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SYSTEMATICS AND ZOOGEOGRAPHY OF THE
AMERICAN CYPRINID FISH *NOTROPIS* (*OPSOPOEODUS*)
*EMILIAE*BY CARTER R. GILBERT¹ AND REEVE M. BAILEY

INTRODUCTION

THE PUGNOSE MINNOW, long known as *Opsopoeodus emiliae* Hay, is one of several small, cyprinid fishes with a black midlateral stripe that are characteristic of quiet, usually weedy waters of eastern United States. Specimens from peninsular Florida differ from those elsewhere: the breeding males lack the characteristic flag-like appearance of the dorsal fin produced by darkening of anterior and posterior interrational membranes (Fig. 1, A and B), the usual dentitional formula is 5-4 instead of 5-5, the mouth is less notably oblique, and nuptial tubercle development on the snout is less extensive. In northern Florida and southern Georgia the two forms intergrade. In this paper we treat the species *emiliae* as a complex of two subspecies. The peninsular Florida race is described as a new subspecies, *peninsularis*, that is less specialized than the more widespread nominate subspecies.

Although five nominal species have been assigned to *Opsopoeodus*, three apply to *emiliae* and two are synonyms of other species. Consideration is given to the evolution and significance of the characters on which generic status has been accorded *emiliae*. We interpret *emiliae* as a specialized derivative of *Notropis*, and on the evidence adduced downgrade *Opsopoeodus* to subgeneric status in *Notropis*.

¹ Florida State Museum, University of Florida, Gainesville, Florida 32601.

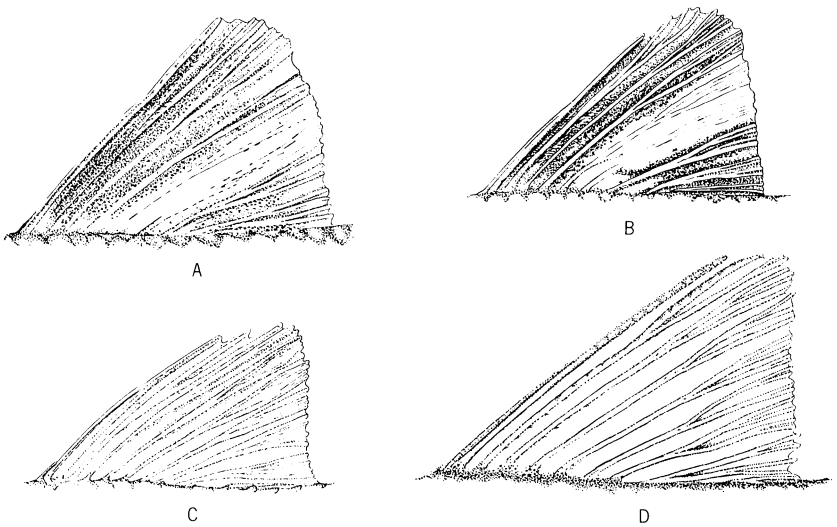


FIG. 1. Dorsal fins in *Notropis emiliae*. A, *N. e. emiliae*, CU 30902, 43 mm. S.L., Savannah River, Barnwell Co., South Carolina, May 1956; B, *N. e. emiliae*, FSU 344, 46 mm. S.L., Bruce Creek, 2.4 mi. N Redbay, Walton Co., Florida, May 27, 1951; C, intergrade, *N. e. emiliae* × *N. e. peninsularis*, FSU 934, 41 mm., Wakulla River, 2.3 mi. SW Wakulla, Wakulla Co., Florida, Mar. 31, 1951; D, *N. e. peninsularis*, UF 6261, 41 mm., Little Lake George, Orange Point, Putnam Co., Florida, Jan. 30, 1947.

MATERIALS AND METHODS

Specimens examined or recorded are from the following museum collections: CAS, California Academy of Sciences; CM, Charleston Museum; CU, Cornell University; FMNH, Field Museum of Natural History; FSU, Florida State University; INHS, Illinois Natural History Survey; TNHC, University of Texas; TU, Tulane University; UF, University of Florida; UG, University of Georgia; UMMZ, University of Michigan, Museum of Zoology; MSUMZ, Memphis State University, Museum of Zoology; UOMZ, University of Oklahoma, Museum of Zoology; USNM, United States National Museum; UT, University of Tennessee. We wish to thank those in charge of these collections for making them available to us. Appreciation is also extended to Paul Laessle, staff artist in the Department of Zoology, University of Florida, for the drawings in Figure 1, to John Tottenham, formerly staff artist of the Museum of Zoology, for those in Figures 2 and 3, and to Martha Lackey, present staff artist of the Museum of Zoology, for Figure 4.

Counts and measurements follow the methods described by Hubbs and Lagler (1958: 19–26). Measurements are expressed in thousandths of standard length; they were taken with dividers and were read to the nearest tenth of a millimeter.

Commonly, a high percentage of counts shows relatively little deviation from the mean. Frequency distributions are expressed thus: (24) 25 to 28 (30), and indicate that at least 90 percent of the total counts fall between 25 and 28.

Vertebral counts include the Weberian complex as four and the urostyle as one. The angle of the mouth, determined with the aid of a special ocular equipped with perpendicular crosshairs (Smith, 1956), was measured between the lower profile of the head and the anteroventral border of the upper lip. The pointer is set at a 0° reading, and one crosshair is directly over the lower part of the head from the isthmus forward. The intersection of the crosshairs is at the hinge of the lower jaw. The ocular is then rotated in a clockwise direction until the horizontal crosshair is in line with the upper lip. The angle is read in degrees; a more steeply inclined mouth has a higher value.

GENERIC REFERENCE

Since the time of its original description the pugnose minnow has been placed in the genus *Opsopoeodus* Hay (1881: 507), of which *Trycherodon* Forbes (*in* Jordan and Gilbert, 1883: 247) is a synonym. Although other species have been assigned to *Opsopoeodus*, these are synonyms either of *emiliae* or of other species currently placed in *Notropis* (see below). *Opsopoeodus emiliae*, as understood from study of the wide-ranging nominate subspecies, is a well-marked and distinctive species. It is a small cyprinid with large scales; dorsal fin distinctively patterned, its origin above insertion of pelvic, and with a modal count of nine principal rays; pharyngeal teeth serrate and uniserial, typically numbering 5–5; mouth tiny, steeply upturned and terminal; intestine short; peritoneum light; premaxillae protractile; barbel usually wanting, but a small one occasionally present on one or both sides at tip of maxilla; and isthmus narrow. Many if not all of the above characters have at times past been regarded as adequate to define genera of American cyprinids. Recent studies have increasingly demonstrated that closely related forms may vary widely in these and other features, and their use as criteria for generic separation has accordingly been devalued or is viewed with renewed caution. Despite its several

diagnostic features, the overall appearance of *emiliae* is that of a species of *Notropis*, a placement supported by agreement in most of the above listed characteristics.

The argument for continued recognition of *Opsopoeodus* as a genus would presumably depend chiefly on dentition, the number of dorsal fin rays and, perhaps, the pigmentation of that fin. The small upturned mouth, a notable specific character, finds a convergent counterpart in *Notropis anogenus* (Bailey, 1959: 119–121), and represents an extreme in the wide variation in mouth configuration found in *Notropis*.

PHARYNGEAL TEETH.—Dental characteristics, especially the number of teeth on the pharyngeal arches, have long been accorded much emphasis in the classification of the American Cyprinidae. For example, Jordan and Evermann (1896: 200–201) wrote: “No progress can be made in the study of these fishes without careful attention to the teeth, as the genera are largely based on dental characters.” This close attention continues to the present. No exhaustive analysis of dental characters of American cyprinids has been performed, but this closely interrelated group, made up largely of the Leuciscinae according to Hubbs (1955), displays far less variation than the more diversified Old World Cyprinidae (Chu, 1935).

The original description of *Opsopoeodus* (Hay, 1881) emphasized dental features—“well-developed masticatory surface, both bounding edges of which are conspicuously serrated, standing in a single row of 5–5 on a prominent process of the pharyngeals.”

The presence of serrations on the cutting edges of the pharyngeal teeth is uncommon in American cyprinids, but it is not unique. At least two other species with steeply inclined mouths and a single row of teeth and presumably similar feeding habits share the character. *Notropis anogenus* has finely serrate teeth (Bailey, 1959: 119). In *Notemigonus crysoleucas* the serrations are stronger than in other American minnows known to us, but they are developed only on the anterior cutting edge of the grinding surface. In *Notropis heterodon*, a species with a tooth in the lesser row, serrations are well developed on the teeth of the principal row. Most cyprinids have entire teeth, but crenulate edges have been noted in several. Although we have examined only a small fraction of American species for this character, we believe that the evolution of crenulate or serrate teeth has proceeded independently in a number of phyletic lines, likely as a common feeding adaptation.

Students of the Cyprinidae have attached much, sometimes too much,

importance to the number of teeth on the pharyngeal arches. Because *Opsopoeodus* has the teeth 5-5, it has uniformly been grouped in keys, in phyletic sequence, and, by presumption, in relationship with other genera having the teeth in the principal row 5-5 or 5-4 (e.g., Jordan and Evermann, 1896; Hubbs and Lagler, 1958; Moore, 1968). We see no other basis for its close association with such genera as *Semotilus*, *Gila*, *Notemigonus*, and *Phoxinus* (including *Chrosomus*). Rather, as stated above, the more intimate relationship appears to be with *Notropis*, all other species of which have a modal count of 4-4 in the main row.

It has been suggested by Chu (1935: 184) that 5,4,3 is the primitive tooth complement of the three rows in the Cyprinidae, from which specializations have taken place by increase or decrease in the main row and by reduction only in the lesser rows. We do not challenge the general evolutionary trend but suggest that even as 5 may be increased to 6, so also may 4 teeth be increased to 5, thus reversing an earlier phyletic reduction. In *emiliae* there are no lesser rows. Throughout most of the range of the species the usual count for the main row is 5-5 (Table 1), with 5 (left) -4 (right) as a variation found in 3 of 51 specimens. In peninsular Florida, however, the typical count is 5-4,

TABLE 1
FREQUENCY DISTRIBUTION OF PHARYNGEAL TOOTH COUNTS IN *Notropis emiliae*

Subspecies and Drainage	Pharyngeal Formula		
	4-4	5-4	5-5
<i>N. e. emiliae</i>			
Upper Mississippi	—	—	16
Lower Mississippi—Gulf Coast	—	3	23
Atlantic Coast	—	—	9
Intergrades	—	6	57
<i>N. emiliae peninsularis</i>	6	59	9

with 4-4 appearing in 6 and 5-5 in 9 of 74 individuals. A count of 5-4 in the main row occurs as an infrequent individual variation in some species of *Notropis*, e.g. *blennius*, *cerasinus*, *shumardi*, and *hudsonius*.

Our hypothesis of an increase in dental count is based on the arrangement of teeth in the arch. Most cyprinids have the teeth rising more or less vertically from the arch, as in *Notropis volucellus* (Fig. 2, A and D). In some species extensive ossification at the bases of the upper (posterior) teeth provides an elevated crest for tooth implantation, as in *Notropis maculatus* (Fig. 2, B and E) and *Lavinia exilicauda*

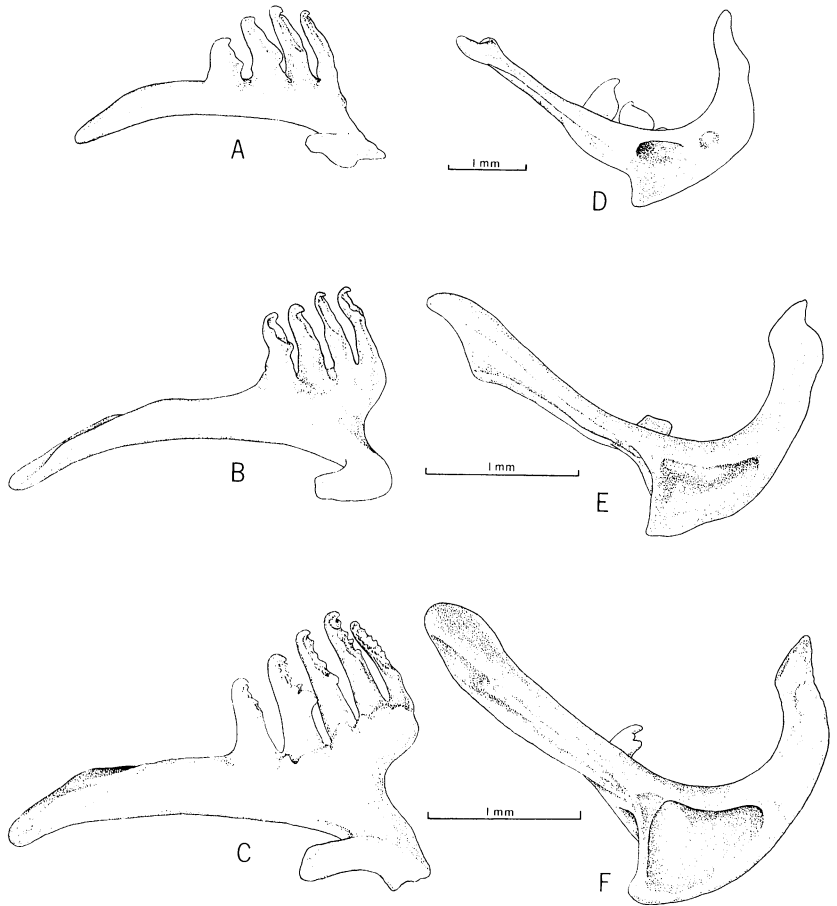


FIG. 2. Left pharyngeal arches in three species of *Notropis*. A, D, *N. volucellus*, UMMZ 164839, 49 mm. S.L., Meramec River, near Steelville, Crawford Co., Missouri, in dorsal and lateral aspects; B, E, *N. maculatus*, UMMZ 166115, 47 mm. S.L., East Branch Hobolochitto Creek, 1 mi. N Picayune, Pearl River Co., Mississippi, in dorsal and lateral aspects; C, F, *N. emiliae emiliae*, UMMZ 166119, 51 mm. S.L., East Branch Hobolochitto Creek, 1 mi. N Picayune, Pearl River Co., Mississippi, in dorsal and lateral aspects.

(Fig. 3, A and C). Functionally this brings the posterior teeth of opposite sides closer together and probably increases the area of contact between the grinding surfaces and the callous pad. (We do not understand the precise kinetics of mastication.) Further extension of the bony crest increases the dentigerous surface, thus providing

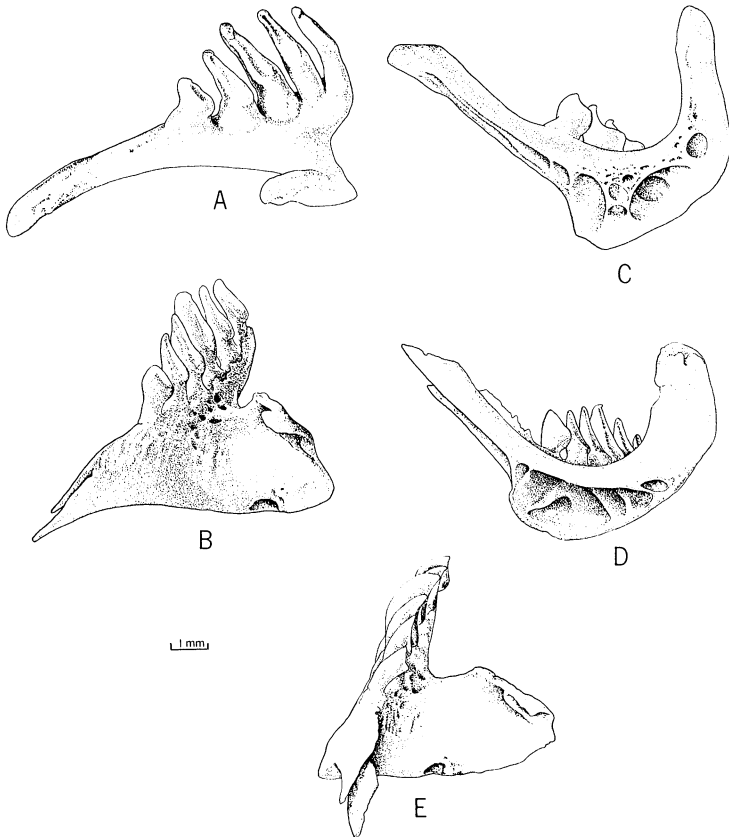


FIG. 3. Left pharyngeal arches in *Lavinia exilicauda* and *Orthodon microlepidotus*. A, C, *Lavinia exilicauda*, UMMZ 94211, 116 mm. S.L., Stony Creek near Orland, Glenn Co., California, in dorsal and lateral aspects; B, D, E, *Orthodon microlepidotus*, UMMZ 86836, 104 mm. S.L., Sacramento River, Sacramento, California, in dorsal, lateral and anteromesial aspects.

support for an additional tooth. This is what we believe has occurred in *emiliae* (Fig. 2, C and F), which displays five teeth, and in *Orthodon microlepidotus* (Fig. 3, B, D, and E), which commonly has six, the maximum count for an American cyprinid. A parallel to the dentition in *Orthodon* is illustrated by Chu (1935: Fig. 141) for *Pseudobrama simoni*, which has from 5 to 7 teeth and was believed by Chu to be related to *Orthodon*. It is not postulated that Figures 2 and 3 represent phyletic series, but they illustrate the morphological gradient that we believe marked an evolutionary increase to 5 and 6 teeth in *Opsopoeodus* and *Orthodon* respectively. We suggest that for any

cyprinid in which the upper tooth is supported by an elevated crest or whose base is closely associated with that of the penultimate tooth, there exist a priori grounds to suspect that dental addition has occurred. For example, in *Notemigonus crysoleucas* the two uppermost teeth arise from a common bony pillar; perhaps the 5-5 count of this species has evolved from an ancestor with 4-4. It is to be recalled that configuration of the mouth, serration of teeth, and perhaps food habits are convergent in *Opsopoeodus* and *Notemigonus*.

DORSAL FIN.—Dorsal fin-ray counts are remarkably constant in American Cyprinidae, with modal numbers between 7 and 11 and total variation from 6 to 13. In eastern United States "*Opsopoeodus emiliae*" is distinctive among described species in having a modal count of nine; all other named species typically have eight but there is an undescribed species of *Notropis*, probably related to *N. welaka*, with 9 or 10 rays. It is not closely related to *emiliae*. Many western cyprinids have increased usual numbers, for example 7 to 9 in *Rhinichthys*, 8 or 9 in *Hesperoleucus*, 8 to 10 in *Ptychocheilus*, 8 to 11 in *Gila*, 9 or 10 in *Orthodon*, 9 in *Pogonichthys*, 10 in *Acrocheilus*, and 10 or 11 (13 in rare variants) in *Lavinia*. None of these appears to be close to *emiliae*. Individual variation in dorsal rays among eastern species is infrequent, but we have noted counts of 7 and 9 in various species. Among 601 specimens of *emiliae* from several localities in peninsular Florida, there are 8 rays in 6, 9 in 593, and 10 in 2. In 132 specimens of *emiliae* from western Florida to Texas and Missouri, there are 7 rays in 1, 8 rays in 8, and 9 in 123. Although the typical occurrence of nine dorsal rays in *emiliae* is a usable taxonomic character, it appears from the above data not to provide an acceptable basis for generic separation from *Notropis*.

Breeding males from most of the range of *emiliae* have the anterior four and posterior three dorsal rays, together with their associated membranes, heavily sprinkled with melanophores; the intervening two rays and adjacent membranes are almost devoid of melanin (Fig. 1, A and B). Although breeding behavior is unknown, this pigmentation is likely of functional significance during the reproductive period. It is highly distinctive among American cyprinids. Its importance is questionable since the "flag fin" is undeveloped in peninsular Florida (Fig. 1, D) and is intermediate in intergrades from the Suwannee, Ochlockonee, and adjacent rivers (Fig. 1, C).

STATUS OF *Opsopoeodus*.—The pugnose minnow agrees closely with *Notropis* in the aggregate of its characters. Two of the most distinctive features of *emiliae*, the pharyngeal tooth count (5-5) and the conspicu-

ous marking of the dorsal fin in breeding males, lose force as "generic" characters in that they vary geographically—in peninsular Florida the teeth number 5-4 and the "flag fin" is undeveloped. The configuration of the pharyngeal arch furnishes evidence that the fifth tooth is a newly derived feature and does not associate *emiliae* with more generalized cyprinids with 5-5 or 5-4 teeth in the main row. The presence of serrations on the teeth is apparently correlated with a steeply inclined mouth and perhaps specialized feeding habits (likely on microcrustaceans); such serrations have developed independently in a number of species of *Notropis* and in *Notemigonus*. In light of this evidence we believe that *emiliae* is a rather highly specialized species of *Notropis* and therefore add *Opsopoeodus* to the synonymy of that genus.

BARBELS AND THEIR SIGNIFICANCE IN THE CLASSIFICATION OF THE CYPRINIDAE

The discovery that *Notropis emiliae*, a species not previously reported to have a barbel, occasionally has a terminal maxillary barbel on one or both sides (p. 10) is the most unexpected development of this study. Students of the New World Cyprinidae have until recently usually regarded the presence or absence of a maxillary barbel as a generic distinction, notwithstanding recognition that occasional individuals vary in this feature. Some workers have placed limited emphasis on barbels in classification; for example, Jordan and Evermann (1896: 202-204) keyed out barbeled minnows in four different couplets and Moore (1968: 56-59) six times, subordinate to such features as length of intestine, dentition, and configuration of mouthparts, thus suggesting that barbels are of multiple origin. Commonly, however, authors have emphasized the barbel by a position of prominence in keys and at least by implication placed high phyletic significance in the character, which has been regarded as primitive among cyprinids. One of us (Bailey, 1951: 192) merged eight nominal genera of cyprinids (*Couesius*, *Erimystax*, *Extrarius*, *Macrhybopsis*, *Nocomis*, *Oregonichthys*, *Platygobio*, and *Yuriria*) with *Hybopsis* because they had a barbel and a range of morphological variation in other characters that was viewed as comparable to that in *Notropis*. *Notropis*, by tradition, has comprised species that lack a barbel. Barbels have been and will remain useful in cyprinid identification, they are commonly consistent within species, and they are in some cases useful indicators of relationship among species. As indicated below, however, they have been overemphasized in classification.

We contend that the presence or absence of barbels should be given

less weight in cyprinid systematics for the following reasons: (1) they are subject not only to individual variation within some species but to bilateral asymmetry; (2) they may be present in some but not all species of intimately related groups—as judged by other characters; and (3) they are highly adaptive and subject to repeated development or loss depending on selectional environmental forces, are heterogeneous in position and structure, hence of polyphyletic origin.

The barbel in *Notropis emiliae*, if present, is always small. It is located at the posterior tip of the maxilla and is similar in location and shape to those of most species of *Hybopsis*, projecting downward and forward and free ventrally from the lip. A tabulation (Table 2) reveals a low incidence of occurrence in the Florida subspecies, of

TABLE 2
FREQUENCY DISTRIBUTION OF MAXILLARY BARBELS IN *Notropis emiliae*

Subspecies	No Barbel	Barbel Unilateral		Barbel Bilateral	N
		Left	Right		
<i>N. e. emiliae</i>	70	15	17	25	127
Intergrades	104	1	5	2	112
<i>N. e. peninsularis</i>	139	9	9	2	159

which 87 percent lack a barbel, 11 percent have a barbel on one side only, and 1 percent (2 individuals of 159) have a pair of barbels. In the area of intergradation the frequencies are comparable: 93 percent lack barbels, 5 percent have a barbel on one side only, and 2 percent have a pair of small barbels. In the nominate subspecies, in contrast, barbels are encountered more often: 55 percent of specimens lack a barbel, 25 percent have one on one side, and 20 percent have them on both sides. Barbels are of frequent occurrence in such scattered areas as Texas, Missouri, Indiana, and Wisconsin. We note no obvious correlation of barbels with size or sex. Cortés (1968: 185–187) has reported variation in barbels in two Mexican species of *Notropis*. Of 20 specimens of *N. moralesi* examined, 12 had a pair of barbels, six had a unilateral barbel, and two lacked barbels. Of 100 specimens of *N. boucardi* examined, 24 had a pair of barbels, 18 had a single barbel, and 48 lacked them (10 specimens are unaccounted for). Mrs. Cortés concluded that the presence and absence of barbels in a species invalidated the character, both at generic and specific levels. In *Rhinichthys osculus* from Oregon, Bisson and Bond (1971) have noted high variability in the occurrence of maxillary barbels, from 0 to 98 percent in various samples. They are usually absent in Warm Springs, present in 60–90 per-

cent in the Harney basin, and in 90–97 percent in the John Day system. The original description of *Notropis harperi* Fowler made no mention of a barbel, so it was presumably overlooked. Hubbs and Crowe (1956: 2) pointed out that the species usually has a small barbel and therefore assigned it to *Hybopsis*, but they observed that the barbel is occasionally lacking on one or both sides, a finding that we corroborate. *N. harperi* has the facies of *Notropis* rather than of *Hybopsis* and differs from *Notropis* only in the usual presence of a barbel. In view of barbel variability in *harperi* we reassign the species to *Notropis*. Other species usually assigned to *Hybopsis* also may vary in the development of the barbel. We have examined specimens of *H. hypsinotus* and *H. amblops winchelli* that lack barbels on one or both sides. Dr. Glenn Clemmer is currently studying a group of cyprinids including *Hybopsis amblops* (the type-species of *Hybopsis*) and *Notropis amnis* and has found considerable variation in barbel development. Nomenclatural changes will likely accompany re-evaluation of relationships among these fishes.

In the polytypic species *Barbus radiatus*, Greenwood (1970: 9) has shown that subspecies *profundus*, restricted to deep water of Lake Victoria, consistently lacks oral barbels whereas two other non-lacustrine subspecies invariably have two pairs of maxillary barbels. Of these the anterior pair are usually minute, the posterior pair vary from minute to 5.6 percent of the standard length.

Other aspects of barbel development involve ontogeny and sex. The species of *Semotilus* have a characteristic flaplike barbel lying in the groove above the upper lip well in advance of its tip. It is undeveloped in young, appearing usually with growth, but many large juveniles lack the barbel, at least on one side. We do not know whether or not it may be undeveloped in adults. As has long been recognized nuptial males of *Pimephales notatus* develop a thick, fleshy, barbel-like protuberance from the posterior angle of the lips. This structure is transient and presumably differs structurally from other barbels.

Although students of American cyprinids commonly utilize the presence or absence of a maxillary barbel to delimit genera, this is not standard practice for Old World forms. Both in Africa (Boulenger, 1911: 3) and in Thailand (Smith, 1945: 166) some species of *Barbus* (or *Puntius*) have rostral and maxillary barbels, others only maxillary barbels, and still others no barbels. In Thailand, the forms of *Osteochilus* may have two pairs of barbels, only maxillary barbels, or only rostral barbels (Smith, 1945: 210); *Cyclocheilichthys* may have two

pairs, only maxillary barbels which may be simple or multifid, or none (Smith, 1945: 141); *Cirrhinus* and *Tylognathus* may possess or lack maxillary barbels (Smith, 1945: 161, 234). Other Oriental genera that display variation in occurrence of barbels include *Garra*, *Epalzeorhynchus*, *Crossochilos*, *Labeo*, *Lobochilos* (Smith, 1945), *Rasbora* (Brittan, 1954), and *Acheilognathus* (Abe et al., 1965: 194–197). African genera in addition to *Barbus* that have barbels in some but not all species are *Labeo* and *Varicorhinus* (Boulenger, 1909: 300, 353). The examples cited represent several subfamilies. It seems obvious from this notable variation that (1) barbels have been evolved and/or lost repeatedly, and (2) that the occurrence of barbels fails of itself to provide an adequate basis for generic distinction in the Cyprinidae.

Among American groups, too, there are obviously interrelated clusters of species, some with barbels and others without them. Of the three genera assigned to the Plagopterini by Miller and Hubbs (1960) the generalized *Lepidomeda* lacks barbels; of the two specialized but closely related genera, *Meda* lacks a developed barbel but *Plagopterus* has a pendant one from the end of the upper lip. *Phenacobius* is treated as a genus in which there is no barbel. In the four clear-water species from the uplands of eastern states (*catostomus*, *crassilabrum*, *teretulus*, and *uranops*), however, we find that deep in the groove between the upper lip and the lachrymal there is a fold of tissue from which emerges a well-formed lappetlike barbel or flap. This is more like the barbel of *Semotilus* than that of *Rhinichthys* and *Hybopsis*. In *Phenacobius mirabilis*, a wide-ranging plains and prairie form tolerant of turbid water, the barbel is obsolescent or wholly absent. Two closely allied eastern cyprinids customarily placed in separate genera are *Parexoglossum laurae* (including *hubbsi*), with more generalized mouthparts, and *Exoglossum maxillingua*. *Parexoglossum* usually has a slender barbel that is pendant from the lower edge of the premaxilla well in advance of its end, but as was noted by Hubbs (1931) this is occasionally lacking on one or both sides. *E. maxillingua* lacks a barbel. These species share numerous features (Hubbs, 1931: 4), especially the bony structure of the lower jaw. We believe that the differences are adequately valued at the species level and regard *Parexoglossum* Hubbs as a synonym of *Exoglossum* Rafinesque, a conclusion reached independently by Jenkins and Lachner (1971).

Cyprinid barbels are evidently of diverse origin. The evolution and elaboration of fingerlike or flaplike projections from soft tissues and membranes on or about the lips and their enrichment with sensory structures provide adaptive enhancement that is especially advanta-

geous to those groups which emphasize senses other than vision in food getting. Absent in the ancestral characoid fishes, barbels occur in many groups of cyprinids, but their diversity in position and structure points to repeated independent development and loss. Superficial examination of most of the groups of American barbeled cyprinids suggests that they can be grouped in several, probably at least six, structural types, perhaps indicative of as many independent evolutionary lines.

Notropis (Opsopoeodus) emiliae (Hay)—pugnose minnow

NOMENCLATURE.—*Opsopoeodus emiliae* was originally described from Artesia, Macon, and Enterprise, Mississippi (Hay, 1881: 507–508). Forbes (in Jordan and Gilbert, 1883: 247) later described, from Illinois, *Trycherodon megalops*, which, as was noted by Jordan (1885: 821), is a synonym of *O. emiliae*. Evermann (1892: 82–83) described a third species, *Opsopoeodus osculus*, from eastern Texas, believing this form to differ from *emiliae* in the absence of the characteristic pigment pattern in the dorsal fin. Despite Jordan's action and the treatment by Ortenburger and Hubbs (1927: 125) of *megalops* and *osculus* as indistinguishable from *O. emiliae*, all three forms were accepted as valid by Jordan and Evermann (1896: 247–249) and by Jordan, Evermann, and Clark (1930: 115). Although examination of the types of *Opsopoeodus osculus* confirms the absence of the characteristic pigment pattern of the dorsal fin, this may be attributed to age of the specimens, none of which is fully adult, and possibly also to the fact that all came from a turbid environment. Examination of other examples of *emiliae* from Texas indicates no appreciable difference from other parts of the range, excluding peninsular Florida.

Hubbs and Lagler (1947: 64–65) believed that populations in the Great Lakes and Mississippi Valley, probably to Texas, differ from those to the southeast (Mississippi to Florida) in which the mouth was said to be less oblique. They applied the subspecific name *megalops* to the northern form and *Opsopoeodus emiliae emiliae* to that from Mississippi to Florida. Our study indicates that *emiliae* and *megalops*, from Mississippi and Illinois respectively, belong to the same taxon.

Two other nominal species have been described in *Opsopoeodus*: *O. bollmani* Gilbert (1890: 226) and *O. borealis* Harper and Nichols (1919: 266). Study of the description shows conclusively that *O. bollmani*, from Buckland Creek, Millen, Georgia, is a synonym of *Notropis maculatus* (Hay), a common cyprinid in lowland areas of southeastern United States. *O. borealis* was described from Lake Athabaska, Alberta,

far from the range of *emiliae*. Study of the description of *borealis*, considered along with the range and habitat of North American cyprinids, indicates that this form likely is a synonym of *Notropis hudsonius* (Clinton).

DIAGNOSIS.—A species of *Notropis* characterized by: pharyngeal teeth in a single row, usually 5–5 or 5–4; dorsal rays nine (this occurs in only one other species of *Notropis*); a small, extremely oblique mouth, that forms an angle of 31°–47° to the plane of the lower profile of the head; and by the thin pigment lines which crisscross in such a way that the scales over most of the body appear diamond-shaped. In addition, populations of *emiliae* except in parts of Florida and Georgia have a characteristic dark-light-dark color pattern in the dorsal fin (see Figs. 1A and B), this character being most pronounced in breeding males.

DESCRIPTION.—Variational data on pharyngeal tooth counts, barbel frequency, scale rows, vertebral counts, body proportions, and mouth angle appear in Tables 1 to 6. The following description was taken from darkly pigmented individuals, which better show certain diagnostic pigmentary features:

Body moderately deep and compressed; mouth small and extremely oblique, with the corners well forward of anterior margin of orbit; snout rounded and blunt; scales of normal shape, only slightly higher than long; predorsal scales crowded, particularly irregular in anterior half of nape; breast and prepectoral area naked (the figure by Moore, 1968, p. 66, is inaccurate); dorsal fin rounded at tip, the first ray not extending as far posteriorly as the second to fourth rays; tip of depressed dorsal fin reaching a vertical above posterior two-thirds of anal-fin base; posterior margin of dorsal fin straight or slightly rounded; anal fin pointed at tip, the first three rays somewhat longer than other rays; posterior margin of anal fin slightly falcate; tip of pectoral fin falling just short of insertion of pelvic fin; tip of pelvic fin just reaching origin of anal fin; lateral line usually complete, if incomplete extending posteriorly at least as far as anal fin. Caudal supporting skeleton with a well-developed free uroneural; its distal end lying just above the base of the upper principal caudal ray. No opercular canal.

Nuptial tubercles (Fig. 4) small, acute but not sharp, situated in compact patches from above angles of mouth upward on snout, either broadly joined or separated at midline, and in a prominent symphyseal cluster on lower jaw; a few tubercles sometimes present on upper lip

TABLE 3
FREQUENCY DISTRIBUTIONS OF SCALE-ROW COUNTS IN *Notropis emiliae*

Subspecies and Drainage	Lateral-line Scales							N	Mean	
	36	37	38	39	40					
<i>N. e. emiliae</i>										
Upper Mississippi ¹	1	4	6					11	37.5	
Lower Mississippi-Gulf ²	1	7	8	1				17	37.5	
Atlantic Coast	1	7	3	1				12	37.3	
Intergrades	2	7	10	7	2			28	38.0	
<i>N. e. peninsularis</i>	5	10	4	4				23	37.3	
<i>Predorsal Scales</i>										
	17	18	19	20	21	22	23	24	N	Mean
<i>N. e. emiliae</i>										
Upper Mississippi ¹		4	2	2	2	1			11	19.5
Lower Mississippi-Gulf ²	2	4	2	7	2				17	19.2
Atlantic Coast	1	2	2	3	2	0	2		12	19.9
Intergrades	1	4	2	7	8	1	4	1	28	20.5
<i>N. e. peninsularis</i>	1	5	11	3	2	1			23	19.1
<i>Body-circumference Scales</i>										
	24	25	26	27	28	29	30	N	Mean	
<i>N. e. emiliae</i>										
Upper Mississippi ¹		2	9					11	25.8	
Lower Mississippi-Gulf ²		1	13	1	2			17	26.2	
Atlantic Coast	1	1	7	3				12	26.0	
Intergrades		2	7	11	6	1	1	28	27.0	
<i>N. e. peninsularis</i>		1	14	6	1	0	1	23	26.5	

¹ South to Indiana and Illinois

² North to Tennessee and Missouri

near corner of mouth; small tubercles present in double file on upper surface of anterior 5-7 branched pectoral rays; tubercles apparently absent otherwise from fins and rest of body.

Body-circumference scales (24) 25 to 28 (30); predorsal scales 17 to 23 (24); lateral-line scales 36 to 39 (40); caudal-peduncle scales 12 or 13 (14); dorsal rays (7) 9 (10); pectoral rays (13) 14 or 15 (16); pelvic rays 8 (9); anal rays (7) 8 (9).

Vertebrae (36) 37 to 39, usually 38 or 39 in the north and along the eastern gulf drainage but most often 37 or 38 in Texas and Florida. Thus, there is a weak clinal gradient with higher average number to the north (Table 4).

Melanophores heavily concentrated on upper and lower lips; gular area and lower jaw usually well pigmented, particularly anteriorly; top

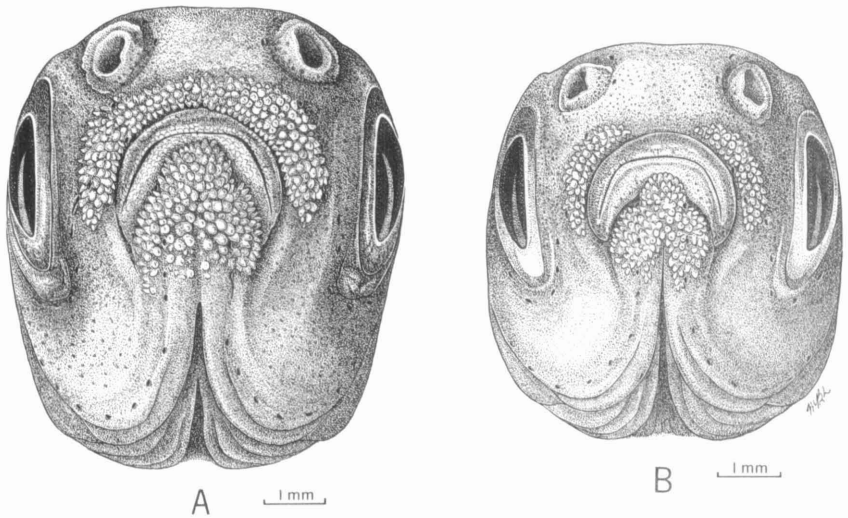


FIG. 4. Anteroventral views of the heads of tuberculate males of two subspecies of *Notropis emiliae*. A, *N. e. emiliae*, UMMZ 111595, 47 mm., Horseshoe Lake, Alexander Co., Illinois, May 14, 1936. B, *N. e. peninsularis*, UMMZ 163356, 42 mm., St. Johns River at Ft. Gates Ferry, Putnam Co., Florida, April 5, 1941.

and upper part of side of head thickly covered with melanophores, these sparse or absent on lower part of cheek, opercle, and branchiostegals; rim of orbit heavily pigmented; upper three-fourths of iris dark, lower fourth sparsely pigmented, the inner fifth (closest to pupil) silvery and devoid of pigment; heavy chains of melanophores along both edges of outer pectoral ray, the melanophores irregular or absent along other pectoral rays; pigment largely or entirely absent from

TABLE 4
FREQUENCY DISTRIBUTION OF VERTEBRAL COUNTS IN *Notropis emiliae*

Subspecies and Drainage	Vertebrae				N	Mean
	36	37	38	39		
<i>N. e. emiliae</i>						
Upper Mississippi ¹		3	50	20	73	38.23
Eastern Gulf of Mexico ²		1	27	4	32	38.09
Texas		16	25	2	43	37.67
Intergrades		1	11	3	15	38.13
<i>N. e. peninsularis</i>	1	26	23		50	37.44

¹ Missouri, Illinois, Indiana, Wisconsin

² Mississippi, West Florida

pelvic fin; flecks of pigment sometimes bordering rays of anal fin, when present usually confined to last four or five rays; pigment present in membranes and along borders of caudal membranes; dorsal fin variously pigmented, in adults usually with melanophores on four anteriormost membranes and on last two-and-one-half membranes, with the inner membranes clear (this pattern not present in some populations); a distinct scapular bar extending from top of opercle about half distance to insertion of pectoral fin; cleithral area sparsely flecked with dark melanophores; predorsal stripe poorly defined to absent; no postdorsal stripe; width of dark lateral stripe on body equal to height of about one-and-one-half lateral-line scales; lateral stripe commencing at margin of upper lip (not encircling snout) and extending posteriorly to base of caudal fin, mostly beneath lateral line in region just back of opercle, then just above (and bordering) lateral line as far as a point under middle of dorsal fin, thence mostly beneath lateral line to caudal fin (where about four-fifths of stripe is below lateral line); periproct and area around anal fin heavily pigmented; scales outlined on all parts of body, except belly, by thin lines of dark pigment that do not follow exact margin of scales, thereby giving impression that scales are diamond-shaped.

Fins in breeding individuals of a series of intergrades from the Suwannee River basin pinkish to blood-red, the color most intense in caudal and anal fins. We do not know that similar colors obtain throughout the range.

RANGE.—*Notropis emiliae* occurs from the Nueces River system of Texas eastward to the Edisto drainage of South Carolina (Fig. 5); it extends as far north as the Mississippi drainage of southeastern Minnesota, the Lake Winnebago drainage of Wisconsin, the southern Lake Michigan drainage in Illinois, to the Lake Erie and Lake St. Clair drainages of Michigan and Ontario, and the Ohio River basin in southeastern Ohio and western West Virginia; an endemic subspecies occurs in peninsular Florida south to Lake Okeechobee.

ECOLOGY.—Except for general statements regarding habitat little has been written on the ecology of *Notropis emiliae*. Although the species is most often found in sluggish, clear, weedy waters, Gerking (1945: 53) stated that in Indiana it "was most frequently taken in sluggish, turbid streams with a muddy bottom. No vegetation was found associated with its occurrence." Trautman (1957: 337), commenting on this seemingly paradoxical situation, said "Gerking's . . . perplexing statement that during 1940-43 surveys in Indiana, the Pugnose was found in turbid

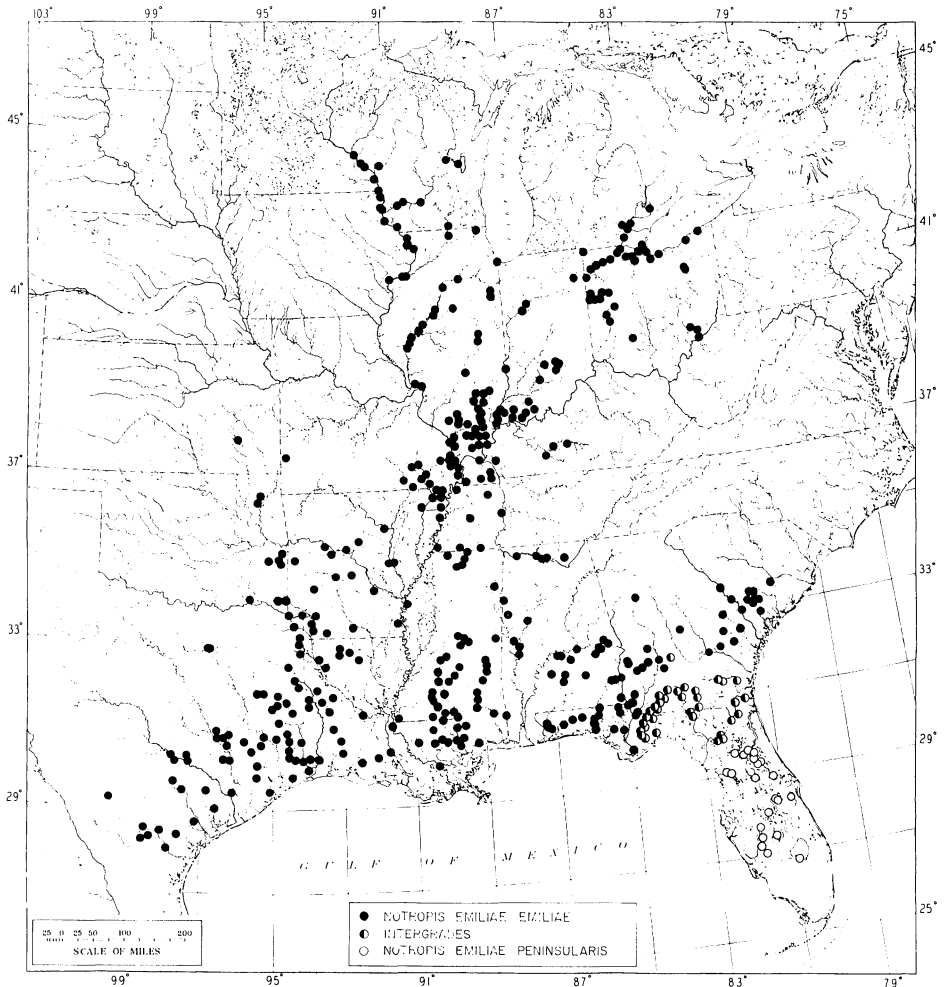


FIG. 5. Distribution by record stations of *Notropis emiliae emiliae*, *N. e. peninsularis*, and intergrades.

waters without vegetation is contrary to the general conception of its environmental requirements. This contradiction can be explained when it is realized that before their final disappearance, relict populations persisted in Ohio for several years after almost all of the aquatic vegetation had disappeared, and after turbidity and siltation had become great. This persistence of small populations to exist for a time after only submarginal conditions remain may have been operating in southern Indiana during the 1940-43 fish surveys."

A reference to feeding habits of the pugnose minnow appears in an unpublished doctoral dissertation by William McLane, who examined specimens from the St. Johns system, Florida. He found, in descending order of frequency, chironomid larvae, filamentous algae, unidentified animal matter, copepods, cladocerans, and hydrachnids, with minute amounts of larval fish (?), fish eggs, and sand. Except for the algae, which may have been ingested incidentally, such items are what one might expect from a species adapted to a carnivorous diet. The strongly oblique mouth suggests that *N. emiliae* feeds on items from mid-water or near the surface.

Breeding occurs during late spring in Illinois, where Forbes and Richardson (1909: 125) reported taking gravid females and tuberculate males between the 10th and 20th of June. Meek (1894: 94) reported individuals from Arkansas breeding in late May. We have prespawning specimens collected in the St. Johns River on April 5, 1941. McLane collected breeding males of *N. emiliae* in Big Lake George (an enlargement of the St. Johns River) from March to September and gravid females from January to September, suggesting that this species has a protracted breeding season in Florida.

RELATIONSHIPS.—No one has yet attempted a comprehensive interpretation of interrelationships of the numerous principal groups within *Notropis*, an effort that if successful will presumably necessitate study of characters not yet employed in the taxonomy of the group. *Notropis emiliae* is well set off structurally from other species and groups of species of the genus, but we do not know its intimate relationships. A casual survey of all species of *Notropis*, with special emphasis on those with a single row of pharyngeal teeth, suggests that *N. maculatus* is perhaps closest to *N. emiliae*. We note especially certain similarities in the pharyngeal arch, including the long anterior arm (Figs. 2B, C, E, and F), body and dorsal-fin pigmentation, size and position of the mouth, and tuberculation of the snout. The scales along the side of the body in both species are outlined with dark pigment, which produces a distinct cross-hatching effect (Pl. 1A–C). There is a large amount of dark pigment, with a depigmented central area, in the dorsal fin of adult males of *N. maculatus*, as also in adult males of the nominate subspecies of *N. emiliae* (Pl. 1A, C). Nuptial tubercles in *N. maculatus* emphasize the lower surface and side of the head, but, as in *N. emiliae peninsularis*, there is a narrow, interrupted bridge of tubercles on the anterior part of the snout. Finally, both species inhabit quiet, sometimes weedy water. The relationship is not intimate.

Notropis emiliae emiliae (Hay)

Opsopoeodus emiliae. Hay, 1881: 507–508 (original description of genus and species; Artesia, Enterprise, and Macon, Mississippi; type-specimen(s), USNM 27429 from Macon, now apparently lost according to Dr. W. R. Taylor, pers. comm.). Hay, 1883: 71 (Tennessee and Mississippi). Jordan and Gilbert, 1883: 246–248 (in part; description; range). Jordan, 1885: 821 (in part; in list; *Trycherodon megalops* a synonym). Meek, 1889: 438 (Maumee River drainage, Ohio). Jordan, 1889: 163, 166 (lower Wabash River system, Indiana). Gilbert, 1890: 226 (eastern Georgia). Gilbert, 1891: 149, 152 (northern Alabama). Woolman, 1892: 263, 271, 274, pl. 51, fig. 1 (description; records for Kentucky). Hay, 1894: 221 (description; Indiana; *Trycherodon megalops* a synonym). Meek, 1891: 250 (in list; range; Arkansas). Meek, 1894: 78, 92, 94 (records from Arkansas and Oklahoma). Kirsch, 1895: 329, 334–335 (Maumee River drainage, Ohio). Meek, 1896: 343, 347 (records from Arkansas and Oklahoma). Jordan and Evermann, 1896: 247–249 (in part; key; description; range). Evermann, 1899: 307 (Mississippi, Louisiana, and Texas). Forbes and Richardson, 1909: 124–125, fig. 27, map 30 (diagnosis; range; habitat; distribution in Illinois). Meek and Hildebrand, 1910: 263–264, fig. 29 (records for Chicago area). Evermann, 1918: 340 (Kentucky). Dymond, 1922: 64 (Lake Erie). Fowler, 1922: 23 (records for Tennessee and Texas). Fowler, 1924: 404 (description; Beaumont, Texas). Hubbs, 1926: 35 (Lake Erie drainage, Michigan). Ortenburger and Hubbs, 1927: 125 (Oklahoma; *Opsopoeodus osculus* and *Trycherodon megalops* are synonyms). Jordan, 1929: 68, 71 (in part; description; range). Jordan, Evermann, and Clark, 1930: 115 (in part; in list; range). Thompson and Hunt, 1930: 23, 44 (habitat; Champaign County, Illinois). Luce, 1933: 115 (Kaskaskia River, Illinois). O'Donnell, 1935: 480 (Illinois). Greene, 1935: 90 (distribution in Wisconsin). Doan, 1936: 59 (first record for Ontario). Hubbs and Cooper, 1936: 24, 35 (key; habitat; Michigan). Hubbs and Lagler, 1943: 78 (Foots Pond, Gibson County, Indiana). Radforth, 1944: 50, map 20 (zoogeography, Ontario). Fowler, 1945: 113 (synonymy; southern Piedmont and coastal plain). Gerking, 1945: 53, map 31 (habitat; distribution in Indiana). Eddy and Surber, 1947: 156 (description; range; upper Mississippi Valley). Harlan and Speaker, 1951: 75 (Iowa records). Bailey, 1951: 192 (occurrence in Iowa). Cross and Moore, 1952: 402 (Poteau River system, Oklahoma and Arkansas). Bailey, Winn, and Smith, 1954: 124 (Escambia River system, Alabama and Florida; *megalops* a synonym of *emiliae*). Scott, 1954:

57 (Ontario). Carr and Goin, 1955: 52–53 (in part; description; Florida). Bailey, 1956: 331 (Iowa). Harlan and Speaker, 1956: 89 (Iowa records). Illick, 1956: 215–218 (sensory canal system; key). Moore, 1957: 107, fig. 2–59 (in part; key; description; range). Eddy, 1957: 100–101, fig. 249 (in part; key; description; range). Hubbs, 1957: 93, 97 (distribution in Texas). Trautman, 1957: 335–337, fig. 75, map 75 (key; description; habitat; distribution in Ohio). Underhill, 1957: 12 (zoogeography; distribution in Minnesota). Hancock and Sublette, 1957: 44 (upper Kisatchie River drainage, Louisiana). Hubbs and Lagler, 1958: 72, 80, fig. 134 (key; habitat; range). Briggs, 1958: 260 (in part; in list; Florida). Slastenenko, 1958: 181, 220 (key; description; Canada). Cook, 1959: 101–102 (description; habitat; Mississippi). Bailey, 1959: 119, 121 (compared with *Notropis anogenus*). Larimore and Smith, 1963: 324, 330 (Champaign County, Illinois). Smith, 1963: 255 (upper Kaskaskia River system, Illinois). Becker, 1964: 43 (Wisconsin records). Cross, 1967: 83–84 (description; Kansas record). Moore, 1968: 66, fig. 2–48 (in part; key; description; range). Smith-Vaniz, 1969: 30, 53, 131, fig. 21 (key; range in Alabama).

Opsopoeodus emiliae emiliae. Hubbs and Lagler, 1947: 64–65 (supposed difference from *O. emiliae megalops*). Cook, 1953: 195 (type locality; distribution in Mississippi).

Trycherodon megalops. Forbes, in Jordan and Gilbert, 1883: 247 (original description of genus and species; Illinois River at Peoria and Peoria, and Mackinaw Creek [near Peoria]; lectotype, here designated, USNM 28406, 40.4 mm., from "Long L., Peoria, Illinois, coll. Oct. 27, 1879, S. A. Forbes;" paratype, CAS 13513, 35 mm., Long River, Peoria, Illinois).

Opsopoeodus megalops. Jordan and Evermann, 1896: 247–249 (key; description; range). Jordan, Evermann, and Clark, 1930: 115 (in list; range).

Opsopoeodus emiliae megalops. Schrenkeisen, 1938: 107 (distinguishing features; northern race of *O. emiliae*; range). Hubbs and Lagler, 1947: 64–65, fig. 135 (key; habitat; range; supposed difference from *O. emiliae emiliae*). Knapp, 1953: 53, 60, fig. 70 (key; range; Texas). Langlois, 1954: 204–205 (western Lake Erie).

Opsopoeodus osculus. Evermann, 1892: 82–83 (original description; compared with *O. emiliae* and *O. bollmani*; Neches River and Long Lake, near Palestine, Texas; Buffalo Bayou, Kilpers Ponds, and Sims Bayou, near Houston; Dickinson Bayou, Nicholstone, Texas. No type designated, but Evermann and Kendall, 1894:

126 and pl. 19, state that their figure is from the type from Buffalo Bayou, Houston. Dr. W. R. Taylor informs us that USNM 45560, 4 specimens, 37.5 to 43 mm. S.L. from Buffalo Bayou, 6 miles above Houston, includes three pale smaller fish, now removed as USNM 205205, paratopotypes, but he believes that the figure (which was republished by Jordan and Evermann, 1900: fig. 108, p. 3240) is from the largest. We regard this as an acceptable designation of a lectotype, despite the indication (Evermann and Kendall, 1894: 105) that Dickinson Bayou specimens are "types." USNM 125143, 36 specimens 40.6 to 50.4 mm. S.L., and CAS 13514, 4 specimens, from Sims Bayou, near Houston, may be regarded as paratypes of *O. osculus*). Jordan and Evermann, 1896: 247-249 (key; description; range). Evermann and Kendall, 1899: 52 (in part; Florida). Jordan, Evermann, and Clark, 1930: 115 (in list; range). Fowler, 1933: 58 (Louisiana).

Opsopoeodus oscula. Evermann and Kendall, 1894: 83, 105, pl. 19, fig. 3 (Texas records; lectotype designated—see above under Evermann, 1892).

Opsopoeodus emiliae osculus. Schrenkeisen, 1938: 107 (lacks dark pigment in dorsal fin; Texas).

DIAGNOSIS.—A subspecies of *Notropis emiliae* with pharyngeal teeth 5-5; a dark-light-dark pigment pattern in the dorsal fin of adults (see page 8), this character pronounced in breeding males (see Fig. 1, A and B); and a more oblique mouth, forming an angle of 36°-47°, mean 40°, to the ventral plane of the head (Table 5). Nuptial tubercles on the snout of breeding males are arranged in a straplike band extending just behind the upper lip from above the corner of the mouth of one side to the other (Fig. 4A).

VARIATION.—*Notropis emiliae emiliae* exhibits surprisingly little morphological variation throughout its range (see Tables 3, 4, 6). There is considerable variation in the degree of pigmentation in the dorsal

TABLE 5
FREQUENCY DISTRIBUTION OF MOUTH-ANGLE MEASUREMENTS IN *Notropis emiliae*¹

Taxon	Mouth Angle (degrees)									N	Mean
	30-31	32-33	34-35	36-37	38-39	40-41	42-43	44-45	46-47		
<i>N. e. emiliae</i>				8	8	8	3	2	1	30	39.7
Intergrades		3	2	5	10	9	1	1		31	38.3
<i>N. e. peninsularis</i>	1	10	17	1	1					30	34.0

¹ Angle between lower profile of head and anteroventral border of upper lip—see text

fin; however, this is a function of both age and sex, the characteristic dark-light-dark color pattern being best developed in breeding males. The intensity of pigment is at times partly determined by the turbidity of the environment. The obliqueness of the mouth varies considerably, even within a single population.

Notropis emiliae peninsularis, new subspecies

Opsopoeodus emiliae. Jordan and Gilbert, 1883: 246–248 (in part; description; range). Jordan, 1885: 821 (in part; in list). Jordan and Evermann, 1896: 247–249 (in part; key; description; range). Jordan, 1929: 68, 71 (in part; description; range). Jordan, Evermann, and Clark, 1930: 115 (in part; in list; range). Schrenkeisen, 1938: 107 (in part; habits; range; related forms). Reid, 1950: 176 (Orange Lake, Florida). Carr and Goin, 1955: 52–53 (in part; description; Florida). Moore, 1957: 107 (in part; key; description; range). Eddy, 1957: 100–101 (in part; key; description; range). Briggs, 1958: 260 (in part; in list; Florida). Moore, 1968: 66 (in part; description; range).

Opsopoeodus emiliae emiliae. Hubbs and Lagler, 1947: 64–65 (in part; characters; Florida).

Opsopoeodus osculus. Evermann and Kendall, 1899: 52 (in part; Florida).

DIAGNOSIS.—A subspecies of *Notropis emiliae* with pharyngeal teeth 5–4 (Table 1); no pronounced pigment pattern in the dorsal fin (Fig. 1, D); and a less oblique mouth, forming an angle of about 31°–39°, mean 34°, to the ventral plane of the head (Table 5). Nuptial tubercles on the snout of breeding males are arranged in a pair of compact clusters lying behind the upper lip, each extending from above the corner of the mouth upward to before the nostril but not joined to the cluster of the opposite side (Fig. 4, B).

TYPES.—The holotype of *Notropis emiliae peninsularis* is an adult male (UMMZ 197672), 44.5 mm. standard length, collected in St. Johns River at Ft. Gates Ferry, T 12 S, R 26 E, Ocala National Forest, Putnam County, Florida, on April 5, 1941 by Carl L. Hubbs and party. Paratopotypes UMMZ 163356 (9 specimens, 40 to 47 mm.) were taken with the holotype. Dr. Hubbs noted that while still fresh, on April 13, the dorsal and caudal fins of the type series were orange amber.

Counts for the holotype are as follows: anal rays 8; dorsal rays 9; lateral-line scales 38; caudal-peduncle scales 12; predorsal scales 18;

TABLE 6
 MEASUREMENTS OF *Notropis emiliae*
 (Proportions expressed in thousandths of standard length)

Measurement	<i>N. e. emiliae</i>			Intergrades	<i>N. e. peninsularis</i>
	Upper Mississippi ¹	Lower Mississippi, Gulf Coast ²	Atlantic Coast		
Number of specimens	12	12	12	14	12
Standard length (mm.)	33.5–48.5 (42.2)	39–48 (45.4)	37.5–44.5 (41.6)	33–47 (40.9)	38.5–45 (41.0)
Predorsal length	451–495 (471)	448–487 (467)	453–485 (470)	457–494 (472)	456–477 (469)
Dorsal origin to base of caudal	528–577 (555)	523–562 (543)	513–561 (543)	515–562 (543)	518–569 (544)
Prepelvic length	426–484 (458)	446–495 (467)	460–480 (471)	448–494 (470)	440–475 (459)
Preal length	609–658 (633)	627–679 (644)	613–683 (647)	614–667 (640)	597–650 (632)
Head length	233–253 (244)	236–256 (243)	231–253 (243)	227–253 (241)	233–251 (243)
Snout length	54–73 (63)	56–74 (65)	56–69 (63)	56–74 (65)	60–74 (68)
Diameter of orbit	73–88 (80)	70–87 (80)	74–92 (80)	73–87 (81)	76–91 (83)

Mouth gape	42-54 (48)	44-54 (50)	41-56 (46)	40-57 (49)	45-56 (50)
Length of lower jaw	65-80 (74)	69-88 (74)	64-80 (71)	64-75 (69)	67-88 (75)
Greatest body depth	188-243 (223)	193-255 (230)	216-257 (236)	178-237 (209)	190-226 (207)
Dorsal origin to lateral line	118-153 (137)	123-154 (142)	123-145 (134)	112-145 (129)	117-143 (128)
Greatest body width	107-147 (124)	107-146 (125)	110-123 (117)	101-133 (116)	117-136 (127)
Caudal peduncle length	240-278 (256)	223-254 (245)	219-254 (239)	217-260 (243)	228-260 (248)
Caudal peduncle depth	89-116 (100)	96-110 (103)	99-116 (105)	95-114 (101)	93-105 (100)
Length of depressed dorsal fin	233-285 (262)	254-292 (273)	243-300 (264)	242-280 (261)	248-279 (265)
Length of pectoral fin	162-198 (181)	174-198 (184)	162-191 (178)	155-198 (179)	175-200 (184)
Length of pelvic fin	156-194 (172)	162-198 (181)	166-198 (178)	155-194 (175)	168-195 (180)
Length of depressed anal fin	196-235 (215)	205-234 (222)	202-234 (220)	194-237 (215)	202-238 (223)

¹ South to Indiana and Illinois

² North to Tennessee and Missouri

circumferential scales 13-2-11 = 26; pectoral rays 15-15; pelvic rays 8-8; pharyngeal formula 5-4; mouth angle 35°; and vertebrae 38.

The following specimens, all from Florida, are designated as paratypes: **Brevard Co.:** UF 6286 (67), Lake Winder; **DeSoto Co.:** FSU 1421 (3), Joshua Cr., 3.8 mi. S Arcadia, hwy. 17; **Hardee Co.:** FSU 1661 (2), Charlie Apopka Cr., 8.3 mi. S Zolfo Springs, hwy. 17; **Lake Co.:** UF 179 (1), UMMZ 106424 (1), Alexander Spring Run; UF 6279 (2), Alexander Spring Run, below hwy. 445; UF 180 (19), UMMZ 106421 (5), Lake Eustis, east shore; UF 228 (2), UF 546 (10), UF 6277 (11), UMMZ 101682 (2), Lake Eustis; UF 4472 (1), Lake Harris, north shore; UF 6275 (146), Haines Cr., near outlet from Lake Eustis; UF 6276 (81), Lake Eustis, mouth Haines Cr.; **Marion Co.:** UF 6282 (2), Withlacoochee R., Dunnellon; FSU 2139 (3), Withlacoochee R., at Stokes Ferry, 6.8 mi. NNE Hernando, Citrus Co. line; **Osceola Co.:** UMMZ 158637 (1), canal between Alligator and Lizzie lakes; UMMZ 158564 (36), East Tohopekaliga Lake, near St. Cloud; **Putnam Co.:** UF 6264 (42), UF 6265 (42), UF 6266 (46), UF 6267 (52), UF 6268 (5), UMMZ 180659 (35), Little Lake George, Johns Landing; UF 6258 (33), UF 6259 (12), UF 6260 (27), UF 6261 (35), UF 6262 (9), Little Lake George, Orange Point; UF 6269 (35), St. Johns R., Dryton Island, Georgetown; UF 6271 (13), St. Johns R., Welaka; UF 6273 (2), St. Johns R., 1 mi. N Welaka; UF 6274 (8), St. Johns R., Jenerson Pt., between Welaka and Georgetown; UF 6270 (5), UF 6281 (4), Oklawaha R., Davenport Landing; **Seminole Co.:** UMMZ 126288 (3), Lake Monroe, Sanford; **Volusia Co.:** UF 6284 (17), Lake Beresford, 4.1 mi. S Deland.

INTERGRADATION

Specimens of *Notropis emiliae* from the Ochlockonee, Suwannee, St. Marys, and Satilla river systems, Georgia and Florida, are interpreted as intergrades between the nominate and the peninsular subspecies. Identification is based primarily on the pigmentation in the dorsal fin, which is of average intermediacy between the two subspecies (Fig. 1, C). In no case has an intergrade been found to exhibit the extremes of pigmentation found in the two subspecies. The angle of the mouth also is of average intermediacy (Table 5), although this is not readily demonstrable because of the relatively small differences between the two subspecies. Surprisingly, the pharyngeal formula is usually 5-5, as in *N. e. emiliae* (Table 1), hence not intermediate.

Only a few small specimens from the Altamaha and Ogeechee river systems were seen; these are classified tentatively with the typical

subspecies on the basis of geography. Additional specimens need to be studied before the overall zone of intergradation can be accurately determined.

ZOOGEOGRAPHY

Two loci of origin of *Notropis emiliae* may be postulated. The precursor to the species, presumably not greatly different morphologically from *peninsularis*, may have arisen in the Mississippi Valley and later spread into the present range (Fig. 5), with one segment becoming isolated in peninsular Florida. This suggestion implies more extensive differentiation in the mainland than on the peninsula. Consideration of the morphology of the two forms, however, invites an alternative possibility. The peninsular subspecies appears to be more generalized than the typical subspecies in its dorsal-fin pigmentation, less oblique mouth, and pattern of nuptial-tubercle development on the snout. If the hypothesis of dental accretion in *Opsopoeodus* (see above) is correct, then the 5-4 formula in the peninsular form represents an intermediate stage in the transition from a primitive 4-4 in most forms of *Notropis* to 5-5, the derived state. Thus, dentition is concordant with the other generalized features of *peninsularis*, and a peninsular origin for *Opsopoeodus* is the more likely.

The northward movement of *Notropis emiliae* during interglacial periods cannot be ascertained, but since today it penetrates only narrowly into the Great Lakes (Fig. 5) its range probably never extended far to the north. It reached the Lake Erie drainage via the Ft. Wayne glacial outlet (Radforth, 1944: 50), and apparently entered tributaries to Lake Michigan through the Chicago (Greene, 1935: 90) and Fox river outlets.

Notropis emiliae, perhaps because of its preference for quiet, often weedy, waters, is one of the relatively few cyprinids in peninsular Florida. During Pleistocene glacial stages peninsular Florida underwent pronounced areal changes, being larger during advances, when ocean levels were lowered because of water bound in glacial ice, and correspondingly smaller during glacial retreat. Until recently it was believed that the peninsula was completely separated from the rest of southeastern United States at maximal submergence during each interglacial period by the so-called "Suwannee Straits," thought to have occupied the area of the present-day Suwannee River Valley (Fenneman, 1938: 42-47; Cooke, 1945; Neill, 1957: 188; Laessle, 1958). Recent geological findings (Alt and Brooks, 1965), however, indicate that the last unquestioned complete separation of peninsular Florida

occurred during late Pliocene, and that maximum rises in sea level have been progressively less during each succeeding interglacial period. This does not invalidate the idea that differentiation of peninsular and nominate subspecies of *N. emiliae* was precipitated by a salt-water channel across the neck of peninsular Florida, but dates this event as older than was formerly thought. It is well established that peninsular Florida is an area of biological differentiation and endemism. Characteristic freshwater fishes include several cyprinodontids that are restricted to the peninsula (*Jordanella floridae*, *Cyprinodon hubbsi*, *Fundulus seminolis*) or have dispersed narrowly from this source (*Leptolucania ommata*, *Lucania goodei*).

Following Pliocene reconnection of insular Florida and the rest of southeastern United States, *N. e. peninsularis* invaded the neighboring river systems to the north, the Suwannee, St. Marys, Ochlockonee, and Satilla, where it came into contact with the typical subspecies. The resultant area of intergradation has partially interrupted the range of the typical subspecies (Fig. 5). Significantly, the northern limit of the range of *N. e. peninsularis* corresponds closely with that of an endemic peninsular subspecies of largemouth bass, *Micropterus salmoides floridanus* (Bailey and Hubbs, 1949: 31, map 1). The areas of presumed intergradation of the subspecies in *N. emiliae* and *M. salmoides* (Bailey and Hubbs, 1949, op. cit.) do not exactly correspond. However, this difference may be more apparent than real. Intergradation of *M. s. salmoides* and *M. s. floridanus* is irregular, particularly to the north. Bailey and Hubbs (1949: 32) suggest "that a natural orderly situation has been complicated by the extensive stocking of northern *salmoides*."

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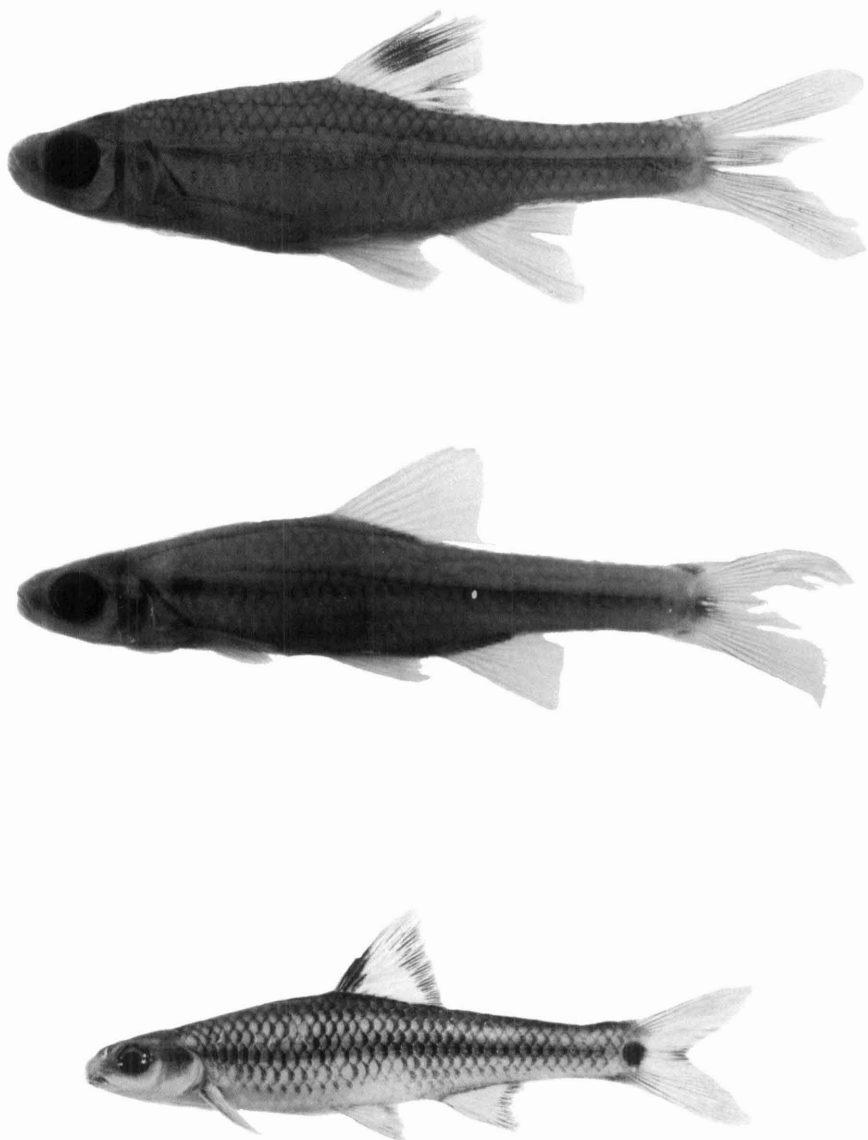


PLATE I

A, *Notropis e. emiliae*, UMMZ 110535, 47.5 mm. S.L., Brazos River system, Texas; B, *Notropis e. peninsularis* (holotype), UMMZ 197672, 44.5 mm. S.L., St. Johns River, 4 mi. above Welaka, Putnam Co., Florida; C, *Notropis maculatus*, FSU 5791, 62.5 mm. S.L., Lake Parker, Polk Co., Florida.

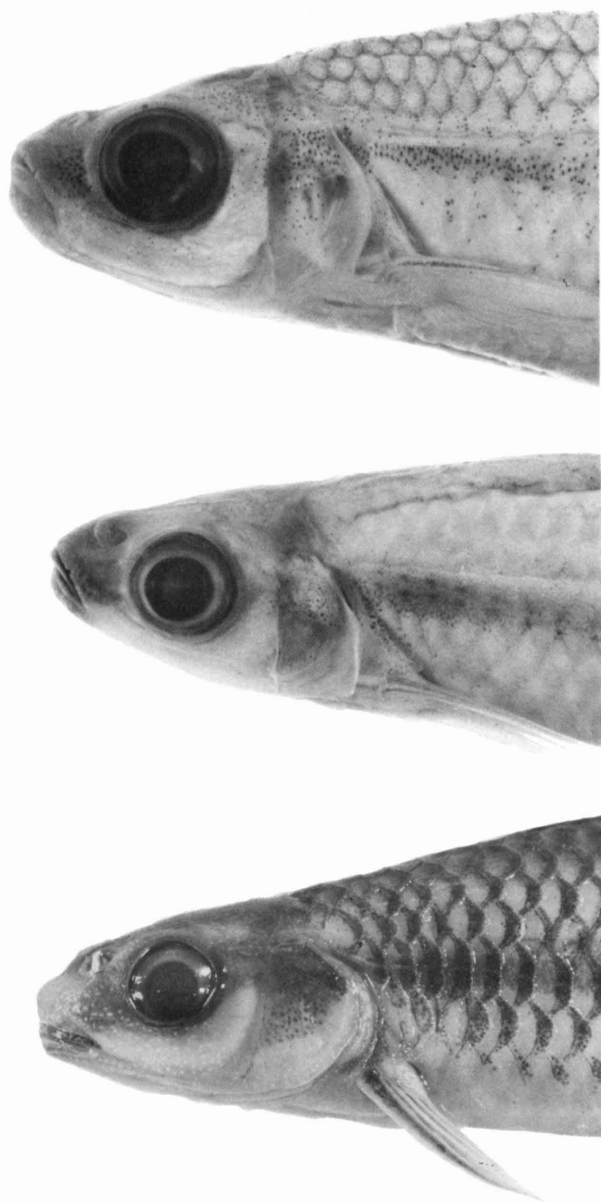


PLATE II

Heads of *Notropis e. emiliae* (A), *Notropis e. peninsularis* (B), and *Notropis maculatus* (C). Specimens and locality data as in Pl. I.

