys cyclotis* and *Ceratichthys micropogon* (as well as another one, *Ceratichthys stigmaticus* on page 278). Lachner and Jenkins (1971) discuss the hybrid nature of Cope's type specimen (ANSP 5061) of *Ceratichthys micropogon* and conclude that it probably represents a hybrid *Nocomis micropogon* × *Notropis cornutus*, based on a number of morphological characters. Lachner and Jenkins (1970) restricted the name *Ceratichthys micropogon* Cope to that presumed parent of the type specimen. But Cope's description of *Ceratichthys cyclotis* involves both *Nocomis biguttatus* and *N. micropogon*. The type material came from Michigan, at Grosse Isle, and from Waterford, Oakland County, from Clinton River, and from Bruce, Macomb County. Hubbs (1926:29) indicated that Cope's description may have been based on the above two species. Cope recorded the dentition as variable,



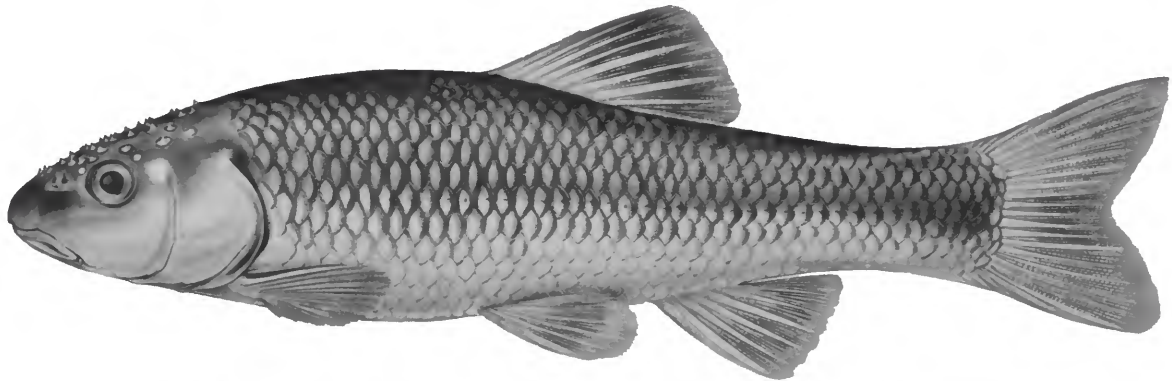


FIGURE 5.—Lateral view of *Noconis biguttatus*, USNM 166459, a nuptial male, 99 mm SL, taken 21 July 1939 from Johnson Creek, Lake Ontario drainage, New York. Drawn by C. B. Gast.

“in some specimens of this species, especially among the half-grown, I find a tooth of the second row of pharyngeals.” Hubbs further commented that Fowler’s (1918:33) redescription of the species amounts to a restriction of the name *biguttatus*. Fowler, however, records the dentition as that of *micropogon*, 4–4.

Examination of the extant types of *Ceratichthys cyclotis* (ANSP 2113–2117, 5 specimens) reveals two species. We designate ANSP 2113, a nuptial male, 132 mm SL, a lectotype of *Ceratichthys cyclotis* Cope, 1864, and place it in the synonymy of *Noconis biguttatus* Kirtland, 1840, because of its dentition, 1,4–4,1, and



FIGURE 6.—Lateral view of head of *Noconis biguttatus*, USNM 193359, a nuptial male, 194 mm SL, collected 7 June 1962 from Brush Creek, White River drainage, Washington County, Arkansas. (The only specimen having an atypical tubercle just below nape on one side. See Lachner and Wiley, 1971, for presence of supernumerary nape tubercles in *N. leptocephalus*).

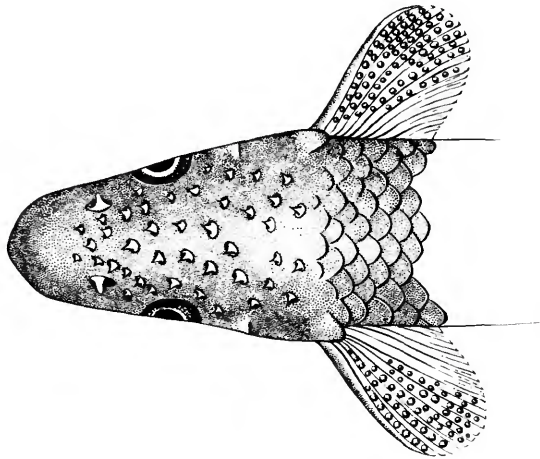
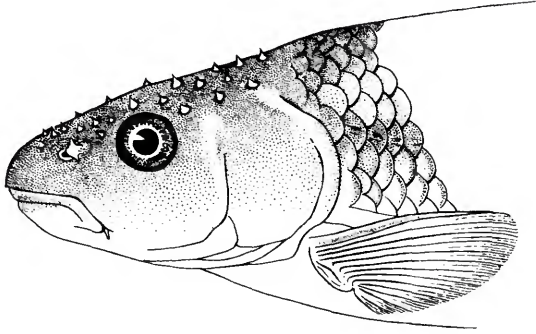


FIGURE 7.—Dorsal and lateral views of the head of a nuptial male *Nocomis biguttatus*, USNM 166459, 99 mm SL. Same specimen as Figure 5. Drawn by C. B. Gast.

the widespread occurrence of tubercle scars, dorsally, on the head, extending from the posterior area of the snout to the occiput. The following numbers are designated paralectotypes: ANSP 2114, 101 mm SL and ANSP 2115, 60 mm SL. Both specimens have two rows of pharyngeal teeth, and indications of a once large dark spot at the base of the caudal fin, or post-orbital head tubercles. ANSP 2116, 62 mm SL, may have had two rows of pharyngeal teeth, but the arches are in poor condition; since the specimen is otherwise

faded and shows no tubercle marks, it may represent either *N. biguttatus* or *N. micropogon*. (We suspect that it is *N. biguttatus*.) ANSP 2117, 142 mm SL, is referred to *N. micropogon* because it has a dentition of 4-4, and the tubercle spots are located in the inter-nasal and subnasal areas. With the above lectotype restriction of *Ceratichthys cyclotis* Cope, 1864, the name is not available for *Ceratichthys micropogon* Cope, 1864.

**SPECIMENS STUDIES.**—*Nocomis biguttatus* has an extensive distribution primarily in the central basin of the United States (Figure 8). It is the key species in understanding the evolution, ecology, and distribution of the species group. The specimens listed below represent material from which morphological data were recorded. An attempt was made to study the larger specimens available in museum collections from samples widely scattered within the various river systems of the area.

#### MISSISSIPPI BASIN

**WHITE DRAINAGE.**—Arkansas: KU 3242 (1), OSUMZ 5994 (2), TU 10130 (5), 44685 (2), 44710 (2), 44817 (1), 46953 (3), 49386 (2), 49473 (1), 49804 (1), UF 14704 (3), UMMZ 123903 (1), 128305 (1), 169890 (1), 170895 (1), USNM 42684 (3), 42677 (1), 193359 (10).

Missouri: KU 11014 (2), UMMZ 102586 (1), 102712 (2), 111459 (1), 151091 (7), 151320 (1), 151367 (1), 152061 (2), USNM 42814 (1), 42882 (1), 204018 (10), 204855 (34).

**ST. FRANCIS DRAINAGE.**—Missouri: UMMZ 139507 (1).

**MERAMEC DRAINAGE.**—Missouri: CU 10783 (4), UMMZ 148338 (1), 148389 (2), 148441 (1), 149630 (2), 149664 (1), 149816 (2).

#### MISSOURI BASIN

**GASCONADE DRAINAGE.**—Missouri: CU 24323 (3), UMMZ 102721 (1), 111436 (2).

**OSAGE DRAINAGE.**—Missouri: UMMZ 86532 (1), 102748 (3), 102804 (1), 111355 (1), 150102 (4), 150092 (2), 150377 (1), 150465 (1), 150881 (1), 150917 (2), 150942 (1), 151944 (1), 152694 (1).

Kansas: KU 2470 (2), 2498 (10), 2605 (7), UMMZ 61214 (1), 126847 (1), 160538 (1).

**MISSOURI DRAINAGE.**—North tributaries: UMMZ 147948 (1), USNM 35876 (1).

**KANSAS DRAINAGE.**—Kansas: KU 426 (1), 427 (1), 429 (1), 438 (1), USNM 3551 (1).

MISSOURI DRAINAGE.—Nebraska: USNM 86694 (1).

Iowa: UMMZ 114088 (3).

#### UPPER MISSISSIPPI BASIN

Missouri: UMMZ 148252 (1).

Illinois: UMMZ 144502 (1), USNM 171692 (2).

Indiana: UMMZ 81365 (4), USNM 66457 (3).

Iowa: TU 14498 (6), UMMZ 87066 (1), 87075 (1), 101200 (1), 101214 (1), 101234 (1), 101244 (1), 101270 (1), 101288 (1), 101308 (2), 101366 (1), 101376 (1), 101387 (2), 101399 (1), 146829 (2), 146849 (2).

Wisconsin: UMMZ 74187 (2), 74362 (1), 75579 (3), 75618 (1), 75648 (2), 75808 (1), 75925 (1), 76699 (2), 76854 (2), 76922 (2), 77031 (1), 77056 (1), 77184 (1), 77238 (1), 77483 (2), 77558 (2), 77574 (1), 77933 (6), 78956 (1), 96137 (4), 96148 (1), 96181 (4), 96227 (2).

Minnesota: USNM 133094 (4).

South Dakota: UMMZ 166896 (6), 167000 (6), 167131 (1).

#### OHIO BASIN

Kentucky: CU 37297 (5), UL 10479 (1), 12465 (1), 12620 (6).

Indiana: UMMZ 6662 (1), UMMZ (IU 9549) (1), 99904 (8), 99952 (2), 112746 (1), 112747 (1), USNM 66449 (1), 69245 (2).

Ohio: UMMZ 86964 (1), 87203 (2), 107667 (1), 118369 (1).

Pennsylvania: CU 33875 (4), 40731 (1), 46677 (2), USNM 166418 (5), 166419 (2), 166420 (7).

#### GREAT LAKES BASIN

New York: CU 659 (3), USNM 166437 (2), 166452 (3), 166456 (6), 166457 (7), 166459 (2), 166460 (6), 166463 (2), 166464 (6), 166465 (7), 166468 (8), 166469 (4), 166475 (19), 166478 (2).

Ontario: UMMZ 85516 (1), 89023 (3), 89078 (1).

Ohio: UMMZ 121801 (2), 121810 (5), 121832 (3), 121853 (2), USNM 40096 (3).

Indiana: UMMZ 114919 (1).

Michigan: UMMZ 55272 (1), 60230 (2), 61387 (1), 68285 (1), 69039 (1), 69060 (1), 69085 (3), 69123 (1), 69129 (3), 69143 (5), 70558 (1), 79096 (1), 79881 (1), 80731 (1), 81500 (2), 82609 (2), 82975 (1), 83087 (1), 83146 (2), 83231 (1), 83267 (1), 83411 (1), 83543 (1), 83771 (1), 83913 (1), 84650 (2), 84681 (2), 84758 (2), 84802 (3), 84951

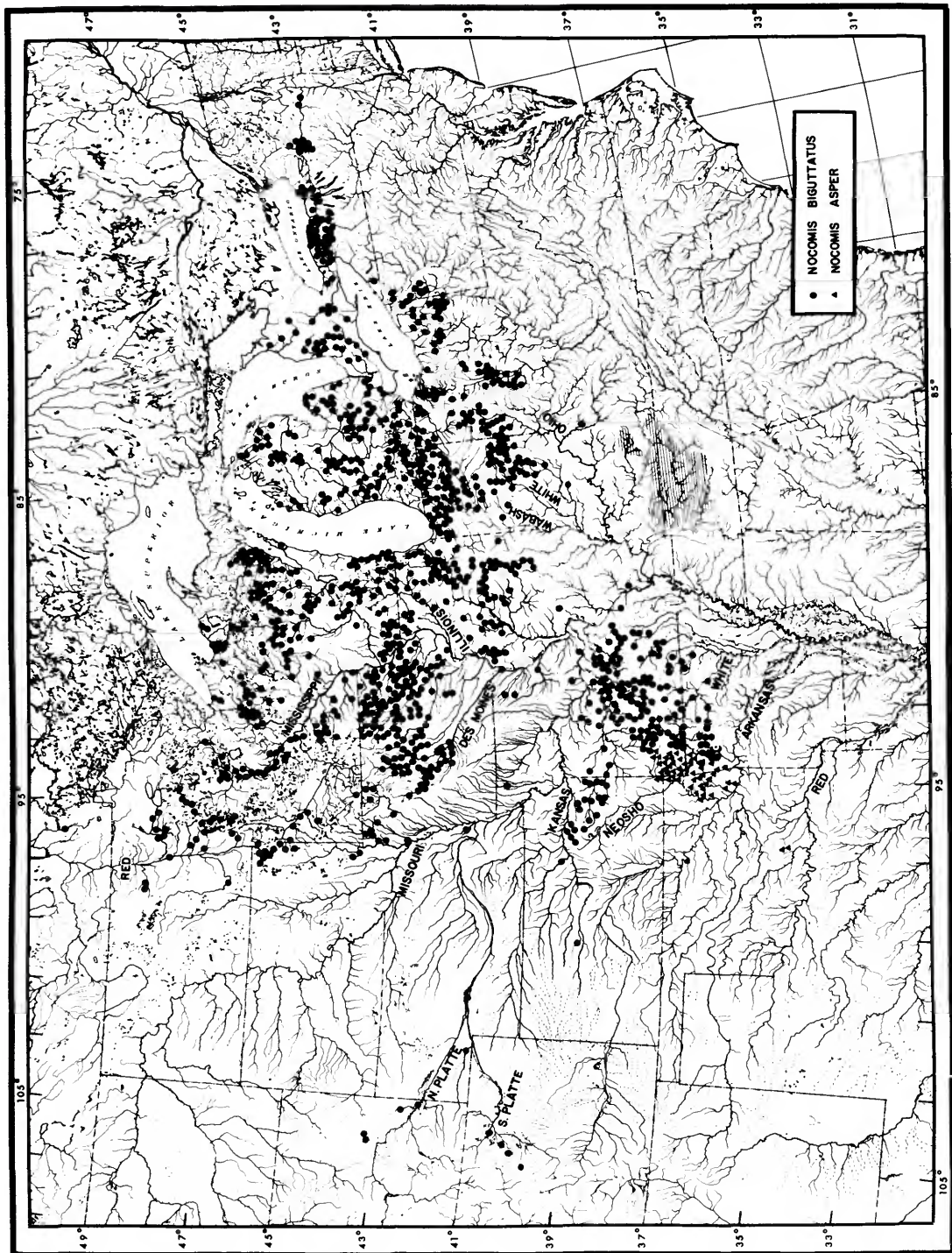
(1), 86292 (2), 89454 (2), 89595 (2), 92108 (1), 96987 (1), 97242 (2), 98410 (2), 101908 (1), 101958 (1), 104120 (1), 106876 (2), 106902 (1), 110352 (1), 113321 (1), 116249 (1), 116335 (1), 116972 (1), 117014 (4), 117137 (1), 131946 (1), 136822 (1), 136944 (1), 137148 (1), 137217 (1), 137287 (1), 137649 (1), 137672 (1), 137692 (16), 137701 (1), 137731 (3), 138070 (5), 139797 (1), 139804 (2), 139834 (2), 140215 (1), 162738 (8), 164288 (19), 164376 (12), 167826 (5), 185397 (3), 185398 (2), 185400 (3), 185406 (3), 185411 (2), 185414 (5).

Wisconsin: UMMZ 64516 (3), 64522 (2), 64663 (3), 64902 (2), 72884 (1), 72975 (4), 73892 (4), 73963 (2), 74087 (1), 74159 (1), 74285 (1), 74894 (5), 74940 (5), 76713 (1), 76763 (1), 77794 (3), 78532 (1), 87029 (2), 97150 (1), 108084 (1), USNM 143015 (3), WSU 466 (7).

The plots on the map for the distribution of *Nocomis biguttatus* (Figure 8) are based on two sets of data. One set includes the specimens listed above, and hundreds of additional collections examined in these museums, which, while of no immediate systematic value, were important in the locality data they provided and contributed to a better understanding of the distribution, ecology, and zoogeography of the group. Because of the thousands of specimens involved, it is prohibitive to list all of these collections herein. Another set of distributional data were taken mainly from comprehensive state faunal surveys. These records, often extremely abundant, were used to round out aspects of the distribution of a local nature, from which we saw no material. The references from which these data were taken, listed by author with the state or province involved, are as follows: Cross (1967, Kansas), Ellis (1914, Colorado), Bailey and Allum (1962, South Dakota), Keleher (1956, Manitoba), Hinks (1943, Manitoba and North Dakota), Cleary (1956, Iowa), Forbes and Richardson (1920, Illinois; *N. micropogon* apparently is confined to the Wabash system in Illinois), Gerking (1945, Indiana), Greene (1935, Wisconsin), Taylor (1954, Michigan), Trautman (1957, Ohio), Raney (1938, Pennsylvania), Underhill (1957, Minnesota), Simon (1946, Wyoming), and Copes and Tubb (1966, North Dakota).

Locality records for collections in the Royal Ontario Museum, Toronto, Canada, were taken from a list provided by W. B. Scott. Distributional records for New York were checked against the data published in the *New York State Biological Survey Reports*.





**DIAGNOSIS.**—*Nocomis biguttatus* is a wide-ranging species, most closely related to *N. asper* in having two rows of pharyngeal teeth. It differs from *N. asper* and *N. effusus* in never having tubercles on the scales of the body, laterally. It is a coarser scaled species than *N. effusus*. The red postocular spot is intermediate in its development in *N. biguttatus*, compared with its two species-group relatives. In *N. biguttatus* the red spot is well developed only in adult males, and is brassy colored or not evident in adult females. In *N. asper* the red spot is conspicuously developed in adults of both sexes. In *N. effusus* the red spot is present, but faint, in the large males only.

#### Comparison of Species in the *Biguttatus* Group

The primary differentiation among the three species is in the tuberculation of the body, the reduction of teeth on the pharyngeal arch from two rows to one row, the development of coarser and finer scaled species, the elongation of certain body proportions, as length of snout and head, and the development of certain nuptial colors in the males.

Counts of the head tuberculation revealed that the three species have about the same number of head tubercles and the same increments in tubercle numbers with increase in body length (Tables 3, 4, and 5). Where large samples of nuptial males were available from particular drainages, great variability existed in the number of head tubercles within any of the groups classified by a range of 10 mm in body length. The group of *Nocomis biguttatus* 70 to 79 mm in size has specimens in which the number of head tubercles exceed others by three times or more. The same variation existed in the larger specimens. All three species had a high variability in the number of head tubercles within any given size-group. Preliminary counts suggested differences in the number of head tubercles among the three species and among drainage populations of *N. biguttatus*, but as more adult specimens became available these differences proved unreal, for they were associated primarily with body size.

*N. biguttatus* is apparently a small species over most of its range, excluding those of the White River drainage, and it is much smaller than *N. effusus* or *N. asper*. Only one specimen was examined which exceeded 150 mm SL (Table 5)—a gravid female, 162 mm from Weber Lake, Lake Michigan drainage. Many males of *N. biguttatus* in the Great Lakes drainage are mature, and with head tubercles enlarged, at 100 mm, and the females are gravid at 90 mm. Apparently, *N. biguttatus* in the White River drainage attains the largest size among the drainage populations and among the members of the species group.

In one collection, USNM 204018, eleven specimens from the North Fork of the White River, Ozark County, Missouri, five males exceeded 200 mm SL (compare data in Tables 3, 4, and 5, and Lachner and Jenkins 1967, Table 1). One of these specimens also had about 155 head tubercles, the highest number found among the three species.

*Nocomis effusus* may be a larger species than *N. asper*; five nuptial males of the former attained body lengths of 161 to 202 mm and averaged 179 mm. Seventeen nuptial males of the latter species ranged from 143 to 182 mm and averaged 167 mm.

Although tuberculation on the body, laterally and on the nape, increases with increase in body length, there are two notable differences in the development of body tubercles among the three species. First, *Nocomis biguttatus* does not develop body or nape tubercles, excluding one or two supernumerary occipital tubercles that may be present in the largest nuptial males. The body tubercles only appear on *N. asper* and *N. effusus*. They also are absent on all numbers of the micropogon group and leptocephalus group. Secondly, the body tubercles on *N. asper* have differentiated significantly from those on *N. effusus* in the number of tubercles per scale. The total number of tubercles on the tuberculated lateral body scales was about the same in both species (Table 6, *N. asper*, seventeen specimens range from 28–112 total tubercles, average 82.2; *N. effusus*, five specimens range from 25–116 total tubercles, average 86.6). Only 3 percent of the tuberculated scales in *N. effusus* had two tubercles per scale, and no scales had more than two tubercles. About 23 percent of the tuberculated scales in *N. asper* had two tubercles (Tables 8 and 9), 2 percent had three tubercles, and one specimen had one scale with four tubercles. There is a great range in *N. asper* in the number of tuberculated scales having either

FIGURE 8.—Distribution of the three species of the *Nocomis biguttatus* species group. Locality data for *N. asper* are listed in "Materials Studied." The basis of the plots used for *N. biguttatus* is explained in the text. The shaded area marks the approximate range of *N. effusus*, which was taken from Lachner and Jenkins (1967, figure 7).

one or two tubercles per scale. Nuptial males may have only 26 scales bearing one tubercle and other larger specimens have 82 to 86. Some specimens have less than 10 scales bearing two tubercles and other specimens may have 30 to 50 scales bearing two tubercles (Tables 8, 9). The smaller nuptial males of both species averaged fewer tuberculated scales (Table 7). In *N. asper*, the 10-mm-size groups from 140 to 180 mm SL, had average values for number of tuberculated scales of 64, 75, 85, 85, and 112.

Tuberculation on the nape was highly variable but the larger specimens of both species had more tubercles. The nape tuberculation is probably more extensively developed and more tubercles are present in *Nocomis asper* than in *N. effusus*. The body tubercles in *N. effusus* are about the size of the average head tubercles, whereas in *N. asper* the body tubercles are much smaller than in *N. effusus*, about one half the size of the average head tubercles. The head tubercles are about equal in size in all three species of the *biguttatus* group.

There is nearly a complete separation of *Nocomis asper* and *N. biguttatus* from *N. effusus* in the pharyngeal dentition. The former two species have two rows of teeth with the following counts: *N. asper*, 1,4-4,1 (22 pairs of arches), 0,4-4,1 (1), 1,4-4,2 (1); *N. biguttatus*, 1,4-4,1 (47), 1,4-4,0 or 0,4-4,1 (5), and 4-4 (1, questionable). *N. effusus* has one row with 4-4 (28 pairs of arches) and 0,4-4,1 (1).

A summary of the differences in squamation among the three species is given in Table 2 involving three different scale counts, the lateral line, circumferential, and caudal peduncle. The data for *Nocomis biguttatus* were grouped by four general areas: (1) the Great Lakes drainage including the Ohio and upper Mississippi River drainage, (2) the Missouri drainage, (3) the lower Mississippi drainage area, and (4) the White River system. We were particularly interested in the White system because of its geographic location between the Arkansas River to the south (and adjacent headwaters) and the northern and eastern systems of the Missouri, Mississippi, and Ohio basins. Although the number of scales is of minor value in the identification of the species, the character has systematic value in showing trends and relationships among the species and among populations of *N. biguttatus*. *N. effusus* is finer scaled, which is shown particularly in the high values of the circumferential count (av-

erage 36.1 scales) and the caudal peduncle count (average 19.7). *N. asper* is somewhat more coarse-scaled than *N. biguttatus* of the White drainage. The northern and eastern populations of *N. biguttatus*, in the Great Lakes, Ohio, and upper Mississippi drainages, were consistently lower in all three scale counts when compared with those from the Missouri, lower Mississippi, and White drainages (and also with those counts of *N. asper* and *N. effusus*).

The vertebral numbers (Table 2) were higher in *Nocomis effusus* (modally 41) compared with those of *N. asper* (modally 40) and *N. biguttatus* (modally 40).

Our first observations of *Nocomis asper*, based on a few large males, indicated that it was a long-head, long-snout form. As more material accumulated, particularly larger specimens, it became possible to test statistically these preliminary observations. Because of the contiguous distribution *N. asper* has with *N. biguttatus*, its close relationship with this species, and probable evolution from *biguttatus* stock, more detailed comparisons of head lengths were made between these two species. The relationship between standard length and head length of *N. asper* and *N. biguttatus* from the White River drainage is shown in Figure 3, based on a sample of measurements of juveniles and adults distributed as widely over the drainages as the collections permitted.

Statistical tests were performed to compare the relationship between standard length and head length of *Nocomis asper* with each of the following populations of *N. biguttatus*: The White drainage, the Missouri drainage, and the Great Lakes drainage including the Ohio and Upper Mississippi drainages. Tests of differences of slopes and heights (intercepts) of pairs of regression lines were performed by analysis of covariance (Simpson, Roe, and Lewontin, 1960). F values yielding probabilities greater than 0.95 were considered significant. The samples tested were randomly selected from several hundred measurements of specimens from each population; these specimens were widely distributed within the area tested. The regression equations are as follows:

$$N. asper, y = .0149X + 26.49, n = 124;$$

$$N. biguttatus \text{ (White drainage)}, y = .0063X + 26.64, n = 70;$$

$$N. biguttatus \text{ (Missouri drainage)}, y = .0141X + 26.48, n = 60;$$

$$N. biguttatus \text{ (Great Lakes)}, y = .0114X + 26.12, n = 100.$$



TABLE 6.—The number of body tubercles per scale in nuptial males of seventeen specimens of *Nocomis asper* and five specimens of *N. effusus*. Under the heading "tubercles per scale" is given the number of specimens and the mean and range of scales bearing from one to four tubercles with this data also in percentages (body tubercles counted on left side)

Species, number of specimens, $\bar{X}$ , range	Tubercles per scale				Total number of tubercles
	1	2	3	4	
<i>asper</i>					
17(167.2).....	17(60.0)	17(11.0)	8(4.3)	1(1)	17(82.2)
143-182.....	26-86	2-42	1-15	—	28-112
In percent:					
$\bar{X}$ .....	(74.9)	(22.8)	(2.3)	—	—
Range.....	45-93	7-47	1-15	—	—
<i>effusus</i>					
5(179.0).....	5(85.6)	3(1.7)	—	—	5(86.6)
161-202.....	25-116	1-3	—	—	25-116
In percent:					
$\bar{X}$ .....	(99.0)	(1.0)	—	—	—
Range.....	97-100	1-3	—	—	—

TABLE 7.—The number of specimens and the mean and range of body tubercles per scale, by size groups, in nuptial males of *N. asper* and *N. effusus*

SL in mm	Tubercles per scale				Total tubercle number
	1	2	3	4	
<i>asper</i>					
140-149.....	2(36.5)	2(19.5)	1(15)	—	2(63.5)
	26-47	2-37	—	—	28-99
150-159.....	3(51.0)	3(22.0)	1(7)	—	3(75.3)
	40-72	3-42	—	—	44-93
160-169.....	3(61.7)	3(23.0)	—	—	3(84.7)
	56-67	13-37	—	—	75-93
170-179.....	8(67.3)	8(18.6)	6(2.0)	1(1)	8(84.9)
	45-82	6-30	1-4	—	55-102
180-189.....	1(86)	1(26)	—	—	1(112)
	—	—	—	—	—
<i>effusus</i>					
160-169.....	2(56.5)	1(1)	—	—	2(57.0)
	25-88	—	—	—	25-89
170-179.....	—	—	—	—	—
180-189.....	1(92)	1(1)	—	—	1(93)
190-199.....	1(116)	—	—	—	1(116)
200-209.....	1(107)	1(3)	—	—	1(110)
	—	—	—	—	—

TABLE 8.—The number of tubercles per scale on the body in nuptial males of seventeen specimens of *N. asper* and five specimens of *N. effusus* (expressed in percent of the total number of scales bearing tubercles)

Species and number of tubercles per scale	Tubercle numbers per specimen in percent of scales bearing tubercles									
	1-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-100
<i>asper</i>										
1					2	—	3	6	3	3
2	2	3	9	1	2					
3	7	1								
4	1									
<i>effusus</i>										
1										5
2	3									

The slope of the regression of head length (as percent of SL) on standard length of *Nocomis asper* is significantly different from *N. biguttatus* of the White drainage ( $F=8.71$ ; 190 degrees of freedom). The slope of the regression of head length (as percent of SL on standard length of *N. asper* was not statistically different from that of *N. biguttatus* of the Great Lakes drainage ( $F=.40$ ; 220 degrees of freedom), but the heights were significantly different ( $F=36.38$ ; 221 degrees of freedom). The slope and height for data of *N. asper* were not statistically different from those of *N. biguttatus* from the Missouri drainage (slope:  $F=.04$ , 180 degrees of freedom; height:  $F=<.05$ , 181 degrees of freedom). It is of interest that *N. asper* and *N. biguttatus* of the White drainage, the two adjacent populations, have the greatest difference in head length.

Many body proportions of the species of *Nocomis* show allometric growth (Lachner and Jenkins 1971; Lachner and Wiley 1971), an increase in body length resulting in an increase in size of structure. The relationship of snout length to standard length of *N. asper* and *N. biguttatus* from the Great Lakes drainage (Figure 4) shows the same general growth trends and differences as head length. Considerable variability occurs in the size of the proportional character within each population and within the 10-mm-size SL groups. Such proportional characters, however, are useful in describing populations and in demonstrating differentiation among populations and species of *Nocomis*.

The three species show consistent differences in life in the intensity of development of the red postocular

spot, in the color of the fins, and in the development of the dark lateral body band. These comparisons pertain mainly to the nuptial males. The red postocular spot is large, conspicuous, and intensely developed in *Nocomis asper* on specimens of subadults to adults (and present in mature females at sizes of 100 mm SL or greater). It is well developed only in the larger, mature males of *N. biguttatus* and is brassy colored in some adult females. It is small and weakly developed in the largest nuptial males of *N. effusus*, often absent in the smaller nuptial males, and absent in all other individuals.

The most intense and noticeable life colors occur in adult males of *Nocomis effusus*, in which the fins—particularly the caudal, pelvic, and anal—are bright orange or reddish orange. The pectoral fin is bright in *N. asper*, being predominantly pinkish yellow to pinkish orange. The pelvic, anal, and caudal fins are mainly pinkish olive or light pinkish orange. *N. biguttatus* develops the weakest fin colors among the three species; the pectoral fins are orange, the pelvics and anal fins are pale orange, and the caudal fin is light orange red.

The dark lateral band on the body is prominent in nuptial males of *Nocomis biguttatus*, weakly developed in *N. asper*, and almost completely absent in *N. effusus*. The young to subadult males and most all-size stages of the females have subdued colorations and they are, other than the differences discussed above, fairly similar in their general color pattern. More detailed descriptions of color and color patterns are given by Lachner (1952) and Lachner and Jenkins (1967).



TABLE 9.—Total number of body tubercles per scale in nuptial males of seventeen specimens of *N. asper* and five specimens of *N. effusus*

Number of tubercles per scale	Tubercle numbers per specimen, of scales bearing tubercles											
	1-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99	100-109	110-119
<i>asper</i>												
1			1	—	4	3	3	4	2			
2	4	5	4	3	1							
3	7	1										
4	1											
<i>effusus</i>												
1			1	—	—	—	—	—	1	1	1	1
2	3											

### Distribution and Ecology

The distribution of the three species of the *biguttatus* group is shown on Figure 8. The extensive distribution of *Nocomis biguttatus* in the central basin contrasts markedly with the restricted distributions of *N. asper* and *N. effusus*. *N. asper* has a center of distribution in the Ozark highland section of the Arkansas River drainage. It is absent in the western tributaries of the Neosho system. Hall (1952:57) reported it only from the upland tributaries of the east side of Grand (Neosho) River. Branson (1967:133) found it "very abundant in most of the eastern clear tributaries but is absent from the main (Neosho) stream."

Three isolated populations of *Nocomis*, two in the Arkansas drainage which possibly represent *N. asper*, and one in the Red drainage, definitely *N. asper*, are apparent evidence of what was once a much greater distribution of the species. In the upper Arkansas drainage of Kansas, Cross (1954) reported *Hybopsis biguttatus* (= *N. asper*?) as rare in the South Fork of the Cottonwood River and that juveniles were common in Cedar Creek, both of the Neosho River system. These localities are plotted on the Kansas map by Cross (1967:87). Cross and Braasch (1969) did not capture the species in their 1967 survey whereas it was present in 1952 (1954 report) in one half of all collections made. We have examined the following *Nocomis* collections from the Neosho River system in Kansas: KU 2704 (1), KU 2718 (16), UMMZ 116059 (1), and UMMZ 120801 (1). All of these specimens were young and juvenile sizes under 83 mm SL, and we

could not specifically identify them because of their small size. These specimens are indicated on Figure 8 by a question mark and they may represent either *N. asper* or *N. biguttatus*. A single, isolated western record (Figure 8) of *Nocomis* in north-central Oklahoma, Arkansas River drainage, is tentatively referred to *N. asper*. One specimen, UOMZ 15475, 71 mm SL, was taken near Turkey Island, Panner County, on 8 April 1933 by George A. Moore, where according to Hubbs and Moore (1940:92) "large springs emerge in the bed of the main river." A third isolated population occurs in south-central Oklahoma (two plots on Figure 8) where we have examined seven collections from the Blue River, Johnston County, Red River drainage. The Blue River is the only portion of the Red drainage inhabited by *Nocomis*. A good series of large specimens had the typical body tuberculation of *N. asper* and otherwise agreed with the characters of this species. *N. asper* was taken from the Blue River in 1947 by Linder (1955:175, as *Hybopsis biguttata*). R. E. Jenkins and F. F. Snelson, Jr., found *N. asper* very common in the Blue River system in 1967.

The disjunct occurrence of these three populations from the main one in the Ozark upland, Arkansas drainage, closely parallels isolated populations of *Notropis pilsbryi*. Cross (1967:110) shows the distribution of *Notropis pilsbryi* in the upper Neosho system where it occurs as a relic, occupying clear, flowing water with a substrate of rubble and gravel. *Notropis pilsbryi* once occurred with *Nocomis asper* at the isolated western station of the Arkansas drainage near Turkey Island, Panner County (Hubbs and Moore

1940: 94, Figure 1; Gilbert 1964: 133, Map 2). It was reported from the Red drainage at three localities, each in a separate tributary by Hubbs and Moore (1940: Figure 1). The species was recently captured from the Blue River, a fourth locality in the Red drainage. These isolated populations of *Nocomis asper* and *Notropis pilsbryi* appear to be remnants of a fauna that was formerly much more widely distributed. They do not seem to be products of introductions or accidental transfer of data, as was suggested by Hubbs and Moore (1940: 94) for *Notropis pilsbryi*. Other evidence suggests a natural distribution of these species, such as the close compatibility between them during spawning. *Notropis pilsbryi* is one of the common nest associates of *Nocomis asper*. While the latter species constructs a gravel mound in the reproductive process, the former species occupies the nest as a spawning site, often in large numbers, with practically no antagonism shown between the two. Both species prefer clear, flowing streams with clean gravel, rubble, and sandy substrates.

The wide distribution of *Nocomis biguttatus* shows interesting gaps, some of which are related to the immediate erosional history of the central basin, while others are associated with the geology and glacial history of the area. Climatic factors, such as droughts, also have affected the general distribution and occurrence of *Nocomis biguttatus*. The hornyhead chub is common on the Ozark upland of Arkansas and Missouri with some scattered populations at lower elevations. The species is fairly common in the low elevation areas of the upper Osage drainage. Deacon and Metcalf (1961) did not collect this species in the Wakarusa River system draining northeastern Kansas. They report (page 316) that it was common in early collections but that it has not been taken since 1924. Its disappearance is probably related to increased siltation and intermittency of stream flow. Metcalf (1966: 105) found the hornyhead chub to have one of the most restricted ranges of any fish in the Kansas River drainage. He lists earlier records and museum specimens, some dating back more than 100 years. Some of these earlier records appear on the distribution map of Figure 8. The occurrence of *Nocomis biguttatus* in the Missouri River drainage today is limited to a few, widely separated populations. Metcalf points out that its extirpation in the Missouri drainage is much like that described in Ohio by Trautman (1957) where fine siltation due to cultivation has covered coarser sedi-

ments. The water has become more turbid, with reductions in flow and volume, and the streams are now intermittent in some areas. The ecological conditions, such as clear, constantly flowing streams with gravel-rubble bottoms that once provided suitable habitat for this gravel-mound, nest-building chub to maintain a wide distribution, are now largely in a state of attrition. Extirpation of the species through change of habitat, and increased competition from species more highly adapted to silt-bearing waters, is now leading to its confinement in numerous scattered localities.

Our single plot (Figure 8) in northwest Missouri is an 1884 record of Jordan and Meek (1885:12) from Hundred and Two River. The plot in eastern Nebraska is based on a specimen from Papillion River (USNM 86694) received from the Museum of Comparative Zoology, Harvard, and was taken by the Hassler Expedition prior to 1872. It is not known whether the species occurs there today. The few scattered records in the Platte River system in Colorado and Wyoming are documented by Ellis (1914) and Simon (1946). The occurrence of the hornyhead chub in the upper Cheyenne system of Wyoming (two plots, Figure 8) is based on several specimens. *Nocomis biguttatus* has some populations in northwest Iowa and southeast South Dakota of the Missouri drainage.

Farther west across the Continental Divide in the Colorado drainage, Cope and Yarrow (1875:651) reported *Nocomis biguttatus*, based on collections taken by H. C. Yarrow and H. W. Henshaw (Wheeler Survey) in 1872, and the locality was given as Harmony, Utah. Two extant collections of Yarrow and Henshaw, USNM 16986 (8 specimens) and ANSP 19854 (1 specimen), were examined by us and these represent *Nocomis biguttatus*. This locality is within the hydrographic boundary of ancient Lake Bonneville, between the southern boundary of Lake Bonneville and the headwaters of the Virgin River (R. R. Miller, personal communication), a present tributary of the Colorado River. Miller and Hubbs (1960:34) consider the locality as unquestionably erroneous and we concur, because extensive field work by them throughout the Great Basin has never revealed any *Nocomis*. Miller and Hubbs (1960) also cite other erroneous locality data associated with collections of the Wheeler Survey of 1871-1874.

The hornyhead chub is widely distributed within the glacial regions of the upper Mississippi River drainage. It is largely absent from the Driftless Area of Wis-

consin (Greene 1935:75, Map 26), as well as the larger western rivers. It is widespread in the upper Red River of the North drainage but apparently absent in the Lake of Woods drainage, both of the Hudson Bay basin. In the northern Ohio River basin *Nocomis biguttatus* is widely distributed, but avoids the non-glaciated areas. The species has a restricted distribution in the Allegheny River system of northwestern Pennsylvania. It is absent in the more upland sections of the Allegheny and Monongahela River systems of western Pennsylvania.

Lachner and Jenkins (1967:576) reported *Nocomis biguttatus* south of the Ohio River in Kentucky based on two collections from Elkhorn Creek, Franklin County, lower Kentucky River drainage. Three additional collections have been examined from Elkhorn Creek or its South Fork, UL 10479, 12465, and 12620. These five collections are represented on Figure 8 by a single plot. We suspect that this isolated population is not natural because of the absence (but high survival potential) of the species elsewhere in the system and south of the Ohio drainage. The area has been an intensive angling site and the population probably represents introduction by bait fishermen or, accidentally, through stocking programs or pond culture.

Several post-glacial routes assisted the entry of *Nocomis biguttatus* into the Great Lakes drainage. These routes are reviewed by Lachner and Jenkins (1971). The hornyhead chub is widespread in drainages of southern Lake Ontario and all or most of Lake Erie and Lake Michigan. It is present on the Atlantic slope only in the Mohawk-Hudson drainage of New York. It is absent from northern Lake Huron and the Georgian Bay region. Its presence in the Lake Superior area is restricted to streams of the southwestern portion.

The distribution and ecology of *Nocomis biguttatus* is compared with *N. effusus* and *N. micropogon* by Lachner and Jenkins (1967). Over much of its range, east of the Mississippi River, *N. biguttatus* is sympatric with *N. micropogon*. The ecology of *N. biguttatus* is treated further in Lachner (1952). As a whole, the species of the biguttatus group are tributary forms, avoiding the main rivers. Clear water streams, small-to-moderate in size, with moderate-to-low gradients, and with clean substrates of gravel, rubble, and some sand are preferred. Generally, the preferred streams have a moderate balance of riffles and pools, but long pools of slack water often exist. Turbid waters or fine

silt-laden situations are usually not inhabited. Streams with some aquatic vegetation appear to be preferred more by *N. biguttatus* and least by *N. effusus*.

The spawning behavior of *Nocomis asper* was observed by the authors at two typical habitats of the Arkansas River drainage in Oklahoma—at Spavinaw Creek, Delaware County, 7 June 1967, with water temperature about 21° C. and at Flint Creek, Delaware County, 12 June 1967, with water temperature about 21.5° C. These small, clear-water streams, 20 to 40 feet in width, have substrates of 70 to 95 percent small-to-large gravel, the remainder of the bottom being sand and rubble. The riffles are shorter in length than the pools; the linear relationship is about 1:2. Most of the riffles are about one-half to two feet in depth, the slack water about two feet deep and the pools three to four feet in depth, the deepest exceeding five feet. The riffles are generally shorter in length than the width of stream. Many nests of *N. asper* were completed, located in the moderately flowing waters, at the head of riffles, and in pools. The active nests, where spawning was observed, also were occupied by the spawning cyprinids *Notropis pilsbryi* and *Dionda nubila*. The common stream inhabitants in Spavinaw Creek were, in addition to *N. asper*, the cyprinids *Dionda nubila* and *Notropis pilsbryi*, the cottoid *Cottus carolinae*, the smallmouth bass *Micropterus dolomieu*, and the percid fishes *Etheostoma flabellare lineolatum* and *Etheostoma spectabile*.

The general habitat and ecology of *Nocomis asper* elsewhere in the Ozark upland of the Arkansas River drainage, particularly in the Neosho River system, is described in relation to other fishes and problems by Cross (1954), Minckley and Deacon (1959), Deacon and Metcalf (1961), Branson (1967), and Cross and Braasch (1969).

### Evolution and Zoogeography

We have postulated (Lachner and Jenkins 1967) that the biguttatus species group is probably primitive within the genus, the assumption based mainly on the general tuberculation pattern of the head and the presence of two rows of pharyngeal teeth. A biguttatus stock(s) was probably the precursor of the three groups of *Nocomis*. The adaptive specialization of head tuberculation among the species of the micropogon and leptocephalus groups involves elaboration and/or reductions of tubercle number, size, and distribution. The head tuberculation within the biguttatus group is



about the same in the three species in regard to size, distribution, and numbers when related to body length.

The minor tooth row of the pharyngeal arch is absent in the micropogon and leptocephalus groups and the loss is considered a derived condition. The primitive condition of two tooth rows, 1,4-4,1, persists in *Nocomis biguttatus* and *N. asper*, but the minor row is absent in *N. effusus*. The loss is regarded as a development independent to the loss in the micropogon and leptocephalus groups.

The evolution of the three groups of *Nocomis* are further compared and discussed by Lachner and Jenkins (1967, 1971). Within the biguttatus species group the body tuberculation in *N. asper* and *N. effusus* possibly represents evolution of another type of tubercle pattern, restricted entirely to this group and these two species of *Nocomis*. *N. asper* has more tubercles per tuberculate scale, laterally, on the side of the body than *N. effusus*. The occurrence of tubercles on the nape and on the scale rows above the lateral line is more widespread in *N. asper* compared with *N. effusus*. The body tubercles are much smaller in *N. asper* than those of *N. effusus*. The reduction in tubercle numbers per scale and distribution on the body, and the increase in tubercle size in *N. effusus* is regarded as a derived condition and correlates with the evolutionary trends of head tubercle development in the other groups of *Nocomis*. *N. biguttatus* is probably the more primitive of its species group, having a general tubercular pattern only on the head. *N. effusus*, because of its reduced dentition and specific body tubercle pattern, is placed at the advanced end of the biguttatus line. It also has the finest scales, narrowest scale margins, and shows the least development of the dark lateral band. *N. asper* is intermediate between *N. biguttatus* and *N. effusus* in character development, having a close affinity to *N. effusus* in its body tuberculation, and a close affinity to *N. biguttatus* in its coarser scales, dark lateral body band, well-developed red post-ocular spot, and two rows of pharyngeal teeth.

The zoogeography of the eastern and southern forms of *Nocomis* are discussed by Lachner and Jenkins (1971) and Lachner and Wiley (1971). The occurrence of the wide-ranging *N. micropogon* and its distributional relationships with *N. effusus* in the southwestern Ohio River basin is treated by Lachner and Jenkins (1967). The interesting aspects of the zoogeography of the biguttatus species group is that two of the species, *N. asper* and *N. effusus*, have restricted

distributions and have been long isolated by a vast lowland; the nominal form is extremely wide ranging. The three species are allopatric.

*Nocomis effusus* probably evolved within the region of the Cumberland, Green, and lower Tennessee drainages. It is unlikely that it had a much wider range because of its inability to traverse the Mississippi River valley. Its preference for moderate-to-low-gradient streams inhibited upstream movement. The closest relative and probable ancestor of *N. effusus*, *N. asper*, is not far west of the range of *N. effusus*, in the Ozark region of the Arkansas River drainage and a restricted portion of the Red River drainage. The lower portions of the Mississippi River tributaries below the mouth of the Tennessee River are not inhabited by members of the biguttatus species group. The range of *N. biguttatus* begins north of that of *N. asper* and is largely north and west of *N. effusus*.

The Ozark upland has additional faunal relationships with the Tennessee and Cumberland drainages, many species of which have almost always been confined to these two areas. Stages of main river development have provided means for species to establish a southern trans-Mississippi River distribution, and for isolation and subsequent differentiation on either side of the river. Trans-Mississippi dispersal of many upland species was probably quite limited and, once a large river was transversed, they would tend to seek conditions upstream within newly occupied systems.

The important early relations among the Mississippi and Ohio Rivers and some of their main tributaries are discussed by Fenneman (1938:87-90). (Also, see Figure 30 of Lachner and Jenkins 1971). The Ohio River once entered the Mississippi appreciably southward of the present mouth of the Ohio. The point of juncture was assumed to have been somewhat below Helena, Arkansas, which is about fifty air miles above the mouth of the Arkansas River. At about that time, the Tennessee River had a more southern confluency with the Ohio, and the Cumberland was probably a tributary of the former. These conditions were extant during part of the Pleistocene, presumably until near-present relations were established in late Pleistocene. Large rivers that were probably often turbid in the past, as the Mississippi, are regarded as both barriers to dispersal for upland, clear-stream fishes, and/or as limited, direct routes of dispersal.

The species of *Nocomis* distinctly disfavor ecological conditions that were probably present in the region of

the lower Mississippi, Ohio, and Tennessee Rivers. Assuming *N. effusus* was derived from *N. asper* stock, however, there had to be eastward dispersal from the Ozark region into the southwestern Ohio River basin. It is most probable that such dispersal occurred before post-Pleistocene conditions. From the mouth of the Arkansas River to the present mouths of the Tennessee River and Cumberland River involves upriver movement over a considerably greater distance and through conditions probably more difficult than those extant when the rivers were confluent farther south. In addition, the evolution of *N. effusus* probably required a greater time span than the age of the present drainage relationships.

Dispersal of *Nocomis effusus* among the three drainages of the southwestern Ohio basin was through main rivers and/or stream capture. It is possible that *N. effusus* used the Ohio River after the close of the Pleistocene, as mouths of the Tennessee, Cumberland, and Green drainages are close to each other. They may have been closer or formed a single river during earlier stages of the formation of the Ohio basin. The fact that *N. effusus* is known from the lower Tennessee and Cumberland drainages lends credence to river dispersal.

It would be more presumptuous to assume that both *Nocomis asper* and *N. effusus* were derived independently from a biguttatus-type stock. If so, the invasion of biguttatus stock into the southwestern Ohio basin would not be difficult to envision.

Problems related to the usage of stream capture in zoogeographic considerations are discussed by Lachner and Jenkins (1971). Although the known geological evidence for stream captures in the southwestern Ohio basin is meager, Wright (1936:246) stated that evidence of capture disappears with active dissection of the capture area. When geological evidence for stream capture is not cited below, the possibility of stream capture is still invoked when biological evidence exists, and the streams involved are adjacent to each other. The drainage in which *Nocomis effusus* evolved is not known. Stream capture, however, probably occurred between the Cumberland and Green and the Cumberland and Tennessee drainages, thus permitting crossing of their divides. Considerable portions of both the Green River and Barren River systems, Green drainage, are adjacent to the range of *N. effusus* in the Cumberland. Campbell (1896:671–672) stated that these divides have migrated toward the Cumberland. Such migration probably involved stream capture. *N. effusus*

would likely have been transferred during headwater capture since it typically inhabits small streams. Many additional small and moderate stream species are shared by the Cumberland and Green drainages. There also are close faunal relationships between the Cumberland and Tennessee drainages. One theater of stream capture may have been in their lower portions where the Duck River system of the Tennessee is bounded almost entirely on the north by the Cumberland.

*Nocomis asper* probably evolved in the Ozark plateau of the Arkansas River drainage. It could have been more widespread at one time, as evidenced by relict populations at Turkey Island, western Arkansas drainage, in the Blue River of the Red River drainage, and by the population in the upper Neosho River system of Kansas. The occurrence of these relict populations is interestingly paralleled by at least one species, *N. pilsbryi*. Although the Arkansas and White drainages have closely adjacent headwater tributaries and their mouths are practically together, there is no known recent exchange of *Nocomis* between these drainages.

The *Nocomis* forms from the Arkansas River and White River drainages have many characters common to each other. We suspected intergradation in body tuberculation and acquired large specimens needed to solve this problem. None from the White River drainage showed any evidence of body tuberculation. Other characters were also found to have differentiated from those of the Arkansas drainage. Drainage exchanges, however, between the White River and the Arkansas River are suggested by Hubbs and Moore (1940:95) involving *Notropis pilsbryi*, and by Branson (1964:746) involving *Notropis galacturus*; Branson (1967:148–152) discusses stream piracy and possible faunal exchanges between these two drainages. *Nocomis* does not appear to be involved in any recent White-Arkansas drainage exchange for the differentiation of the two forms is complete and constant in all tuberculate specimens.

The population of *Nocomis biguttatus* in the White drainage is morphologically similar to that of the Missouri basin. The distribution of the hornyhead chub in the Missouri basin consists of scattered, local populations, some of which are at a low level of survival, and others are known only by collections of early explorers. The present range of *N. biguttatus* in the Missouri basin indicates an early, wider distribution. A progressive restriction in the distribution is attributed to the

erosional history of the area, recent agricultural practices, and to unfavorable climatic conditions.

The present distribution of *Nocomis biguttatus* indicates that refugia existed south of the glacial limits in the Mississippi-Missouri basins during Pleistocene times. With glacial retreat, *N. biguttatus* invaded the upper Mississippi and Ohio basins. Its entrance in the Great Lakes at several different, broad postglacial connections and times, and entry into The Red River of the North, is discussed by Greene (1935), Radforth (1944), Gerking (1945), Underhill (1957), Trautman (1957), Hubbs and Lagler (1958) and Bailey and Allum (1962). The absence of *N. biguttatus* from above the falls of the Genesee River system in New York and in the upland Allegheny River system indicates that it entered the Lake Ontario drainage from the west rather than through the Allegheny-Genesee (Cuba) postglacial outlet. Entry of *N. biguttatus* into the Mohawk-Hudson drainage was probably during the Mohawk glacial outlet. Although *N. biguttatus* and *N. micropogon* today are sympatric over extensive portions of their ranges, *N. biguttatus* probably had central basin refugia during glacial times and *N. micropogon* had a more easterly refuge (Lachner and Jenkins 1971: Figure 30).

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