

ROBERT E. JENKINS
and ERNEST A. LACHNER

*Criteria for Analysis
and Interpretation of
the American Fish
Genera *Nocomis* Girard
and *Hybopsis* Agassiz*

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Lines on the indicated pages should read as follows:

Page 3, 1st column, 5th line from bottom --

"Hybopsis (sensu lato or sensu stricto)."

Page 3, 2nd column, 12th line from bottom --

"38 to 44, precaudal vertebrae number 20 to 24. De--"

Page 9, 1st column, 2nd line from top --

"ferences between the subspecies of Hybopsis (Eri--"

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ABSTRACT

Robert E. Jenkins and Ernest A. Lachner. Criteria for Analysis and Interpretation of the American Fish Genera *Nocomis* Girard and *Hybopsis* Agassiz. *Smithsonian Contributions to Zoology*, number 90, 15 pages, 1 figure, 1971.—Until recently *Nocomis* Girard has been included as a subgenus in the polymorphic genus *Hybopsis* Agassiz along with *Couesius* Jordan and six additional nominal American cyprinid genera. *Nocomis* is diagnosed and recognized as a genus primarily on the basis of sexual dimorphic features, its mound-nest building behavior, general coloration, physiognomy, scale radii, and vertebral numbers. *Nocomis* and *Couesius*, also given generic rank, are probably more closely related to the genus *Semotilus* Rafinesque than to any group remaining in *Hybopsis*. *Parexoglossum* Hubbs is merged with *Exoglossum* Rafinesque and these are implicated to be related to *Semotilus*.

Characters previously employed to diagnose *Hybopsis* are widely shared with other American cyprinids, such as the maxillary barbels which may be highly variable. Certain subgenera of *Hybopsis* are probably more closely related to other American cyprinid genera than to *Hybopsis* sensu stricto. Species of some subgenera of *Hybopsis* merit reallocation to other subgroups of *Hybopsis* or *Notropis*. Additional nomenclatural changes in *Hybopsis* are not recommended until more comprehensive studies are available.

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Criteria for Analysis and Interpretation of the American Fish Genera *Nocomis* Girard and *Hybopsis* Agassiz

Introduction

The group of nest-building barbeled cyprinid fishes herein recognized as *Nocomis* Girard has had a history of instability regarding its level within the genus-group category. A nomenclatural review of *Nocomis* is given by Lachner and Jenkins (1971a) and of *Hybopsis* by Reno (1969a).

Bailey (1951:192) submerged *Nocomis* and seven additional nominal genera, including *Couesius* Jordan, in *Hybopsis* Agassiz. The nine nominal genera are listed in Table 1. Bailey's arrangement has been generally followed, with recognition of *Nocomis* as a subgenus. However, Hubbs and Crowe (1956) commented that "... the reexpanded genus *Hybopsis* rests on an unsteady basis. . . ." Lindsey (1956:771) did not follow Bailey's actions, partly by reason of the latter's failure to provide data for his contentions. Bailey and Allum later (1962:36-37) attempted to support lumping of *Nocomis* with *Hybopsis*. Recent studies of brain and gustatory structures by Davis and Miller (1967) and on the cephalic lateral-line system by Reno (1967; 1969b), combined with our work indicate that *Hybopsis* is an unnatural assemblage. Lachner and Jenkins (1967:558) regarded *Nocomis* as a valid genus but reserved discussion of this allocation for the present paper. *Couesius* is herein recognized as a genus rather than a subgenus of *Hybopsis*. *Hybopsis*, excluding *Nocomis* and

Couesius, is still morphologically and biologically a very diverse assemblage of about twenty species.

Our primary purpose is to define the genus *Nocomis* as it relates to the remaining groups in the currently recognized genus *Hybopsis* and to its apparent close relatives. Additionally, we discuss the status of *Hybopsis* and make suggestions for future realignment of some of the subgenera and species included under it.

We have evaluated characters previously employed in the classification of the genera and subgenera treated herein with respect to their utility and importance. Most characters treated are external, but some internal anatomical features have been considered. The morphology upon which some of the statements given below are partly based will be presented for *Hybopsis* sensu stricto (the amblops group) by Glenn H. Clemmer and for other groups of *Hybopsis* and relatives by Jenkins and others. We place more emphasis than some previous workers on basic pigmentation patterns, aspects of physiognomy, sexual dichromatism and dimorphism, behavior, and ecology as useful group characters. Various aspects of nuptial tuberculation, in particular, have been of utmost importance as indications of relationship. The systematic significance of tubercle characters was discussed by Lachner and Jenkins (1967:567 and 1971a).

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TABLE 1.—Comparison of characters distinguishing subgenera of *Hybopsis*, *Couesius*, and *Nocomis*

Genus-group	Breeding coloration	Nest (mound) builders	Nuptial head tubercle size	Nuptial crests or swellings	Pharyngeal dentition	Range: Total number of scale radii	Range: Total number of vertebrae	Feeding type ¹	Cephalic lateral line system ²
<i>Hybopsis</i>									
(<i>Hybopsis</i>)	No (except <i>labrosa</i>)	No	Tiny to large	None	1,4-4,1	5-24	31-37	III, Mouth tasters (except <i>labrosa</i>)	Unique (excluding <i>labrosa</i>)
(<i>Yuriria</i>)	No	No	Small	None	4-4	16-21	34-37
(<i>Erimystax</i>)	No	No	Small to moderate	None	4-4	6-26	32-39	I, Sight feeders	As in <i>Macrhybopsis</i> and <i>Extrarius</i> (excluding <i>harperi</i>)
(<i>Platygobio</i>)	No	No	Small	None	2,4-4,2	13-18	40-47	II, Skin tasters	As in <i>Hybopsis</i> , but with many goblet cells
(<i>Macrhybopsis</i>)	No	No	Small	None	1,4-4,1	7-20	35-39	II, Skin tasters	As in <i>Erimystax</i> and <i>Extrarius</i>
(<i>Extrarius</i>)	No	No	Tiny	None	4-4	4-12	30-35	I, Clear water forms II, Silty water forms	As in <i>Erimystax</i> and <i>Macrhybopsis</i>
(<i>Oregonichthys</i>)	No	No	Moderate	None	1,4-4,1	7-13	31-32	I, Sight feeders	Unique
<i>Couesius</i>	Yes	No	Small	None	2,4-4,2	15-22	36-39	I, Sight feeders	Unique
<i>Nocomis</i>	Yes	Yes	Large to very large	Typical of two species-groups	1,4-4,1 4-4 to 3-3	23-54	34-40	I, Sight feeders	Unique

¹ After Davis and Miller, 1967² After Reno, 1967 and 1969b.

of Natural History: Kenneth Karb assisted in much of the work on scale analysis; Dorothy Hubbs and Martin L. Wiley aided considerably in taking and reading some of the radiographs. Frank B. Cross, University of Kansas, permitted use of his vertebral counts for *Hybopsis gracilis*. We have profited in our knowledge of *Hybopsis* through discussion with Glenn H. Clemmer, Mississippi State University.

The Genus *Nocomis*

Nocomis is perhaps the most distinctive group that has been relegated to *Hybopsis*. It is unique in two and nearly unique in two others of the first four characters, which are concerned with reproduction, in Table 1. It differs almost entirely in number of total scale radii (Table 2) and considerably in precaudal vertebral numbers (Table 4). Its cephalic lateral-line system is unique only in that long canaliculi develop in apparent compensation for increase in thickness of facial integumental areas (Reno, 1967: 72, 107; 1969b:757). *Nocomis* shows homogeneity in its lateral-line development, brain pattern, barbel origin and morphology, and its taste-bud sensory systems, but in these characters it is essentially similar to several other *Hybopsis* subgroups. It is a well-marked group in having a robust body (not shared with several other so-called chubs in *Hybopsis sensu lato*), specific contours of the head in juveniles, and a characteristic body coloration.

Bailey and Allum (1962:36-37) mentioned character trends associated with reproductive behavior in *Nocomis* and other cyprinid genera and stated that the resultant developments (such as large tubercles) should not be over-emphasized in classification. We place considerable importance upon the fundamental fact that all *Nocomis* build a mound nest and all other *Hybopsis* do not. Elaborations of sexual dimorphic features apparently are positively correlated with the nest building behavior, and as such they may be regarded as forming a single character complex. However, even if these characters are disregarded, there is still virtually no evidence for close relationship between *Nocomis* and *Hybopsis* (*sensu lato* or *sensu stricto*).

Bailey and Allum (*loc. cit.*) apparently regarded monotypy or oligotypy of phyletic groups to merit reduced weight in classification. We do not subscribe to this opinion, and, in addition, note that a

greater amount of differentiation has occurred within *Nocomis* than was indicated by Bailey and Allum; three species groups have evolved.

No group remaining in *Hybopsis s.l.* approaches *Nocomis* in its combination of morphology, coloration, and habits. In the event of further dismemberment of *Hybopsis*, *Nocomis* will obviously not be associated with the name *Hybopsis*, because its relation to the *H. amblops* complex (the type species of *Hybopsis*) is quite remote; there are no extant forms transitional between the *H. amblops* complex and *Nocomis*.

We regard *Nocomis*, which has recently been recognized as a genus by Douglas and Davis (1968), Raney (1969), Scott and Crossman (1966), Smith-Vaniz (1968), and Suttkus and Ramsey (1967), as a natural unit of generic rank, marked by the following characters: Nuptial males (1) construct a mound-nest by transportation of stones in the mouth; (2) have large to very large breeding tubercles on the head and, in two species, on the body; (3) have an expansive cephalic crest or swelling except in one species group; (4) develop on the body elaborate breeding coloration of pink-rosy, orange, and/or bluish; (5) attain a moderate to large body size, adult males 100 to 250 mm SL (Standard Length). Other characters common to both sexes follow: (6) coloration dark above, light below with broad dark scale margins and post-opercular bar; (7) large scales, the lateral line scales almost always fewer than 44 and body circumferential scales fewer than 37 (caudal peduncle scales 16-20); (8) mouth normal, moderate to large in size, subterminal; (9) barbels small, one terminal maxillary pair; (10) pharyngeal tooth count 1,4-4,1; 4-4; or 3-3; (11) scales with radii on posterior field only, the total number of radii in adults 23-54; (12) total vertebrae number 38 to 43, precaudal vertebrae number 21 to 24. Descriptions of the species groups of *Nocomis* are given by Lachner and Jenkins (1971a).

The closest relatives of *Nocomis* are probably the nest-building species of *Semotilus* Rafinesque, *S. atromaculatus* and *S. corporalis*. In addition to reproductive behavior (nest building), these species are similar to at least the more primitive *Nocomis* in their reddish nuptial colors and pattern, pectoral fin tuberculation, head and body physiognomy, scale characters, vertebral numbers, and general body color pattern. The *Couesius* group shows affinity

with *Semotilus*, particularly with *Semotilus margarita*, in the following characters: barbel position; squamation pattern; opercular, branchiostegal, and breast tuberculation; breeding color (see painting in Raney, 1969); scale morphology; vertebral numbers; and other features. The data indicate that if *S. margarita* merits inclusion in the genus *Semotilus* (Bailey and Allum, 1962:36-37), so does *Couesius*. The mound-nesting behavior and other characters of the *Exoglossum* group suggest that it, too, may be related to *Semotilus*.

Scale Morphology

METHODS.—Scale samples were taken from adult or subadult specimens. The scales were selected from the dorsolateral portion of the body below the dorsal fin. Only typical scales were studied, and those showing any regeneration were discarded. Scales were studied from about ten specimens of 19 of the species of *Hybopsis*, the one species of *Couesius*, and all species of *Nocomis*. In addition, the scales from three specimens of each of 89 species of *Notropis* were studied, as were scales of other American cyprinid genera.

Preliminary studies revealed that among the various characters of scale morphology, the best comparative character between the genera was the number of radii. In *Hybopsis* and *Nocomis* the radii are found only on the posterior field. The radii were subdivided initially into two groups, primary and secondary. The secondary radii were considered, for convenience, as those one-half or less of the length of the longest radii. All others were considered primary radii. The number of primary and/or secondary radii were compared as a percentage of the total number, and various differences among the species were observed, but the most useful comparison was the total count (Table 2).

The use of scale morphology as a systematic character was initiated mainly by Agassiz in 1833 with his work on fossil and recent fish scales. Later studies in lepidology, such as those of Cockerell (1911; 1913), Lagler (1947), Kobayasi (1951, 1952-1955) and McCully (1961) reviewed scale characters on a family or major group level. When our preliminary studies revealed possible meristic differences in the number of scale radii, we undertook a comprehensive survey, although we were aware that con-

TABLE 2.—Total number of radii in the posterior field of scales of *Hybopsis*, *Couesius*, and *Nocomis*

(Genus-group)	Species	Mean	Range	Specimens
<i>Hybopsis</i>				
(<i>Hybopsis</i>)	<i>a. amblops</i>	19.2	15-25	9
	<i>rubrifrons</i>	13.7	9-19	10
	<i>hypsinotus</i>	9.6	8-14	10
	<i>labrosa</i>	7.0	5-9	10
	sp., cf. <i>labrosa</i>	11.5	8-15	11
	<i>storeriana</i>	18.5	14-24	12
(<i>Yuriria</i>)	<i>alta</i>	17.7	16-21	12
(<i>Erimystax</i>)	<i>d. dissimilis</i>	12.3	9-17	10
	<i>x. x-punctata</i>	7.6	6-16	11
	<i>i. insignis</i>	8.4	7-10	9
	<i>cahni</i>	5.7	5-7	5
	<i>monacha</i>	9.7	7-11	10
	<i>harperi</i>	18.5	13-26	11
(<i>Platygobio</i>)	<i>g. gracilis</i>	14.8	13-18	10
(<i>Macrhybopsis</i>)	<i>gelida</i>	13.7	11-20	10
	<i>meekei</i>	10.0	7-13	9
(<i>Extrarius</i>)	<i>aestivalis</i>	6.9	4-12	10
(<i>Oregonichthys</i>)	<i>cramerii</i>	10.8	7-13	11
<i>Couesius</i>	<i>plumbeus</i>	18.5	15-22	11
<i>Nocomis</i>				
	<i>biguttatus</i>	33.4	26-40	9
	<i>asper</i>	29.2	23-36	10
	<i>effusus</i>	40.7	25-49	18
	<i>platyrhynchus</i>	34.0	24-48	12
	<i>raneyi</i>	31.9	25-36	9
	<i>micropogon</i>	40.8	24-54	12
	<i>leptocephalus</i>	28.6	24-35	10

siderable variation in many aspects of scale structure existed in any single species. Lagler (1947:153) noted that the characters "least usable for diagnostic purposes, even at the major taxonomic level of families, are absolute size, shape, numbers of various countable structures, and position of the focus." Chu (1935:21) in his studies of Chinese cyprinids, pointed out that, "Granting sufficient allowance for variations, the number of radii in the various fields may be stated as fairly characteristic for certain forms or groups."

RESULTS.—Table 2 giving the average values for the total number of radii in all the recognized species of *Hybopsis*, *Couesius*, and *Nocomis* illustrates a major difference among these genera. The highest individual counts of only three species of *Hybopsis* (*amblops*, *storeriana*, and *harperi*) approach or

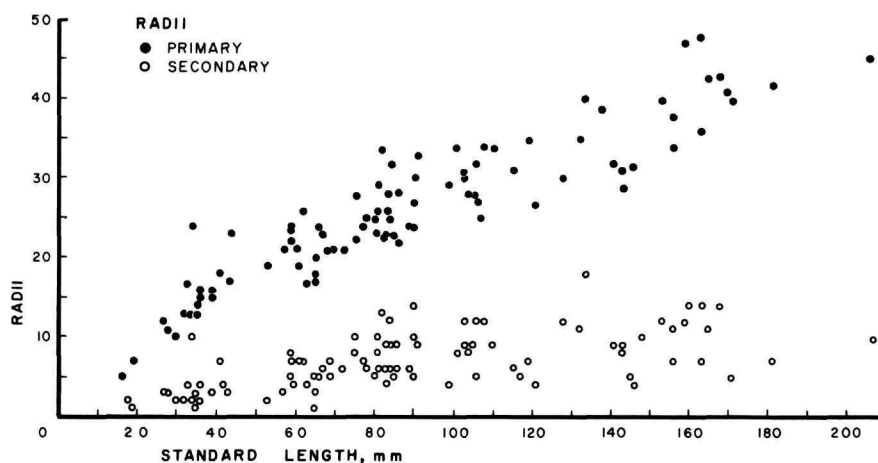


FIGURE 1.—The relationship of the number of primary and secondary radii with increase in body length in 91 specimens of *Nocomis micropogon*, ranging in size from 16 to 207 mm in Standard Length (SL).

slightly overlap the lowest individual counts in *Nocomis*. Obviously, both higher and lower counts in all species may be expected with increase in size of sample, but modal values should remain about the same.

In order to obtain some idea of ontogenetic differences and variations in number of radii, 91 specimens of *N. micropogon* ranging from about 16 to 207 mm SL were studied (Figure 1). This slightly curvilinear relationship shows a fairly uniform increase in the number of primary and secondary radii with increase in body length and also that, for any size, the range of variation is moderate. The rate of increase is greater in primary than in secondary radii. The number of primary radii in relation to secondary radii was comparatively high in *Nocomis* (Figure 1), and the relationship was similar among all of the species. The average number of primary radii, in percent of the total number in species of *Nocomis* was: *effusus* 66, *raneyi* 71, *platyrhynchus* 72, *micropogon* 75, *leptocephalus* 75, *asper* 78, and *biguttatus* 80. Mean values for species of *Hybopsis* ranged from about 18 to 90 percent.

Cockerell and Allison (1909:161–162) distinguished *Nocomis* from *Hybopsis* on the basis of the broader nuclear scale area in *Nocomis*, the “apical radii almost parallel” (i.e., less convergent). We cannot agree with this distinction. In species of *Hybopsis* with high numbers of primary radii, the convergence of the radii in the nuclear area is gen-

erally less than in species with fewer primary radii. There are also differences in the convergence of the radii in species with low numbers of radii, some meeting on a much wider nuclear area than others.

The survey of the total number of radii in 89 species of *Notropis* (of the 101 species recognized as valid) showed great differences among the species; the average values ranged from about 5 to 20. These values are very similar to those of *Hybopsis* (mean values, 5.7 to 19.2) and unlike all species of *Nocomis* (mean values, 29.2 to 40.8). Species of the subgenus *Luxilus* as well as the *Notropis* species *dorsalis*, *anogenus*, *signipinnis*, *bairdi*, *heterolepis*, *atrocaudalis*, *petersoni*, *longirostris*, and other *Notropis* species had mean values from about 13 to 20. Many species, such as members of the subgenera *Cyprinella* and *Lythrurus*, had total radii counts ranging only from about 5 to 13. Our data are in general agreement with many of the radii counts given by Cockerell and Callaway (1909:190). Both sets of data indicate the numbers of radii are lower characteristically in *Notropis* than in *Nocomis*.

INTERPRETATION.—Cockerell and Allison (1909:163) linked *Nocomis* with *Semotilus*, *Couesius*, and *Phenacobius* on the basis of several scale characteristics. *Phenacobius* was certainly misplaced by Cockerell, if one considers the scale characters he regarded significant. *Phenacobius* develops few radii (about 8–15) and these converge broadly in the area of the focus, whereas in *S. atromaculatus* and *S. cor-*

TABLE 3.—Total vertebral numbers in *Hybopsis*, *Couesius*, and *Nocomis*

Genus-group	species	Total vertebrae												
		34	35	36	37	38	39	40	41	42	43	44	45	46
<i>Hybopsis</i>														
(<i>Hybopsis</i>)	<i>a. amblops</i>		6	44	20	2								
	<i>rubrifrons</i>			2	20	23	1							
	<i>hypsiniotus</i>			2	18	4								
	<i>labrosa</i>						11	19	1					
	sp., cf. <i>labrosa</i>				5	32	2							
	<i>storeriana</i>						12	6	1					
(<i>Yuriria</i>)	<i>alta</i>					6	24	20	1					
(<i>Erimystax</i>)	<i>d. dissimilis</i>						5	11	8					
	<i>dissimilis harryi</i>								3	3	2			
	<i>x. x-punctata</i>				1	1	14							
	<i>x-punctata trautmani</i>				2	12	4							
	<i>i. insignis</i>					12	33	6						
	<i>insignis eristigma</i>					6	4							
	<i>cahni</i>						13	6						
	<i>monacha</i>								3	15	1			
	<i>harperi</i>			9	33	4								
(<i>Platygobio</i>)	<i>g. gracilis</i>											5	15	6
	<i>gracilis:gracilis x gulonella</i>								18	37	37	8	2	
	<i>gracilis gulonella</i>							19	18	14	1			
(<i>Macrhybopsis</i>)	<i>gelida</i>						15	12	6					
	<i>meekei</i>									14	26			
(<i>Extrarius</i>)	<i>aestivalis</i>	3	13	29	26	9	1							
(<i>Oregonichthys</i>)	<i>crameri</i>		8	18										
<i>Couesius</i>	<i>plumbeus</i>							1	16	18	2			
<i>Nocomis</i>	<i>biguttatus</i>					1	46	124	19					
	<i>asper</i>						1	12	3					
	<i>effusus</i>							10	47	1				
	<i>platyrhynchus</i>						2	59	94	7				
	<i>raneyi</i>							27	204	111	8	1		
	<i>micropogon</i>					1	5	168	278	70				
	<i>leptocephalus</i>					24	188	134	10					

poralis the radii are numerous (about 25–40) and they converge comparatively sharply in the area of the focus.

The scale morphology of *Nocomis*, in numbers of radii and in scale configuration and development, agrees closely with that of *S. atromaculatus* and *S. corporalis*. The small-scaled form *Semotilus margarita* has a moderate number of radii (15–21), but otherwise its scale morphology generally agrees with that of *Nocomis* and *Semotilus*. *Couesius plumbeus* (15–22 total radii) is also close to this relationship in scale morphology, particularly to *S. margarita*. The scales of *N. biguttatus*, *N. leptocephalus* and *N. mi-*

cropogon were illustrated by Lachner (1952:442, Figures 1–5); *N. biguttatus* by Lagler (1947, Plate 4, Figure 21); *N. effusus* (as *N. kentuckiensis*) by Cockerell (1913, Plate-figure 32:6); *S. atromaculatus* and *S. corporalis* by Cockerell and Allison (1909, Plate 3, Figures 4, 5); and *S. atromaculatus* by Ellis (1914, Plate 12, Figure 61).

We present our scale data with a cautious attitude in regard to its use as a systematic character. The difference, however, between the scale morphology of *Nocomis* and that of *Hybopsis* s.l. and *Notropis* is of such magnitude that it cannot be omitted as criteria in the evaluation of these generic groups. The scale

TABLE 4.—Precaudal and caudal vertebral numbers in *Hybopsis*, *Couesius*, and *Nocomis*

Genus-group	species	Precaudal										Caudal							Difference ¹ P or C
		16	17	18	19	20	21	22	23	24	16	17	18	19	20	21	22	23	
<i>Hybopsis</i>																			
(<i>Hybopsis</i>)	<i>a. amblops</i>		2	37	33							22	41	9				=	
	<i>rubrifrons</i>			14	29	3						3	12	25	6			=	
	<i>hypsinothus</i>			1	15	8						7	15	2				P 1	
	<i>labrosa</i>			2	22	7									16	14	1	C 1	
	sp., cf. <i>labrosa</i>				34	3						8	27	2				=	
	<i>storeriana</i>				1	8	8	1				3	14	1				P 1.5	
(<i>Yuriria</i>)	<i>alta</i>					2	36	13				4	38	9				P 3	
(<i>Erimystax</i>)	<i>d. dissimilis</i>					1	15	7				1	6	11	5			P 2	
	<i>dissimilis harryi</i>							3	5					1	4	3		P 2	
	<i>x. x-punctata</i>				3	8	2					1	4	7	1			P 1	
	<i>x-punctata trautmani</i>				7	9						7	8	1				P 1	
	<i>i. insignis</i>				24	26	1					4	27	19	1			P 1	
	<i>insignis eristigma</i>				7	3						1	7	2				=	
	<i>cahni</i>				1	13	2					1	9	6				P 1	
	<i>monacha</i>						2	10							10	2		=	
	<i>harperi</i>			5	38	3						10	29	7				P 1	
(<i>Macrhybopsis</i>)	<i>gelida</i>			4	20	8								2	14	12	4	C 1	
	<i>meeki</i>					5	2									4	3	C 2	
(<i>Extrarius</i>)	<i>aestivalis</i>	8	46	20	4							1	5	14	26	29	3	C 3	
(<i>Oregonichthys</i>)	<i>crameri</i>			12	12								19	5				P 1.5	
<i>Couesius</i>	<i>plumbeus</i>						1	15	18	1				7	21	7		P 4	
<i>Nocomis</i>	<i>biguttatus</i>						2	131	55			6	87	105	6			P 4	
	<i>asper</i>							3	13				11	5				P 6	
	<i>effusus</i>							2	37	19			28	28	2			P 5.5	
	<i>platyrhynchus</i>					16	93	19					4	47	69	8		P 3	
	<i>raneyi</i>							34	160	11			7	166	101	10		P 5	
	<i>micropogon</i>				1	33	324	61				10	151	221	43			P 4	
	<i>leptocephalus</i>					5	117	35				13	108	35				P 5	

¹ P = precaudal, C = caudal. Region with higher mode, if any, in left column; approximate difference between modal values of precaudal and caudal vertebrae in right column.

data support our concept that *Nocomis* is unique among the *Hybopsis-Notropis* complex and that its relationships are close to the *Semotilus* group.

Vertebral Counts

METHODS.—Total and precaudal counts include the Weberian vertebrae, counted as four, and urostylar vertebra counted as one. Of the 18 references cited herein for cyprinid vertebral counts, only 4 excluded the Weberian vertebrae from the total: Olund and Cross (1961), Al-Rawi and Cross (1964), Cross (1967, [apparently excluded only for *N. biguttatus* and the subspecies of *H. (Platygobio) gracilis* but

not in the total given for the latter species]), and Lachner and Jenkins (1967). Their data, before being used herein (Tables 1, 3, and 4), were adjusted by adding four for the Weberian complex.

Counts were made from radiographs over a light-box with an opaque plastic top. For smaller specimens a focusing magnifying lens mounted in a plastic cylinder was used. A pointer mounted below the lens in the cylinder facilitated counting.

An attempt was made to minimize possible environmental influence upon the data by using samples obtained from localities scattered throughout the ranges of the species. This was not possible for all species. Garside (1966) includes keys to, or sum-

maries of, the literature and a critical discussion of the effect of environment upon vertebral number.

An attempt to distinguish between precaudal and caudal vertebrae was also made. If a haemal spine was distinctly longer (by about 25 percent or more), than an adjacent anterior haemal element, the vertebra on which such a spine occurred was counted as the first caudal vertebra. This method probably yields a close approximation of the actual line of division, which usually occurred in the region of the tip of the anteriormost anal pterygiophore, the succeeding haemal spines being approximately equal in length. Such a distinction was not obvious in some specimens. Thus for some species the total of the precaudal and caudal counts is less (Table 4) than the total shown in Table 3. Precaudal and caudal vertebral counts of American cyprinids appear to have been published only by Suttkus and his collaborators (see Literature Cited); the present study indicates the importance of their consideration.

In Tables 3 and 4 the data are segregated by currently recognized subspecies except for those of three species: *H. (Extrarius) aestivalis*, which shows a complex pattern of variation (Hubbs and Ortenburger, 1929:23–28; Yerger and Suttkus, 1962:327; Metcalf, 1966:108–110; Davis and Miller, 1967:16–20); and *H. (Erimystax) harperi* and *Couesius plumbeus*, in which the recognition of subspecies was questioned by Howell (1961) and Lindsey (1956:769–771), respectively. *Hybopsis (Hybopsis) labrosa* and *H. (Hybopsis) sp. cf. labrosa* are closely related to each other.

RESULTS.—*Nocomis* is relatively homogeneous with respect to the number of vertebrae; among the seven species, the modes for total vertebrae (Table 3) range from 39 to 41 and the modes for total precaudal and caudal vertebrae (Table 4) range, respectively, from 22 to 23 and from 17 to 19. Total number of vertebrae average higher in *Nocomis* than in most *Hybopsis* s.l., the differences being due to the higher counts in the precaudal and lower counts in the caudal regions of *Nocomis*. The precaudal counts in *Nocomis* show complete separation from 11 of the 20 forms of *Hybopsis* and a high percentage of separation of specimens from most of the remainder (excluding the single specimen of the 419 *N. micropogon* examined, with 20 precaudals). In the 20 forms of *Hybopsis* the modal values for precaudal and caudal counts are about the same in 5

forms, the precaudal count is lower than the caudal in 4, and the precaudal is higher in 11 forms (9 species). The magnitudes of the differences between precaudal and caudal counts are pertinent. In the 11 *Hybopsis* forms whose precaudal count is higher than the caudal, the differences between the modes are about 1 vertebra in 7 forms, 2 in 3 forms, and 3 only in *H. (Yuriria) alta*. The differences between the precaudal and caudal modes in *Nocomis* are greater than 3 in all but one species, 3 in *N. platyrhynchus*, 4 in *N. biguttatus* and *N. micropogon*, 5 in *N. raneyi* and *N. leptocephalus*, 5.5 in *N. effusus*, and 6 in *N. asper*.

With respect to vertebral count, *Couesius* and *Semotilus* have modal values similar to or distinctly higher than those of *Nocomis*: The modal value for *Couesius* is 42; for the three species of *Semotilus* the ranges are 40–42 for *S. margarita*, 42–44 for *S. atromaculatus* (42–45 for Kansas material, Cross, 1967), and 44–46 for *S. corporalis*. *Couesius* and *Semotilus* have the large precaudal-caudal differences characteristic of *Nocomis*; the precaudal has modally from 4 to 6 vertebrae more than the caudal in these two groups. These data again support a possible relationship among *Nocomis*, *Couesius* and *Semotilus*.

A survey was made of vertebral counts published for American cyprinids. The references and groups follow: Miller and Hubbs, 1960 (Plagopterini); Miller, 1963 (*Gila crassicauda*); Snyder, 1908 (*Ptychocheilus*); Barbour and Contreras, 1968 (*Algansea*); Jordan and Evermann, 1896 (*Gila*, *Ptychocheilus*, *Orthodon*, *Pogonichthys*, *Semotilus*); Fingerman and Suttkus, 1961, and Al-Rawi and Cross, 1964 (*Hybognathus*); Minckley and Craddock, 1962 (*Phenacobius*). The following presented counts for various species or groups of *Notropis*: Bailey and Suttkus (1952), Suttkus (1955), Suttkus and Raney (1955), Suttkus (1959), Bailey and Allum (1962), Gilbert and Bailey (1962), Gilbert (1964), Snelson (1968), Suttkus and Clemmer (1968). Cross (1967) gave the range for all cyprinids of Kansas, presumably based upon Kansas specimens, thus making available counts for six groups in addition to those listed above: *Notemigonus*, *Chrosomus*, *Opsopoeodus*, *Dionda*, *Pimephales*, and *Campostoma*. Counts for *Hemitremia*, *Semotilus*, certain species of *Phenacobius*, and the *Notropis boucardi* group were obtained by the authors.

Distinctive specific differences exist between some

species of *Hybopsis*, and there also appear to be differences between the subspecies of *Hybopsis* (*Erimystax*) *dissimilis*. Of particular interest is *H. (Platygobio) gracilis*, in which two subspecies were recognized by Olund and Cross (1961) on the basis of several characters in addition to the vertebrae numbers. Bailey and Allum (1962:44-45) did not recognize these subspecies, addressing their remarks apparently only to the difference in the number of vertebrae. They gave counts for 476 specimens from South Dakota, and their interpretation of the data was that these differences in number of vertebrae strongly indicated environmental modification. This may be true, as is evidenced by the fact that the greatest and second greatest ranges in total vertebrae, 7 and 6, respectively, appear in *H. gracilis* and the rather polytypic *H. aestivalis*, species that apparently occur in the widest range of ecological conditions. Metcalf (1966:103-104) summarized additional information indicating that differences in vertebral counts among subspecies of *H. gracilis* are not solely due to phenotypic responses to temperature; he also gave a logical zoogeographic hypothesis concerning the origin and intergradation of the subspecies.

The vertebrae count of a broad sample of American cyprinids ranges from 33 to 47. *Notropis* tends to have lower counts (more than 75 percent of the 34 species surveyed have modal values less than 40), whereas the elongate *Phenacobius*, the larger sized *Semotilus*, and a number of western groups have higher counts. Apparent trends in body form and size, and vertebrae count in percids (Bailey and Gosline, 1955) seem to be roughly paralleled in cyprinids.

Scope of the Genus *Hybopsis*

The characters most frequently used to describe *Hybopsis* s.l. are: (1) pharyngeal teeth in major row 4-4 (in minor row 0-2); (2) upper jaw protrusile, no frenum; (3) mouth subterminal to inferior; (4) barbels present, their origin terminal or near terminal on maxillae; (5) intestine not whorled (except one species); (6) scale radii restricted to posterior field (Jordan and Evermann, 1896:314; Bailey, 1951:216; Moore, 1968:67). To evaluate these characters we compared *Hybopsis* with a large majority of other American cyprinid genera, particularly *Notropis*. On the basis of our studies and

through reference to the general treatments of Jordan and Evermann (1896) and Moore (1968), we found that characters 1, 2, 3, 5, and 6, are widely shared with other cyprinid groups, and (except for character 3) by about 50 to 75 percent of the extant American cyprinid species, so that emphasis upon any one of these characters, or all in combination, as a principal support for merging genus-groups under *Hybopsis* appears questionable.

As for item 4, the possession of a barbel pendant from or very close to the lip angle (terminal maxillary position) seems to have been a chief requisite for inclusion of fishes in *Hybopsis*. Histologically, this basically gustatory structure in *Hybopsis* and *Nocomis* is fleshy and lacks osseous, cartilaginous, and muscular support, according to Davis and Miller (1967:13), who give (p. 15) for most species, the number and size of taste buds on barbels. The barbels have, in effect, been the key character for distinguishing between *Hybopsis* and *Notropis*, species lacking these structures being assigned to the latter genus. However, the barbel in some American cyprinid species and genus-groups is now thought to be a variable and labile character. Their occurrence in certain groups is probably an advanced rather than primitive condition that has been developed through several evolutionary pathways. The observed variation in barbels and lips indicates opportunity for their selective change as environmental conditions may warrant. We cite some of the known cases that support these statements:

(1) In specimens of some species of *Hybopsis* (in part, Moore, 1968) and other typically barbeled groups (e.g., *Rhinichthys*, Hubbs and Miller, 1948:16-17; *Semotilus*, Gould and Brown, 1968, and our studies; *Nocomis* and *Exoglossum*, our studies), the barbel or barbels are occasionally absent.

(2) In some species of *Hybopsis* (particularly the subgenus *Erimystax*) and at least one other group (including *Phenacobius*) a small flap or fold of skin occurs, extending from beneath the anterior end of the lachrymal bone to the posterior end of the maxilla. Sometimes part of this flap is excised or nearly so, somewhat resembling a *Semotilus*-type barbel.

(3) Sometimes there occurs along the ventral edge of this flap an elongate, apparently compound, taste bud that resembles a tiny barbel and may function as such. A series of elongate pendent "barbels" oc-

curs along the flap in some specimens of *Hybopsis* (*Erimystax*) *x-punctata*; these were roughly sketched and termed sensory bristles by Branson (1962).

(4) Occasional specimens of *Nocomis*, *Semotilus*, the subgenus *Erimystax*, and of species of other groups were found with a deeply cleft barbel or two barbels, completely separated, usually small and on one side of the mouth.

(5) The individuals of certain populations of *Hybopsis* (*Extrarius*) *aestivalis* typically possess two well-developed pairs of barbels rather than one (Hubbs and Ortenburger, 1929:23–28; Yerger and Suttkus, 1962:327). The evidence presented by the former authors indicates that the tetranemus condition, unique to *aestivalis* among American cyprinids, evolved within this species independently from Old World groups (and perhaps more than once).

(6) Discrete differences exist in details of barbel origin and form among species-groups of *Hybopsis* s.l., some of which were mentioned by Branson (1962). These data indicate that barbels may have arisen independently several times.

(7) *Notropis bairdi*, a turbid-river dweller, shows a tendency toward prolongation of the lip angle into a barbel-like structure whereas its two close relatives apparently do not show this condition (Cross, 1953:254).

(8) Nuptial males of *Pimephales notatus* develop a transitory barbel-like structure derived from tissue at the lip angle. It apparently is at least partly associated with increase in cephalic epidermal gibbosity in nuptial males that forces the lip angle downward. This is the only species of *Pimephales* known to possess the structure and was considered on the basis of trophic, nuptial, and other characters to be the most specialized in its group (Hubbs and Black, 1947:9–13).

(9) The presence of a barbel in *Plagopterus* is regarded as an advanced state in the Plagopterini. This genus seems to be the most highly specialized plagopterin (Miller and Hubbs, 1960:6–11), most of its modifications apparently being related to life in turbid waters. The ancestral plagopterin was suggested by Miller and Hubbs to be a species of *Gila*, all known members of which lack a barbel, or "a similar, relatively unspecialized cyprinid genus."

(10) The possibility of close relationship between the non-barbeled *Notropis amnis* and usually barbeled *Hybopsis* (*Hybopsis*) *amblops winchelli* was

suspected by Hubbs (1951:5; and more so in Moore, 1968:72). Study of this possibility by Glenn H. Clemmer shows that these forms are intimately related; they are regarded as congeneric by Clemmer and by us.

We conclude that, for groups under consideration herein, the barbel alone (its occurrence, position, and morphology) is not necessarily of decisive significance in classification. It is conceivable that a genus may include both barbeled and non-barbeled forms. The only current New World examples of such groups are *Notropis*, to which the barbeled boucardi group was recently referred by Cortes (1968), and *Exoglossum*, to which we assign the barbeled *Parexoglossum*.

The presence of barbels in some but not all members of a group or species reduces the systematic value of this character, although contrary to Cortes (1968) and the opinions of others, its usage at the generic level has not been invalidated. Barbels remain important in the determination and delimitation of phyletic lines and generic groups, particularly when considered with other details of morphology, sensory functions, and group life history. We concur with a statement by Hubbs and Miller (1948:16–17) that, "The capacity to develop a barbel . . . is of more significance than its actual presence or absence."

This review of six important diagnostic characters given for *Hybopsis* s.l., the first five of which are trophic ones, reveals that the group is probably insecure; the lack of other cohesive characters, such as melanophore pigmentation patterns, head and body physiognomy, nuptial features, and life histories further substantiates this point. No additional specialized feature is known that is common to most species. The subgroups of *Hybopsis* comprise an extremely heteromorphic assemblage, one that Jordan and Evermann (1896:314) regarded to show ". . . a range of variation as wide as that in *Notropis*, though with a [considerably] smaller number of species." *Hybopsis*, at that time, did not include *Platygobio* and *Couesius*. The geographic range of *Hybopsis* extends from Arctic Canada southward into Mexico and from the Atlantic to the Pacific slope; if this were a natural group it would be the most wide-ranging American cyprinid genus.

On the basis of several studies in progress, some tentative summaries concerning relationships among

and within groups of *Hybopsis* and other cyprinid genera now can be made. Davis and Miller (1967) and Reno (1967) restricted their studies to *Hybopsis* s.l. and therefore could not determine the wider systematic significance of their results; their findings concerning divergence in sensory structures among and within previously established subgroups, however, usually correlate with studies of other character complexes.

We have already indicated that *Couesius* probably is closely related to *Semotilus*, particularly through the species *Semotilus margarita*. The subgenera *Platygobio*, *Macrhybopsis*, and *Erimystax* are near allies of each other and are probably closer to *Phenacobius* than to *Hybopsis* s.s. *Hybopsis* (*Hybopsis*) *storeriana* is misplaced in the subgenus *Hybopsis* and appears to be a close relative of *Platygobio*. *Hybopsis* (*Erimystax*) *harperi* is probably referable to *Notropis*. *Hybopsis* (*Hybopsis*) *labrosa* and *Hybopsis* (*Hybopsis*) sp., both from southeastern United States, are related to the *Notropis* (Cyprinella) group. The relations of the latter four species with *Hybopsis* s.s. are distant. Also, *Hybopsis* s.s. is probably more closely related to a *Notropis* lineage than to the remaining subgenera of *Hybopsis* s.l.

There is too great a diversity engendered by the groups just mentioned (including *Nocomis* and its closest relatives) to place them into a single genus. At least three rather distantly related phyletic lines are represented in *Hybopsis* s.l., only one of which seems to have an (apparently advanced) end in *Hybopsis* s.s. The eventual dismemberment of *Hybopsis* s.l. and some of its subgroups, and indication of their relationship with other genera, will lead to considerable nomenclatural changes, a necessary reaction to earlier uncritical study and understanding. Although we are certain that changes will be necessary, we do not recommend nomenclatural alterations until further studies are completed.

Materials

A list of the material of *Hybopsis* and *Couesius* used for vertebral data is given below. The samples of *Nocomis* are from localities scattered throughout the ranges of the species and are reported in papers by Lachner and Jenkins (1967; 1971a) and Lachner and Wiley (1971). Numbers in parentheses refer to the specimens on which counts were made. Abbrevi-

ations for institutions are: Cornell University (CU); University of Kansas (KU); Tulane University (TU); University of Michigan, Museum of Zoology (UMMZ); National Museum of Natural History (USNM). The locality data and identifications for all series of the *Hybopsis* (*Platygobio*) group were listed by Olund and Cross (1961) or are from their original data sheets.

Hybopsis (*Hybopsis*) *a. amblops* (Rafinesque)

White R. drainage: USNM 42681, Missouri, Texas Co., N. Fk. White R., 1889 (10); USNM 59310 and 59311, Arkansas, Washington Co., Mid. Fk. White R. (3 and 5); USNM 59313, Arkansas, Washington Co., White R. (1); USNM 59312, Arkansas, Newton Co., Little Buffalo R. (3).

Tennessee R. drainage: USNM 63084, Alabama, Colbert Co., Tusculumbia, 1909 (11); USNM 188710, North Carolina, Yancy Co., Cane Cr., 1964 (5); USNM 40535, North Carolina, Madison Co., Spring Cr., 1888 (6); USNM 194857, Virginia, Smyth Co., Mid. Fk. Holston R., 1958 (6); USNM 190960, Virginia, Smyth Co., N. Fk. Holston R., 1959 (5).

Green R. drainage, Kentucky: USNM 107208, Mammoth Cave, 1929 (5); USNM 163099, Metcalfe Co., trib. Russell Cr., 1952 (7); USNM 163101, Adair Co., Russell Cr., 1952 (3); USNM 163100, Casey Co., trib. Green R., 1952 (2).

H. (Hybopsis) rubrifrons (Jordan)

Savannah R. drainage: USNM 165721, Georgia, Madison Co., trib. Broad R., 1952 (5); USNM 168122, South Carolina, Oconee-Pickens Co. line, Keowee R., 1954 (6); USNM 168103, South Carolina, Oconee Co., Chauga Cr., 1954 (2).

Altamaha R. drainage, Georgia: USNM 165729, Walton Co., trib. 1 mi NE Monroe, 1952 (4); TU 26141, Gwinnett Co., Yellow R., 1962 (29).

H. (Hybopsis) hypsinotus (Cope)

Pee Dee R. drainage: USNM 104100, Virginia, Carroll Co., Lovels Cr., 1937 (10); USNM 162921, North Carolina, Wilkes Co., trib. Yadkin R., 1952 (1); USNM 166285, North Carolina, Wilkes Co., trib. Yadkin R., 1947 (1).

Santee R. drainage, South Carolina: USNM 192851, Greenville Co., Oil Camp Cr., 1964 (5); USNM 162954, Spartanburg Co., Fair Forest Cr., 1952 (7).

H. (Hybopsis) labrosa (Cope)

Santee R. drainage: USNM 168129, North Carolina, Iredell Co., Buffalo Cr., 1956 (2); USNM 192853, South Carolina, Spartanburg Co., N. Pacolet R., 1954 (2); TU 26207, South Carolina, Anderson Co., Brushy Cr., 1962 (27).

H. (Hybopsis) sp., cf. labrosa

Pee Dee R. drainage: USNM 162928, North Carolina, Surrey Co., Mitchell R., 1952 (2); USNM 162929, North Carolina, Wilkes Co., Bugaboo Cr., 1952 (1); USNM 162251, North Carolina, Wilkes Co., trib. Yadkin R., 1947 (10); USNM 105075, Virginia, Carroll Co., Ararat R., 1933 (2).

Santee R. drainage: USNM 162356, South Carolina, Greenville

- Co., N. Saluda R., 1947 (10); USNM 67996, North Carolina, Burke Co., Johns R., and McDowell Co., Bucks Cr., 1888 (7); USNM 40551, North Carolina, Burke Co., Johns R., 1888 (7).
- H. (Hybopsis) storeriana* (Kirtland)
Mobile R. drainage: USNM 167997, Alabama, Choctaw Co., Tombigbee R., 1955 (7).
Tennessee R. drainage, Alabama: USNM 108552, Lauderdale Co., Shoal Cr., 1938 (2); USNM 108558, Wheeler Res., 1938 (10).
- H. (Yuriria) alta* (Jordan)
Mexico: USNM 48905 and 125131, Río Lerma, Salmanca (5 and 3); USNM 55757, Aguas Calientes (7); USNM 37819 and 41819, Guanajuato (3 and 1); TU 30663, Zacatecas state, Río Juchipila, 1963 (32).
- H. (Erimystax) d. dissimilis* (Kirtland)
Tennessee R. drainage, Virginia: USNM 195832, Smyth Co., N. Fk. Holston R., 1958 (8).
Wabash R. drainage, Indiana: USNM 66892, Marshall Co., Tippecanoe R., 1890 (6).
Upper Ohio R. drainage, Pennsylvania: USNM 116420, Westmoreland Co., Loyalhaune Cr., 1893 (6); USNM 161903, Mercer Co., French Cr., 1947 (4).
- H. (Erimystax) dissimilis harryi* Hubbs and Crowe
White R. drainage, Missouri: CU 24242, Barry Co., White R., 1956 (5); CU 38345, Stone Co., Indian Cr., 1958 (1); CU 32874, Ripley Co., Current R., 1953 (2).
- H. (Erimystax) x. x-punctata* Hubbs and Crowe
Ouachita R. drainage, Arkansas: USNM 36428, Clark Co., Ouachita R., 1884 (7); USNM 36462, Saline Co., Saline R. (7).
- H. (Erimystax) cahni* Hubbs and Crowe
Tennessee R. drainage, Tennessee: UMMZ 157709, Claiborne Co., Powell R., 1939 (4); UMMZ 103462-63 Anderson Co., Clinch R., 1936 (4); USNM 70580 and 201454, Clinch R., Walkers Ford, 1893 (5 and 6).
- H. (Erimystax) monacha* (Cope)
Tennessee R. drainage: USNM 36664, Alabama, Lauderdale Co., Shoal Cr., 1884 (2); USNM 190644, Tennessee, Rhea-Roane Co. line, White Cr., 1959 (7); USNM 70580, Tennessee, Clinch R., 1893 (1); USNM 70581, Tennessee, Indian Cr., Cumberland Gap (2); USNM 40499, North Carolina, Madison Co., Spring Cr., 1888 (1); USNM 177367, Tennessee, Hawkins-Sullivan Co. line, N. Fk. Holston R., 1954 (1); CU 46397, Tennessee, Sullivan Co., N. Fk. Holston R., 1963 (2); USNM 40475, Virginia, Smyth Co., N. Fk. Holston R., 1888 (3).
- H. (Erimystax) harperi* (Fowler)
Florida: TU 20358, Wakulla Co., Wakulla R., 1959 (36); USNM 133245, Lake Co., Juniper Springs, 1946 (10).
- H. (Platybio) g. gracilis* (Richardson)
UMMZ 166845 (9); KU5127 (3); KU5128 (2); UA uncataloged, Simonette R. (2); UA uncataloged, Peace R. (5); ROMZ 14500 (5).
- H. (Platybio) gracilis: gracilis x gulonella*
KU 1841 (10); MSC 1878 (7); MSC 2021 (6); ROMZ 3885 (2); UMMZ 166803 (9); MSC 1960 (5); KU 2140 (2); KU 4863 (12); UMMZ 134813 (9); UMMZ 135280 (10); UMMZ 135786 (7); UMMZ 114644 (8); UMMZ 127681 (15).
- H. (Platybio) gracilis gulonella* (Cope)
KU 4742 (5); KU 4769 (5); MSC 2010 (5); KU 4266 (5); KU 4269 (6); KU 3409 (10); KU 4235 (5); WU 2084 (4); WU 2095 (3).
- H. (Macrhybopsis) gelida* (Girard)
UMMZ 164849, Illinois, Jackson Co., Mississippi R. (4).
Missouri R. drainage: UMMZ 161909, South Dakota, Pennington Co., Cheyenne R., 1950 (7); USNM 125133, Nebraska, Hall Co., Platte R., (5); USNM 76049, Wyoming, Sheridan Co., 1893 (4); USNM 59137 and 174890, Wyoming, Sheridan Co., Powder R., (10 and 2); USNM 174889 Wyoming, Converse Co., Platte R., (1).
- H. (Macrhybopsis) meeki* Jordan and Evermann
Missouri R.: USNM 35889, Missouri, Buchanan Co., (1); KU 9675, Missouri, St. Louis Co., 1963 (10); KU 9783, Missouri, Lafayette Co., 1963 (8); KU 9688, Missouri, St. Charles Co., 1963 (9); CU 30323, South Dakota, Yankton Co., 1952 (5); UMMZ 166966, South Dakota, Charles Mix and Gregory Co., 1952 (7).
- H. (Extrarius) aestivalis* (Girard)
Mexico: USNM 55727, Nuevo León state, trib. San Fernando R., (4); CU 24390, San Fernando R., Tamaulipas, 1952 (7).
Colorado R. drainage: USNM 36582, Texas, Travis Co., Rio Colorado, 1884 (9).
San Antonio R. drainage: USNM 46229, Texas, Comal Co., Rio San Marcos (7).
Red R. drainage: USNM 173317, Louisiana, Bossier Parish, 1956, (4); USNM 36342, Arkansas, Hempstead Co., Red R., 1884 (10).
Ouachita R. drainage, Louisiana: USNM 172285, Union Parish, Ouachita R., 1956 (2); USNM 172361, 172381, and 172394, Ouachita Parish, Ouachita R., 1956 (2, 2, and 1).
Arkansas R. drainage, Arkansas: USNM 36374, Sebastian Co., Arkansas R., 1884 (5); USNM 16136, Oklahoma, Payne Co., Cimarron R., 1935 (10).
Missouri R. drainage, Nebraska: USNM 76047 and 125132, Buffalo Co., 1893 (3 and 5).
Wabash R. drainage, Indiana: CU 32229, Posey Co., Wabash R., 1958 (7).
Green R. drainage, Kentucky: CU 46651, Green Co., Green R., 1963 (3).
- H. (Oregonichthys) crameri* Snyder
Umpqua R. drainage, Oregon: USNM 58116, Douglas Co., S. Umpqua R., (1); USNM 58132, S. Umpqua R., (4).
Williamette system of Columbia R. drainage, Oregon: UMMZ 166728, Lane Co., Cottage Grove Reservoir, 1950 (7);

CU 20988 and 31026, Benton Co., McFaddens Pond, 1946 and 1951 (4 and 3); CU 43623, Benton Co., Willamette R., 1952 (7).

Couesius plumbeus (Agassiz)

Alberta: USNM 125198 (4).

Saskatchewan R. drainage, Montana: USNM 104725, Upper Waterton L., 1934 (7).

L. Superior drainage, Michigan: USNM 193063, Houghton Co., Otter R., 1953 (7).

Missouri R. drainage, Idaho: USNM 125200, Bonner Co., Pend Oreille R., 1892 (1).

Labrador: USNM 165435, Northwest R., 1951 (3).

Maine: USNM 57004, Telos L. (9).

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