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Cyprinid Fishes of the Subgenus Cyprinella of Notropis. IV The Notropis galacturus camurus Complex

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ABSTRACT: The species Notropis galacturus and N. camurus are redescribed and differentiated from other species of the subgenus Cyprinella and synonymies are given. These two species form a distinct unit within the subgenus, distinguished by the presence of depigmented basicaudal areas, a hiatus between nuptial tubercles of the snout and those of the top of the head, two rows of tubercles on each chin ramus, and red pigment in dorsal and anal fins of breeding males. Populations of N. galacturus east and west of the Mississippi have differentiated slightly. Lower Mississippi populations of N. camurus are racially distinct from those in the Arkansas system. The two species are probably derived from a common stock which became divided into eastern and western portions. N. galacturus has crossed the Mississippi, but the range of N. camurus appears to have contracted, leaving the two present populations.

The systematic situation in the subgenus Cyprinella has been outlined in the first paper of this series, and the two variable species N. spilopterus and \hat{N} . venustus treated in subsequent parts (Gibbs, 1957a, b, c). Notropis galacturus and Notropis camurus stand apart from most of the species of Cyprinella as a unit, defined by a number of characters which they have in common. First, and most notable, both have depigmented areas at the caudal base which, at their fullest development, are quite prominent. Occasionally in other species of Cyprinella a specimen is found which has such depigmentation, but the character is never common. An unrelated species which is sympatric with N. galacturus in the Tennessee system, Notropis coccogenis, also has prominent depigmented caudal areas, but this is surely a case of parallelism. The breeding males of both N. galacturus and N. camurus have greatly enlarged dorsal fins and red pigment in both dorsal and anal. Their tubercle patterns are similar, notably in the lack of a hiatus between the tubercles of the top of the head and those of the snout, in the minuteness of the nape tubercles, and in the presence of two rows on each chin ramus.

This paper redescribes the species N. galacturus and N. camurus, treats their intraspecific variation, and discusses their possible origin and means of dispersal.

MATERIALS AND METHODS

Specimens used in this study were from the following institutions: Academy of Natural Sciences of Philadelphia (ANSP); Cornell University; University of Georgia; Museum of Zoology, University of Michigan; Tulane University; and United States National Museum (USNM). To staff members of these institutions, I owe my deepest appreciation.

Counts and measurements were made in accordance with Hubbs and Lagler (1958), except postdorsal length (dorsal origin to caudal base) and dorsal origin to lateral line. All measurements were made on specimens between 50 and 60 mm, and are recorded as per cent of standard length.

This paper is based on a doctoral thesis, done at Cornell University under Dr. Edward C. Raney. To him, and to the many colleagues who gave constructive criticism or aid in the field, I extend my sincere thanks.

Notropis galacturus Whitetail Shiner

- Hypsilepis galacturus. Cope, 1867:160 (orig. descr.; Holston system, Va.); 1869:229 (Holston system, Va.), 1870:459 (French Broad, Clinch, Cumberland systems).
- Leuciscus kentuckiensus. Günther, 1868:251 (specimens from Cope from Holston R.).
- Cyprinella galactura. Jordan and Copeland, 1876:153; Jordan, 1929:81 (char., distr.); Pratt, 1935; 76 (char., distr.); Schrenkeisen, 1938:130 (char., distr.).
- Luxilus galacturus. Jordan, 1877:339, 370, 373 (Tennessee and Cumberland systems); 1878a:294 (char., distr.); 1878b:421, 1879:110 (distr.).
- Photogenis galacturus. Jordan and Brayton, 1878:18, 64, 91 (Tennessee, Cumberland and Savannah systems).
- Hudsonius galacturus. Jordan, 1880:292 (char., distr.); 1884:292 (char., distr.).
- Cliola galactura. Jordan and Gilbert, 1883:179 (char., distr., syn.).
- Notropis galacturus. Jordan, 1885:814; Call, 1887:76 (Shannon Co., Mo.); Jordan and Gilbert, 1887:2 (White R., Ark.); Jordan, 1889:145, 152 (Holston and French Broad systems); Gilbert, 1891:147 (Tennessee system, Ala.); Meek, 1891 (Neosho, White and Black systems, Ark. and Mo.); Kirsch, 1892:291 (Cumberland system, Ky.); Woolman, 1892:266 (Cumberland system, Ky.); 1893:260-267 (Cumberland system, Ky. and Tenn.); Evermann and Kendall, 1895: 470 (White system, Mo.); Meek, 1895:77, 82 (White system, Ark.); Jordan and Evermann, 1896b:256 (distr., syn.); 1896a: 257 (char., distr., syn.); Smith, 1907:93 (French Broad system, N.C.); Goldsborough and Clark, 1908:35 (Monongahela system, W. Va. doubtful); Fowler, 1910:283 (variation); Jordan, 1910:58 (char., distr.); Cockerell, 1911:384 (scale illustrated); Evermann and Hildebrand, 1916:444 (E. Tenn.); Jordan, 1916 (char., distr.); Evermann, 1918:364 (Ky. and Tenn.); Fowler, 1923:16 (Catawba doubtful and French Broad systems, N.C., Cumberland system, Tenn.); Pratt, 1923:80 (char., distr.); Pickens, 1928:30 (S.C.); Hildebrand, 1932:66 (Tuckasegee R., N.C.; char.); Kuhne, 1939:50 (Tenn.); Shoup and Peyton, 1940:111, 113 (Cumberland system, Tenn.); Shoup, Peyton and Gentry, 1941:69 (Obey R., Tenn.); Fowler, 1945:115, 343 (N.C., Ala.).
- Erogala galactura. Jordan, Evermann and Clark, 1930:129 (distr., syn.); Fowler, 1936a:192 (Holston system, N.C.); 1936b:111 (Charter, Tenn.); Driver, 1942:274 (distr., char.); 1950:287 (char., distr.).

Types.—One specimen of Hypsilepis galacturus, collected by Prof. E. D. Cope in North Carolina, is located in the U.S. National Museum. This specimen, a male, 83.8 mm, USNM 14981, is herein designated lectotype. In the Academy of Natural Sciences at Philadelphia there are 64 syntypes, ANSP 3381-3444, collected by Cope in the Holston River, Virginia.

Collections examined by river system.—Savannah, 1; Santee, 1; Tennessee, 92; Cumberland, 14; White, 52; St. Francis, 4; Mississippi, 1. Kanawha system collections not seen.

Comparative diagnosis.—Notropis galacturus occurs sympatrically with N. s. spilopterus, N. whipplei, and N. v. venustus of the subgenus Cyprinella. There are few records of its being taken with N. camurus, although in the White system there is apparently a small, perhaps introduced, population of N. camurus together with the abundant N. galacturus. The differentiation of N. galacturus from N. camurus may be seen in Tables I-IV. N. camurus has fewer lateral-line scales, a smaller predorsal length, accompanied by a longer postdorsal length, a longer head, generally deeper body, as expressed in body depth, dorsal origin-lateral line and caudal peduncle depth, and a slightly larger orbit and longer upper jaw. In addition, the depigmented caudal base of N. camurus is much less bipartite than that of N. galacturus, often appearing as a bar across the base of the fin rays, and the snout is extremely blunt.

N. whipplei, and particularly N. spilopterus, are likely to be the most confusing species. Specimens of N. galacturus which have less-prominent depigmented caudal areas very strongly resemble N. spilopterus, and in fact, this study has revealed specimens which are surely hybrids between the two.

In the river systems east of the Mississippi, N. galacturus differs from N. s. spilopterus in the following characters: (1) usually 39-41 laternal-line scales instead of 37-39, (2) usually 15 or 16 pectoral rays, instead of 13-15, (3) a more slender body, usually 21-23% of standard length, instead of 22-26% (4) caudal peduncle depth usually 10-11% of standard length, instead of 11-12%, (5) pigment present along base of anal fin and along the midventral caudal peduncle, (6) the presence from an early age of at least a moderate amount of pigment in all dorsal fin membranes, while N. spilopterus, except in breeding males, has little or no pigment in the first three membranes, and (7) the presence of depigmented basicaudal patches.

In the same eastern systems and also west of the Mississippi, N. galacturus differs even more trenchantly from N. whipplei in most of the same characters. N. whipplei has: (1) usually 37 or 38 lateral-line scales, (2) usually 14-16 pectoral rays, (3) body depth 24-28% of standard length, (4) caudal peduncle depth 10-12% of standard length, (5) no pigment along anal base or midventral caudal peduncle, (6) pigment in all dorsal membranes, thus not differing from N. galacturus, and (7) no depigmented basicaudal patches. West of the Mississippi, N. galacturus may be distinguished from N. spilopterus hypsisomatus, with which it is not sympatric, by its greater number of lateral-line scales, 39 or 40, instead of 35-38; by its 15 or 16 pectoral rays, instead of 13-15; by its smaller body depth, 19-22% of standard length, instead of 10-13%; and by its smaller distance from dorsal origin-lateral line, 12-15% of standard length, instead of 14-19%. In pigmentary differences, the two forms may be told apart as in the comparison of N. s. spilopterus and N. galacturus above.

Notropis v. venustus, the only remaining Cyprinella likely to be confused, has a prominent black caudal spot which N. galacturus lacks, and itself lacks the depigmented basicaudal patches of N. galacturus.

It might be possible to confuse N. galacturus in the Tennessee and Cumberland with Notropis coccogenis, which is not a species of Cyprinella, but which has a depigmented caudal base. N. coccogenis has 2,4-4,2 teeth, and lacks the distinctive Cyprinella characters of narrowly outlined scales which appear diamond-shaped, and contrastingly dark posterior dorsal membranes. It further lacks tubercles on top of the head, these being present only at the tip of the snout and lower jaw.

Description.—Teeth 1,4-4,1, hooked, the grinding surfaces narrow, elongate, concave, and usually not serrated. Anal rays 9. Pectoral rays usually 15 or 16. Lateral scales with exposed portions higher than wide. Lateral-line scales usually 39-41; predorsal circumferential scales 13-2-11; caudal peduncle scales 7-2-5. No crowding before dorsal. Dorsal fin moderate in size in non-breeding adults, the first or second principal ray longest, the middle rays longest in the depressed fin; origin nearer caudal base than snout tip.

Head subconical. Orbit usually about 7% of standard length, shorter than snout, 3-4 in head. Mouth terminal or subterminal, oblique, moderate in size; upper jaw reaches about to level of anterior edge of orbit. Upper jaw slightly longer than either lower jaw or orbit. Body, slender, terete, body depth usually 20-23% of standard length. Caudal-peduncle depth usually 10-11% of standard length. Lateral line slightly decurved from opercular margin to below middle of dorsal fin.

Breeding males with scattered tubercles on top of head, snout, and area between eye and snout, most dense in the latter two areas. No hiatus present between head and snout tubercles. Chin rami with two or more rows smaller than those of top of head. Nape tubercles very small; those of rest of notal ridge absent or almost invisible. Extremely small prickles on all body scales except belly, partially arranged in rows on exposed scale margins. Small tubercles on all fin rays, following their branching, often weak in dorsal and caudal.

Coloration.—Dorsal scales and a row or two below the lateral line narrowly edged in black, appearing diamond-shaped. A poorly developed lateral stripe present behind the level of the dorsal fin, the

narrow dark line which marks its dorsal outline continued forward almost to opercle. A very diffuse band, slightly denser than the background color, runs in a straight line from opercle to caudal base, its lower half merging with the lateral stripe posteriorly. A narrow middorsal line present along entire dorsum both before and behind dorsal fin.

The most prominent character of the species is the depigmented caudal base, which takes the form of two patches whose margins extend from the bases of the most-anterior procurrent rays to the middle of the junction between scales of caudal peduncle and caudal rays, and out to the distal end of the longest procurrent ray (see Fig. 1).



Fig. 1.—Left lateral views of: (top) Notropis galacturus, CU 25992, male, 60.3 mm, Tennessee drainage, Franklin Co., Tenn.; (middle) N. camurus, CU 23357, male, 61.1 mm, Arkansas drainage, Cherokee Co., Okla.; (bottom) N. camurus, CU 24931, female, 64.7 mm, Mississippi drainage, De Soto Co., Miss. Photography by Douglass M. Payne of Cornell University.

Belly immaculate. Sides of anal fin and midventral caudal peduncle with more or less prominent pigment.

Top of head dark, covered with small melanophores which reach the lower edge of the lachrymal and circle the eye. The upper part of the preopercle and the entire opercle are covered with diffuse, larger melanophores. The pigment of the lips is similar to that of the snout. Remainder of head immaculate. Deep-lying bar of pigment between chin rami hardly visible.

Dorsal fin usually well pigmented on all membranes, the last two noticeably darker than the rest. Caudal lightly pigmented except in basal patches, the pigment along outer edges of rays often very dark, adding to the contrast of the depigmented areas. Pectoral fin rays usually with melanophores lining the leading rays. Pelvics and anal lack pigment.

Breeding males assume a dusky gray cast, all fins are filled with milky pigment, and the anal and enlarged dorsal fin are red.

Infraspecific variation.—Exchange of genetic material between stocks of N. galacturus in the Tennessee-Cumberland and those in the Ozark region appears to have been sufficient and/or recent enough to minimize the differences between these portions of the range. Fishes from the two regions, however, show slight but definite signs of drift from one another. These trends are illustrated in Tables I, III, IV. The number of lateral-line scales is different, the mean being 39.50 or less in the Ozarks, 40.00 or more in the East. A slight trend is present in pectoral rays, of which the Ozark populations have slightly more than the East. Among proportional characters, predorsal length, head length, caudal peduncle depth, body depth, and dorsal origin-lateral line show a shift. None of these differences is of such magnitude as to warrant nomenclatorial recognition, or even racial status, although the latter, merely on the basis of geographical isolation would not seem unreasonable.

Range.—Tennessee, Cumberland, and upper Savannah, Santee, and Kanawha systems east of the Mississippi; Ozark Plateau and Ouachita Mountain portions of the White and St. Francis systems west of the Mississippi. One collection in the U.S. National Museum, according to the accompanying data, was made in Wyatt, Missouri. Wyatt is in Mississippi County and is well outside the range of either eastern or western segment of the species. Further, N. galacturus habitat is probably not found in this region. Although the record is possible, it must be the subject of considerable doubt.

Habitat.—Cool, clear streams, most commonly in the vicinity of mountains. Although it is most often found in moderate-sized waters, it has been taken on occasion in small headwater streams.

Etymology.—The name *galacturus* is derived from the Greek *gala* (genetive *galactos*), milk and *oura*, tail, with reference to the white basicaudal marks.

				Ľ	teral-lin	Lateral-line scales							
River System	35	36	37	38	39	40	41	42	43	z	×	SD	\mathbf{SE}
N. galacturus													
Cumberland	:	;		1	13	33	13		1	60	40.0	.71	60.
Tennessee	;	;	:	5	36	116	76	16	4	250	40.3	.88	.06
Savannah	1	1	:	1	:	1		:	:	1	41.0		;
White	1	1	:	5	34	32	3			75	39.5	.75	60.
St. Francis	;	:	:		4	1	-	1	i	9	39.5	.84	.34
(Mississippi)	:		1	1	4	3		ł	i	8	39.3	.71	.25
Total eastern	:	:	ł	2	49	149	89	18	4	311	40.3	.86	.05
Total western	:		1	5	38	33	4		1	81	39.5	.75	.08
N. camurus													
Osage	:	4		:	:	:	1		1	5	36.2	.45	.20
Arkansas	3	91	60	5	:	1	1	1	i	169	36.3	.76	.04
Total Arkansas Race	13	65	61	ß		1	:	-		174	36.3	.66	.05
Lower Miss. Race	1	10	45	29	2	:	:	:	1	86	37.3	.69	.05
					Pectoral rays	rays		1					
N. galacturus	13	14	15	16	17	18	z	×	SD	\mathbf{SE}			
Cumberland		12	58	43	9	:	119	15.4	.73	.07			
Tennessee	:	59	271	167	16		514	15.3		.03			
Savannah	;	ł	:	5	!	1	5	16.0		!			
White	1	6	72	79	10	1	170	15.5		.05			
St. Francis	ł	!	9	5		;	12	15.6	.67	.19			
(Mississippi)	1	!	6	9	:	1	15	15.4		.13			
Total eastern	:	71	329	212	22	1	635	15.3		.03			
Total western	:	6	78	84	11	:	182	15.5		0.5			
N. camurus													
Osage	1	1	9	4	1	1	10	15.4	.52	.16			
Arkansas	4	19	145	150	26	:	344	15.5	.76	0.4			
Total Arkansas race	4	19	151	154	26	1	354	15.5	.76	.04			
Lower Miss. race	:	11	81	17	6	;	178	15.5	.69	.05			

Notropis camurus (Jordan and Meek) Bluntface Shiner

Cliola camura. Jordan and Meek, 1885:474 (orig. descr.; Fort Lyon, Colo.). Notropis camurus. Cragin, 1885:108 (Neosho system, Kans.); Jordan, 1885:814; 1891:18 (Arkansas R., Wichita, Kans.); Gilbert, 1886:208 (Neosho R., Oswego, Kans.); Jordan and Evermann, 1896b:256 (distr., syn.); 1896a:279 (char., distr., syn.); Gilbert, 1889:39 (Neosho system, Kans.); Jordan, 1899:58 (char., distr.); 1910:58 (char., distr.); 1916:58 (char., distr.); Jordan, 1928:370 (distr.); Moore and Paden, 1950:85 (Illinois R., Okla.); Moore, 1952 (Okla.).
Cyprinella whipplei. Graham, 1885:73 (misidentification).

Erogala camura, Jordan, Evermann and Clark, 1930:129 (distr., syn.).

TABLE II.—Frequency distribution of meristic characters of Notropis galacturus and N. camurus

		Pred. o	circumf. s	scales at	ove L	Ĺ
River System	11	12	13	14	15	N
N. galacturus						
Cumberland			55	2	3	60
Tennessee	8	9	215	11	12	255
Savannah			1			1
White			58	6	12	76
St. Francis			6			6
(Mississippi)			5	1	2	8
Total eastern	8	9	271	13	15	311
Total western		.	64	6	12	82
N. camurus						
Osage			1	1	3	5
Arkansas		1	85	41	43	170
Total Arkansas Race		1	86	42	46	175
Lower Miss. Race	3	4	76	3	1	87
			Ana	l rays		
River System		8	9	10		N
N. galacturus						
Cumberland			56	3		59
Tennessee		18	228	11		257
Savannah			1			1
White		6	78	2		86
St. Francis			6			6
(Mississippi)			8			8
Total eastern		18	295	14		317
Total western		6	84	2		92
N. camurus						
Osage			5			5
Arkansas		9	157	5		171
Total Arkansas Race		9	162	5		176
Lower Miss. Race			81	8		89

Cyprinella camura. Pratt, 1935:76 (char., distr.); Schrenkeisen, 1938:130 (char., distr.).

Notropis camura. Cross, 1954:309 (Neosho system, Kans.).

Types.—Cliola camura Jordan and Meek USNM 15256. Fort Lyon, Colo., Dr. E. Palmer. Two specimens were in this type series. One of these, a very highly developed male, 80.0 mm in standard length, with an extremely arched dorsal profile, is herein designated lectotype and retains the original catalogue number. The other is a specimen which had previously been reidentified as *Hybognathus* nuchalis placita. This has been recatalogued as USNM 163962.

Collections examined by river system.—Arkansas, 61; White, 1; Osage, 1; Lower Mississippi tribs. in Miss. and La., 25.

Diagnosis.—Although Notropis camurus is sympatric with only two species of Cyprinella, Notropis spilopterus hypsisomatus and Notropis v. venustus, it actually most closely resembles N. whipplei.

One would be hard-put to distinguish N. camurus from N. whipplei on the basis of meristic characters, and proportional characters show few distinctions. The head length is usually 26-28% of standard length in N. camurus, instead of 25-26%, and the upper jaw is usually 8-9% of standard length, instead of 8%. Thus it is clear that identification must rest on conformation and coloration. N. camurus has the depigmented caudal base, which N. whipplei lacks, and has a much blunter snout, although the Lower Mississippi form of N. camurus is less extreme in the latter character. Breeding males of N. camurus may be distinguished by their red dorsal and caudal fins, and by the lack of a hiatus between tubercles of head and snout (Fig. 2).

From Notropis spilopterus hypsisomatus, N. camurus may be identified by its 15 or 16 pectoral rays, instead of 13-15; by its larger upper jaw, usually 8-9% of standard length, instead of 7-8%; by its longer postdorsal length, usually 51-54% of standard length, instead of 48-51% (dorsal fin about equidistant between snout and caudal base); and importantly, by its nine anal rays, rather than eight. The blunt snout, depigmented caudal base, and tubercle characters by which N. camurus was distinguished from N. whipplei will also serve for N. spilopterus, and in addition, breeding male N. spilopterus have moderately large tubercles on the nape and notal ridge, and lack an enlarged dorsal fin.

N. v. venustus may be easily distinguished by the presence of its black caudal spot and eight anal rays, and by its lack of the contrasting black pigment of the posterior dorsal membranes or depigmented caudal base.

Description.—Teeth 1,4-4,1, hooked, the cutting surfaces narrow, concave, and with or without serrations. Anal rays 9, pectoral rays usually 15 or 16. Dorsal fin moderate in size in non-breeding adults, the third principal ray longest, the rays about equal in the depressed fin; origin about equidistant from tip of snout and caudal base.

THE AMERICAN MIDLAND NATURALIST

Exposed portions of lateral scales higher than wide. Lateral-line scales usually 36-38; predorsal circumferential scales 13-2-11, sometimes 15-2-11. It is worthy of note that a small number of collections show a departure from the count of 11 below the lateral line, which is so dominant in most of the species of *Cyprinella*. These collections have a majority of 12 and 13 counts. Caudal peduncle scales 7-2-5. Scales not crowded before dorsal.

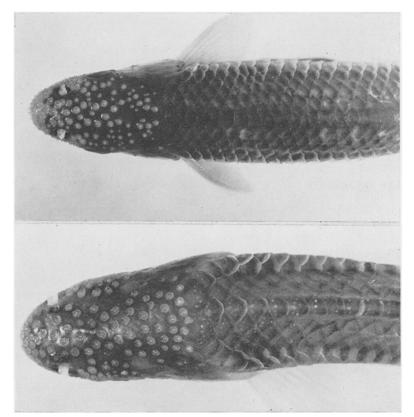


Fig. 2.—Typical breeding tubercle pattern on top of head and back in: (top) Notropis galacturus and (bottom) N. camurus. The absence of a hiatus between tubercles of snout and those of the top of the head is characteristic of these two species alone among the Cyprinella.

Head bluntly triangular. Orbit usually 7-8% of standard length, as long as snout or slightly shorter, $3\frac{1}{2}$ -4 in head. Snout quite blunt and rounded. Mouth terminal or subterminal, oblique, moderate in size, upper jaw usually 8-9% of standard length; the upper jaw usually reaches just behind the anterior margin of the orbit and is slightly longer than orbit.

Body moderately deep, usually 24-27% of standard length, somewhat compressed; caudal peduncle depth 11-13% of standard length. Lateral line slightly to moderately decurved from opercular margin to below posterior part of dorsal fin.

Breeding males with tubercles similar to N. galacturus. Head, snout and area between eye and snout with concentrations of scattered tubercles; no hiatus between those of head and snout. Two rows on each chin ramus. Nape tubercles very small, becoming almost invisible on the notal ridge before the dorsal fin. Tiny pearl organs over most body scales and on fin rays, following the branchings.

Coloration.—Lateral scales narrowly outlined in black, appearing diamond-shaped. An indistinct lateral stripe present on the posterior half of the body. A poorly-developed dark humeral bar present, extending from opposite upper opercular margin to base of pectoral fin. Dorsum with a narrow stripe before and after the dorsal fin, extending to the procurrent caudal rays. Venter immaculate below a scale row or two under the lateral line.

The depigmentation of the caudal base is not as well defined as it usually is in N. galacturus. Commonly it forms a light bar at the base of the caudal rays, flaring slightly dorsally and ventrally. Often it is a shallowly emarginate area, reminiscent of the basicaudal patches of N. galacturus.

The dorsal fin is well-pigmented on all its membranes from an early stage, the last two membranes prominently darker than the rest. The caudal fin is lightly pigmented except for the blanched base, and there is sometimes a row of pigment along some of the leading pectoral rays. The pelvics and anal are without melanophores.

Breeding males have red dorsal and caudal fins, and all fins are suffused with milky pigment.

Races.—Two distinct populations of Notropis camurus are known, one in tributaries of the Arkansas River, the other in Mississippi River tributaries in Mississippi. Tables I, II, IV indicate that a fairly wide divergence has taken place between these two populations. For example, a line drawn between 36 and 37 lateral-line scales results in an index of divergence of 76.3. A far greater proportion of Arkansas specimens have more than 13 predorsal circumferential scales above the lateral line than do Lower Mississippi fish. In proportional characters, the Lower Mississippi population tends toward a more streamlined form, approaching N. whipplei, rather than the straight contours of Arkansas River N. camurus. While body depth shows little difference, the caudal peduncle of the Lower Mississippi population tends to be less deep. Dorsal origin-lateral line is somewhat less in the Lower Mississippi forms than in those from the Arkansas, and both eye and upper jaw tend to average larger. By some standards, these two populations might be called subspecies,

			I	Predo	orsal	lengt	h			
River System	50	51	52	53	54	55	56	57	Ν	
N. galacturus										
White			8	4	3		1		16	
Tennessee-Cumberland	1	1	1	8	11	12	1	1	36	
N. camurus										
Osage		.			1	1			2	
Arkansas	2	6	14	4	1				27	
Lower Mississippi		2	6	6	4	1			19	
	46	47	$\frac{P}{48}$	ostdo 49	orsal 1 50	lengt 51	h52	53	54	
N. galacturus										
11. guiuoru/us										
White		1	4	5	6					
	 2	$\frac{1}{3}$	$\frac{4}{12}$	5 13	6 4	 2	····	····	 	
White	2					2	 	 	 	
White Tennessee-Cumberland	2					2 2 2	 	 	·····	
White Tennessee-Cumberland N. camurus	2 					_	 9	 4	 1	

TABLE III.—Frequency distribution of body proportions, expressed as per cent of standard length, of Notropis galacturus and N. camurus

TABLE III.--(continued)

			He	ad len	gth		
River System	23	24	25	26	27	28	Ν
N. galacturus							
White	1	6	5	4			16
Tennessee-Cumberland		4	14	15	3		36
N. camurus							
Osage				1	1		2
Arkansas	•		2	12	11	2	27
Lower Mississippi			2	7	6	4	19

		Caud	al ped	luncle	depth	
	9	10	11	12	13	N
N. galacturus	1 111 / · · · · · · · · ·					
White	2	13	1			16
Tennessee-Cumberland	1	18	17			36
V. camurus						
Osage					2	2
Arkansas				18	9	27
Lower Mississippi			8	11		19

TABLE IV.—Frequency distribution of body proportions, expressed as per cent of standard length, of Notropis galacturus and N. camurus

			-1	Body depth	lepth							δ	Orbit length	gth				
River System	19	20	21	22	23	24	25	26	27	28	29	30	z	9	7	8	6	z
N. galacturus White	5	4	æ	7	1	:	:	:	i	1	i	1	16	5	11	ŝ	1	16
Tennessee-Cumberland	:	1	10	12	10	3	1	1	:	:	:	:	36	5	26	8	:	36
N. camurus Osage	ł	i	i	ł	:	1		:	i	ł	ł	73	5		-	1	1	5
Arkansas	:	:	:	1	1	3	7	10	9	1	1	1	27	1	17	10	:	27
Lower Mississippi	!	:	:	1	1	4	ŝ	9	4	Ţ	;	:	19	:	ł	15	4	19
		Dorsal	Dorsal origin	- 1	1	Lateral line	line		• 1	Upper	Upper jaw length	length						
	12	13	14	15	16	17	18	19	z	7	8	6	z					
N. galacturus White	T	4	10	1	1	:	!	:	16	6	7	:	16					
Tennessee-Cumberland	1	0	19	12	5	-	:	:	36	7	27	2	36					
N. camurus Osage	I	1	1	1	1	1	i	5	5	:	1	5	5					
Arkansas Lower Mississinni	-			~	10 2	16 5	~	:	27 19	:	11	16 18	27 19					
Iddiserseitht IDMOR	:	:	-	,		,	:	:		:	-	2	21					

at least on the basis of the divergence in lateral-line scales. The mode of the Lower Mississippi population, however, overlaps the Arkansas population at a high point in the latter's distribution, so that actual separation would be quite difficult. In this study, therefore, the two populations are considered as races, the Arkansas Race and the Lower Mississippi Race.

A single sample from the Osage, a tributary of the Missouri River, falls extreme in many proportional characters, but is tentatively included in the Arkansas race. No data are available for the sparse material from the upper White River system, where N. camurus occurs with N. galacturus.

Range.—Upper Arkansas River and tributaries in Arkansas, Missouri, Oklahoma, Kansas and Colorado. Particularly abundant in the Neosho and Illinois Rivers. Rare in Osage River. Tributaries of the Lower Mississippi River in Mississippi and Louisiana.

Habitat.—Cross (1954: 309) states that the species in Kansas prefers moderately fast, clear water, and its abundance in the two Ozark streams, the Neosho and Illinois Rivers, would seem to bear this out. Moore (*in litt.*) however, has indicated that in the more westerly portions of its distribution, the species is found in warmer, more turbid waters. The habitat of the Lower Mississippi race has been described by Bailey and Taylor (1950: 37) in their discussion of Noturus (= Schilbeodes) hildebrandi. The race appears to favor those high gradient streams with clear waters and sandy bottoms, and probably will not be found in more sluggish, flood-plain tributaries.

Etymology.—The name *camurus* is apparently derived from the Latin *camur*, turned inward, in allusion to the blunt snout.

DISPERSAL AND SPECIATION IN THE COMPLEX

From the close relationship of N. camurus and N. galacturus, it seems obvious that they were derived from a common stock in the distant past. This stock was presumably divided into eastern and western portions, and the two species evolved (see Fig. 3).

Probably N. camurus was at one time far more widely distributed than at present, as indicated by the type locality in eastern Colorado, far west of the nearest recent record, and perhaps by the specimens in the White drainage, which may be remnants of a population which has been unable to meet competition successfully. The presence of the Lower Mississippi race may be evidence of a former occupation of much of the lower Mississippi Valley. It seems that the range of the species is contracting at present, and that the southwestern Ozark region is its stronghold. The precise competitive status of the Lower Mississippi race is too poorly known to permit speculation, but where it is found, the species seems to flourish.

GIBBS: STUDIES ON NOTROPIS

1961

N. galacturus probably differentiated in the Tennessee system, becoming adapted to the cool, mountain waters of the uplands. At a comparatively recent date, possibly when glacial effects brought about the presence of cool connections to the Arkansas, White and St. Francis systems, the species crossed the Mississippi and became established in cooler waters to the west. If it was ever present in the Arkansas, there is no longer any evidence, but it is possible that the

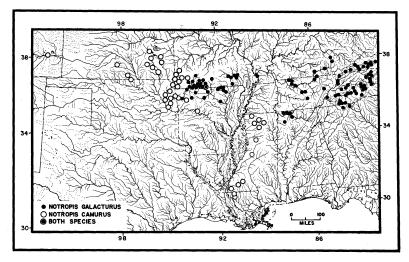


Fig. 3.—Distribution of collections examined of *Notropis galacturus* and *N. camurus*. Records of Ross and Perkins (1959) from the upper Kanawha system are not shown. Dotted line at right marks part of the divide between Tennessee and Atlantic coastal drainages.

warming following the last glacial period has caused a more extensive range to shrink, until it became confined to the faster, cooler portions of the White and St. Francis. That connections may be possible even at present between the populations east and west of the Mississippi is indicated by the collection of N. galacturus supposedly taken at Wyatt, Missouri, almost halfway between the two ranges, but much nearer the mouth of the Tennessee than that of the White.

The occurrence of N. galacturus in headwater tributaries of the Savannah and Santee systems is doubtless due to stream piracy across the Appalachian divide from Tennessee River tributaries. Ross and Perkins (1959) have recently reported the species from the upper New River in Virginia (Kanawha system). This is apparently due to piracy involving the New and upper Tennessee tributaries, both to the west of the east-west divide.

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