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STATUS, SUBSPECIES, AND VARIATIONS OF *NOTROPIS CUMMINGSAE*, A CYPRINID FISH OF THE SOUTHEASTERN UNITED STATES*

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INTRODUCTION AND ACKNOWLEDGMENTS

FOR many years it has been evident that the southeastern states of the United States constitute one of the most fertile fields for ichthyological discoveries. In each of the stream systems of that region the student of fishes may find new kinds, or new facts regarding the status, distribution, and life ways of forms already described. This is particularly true of the smaller fishes, including the almost endless array of shiners comprising the genus *Notropis*. In addition to the present paper dealing with the dusky shiner, *Notropis cummingsae* Myers, 3 reports on the southeastern species of *Notropis* have been prepared recently (Hubbs, 1941; Hubbs and Raney, 1947, 1948).

We wish to acknowledge especially the assistance of Reeve M. Bailey, curator of fishes, Museum of Zoology, University of Michigan, who made available the specimens under his care, some of which he and Marian K. Bailey had collected. He also provided certain fin ray counts and performed other services. Specimens of critical value were kindly furnished by Leonard P. Schultz, curator of fishes, United States National Museum, E. Milton Burton of the Charleston Museum, F. E. Guyton of the University of Alabama, Elmer E. Brown of Davidson College, Harry W. Freeman of the University of South Carolina (now at Stanford University), and Donald J. Ameel, now of Kansas State College. Other collections were made by Edwin P. Creaser and Herbert R. Becker, O. K. Fletcher, Jr. and W. H. Fletcher, William

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M. McLane and Gil Nelson, O. C. Van Hyning, and C. R. Aschemeir. To all of these collectors we express our gratitude. For aid in processing data we again owe thanks to Laura C. Hubbs.

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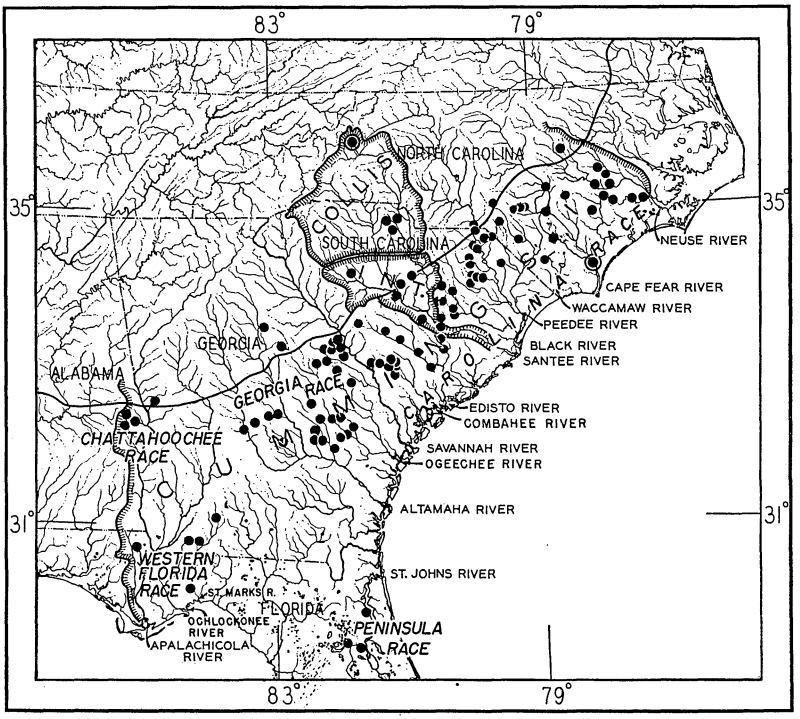
GENERAL DISTRIBUTION

In its various local forms *Notropis cummingsae* ranges from the Neuse River system in east-central North Carolina through the Cape Fear, Waccamaw, Peedee, Black, Santee, Edisto, Combahee, Savannah, Ogeechee, and Altamaha drainage basins of the Carolinas and eastern Georgia to the St. Johns River system in northeastern Florida and to the St. Marks, Ochlockonee, and Apalachicola River systems in western Florida, southwestern Georgia, and southeastern Alabama (Map 1). Like some other species it seems to avoid most of the Florida peninsula. Except in the Santee River system, where its upland subspecies, *N. c. collis,* ranges across the Piedmont into the Mountains, it is essentially a fish of the Coastal Plain (including the relatively low Tifton Upland), only rarely, locally, and to a limited distance passing above the Fall Line (Map 1). The habitats where the lowland subspecies has been taken 6 or 7 times just above the Fall Line, as mapped, are in no way unusual for this form. As a rule, the species inhabits more lowland waters in the north than in the south, much as do many other fishes, including, among Atlantic Coast species, the recently described darter, *Hadropterus notogrammus* (Raney and Hubbs, 1948: 21). The upland subspecies of *N. cummingsae,* however, occurs near the middle of the range of the species and the area of intergradation between the two subspecies appears to disrupt the range of the typical race of *N. c. cummingsae.*

Because of its habitat on the Coastal Plain, *N. cummingsae* has a distribution that usually complements that of the essentially Piedmont



Map 1. Record stations for *Notropis cummingsae* and distribution of the subspecies, intergrades, and races.

All records are original except that for the type locality of *N. c. cummingsae* and all are based on specimens examined. The type localities of the subspecies are indicated by ringed dots. The heavy line approximates the Fall Line (note that only 6 or 7 records of *N. c. cummingsae* lie slightly above the Fall Line). The hachured lines bound the northeastern and southwestern known limits of the range of *N. c. cummingsae* and enclose the inferred ranges of the intergrades and of *N. c. collis*. The races are only provisionally recognized. The figure is based on a section of an outline drainage map of the United States prepared by Walter Johnson and others under the direction of the senior author, as a modification of the United States Geological Survey base map, and printed for the University of Michigan Museum of Zoology in July, 1940. Final drafting of this figure was by Norman J. Wilimovsky, with additions by William L. Cristanelli, Donald B. Sayner, and William L. Brudon. The trivial name has now been emended to *cummingsae*.

species, *N. altipinnis*. In 2 regions, however, the species occur together. In the Neuse River system, where *N. altipinnis* occupies a Coastal Plain habitat, the local subspecies, *N. a. neusensis,* lives with *N. c. cummingsae*. In the upper part of the Santee River system, where *N. cummingsae* takes to the hills, its upland form, *N. c. collis,* occurs with *N. altipinnis wrighti*. In both areas of cohabitation the representatives of the 2 species look surprisingly alike, so much so that some degree of introgressive hybridization (Anderson, 1949) is suggested, though no evidence was found of hybridization or intergradation at the present time. The similarity, however, may merely reflect like responses to the same environment.

SUBSPECIATIONAL PATTERN

Like a number of other southeastern fresh-water fishes, including *Notropis altipinnis* (Hubbs and Raney, 1948), *N. cummingsae* is divisible into subspecies. The pattern of subspeciation, however, contrasts with that of *N. altipinnis*. In harmony with their upland habitats, the local forms of *altipinnis* are stream-system isolates, whereas in *cummingsae* the sharpest segregation is altitudinal. In *altipinnis* the subspecific intergradation involves characters only, for no interbreeding is possible; subspecies status is justified by the inference that differentiation has not become complete. Within *cummingsae,* in contrast, a real intergradation takes place in the lower elevations of the Santee River system, to which the upland subspecies and the intergrades seem to be confined. There is evidence of some altitudinal variation also within the Apalachicola River system, but this differentiation is now interpreted as being below the subspecies level.

The contrast between *cummingsae* and *altipinnis* in respect to geographical variation does not appear to be complete, however, for there are indications of at least racial differentiation between the populations of certain groups of stream systems. Thus, the series from the Neuse to the Combahee, those of the Savannah, the Ogeechee, and the Altamaha, those from peninsular Florida, and the 2 types from the western limits of the species all show average differences that appear more or less definitely to indicate distinct raciation (pp. 12–16).

The pattern of the subspecies now recognized in *Notropis cummingsae* very strikingly parallels the probably subspecific differentiation in *Hadropterus notogrammus,* a percid fish occurring farther north along the Atlantic Coast (Raney and Hubbs, 1948: 20–26, Map 1). Each species has a wide-ranging coastal form, with an upland representative in a single major stream system. In both species the

character gradient is in the expected direction. In the darter (*H. notogrammus*) the upland form, as would be expected in a fish of cool swift waters, has an increased number of scales and rays in the vertical fins. In the shiner the number of anal rays decreases in the upland forms following a variational pattern that is exhibited by a number of American cyprinids, notably *Richardsonius* and *Notemigonus* (Hubbs, 1926: 67; Schultz, 1927).

LOWLAND DUSKY SHINER

Notropis cummingsae cummingsae Myers
(Pl. I, Figs. 1–2; Map 1)

Notropis cummingsi.—Myers, 1925: 1–4, Fig. 1 (original description; habitat; associates). Fowler, 1945: 114 (paratype compared with *N. hypselopterus*). Hubbs and Raney, 1948: 7–9 (close resemblance to the Neuse subspecies of *N. altipinnis;* Coastal Plain in Neuse River system).

Cyprinella cummingsi.—Jordan, 1929: 80–82 (compiled).

Hybopsis cummingsi.—Jordan, Evermann, and Clark, 1930: 133. Schrenkeisen, 1938: 138 (compiled).

As indicated in the preceding synonymy, *N. c. cummingsae* has been known only from Myers' description of the type specimens from Burnt Mill Creek, Wilmington, North Carolina; from a brief statement by us, anticipating a conclusion elaborated below; and from some remarks by Fowler, based on a paratype. The other references have been in check lists and manuals, in which the species has been referred to genera into which some recent authors have uncritically divided *Notropis.* This disruption of the genus does not appear to be wise or justified, at least until the whole group has been more thoroughly studied and revised.

The trivial name is emended to *cummingsae* to conform with a recent ruling of the International Commission on Zoological Nomenclature *(Bull. Zool. Nomen.,* 4: 68, 206–7). Myers definitely indicated that the species was "named for Mrs. J. H. Cummings."

Material and Range

We can now show that *N. c. cummingsae* has an extensive range in the Austroriparian region. A total of 3,150 specimens from 93 localities was examined.

List of New Material of Notropis cummingsae cummingsae

The new material of *N. c. cummingsae* includes all that is known except for the single type lot, which has also been examined. Most

of the specimens are deposited in the University of Michigan Museum of Zoology and in the Cornell University collections. Others are in the United States National Museum, Charleston Museum, and University of Florida. We have examined all material listed. The locations are all plotted on Map 1. In parentheses are indicated the number of specimens and the range of standard lengths in millimeters. In addition to standard compass directions, with the following "of" deleted, these abbreviations are used: Br. = branch, Co. = county, Cr. = creek, L. = lake, mi. = mile or miles, R. = river, trib. = tributary (of).

Neuse River System, North Carolina.—Wake Co.: Buffalo Cr., 0.5 mi. W. Wendell (1, 38). Wayne Co.: Walnut Cr., 7 mi. WNW. La Grange (6, 38–44); Brooks Swamp, 3.5 mi. N. Mt. Olive (65, 22–51); Nahunta Swamp, 1 mi. N. Pikeville (70, 30–54). Lenoir Co.: Falling Cr., 6 mi. W. Kinston (1, 34); headwaters, Trent R., 1 mi. S. Deep Run (16, 30–54). Craven Co.: tribs. Trent R., 4.5 and 7 mi. WSW. New Bern (25, 34–45). Wilson Co.: Black Cr., 9 mi. N. Fremont (35, 30–54).

Cape Fear River System, North Carolina.—Sampson Co.: trib. Great Coharie R., 4 mi. S. Newton Grove (60, 35–53). Duplin Co.: trib. Northeast Cape Fear R., 1 mi. N. Kenansville (3, 31–35). Cumberland Co.: trib. South R., 1 mi. S. Stedman (10, 28–42); trib. Little Rockfish Cr., 9 mi. W. Fayetteville at State Fish Hatchery (3, 17–39). Bladen Co.: Hammond Cr., trib. Cape Fear R., 1 mi. S. Elizabethtown (66, 18–51). Hoke Co.: tribs. Rockfish Cr., 4.8 mi. NE. Raeford (5, 25–42), and 6 mi. W. Hope Mills (5, 45–51). Harnett Co.: Stuarts Cr., 2 mi. W. Erwin (12, 22–44).

Waccamaw River System, North Carolina.—Columbus Co.: trib. White Marsh, 4 mi. SW. Clarkton (3, 41–42).

Peedee River System, North Carolina and South Carolina.—Moore Co., N. C.: trib. outlet of Aberdeen L., 0.2 mi. S. Aberdeen (98, 25–55). Richmond Co., N. C.: Mark Cr. at Evers Mills (2, 41–44). Scotland Co., N. C.: Drowning Cr., 11 mi. NE. Laurinburg (2, 46–47). Robeson Co, N. C.: Bear Cr., 10 mi. W. Lumberton (4, 40–49). Florence Co., S. C.: Middle Swamp, 3 mi. S. Florence (18, 33–38); Sparrow Swamp, 1 mi. W. Timmonsville (87, 26–50); trib. Jeffreys Cr., 6 mi. SW. Florence (46, 24–54); Jeffreys Cr., 4 mi. W. Florence (34, 22–44). Chesterfield Co., S. C.: trib. Peedee R., 2 mi. NW. Society Hill (96, 22–50). Darlington Co., S. C.: tribs. Peedee R. at Society Hill (57, 28–46) and 11 mi. SW. Society Hill (3, 25–42); trib. Black Cr., 6 mi. NW. Darlington (7, 31–48). Dillon Co., S. C.: Catfish Cr., 1 mi. SW. Latta (125, 29–56). Marlboro Co., S. C.: Beaver Dam Cr., 1.2 mi. NE. McColl (85, 21–60); Whites Cr., 5.5 mi. N. Cherow (1, 50); Crooked Cr., 6 mi. NW. Bennettsville (24, 36–50).

Black River System, South Carolina.—Sumter Co.: 4 mi. W. Sumter (1, 42); trib. Pocotaligo R., 1 mi. W. Sumter (33, 38–49). Sumter–Lee Co. line: Black R., 1 mi. N. Mayesville (27, 29–42). Lee Co.: trib. Black R., 11.3 mi. SW. Bishopville (7, 35–40). Clarendon Co.: tribs. Pocotaligo R. near Alcohe (4, 34–40) and at Manning (2, 38–45); trib. Black R., 2.2 mi. S. Paxville (26, 17–45).

Edisto River System, South Carolina.—Colleton Co.: near Edisto R. at Weeks (Canadys) (15, 37–43). Orangeburg Co.: Goodland Cr., trib. South Edisto R. near Springfield (22, 27–51); tribs. Edisto R. at Branchville (58, 25–49) and 10.3 mi. SW.

Orangeburg (59, 18–57); tribs. Four-Hole Swamp, 5.6 mi. S. Santee (2, 34–40) and 8 mi. S. Santee (35, 23–43). Aiken Co.: Shaws Cr., 4 mi. N. Aiken (18, 30–55).

Combahee River System, South Carolina.—Allendale Co.: trib. Jackson Br., 1.8 mi. S. Sycamore (242, 22–48); trib. Salkehatchie R., 3.4 mi. S. Ulmers (78, 26–52). Barnwell–Bamberg Co. line: trib. Salkehatchie R., 2.6 mi. W. Olar (137, 15–46). Bamberg Co.: trib. Salkehatchie R., 2 mi. S. Olar (138, 19–35).

Savannah River System, South Carolina and Georgia.—Allendale Co., S. C.: tribs. Lower Three Run, 3.6 mi. NW. Appleton (57, 26–43) and 4 mi. NW. Martin (137, 29–48). Richmond Co., Ga.: trib. McBean Cr., 15 mi. S. Augusta, 2 mi. SE. Hepsibah (18, 16–28); Rocky Cr. just below New Savannah Road, about 5 to 8 mi. S. Augusta (38, 24–42); drainage ditch, 4.5 mi. S. Augusta (27, 18–38); trib. Butler Cr., 1 mi. SW. Augusta city limits on U. S. Route 1 (137, 26–43); Boggy Gut Cr., 9 mi. NE. Wrens (90, 20–46); Spirit Cr., 11 mi. SW. Augusta (76, 25–37). Jefferson Co., Ga.: Brushy Cr., 1 mi. S. Wrens (3, 30–44).

Ogeechee River System, Georgia.—Jefferson Co.: Big Cr., 6 mi. S. Wrens (4, 31–40). Burke Co.: Rocky Cr., 9.8 mi. E. Vidette (26, 18–38). Candler Co.: Fifteen Mile Cr., 3.5 mi. W. Pulaski (21, 19–32); Canoochee R., 5 mi. W. Metter (2, 22–23). Bullock Co.: Lotts Cr., 7.4 mi. S. Statesboro (11, 22–32). Hancock Co.: trib. Ogeechee R., 1.7 mi. E. Sparta (4, 37–46). Evans Co.: trib. Canoochee R., 1 mi. NW. Claxton (36, 19–33). Evans–Bryan Co. line: Canoochee R., 2.3 mi. W. Grovel (2, 27–31).

Altamaha River System, Georgia.—Pulaski Co.: Town Cr., trib. Ocmulgee R. at N. limits of Hawkinsville (3, 17–32). Bleckley Co.: trib. Little Ocmulgee R. about 3 mi. E. Cochran (1, 30). Laurens Co.: Rocky Cr., 2 mi. from Bleckley Co. line, near Dudley (17, 23–33); Hunger and Hardship Cr., 5 mi. SW. Dublin (20, 20–33). Emanuel Co.: Ohoopee R. about 15 mi. S. Swainsboro (1, 19); Little Ohoopee R., 9.2 mi. W. Swainsboro (2, 14–27). Greene Co.: Richland Cr., 1.5 mi. W. Greensboro (29, 21–30). Toombs Co.: Swift Cr., 1.5 mi. N. Lyons (6, 17–23); Rocky Cr., 6 mi. SW. Lyons (6, 16–19); trib. Ohoopee R., 3.1 mi. S. Lyons (17, 33–40). Telfair Co.: Little Ocmulgee R., 1.2 mi. N. McRae (6, 22–28). Tatnall Co.: Brazells Cr., 2.3 mi. W. Reidsville (101, 30–46).

St. Johns River System, Northeastern Florida.—Marion Co.: Oklawaha R. at Davenport Landing, about 7 mi. from mouth (8, 19–26); trib. Oklawaha R., 1 mi. W. Orange Springs (6, 19–36). Clay Co.: Clark Cr., 7.3 mi. N. Bostwick (1, 23).

St. Marks River System, Western Florida.—Wakulla Co.: Wakulla R. near Wakulla Springs (4, 20–31).

Ochlockonee River System, Southwestern Georgia.—Grady Co.: trib. Ochlockonee R., 1.6 mi. E. Cairo (131, 19–39); Attapulgus Cr., 3. mi. E. Climax (9, 21–38). Colquitt Co.: Bridge Cr., 4.1 mi. W. Funston (1, 30).

Apalachicola River System, Lower Part, Florida.—Jackson Co.: Spring Cr., 3 mi. SE. Marianna (5, 23–35).

Apalachicola River System (Chattahoochee River Division), Georgia and Alabama.—Harris Co., Ga: Standing Boy Cr., 2.5 mi. SW. Cataula (2, 34–42). Russell Co., Ala.: Watoolee Cr., trib. Uchee Cr., S. Marvyn (1, 39); Brush Cr., trib. Uchee Cr., S. Marvyn (90, 24–43); Uchee Cr. at Marvyn (8, 26–42).

Habitat

This shiner inhabits various types of streams on the Coastal Plain. It is not confined to swift unstained waters like those of Burnt Mill Creek where the types were secured (Myers, 1925: 3). Some specimens were seined over sand and gravel on riffles, but most were secured over silt-covered detritus and sand in quiet waters or in schools below trailing aquatic weeds in moving water. The color of water was noted as slightly brownish to almost black. Aquatic vegetation grew at some of the collecting stations. Like most other kinds of *Notropis, N. c. cummingsae* is gregarious. It is often seen in schools of more than 100 individuals.

Relationships

In the maze of species groups that constitute *Notropis* the relationships of *N. cummingsae* are not very obvious. In general appearance it simulates *N. altipinnis,* with which it is compared below, and other kinds having 2, 4–4, 2 teeth, but Myers gave the dental formula as 1, 4–4, 1. For 57 specimens taken throughout its range we count (from left to right): 1, 4–4, 1 in 50; 0, 4–4, 1 in 3; 1, 4–4, 0 in 3; and 1, 4–3, 0 in 1 (the one with only 3 teeth on the right side, a most unusual number, shows no sign of a missing alveolus or gap, and the 3 teeth are sufficiently broad-based to fill the dentigerous space). There is little similarity in specific characters between this species and any previously described form having 1, 4–4, 1 as the usual tooth complement.

Most shiners that have a definite blackish band like that of *cummingsae* differ in having 2, 4–4, 2 teeth. The several species of the *N. hypselopterus* group, which agree with *cummingsae* in having a broad dark lateral stripe, differ in having considerable dark pigment on the dorsal and anal fin membranes; they also differ in many other respects. Contrary to the statements usually seen in the literature, the members of the *hypselopterus* group have been found by Royal D. Suttkus to have the teeth normally 2, 4–4, 2, and occasionally 1, 4–4, 1. Fowler (1945: 114) compared *cummingsae* only with *N. hypselopterus* (Günther), but these species are neither similar in appearance nor close in relationship.

In the typical number (10 or 11) of anal rays (Table I), *N. c. cummingsae* differs sharply from the black-striped shiners with 4–4 teeth, such as *N. alborus* Hubbs and Raney (1947), which has 7 anal rays. The high number of anal rays likewise distinguishes *N. c. cummingsae* from *N. chalybaea* (Cope), which usually has 8 anal rays and 2, 4–4, 2

teeth, and from *N. petersoni* Fowler (1942: 1–2, Figs. 1–2), which has 7 anal rays and either 1 or 2 teeth in the lesser row. Two nominal species that we surmise are synonyms of *N. petersoni,* namely *N. norrisi* Fowler (1945: 235, Figs. 114–16) and *N. williami* Fowler (1945: 236, Figs. 117–19), were described as having a dark lateral stripe and as having the teeth, respectively, 1?, 4–4, 1? and 1, 4–4, 1, and the anal rays only II, 6 or II, 7 and III, 6 (presumably equivalent to 7 or 8, and 7 principal rays).

N. cummingsae collis, which usually has 9 anal rays, differs less sharply in this one respect from the species mentioned.

Notropis c. cummingsae differs otherwise from *N. chalybaea,* with which it often occurs. The distal margin of the anal fin is distinctly instead of scarcely concave. The other fins are more rounded. The fins are all shorter and the height of the dorsal is less than the head length, rather than being equal to or greater than that measurement. The dorsal origin is nearer to the caudal base than to the tip of the snout, rather than equidistant between those points or, as is usual, nearer the snout tip. The lateral stripe is broader, is less sharply limited below, and passes well below the lateral line at its lowest extent. The narrower and usually blacker stripe of *chalybaea,* in contrast, is sharply delimited and passes below the lateral line only where the black specks cluster about the lateral-line pores. The basicaudal spot of *cummingsae,* instead of ending abruptly, streaks backward on the membranes. On the opercle the stripe extends well below the middle in *cummingsae* but is limited to the upper half in *chalybaea.* The breast and the belly are immaculate or have few small scattered chromatophores, whereas in *chalybaea* these parts have many large melanophores. The underside of the caudal peduncle bears few scattered chromatophores, rather than numerous conspicuous specks that are more or less continuous in 2 lines on the anterior two-thirds of the peduncle.

Notropis cummingsae is probably most intimately related to *N. ortenburgeri* Hubbs, a species of western Arkansas and eastern Oklahoma (Hubbs, in Ortenburger and Hubbs, 1927: 127; Hubbs and Ortenburger, 1929: 72–73). The two agree closely in size, pigmentation, physiognomy, proportions, and ray counts. The most notable difference is in dentition, for *ortenburgeri* consistently has only 4–4 teeth. In this respect it departs further from expectation than does *cummingsae,* for nearly all species of *Notropis* with the external characters of *cummingsae* and *ortenburgeri* have 2, 4–4, 2 teeth. Within the *Notropis* complex such indications of relationship minimize the probable taxonomic significance of the number of teeth in the lesser row.

Comparison with Notropis altipinnis

In many respects *N. c. cummingsae* agrees closely with *N. altipinnis* (for synonymy, characters, and range see Hubbs, 1941, and Hubbs and Raney, 1948). In general coloration and in number of anal rays they are very similar. Attention to detail, however, brings out numerous differentiae in addition to the dental distinction already indicated.

Some of the best differences are in mouth structure. The gape is less oblique in *cummingsae* than in *altipinnis*. The upper lip averages thicker and is hooked slightly downward anteriorly. The lower jaw is not hooked upward as it is, more or less, in *altipinnis*. As seen from the front, the mouth is more broadly U-shaped. These distinctions are not very striking, though they are still evident, at least on the average, when the Neuse River race of *N. altipinnis (neusensis)* is compared with *N. cummingsae*. The angle between the edge of the premaxillary and the top of the head, which in 35 adults of *N. c. cummingsae* varies from 45° to 62°, with an average of 56°, is generally less than in most forms of *N. altipinnis* (Hubbs and Raney, 1948: 9).

The fins are usually shorter and more rounded in *N. c. cummingsae* than in *N. altipinnis*. *N. a. neusensis*, however, differs little from *cummingsae* in this respect. For this character the sexes should be compared separately because in both species, as is usual in minnows, the males have higher and sharper fins than do the females.

The nuptial tubercles are coarser in *N. c. cummingsae* than in *N. altipinnis* and are differently arranged. The distinctions will be appreciated on comparing the following description of the tubercles in *cummingsae* with the detailed account of these structures in *altipinnis* (Hubbs, 1941: 171). In *N. c. cummingsae* the tubercles are enlarged on the muzzle, especially in a definite row along the edge of the snout. Those on the mandible are also somewhat enlarged. The largest mandibular tubercles, pointing somewhat outward, border the outer edge of each ramus. On the pectoral rays they are uniserial toward the extreme base, elsewhere biserial. In each series there are about 3 pointed tubercles on each ray segment. Minute tubercles are scattered along the dorsal and pelvic rays, often several per segment.

The lateral band is wider in *N. c. cummingsae* than in *N. altipinnis*. It covers most of the opercle and extends as a solid band below the lowest part of the lateral line. In *altipinnis*, in contrast, the band is restricted to the upper half of the opercle and extends below the lateral line only where melanophores are clustered about the lateral-line pores. In the more typical races of *altipinnis* the band does not even reach the lateral line where it is arched downward.

The pigmentation on the top of the head is less variegated than in *N. altipinnis,* and the snout is lighter in the ring adjoining the nostrils. *N. c. cummingsae* lacks the dark blotch that is developed on the middle of the front of the snout in *altipinnis. N. a. neusensis,* however, approaches *N. c. cummingsae* in this character also, but the distinction is not obliterated.

There are also differences in the detailed pigmentation of the body. The median predorsal dark streak is rather well developed in *N. c. cummingsae* but is weak to obsolete in *N. altipinnis.* The lower edge of the caudal peduncle bears a number of scattered melanophores in *N. c. cummingsae* but usually few to none in *N. altipinnis.* This distinction largely breaks down in the Neuse River system. The region about the front of the anal fin and about the anus is deeply charged with black pigment in *N. c. cummingsae* instead of being nearly or quite clear. In this feature, too, *N. altipinnis neusensis* approaches *N. c. cummingsae* but remains separable.

It will be clear from the foregoing comparison that the Coastal Plain form, *N. c. cummingsae,* differs sharply and very obviously from the essentially Piedmont species, *N. altipinnis,* but that the distinction is impaired in the Neuse River system, where *N. a. neusensis* occurs on the Coastal Plain in company with *N. c. cummingsae.* The 2 species also show superficial similarity where a subspecies of *N. cummingsae (collis)* lives with *N. altipinnis wrighti* in the uplands of the Santee River system. The differentiation in external features is not completely broken down, however, and all specimens of *cummingsae* and *altipinnis* in the restricted areas of joint occurrence are separable on close scrutiny. Their specific rather than subspecific separation is therefore indicated. The diagnosis based on characters of pigment and form is confirmed by an examination of the pharyngeal teeth, for the aberrant subspecies of *altipinnis* in the Neuse system retains the dental formula 2, 4–4, 2, and *N. c. collis* has 1, 4–4, 1 teeth.

Other Characters

Notropis c. cummingsae is a small shiner, rarely if ever attaining a total length of 3 inches. The largest of the 3150 specimens examined is only 60 mm. in standard length.

Proportional measurements, taken to correspond with those given by Hubbs (1941) for *N. altipinnis* and *N. scepticus* and by Hubbs and Raney (1948) for the subspecies of *N. altipinnis,* are given in Table IV. Fin rays in 20 specimens from various localities are: dorsal, 8 in

all; pectoral, 14–14 to 16–16 (average 14.6); pelvic, 8–8 (rarely 7–7 or 9–9, less rarely 8–9 or 9–8). Anal ray counts are detailed in Tables II and III.

TABLE I

FREQUENCY DISTRIBUTION OF LARGEST SPECIMEN IN EACH COLLECTION OF NOTROPIS CUMMINGSAE

Subspecies and Race	Standard Length in mm.				
	15–24	25–34	35–44	45–54	55–64
Notropis c. cummingsae					
Carolina	..	5	24	21	2
Georgia	4	12	9	4	..
Peninsular	1	1	1	..	..
Western Florida	..	2	3	..	..
Chattahoochee	..	..	4	..	..
Intergrades	..	2	2	3	..
Notropis c. collis	..	1	3	..	..

The nuptial colors, as indicated by a specimen taken in Alabama on May 10, 1939, and examined after 14 days in formalin, are only moderately bright. There is some pale orange on the caudal lobes and a trace of orange on the dorsal rays. The back is waxy green, with a deep-lying wash of pale orange just above the dark stripe. The blackish lateral stripe and the adjacent parts of the silvery white lower trunk are washed with purplish rose. In live specimens from North Carolina, the dark lateral stripe is greenish and is paralleled above by a narrow orange stripe.

Females average larger and stouter than males. The collection from Rocky Creek, near Augusta, Georgia, taken April 27, 1941, contained 16 nuptial males 30 to 38 mm. in standard length, averaging 34.1 mm., and 20 gravid females 32 to 42 mm. long, averaging 37.0 mm.

Geographical Variation

Even after the separation of the upland subspecies, *N. c. collis,* described below, *N. c. cummingsae* remains a complex of local forms, most or all of which are probably genetic races. Some of these stocks may warrant subspecific separation after the rich cyprinid fauna of the southeast has been subjected to more critical study. Five such races are provisionally recognized:

CAROLINA RACE.—In the stream systems from the Neuse in North Carolina to the Combahee in South Carolina, *N. cummingsae* is characterized by the comparatively large size attained (Table I), the high

average number of anal rays (Tables II and III), and the relatively robust build and dark color (Pl. I, Figs. 1–2). The largest specimen in each collection is nearly always more than 34 mm. long (standard length) and is usually 45 to 54 mm. long in a series of 5 or more specimens. The anal rays frequently number 11, occasionally 12, with a grand average of 10.28 and with means for stream systems ranging from about 10.3 to 10.4, except in the Edisto Basin. The specimens from that stream system, next to the southernmost in the range of this race, almost equal those from the Georgia streams in having an average of only 10.12 anal rays, but in size and appearance they more closely resemble the examples from streams farther north.

GEORGIA RACE.—The 897 specimens from the Savannah, Ogeechee, and Altamaha river systems in Georgia are smaller on the average than

TABLE II

NUMBER OF ANAL RAYS IN NOTROPIS CUMMINGSAE
Consistency within certain stream systems is indicated in Table III.

Subspecies, Race, and Stream System	Number of Anal Rays							
	8	9	10	11	12	No.	Mean	SE
N. c. cummingsae	1	193	2102	815	39	3150	10.22	.01
Carolina race	1	96	1260	597	33	1987	10.28	.01
Neuse River	..	5	134	75	4	218	10.36	.04
Cape Fear River	..	6	94	67	6	173	10.42	.05
Waccamaw River	..	..	2	1	..	3	10.33?	..
Peedee River	..	49	431	195	14	689	10.25	.02
Black River	..	1	56	41	2	100	10.44	.06
Edisto River	1	12	157	38	1	209	10.12	.03
Combahee River	..	23	386	180	6	595	10.28	.02
Georgia race	..	72	676	147	2	897	10.09	.02
Savannah River	..	49	449	84	1	583	10.06	.02
Ogeechee River	..	10	77	18	1	106	10.09	.05
Altamaha River	..	13	150	45	..	208	10.15	.03
Peninsular race								
St. Johns River	..	1	12	2	..	15	10.07	.12
Western Florida race ...	..	6	75	65	4	150	10.45	.03
St. Marks River	..	..	1	3	..	4	10.75?	..
Ochlockonee River ..	..	6	71	60	4	141	10.44	.05
Lower Apalachicola R.	..	..	3	2	..	5	10.40?	..
Chattahoochee race								
Chattahoochee River ..	..	18	79	4	..	101	9.86	.04
All races except								
Chattahoochee	1	175	2023	811	39	3049	10.23	.01
Intergrades								
Santee River System ..	..	28	40	5	..	73	9.68	.07
6 small collections ...	..	5	4	1	..	10	9.60	.22
2.8 miles W. Summerton	..	23	36	4	..	63	9.70	.07
N. c. collis	1	30	3	..	..	34	9.06	.06
Grand total for species	2	251	2145	820	39	3257	10.20	.01

the Carolina specimens (Table I). They are relatively frailer, deeper bodied, and usually paler than examples of the Carolina race. Since nearly all this material came from the Tifton Upland, where most of the streams are relatively clear and sandy, the small size, wafery build, and palish color may be, in part at least, the direct imprint of the environment. The anal rays are seldom 11 and average 10.09.

On the basis of the anal ray counts alone a subspecific separation of the Carolina and Georgia races is not admissable. On the basis of other characters, such as size, deepness of pigmentation, and general fragility, a subspecies separation might appear warranted, should it appear highly probable that these differences are genetic.

PENINSULAR RACE.—In their small size, large eyes, fragile structure, and in their low average number (10.07) of anal rays, the 15 specimens from the St. Johns River system in Florida resemble the Georgia stocks, but differ in being very dark and in having dark flecks on the lower sides (perhaps a purely environmental response). The large melanophores that are scattered over the peritoneum of all the races show through the body wall in the Florida specimens.

WESTERN FLORIDA RACE.—The 150 specimens from the St. Marks and lower Apalachicola river systems in western Florida and from the Ochlockonee River system in southwestern Georgia, just north of western Florida, seem to be intermediate between the Georgia and Carolina races in size (Table I) and general appearance, but have the anal rays at least as numerous, on the average (10.45), as in the Carolina stocks. They have none of the characteristics of the Chattahoochee race. Material is inadequate to show whether the forms in the St. Marks and the lower Apalachicola river systems differ from the Ochlockonee type, which alone is well represented by specimens.

CHATTAHOOCHEE RACE.—Most distinctive among the races left in *N. c. cummingsae* is one represented by 3 series from the basin of Uchee Creek, eastern Alabama, and by 1 series from Standing Boy Creek, Georgia, all in the Fall Line Hills section (Fenneman, 1938: 67, Fig. 21) of the Chattahoochee River division of the Apalachicola River system. The specimens of this race have on the average a deeper and thicker body and a deeper caudal peduncle than do those from other stream systems. They also show a reduced average number of anal rays (Table II). In this respect they approach *N. c. collis*, no doubt as the result of independent variation. There are also suggestions of aberrancy in other proportional measurements (Table IV). It is not certain, however, that the robust body and other differential propor-

TABLE III

RELATIVE STABILITY IN NUMBERS OF ANAL RAYS OF NOTROPIS C. CUMMINGSAE WITHIN CERTAIN STREAM SYSTEMS

Localities are specified in more detail on pages 6–7. Counts for small series are deleted from this table but are included in the compilations in Table II.

Race, River System, and Locality	Number of Anal Rays							
	8	9	10	11	12	No.	Mean	SE
Carolina race								
Neuse River System, N.C.								
Trent River tributaries	..	..	25	15	..	40	10.37	.10
Brooks Swamp	..	3	37	25	..	65	10.34	.07
Nahunta Swamp	..	1	40	26	3	70	10.44	.07
Black Creek	..	1	24	9	1	35	10.29	.10
Cape Fear River System								
Trib. of Great Coharie R.	..	2	32	25	1	60	10.42	.08
Hammond Creek	..	3	41	20	2	66	10.32	.08
Peedee River System								
Outlet of Aberdeen L.	..	7	64	25	2	98	10.22	.06
Sparrow Swamp	..	6	57	19	5	87	10.26	.07
Trib. of Jeffreys Creek	..	3	26	16	1	46	10.33	.09
Jeffreys Creek	..	4	18	11	1	34	10.26	.12
Tribs. of Peedee River								
NW. of Society Hill	..	4	58	34	..	96	10.31	.06
At Society Hill	..	2	41	14	..	57	10.21	.06
Catfish Creek	..	11	80	33	1	125	10.19	.05
Beaver Dam Creek ..	..	7	50	25	3	85	10.28	.07
Black River System								
Trib. of Pocotaligo R., Sumter County	..	1	17	15	..	33	10.42	.10
Black River	..	..	17	8	2	27	10.44	.12
Trib. of Black River, Clarendon County..	..	..	14	12	..	26	10.46	.10
Edisto River System								
Tribs. of Edisto River								
At Branchville	..	4	43	11	..	58	10.12	.07
Trib. of Edisto River SW. of Orangeburg	..	2	44	12	1	59	10.20	.07
Trib. of Four-Hole Swamp	1	5	22	7	..	35	10.00	.12
Combahee River System								
Trib. of Jackson Br...	..	15	163	60	4	242	10.22	.04
Tribs. of Salkehatchie R.								
South of Ulmers ...	..	3	47	28	..	78	10.32	.06
West of Olar	..	3	88	45	1	137	10.32	.04
South of Olar	..	2	88	47	1	138	10.34	.04
Georgia race								
Savannah River System								
Tribs. of Lower Three-Run								
Near Martin	..	3	104	29	1	137	10.20	.04
Near Appleton	..	3	46	8	..	57	10.09	.06
Spirit Creek	..	4	55	17	..	76	10.17	.06
Boggy Gut Creek	..	11	65	14	..	90	10.03	.05
Trib. of Butler Creek	..	18	107	12	..	137	9.96	.04
Trib. of McBean Creek	..	6	65	11	..	82	10.06	.05
Rocky Creek	..	8	27	3	..	38	9.87	.09
Ditch near Augusta ..	..	1	26	..	..	27	9.96	.04
Ogeechee River System								
Trib. of Canoochee R.	..	3	28	4	1	36	10.08	.09
Rocky Creek	..	1	21	4	..	26	10.12	.08

tions are of racial rather than direct environmental basis. Were it not for this doubt, we would probably describe this race as another distinct subspecies.

The geographical variation in the average number of anal rays (Tables II and III) seems to have an environmental correlation even within *N. c. cummingsae*. Toward the western limits of the species, for example, there seems to be a marked upstream reduction in the average number (from 10.45 to 9.86), which parallels the distinction between the lowland Carolina race (averages from 10.12 to 10.44) and the upland subspecies, *N. c. collis* (average 9.06). In correlation with the slight reduction in the average number of anal rays in the sandy waters of the Savannah and Altamaha systems, these streams are of a more upland and presumably of a cooler type than are those of the Carolina lowlands. In fact, most of the collections of this race have come from a slightly elevated region that has been named the Tifton Upland (Fenneman, 1938: 40–42, 68, 77–79, 118, Figs. 15, 21; Pl. 3). The 15 specimens from the St. Johns River system in Florida yield an average of only 10.07 rays, and it may be significant that the stream in which most specimens were taken, the Oklawaha River, originates in a giant spring. Within stream systems from North Carolina to Georgia, below the Fall Line, the number of rays is rather constant (Table III).

The most obvious geographical variant in the species, the upland form of the Santee River system of South Carolina and North Carolina, obviously warrants subspecific separation and is defined as:

UPLAND DUSKY SHINER

Notropis cummingsae collis, new subspecies

(Plate I, Fig. 3; Map 1)

The type material comprises 34 specimens from 5 localities. In addition, 73 examples in 7 collections are regarded as intergrades, *Notropis cummingsae: collis* × *cummingsae*. All known material is deposited in the University of Michigan Museum of Zoology (UMMZ), Cornell University (CU), and the Charleston Museum (CM). In the following lists of specimens the same abbreviations are used as in the list of material of *N. c. cummingsae*.

TYPE SPECIMENS.—The holotype, UMMZ No. 160557, an adult female 34 mm. in standard length, was collected by Elmer E. Brown on September 6, 1946, in Roses Creek, a small stream in the Catawba River system, 1.5 mi. S. of Smyrna on State Highway 181, Burke Co., North Carolina. The 5 paratypes, UMMZ 160558 (2), and CU 11218

(3), 30 to 36 mm. long, are from same locality (ringed on Map 1). The additional paratypes bear the following data: UMMZ 94556–57 (18, 25–43 mm.), Donald J. Ameel, Nov. 11, 1931, creek in Santee R. system (trib. to either Catawba R. or Broad R.), near York, York Co., S. C.; UMMZ 94553 (1, 27), Ameel, Nov. 11, 1931, Steele Creek, Catawba R. system, near Rock Hill, York Co., S. C.; CU 11269 (9, 29–37), Brown, Aug. 13, 1946, South Fork Cr., Catawba R. system, between Rock Hill and Chester, Highway 21, Chester Co., S. C.

DATA ON INTERGRADES, *Notropis cummingsae: collis* × *cummingsae,* ALL FROM THE LOWER SANTEE RIVER SYSTEM, SOUTH CAROLINA.—UMMZ 143214 (1, 31 mm.), E. Milby Burton, Aug. 18, 1931, Beaver Dam Cr., trib. Saluda R., 5 mi. from Newberry on the Newberry–Saluda Road, Newberry Co. CU 11270 (3, 42–48), Harry W. Freeman, June 17, 1947, North Br. Crane Cr., 12 mi. N. Columbia, Richland Co. CU 11271 (1, 47), Freeman, Aug. 1, 1947, Twenty Five Mile Cr., near Blythewood, Richland Co. UMMZ 143247 (2, 26–27) and 1 returned to CM, Burton, Aug. 19, 1931, Millwood Pond, St. Matthews, Calhoun Co. Collected by R. D. Suttkus and parties, 1949, as follows: CU 15295 (1, 44), June 8, Congaree Cr., 2.5 mi. SSW. Cayce, Lexington Co.; CU 15245 (1, 37), June 8, Congaree Cr., 0.6 mi. farther south; CU 18417 (63, 17–45), Dec. 27, trib. Santee R., 2.8 mi. W. Summerton, Clarendon Co.

DISTRIBUTION AND HABITAT.—*Notropis cummingsae collis* is known only from the Piedmont and Mountain streams of the Santee River system in South Carolina and North Carolina (Map 1). It is probably of wide occurrence throughout these waters, but there is no evidence of its living in any other stream system. Three of the 4 record stations are in the Catawba River division of the Santee complex and the fourth is from either that division or from the Broad River branch. Though provisionally placed in the supposed area of intergradation, a station in the Saluda River division may pertain to *collis* (the single specimen, like *collis,* has 9 anal rays, but the intergrades have about an even chance of having that number). The probable occurrence of an intergrade in the Saluda branch suggests that *N. c. collis* occurs farther upstream in that branch. Assuming that it does occur there, we tentatively map the range of that subspecies as the entire upland part of the Santee River system.

The limited data suggest that *N. c. collis* inhabits small, more or less clear streams, with slow to moderate current and with sandy bottom partly covered with fine sediment.

DIAGNOSIS AND STATUS.—This small form of *Notropis* is essentially like *N. c. cummingsae* in dentition (1, 4—4, 1) and in other characters, but usually has 9 rather than 10 or 11 principal anal rays. Subspecific status is indicated by the overlap in anal ray counts and in other characters and, especially, by the areal intergradation.

INTERGRADATION.—Series interpreted as intergrades between the upland form, *N. c. collis,* and the wide-spread lowland form, *N. c. cummingsae,* have been taken in the Santee River system near and below the Fall Line (Map 1). Unfortunately, only 7 series can be so identified and, with the exception of one set of 63 fish, they each comprise only 1 to 3 specimens. Since the main distinction involves only 1 anal ray and since the intergrades should have either 9 rays as in *collis* or 10 as in typical *cummingsae,* the identification of single specimens is rather arbitrary and the allocation of small samples is insecure. Large series are needed to establish beyond doubt the intermediacy of the stock at each locality and to delimit more precisely the area of intergradation.

That the 2 forms intergrade, rather than overlap without fusion, is definitely indicated by the characters of the one adequate series, which came from the station of lowest elevation. In this series, which is essentially uniform in its characters, the anal rays average 9.70. In the 6 smaller series regarded as intergrades, the mean is 9.60. Both values are intermediate between the average for typical *collis* (9.06) and the means for the river systems on either side of the Santee, namely 10.44 for the Black and 10.12 for the Edisto. Since the smaller series of putative intergrades are relatively uniform in appearance and stem from a small region where intergradation is expected, we feel little doubt in our inference that *collis* and *cummingsae* intergrade not only below but also near the Fall Line.

It is probable that the area of intergradation extends throughout the lower Santee River system, splitting the range of *N. c. cummingsae.* Downstream dispersal of *collis* into a lowland area formerly inhabited by the nominate subspecies probably produced this pattern of intergradation.

The anal ray counts for the 7 series identified as intergrades are: UMMZ, No. 143214—9(1); CU, No. 11270—9(1), 10(2); CU, No. 11271—10(1); UMMZ, No. 143247, and CM—9(2), 10(1); CU, No. 15295—11 (1); CU, No. 15245—9(1); CU, No. 18417—9(23), 10(36), 11 (4).

A trend toward intergradation may be shown by the specimens from the southernmost station mapped for *N. c. collis.* Of the 9 specimens, 7 have 9 anal rays and 2 have 10. In the 25 other specimens referred

to *N. c. collis* the only variation from 9 anal rays is in one series (UMMZ, 94556–57), in which the counts are: 8(1), 9(16), 10(1).

Comparison with *N. c. cummingsae.*—In *N. c. collis* the number of anal rays is typically 9, rarely 8 or 10, whereas in *N. c. cummingsae* the number is usually 10, often 11 (especially in the typical Carolina race), rarely 8 or 12 (Table II). The 9 paratypes of *N. cummingsae* examined have 9 rays in 1, 10 in 4, and 11 in 4. The number in *N. c. cummingsae* (Tables II and III) is rather consistent and shows a slightly confusing and presumably independent approach toward the reduced number of *N. c. collis* in the Chattahoochee race (possibly a subspecies), which is otherwise aberrant (p. 14). When we exclude that race and the intergrades and draw the line of distinction between 9 and 10 anal rays, we find that 94 per cent of the specimens of *N. c. cummingsae* are separable from 91 per cent of known examples of *N. c. collis.* This difference alone seems sufficient to warrant subspecific separation. The low number of anal rays is reflected in the reduced length of the anal base (Table IV).

Long comparison reveals few other distinctions and none as trenchant or as trustworthily genetic as the difference in the number of anal rays and the length of the anal base. Most proportional measurements are similar (Table IV). The body averages a little deeper and wider than in the typical Carolina race of *N. c. cummingsae,* but less deep and less wide than in the Chattahoochee race. The caudal peduncle averages slightly longer, but the overlap is very wide. The interorbital averages wider. The dorsal averages a little higher. *N. c. collis* may average somewhat smaller than the typical or Carolina race of *N. c. cummingsae,* for the largest specimens of the 2 forms are 43 and 60 mm. in standard length, respectively, and the largest specimen in almost half the lots of the Carolina race of *cummingsae* is more than 43 mm. long (Table I). The upland form *(collis),* however, averages larger than the Georgia race of the lowland subspecies.

As a rule, *N. c. collis* is less dusky than typical *N. c. cummingsae* (Pl. 1). The difference is particularly noticeable on the top of the head and on the snout. In *N. c. collis* relatively few melanophores cross the front of the clear light streak that rings the snout from eye to eye, passing through the nostrils, whereas in typical *N. c. cummingsae* the light ring is more or less disrupted anteriorly by a darkish bar. In *N. c. collis* the light triangle just above and behind the eye, as well as the light dash that connects this mark with the pale streak above the dark lateral band of the body, is typically clearer of dark pigment and, therefore, more conspicuously light. In *N. c. collis* the sides below the

TABLE IV

MEASUREMENTS OF NOTROPIS CUMMINGSAE IN THOUSANDTHS OF STANDARD LENGTH

Under each series there is given for each character the range of variation and, in parentheses, the average. Under *collis*, the bold-face figure in each second row is the value for the holotype. For methods of measuring see Hubbs and Lagler (1941 and 1947).

Subspecies	*Notropis cummingsae cummingsae*						*N. c. collis*
Race	Carolina				Chatta-hoochee	Both	
Stream System	Neuse	Cape Fear	Peedee	Edisto	Chatta-hoochee	All 5	Santee
State	N. C.	N. C.	S. C.	S. C.	Ala.	N.C.–Ala.	N.C.,S.C.
Stream	Walnut Cr. & Trent R.	Hammond Cr. & trib. South R.	Crooked Cr.	Trib. near Edisto R.	Brush Cr.	All Streams	All Streams
Number of specimens	8	8	8	7	8	39	9
Standard length, mm.	39–49 (44.3)	39–49 (41.5)	35–50 (39.7)	35–42 (38.6)	34–41 (38.4)	34–49 (40.6)	33–42 **34**(36.4)
Predorsal length	511–555 (539)	520–555 (538)	525–556 (541)	536–567 (548)	492–546 (528)	492–567 (538)	508–562 **530**(537)
Dorsal to occiput	338–361 (352)	319–353 (340)	307–353 (334)	323–354 (342)	308–339 (327)	307–361 (339)	325–361 **325**(340)
Prepelvic length	477–497 (487)	472–504 (486)	470–500 (482)	474–500 (489)	472–512 (492)	472–512 (487)	474–505 **479**(491)
Body depth	181–209 (196)	183–242 (208)	203–249 (220)	216–229 (221)	226–244 (235)	181–249 (216)	209–243 **222**(224)
Body width	103–128 (116)	106–143 (120)	102–131 (118)	116–135 (128)	143–166 (152)	102–166 (127)	117–151 **124**(134)

Caudal peduncle depth	84–96 (89)	85–105 (94)	88–101 (96)	90–106 (98)	101–118 (106)	84–118 (97)	96–104 **98**(100)
Caudal peduncle length	209–236 (225)	202–257 (218)	200–242 (212)	186–212 (201)	201–228 (217)	186–257 (215)	206–251 **231**(230)
Head length	236–251 (244)	236–252 (245)	237–254 (246)	243–253 (248)	241–261 (250)	236–261 (247)	236–258 **249**(251)
Head depth	146–164 (157)	149–163 (157)	152–168 (160)	156–164 (160)	164–176 (167)	146–176 (160)	155–175 **163**(167)
Snout length	68–73 (71)	69–79 (73)	67–76 (72)	64–74 (70)	65–76 (71)	64–79 (71)	66–82 **77** (76)
Eye length	72–81 (77)	73–86 (80)	77–87 (85)	75–85 (81)	78–89 (85)	72–89 (82)	79–89 **89** (85)
Interorbital, least fleshy width	78–89 (84)	84–93 (89)	82–95 (88)	83–93 (86)	84–89 (86)	78–95 (87)	91–100 **95** (98)
Upper jaw length	77–91 (82)	73–86 (79)	72–85 (78)	78–85 (81)	76–89 (83)	72–91 (81)	71–92 **80** (83)
Dorsal origin to lateral line	124–145 (135)	117–155 (134)	141–155 (147)	128–147 (141)	150–173 (158)	117–173 (143)	138–165 **142**(150)
Pelvic insertion to lateral line	47–70 (61)	57–99 (74)	62–93 (77)	67–93 (83)	89–100 (94)	47–100 (78)	78–97 **92** (88)
Dorsal height	224–268 (241)	217–269 (246)	231–268 (251)	215–241 (233)	221–269 (238)	215–269 (242)	229–273 **246**(246)
Anal height	194–221 (208)	191–233 (209)	192–229 (208)	181–229 (201)	175–208 (195)	175–233 (204)	185–218 **198**(201)
Anal base	134–181 (158)	143–181 (157)	145–192 (170)	156–167 (162)	143–167 (152)	134–192 (160)	125–147 **136**(133)
Pectoral length	176–209 (191)	179–234 (198)	182–209 (201)	181–221 (194)	191–223 (200)	176–234 (197)	185–221 **204**(199)
Pelvic length	149–190 (165)	139–188 (164)	154–198 (176)	141–184 (162)	149–187 (160)	139–198 (166)	147–184 **154**(161)

lateral band are immaculate, with few or no melanophores, whereas in *N. c. cummingsae* black specks frequently encroach from above into this light area.

RAY AND SCALE COUNTS IN HOLOTYPE (AND PARATYPES).—Dorsal, 8 (7 in 2, 8 in 28). Anal, 9 (all counts in Table II). Caudal, 19, consistently. Pectorals, 14—14 (usually 14—14, occasionally 13—14, 14—13, or 13—13). Pelvic, 7—8 (7—7 in 1, 7—8 in 4, 8—7 in 1, and 8—8 in 25). Scales 6 (5 to 7, usually 6)—37 (35 to 37, most frequently 36, often 37)—4 (3 to 4, usually 4).

SUMMARY

The dusky shiner, *Notropis cummingsae* Myers, has previously been known only from the type locality in North Carolina, but is now reported from more than 100 other localities, ranging from the Neuse River system in east-central North Carolina to the Apalachicola system in southwestern Georgia, western Florida, and southeastern Alabama. Like many other fishes, it largely avoids the Florida peninsula. As a rule it seems to select more lowland habitats toward the north, as do many other fishes. With one notable exception, its populations are characteristic of the Austroriparian region and of the Coastal Plain. It closely resembles the essentially Piedmont species, *N. altipinnis,* and these species are usually complementary in distribution. Probably as a result of parallel speciation rather than of introgressive hybridization, they are confusingly alike in the 2 areas where they occur together—in the Neuse River system, where *N. altipinnis* is represented by the lowland subspecies *N. a. neusensis,* and in the upper Santee system, which is jointly occupied by the new upland subspecies *N. cummingsae collis* and by *N. altipinnis wrighti.* Even in these areas of cohabitation, however, the 2 species are consistently distinguishable, particularly in details of pigmentation. Furthermore, they differ trenchantly in tooth formula and show no sign of intergradation. Unlike *altipinnis* and other species of similar appearance, *cummingsae* has only 1 tooth in the outer row. It is probably most closely related to *N. ortenburgeri,* of Arkansas and Oklahoma, which is still more aberrant among shiners of this type in the complete lack of the outer row of teeth.

The pattern of subspeciation in *N. cummingsae,* strikingly like that of *Hadropterus notogrammus,* is featured by relative uniformity in the lowlands, by a subspecific segregate in the Piedmont and Mountain districts of a single stream system (that of the Santee River), and by intergradation near and below the Fall Line. The intergrades

occupy the lower Santee River system and appear to split the range of *N. c. cummingsae*. Downstream dispersal and hybridization seem to have caused this pattern of intergradation. There is evidence of altitudinal differentiation also in the Apalachicola River system. The Chattahoochee race, living in the Fall Line Hills, is perhaps also worthy of subspecific separation. In addition to this race and *N. c. collis,* 4 lowland races of *N. c. cummingsae* are tentatively recognized, namely the Carolina race, the Georgia race, the Peninsular race, and the Western Florida race.

In line with a general trend among American cyprinids there seems to be a negative correlation between the number of anal rays on the one hand and the altitude and the water temperature on the other. In the Carolinas the anal rays average about 10.1 to 10.4 in the populations of *N. c. cummingsae* and 9.06 in the upland subspecies, *N. c. collis.* In the Apalachicola and adjacent river systems the averages are 10.45 for the lower elevations and 9.86 for the Fall Line Hills. The Georgia race, chiefly from the Tifton Upland, has on the average 10.09 anal rays and, as a rule, inhabits waters of a more upland type and presumably of cooler temperatures than does the Carolina race. The Peninsular race, largely from a stream originating in a huge spring, has 10.07 anal rays as the mean.

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PLATE I

Subspecies of *Notropis cummingsae*

FIG. 1. *Notropis cummingsae cummingsae,* Carolina race: adult male, 34 mm. in standard length, from a tributary of South River, 1 mile south of Stedman, Cumberland County, North Carolina. Photograph by Art Smith.

FIG. 2. *Notropis cummingsae cummingsae,* Carolina race: adult female, 53 mm. long, from Nahunta Swamp, 1 mile north of Pikeville, Wayne County, North Carolina. Photograph by Douglass M. Payne.

FIG. 3. *Notropis cummingsae collis,* holotype: adult female, 34 mm. in standard length, from Roses Creek, Burke County, North Carolina. Photograph by Douglass M. Payne.

PLATE I

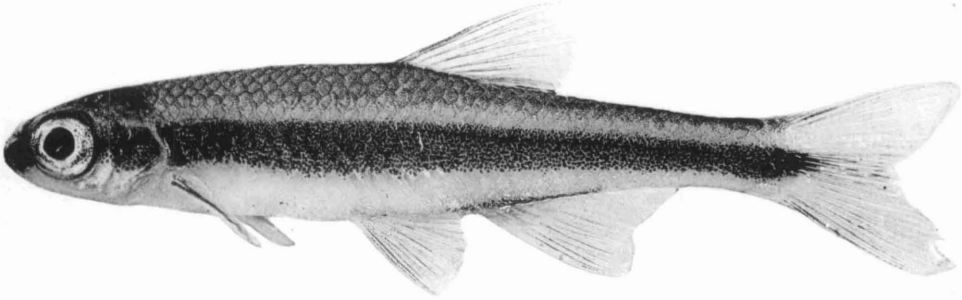

FIG. 1

FIG. 2

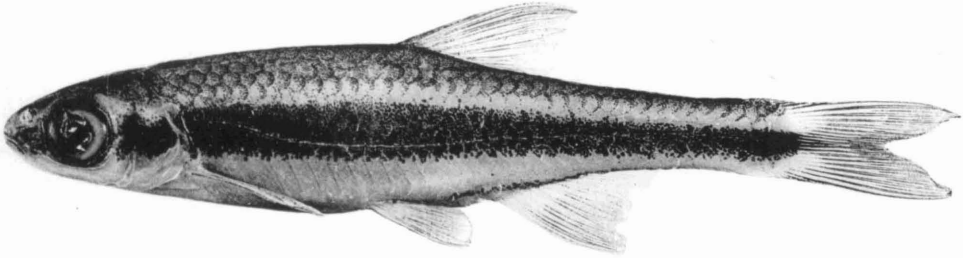

FIG. 3