December 16, 1994

Occasional Papers
Tulane University
Museum of Natural History

Two new darters, *Percina* (*Cottogaster*), from the southeastern United States, with a review of the subgenus

Number 4

OCCASIONAL PAPERS TULANE UNIVERSITY MUSEUM OF NATURAL HISTORY

Henry L. Bart, Jr., Editor

Occasional Papers is a scientific publication of the Tulane University Museum of Natural History dedicated primarily to studies of systematics, natural history, biogeography, and environmental biology. It appears irregularly in consecutively numbered issues. Previously published issues are listed in the back pages.

For information on orders and exchanges, please contact:

The Editor, Occasional Papers
Tulane University Museum of Natural History
Belle Chasse, LA 70037
(504) 394-1711
piscine@mailhost.tcs.tulane.edu

Please consult the instructions for authors inside the back cover for information on style, editorial policy, and format for submission of manuscripts.

Authors are requested to use the following abbreviation when citing this publication: Occ. Pap. Tulane Univ. Mus. Nat. Hist.

Publication of this issue was partially supported by the Mississippi Department of Wildlife, Fisheries and Parks, Mississippi Museum of Natural Science.

Cover photo: Strong River rapids, Simpson Country, Mississippi (type locality of *Percina aurora*), 25 March 1994, by Jayson S. Suttkus.

Two new darters, *Percina* (*Cottogaster*), from the southeastern United States, with a review of the subgenus

Royal D. Suttkus
Tulane University Museum of Natural History
Belle Chasse, LA 70037

Bruce A. Thompson[1,2]
Coastal Fisheries Institute
Louisiana State University
Baton Rouge, LA 70803-7503

Henry L. Bart, Jr.
Tulane University Museum of Natural History
Belle Chasse, LA 70037

ABSTRACT

The subgenus *Cottogaster* Putnam has long been considered monotypic and recent characterizations of it have been based primarily on the channel darter, *Percina copelandi*. In this paper, we describe two new species of *Cottogaster*, revise the characterization to include the wealth of accumulated data on *Percina copelandi* and the two new species, and summarize available information on habitat, biology, and conservation status. *Percina aurora*, from the Pearl and Pascagoula river drainages in Mississippi is distinguished by its large average body size, lack of tubercles and heavy pigmentation of breeding males, high number of marginal spines on the modified belly scales of breeding males, and fully scaled cheek. *Percina brevicauda*, from the Mobile Bay drainage, Alabama, is distinguished by its short fins, heavy pigmentation, tubercular ridges on fins, and low number of marginal spines on the modified belly scales of breeding males, low number of vertebrae, and naked cheeks. We do not consider the subgenus *Cottogaster* to be closely related to subgenus *Imostoma* as previously suggested. We present evidence which suggests a closer affinity to a restricted group of subgenus *Alvordius*.

[1] The order of the junior authors reflects the order of description of the two new forms.

[2] Contribution LSU CFI–94–03 from LSU's Coastal Fisheries Institute.

Introduction

The subgenus *Cottogaster* Putnam, 1863 has been considered as monotypic for a number of decades and recent characterizations of it (Page, 1983; Kuehne and Barbour, 1983) have been based primarily on the channel darter, *Percina copelandi*. The purpose of this paper is to describe two new species of darters that we place in *Cottogaster*. A secondary objective is to revise the characterization to include the wealth of accumulated data on *Percina copelandi* and the two new species.

Putnam (1863) recognized Thompson's (1853) *Boleosoma tessellatum* to be distinct from *B. tessellatum* of DeKay (1842). He erected the genus *Cottogaster* for this form and specified *Boleosoma tessellatum* as type species. The name *copelandi* originated with Jordan (1877a: 9–10) who erected the genus *Rheocrypta* for the channel darter at the time of his original description. He characterized *Rheocrypta* as follows: "allied to *Imostoma* and *Alvordius*. Body rather slender and elongate, with a pretty large, rather long, and somewhat narrowed head, resembling that of *Boleosoma*; mouth small, horizontal, subinferior, with weak teeth in the jaws, five or six teeth on the vomer, and none on the palatines; upper jaw protractile, separated by a distinct furrow from the forehead; two distinct dorsal fins, of which the second is rather smaller than the first and than anal; anal with two distinct spines; ventral region with a series of enlarged plates, as in *Alvordius* and *Percina*, these caducous, in many specimens replaced by a scaleless strip; cheeks naked; opercles with a few scales; lateral line complete."

In the next paragraph Jordan stated, "This genus is perhaps nearest *Imostoma*, with which it agrees in the protractile mouth. It differs from *Imostoma* and agrees with *Alvordius* Grd. in the presence of ventral plates. The name *Rheocrypta* (ῥέω, to flow rapidly; κρυπτός, concealed, i.e., hiding in the rapids) is given in allusion to the peculiar habits of this interesting species." Jordan and Gilbert (1883) placed *Rheocrypta* Jordan in the synonymy of *Cottogaster* Putnam and specified *Boleosoma tessellatum* Thompson as type species.

Subsequent to Jordan's (1877a) description most treatises characterized (genus or subgenus) *Cottogaster* by a single feature, the typical lack of a premaxillary frenum. An additional character, a rudimentary air bladder, was suggested by Hubbs and Lagler (1939:30) but few subsequent workers repeated mention of that character. We follow Winn (1953:26) in his decision that the development of the air bladder is variable and has little value as a distinguishing systematic character.

Materials and Methods

Specimens of the new species and comparative material used are from the collections of Academy of Natural Sciences of Philadelphia (ANSP); Auburn University (AUM); Cornell University (CU); Eastern Kentucky University (EKU); Geological Survey of Alabama (GSA); Illinois Natural History Survey (INHS); Kansas University (KU); Louisiana State University (LSUMZ); Museum of Comparative Zoology, Harvard (MCZ); Northeast Louisiana University (NLU); Ohio State Museum (OSUM); Texas Natural History Collection (TNHC); Tulane University Museum of Natural History (TU); University of Alabama Ichthyological Collections (UAIC); University of Georgia (UGAMNH); University of Michigan Museum of Zoology (UMMZ); University of New Orleans (UNOVC); University of Southern Mississippi (USM); National Museum of Natural History (USNM); and University of Tennessee (UT).

Counts and measurements were made as described in Hubbs and Lagler (1958) except as follows. Transverse body scales were counted from the origin of the anal fin diagonally upward to the base of the spinous dorsal fin. Gill rakers, counted on the anterior arch of either left or the right side, include both dorsal and ventral rudiments. Marginal spines were counted on the modified ventral scales of the breast, pelvic region and the belly. The premaxillary groove and/or frenum was categorized in three ways: 1. deep groove, premaxillaries fully protractile—frenum absent 2. low ridge with only shallow groove present, premaxillaries somewhat protractile—frenum, slight to intermediate 3. no groove, premaxillaries essentially non-protractile—frenum present (narrow). Measurements were made with needle-point dial calipers and recorded to the nearest 0.1 mm. Names used for associated fish species follow Robins et al. (1991), except *Etheostoma chlorosoma* (Simons, 1992).

Data for 17 body measurements, including standard length, were gathered for samples of 25 males and 10 females each from Ohio and Red river system populations of *Percina copelandi* (Ohio River: EKU 542, EKU 592, OSM 943, UT 91.662, Red River: CU 36536, CU 52416, NLU 18390, NLU 18766, NLU 25527, NLU 30418, TU 93159, UT 91.946); 26 males and 10 females from the Pearl River drainage population of *P. aurora* (HOLOTYPE, TU 17732, TU 55249, TU 56493, TU 56615, TU 56852); and (depending on the measurement) from 28–60 males and 10–34 females from the Cahaba River system population of *P. brevicauda* (HOLOTYPE, TU 37661, TU 121402, TU 121415, TU 125420). In most instances, specimens selected for measurement were at or near the height of the breeding condition. Thus, the analysis of body proportions reveals sexual dimorphism within species as well as differences among taxa. Data for 16 body measurements were converted to ratios of standard length. Normality tests were performed on the ratio data grouped by species/population and sex within species/population to assess the appropriateness of using the ratios in direct statistical comparisons. The null hypothesis that the data represented a random sample drawn from a normally distributed population was not rejected in any of the tests. Means were computed for the above groupings and tested for significant differences at the $\alpha = .05$ level using Student-Newman-Keuls multiple range tests.

The mensural data were also subjected to principal components analysis (PCA) to characterize shape differences among the three species. Data for males and females were analyzed separately. PCA was first performed on data for all 17 measurements to illustrate the effect of body size differences among the species. In a second analysis, data for 16 measurements were regressed on standard length and the residuals retained for PCA. This partial regression procedure removed variation in the data attributable to standard length and had the effect of adjusting data for the remaining characters to a common body size. All statistical analyses were performed on a personal computer with Statistical Analysis System (SAS) Inc., software.

In the listings of type material for the two new species each catalog number is followed by the number of specimens examined and the range of standard length (SL) in millimeters, e.g., (8, 35–42). In addition to standard compass directions (with the following "of" deleted), the following abbreviations are used: mi = mile(s), airmi = airmile(s), hwy = highway, rd = road, T = Township, R = Range, Sec = Section. In lists of *Percina copelandi* materials and of non-type specimens of the two new species, the catalog number is followed by the number of specimens examined, enclosed in parentheses. For the sake of completeness and for convenience to the reader we include the names of collectors for all material that predates the year 1900.

Nomenclatural and Systematic Chronology of *Cottogaster*

Thompson (1853: Appendix, 31) figured and described what he thought was *Boleosoma tessellatum* DeKay. In the preface of DeKay's (1842) *Natural history of New York* reference is made to specimens from Lake Champlain sent to DeKay by Thompson. Although the reference provides no clues to the identity of the specimens, Thompson (1853: Appendix) specifically mentions collecting and observing specimens of *B. tessellatum*, so this form may have been among the specimens Thompson sent to DeKay. DeKay's illustration of *B. tessellatum* (plate 20, fig. 57) appears to be a composite of *Etheostoma olmstedi* Storer (=*B. tessellatum* DeKay, Agassiz 1850) and *Percina copelandi*. The pattern on the side appears to be more like the lateral blotches of *P. copelandi* than the X- or W-shaped markings of *E. olmstedi*. If DeKay's count for the anal fin of "A.10 of which the first two are short" is interpreted as two spines plus eight rays, then this too is more typical of *P. copelandi* (*E. olmstedi* typically has one anal spine, Cope 1868). The size of *B. tessellatum*, as inferred from DeKay's illustration (denoted "natural size") agrees with *E. olmstedi*, but is large for *P. copelandi*. This and other evidence from DeKay's description of *B. tessellatum* (e.g., "occurs in most of the freshwater streams of the state") leads us to believe that he was in part referring to the form recognized today as *E. olmstedi* Storer. The contradictory evidence presented above, though anecdotal (DeKay's original specimens of *B. tessellatum* are no longer extant, Collette and Knapp, 1967), causes us to wonder whether DeKay's description of *B. tessellatum* was also partly based on specimens of *P. copelandi* provided by Thompson. Thompson's (1853) illustration of *B. tessellatum* leaves little doubt that his "Darter" was in fact *P. copelandi*.

Putnam (1863: 4–5) recognized Thompson's species as distinct from *B. tessellatum* DeKay and proposed a new genus, *Cottogaster*, thus *Cottogaster tessellatus*. Jordan (1876: 222) placed *B. tessellatum* Thompson, nec DeK., Vermont Darter, L. Champlain, under subgenus *Cottogaster* Putnam, genus *Boleosoma*. Jordan and Copeland (1877) listed *Boleosoma tessellatum* Thompson nec DeKay as a doubtful species under *Boleosoma* DeKay, 1842. Jordan and Gilbert (1877: 93) listed *Cottogaster* Putnam and gave *Boleosoma tessellatum* Thompson, 1853 as the type species. Jordan (1877a: 7) in his description and discussion of *Hadropterus tessellatus* stated that Putnam (1863) considered his *Cottogaster tessellatus* to be a species of *Boleosoma*. We believe Jordan misinterpreted what Putnam said. Putnam said, "General form of body, and position of mouth as in *Bolesoma*." Then he erected the genus *Cottogaster*, gave a brief description of it, gave the full name *Cottogaster tessellatus* Putnam, MS. 1860, and then placed *Boleosoma tessellatum* Thompson, App. Hist. Vt., p. 31, 1853 (not of DeKay) as a synonym. Had Putnam believed that Thompson's species was a *Boleosoma* he would have substituted a new species name and retained it in the genus *Boleosoma*. Collette and Knapp (1967) determined *Hadropterus tessellatus* Jordan (1877a) to be = *Etheostoma variatum* Kirtland. No further discussion of *Hadropterus tessellatus* is necessary.

Jordan (1877a: 9) described a new genus and species of darter from the White River, Indiana. He named this darter *Rheocrypta copelandi* and stated that *Rheocrypta* is allied to *Imostoma* and *Alvordius*. Further on he stated that *Rheocrypta* perhaps is nearest to *Imostoma*, with which it agrees in the protractile mouth. Then he said it differs from *Imostoma* and agrees with *Alvordius* Girard in the presence of ventral plates. Jordan (1877b: 311, 376) placed [? > *Cottogaster* Putnam, Bull. M.C.Z., 1863, 4. (Type *B. tessellatum*, Thompson.)] in synonymy of *Boleosoma* DeKay, N.Y. Zoology, 1842, 20. (Type *B. tessellatum*). On page 376 he listed *Rheocrypta copelandi* as rare in the White River of Indiana. Jordan (1878a: 82) listed *Rheocrypta copelandi* in his tabulation of species in the Ohio River basin. Jordan (1878b: 438) listed *Rheocrypta copelandi* in the Wabash Valley. Jordan (1878c: 222) listed *Rheocrypta copelandi* with a brief description; Jordan (1880: 222, 3rd edition) and Jordan (1884: 222, 4th edition) repeated the same information as in the (1878c) 2nd edition of the Manual of Vertebrates.

Jordan (1882: 969) repeated the name *Cottogaster copelandi*. Jordan and Gilbert (1883: 497–498, 511) in their *Synopsis of the fishes of North America* placed *Rheocrypta* Jordan in the synonymy of *Cottogaster* Putnam and specified the type species as *Boleosoma tessellatum* Thompson.

On page 498 they furnished a description of *Cottogaster copelandi* and it is interesting that in the second sentence they stated, "Head rather large and long, somewhat narrowed, resembling that of *Boleosoma*." Immediately below the characterization of *C. copelandi* they described a new species, *C. putnami*, from Lake Champlain based on specimen USNM 1314. Jordan (1885: 78–79, or 866–867) listed *Cottogaster copelandi* and *Cottogaster putnami*. Jordan and Eigenmann (1886: 69) again used the name *Cottogaster copelandi*. Jordan and Gilbert (1886: 9, 12) listed *Cottogaster copelandi* from tributaries to the Arkansas River near Fort Smith, Arkansas, and stated that it was the first record other than the original locality in the White River at Indianapolis, Indiana. They listed additional specimens of *Cottogaster copelandi* from the Washita River at Arkadelphia and Saline River at Benton, Arkansas. Some of these specimens were deposited at Indiana University and were part of the material reported in the 1886 paper. Dr. Reeve M. Bailey informed one of us (R.D.S.) in a letter dated 6 April 1976 that specimens formerly cataloged as *Cottogaster copelandi* in the Indiana University collection and subsequently recataloged into the University of Michigan collection were reidentified as follows:

I.U. No.	UMMZ No.	Locality	RMB Identification
4642	198762	Ark: Saline R. Benton Co.	*E. stigmaeum* (part)
4642	198757	Ark: Saline R. Benton Co.	*E. chlorosoma* (part)
4643	198758	Ark: Washita R. Arkadelphia	*E. chlorosoma*

Jordan (1888: 121–134) in his Manual of Vertebrate Animals, 5th Edition, placed all darters, including *copelandi* and *putnami*, in the genus *Etheostoma* Rafinesque. Henshall (1889: 126) used *Etheostoma copelandi* following Jordan's Manual, 5th Edition.

Jordan (1890: 164, 167) reported *Etheostoma copelandi* from Wabash River at Vincennes and from Wabash River at Terre Haute, Indiana. One lot from the latter locality was reidentified as follows:

I.U. No.	UMMZ No.	Locality	RMB Identification
5126	198759	Ind: Wabash R. Terre Haute	*E. gracile*

Meek (1891: 127, 139) reported three specimens of *Etheostoma copelandi* from Shoal and Hickory creeks, Neosho, Missouri, and seven specimens from the Ouachita River near Crystal Springs, Arkansas. One lot from the former locality was reidentified as follows:

I.U. No.	UMMZ No.	Locality	RMB Identification
5563	198763	Mo: Shoal & Hickory Cr. Neosho	*E. stigmaeum*

Gilbert (1891: 155) reported *Etheostoma copelandi* from the Black Warrior at Tuscaloosa (= *Percina brevicauda*). Also he stated that he was no longer able to distinguish *putnami* from *copelandi* and placed *putnami* as a synonym. McCormick (1892: 29) reported *E. copelandi* from Lorain County, Ohio. Woolman (1892: 253, 259) reported lateral-line scale counts for *Etheostoma copelandi* from the lower and upper Green River in Kentucky and questioned whether *copelandi* and *putnami* were distinct species. Kirsch (1893: 265) reported one specimen of *Etheostoma copelandi* from Obeys River, near Olympus, Tennessee. Attempts to locate the specimen have been unsuccessful. Garman (1894: 43) listed two literature records for *Etheostoma copelandi*.

Hay (1894: 267, 269) was the first to break ranks with Jordan's (1888) placement of the darters, including *copelandi*, in the genus *Etheostoma*. However, Hay's placement of *Boleosoma*, *Vaillantia*, *Ulocentra*, *Cottogaster*, and *Imostoma* of Jordan and Gilbert's (1883) "Fishes of North America," in the genus *Boleosoma* DeKay did not resolve the systematic position of *Cottogaster* and in fact no one followed this systematic arrangement.

Boulenger (1895: 90–92) placed *Boleosoma* DeKay, *Arlina* Girard, *Estrella* Girard, *Cottogaster* Putnam, *Rheocrypta* Jordan, *Imostoma* Jordan, *Vaillantia* Jordan, and *Etheostoma*, in part., Gilbert under genus *Boleosoma*. Then in his listing of species in the genus *Boleosoma* he included *copelandii* and *shumardii* (with '*ii*' ending).

Meek (1895: 90, 91, 93) repeated the records of *Etheostoma copelandi* of Jordan and Gilbert (1886) and of Meek (1891) and thus a perpetuation of misidentifications of Arkansas and Missouri specimens as indicated above. Moreover, Evermann and Kendall (1895: 469, 471) repeated Meek's (1891) records of *Etheostoma copelandi* from Shoal Creek, Missouri and thus identification is suspect.

Kirsch (1895: 331) reported *Etheostoma copelandi* from the Maumee River at Toledo, Ohio. The species apparently no longer exists there; Trautman (1957) reported that the last specimens were taken in 1922.

Jordan and Evermann (1896b, pt. 1: 1045–1046, 1049) discontinued the practice (initiated with Jordan 1888) of placement of all darters in the genus *Etheostoma* Rafinesque. They again recognized the genus *Cottogaster* Putnam and subdivided it into two subgenera, *Cottogaster* Putnam and *Imostoma* Jordan. *Cottogaster uranidea* Jordan and Gilbert and *Cottogaster copelandi* (Jordan) were placed in the subgenus *Cottogaster* and a single species, *Cottogaster shumardi* (Girard), was placed in the subgenus *Imostoma*. They continued to recognize *putnami* as a subspecies of *copelandi* on the basis of larger scales (44–48) versus 53–56 lateral-line scales for *copelandi*, even though they cited Gilbert (1891) and Woolman's (1892) remarks in footnotes. On page 1049, *Ulocentra gilberti* Evermann and Thoburn was described as a new species and included under the genus *Ulocentra*. In the description of *gilberti* reference was made to "coloration much as in *Cottogaster copelandi*."

Evermann and Kendall (1898: 129) described *Cottogaster cheneyi* from the Racket [=Raquette] River, Norfolk, New York. They said it was most closely related to *Cottogaster shumardi*. Jordan and Evermann (1898, pt. 3: 2851–2852) presented a full description of *Cottogaster cheneyi*.

In Jordan's 8th (1899), 9th (1904), 10th (1910), 11th (1914), and 12th (1916) editions of manual of vertebrates all darters are included under the genus *Etheostoma* in the text, but in the appendices the nomenclatural arrangement of the darters is as presented in Jordan and Evermann (1896b, pt. 1).

Jordan and Evermann (1900, pt. 4: pl. 169, figures 445, 446) illustrated *Cottogaster cheneyi* and *Ulocentra gilberti*. Thereafter most references followed Jordan and Evermann in the use of the generic name *Cottogaster*: Evermann (1902: 96); Bean (1903: 509–511); Nash (1908: 94–95); Evermann and Hildebrand (1916: 449, and *Ulocentra gilberti*, p. 450); Evermann (1918: 356, 365, 367); Jordan (1919: 328, 390); Conger (1920: 31); Turner (1921: 49–50, 56); Dymond (1922: 71); Hubbs (1926: 56, 61, "*C. putnami* appears to be inseparable from *C. copelandi*"). Hubbs and Greene (1928: 382–384, 391, revised the thinking expressed by Hubbs (1926) and resurrected the genus *Rheocrypta* for *copelandi*. They retained *Cottogaster* for *putnami* and treated *C. cheneyi* as a synonym of *C. putnami*.

Jordan (1929, 13th ed.: 156–157, 159) erected a new genus, *Anemoces*, for the species *gilberti*, that was formerly described and considered as a species of *Ulocentra*. Jordan continued the use of the name *Cottogaster* for *copelandi* and considered *putnami* as a subspecies of *copelandi*. Further, he based his description of *C. c. putnami* on the account of *C. cheneyi* by Evermann and Kendall and added that it is, "a similar species probably identical with *C. putnami*."

Hubbs and Ortenburger (1929: 101) corrected the error made by Hubbs and Greene (1928) with regards to *copelandi* as generically distinct from *C. putnami* and added that, "The two forms now appear to be at most subspecifically distinct."

Greeley (1929: 176) reverted back to the use of *Rheocrypta copelandi* as the name for Copeland's darter, presumably because of Hubbs and Greene's (1928) paper. Greeley (1930: 84–85, 89) returned to the use of *Cottogaster copelandi* for the same species.

Hubbs (1930: 433–434) presented a fuller explanation, than that in the Hubbs and Ortenburger paper (1929), of the errors committed in the Hubbs and Greene (1928) paper and said that even subspecific distinction of *C. putnami* from *C. copelandi* was questionable.

Jordan, Evermann, and Clark (1930: 285–286) listed *Cottogaster copelandi* (Jordan) and *Cottogaster putnami* as two separate species with the remark that *C. putnami* probably intergraded with *C. copelandi*. They listed *Ulocentra gilberti* Evermann and Thoburn (apparently *Anemoces* Jordan had a very short life) and *Cottogaster cheneyi* Evermann and Kendall as *Imostoma gilberti* and *Imostoma cheneyi*. Thus they retained four species that eventually were reduced to a single species.

Greeley and Greene (1931: 91) used the name *Cottogaster copelandi* for St. Lawrence River, New York specimens and Greeley and Bishop (1932: 89) continued the use of *Cottogaster copelandi* for Oswegatchie and Black river, New York specimens. Fish (1932: 373) gave the name *Rheocrypta copelandi* Jordan first and then in brackets gave the name *Cottogaster copelandi*. Greeley (1934: 106, pl. No. 11), used the name *Cottogaster copelandi* and this same combination was applied by Welter (1938: 67) and Blatchley (1938: 89).

Bangham and Hunter (1939: 406) presumably were not current with their fish nomenclature and used the name *Rheocrypta copelandi* in their article on fish parasites of Lake Erie.

Kuehne (1939: 92); Hubbs and Lagler (1939: 30); Hubbs and Lagler (1941: 70, 74); Gerking (1945: 88, Map 33); and Hubbs and Lagler (1947: 83, 87) used the name *Cottogaster copelandi* and referred to the species as the river darter.

Bailey (1951: 229–231) proposed a reduction to five genera of darters: *Hadropterus, Percina, Crystallaria, Ammocrypta*, and *Etheostoma*. Thus by inference *Cottogaster* was reduced to subgeneric status under *Hadropterus*.

Cross and Moore (1952: 408), which may have been in press at the time Bailey's paper was published, used the name *Cottogaster copelandi* for the river darter. Winn (1953: 26–27) at Reeve M. Bailey's suggestion, studied the characters that were considered as a basis for the generic status of *Cottogaster*. He concluded that there was insufficient evidence to consider *Cottogaster* as a monotypic genus, and that *copelandi* should be referred to the genus *Hadropterus*. Following Winn (1953) subsequent authors used the new combination, *Hadropterus copelandi*. Legendre (1954: 5) suggested the common name channel darter for *Hadropterus copelandi*.

Bailey, Winn, and Smith (1954: 139–140) further reduced darter genera from five to the currently recognized three. Bailey assumed responsibility for the reduction of *Hadropterus* Agassiz, 1854 to the synonymy of *Percina* Haldeman, 1842. Scott (1955: 151) used the name *Hadropterus copelandi* for the channel darter.

Bailey and Gosline (1955: 10, Table 1, 37) recognized *Cottogaster* as one of eight subgenera in the genus *Percina*.

Schelske (1957: 49) used the name *Hadropterus copelandi*. Trautman (1957: 549–551); Moore (1957: 178, 182); and Winn (1958a: 202) used the name *Percina copelandi*. Winn (1958b: 186, Figure 7) used *Hadropterus copelandi* in the text and then, in his phylogenetic tree (p. 186), placed *P. copelandi* as a species in the subgenus *Imostoma*, genus *Percina*. Hubbs and Lagler (1958: 103, 107, Figure 209) remained with *Hadropterus copelandi* for the channel darter.

The combination *Percina copelandi* appeared in Clarke, Breukelman, and Andrews (1958: 169); Metcalf (1959: 379, 388, 393–394); Blair (1959: 2, 5, 8, 10, 12); Bailey et al. (1960: 29); Deacon (1961: 400); Scott (1963: 124); Collette (1965: 582); New (1966: 28); Collette and Knapp (1967); Cross (1967: 296–297); Branson (1967: 143); Moore (1968: 135, 138); Scott and Crossman (1969: 69); Bailey et

al. (1970: 38); Pflieger (1971: 428, 546, Map 167); Jenkins, Lachner, and Schwartz (1972: 55, 97); Olmsted, Hickman, and Cloutman (1972: 16); Comiskey and Etnier (1972: 143); Miller and Robison (1973: 219–220); Buchanan (1973: 55, Map 184); Scott and Crossman (1973: 801–802); Douglas (1974: 372, 376–377, in part); Page (1974: 66–68, 70–72, 74–82, 84–86); Cloutman and Olmsted (1974: 264); Pflieger (1975: 283, 305–306); Clay (1975: 295, 298–299); and Cross and Collins (1975: 152).

The only exceptions to the placement of *copelandi* in *Percina* we are aware of during the period 1958–1975 were Hoffman (1970: 380, 2nd printing) who used *Cottogaster copelandi* for Copeland's darter in his *Parasites of North American Freshwater Fishes* and Hubbs and Bryan (1975: 623–625) who used the name *Hadropterus copelandi* for the channel darter. Thereafter, only the name *Percina copelandi* was used (Denoncourt, 1976: 58; Page 1976: 256–257, 259–260, 263; Cloutman and Olmsted 1976: 40–41, 106, Map 83; Starnes et al. 1977: 784; Page 1977: 472; Jenkins and Musick 1980: 353, 362; Gilbert and Burgess 1980: 721, in part; Robins et al. 1980: 41; Werner 1980: 165; Burr 1980: 79; Page 1981: 4, 6–7; Trautman 1981: 633–635; Branson et al. 1981: 81; Warren 1981: 135; Cooper 1983: 202; Page 1983: 44; Kuehne and Barbour 1983: 12, 48, in part, pl. 4; Burr and Page 1985: 313; Starnes and Etnier 1985: 346; Underhill 1985: 113; Hocutt, Jenkins, and Stauffer, Jr. 1985: 177; Cross, Mayden, and Stewart 1985: 371; Smith 1985: 316, 340; Burr and Warren, Jr. 1986: 324; Coad 1987: 49; Mayden 1987: 213; Johnson 1987: 25, 30, 34, 40; Robison and Buchanan 1988: 448–449; Bailey and Etnier 1988: 3, 6; Facey and La Bar 1989: 3, 20, 23; Gilbert and Walsh 1991: 14; Etnier and Starnes 1991: 129; Robins et al. 1991: 50; Burkhead and Jenkins 1991: 393–394, pl. 156; Page and Burr 1991: 282, pl. 39, map 321, in part; Campbell 1992: 4; Coburn and Gaglione 1992: 995–996, 1000).

In summation, the period between 1863 and 1890 understandably was one of confusion with regards to darter systematics because of the rapidly emerging new descriptions and new distributional information. Jordan's (1888) placement of all darters known at that time in the genus *Etheostoma* Rafinesque was a revolutionary change in thinking. He was followed almost without exception until 1896. In *The Fishes of North and Middle America* (1896b, pt 1), Jordan and Evermann discontinued the placement of all darters in the genus *Etheostoma*. New groups of species were formed, subgenera were elevated to genera, new names were proposed, etc., and the generic name *Cottogaster* was reestablished. Collette and Knapp (1967) determined *Cottogaster cheneyi* Evermann and Kendall, *Cottogaster putnami* Jordan and Gilbert, and *Ulocentra gilberti* Evermann and Thoburn to be synonyms of *Percina (Cottogaster) copelandi* (Jordan).

Our current understanding of the subgeneric groups of darters in the genus *Percina* is based primarily on Bailey (1951), Bailey, Winn, and Smith (1954), Bailey and Gosline (1955), Bailey and Etnier (1988), Page and Whitt (1973a, b), and Page (1974, 1976, 1981, and 1983).

Percina copelandi (Jordan, 1877)
Channel Darter
Figures 1, 4, 7, and 8

Rheocrypta copelandi. Jordan, 1877a: 9 (original description, White River, 5 miles N Indianapolis, Indiana).

Cottogaster putnami. Jordan and Gilbert, 1883: 498 (original description, Westport Br. Lake Champlain, New York).

Ulocentra gilberti. Evermann and Thoburn in Jordan and Evermann, 1896: 1049 (original description, Clinch River at Walker's Ford, Tennessee).

Cottogaster cheneyi. Evermann and Kendall, 1898: 129, pl. 8, fig. 8 (original description, Racket [Raquette] River near Norfolk, St. Lawrence County, New York).

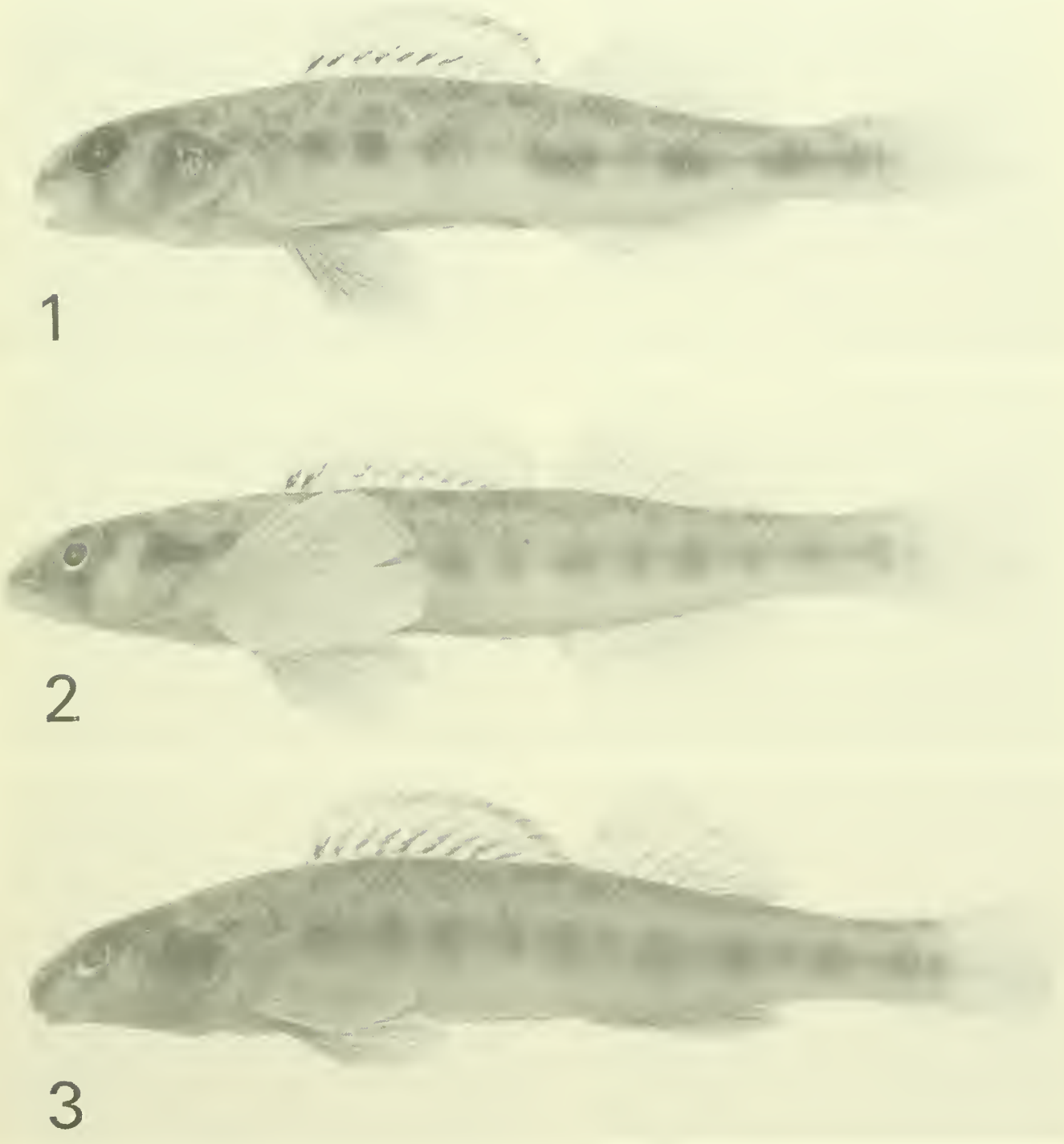
LECTOTYPE: Adult male, USNM 20143, designated by Collette and Knapp, 1967 (examined by us).

PARALECTOTYPES: Adult males, USNM 197996, removed from USNM 20143; adult male 23461, designated by Collette and Knapp, 1967 (examined by us). Adult male, MCZ 24392, and BMNH 1880.1.21.36–37 (2♂♂, 43–45), designated by Collette and Knapp, 1967 (not examined by us).

We present data (Table 1) for some of the type specimens of nominal species of the subgenus *Cottogaster* that are currently housed in the National Museum of Natural History (USNM).

Material from the Great Lakes region, Ohio River system, Cumberland and Tennessee river systems, and Arkansas and Red river systems is listed in the following order: Great Lakes, from eastern Michigan to western Vermont and southern Quebec; Ohio River system, from Wabash River system of western Indiana to Muskingum River system of eastern Ohio, from western Kentucky to eastern Kentucky and western West Virginia and from central to eastern Tennessee; Arkansas River system from central to eastern Kansas and southwestern Missouri, from eastern Oklahoma to western Arkansas; and Red River system from southeastern Oklahoma to southwestern Arkansas and north central Louisiana. All material listed (a total of 2017 specimens) was examined by us.

GREAT LAKES REGION. MICHIGAN. MONROE COUNTY: UMMZ 138009 (12), Huron River, 1 mi NW Rockwood, 19 October 1941. **WAYNE COUNTY:** UMMZ 162976 (11), Detroit River at Sugar Island, 9 September 1952. **ONTARIO. ESSEX COUNTY:** UMMZ 130893 (3), Detroit River opposite south end Bois Blanc Island, about 1 mile S Amherstburg, 30 August 1940. **MICHIGAN. HURON COUNTY:** UMMZ 91400 (8), Saginaw Bay at Lone Tree Island, 6 August 1930; UMMZ 92209 (20), 12 September 1930; UMMZ 91168 (10), Saginaw Bay 1/4 mi N Fish Point, 10 July 1930. **ARENAC COUNTY**: UMMZ 91349 (13), Saginaw Bay at Point Lookout, 30 July 1930. **IOSCO COUNTY:** UMMZ 73136 (15), Au Sable River immediately below Foote Dam, 30 April 1925. **ALCONA COUNTY:** UMMZ 174668 (1), Pine River (T25N, R8E, Sec 36), 5 August 1957. **ALPENA COUNTY:** UMMZ 67303 (8), Devil River below railroad bridge at Ossineke (T29N,



Figures 1-3. *Percina* species of the subgenus *Cottogaster*. 1. *P. copelandi*, CU 52416, adult male 45mm SL. Blue River at Hwy 99 bridge in Connerville, Johnston Co., Oklahoma. 2. *P. aurora*, TU 101392, holotype, adult male, 60mm SL. Strong River, tributary to Pearl River, 2 mi W Pinola, Simpson Co., Mississippi. 3. *P. brevicauda*, TU 101393, holotype, adult male, 46mm SL. Cahaba River, tributary to Alabama River, 3.2 mi W Helena, Shelby Co., Alabama. Photos by Jeanne R. Suttkus.

R8E, Sec 12 and 13), 28 August 1925. **CHEBOYGAN COUNTY:** UMMZ 79040 (12), Black River between Black Lake and city of Cheboygan at power dam, 13 June 1926; UMMZ 116208 (17), Cheboygan River below paper mill dam at Cheboygan, 2 July 1937; UMMZ 162988 (15), Cheboygan River at Cheboygan, 1/4 mi below dam, 2 July 1951. **OHIO**. USNM 69496 (75), [Lake Erie] Kelley Island bathing beach, collected by Cloudsley M. Rutter, 9 July 1894; USNM 69935 (89), **[OHIO] PENNSYLVANIA**. Lake Erie at Catawba collected by Cloudsley M. Rutter, 25 July 1894. **OHIO**. UMMZ 177547 (17), Lake Erie, north shore South Bass Island, August 1930. **ONTARIO**. UMMZ 85919 (34), Lake Erie at Fish Point, Pelee Island, 21 July 1928. **NEW YORK**. USNM 69965 (15), Canadaway Creek at Dunkirk, collected by Albert J. Woolman, 5 August 1893; USNM 69964 (28), Canadaway Creek at Dunkirk, collected by Cloudsley M. Rutter, 28 June 1894. **ST. LAWRENCE COUNTY:** USNM 48781 (1), lectotype, USNM 48782 (4), paratypes, USNM 126978 (4), paratypes, *Cottogaster cheneyi* (= *Percina copelandi*), Racket [Raquette] River at Norfolk, collected by Barton W. Evermann and Barton A. Bean, 18 July 1894; UMMZ 95803 (1), Sawyer Creek (tributary 68 to Oswegatchie River, 1/4 mile above mouth, 5 June 1931; UMMZ 95644 (2), St. Lawrence River, 3/4 mile below Ogdensburg hatchery, 6 June 1931; UMMZ 95597 (4), St. Regis River at Hogansburg, below dam, 15 July 1930. **[ESSEX COUNTY]**: USNM 1314 (1), lectotype, USNM 198000 (27) paralectotypes, *Cottogaster putnami* (= *Percina copelandi*), UMMZ 86458 (5) (formerly MCZ 24538 + 24610), Lake Champlain at Westport Brook, all collected by Spencer F. Baird, 12 September 1853. **CLINTON COUNTY**: UMMZ 140505 (6), (two questionable), Lake Champlain in first bay north of Plattsburg, 31 May 1928. **VERMONT. RUTLAND COUNTY:** MCZ 60631 (52), Poultney River at West Haven, from Coggman Bridge downstream about 0.8 mile, 25–29 July 1983, MCZ 62167 (11), 25–29 July 1983. **QUEBEC**. UMMZ 133760 (1), Chateauguay River at base of dam, tributary to Lake St. Louis of St. Lawrence River, 15 May 1941; UMMZ 142921 (1), River St. Francois, 3 miles SE Pierreville, 12 July 1944.

OHIO RIVER SYSTEM. INDIANA. USNM 20143 (1), lectotype *Rheocrypta copelandi* (= *Percina copelandi*), USNM 23461 (1), paralectotype, USNM 197996 (1), paralectotype, White River 5 miles N Indianapolis, collected by David S. Jordan and Herbert E. Copeland; USNM 40964 (1), Wabash River at Terre Haute, collected by David S. Jordan, 1888; USNM 66888 (1), Wabash River at Terre Haute, collected by Barton W. Evermann, no date; USNM 40982 (1), Wabash River at Vincennes, collected by David S. Jordan and Charles H. Bollman, 1888; UMMZ 198769 (1), Wabash River at Vincennes, no collector named, no date, Indiana University Museum No. 4984; USNM 40970 (1), Wabash River at New Harmony, collected by David S. Jordan, 1888. **POSEY COUNTY**: TU 19291 (1), Wabash River at old dam, 4 miles SW New Harmony, 28 August 1958. **OHIO. HAMILTON COUNTY**: OSUM 5221–A (3), Ohio River at mouth of Miami River, 16 October 1942; OSUM 10571 (4), Miami River near mouth, 26 May 1931, OSUM 10566 (10), White Oak Creek, 17 August 1930. **LAWRENCE COUNTY:** OSUM 597 (3), Ohio River at dam 29, Perry Township, 22–23 August 1939. **WASHINGTON COUNTY:** OSUM 10565 (7), Muskingum River, 29 September 1929. **MUSKINGUM COUNTY:** OSUM 943 (10), Muskingum River, Washington Township, 19 October 1939. **KENTUCKY. CALLAWAY COUNTY:** UMMZ 202531 (5), Tennessee River at head of Blood Island, Quadrangle 18 NE, 22 October 1942. **HART COUNTY:** UMMZ 88021 (4), Green River, 27–28 August 1929. **GREEN COUNTY:** TU 19388 (2), Green River at Kentucky Hwy 88, 3.8 mi ENE Donansburg, 7 September 1958; UMMZ 198767 (4), Green River at Greensburg (Indiana University Museum No. 4839), collected by Albert J. Woolman, 7–8 August 1890; UMMZ 165305 (1), Green River at Greensburg, 5 April 1953. **CUMBERLAND COUNTY:** UMMZ 177905 (2), Cumberland River, 6 to 9 mi NE Burkesville, 12 July 1956. **OWSLEY COUNTY:** EKU 596 (4), South Fork Kentucky River at south edge of Booneville, 26 June 1971; EKU 602 (1), South Fork Kentucky River at Eversole, 19 June 1971; UMMZ 177829 (17), Redbird Creek at mouth of Sexton Creek, 8 mi N Oneida, 25–26 May 1956. **LEE COUNTY:** EKU 567 (1), Middle Fork Kentucky River at Tallega, 24 June 1972. **BREATHITT COUNTY**: EKU 592 (10), Middle Fork Kentucky River at Kentucky Hwy 30, 1 July 1972, EKU 593 (2), 6 January 1970; UMMZ 154420 (1), Quicksand Creek, 3.8 mi above mouth, 3.5 mi NE Quicksand, 6 April 1947; TU 120014 (3), Buckhorn Creek, 0.4 mi NE of Kentucky Hwy 476, 19 June 1978. **LESLIE COUNTY:** EKU 552 (2), Middle Fork Kentucky River at Hyden, 22 September 1973. **PENDLETON COUNTY:** EKU 341 (1), Licking River at Butler, Kentucky Hwy 609, 4 August 1964. **NICHOLAS COUNTY:** UMMZ 171460 (18), Licking River at Kentucky Hwy 32, at confluence of Licking River and Cassady Creek, 12 September 1955. **FLEMING COUNTY:** EKU 542 (65), Licking River at covered bridge, Kentucky Hwy 11, 10 November 1973. **ROWAN COUNTY:** UMMZ 126946 (5), Licking River near Farmers, 7 October 1939; EKU 134 (15), Licking River at Kentucky Hwy 60, at county line, 4 October 1968. **WEST VIRGINIA. KANAWHA COUNTY:** UMMZ 119356 (6), Kanawha River at mouth of Paint Creek, 1 August 1935. **TENNESSEE. SCOTT COUNTY:** UT 91.425 (30), Big South Fork Cumberland River at mouth of Station Camp Creek, 16 and 22 September 1968, UT 91.662 (7), 20 May 1972; UT 91.427 (17), Big South Fork Cumberland River at or near Leatherwood Ford, 17 July, 30 August, and 12 September 1968; INHS 75555 (12), North Whiteoak Creek, 0.5 mi above Big South Fork Cumberland River, 5 July 1968; UT 91.419 (37), Clear Fork River at Burnt Mill bridge about 3.8 mi above mouth, 24 July 1968. **UNION COUNTY:** UMMZ 113025 (1), Bull Run Creek, 3 October 1936. **ANDERSON COUNTY:** UMMZ 104209 (2), creek between Norris and Andersonville, 5 May 1937. **CLAIBORNE COUNTY:** UT 91.299 (6), Powell River at US Hwy 25E, 25 January 1969 and Powell River, 3.5 mi SW US Hwy 25E bridge at Southern railroad trestle, 2 October 1970. USNM 47531 (1), holotype, USNM 125373 (1), paratype, *Ulocentra gilberti* (= *Percina copelandi*), Clinch River at Walker's Ford, near Tazewell, collected by Barton W. Evermann, Josiah T. Scovell, and R. R. Gurley, 12 October 1893. **HANCOCK COUNTY:** TU 95686 (2), Clinch River at Frost Ford, UT 91.1214 (26), 1 May 1976; UT 91.318 (9), Clinch River at gravel shoal 0.3 mi below bridge at Kyles Ford, 20 June 1969, and Clinch River 4.9 road miles above junction of county road 2499 and Tennessee Hwy 70, at road 2499, 22 July 1970. **GREENE COUNTY**: UMMZ 157290 (3), Franks Cr. [= College Cr., next trib to north side of Nolichuckey R. upstream from Holley Cr.], 17 February 1947. **KNOX COUNTY**: USNM 70686 (7), Tennessee River at mouth of Lyon Creek, 5 mi W Knoxville, collected by Barton W. Everman, Josiah T. Scovell and Revere R. Gurley, 28 September 1893 (see Evermann and Hildebrand, 1916).

ARKANSAS RIVER SYSTEM. KANSAS. CHAUTAUQUA COUNTY: INHS 75553 (6), Big Caney River (T34S, R8E, Sec 12), 8 August 1959. **ELK COUNTY:** KU 14355 (49), Elk River at Kansas Hwy 99, 27 April 1970. **CHASE COUNTY:** KU 12572 (30), Cedar Creek , 2.5 mi S Cedar Point (T21S, R6E, Sec 13), 17 August 1967. **CHEROKEE COUNTY:** KU 3188 (1),

Shoal Creek at Kansas Hwy 26 at Galena (T34S, R25E, Sec 35), 11 April 1954, KU 3591 (5), 6 April 1956, KU 3660 (1), 22 August 1956, KU 3771 (6), 11 May 1957, KU 4618 (12), 25 April 1959, KU 7890 (1), 12 May 1963, KU 9899 (4), 9 April 1965, INHS 75554 (5), 9 April 1965; UAIC 1639 (3), Shoal Creek near Galena, 19 June 1965; KU 3779 (2), Spring River (T34S, R25E, Sec 36), 11 May 1957. **MISSOURI. BARTON COUNTY:** UMMZ 164835 (1), Muddy Fork, Spring River, 19 September 1946. **OKLAHOMA. WAGONER COUNTY:** UMMZ 109044 (2), Neosho River, 5 mi SE Wagoner, Oklahoma Biological Survey, 12 July 1929. **PITTSBURG COUNTY:** UMMZ 109043 (1), tributary to Gaines Creek of South Canadian River, 6 mi NE McAlister, Oklahoma Biological Survey, 28 June 1929. **LEFLORE COUNTY:** UMMZ 137913 (40), Poteau River, Slate Ford, near Shady Point, 12 April 1941. **ARKANSAS. CRAWFORD COUNTY:** TU 86324 (5), Lees Creek, tributary to Arkansas River at Oklahoma state line (T11N, R33W, Sec 25), no date; TU 52930 (8), upper end of Lake Ft. Smith, 3 mi N Mountainburg, 21 October 1960. **FRANKLIN COUNTY:** TU 103416 (3), Arkansas River at River Mile 246, 12 August 1975. **JOHNSON COUNTY:** UAIC 1012 (1), Spadra Creek at Clarksville, 9 June 1963. **LOGAN COUNTY:** TU 93725 (4), Petit Jean River at Arkansas Hwy 23, 1 mi S Booneville, 14 September 1974. **FAULKNER COUNTY:** CU 42257 (4), North Fork Cadron Creek at US Hwy 65, 6.1 mi S Damascus, 26 April 1962. **YELL COUNTY:** TU 97099 (6), Fourche LaFave River, county rd 307, 2 mi S Briggsville, 25 April 1975.

RED RIVER SYSTEM. OKLAHOMA. JOHNSTON COUNTY: CU 52416 (7), Blue River at Oklahoma Hwy 99 at Connerville, 4 June 1967, TU 92701 (6), 27 April 1968. **ATOKA COUNTY:** UMMZ 109042 (1), McGee Creek, tributary to Boggy Creek, 7 mi SW Daisy, Oklahoma Biological Survey, 27 June 1929. **PUSHMATAHA COUNTY:** USNM 165800 (13), Little River at Honobia, 25 April 1952; CU 36536 (30), Little River below confluence with Black Fork, 3.2 mi SE Nashoba, 18 April 1959. **MCCURTAIN COUNTY:** NLU 15908 (5), Glover Creek at county rd 198, 5 mi E Wright City, 11 April 1970; NLU 5700 (7), Little River at Marleys Fish Camp, September 1963; TU 103418 (3), Little River at Goodwater, 22 May 1976; UT 91.541 (14), Mountain Fork River at US Hwy 70, 26 April 1969. **ARKANSAS. POLK COUNTY:** TU 103417 (2), Mountain Fork River at Arkansas Hwy 246, 3 April 1976; LSUMZ 10111 (3), Ouachita River at county road 63, WSW Cherry Hill (T2S, R29W, Sec 23), 19 September 1992. **HOWARD COUNTY:** TNHC 8191 (4), Cossatat River at Gillham Dam site, 24 April 1971, TU 93159 (10), 25 March 1972. **SEVIER COUNTY:** NLU 17041 (6), Rolling Fork River at unmarked road, 3 mi N DeQueen, 8 August 1970; TU 97100 (3), Cossatat River at Arkansas Hwy 380, Ladd Bridge, 3 mi E King, 25 March 1972, NLU 25527 (4), 20 October 1972; NLU 28220 (26), Cossatat River at Arkansas Hwy 24, W Lockesburg, 1 September 1973; NLU 30418 (2), Cossatat River at county road, 8 mi S Lockesburg, 13 July 1974. **PIKE COUNTY:** NLU 28148 (7), Little Missouri River off Arkansas Hwy 84, approximately 2 mi SW Langley, 8 September 1973; UT 91.946 (2), Caddo River at US Hwy 70 in Glenwood, 23 May 1974. **OUACHITA COUNTY:** LSUMZ 10112 (25), Little Missouri River, 5 airmi N Chidester (T11S, R19W, Sec 22), 20 September 1992. NLU 24132 (86), Little Missouri River approximately 10 mi NE Chidester (T11S, R18W, Sec 3), 28 July 1972; NLU 25040 (123), Little Missouri River approximately 11 mi NE Chidester (T11S, R18W, Sec 1), 7 September 1972. **CLARK COUNTY:** TU 97098 (1), Caddo River at Arkansas Hwy 84, 2.7 mi NE Amity, 24 May 1973; NLU 18766 (227), Caddo River at control dam spillway, 2 mi W Caddo Valley, 4 April 1971; NLU 18390 (51), Caddo River at Interstate Hwy 30 at south edge of Caddo Valley, 19 March 1971, TU 85397 (7), 9 June 1973; NLU 24235 (18), Caddo River between Interstate Hwy 30 and US Hwy 67, 5 August 1972; NLU 31929 (135), Ouachita River 2 mi N of junction of Arkansas Hwy 7 and US Hwy 67, 500 yards E of Carter Road, 28–29 June 1975. **MONTGOMERY COUNTY:** CU 52333 (5), South Fork Ouachita River at US Hwy 270, 5.0 airmi NW Mt. Ida, 30 May 1967. **HOT SPRINGS COUNTY:** NLU 31924 (11), Ouachita River near Friendship, 1 mi E of US Hwy 67, 29 June 1975. **SALINE COUNTY:** NLU 16437 (10), North Fork Saline River, 7.4 airmi NNW Benton (T1S, R15W, Sec 8), 28 May 1970; NLU 16426 (17), Saline River at south edge of Benton, near Chicago Pacific railroad crossing (T2S, R15W, Sec 21), 28 May 1970. **GRANT COUNTY:** TU 97101 (20), Saline River at US Hwy 270, 3 mi E Poyen, 10 June 1972. **LOUISIANA. UNION PARISH:** NLU 20434 (8), Ouachita River at Alabama Landing, 10 mi E Haile, 16 October 1971. **OUACHITA PARISH:** USNM 172367 (1), Ouachita River, 3.5 airmi SW Ouachita (T20N, R4E, Sec 31—east shore and T20N, R3E, Sec 36), 28 January 1956.

DIAGNOSIS: *Percina copelandi* typically lacks a premaxillary frenum and is one of the smallest species of *Percina*, reaching a maximum of 52 mm standard length. Squamation of head is variable; the cheek is usually naked in Great Lakes and Ohio River system specimens but partially to entirely covered with scales in Cumberland, Tennessee, Arkansas, Ouachita, and Red river specimens; the nape is infrequently naked in Great Lakes and Ohio River system specimens but more often ranges in squamation from a few scales to being completely covered. In general the nape of southern specimens is more extensively scaled. The number of modified belly scales on males is also variable, ranging from 2 to 16; Great Lakes males have the lowest mean number (6.1) and Caddo River system males have the highest mean number (9.7). Nuptial males develop moderately darkened bodies and fins, especially the ventral part of head and body. They also develop fleshy tubercular ridges along spines and anterior rays of anal fin and along ventral side of spine and soft rays of pelvic fins. Occasionally small tubercles occur along the crests of the fleshy ridges on the ventral side of the pelvic fin rays.

ILLUSTRATIONS: The literature pertaining to *Percina copelandi* and its synonyms is rather extensive and illustrations are quite numerous. Thompson (1853) illustrated (drawing) "The Darter," *Boleosoma tessellatum* DeKay. Putnam (1863) said Thompson's species was not *tessellatum* of DeKay (1842) but an unnamed species for which he proposed the new generic name, *Cottogaster*. Jordan and Gilbert (1883) described *Cottogaster putnami*. Jordan and Evermann (1896b, pt. 1: 1045–1046) gave a full description of *Cottogaster copelandi* and considered *putnami* as a subspecies. Evermann and Thoburn (1896: 1049) described *Ulocentra gilberti*. Evermann and Kendall (1898) presented a drawing of *Cottogaster cheneyi*. A full description of *Cottogaster cheneyi* was given in Jordan and Evermann (1898, pt. 3: 2851–2852) and Jordan and Evermann (1900, pt. 4) illustrated (drawings) *Cottogaster*

cheneyi and *Ulocentra gilberti*, pl. 169, figures 445 and 446 respectively. Evermann and Hildebrand (1916: 449) gave a line drawing of *Cottogaster copelandi*. Fish (1932: 373, fig. 103) presented a line drawing of a 6.1 mm *Rheocrypta copelandi*. The first color illustration (painting) of *Cottogaster copelandi* appeared in Greeley's (1934, pl. 11) fishes of the Raquette watershed. Hubbs and Lagler (1947; 1958—as *Hadropterus copelandi*) presented a black and white photograph of *Cottogaster copelandi*. Trautman (1957 and 1981) illustrated (drawings) a male and a female *Percina copelandi*. The next chronological illustration (drawing) was that of Cross (1967; Cross and Collins, 1975) of *Percina copelandi*. Miller and Robison (1973) presented a black and white photograph of *Percina copelandi*. Scott and Crossman (1973) included a drawing of *Percina copelandi*. McAllister and Coad (1974) included a drawing of *Percina copelandi*. Pflieger (1975) presented a drawing of *Percina copelandi*. Clay (1975) included a black and white photograph of *Percina copelandi*. The photograph of *Percina copelandi* in Lee, et al. (1980) [is of a specimen] from the Au Sable River, Iosco Co., Michigan. Cooper (1983) included a black and white photograph of *Percina copelandi*. Page (1983) presented a color photograph of a male (Pl. 5G) *Percina copelandi* from Blue River, Johnston County, Oklahoma and a female (Pl. 5H) from Ouachita River, Polk County, Arkansas. Kuehne and Barbour (1983) also presented a color illustration (Pl. 4) of an adult male *Percina copelandi* from Licking River, Kentucky (see Gilbert and Walsh, 1991: 14). Smith (1985) presented one drawing of *Percina copelandi* in the key, p. 316), and another drawing in the species account, p. 340. Robison and Buchanan (1988) include a color photograph of *Percina copelandi* by B.H. Bauer. Burkhead and Jenkins (1991) include a color photograph of *Percina copelandi*. The next illustration of *Percina copelandi* was included in Plate 39 (painting) of Page and Burr (1991). The most recent illustrations (photographs) appear in Jenkins and Burkhead (1994), Etnier and Starnes (1994), and Robde et al. (1994).

Thus there are numerous drawings, paintings, photographs and descriptions of *Percina copelandi*. Some of the descriptions are brief but others are extensive and in detail.

SIZE: A review of the literature reveals a number of inconsistencies with regards to size of the channel darter, *Percina copelandi*. Some of the inconsistencies were the result of limited observations by the various authors. Recent literature: Scott and Crossman (1973); Gilbert and Burgess (1980); Trautman (1981); Page (1983); Kuehne and Barbour (1983); Robison and Buchanan (1988); Bailey and Etnier (1988); Burkhead and Jenkins (1991); and Coburn and Gaglione (1992) reported either standard or total lengths for *Cottogaster*. Standard lengths ranged from 55 to 64 mm, total lengths from 61 to 64 mm. We believe *Percina copelandi* and the new species from the Mobile River basin to be the two smallest species of *Percina*. We measured 531 specimens of *P. copelandi* from the Great Lakes region including Lake Champlain specimens; 386 specimens from the combined Ohio, Cumberland, and Tennessee river systems; 200 specimens from the Arkansas River system and 900 specimens from the combined Little Missouri, Caddo, Ouachita, Saline and Red river systems, or a grand total of 2017 specimens. The largest male is 51.3 mm SL and the largest female is 52.2 mm SL. The largest specimen in most of the large series typically is a male.

DESCRIPTION: Frequency distributions of scale and fin ray counts are presented in Tables 1–6. Number of vertebrae, branchiostegal rays, gill rakers, number of modified belly scales on males, number of modified belly scales on females, number of marginal spines on modified ventral scales of males, and number of pores in infraorbital and preoperculomandibular canals are given in Tables 7–12. Squamation of cheek, opercle, and nape is described in Tables 13–15.

The lateral line is usually complete with (42) 46–64 (67) scales. Northern populations (Great Lakes, Ohio, Cumberland, and Tennessee river systems) have the lowest number of lateral line scales, $\bar{x}$ = 50.8, and southern populations (Ouachita and Red river systems) have the highest number, $\bar{x}$ = 58.2. The Arkansas River population has an intermediate number of lateral line scales, $\bar{x}$ = 55.4. The northern populations average approximately ten scales fewer than the Red River population, the most southern. Lateral-line scale counts given by Jordan (1882: 969), Meek (1891: 127), Gilbert (1891: 155) and Woolman (1892: 253, 259) fall within the range of our counts for the respective areas. Transverse scale counts show a similar north-south trend. Northern populations range from 11 to 17 scales, $\bar{x}$ = 13.6 in 709 specimens. Transverse scales in the Arkansas River population range from 12 to 19 scales, $\bar{x}$ = 15.8 in 158 specimens, and in the Red River population range from 14 to 22, $\bar{x}$ = 17.6 in 98 specimens. Thus northern populations average approximately four transverse scales fewer than the Red River specimens. Caudal peduncle scale rows number 13 to 20, $\bar{x}$ = 16.3 in 723 specimens from the Great Lakes, Ohio, Cumberland, and Tennessee river systems; 16 to 23, $\bar{x}$ = 18.4 in 158 specimens from the Arkansas River system; and 16 to 22, $\bar{x}$ = 18.4 in 252 specimens from Ouachita and Red river systems. First dorsal fin has 9 to 13, $\bar{x}$ = 10.2 spines in northern populations (Great Lakes, Ohio, Cumberland and Tennessee river systems) and 10 to 14, $\bar{x}$ = 11.3 spines in the Arkansas, Ouachita, and Red river systems. The second dorsal fin has 9 to 14, $\bar{x}$ = 11.2 rays in northern populations; 10 to 13, $\bar{x}$ = 11.7 rays in Arkansas River specimens; and 11 to 14, $\bar{x}$ = 11.7 rays in Ouachita and Red river systems. Anal fin typically has 2 spines and (6) 7–9 (10), modally 8 soft rays in all populations. Woolman's (1892: 259) counts for dorsal and anal fin fall within our counts for the respective fins. Pectoral fin has 12 to 15 rays, modally 13 rays in Cumberland, Tennessee, and Ouachita river systems and modally 14 rays in Great Lakes, Ohio, Arkansas, and Red river systems. Jordan and Eigenmann (1886: 69) gave vertebral number for *Cottogaster copelandi* as 18 + 20 = 38. Bailey and Gosline (1955: Table 1) gave

38(14), 39(13) or 40(2) as vertebral number for 29 specimens from Ontario and Michigan. Our observations reveal vertebral number as 36 to 41, $\bar{x}$ = 38.4 in 1022 specimens.

Agassiz (1850:24) was quoted by Cabot as having said that all the percoids have three caecal appendices from the pyloric extremity of the stomach; Jordan and Eigenmann (1886:69) in reference to *Cottogaster copelandi* gave 3 as the number of pyloric caeca. Our observations are as follows: Lake Champlain drainage, Poultney River in Vermont, pyloric caeca number 4(2), 5(6), and 6(2); Ouachita River in Arkansas, 3(2) and 4(8); Caddo River in Arkansas, 4(8) and 5(2); Little Missouri River in Arkansas, 5(4) and 6(1). Branchiostegal rays range 5—5 to 7—7, but typically are 6—6 in number (Table 7); gill rakers on first arch number 9 to 15, $\bar{x}$ = 12.7 in 633 specimens (Table 8). Smith (1985: 346, Table 36) reported a gill raker count of 16—17 (presumably left and right arch) for a single specimen. Our highest gill raker count for Great Lakes and Lake Champlain specimens was 15. Counts on 15 specimens from the Poultney River in Vermont resulted in 10(1), 11(3), 12(7), and 13(4), these counts are included under Great Lakes in Table 8. Branson and Ulrikson (1967:371–389) gave total number of rakers and gill filaments on all four (4) arches on the left side so their counts are not comparable to ours. Modified belly scales on males number 2 to 16, $\bar{x}$ = 8.2 in 994 specimens (Table 9). Jordan (1877a: 9) considered the ventral modified scales as caducous and this belief was repeated by a number of subsequent authors. We concur with Page (1976: 256–257) that the ventral scales are not caducous. During the height of the breeding season the marginal spines on the modified scales of the nuptial males assume a semierect or erect position, that is, perpendicular to the surface of scale. Modified belly scales are present on some females; 129 (29 percent) of 451 females have them. The number of modified belly scales on these 129 females ranges from 1 to 7, with a mean of 2.4 (Table 10). Marginal spines on the modified ventral scales on males number 3–13, $\bar{x}$ = 5.7 in 25 specimens (253 modified scales) from Arkansas River and 0–13, $\bar{x}$ = 4.6 in 25 specimens (283 modified scales) from Caddo River (Table 11). Infraorbital and preoperculomandibular pores on the left side only were counted. Infraorbital pores number 6 to 10, $\bar{x}$ = 8.1 in 539 specimens (Table 12). Eight infraorbital pores is the modal number in most populations, however Cumberland River specimens are nearly equally divided between eight and nine pores and Caddo River fish are somewhat skewed toward a lower count of seven. Ten preoperculomandibular pores is the modal number throughout our samples.

Squamation of cheek is variable. The cheek is naked in most of the Great Lakes specimens and the majority of the Ohio River samples excluding the Cumberland and Tennessee river specimens. The cheek of nearly all of the latter specimens is partially to fully covered with scales as is the cheek of most of the specimens from the Arkansas, Ouachita, and Red river systems (Table 13). The opercle typically is partially to fully scaled in all populations. A naked opercle or the presence of 1–4 scales is a rarity and occurs only in Great Lakes or Ohio River specimens (Table 14). The nape varies from having few or no scales to being fully covered in all populations; however, 21 percent of Great Lakes specimens and 24 percent of Ohio River fish have a naked nape or 1–4 scales versus only 5 percent of Cumberland River and none of the Tennessee River specimens (Table 15). A premaxillary frenum is present in 20 percent of the 1020 *Percina copelandi* examined. Great Lakes specimens have the highest percentage (36 percent) with a frenum, the combined Arkansas, Ouachita, and Red river samples have the next highest percentage (16 percent), and the combined Cumberland and Tennessee river samples have the lowest (4 percent) with a frenum (Table 16). Winn (1953: 26) reported that 13 percent of 297 *copelandi* from various parts of its range had a premaxillary frenum.

Proportional measurements for males and females are presented in Table 17 and 18, respectively, and are discussed later in comparison to the two new species.

We are in agreement with Page's (1983) color description of the channel darter. Based on three series (CU 36536, NLU 18390, NLU 18766) that were collected during the breeding season in southeastern Oklahoma and southwestern Arkansas, males are heavily pigmented in contrast to females. The chin, gular area, branchiostegal membranes, breast, belly and base of the genital papilla are darkened with pigment in the male. Although the suborbital and preorbital bars are areas of concentrated pigment in the male, the cheek area between the preorbital and suborbital bars and the area posterior and ventral to the suborbital bar are also pigmented, thus diminishing the distinctness of the bars. Typically the entire ventral region of the female is immaculate; occasionally there may be a few melanophores on the chin or anterior gular area. The genital papilla of the female is without pigment. The preorbital bar is distinct but the suborbital bar is faint or represented by as few as six melanophores and the surrounding suborbital area is devoid of melanophores. We are in agreement with Page (1983) with regards to number of dorsal saddle and lateral blotches. However, we observed that many of the lateral blotches are oval, diamond, or quadrate in shape rather than oblong. The black basicaudal spot is typical for both sexes. The pigmentation of other parts of the body and of the fins is essentially as described by Page (1983). Pigmentation of the first dorsal fin of the male is as illustrated by Page (1983, Pl. 5G): a moderately broad black band across the fin near its base, a broader clear or lightly pigmented area distal to the basal band, and a narrow marginal or submarginal dark brown to black band.

An overview of variation in numerous characters reveals regional differentiation between northern and eastern populations (east of the Mississippi River) and southwestern populations (west of the Mississippi River). Page and Whitt (1973a, b) reported a difference in isozyme mobility for samples representative of these two regions. Additional studies of this type should be done to determine the uniformity of their findings within the two regions. Detailed

analysis of variation in external morphology within *P. copelandi* will be the subject of a subsequent paper. We do not favor splitting the taxon until this effort has been completed.

DISTRIBUTION: *Percina copelandi* occurs from eastern Michigan eastward in the Great Lakes region along shores of Lake Erie and Lake Ontario to upper tributaries to the St. Lawrence River in southern Quebec and to both western and eastern shores of Lake Champlain in New York and Vermont respectively. It occurs in various tributaries to the Ohio River from the Wabash River system of western Indiana eastward along southern Ohio and northern and central Kentucky to west central West Virginia and in the upper part of the Cumberland and Tennessee river systems in northern Tennessee to southwestern Virginia. There is also a disjunct distribution west of the Mississippi River that extends from southeastern Kansas and eastern Oklahoma southeastward through southwestern Missouri and western Arkansas to north central Louisiana (Figure 4). Figure 4 includes only the material that we personally studied and not all the distributional records made available to us by Reeve M. Bailey and Frank B. Cross. The species has disappeared from some of its former range east of the Mississippi River and also is diminished in relative abundance.

HABITAT AND BIOLOGY: Jordan's original material came from a broad ripple on White River at the "Red Bridge" about five miles north of Indianapolis. He proposed the name *Rheocrypta* in allusion to the habit of hiding in the rapids. Jordan (1882: 970) stated that *Percina copelandi* lived in rapids in clear water and did not ascend small streams. Woolman (1892: 252, 253 and 255, 256, 259) described Rough Creek, tributary to lower Green River at Hartford, Kentucky, July 25, 1890 as one of the largest northern tributaries supporting *copelandi*. He noted that at low water the stream was broken up into ponds by numerous ripples. The ripples flowed over beds of coarse gravel, while between them the bottom consisted of stone with more or less mud. The channel darter, *Percina copelandi* was taken at two sites along the upper Green River; the first was 5 miles southwest at Greensburg, August 7, 1890, where the river was "about 200 yards wide, flowing over very large beds of gravel and sand." The second site was one-half mile east of Greensburg, August 8, 1890, character of stream much the same as at the last station, however, fewer fishes were taken, "the water being swift and the ripples covered with large stones." He added that 43 species were taken at the latter site.

Kirsch (1893: 263, 265) took one specimen of *Percina copelandi* from the Obeys River at Olympus, Tennessee on August 28, 1891 and stated, "The river has a width of 180 feet, a solid limestone bottom with occasional outcrops of shale, and many gravelly shoals." Greeley (1929: 176) found ripe males in Eighteen-mile Creek on July 11 in riffles about 1/4 mile from the mouth (at Lake Erie). Greeley (1930: 84–85) took a specimen in rapids of the Big Chazy River at the town of Champlain, New York, on July 9. Greeley and Greene (1931: 91) collected *Percina copelandi* at rocky shoals along the St. Lawrence River and in shallows near the foot of rapids in the lower parts of tributaries. Greeley and Bishop (1932: 89) took a single adult male in breeding condition on June 5 from the lower part of Sawyer Creek (tributary 68 of the Oswegatchie River in New York). In the 1929: 176 account Greeley stated that *Percina copelandi* and *Percina caprodes* ascend streams to spawn. Fish (1932: 373) in reference to *Percina copelandi* stated that the fact that many adults seek tributary streams in which to spawn accounts for the few young found in lake (Lake Erie) towings. Hubbs and Lagler (1941: 74) gave the habitat of *Percina copelandi* as in the main lakes and in the deep current of the lower sections of tributaries; seldom on fast riffles. Gerking (1945: 88) took *Percina copelandi* on a sand and gravel bottom in turbid water with a moderate to fast current. Winn (1953: 27–28) described the spawning ground of *Percina copelandi* in the Cheboygan River in the city of Cheboygan, Michigan as an area below a power dam and a pulp mill. The river at the spawning area was characterized by a swift current over a substratum composed of a mixture of rocks, gravel, and sand. Moreover, Winn noted that when the flow through the paper mill was diminished this resulted in reduced current over the breeding ground and all courtship and breeding activity stopped. Scott (1955: 151) reported *Percina copelandi* from along the north shore of Lake Erie in southern Ontario. Specimens were taken from over sand and gravel beaches. Trautman (1957: 551; 1981: 635) reported *Percina copelandi* on coarse sand and fine gravel beaches of Lake Erie and on sand and gravel bars below dams on the Muskingum River, Ohio. He said that the channel darter was an inhabitant of extensive beaches and bars where currents were sluggish. Winn (1958: Table 2, p. 160, 161) gave lake shores and stream gravel raceways as the reproductive habitat of *Percina copelandi* and said spawning occurred in July in the Michigan area. Blair (1959: 10) stated that *Percina copelandi* inhabited large streams of somewhat deep water, either quiet or fast, but did not discuss spawning habitat. Cross (1967: 297) and Cross and Collins (1975: 152) described the habitat of the channel darter in two streams in Kansas. In Shoal Creek in Cherokee County *P. copelandi* occurred mainly along the steep inclined edges of deep beds of gravel, where riffles terminate in pools. In Elk River the channel darter occurred in moderate current over bottoms of bedrock littered by large, angular stones. He also stated, "Seemingly, the channel darter finds its principal habitat in pools having a rocky substrate and sufficient current to sweep the bottom free of sediment." Branson (1967: 143) identified seasonal habitats for the channel darter. He said that from early April on the channel darter moved out of its wintering habitat into the channels of the Neosho River and its eastern tributaries in northeastern Oklahoma where it was seldom found in swiftly flowing riffles but at times became abundant over sand in slow current. Late in the year

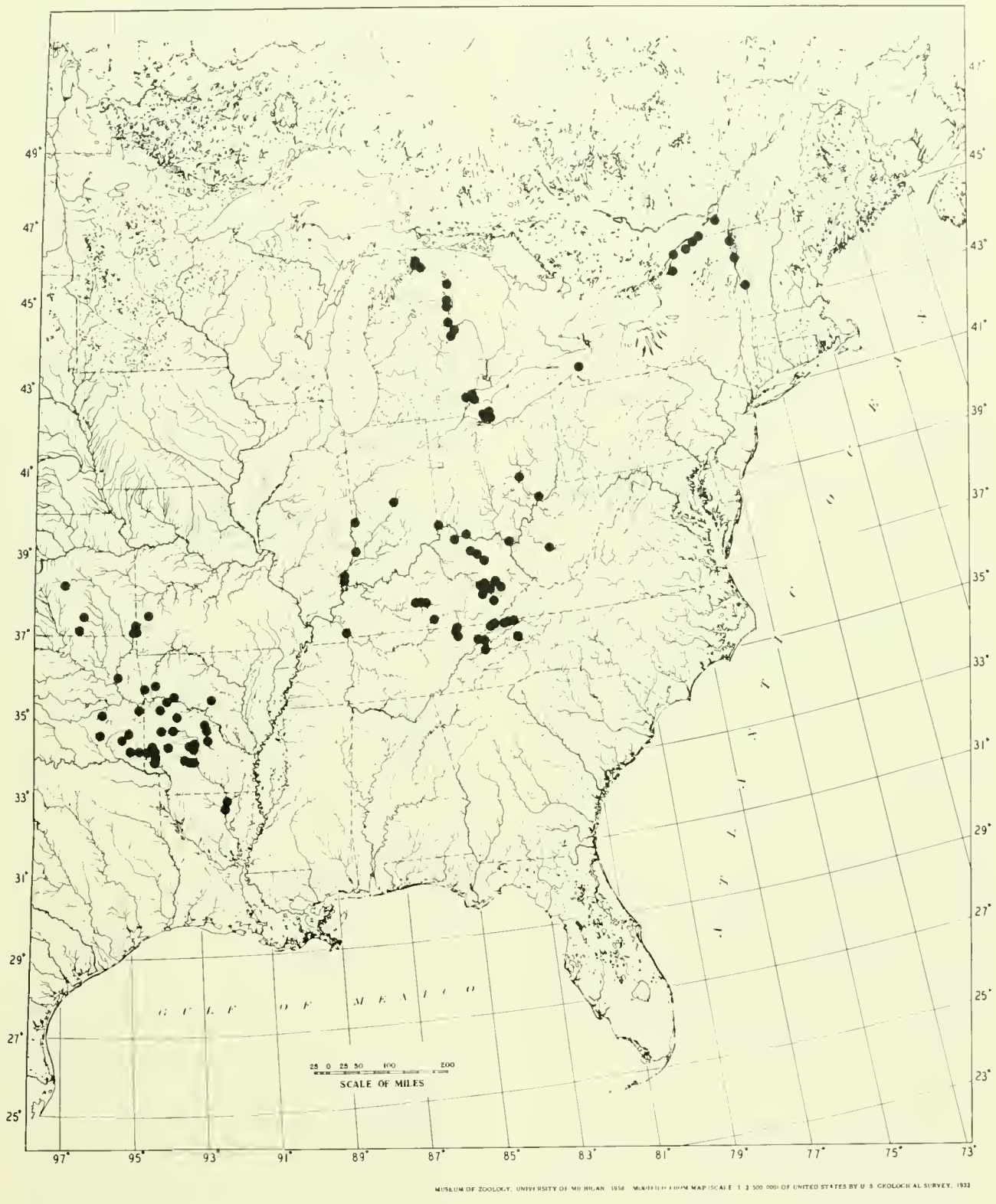


Figure 4. Collection sites of *Percina copelandi* in eastern and central United States, southern Ontario and Quebec (solid dots = sites for material used in this study).

the channel darter moved back into quite backwaters where it overwintered. Pflieger (1971: 428, 1975: 306) stated that the channel darter was common in the larger streams of the Neosho River system where it occurred "on sluggish riffles or in pools having enough current to create silt-free rocky or gravelly bottoms." Jenkins, Lachner, and Schwartz (1972: 55, Table 1) gave habitat of the channel darter as lowland and upland stretches of big rivers (Kanawha River: below falls, Big Sandy River, Cumberland River: below falls, and Tennessee River). Olmsted, Hickman, and Cloutman (1972: 16) gave the habitat as gravelly riffles with moderate flow in the middle portion of the Mulberry River, tributary to the Arkansas River in Arkansas. Comiskey and Etnier (1972: 143) found that in the Big South Fork of the Cumberland River system in Tennessee the channel darter was "uncommon in shallow pools and along the edges of riffles in the main river, Clear Fork, and North Whiteoak Creek." Hubbs and Bryan (1975: 623) stated that the channel darter *Percina copelandi* "breeds in riffles of moderate to large rivers." Page (1983: 45) stated that "the channel darter inhabits lake shores and stream pools with sufficient current to maintain a bottom of sand or of sand mixed with gravel and rocks." However, he also (1983, 174–177 Fig. 33, Table 28, Fig. 34) categorized *P. copelandi* as a "quiet pool, benthic form" and described various morphological adaptations for this habitat.

Kuehne and Barbour (1983: 49) stated that, "the channel darter generally inhabits rivers and large creeks in areas of moderate current, usually over sand and gravel substrates. Such conditions are usually found at the lower ends of riffles or at the edges of deep channels. Seasonally these darters may move into the slower current of pools." Burr and Warren (1986: 334) said that the channel darter "inhabits large upland streams, rivers, and big rivers in moderate currents of raceways over substrates of gravel and sand; avoids deep sluggish pools, headwater creeks, lacustrine/palustrine environments." Robison and Buchanan (1988: 448–449) stated that, "in Arkansas the channel darter is found primarily in small to moderate-sized rivers and large creeks where it typically occurs in riffles of moderate to swift current over a gravel or rocky substrate. It prefers clear water and a silt-free bottom." Burkhead and Jenkins (1991: 393) stated that, "in Virginia and eastern Tennessee, the channel darter is associated with moderate and swift riffles and runs having mixed small gravel to medium rubble substrates." Page and Burr (1991: 282) gave habitat of the channel darter as "pools and margins of riffles of small to medium rivers over sand or gravel bottoms, shores of lakes."

We believe the foregoing statements to be more or less based on direct observations. Our direct observations of northern populations are limited but do agree with the majority of those cited above. Our observations, plus data that accompanied the many series on loan to us, suggest that the channel darter prefers moderate to fast current over gravel, rubble or rock strewn bedrock, not sand, as spawning habitat. Post spawning habitat more often may be slower current over sand substrate as well as over gravel, rubble and bedrock. Our observations do not support Page's (1983: 174–178, Fig. 33, Table 28, Fig. 34) contention that *P. copelandi* is a quiet pool, benthic species. However, we do not dispute the recorded observation of *P. copelandi* overwintering in quiet waters (Branson, 1967a: 143). We do suggest that early seasonal retirement to deeper and slower current habitat may be due to historical events in western regions. In summer and fall the flow in many streams is greatly reduced leaving insufficient depth over preferred substrates. In contrast to *P. copelandi*, Page (1983) considered *P. sciera* as a gravel raceway, midwater species. We have many observations that demonstrate the gravel raceway, midwater habitat to be seasonal and like *P. copelandi*, *P. sciera* often overwinters in eddy pools or in slow current amongst organic debris lodged around snags or along the bank.

Spawning of *Percina copelandi* occurs in June and July in the Great Lakes area (Greeley, 1929; Greeley and Bishop, 1932; Winn, 1953). Based on three collections from southeastern Oklahoma (CU 36536, 18 April 1959) and southwestern Arkansas (NLU 18390, 19 March 1971, and NLU 18766, 4 April 1971) spawning extends from mid-March through mid-April. The sex ratio is skewed toward more males in these collections but may reflect early aggregations of males over spawning areas. The Oklahoma series contains 30 specimens, 22 males (73 percent) and 8 females (27 percent). Males range from 26.1 to 46.9 mm SL with a mean of 40.9; the females range from 35.3 to 42.0 mm SL with a mean of 37.6. The NLU 18390 series contains 51 specimens, 43 males (84.3 percent) and 8 females (15.7 percent). Males range from 36.3 to 43.9 mm SL with a mean of 39.7; the 8 females range from 34.9 to 42.3 mm SL with a mean of 37.7. The NLU 18766 series contains 228 specimens, 181 males (79.4 percent) and 47 females (20.6 percent). Males range from 32.2 to 45.2 mm SL with a mean of 37.3; females range from 30.2 to 41.5 mm SL with a mean of 34.3. Fleshy tubercular ridges are present on the ventral surface of the pelvic spinous and soft rays and also project laterally on either side of anal spinous and soft rays of the males. Most males in all three series have some development of the tubercular ridges. Some males in each of the three series have small projections, "tubercles," along the crests of the tubercular ridges on the central rays of the pelvic fins. Moreover the marginal spines on the modified belly scales project ventrad at a 45 degree angle or nearly at a right angle to the body surface. Too, scales along base of anal fin of some males have the marginal spines (ctenii) enlarged. Numerous males in the CU 36536 series have several scales on either side of anterior base of anal fin with enlarged ctenii (marginal spines) and in addition, have scales along ventral side of caudal peduncle with enlarged ctenii that project away from body surface similar to the marginal spines on the modified belly scales. Ovaries of females in all three series have a mixture of ova sizes. There were some relatively large orange ova, some medium size, and some small white ova in each of the ten plus specimens examined. Two specimens in the 19 March 1971 series have compara-

tively huge ova. Obviously these individuals were in the midst of spawning when collected.

Hubbs (1926:61), under the species account for *Percina caprodes*, indicated that he had seen hybrids between *Percina* and *Cottogaster*. Hubbs (955:15, Fig. 7) indicated hybrids in nature between *Percina* and both *Imostoma* and *Cottogaster*. Jenkins and Burkhead (1994: 789) questioned the validity of the hybrid combination of *Percina* and *Cottogaster*. However, Thompson and Hartel (1994: 132) reported on six hybrid specimens between *Percina caprodes semifasciata* and *Percina copelandi*.

Percina ***aurora*** Suttkus and Thompson, new species
Pearl Darter
Figures 2, 5, 7, and 8

Percina copelandi Collette, 1965: 582 (in part, misidentification, reference to TU 17732, tuberculation). Smith-Vaniz, 1968: 108 (misidentification, reference to TU 19379, Pascagoula drainage). Wallus and Douglas, 1973: 117 (misidentification, records from Strong River). Douglas, 1974: 376 (in part, misidentification, Pearl River records). Seehorn, 1975: 23 (misidentification, DeSoto National Forest records in Pascagoula River drainage, in part). Page, 1983: 45 (in part, misidentification, records from Pearl and Pascagoula). Kuehne and Barbour, 1983: 48 (in part, misidentification, distribution map, reference to Pearl and Pascagoula rivers, treated as distinct by other authors). Suttkus, 1985: 225–227 (misidentification, Pearl River specimens).

Percina (Cottogaster) sp. Jenkins 1976:644 (presumed reference to *P. aurora*). Deacon et al., 1979: 42 (Pearl Channel darter, Louisiana and Mississippi, T1 classification). Gilbert and Burgess, 1980: 721 (reference to Pearl and Pascagoula river drainages). Page, 1981: 1–69 (relationships, TU 17732). Williams et al., 1989: 12 (Pearl Channel darter, T1 classification).

Percina cf. *copelandi* Swift et al. 1985: 225 (considered as Pearl River endemic).

Percina sp. Ross, Heins, and Burris, 1992: 8 (Okatoma Creek record, Pascagoula River drainage).

HOLOTYPE: Adult male, TU 101392, 59.7 mm standard length (SL), Strong River, tributary to Pearl River at rapids, 0.2 mile upstream from Miss. Hwy 28 bridge, 2 miles west Pinola (T1N, R3E, Sec 28), Simpson County, Mississippi, 12 March 1969, R. D. Suttkus and Dawn O'Donnell Remington.

PARATOPOTYPES: TU 56852 (5, 52–59), collected with holotype; TU 17732 (68, 40–57), 3 April 1958, distributed as follows: TU 17732 (53), ANSP 171101 (2), CU 73971 (2), INHS 32133 (1), MCZ 102026 (1), OSUM 77215 (1), UAIC 10883.01 (2), UF 95412 (2), USNM 327768 (2), and UT 91.4441 (2); TU 18078 (3, 49–55), 3 May 1958; TU 19785 (6, 40–58), 8 May 1959; TU 23760 (1, 41), 4 July 1960; TU 28814 (10, 45–57), 29 December 1962; TU 30137 (2, 50–51), 6 November 1963; TU 39458 (1, 46), 13 December 1965; TU 39845 (8, 37–52), 5 March 1966; TU 40131 (1, 41), 18 March 1966; TU 43392 (2, 48–50), 17–18 February 1967; TU 43890 (3, 39–53), 1 March 1967; TU 53618 (4, 48–52), 14 September 1968; TU 54393 (1, 53), 24 October 1968; TU 55249 (5, 49–56), 21 November 1968; NLU 11986 (2, 48–53), 22 November 1968; TU 55525 (11, 49–64), Osteology collection, TU 960 (2–cleared and stained), 13 December 1968; TU 56074 (4, 39–59), 18 January 1969; TU 56493 (16, 44–61), 15 February 1969; TU 56615 (13, 47–59), 22 February 1969, distributed as follows: TU 56615 (10), UMMZ 224805 (3); TU 57298 (3, 50–55), 23 April 1969; TU 57596 (2, 48–51), 11 May 1969; NLU 13280 (2, 49–55), 16 May 1969; NLU 13567 (1, 42), 6 June 1969; TU 57843 (1, 49), 23 June 1969; TU 61141 (3, 54–61), 29 December 1969; TU 61257 (2, 60–62), 27–28 January 1970; NLU 14937 (1, 46), 8 February 1970; TU 62467 (2, 45–51), 28 February 1970; NLU 15531 (12, 41–62), 24 March 1970; NLU 15933 (2, 51–55), 17–18 April 1970; TU 62517 (2, 56–57), 18 April 1970; TU 64475 (1, 62), 9 June 1970; TU 64442 (1, 50), 30–31 July 1970; NLU 19229 (2, 45–45), 24 June 1971; and NLU 19532 (1, 45), 13 July 1971. Total number of type specimens is 207.

ADDITIONAL MATERIAL EXAMINED BUT NOT DESIGNATED AS TYPES: PEARL RIVER DRAINAGE, MISSISSIPPI. SIMPSON COUNTY: NLU 19411 (1), Strong R. at bridge 3.2 mi SE Miss Hwy 28 (T10N, R12W, Sec 11), 30 June 1971. **LAWRENCE COUNTY:** TU 81198 (3), Pearl R. just above mouth of Pretty Branch, 1.2 mi E Rosella (T8N, R21W, Sec 27), 21 February 1973; TU 81289 (1), Pearl R. just above new Silver Creek Hwy bridge, 4.5 mi N Monticello (T8N, R11E, Sec 34), 21 February 1973; TU 24289 (1), Pearl R. at US Hwy 84, 1.4 mi E Monticello (now Atwood Water Park) (T7N, R21W, Sec 26), 25 November 1960, TU 27195 (1), 28 August 1962, TU 81646 (1), 16 February 1973, TU 82083 (2), 3 May 1973; TU 82715 (2), Pearl R. just below mouth of Nim Branch (T7N, R21W, Sec 26), 1 August 1973; TU 27228 (1), Pearl R. at upper end of cut-off channel, about 2.5 mi SE Monticello (T6N, R11E, Sec 2), 28 August 1962; TU 82065 (1), Pearl R. at sand bar opposite mouth Silver Cr. (T6N, R11E, Sec 2), 4 May 1973; TU 27238 (6), Pearl R. about 2 mi downriver from Wilson Lake, about 5 mi SE Monticello (T6N, R11E, Sec 23), 28 August 1962. **MARION COUNTY**: NLU 8403 (1), Pearl R. 1 mi W Goss (at Miss Hwy 13) (T4N, R19W, Sec 5), 24 November 1967 and NLU 11444 (3), 11 October 1968; TU 27174 (3), Pearl R. about 1.5 mi SE Morgantown (T4N, R13E, Sec 10), 30 August 1962; TU 486 (14), Pearl R. at Miss Hwy 24 between Foxworth and Columbia (T3N, R13E, Sec 12), 28 October 1950, TU 18887 (2), 9 July 1958, and TU 27271 (2), 1 July 1962; TU 28280 (2), Pearl R. about 1.5 mi SE Foxworth (T3N, R13E, Sec 13), 17 October 1962, TU 28053 (2), 1 December 1962, and TU 28537 (1), 19–20 December 1962; TU 33 (1), Upper Little Cr., trib. to Pearl R. at Miss Hwy 13, 4.8 mi SE Columbia (T3N, R18W, Sec 27), 28 October 1950 and TU 3968 (10), 23 May 1952; TU 28379 (1), Pearl R., 1.5 mi NE Sandy Hook (T1N, R14E, Sec 22), 19 October, 1962; TU 1866 (2), Pearl R., 2.3 mi E Sandy Hook (T1N, R14E, Sec 27), 24–25 November 1951 and TU 28711 (1), 21 October 1961. **PEARL RIVER COUNTY**: TU 40996 (1), Pearl R. along left bank at River Mile 54, 2.3 mi SE Bogalusa (T3S, R18W, Sec 32), 3 July 1966; TU 47094 (1), Pearl R. just above Pools Bluff Sill, 4 mi S Bogalusa (T4S, R18W, Sec 37), 13 July 1967; TU 31132 (2), Pearl R. just below Pools Bluff Sill, 4 mi S Bogalusa (T4S, R18W, Sec 37), 27 April 1963, TU 31592 (1), 13 June 1963, TU 31163 (5), 24 June 1963, TU 29936

(2), 30–31 August 1963, TU 30004 (2), 29 September 1963, TU 30035 (6), 25 October 1963, TU 33735 (1), 11 August 1964, TU 39379 (1), 12 December 1965, TU 40241 (2), 25 March 1966, TU 40635 (1), 22 April 1966, TU 41889 (1), 17 October 1966, TU 42103 (3), 22 October 1966, TU 42120 (9), 22 October 1966, TU 42161 (30), 29 October 1966, TU 42196 (14), 4 November 1966, TU 42444 (2), 27 November 1966, TU 42708 (3), 16 December 1966, TU 42970 (4), 18 January 1967, TU 43025 (3), 28 January 1967, TU 43274 (1), 8 February 1967, TU 43830 (1), 28 February 1967, TU 44254 (12), 11 March 1967, TU 44543 (11), 21 March 1967, TU 45081 (15), 1 April 1967, TU 45284 (3), 9 April 1967, TU 46040 (8), 25 April 1967, TU 46000 (5), 26 April 1967, TU 47170 (1), 11 May 1967, TU 48103 (2), 4 October 1967, TU 49071 (3), 7 December 1967, TU 50377 (26), 21 February 1968, TU 50540 (13), 6 March 1968, TU 50751 (2), 21 March 1968, TU 50859 (2), 28 March 1968, TU 50924 (1), 28 March 1968, TU 52545 (3), 8 June 1968, NLU 11392 (3), 11 October 1968; TU 53944 (2), 23 October 1968, NLU 11668 (1), 30 October 1968, TU 55179 (1), 10 November 1968, TU 56036 (4), 17 January 1969, TU 56131 (4), 24 January 1969, TU 56450 (4), 7 February 1969, TU 59528 (1), 28 October 1969, TU 76194 (6), 22 December 1970, TU 69079 (1), 14 January 1971, TU 68776 (3), 20 April 1971, TU 72446 (1), 26 October 1971, TU 76667 (1), 18 April 1972, and TU 79420 (3), 17 October 1972. **LOUISIANA. ST. TAMMANY PARISH**: TU 75952 (1), Pearl R. at River Mile 52, 11.5 mi below Pools Bluff Sill (T5S, R14E, Sec 7), 27 October 1971; TU 38439 (5), Pearl R. at River Mile 47, 16.5 mi below Pools Bluff Sill (T5S, R14E, Sec 20), 28 August 1965; TU 34180 (1), Pearl R. at River Mile 46, 17.5 mi below Pools Bluff Sill (T5S, R14E, Sec 29), 21 August 1964, TU 42528 (1), 29 November 1966, TU 49511 (1), 26 November 1967, TU 54927 (4), 12 November 1968, and TU 61927 (1), 25 November 1969; NLU 11712 (2), Bogue Chitto R. at Pearl River Canal (T5S, R13E, Sec 45), 31 October 1968; TU 31451 (2), confluence of Wilson Slough with West Pearl R., 3.5 mi E Talisheek (T6S, R18W, Sec 44), 10 September 1963. **WASHINGTON PARISH**: NLU 20637 (17), Bogue Chitto R., 3 mi S Warrenton, off La Hwy 25, 8 October 1971. Total non-type specimens from the Pearl River Dr. is 338.

PASCAGOULA RIVER DRAINAGE. MISSISSIPPI. JACKSON COUNTY: USNM 129182 (6), Pascagoula R. at Dead Lake, collected by Samuel F. Hildebrand, 12 May 1933. **STONE COUNTY**: TU 144228 (1), Black Cr. at large loop along right bank, SE Board and Horseshoe lakes (T2S, R10W, Sec 2), 30 November 1985. **PERRY COUNTY**: TU 144698 (1), Black Cr. at Miss Hwy 318 (T1S, R10W, Sec 34), 4 April 1986, and TU 148420 (3), 24 April 1987. USM 8148 (3), Leaf R., 1.1 mi downstream of Wingate Bridge, 23 October 1989; USM 9137 (1), Leaf R., 2.8 mi below Hwy 29, 7 August 1990; USM 9575 (1), Leaf R., 4.6 mi above Hwy 29, 2 August 1990; USM 8785 (2), Leaf R., 5 mi upstream from Hwy 29, 9 March 1990. **COVINGTON COUNTY**: USM 6151 (2), Okatoma Cr., 1.2 airmi S Sanford, 5 October 1979. **GEORGE COUNTY**: USM 4293 (4), Pascagoula R., 1.3 mi above Jackson County line, 23 June 1988; TU 65841 (3), Pascagoula R., 6 mi SE Benndale (T3S, R8W, Sec 1), 14 November 1970, and TU 89772 (2), 13 July 1974; TU 100135 (3), Pascagoula R. along right bank opposite Merrill (T1S, R7W, Sec 19), 22 October 1976; TU 100159 (2), Pascagoula R. and lower Leaf River along right bank, 0.5 mi W Merrill (T1S, R7W, Sec 19), 22 October 1976, and TU 100202 (3), 29 October 1976. **JONES COUNTY**: NLU 20547 (1), Leaf R. at mouth of Eastabuchie Branch (T6N, R13W, Sec 33), 7 October 1971. **GREENE COUNTY**: USM 4444 (1), Chickasawhay R. at bend about 1.8 mi above Mineral Branch, 6 August 1988; USM 4242 (1), Chickasawhay R., 3.3 mi above Mineral Branch, 19 June 1988; USM 4975 (1), Chickasawhay R., 4.6 mi below Hwy 63, 17 July 1988. **CLARKE COUNTY**: TU 19379 (1), Chickasawhay R. at US Hwy 45, 1 mi S Shubuta (T10N, R7W, Sec 10), 21 August 1958. **LAUDERDALE COUNTY**: TU 121097 (1), Chunky Cr., 4 mi N US Hwy 11 at Enterprise (T5N, R14E, Sec 36), 18 August 1979; UT 91.2159 (1), Chunky Cr. at Interstate Hwy 59, 18 May 1981. Total non-type specimens from Pascagoula River Dr. is 44.

DIAGNOSIS: *Percina aurora* is a member of the subgenus *Cottogaster*. It typically lacks the premaxillary frenum. *Percina aurora* has a series of oval to quadrate or slightly oblong blotches along the midside and a black basicaudal spot. It is the largest of the three members of the subgenus and attains a maximum of 64 mm SL. Nuptial males are not heavily pigmented, the pelvics are only slightly dusky. Nuptial males lack tubercular ridges and are non-tuberculate. The fins of the male are well developed. The dorsal fins are moderately elevated and the caudal fin is relatively large. The modified belly scales are large and broad with a high number of marginal spines. The cheek is typically fully or nearly completely covered with exposed ctenoid scales whereas the nape is typically naked. The naked region of the nape is relatively wide (estimated to be 10–12 scale rows in width), not just a narrow midline strip.

DESCRIPTION: *Percina aurora* reaches a maximum of 57 mm SL, 67 mm TL (females) to 64 mm SL, 75 mm TL (males). Frequency distributions of scale and fin ray counts are given in Tables 1–6. Number of vertebrae, branchiostegal rays, gill rakers, number of modified belly scales on males and females, number of marginal spines on modified ventral scales of males, and number of pores in infraorbital and preoperculomandibular canals are given in Tables 7–12. Squamation of cheek, opercle, and nape is described in Tables 13–15. Status of premaxillary frenum is presented in Table 16 and proportional measurements for males and females are presented in Tables 17 and 18 respectively.

The lateral line is usually complete with (50) 53–58 (61) scales. Transverse scale rows number (15) 16–19 (21). Caudal peduncle scale rows number 19–21 (23). First dorsal fin has (9) 10–11 (12) spines and the second dorsal fin has (11) 12–13 (14) soft rays. The anal fin has 1–3 spines, modally 2 and (7) 8–9 (10), modally 8, soft rays. Pectoral fin rays number (12) 13–14 (15), modally 14 rays. Vertebral number is 38 (25), 39 (120), 40 (8) or 41 (1), modally 39 in 154 specimens. All ten specimens examined for number of pyloric caeca have four. Branchiostegal rays number 6—6 in 164 of 175 specimens (range 5—5 to 7—7, Table 7). Gill rakers on first arch number 11 to 17, $\bar{x}$ = 13.8 in 101 specimens (Table 8). Modified belly scales on males number 5 to 11, $\bar{x}$ = 7.9 (6–9 in over 90 percent) in 117 specimens (Table 9). Modified belly scales are present on 21 of 58 females examined (36 percent). The number of modified belly scales range from 1–6 with a mean of 2.6 per female with modified belly scales (Table 10). Marginal spines on the modified ventral (breast, interpelvic and belly) scales on males number 2 to 20, $\bar{x}$ = 8.5 (5–13 in over 90

percent of counts) in 250 scales from 25 specimens—Table 11. Number of infraorbital pores range from 7 to 10, modally 8 and preoperculomandibular pores range from 9 to 11, modally 10 in 73 specimens. The cheek is typically covered with scales: of 131 specimens the cheek is 2/3 to completely covered in 127, two specimens have the cheek 1/4 to 1/2 scaled, and the remaining two specimens have only 1–4 scales. The opercle of all 131 specimens is from 2/3 to completely covered with scales. Five of 129 specimens have some scales on the nape area and these five have only 1–4 scales. A premaxillary frenum is present in 23 percent of the 108 *Percina aurora* examined for this character (Table 16). *Percina aurora* males have relatively high (elevated) spinous and soft-rayed dorsal fins, a long upper jaw, and an enlarged caudal fin.

Colors of living and freshly preserved nuptial males collected on 15 February and 12 March 1969 are described from Strong River specimens taken at the type locality. There is a pearly, pastel blue iridescence on the ventrolateral and ventral surface of the head. The bluish iridescence on gular region extends posteriorly and laterally on the rami of the lower jaw and along ventral margin of the opercular series, along the lateral two branchiostegal rays and the intermediate membranes on either side, and extends dorsally to the lower one-third of both the cheek and the opercle. Here the iridescence diminishes in intensity and fades out.

There is a narrow band of iridescent blue that extends from just behind the eye posteriorly along upper margin of cheek and opercle. There is a bluish iridescence on the lateral area of the body. The bluish from the lateral area extends dorsally into the lower part of a golden-yellow chain pattern along the upper side of body. There is a pronounced iridescence on the base and prebasal area of the pectoral fin. The iridescence on the jaws is developed early in February and persists until early May based on recorded observations at the time of capture. Reexamination of material in 1993 showed little evidence of iridescence in old February, early March, and May specimens. However, specimens from mid-March through April retained some evidence of former iridescence. The series (TU 17732) taken on 3 April 1958 had clearly defined pale areas that were formerly iridescent. The iris is golden, the upper part of the orbit is cream to golden, and there are golden blotches on dorsal aspects of the snout and golden areas on the naked nape. Golden color occurs along the spines of the first dorsal fin and along rays, between the darkly pigmented blotches, of the second dorsal fin. The caudal fin has a similar pattern as that in the second dorsal fin, in that the caudal rays, especially the central rays, are bright golden between the dark blotches along the rays. The rays of the pelvic fins are glazed with golden.

There are eight to twelve, modally ten, dark brown to blackish oval, quadrate to slightly oblong lateral blotches and six to nine, modally seven, dorsal saddles. Commonly there is an additional small dorsal saddle on the anterior part of the nape. There are flecks and vermiculations of brown along the upper sides of body underlying the golden-yellow chain pattern. Nuptial males have two dark bands across the spinous dorsal fin, a broad, diffuse, dusky marginal band, and a pronounced dark band across fin near its base. The first two blotches of the latter band are darker than the rest. The basal half of the second dorsal and anal fins is dusky. Interradial membranes of pelvic fins are moderately pigmented; tip of spine and outer soft rays are somewhat thickened. There is a dusky suborbital bar. The basicaudal dark spot typically is present in males. The ventral surface of head and body is dusky in the nuptial male but never as dark as in *Percina copelandi* nuptial males. The base of the genital papilla is pigmented.

Nuptial females are essentially devoid of pigmentation on the ventral surface of head and body. Some females have a few melanophores on the tip of the jaw and anterior gular area. The preorbital bar is prominent but the suborbital varies in development from a dozen or so melanophores to a faint bar. Ventrally the area surrounding the suborbital pigmentation is immaculate. The entire breast and belly is immaculate. Also, the genital papilla is devoid of pigment. The pale pastel blue iridescence is present on the jaws of the nuptial female. The basicaudal dark spot is quite prominent.

DISTRIBUTION: *Percina aurora* is known from the Pearl and Pascagoula river drainages (Figure 5). Many of our specimens came from Strong River, a major tributary to the upper Pearl River. Most of the other series came from the main channel of the Pearl River between Monticello, Mississippi and the West Pearl River near Talisheek, Louisiana. There are single specimens or small series from a scattering of sites in the Pascagoula River drainage (Figure 5).

HABITAT AND BIOLOGY: Strong River at rapids (type locality), 0.2 mi upstream from Miss. Hwy 28 is the only site in the two drainages from which we obtained specimens in reproductive condition. In 1969, the width of Strong River at the foot of the rapids was 243 feet (74 meters). Strong River, a major tributary to the Pearl River, flows in a southwesterly direction across two physiographic districts or belts of the eastern Gulf Coastal Plain. The northern 20 miles of the river drains the relatively smooth clay formations of the Jackson Prairie district and the lower 40 miles of the Strong River cuts through the dissected upland of the Longleaf Pine Hills or Southern Pine Hills physiographic district. The latter district is underlain primarily by the sandy, porous Citronelle Formation which is exposed at the rapids (Lang, 1967). The type locality is approximately 10 miles above the mouth of Strong River at its confluence with the Pearl River. There are some additional exposed sections of bedrock below Miss. Hwy 28 crossing. Several strips of bedrock extend upstream from the central part of the rapids. There are grooves and sharp edged pot-holes just above the irregular broken edge of the bedrock at the foot of the rapids. In some places the grooves continue as troughs through the lip of the bedrock and during low water a fast flowing chute exists. Gravel bars

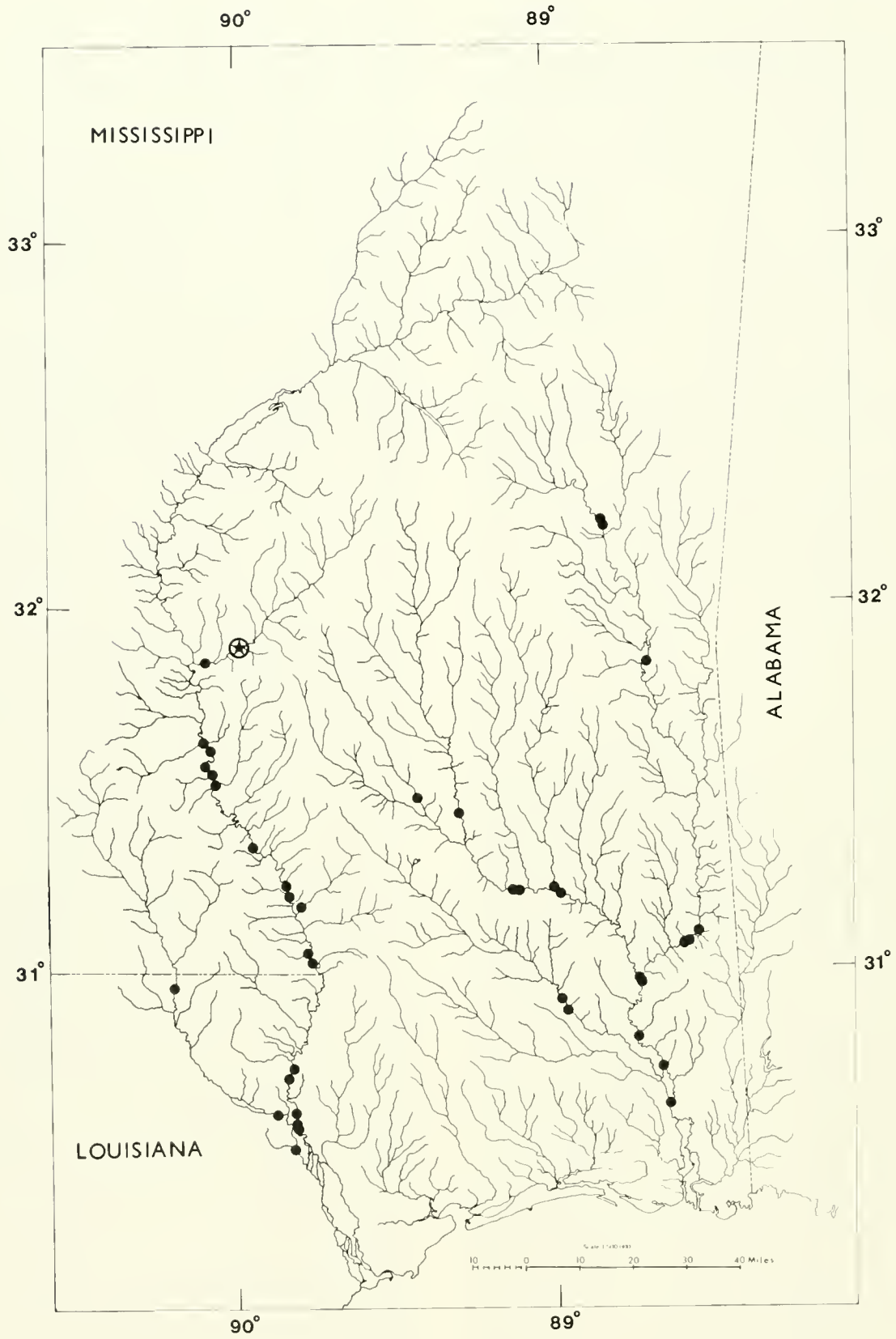


Figure 5. Distribution of *Percina aurora* in Mississippi and Louisiana (solid dots = material used in our study; star in open circle = type locality).

exist downstream from the broken pieces of bedrock and the edge of the bedrock. Along the east bank, on the inside of the bend (left bank), the current is somewhat reduced and the bars are composed of gravel at the upstream end and sand to silt on the lower end. From 1958 to 1967 the entire bedrock area and the broken rubble immediately below the lip of the bedrock was covered with a luxuriant growth of river weed, *Podostemum ceratophyllum*. However, in recent years siltation has greatly increased and we believe both the riverweed and the Pearl darter have been severly impacted as a result.

During low to moderate flows the pearl darter, *Percina aurora*, usually was taken in the slower current along the left bank. During flood, specimens were obtained from along the steep permanent bank in the swift current.

Other than the Strong River rapids site the Pearl River just below Pools Bluff Sill was the only site where we obtained many specimens (April 1963 to October 1972) but very few large adults were taken at this site and none was observed to be in reproductive condition. The current is swift below the dam and the collecting site is divisible into two types. The wing of the dam is rock substrate and there is a continuous eddy current over the rock but downstream of the wing the current resumes its downriver course. Along this stretch the substrate is primarily gravel and eventually changes to sand and silt about a hundred yards downriver. Nearly all the specimens of *Percina aurora* were taken from over the gravel substrate in depths of 18 inches to three feet or more.

Based primarily on our 1969 collections at the type locality ripe males were observed on 17 February, 12 March, 23 April, and 11 May 1969. In addition, series collected on 3 April 1958, 1 March 1967, and 24 March 1970 apparently were in reproductive condition at the time of capture although descriptive notes were not recorded at the time of capture. Two specimens, a male and a female collected on 11 May 1969, appeared to be nearly spawned out at the time of capture. Although our data are somewhat limited, males predominate at the spawning area during February and then in March and April females become equally or more abundant than males. Sixteen ripe males that ranged from 43.5–61.0 mm SL, mean 54.4 mm, were collected on 15 February 1969 when the water temperature was 8 degrees C. None of the males had any of the marginal spines of modified belly scales in an erect or a semierect position. A series of 13 specimens taken on 22 February 1969 in water 9.5 degrees C contained 11 males that ranged from 51.4–58.6 mm SL, mean 55.7 mm, and two females, 47.3 and 48.0 mm SL, mean 47.6 mm. Nuptial coloration was recorded at the time of capture. A few of the males had semierect marginal spines on the modified belly scales, however most males had the marginal spines tightly appressed to the belly. A sample of six specimens taken on 12 March 1969 in water 9 degrees C had five males that ranged from 53.6–59.7 mm SL, mean 56.5 mm, and a single female 51.7 mm SL. Two of the males were ripe at the time of capture. Marginal spines on modified belly scales of some males were in a semierect position. Another sample of three specimens taken on 23 April 1969, water temperature 17 degrees C, contained two ripe males 55.1 and 55.2 mm SL, and a single female is 50.4 mm SL. Marginal spines on modified belly scales were erect in both males. Two specimens, a male and a female, obtained on 11 May 1969, water temperature 21 degrees C, were both ripe at the time of capture and appeared to be nearly spawned-out. The male was 51.0 mm SL and the female was 48.3 mm SL. Marginal spines on modified belly scales of the male were in an erect position.

Our earliest collection from the type locality (Strong River at rapids, 2 miles west of Pinola, Simpson County, Mississippi) was obtained on 3 April 1958, and although we failed to record reproductive information at time of capture, recent examination revealed that the specimens were in reproductive condition. Males have dusky pigmentation on ventral areas of head and body and in the fins as described above. There are visible pale areas on chin, gular region, and rami of lower jaws which we presume were iridescent at the time of capture. Marginal spines on the modified belly scales are directed outward away from body at a 45 to 90 degree angle. The ctenii on the scales on either side of the anterior base of anal fin are enlarged and also directed away from the body surface. Some males have additional scales with enlarged ctenii projecting away from the body surface along the base of the anal fin and on the ventral and ventrolateral surfaces of the caudal peduncle. We believe these latter modified scales function in a similar way as the modified belly scales, that is, as contact structures. No tubercular ridges are developed on the ventral side of the pelvic rays nor along the anal soft rays. The first anal spine is noticeably broad and appears to be similar to the anal rays as described above for *Percina copelandi*, however the second spine is not broadened. Also, no tubercles were observed anywhere on the fins of nuptial males. There are 67 specimens in the 3 April series, nine males that range from 51.4–56.6 mm SL, mean 54.9 mm, and 58 females that range from 39.1–54.9 mm SL, mean 49.2 mm.

Twelve specimens (NLU 15531) collected on 24 March 1970 appear to have been in reproductive condition at the time of capture. The males have the typical dusky pigmentation of nuptial individuals and the marginal spines on the modified belly scales are in various stages of erection. The ovary of one female was examined and a mixture of ova sizes was observed. There are some large orange ova, and some white medium and small ova. The six males range from 47.8–62.2 mm SL, mean 58.8 and the six females range from 40.5–57.5 mm, mean 52.6 mm.

A sample collected on 1 March 1967 contains one male (53.3 mm SL) and two females (38.9 and 48.2 mm SL). The male has some marginal spines on modified belly scales in a semierect position. A sample collected on 13 December 1968 contains eight males (53.5–64.2 mm SL, mean 57.7 mm) and 3 females (49.4–50.0 mm SL, mean 49.6). None of the males has any erect marginal spines on the modified belly scales. A sample collected on 29 December 1962 has

five males (52.3–56.1 mm SL, mean 54.3 mm) and five females (44.6–49.5 mm SL, mean 46.7 mm). None of the males has any erect marginal spines on the modified belly scales.

The ten series cited above total 143 specimens of which there are 64 males (44.8 percent) and 79 females (55.2 percent). The males range from 43.5 to 64.2 mm SL, mean 55.7 mm and the females range from 38.9 to 57.5 mm, mean 49.2 mm. We have cited these various samples for the purpose of illustration of change in sex ratio and erection of marginal spines on the modified belly scales of the males with relation to the spawning season.

The species associates of *Percina aurora* at the type locality, based on 40 collections taken between 3 April 1958 and 31 July 1970, are as follows: *Ichthyomyzon gagei, Lampetra aepyptera, Lepisosteus osseus, Anguilla rostrata, Dorosoma cepedianum, D. petenense, Hiodon tergisus, Esox americanus, Carpiodes cyprinus, C. velifer, Erimyzon oblongus, Hypentelium nigricans, Minytrema melanops, Moxostoma carinatum, M. poecilurum, Cyprinella camura, C. venusta, Hybognathus hayi, H. nuchalis, Luxilus chrysocephalus, Lythrurus roseipinnis, Macrhybopsis aestivalis, M. storeriana, Nocomis leptocephalus, Notemigonus crysoleucas, Notropis atherinoides, N. buccatus, N. longirostris, N. texanus, N. volucellus, N. winchelli, Opsopoeodus emiliae, Pimephales notatus, P. vigilax, Semotilus atromaculatus, Ictalurus melas, I. natalis, I. punctatus, Noturus funebris, N. leptacanthus, N. miurus, N. munitus, N. nocturnus, Pylodictis olivaris, Aphredoderus sayanus, Strongylura marina, Fundulus olivaceus, Gambusia affinis, Labidesthes sicculus, Ambloplites ariommus, Centrarchus macropterus, Elassoma zonatum, Lepomis cyanellus, L. gulosus, L. macrochirus, L. megalotis, L. microlophus, L. punctatus, Micropterus punctulatus, M. salmoides, Pomoxis annularis, P. nigromaculatus, Ammocrypta beani, A. vivax, Etheostoma chlorosoma, E. histrio, E. lynceum, E. parvipinne, E. proeliare, E. stigmaeum, E. swaini, E. whipplei, Percina lenticula, P. maculata, P. nigrofasciata, P. sciera, P. shumardi, P. vigil, P. (Percina)* sp. cf. *caprodes*, and *Mugil cephalus* (sight records only).

ETYMOLOGY: The name *aurora* is Latin meaning dawn or morning and we use it in allusion to the similarity of the colors of the rising sun and the golden-yellow pattern on the dorsal and dorso-lateral area of the body and the golden patches distributed along rays of the dorsal and caudal fins.

The common name, pearl darter, is in reference to the pearly iridescence of the lower jaws and the likeness to the nacre of freshwater mussels.

Percina ***brevicauda*** Suttkus and Bart, new species
Coal Darter
Figures 3, 6, 7, and 8

Etheostoma copelandi Gilbert, 1891: 155, 157 (misidentification, Black Warrior River record, synonymized *Etheostoma putnami*).

Percina copelandi Moore 1957: 182 (misidentification, distribution). Suttkus and Ramsey, 1967: 140 (misidentification, species associates). Smith-Vaniz, 1968: 94, 108, Fig. 143 (misidentification, characters in key, black and white photograph of nuptial male 50 mm SL from Black Warrior River, Blount County, Alabama). Moore, 1968: 138 (misidentification, distribution). Barclay and Howell, 1973: 131,136 (misidentification, Black Warrior R. records). Seehorn, 1975: 23 (misidentification, Talladega National Forest records in Cahaba River system, in part). Mettee, 1978: 151–152 (misidentification, reference to undescribed form, black and white illustration; characters and distribution, in part). Page, 1983: 45 (in part, misidentification, reference to Mobile Bay). Kuehne and Barbour, 1983: 48 (in part, misidentification, map of *Percina copelandi*, text indicates that Mobile basin populations are distinct). Page and Burr, 1991: 282 (in part, misidentification, distribution on Gulf Slope in Mobile Bay).

Percina (*Cottogaster*) sp. Gilbert and Burgess, 1980: 721 (undescribed species in Mobile Bay basin). Williams et al., 1989: 12 (Alabama channel darter, T1 classification)

Percina sp. cf. *copelandi* Ramsey et al., 1980: 58 (distribution and status in Cahaba River). Ramsey et al., 1984: 13 (distribution and status). Swift et al., 1986: 228 (stated as endemic to Cahaba River drainage, but not indicated as such on p. 265). Pierson et al., 1989: 179 (distribution in Cahaba River system, habitat, biology and relationship). Mettee et al., 1989a: 196 (distribution in Black Warrior River system, habitat and biology). Mettee et al., 1989b: 161 (distribution in Black Warrior River system). Boschung, 1992: 125 (distribution in Black Warrior, Cahaba, and Coosa drainages).

HOLOTYPE: Adult male, TU 101393, 45.8 mm standard length (SL), Cahaba River, tributary to Alabama River at Alabama Hwy 52, 3.2 miles west of Helena (T20S, R3W, Sec 20), Shelby County, Alabama, 10 May 1965, R.D. Suttkus and Glenn H. Clemmer.

PARATOPOTYPES: TU 37661 (84, 35–47), collected with holotype are distributed as follows: TU 37661 (75), UMMZ 224803 (5), USNM 327767 (4); TU 32720 (12, 36–45), 31 May 1964; TU 35245 (4, 34–39), 28 June 1964; TU 38200 (5, 40–43), 24 June 1965; AUM 2570(13, 36–42), 13 May 1969; AUM 17060 (2, 43–44), 15 April 1978; AUM 17541 (6, 37–43), 13 July 1978; TU 168925 (8, 31–43), 25 October 1978; AUM 18461 (5, 30–43), 5 December 1978; TU 121402 (79, 36–47), 15 May 1981, distributed as follows: TU 121402 (74), CU 73970 (5); TU 121415 (150, 36–45) and UAIC 6366 (34), 16 May 1981, distributed as follows: TU 121415 (112), ANSP 171100 (4), INHS 32132 (4), KU 23215 (4), MCZ 102025 (4), OSUM 77214 (4), UAIC 10882.01 (4), [UAIC 6366 (34)], UF 95411 (4), UMMZ 224804 (5), UT 91.4440 (5); AUM 21192 (31, 37–44), 17 May 1981; AUM 21193 (17, 37–44), 21 May 1981; TU 121559 (39, 36–46), 5 June 1981; TU 125420 (12, 33–50), 15 May 1982, GSA 5152.17 (2, 34–35), 31 May 1990; GSA 5197.14, (1,41), 13 August 1990; GSA 5277.18 (1,43), 8 November 1990; GSA 4544.13, (4,39–42), 3 June 1993; and GSA 4537.14 (6, 36–42), 8 July 1993. Total number of type specimens is 516.

ADDITIONAL MATERIAL EXAMINED BUT NOT DESIGNATED AS TYPES: ALABAMA. CAHABA RIVER SYSTEM. BIBB COUNTY: UMMZ 171761 (6), Cahaba R. at Bibb County Hwy 27, 8.5 mi N Centreville (T24N, R10E, Sec 33), 28 May 1956, TU 19895 (2), 9 May 1959, TU 34044 (5), 28 June 1964, UAIC 1611 (1), 5 June 1965, UAIC 2580 (1), 13 April 1967, AUM 6194 (3), 16 May 1970, TU 69115 (2), 9 April 1971, TU 106781 (1), 14 April 1978, AUM 17173 (2), 10–11 June 1978, TU 168926 (1), 15 June 1978, AUM 17265 (4), 15–16 June 1978, AUM 17304 (1), 22–23 June 1978, GSA 5166.19 (3), 3 July 1990, and GSA 5200.20, (1), 16 August 1990; AUM 17350 (1), Six mile Cr., about 0.2 mi. upstream from confluence with Little Cahaba R. (T24N, R10E, Sec 23), 6 July 1978; and AUM 18382 (1), Cahaba R., 3.0 airmi ESE West Blocton, Hwy 24 (T24N, R10E, Sec 3), 23 October 1978, AUM 18424 (5), 15 November 1978. **JEFFERSON COUNTY:** TU 168927 (9), Cahaba R. at US Hwy 280 (T19S, R1W, Sec 26), 27 April 1978, and TU 168928 (1), 7 September 1978; UMMZ 168633 (1), Cahaba R., 4 mi W Leeds at US Hwy 78 (T17S, R1W, Sec 23), 3 September 1954. **SHELBY COUNTY:** AUM 5702 (6), Cahaba R., 2.6 airmi N Marvel or 4.7 mi NW Pea Ridge at Booth's Ford (T21S, R4W, Sec 30), 16 May 1970, AUM 17321 (1), 22 June 1978, AUM 17495 (1), 7 July 1978, AUM 18076 (3), 29 August 1978, AUM 18432 (2), 10 November 1978, AUM 18741 (1), 16 May 1979, and AUM 18756 (1), 31 May 1979; GSA 4535.12 (1), Cahaba R., 5.7 mi NNE Pelham, US Hwy 31 (T19S, R3W, Sec 24), 3 August 1992; and GSA 4535.12 (1), 1 June 1993. **COOSA RIVER SYSTEM. COOSA COUNTY:** AUM 16770 (3), Hatchet Cr. at old US Hwy 231, 3.8 airmi N Rockford (T23N, R18E, Sec 36), 20 May 1978, AUM 17505 (5), 7 July 1978, AUM 18037 (1), 14 July 1978, AUM 18071 (1) 1 August 1978, AUM 18180 (1), 8 September 1978, AUM 18459 (1), 15 November 1978, AUM 18655 (2), 20 March 1979, AUM 20917 (5), 9 May 1981, AUM 21482 (19), 25 May 1981, AUM 21195 (11), 21 June 1981, TU 129241 (8), 19 May 1983, and UNOVC 9282 (4), 19 May 1983. **TALLADEGA COUNTY:** UGAMNH 139 (2), Coosa R. near Childersburg (before impoundment) (T20S, R2E, Sec 24), 3 September 1949, and AUM 8659 (1), 30 June 1950. **BLACK WARRIOR RIVER SYSTEM. TUSCALOOSA COUNTY:** USNM 43476 (5) and UMMZ 198765 (1), Black Warrior R. at Tuscaloosa (before impoundment) (T21S, R10W, Sec 21), collected by P. H. Kirsch, W. M. Andrews, and E. O. Jones, 21 May 1889. **BLOUNT COUNTY:** UAIC 2512 (21), Blackburn Fork (T13S, R1W, Sec 11), 25 March 1967, TU 60061 (3), 20 October 1969, and UAIC 5372.16 (16), 24 May 1977 (=Little Warrior River, Barclay and Howell, 1973); AUM 21196 (5), Locust Fork Black Warrior R. 1.7 airmi S Nectar (T13S, R1W, Sec 3), 28 June 1981. Total number of non-type specimens = 183.

DIAGNOSIS: *Percina brevicauda* is a member of the subgenus *Cottogaster*. It typically lacks the premaxillary frenum and is the smallest (maximum of 50 mm SL) of the three members of the subgenus. Nuptial males are heavily pigmented including the entire ventral surface of head and body and in addition the small rounded or elongate-oval, modified belly scales are partially encircled or edged with jet-black pigment. Males of *Percina brevicauda* have a low number (modally 3) of marginal spines on the modified ventral scales. The cheek is typically naked. Males have the longest snout and the shortest pectoral and caudal fins of the three members of the subgenus *Cottogaster*. Tubercular ridges are well developed on the ventral side of pelvic fin rays and laterally on both sides of the anal fin rays in the nuptial males. Occasionally small protuberances are present along the crests of the tubercular ridges on the ventral side of the pelvic fin rays.

DESCRIPTION: *Percina brevicauda* reaches a maximum of 49 mm SL (females) to 50 mm SL (males). Frequency distributions of scale and fin ray counts are given in Tables 1–6. Number of vertebrae, branchiostegal rays, gill rakers, number of modified belly scales on males and females, number of marginal spines on modified ventral scales of males and number of pores in infraorbital and preoperculomandibular canals are given in Tables 7–12. Squamation of cheek, opercle, and nape is described in Tables 13–15. Status of premaxillary frenum is presented in Table 16, and proportional measurements for males and females are presented in Tables 17 and 18 respectively.

The lateral line is usually complete with (50) 55–60 (66) scales. Transverse scale rows number (15) 16–19 (22). Caudal peduncle scale rows number (17) 19–21 (23). First dorsal fin has (9) 11–12 spines and the second dorsal fin has (10) 11–12 (13) soft rays. The anal fin has 1–3 spines (98 percent of 183 specimens have 2), and 6 to 9 softrays (74 percent of 183 have 8. Pectoral fin rays number (12) 13–14, modally 13 rays. Vertebral number ranges from 36 to 39, 93 percent of 118 specimens have 38. In the 10 specimens examined for pyloric caeca, seven specimens have 4 and three have 5. Branchiostegal rays number 5—6 to 6—7 or 7—6, 93 percent of 148 specimens have 6—6. Gill rakers on first arch number 11 to 16, $\bar{x}$ = 12.8 in 145 specimens. Modified belly scales on males number 1 to 13, $\bar{x}$ = 9.3 (7 to 10 in over 90 percent of counts). Modified belly scales are present on some females. Eight (10 percent) of 77 females have modified belly scales. The number of modified belly scales range from 1–5 with a mean of 2.6 per female with modified belly scales (Table 10). The marginal spines on the modified ventral (breast, interpelvic and belly) scales on the males number 0 to 10, $\bar{x}$ = 3.9 (2 to 6 in 90 percent of counts of 289 modified scales in 25 specimens—Table 11). Number of infraorbital pores range from 7 to 10, modally 8 and preoperculomandibular pores range from 9 to 11, modally 10 in 115 specimens (Table 12). The cheek is typically naked, of 153 specimens only two have any scales. The opercle is naked in three, has one to four scales in five, is 1/4 to 1/2 covered with scales in 71, and is 2/3 to completely covered with scales in remaining 74 of the 153 specimens. The nape of *Percina brevicauda* ranges from naked to being 2/3 to completely covered with scales. A premaxillary frenum is present in five (three percent) of the 150 specimens examined for this character (Table 16).

Proportional measurements are presented in Tables 17 and 18. All 27 males and 10 females came from the type locality and were in nuptial condition. Five males and five females were from 10 May 1965, four males from 15 May 1981, 13 males and three females from 16 May 1981, and five males and two females from 15 May 1982 collections.

Thirty three additional specimens—14 from the type

locality and 19 from the Black Warrior River system—were measured to supplement fin measurements presented in Tables 17 and 18 (see Table 19). The additional measurements for longest dorsal spine, longest dorsal soft ray, and longest anal soft ray were based only on specimens with erect fins. The maximum caudal fin length measurement (205) expressed in thousandths of SL, was initially suspect but proved to be valid on remeasurement. The total of 60 specimens (inclusive of the specimen with the extreme caudal fin length) resulted in a mean of 173 and a standard deviation (S.D.) of 14.7 for the caudal fin length. Thus *P. brevicauda* males have the shortest caudal fin of the four samples of *Cottogaster* (Table 17). Pectoral fin length measurements for the same 60 specimens resulted in a mean of 216 versus 218 as given in Table 17 for 25 males. This new value substantiates the conclusion that *P. brevicauda* males also have the shortest pectoral fins of the four samples of *Cottogaster* (Table 17). However, pelvic fin length measurements for the same 60 specimens resulted in a mean of 196. Although lower than the mean (201) based on 25 specimens (Table 17), this value is nearly equal to the mean (194) for 25 specimens of *P. aurora*. Seven specimens each from the type locality—Cahaba River system and Black Warrior River system were used for additional longest dorsal spine measurement; nine specimens from the type locality and seven from the Black Warrior River were used for additional longest dorsal soft ray measurements; eight specimens from the type locality and seven from the Black Warrior River were used for additional longest anal soft ray measurements. Means based on the additional specimens are 95, 124, and 120, respectively, for longest dorsal spine, longest dorsal soft ray, and longest anal soft ray. Based on these samples *P. brevicauda* males have the shortest dorsal spines and anal soft rays of the three species of *Cottogaster* (Table 17). Twenty three additional females from the type locality (2) and Black Warrior River system (21) were measured for caudal fin length, pectoral fin length, and pelvic fin length. The revised means are 170, 216, and 191, respectively. Compared to the means based on 10 specimens (Table 18) the revised mean for caudal fin length is the same, that for pectoral fin length is slightly greater, but the mean for pelvic fin length is somewhat less (see Table 19). The revised mean for pelvic fin length of *P. brevicauda* females is equal to that for *P. aurora* females. Based on eight additional specimens from the Black Warrior River system, the revised mean (92) for longest dorsal spine is slightly lower than in Table 18. Based on nine additional specimens from the Black Warrior River system the revised mean (113) for the longest dorsal soft ray is also slightly lower than in Table 18 and based on the same nine specimens the revised mean (110) for the longest anal soft ray is considerably lower than in Table 18. Thus in general the fins of female *P. brevicauda* are as small as or smaller than fins of females of the other two species.

Colors are described for live and freshly preserved nuptial male specimens, collected in May during different years from Cahaba River system. Light iridescent blue extends posteriorly from anterior suborbital area across cheek and across lower half of opercle and continues on prepectoral area to the base of the pectoral fin. There is a narrow extension of the blue iridescence from the upper cheek area diagonally upward toward the occiput. Also, there is an iridescent greenish-blue stripe along the body from the pectoral fin insertion to the base of the caudal fin. This stripe borders the lower edge of the dark brown to black lateral blotches. These blotches are variously connected by intermediate dark brown pigmentation. Above the lateral blotches the dorso-lateral area and the dorsum is a uniform yellowish or golden-olive with a scattering of brown flecks in the shape of M's, W's and X's. There are two pronounced yellow patches at the base of the caudal fin, above and below the black basicaudal spot. The upper and lower procurrent margins of the caudal fin are pale and the longer procurrent rays plus the first upper and lower principal rays are heavily pigmented in contrast to the lighter pigmentation of the central rays of the caudal fin. This caudal fin pattern of pigmentation is not unlike that of nuptial males of the various populations of *Percina copelandi*. The ventral part of the body shades from olive immediately below lateral blotches to dirty white on the belly. The upper part of the iris is black whereas the lower part is golden color and there is a fine golden rim to the pupil. The preorbital and suborbital bars are dark brown. The overlay of iridescent blue partially obliterates the distal portion of the suborbital bar. The top of the head is dark brown with some olive blotches. The spinous dorsal fin has two black bands across its entire length; the basal band is the broadest and covers nearly two-thirds of the fin. In some males the narrow stripe between the marginal and the basal bands is nearly non-existent especially toward the posterior part of the fin. Anteriorly this interspace has an overlay of iridescent blue in some males. Most of the spines are golden. The soft-rayed dorsal fin has a checkered pattern of coloration; the rays have an alternation of dark and golden blotches along their lengths. The pectoral fins appear to be clear in life but the rays have a fine edging of dark pigment. The interradial membranes of both the pelvic and anal fins are heavily pigmented, the basal one-third to one-half is jet-black. The tips of the spine and soft rays of the pelvic fins are somewhat enlarged and milky white. The tubercular ridges are well developed on the anal spines and soft rays of the nuptial males. These tubercular ridges are milky white and contrast with the dark pigmentation of the interradial membranes.

After the iridescence and yellowish or golden-olive has faded the dark pigmentation becomes entirely visible. The entire head, breast, and belly including the modified belly scales are heavily pigmented. Moreover the posterior margins of the belly scales are outlined or edged with jet-black pigment. The genital papilla has a band of pigment around mid-section. Body scales, especially on ventral surface of body, are nearly completely covered with melanophores.

Unfortunately we did not record detailed color notes for nuptial females. In general pigmentation is much less than

in males. The pectoral, pelvic, and anal fins are mostly clear. The caudal fin is mostly clear although there are narrow dusky margins along outer two principal rays.

The soft dorsal fin has little pigment, only a slight amount near base on interradial membranes and along rays. The spinous dorsal fin has an incomplete submarginal band and a moderately wide basal band across the fin. Because of the reduced widths of the two dark bands the intervening clear area is continuous across the length of the fin and much wider than respective area in spinous dorsal fin of the nuptial male.

In general the scales on the lateral and dorsal areas of the body are less pigmented than those in the nuptial males. Most of the pigment is concentrated along posterior margin of scale leaving a relatively large unpigmented anterior area.

The entire breast, belly and ventrolateral area of body of the female is devoid of pigment. The dorsal portion of the head is moderately dark with pigmentation. There is some pigment on anterior part of upper lip, a small patch of melanophores on chin, the suborbital bar is prominent because the surrounding area of the cheek, gular area and gill membranes are immaculate. The bulbous genital papilla is also devoid of pigment.

Dorsal saddles are brown and vary from 8 to 10. The major lateral blotches are brown and vary from 8 to 12, usually 9, 10, or 11 with 3 or 4 smaller intermediate blotches. Occasionally the lateral blotches are somewhat connected by a narrow strip of brown pigment.

DISTRIBUTION: *Percina brevicauda* is confined to the eastern part of the Mobile basin (Figure 6). Within the basin it occurs disjunctly in the lower section of the Coosa River system above the Fall Line, throughout the upper part of the Cahaba River system above the Fall Line and in a few places below the Fall Line (Pierson et al., 1989), and in a small localized section of the upper Black Warrior River system above the Fall Line. No doubt the species had a more continuous distribution in the past. Based on an early collection from the Black Warrior River at Tuscaloosa, Alabama (1889), at the lower border of the Fall Line Hills, and two comparatively recent records (1949 and 1950) from the main channel of the Coosa River, the coal darter was probably continuously distributed in sections of the Black Warrior and Coosa river systems before impoundment.

HABITAT AND BIOLOGY: The Cahaba River is a small river at the type locality. Immediately above the bridge crossing, the river is deep with moderate to swift current. Down river from the bridge the river flows over substrates that vary from bedrock and rubble to gravel and sand. The bedrock is uneven and in places there are grooves or troughs that form raceways or chutes during moderate to low flows. Along the east bank there are gravel bars with down river extensions composed of a mixture of gravel and sand. The water is shallow over these gravel bars and forms rather extensive riffle areas. Water willow, *Justicia americana*, and river weed, *Podostemum ceratophyllum*, are common aquatic plants in the area. Water willow occurs along the edges and over the surface of the gravel beds, whereas the river weed is developed on the bedrock and rubble substrates.

Spawning of *Percina brevicauda* occurs from early May (Pierson et al., 1989) to early June in the upper part of the Cahaba River. Water temperature ranged from 18 to 23 degrees C during the spawning observations. Water willow, *Justicia americana*, was in bloom during the 15 and 16 May 1981 collections.

Four collections from the type locality were analyzed for sex ratio, size range, and average size of nuptial specimens: one on 10 May 1965 has 79 males and 6 females; another on 15 May 1981 has 72 males and 7 females; one on 16 May 1981 contained 184 specimens (34 specimens sent directly to the University of Alabama (UAIC)): 131 males and 19 females; and the fourth on 15 May 1982 has 10 males and 2 females. The total is 326 specimens, 292 males (89.6%) versus 34 females (10.4%). The males range in SL from 32.6 to 49.9 mm, mean 40.8 mm; the females range from 35.7 to 44.1 mm, mean 39.6 mm.

Many of the 229 specimens of *Percina brevicauda* collected during 45 minutes on 15 May 1981 and during 1 hour 45 minutes on 16 May 1981 were taken from the same trough in the bedrock near the foot of the rapids. A short haul with a 10 foot seine in the trough or chute which was two to three feet wide would yield a dozen or more specimens. So many specimens were taken from this single area during both days that it was inconceivable that males could be maintaining spawning territories the size of those described by Winn (1953). Direct observations of individuals were not attempted because of the turbulence. Numerous males and females were observed to be ripe when taken from the seine. Marginal spines on the modified belly scales of the males were in an erect position, and most males were observed to have tubercular ridges along rays of anal fin and along ventral side of pelvic rays. Examination of specimens after return to the laboratory revealed that some males have tubercles along tubercular ridges on pelvic fin rays.

Twelve specimens of *P. brevicauda* were taken at the type locality on 31 May 1964. Only one of the ten males was ripe. The specimens were taken from over gravel at the head of a fast riffle.

Another collection of 39 specimens was taken at the type locality on 5 June 1981. None was observed to be ripe at the time of capture, however most of the 29 males had some nuptial coloration. Careful examination with a dissecting scope revealed that three of the 29 males have a few tubercles and eight males have semi-erect marginal spines on some modified belly scales.

The species associates of *Percina brevicauda* at the type locality area are as follows: *Alosa alabamae, A. chrysochloris, Campostoma oligolepis, Cyprinella caerulea, C. callistia, C. trichroistia, C. venusta, Luxilus chrysocephalus, Lythrurus bellus, Notropis cahabae, N. stilbius, N. volucellus, N. winchelli, Phenacobius catostomus, Pimephales vigilax, Semotilus atromaculatus, Hypentelium*

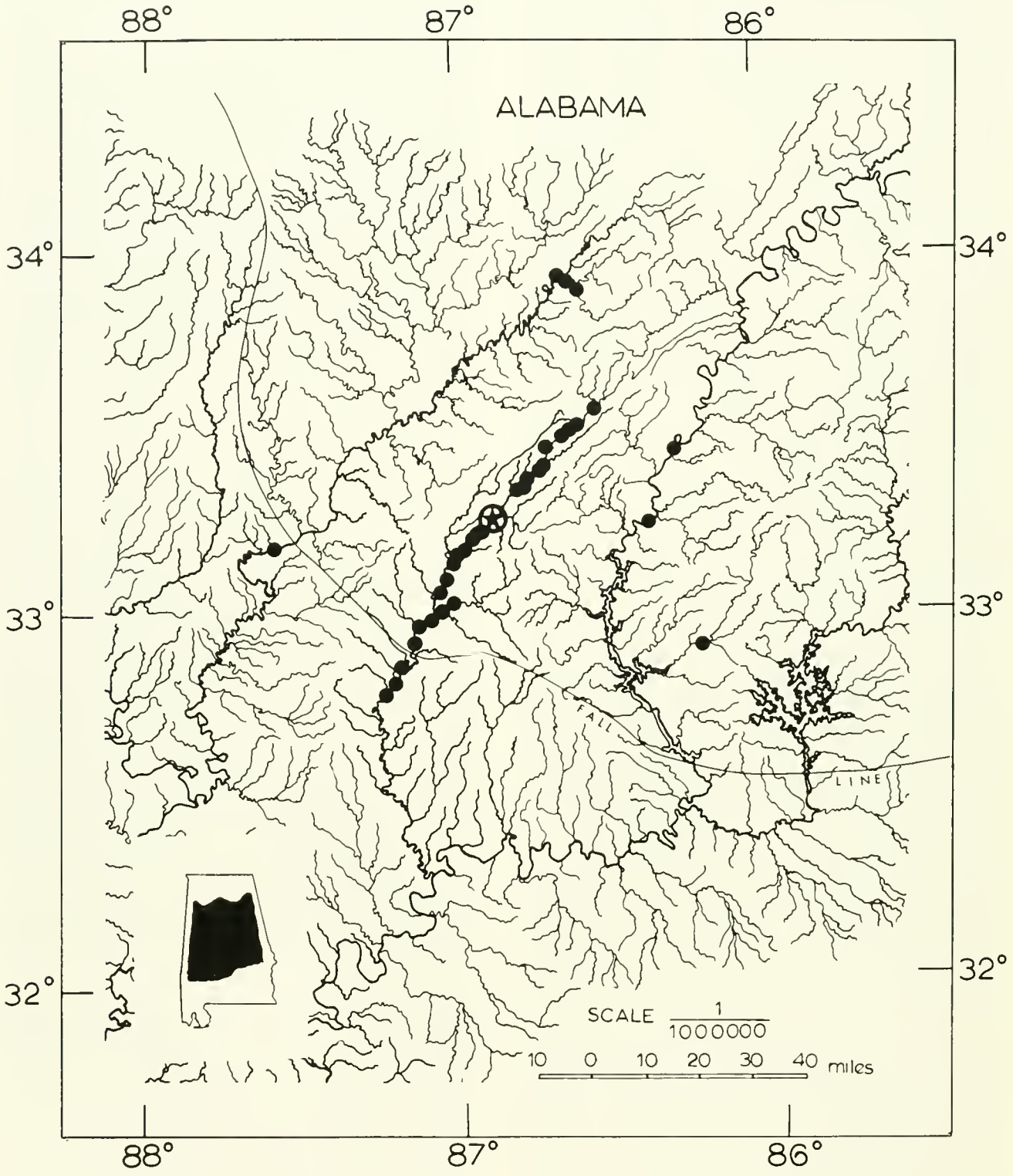


Figure 6. Distribution of *Percina brevicauda* in Alabama (solid dots = sites for material used in this study and additional localities cited in Pierson, et al., 1989, and Mettee, et al., 1989a; star in open circle = type locality).

etowanum, Minytrema melanops, Moxostoma duquesnei, M. erythrurum, M. poecilurum, Ictalurus punctatus, Pylodictis olivaris, Fundulus olivaceus, Gambusia affinis, Ambloplites ariommus, Lepomis cyanellus, L. macrochirus, L. megalotis, L. microlophus, Micropterus coosae, M. punctulatus, Etheostoma jordani, E. rupestre, Percina aurolineata, Percina sp. cf *caprodes, P. nigrofasciata, Aplodinotus grunniens,* and *Cottus carolinae.*

VARIATION: Little or no variation was detected in either meristic or mensural data among populations from the three river systems. However, specimens from Hatchet Creek (AUM 21482) in gravid condition are distinctive in lacking the dark pigment on both fins and body that is characteristic of *P. brevicauda* from Black Warrior and Cahaba river systems.

ETYMOLOGY: The name, *brevicauda*, is Latin that is descriptive of the short caudal fin. We suggest the vernacular name, coal darter, in reference to the over-all dark pigmentation of the nuptial male.

Interspecific Comparisons

There is considerable overlap in meristic features among the three species of *Cottogaster* (Tables 2–15). *Percina copelandi*, geographically the widest ranging species of the three has lateral-line scale, transverse scale row, and scales around caudal peduncle counts that vary from low counts in the Great Lakes region to high counts in the southwestern populations. The range in each of these three meristics for *P. copelandi* overlaps or is nearly equal to that for *P. aurora* and *P. brevicauda*. The highest average number of scales around the caudal peduncle is in *Percina aurora*. *Percina brevicauda* has the next highest average number, and all populations of *P. copelandi* except for Red River system, are considerably lower. Fin ray counts are nearly identical for the three species. Branchiostegal rays typically number 6—6 in each species. *Percina brevicauda* has the lowest number of vertebrae. *Percina aurora* and the Arkansas and Red river populations of *P. copelandi* have the highest number of vertebrae.

Number of pyloric caeca varies among the populations of *P. copelandi*. Based on 35 specimens the number of caeca ranges from 3 to 6, modally 4. All ten of the *P. aurora* examined have 4 pyloric caeca but in ten specimens of *P. brevicauda* seven have 4 and three have 5 caeca. *Percina aurora* exceeds both *P. copelandi* and *P. brevicauda* in the number of gill rakers. The number of modified belly scales of males is variable among the populations of *P. copelandi*. Great Lakes has the lowest average (6.1) and the Caddo River system of the Ouachita River system has the highest average (9.7) number of modified belly scales. Although the average (10.8) for the Coosa River system is the highest the sample size is inadequate for comparison with other samples. The Pearl River system average (7.6) is more or less intermediate between the Great Lakes (6.1) and the Caddo River system (9.7). The Cahaba River (8.5) is also intermediate but slightly higher than the Pearl River (7.6).

The number of females with and without modified belly scales is variable among the populations of *P. copelandi* (Table 10). Populations represented by a sample size of 50 or more females range from 47.1 to 88.1 percent without modified belly scales. Pearl River females (*P. aurora*) (58) have a moderately low percentage (63.8 percent) without modified belly scales. In contrast, *P. brevicauda* females are mostly naked on the belly, with 89.6 percent without modified scales.

Marginal spines were counted on the modified ventral scales (breast, interpelvic, and belly) of 25 male specimens of *P. copelandi* from Arkansas and Caddo river systems, 25 male specimens of *P. aurora* from Pearl River system, and 25 male specimens of *P. brevicauda* from Cahaba River system (Table 11). There are 253, 283, 250, and 289 modified scales for the respective samples. The Cahaba River sample (*P. brevicauda*) has the lowest number, mean 3.9; the Pearl River sample, *P. aurora*, has the highest number of marginal spines, mean 8.5, and the two samples of *P. copelandi* have intermediate numbers.

The number of pores in infraorbital and preopercular-mandibular canals usually 8 and 10 respectively, are quite similar throughout the samples of the three species (Table 12).

The extent of squamation of the cheek is variable among the samples of *P. copelandi* (Table 13). A high percentage of Ohio River specimens has a naked cheek and Great Lakes specimens are typically naked. Cumberland, Tennessee, Arkansas, Ouachita, and Red river specimens typically have cheeks that are partially to completely covered with scales. *Percina aurora* typically has the cheek completely covered with scales, but *P. brevicauda* almost invariably has a naked cheek, as in northern *copelandi*.

Percina copelandi and *P. brevicauda* typically have opercles partially to completely covered with scales. All specimens of *P. aurora* have the opercles completely covered with exposed ctenoid scales (Table 14).

Percina aurora invariably has a naked nape and the strip without scales is relatively wide (Table 15). The nape of Great Lakes, Ohio, Ouachita, and Red river samples of *P. copelandi* varies from naked to completely covered with scales. With few exceptions, the nape of Cumberland, Tennessee, and Arkansas river specimens is partially to completely covered with scales. The squamation of the nape of *P. brevicauda* ranges from naked to partially covered with scales.

The samples of *P. copelandi* vary in the percentage of individuals with a developed premaxillary frenum. The Great Lakes sample has the highest percentage (36 percent) with a frenum, the Ohio River sample is next with (27 percent), and the Cumberland and Tennessee river samples with 6 and 2 percent respectively for the lowest of the *P. copelandi* samples. The Arkansas, Ouachita, and Red river samples range from 8 to 19 percent with a frenum. Although most *P. aurora* have fully or partially protractile premaxil-

lae, 26 percent have a developed frenum. None of the 91 specimens of *P. brevicauda* from the Cahaba River has a frenum. Five (8 percent) of the 49 specimens of *P. brevicauda* from the Coosa and Black Warrior rivers have a premaxillary frenum (Table 16).

There is a distinct difference in maximum size of *P. aurora* and the other two species, *P. copelandi* and *P. brevicauda*. Based on 589 specimens the largest male *P. aurora* is 64.2 mm SL, the largest female is 57.5 mm. Among 2017 specimens of *P. copelandi* the largest male is 51.3 mm, the largest female is 52.2 mm, and from 543 specimens of *P. brevicauda* the largest male is 50.3 mm, the largest female 48.4 mm.

None of the nuptial male *P. aurora* has tubercular ridges on the anal fin rays nor on the ventral side of the pelvic fin rays. Collette (1965: 582) did not find tubercles on the fins of specimens in TU 17732 nor did we find any tubercles on any specimens in the numerous series of *P. aurora*. In contrast, we observed tubercular ridges on many nuptial males of *P. copelandi* and *P. brevicauda*. Moreover, we observed tubercles on some nuptial males of both *P. copelandi* and *P. brevicauda*. In every instance the tubercles in *P. copelandi* and *P. brevicauda* are weakly developed and not like those on the anal fin rays of nuptial *P. vigil* and *P. shumardi* males.

A tabular comparison of salient characteristics of nuptial males of *Percina copelandi*, *P. aurora*, and *P. brevicauda* is presented in Table 20.

Morphometric comparisons

Table 19 lists means for 16 measurements, expressed as thousandths of standard length, for samples of males and females from two populations of *Percina copelandi* (Ohio and Red river systems), the Pearl River population of *P. aurora*, and *P. brevicauda* from the Cahaba River system. All differences referred to in the following discussion are significant at the $\alpha = .05$ level.

Sexual dimorphism in body proportions is evident in some characters but varies in expression among species. The sexual dimorphism in body depth (females deeper bodied than males) seen in all but the Red River population of *P. copelandi*, is undoubtedly related to the gravid condition of females in the samples as compared to the somewhat emaciated state of the breeding males. Similarly, females of *P. brevicauda* and those from the Red River population of *P. copelandi* have wider bodies than males from the same areas, a condition that may also relate to the reproductive state of the specimens. Other sexual dimorphisms noted in Table 19 are as follows: males of the Red River population *P. copelandi* have a deeper caudal peduncle than females; males of *P. brevicauda* have longer snouts than females; females of *P. aurora* and females of the Red River population of *P. copelandi* have larger eyes (greater orbit diameter) than males; the longest dorsal spine is longer in males than in females in *P. brevicauda* and Ohio and Red river populations of *P. copelandi*; the longest soft dorsal ray is longer in males than in females in *P. aurora*, *P. brevicauda*, and Red River *P. copelandi*; the longest anal ray is longer in males than in females in *P. brevicauda* and the Red River population of *P. copelandi*; males from the Red River population of *P. copelandi* have longer pelvic fins than females.

In terms of the differences noted between species, males of *P. copelandi* from the Ohio River drainage have proportionally less depth of caudal peduncle and longer pectoral fins than males of other species/populations; males from the Red River population of *P. copelandi* have deeper bodies, smaller eyes, and more elevated anal fins than males of other species/populations; males of *P. aurora* have more elevated soft dorsal fins, longer upper jaws, and smaller pectoral fins than other males; males of *P. brevicauda* have longer snouts and shorter pectoral fins than other males; females of *P. aurora* have narrower bodies than other females; males and females of *P. copelandi* from the Ohio River drainage have longer pectoral fins and shorter upper jaws than specimens from other species/population, male or female; and males and females of *Percina aurora* have more elevated spinous dorsal fins.

Principal Components Analysis

Body size variation accounted for a large proportion of the variation in the data for both sexes in the principal components analysis (PCA). The first principal component (PC) derived in the analysis of data for males accounted for 87 percent of the variation, whereas, the first PC derived in the analysis of data for females accounted for 84 percent of the variation. Figure 7 a) is a plot of the projection of data for males on the first two PC's; Figure 7 b) is the same plot for females. The plots account for 90 and 89 percent of the variation in the data for males and females, respectively. In both plots, clusters for *P. brevicauda* and the two populations of *P. copelandi* show high degrees of overlap and are centered on the negative side of PC1, whereas the cluster for *Percina aurora* is distinctly separated and on the positive side of the axis, indicating that males and females of *P. aurora* have higher values than the other two species of body measurements loading positively on PC1.

In a second analysis data for 16 measurements were regressed on standard length and the residuals retained for PCA. This partial regression procedure removed variation in the data attributable to standard length and had the effect of adjusting data for the remaining characters to a common standard length. The adjustment for standard length also effectively removed a strong size effect in PC1. After partialling out standard length, PC1 accounted for only 35 percent of the variation in the data for males and 30 percent of the variation in the data for females. Figure 8 a) is a plot of PC1 versus PC2 from the partial regression PCA on data for males; Figure 8 b) is the same plot for females. Compared to plots from the first PCA, these plots explain only 50 and 52 percent of the variation in the data for males and females, respectively. Moreover, *P. aurora* clusters with the other species, indicating that body proportions in this species are similar to those in the other species after taking

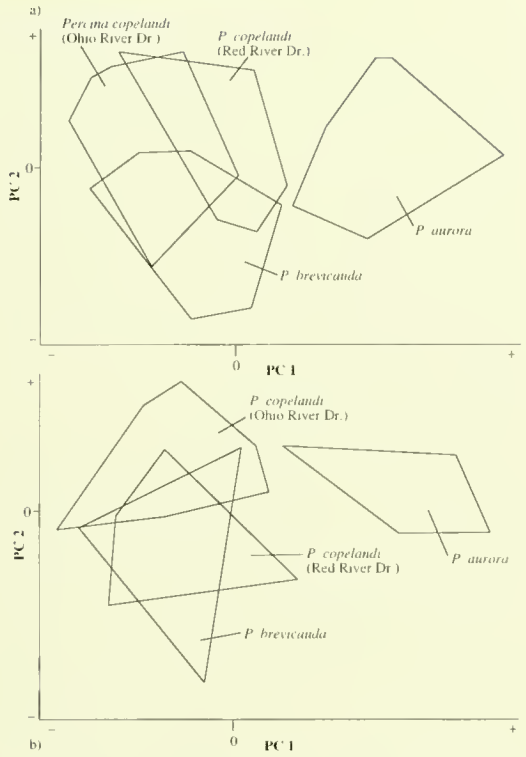


Figure 7. Polygons representing projections of unadjusted morphometric data on the first two PCA axes for males (a) and females (b) of *Percina aurora*, *P. brevicauda*, and Ohio and Red river populations of *P. copelandi*.

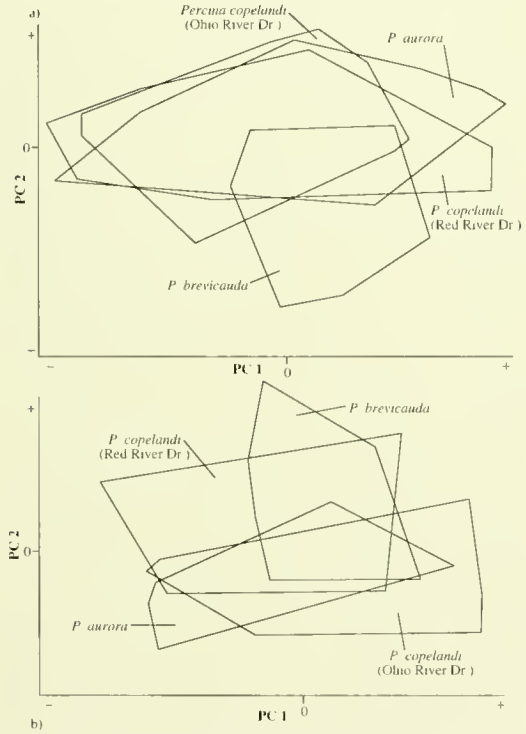


Figure 8. Polygons representing projections of standard length-adjusted morphometric data on the first two PCA axes for males (a) and females (b) of *Percina aurora*, *P. brevicauda*, and Ohio and Red river populations of *P. copelandi*.

size differences between the species into consideration. The greatest separation among the clusters is along PC2. A number of fin measurements (longest dorsal spine, longest anal ray, caudal fin length and pectoral fin length) load highest on PC2. Males of *P. brevicauda* separate out the most, tending to cluster on the negative side of PC2 (Figure 8 a), indicating that they have smaller fins than the other species.

Diagnosis of Subgenus *Cottogaster*

Herein we recognize three species in the subgenus *Cottogaster*. The three species are characterized by small maximum size. Two of the species, *Percina brevicauda* and *P. copelandi* are among the smallest species of *Percina*. *Percina brevicauda* has a maximum size of 50 mm SL and *P. copelandi* has a maximum size of 52 mm SL (our observations), and thus are smaller than *P. roanoka* (maximum SL, 60 mm) which Mayden and Page (1979:416) considered to be the smallest species of *Percina*. *Percina aurora* reaches a maximum size of 64 mm SL. The three species typically lack a premaxillary frenum, although 36% of the Great Lakes specimens of *P. copelandi* have a narrow premaxillary frenum; branchiostegal membranes are separate; modified belly scales are typical on males and present of from 9–53% of females in various stream systems; modified belly scales on males range from one to 16; marginal spines per modified ventral scale of males vary from none to 20; no serrae on the margin of the preopercle; a small medial black basicaudal spot (sometimes nearly obliterated in heavily pigmented nuptial males of *P. brevicauda* and *P. copelandi*); no extensive areas of bright color; tubercular ridges developed on pelvic and anal rays of nuptial males of *P. brevicauda* and *P. copelandi*; none on fin rays of *P. aurora*; breeding "tubercles" weakly developed on some nuptial males of *P. brevicauda* and *P. copelandi*, no tubercles observed on any *P. aurora*. Ctenii enlarged on some scales at anterior base of anal fin, along base of anal fin, and on ventral side of caudal peduncle in an occasional nuptial male of *P. copelandi* and *P. aurora* but none observed on nuptial males of *P. brevicauda*.

ADDITIONAL CHARACTERISTICS: Lateral-line scales range from 42–67, mean number for various drainage systems range from 50.1 to 60.0; transverse scale rows, 11–22, sample means range from 13.1 to 17.9; number of scales around caudal peduncle, 13 to 23, sample means range from 15.7 to 20.9; dorsal spines, 9–14, sample means range from 9.9 to 11.7; dorsal soft rays, 9–14, sample means range from 10.5 to 12.3; anal spines, 0–3, typically 2; anal soft rays, 6–10, sample means range from 7.6 to 8.4; pectoral fin rays, 12–15, sample means range from 13.0 to 13.8; number of vertebrae, 36–41, sample means range from 38.0 to 39.1; branchiostegal rays, 5—5 to 7—7, modally 6—6; gill rakers on first arch number 9–17, sample means range from 11.8 to 13.8; infraorbital pores number 6 to 10, modally 8; and preoperculomandibular pores number 8 to 11, modally 10.

RELATIONSHIPS: Jordan and his colleagues linked *Cottogaster* with *Imostoma* as late as 1930. Winn (1958b) in his Figure 7 indicated *Percina copelandi* as a member of subgenus *Imostoma*. Page (1974) implied a closeness between *Cottogaster* (represented by a single species, *P. copelandi*, in his study) and *Imostoma* (represented by three species in his study) in four of the five phenograms (Figures 1–4). We believe his analyses resulted in an artificial arrangement of relationships among some subgenera and between species within subgenera because of improper weighting of some of the characters. Page (1974: 85) gave the following as derived character states for *Cottogaster*: small size; breeding tubercles present; extremes in reduced meristics; and absence of premaxillary frenum. We concur with Bailey and Etnier (1988) that the capacity for a protractile premaxillary was developed secondarily. Further we believe this capacity was developed independently in the various groups of darters that have protractile premaxillaries, in particular we believe this ability was derived independently in *Cottogaster* and *Imostoma*. Secondly, meristic counts for *P. copelandi*, although low, are not extreme when large samples from over its entire range are analyzed. Also, variation in meristic counts for *P. aurora* and *P. brevicauda* tends to weaken this as a derived character state for the subgenus *Cottogaster*. Thirdly, too much emphasis was placed on presence of breeding tubercles. Considering the sporadic occurrence of breeding "tubercles" on nuptial males of *P. copelandi* and *P. brevicauda* and the fact that these are only weakly developed protuberances on the crests of the tubercular ridges, we do not consider them homologous to the breeding tubercles on the fins, particularly the anal, of members of the subgenus *Imostoma*.

The type species for *Imostoma* is *Hadropterus shumardi* (Jordan 1877, by original designation). (Eschmeyer and Bailey 1990). *Percina vigil, uranidea, tanasi, and antesella* are "brother species," that is, similar by virtue of one or more masculine traits. *Percina shumardi* and the four saddle-back species are similar in the greatly enlarged, tuberculate anal fin of nuptial males (Table 21). The presence of dorsal saddle blotches on the other four species unite them into a group slightly apart from *P. shumardi* (Etnier, 1976). The saddle blotches typically are present in the same position and number in both sexes of the four species, thus we refer to the saddle pattern as a sibling trait. The saddle markings were not emphasized by Page (1974) but were described by Etnier (1976) and described and discussed by Bailey and Etnier (1988).

Page (1974: 79) stated that *P. (Cottogaster) copelandi* and *Imostoma* shared certain characteristics associated with living on sand. Page and Swofford (1984:149) and Bailey and Etnier (1988: 10) stated that specialized ventral scales were reduced or occasionally lost secondarily in *Imostoma*, a subgenus in which the belly and breast, as in *Ammocrypta*, have reduced ventral scales associated with a sand habitat. Our observations do not support the above view, specifically with regard to *Imostoma*. We have collected hundreds of samples of all five recognized species of *Imostoma*, and invariably took specimens from moderately swift to swift current over gravel, rubble or rocky substrate, especially during the breeding season. Occasionally during pre- or postspawning movements an adult will be found over sand substrate. Juveniles of *P. vigil* are not uncommon over sand, and perhaps of significance is that their saddle marks are not as prominent. Certainly, if the reduction or lack of development of ventral scales was an adaptation to a sand substrate it would be counter to the retention of the bold dorsal saddle blotches which in our view blend or are cryptic with a multicolored gravel substrate. Thus, we do not attribute the reduction or lack of development of ventral scales in *Imostoma* to association with substrate.

We believe reproductive success to be the major factor controlling development of these traits. *Cottogaster* and *Imostoma* exhibit two different modes of secondary sexual development. In *Cottogaster* the primary feature is the development of the ventral modified scales in all three species and anal fin rays of adult males not notably elevated. Two of the species (*Percina copelandi* and *P. brevicauda*) also develop tubercular ridges on pelvic and anal fin rays with "tubercle-like" protuberances on pelvic fin rays of some individuals. In *Imostoma* the primary feature is the development of the enlarged, tuberculate anal fin of the nuptial male, with some tubercle development on other fins and on the body. We hypothesize that the modified ventral scales are reduced in *Imostoma* because their function in reproduction has been supplanted by tuberculation, particularly on the enlarged anal fin. Direct observations of breeding behavior in nature would help to substantiate this hypothesis.

In summary, we know of no shared unique similarities between *Cottogaster* and *Imostoma* and conclude that they are not close subgeneric relatives. *Cottogaster* does share features with members of the subgenus *Alvordius*, especially if the latter group is restricted to six species (*P. gymnocephala*, *P. macrocephala*, *P. maculata*, *P. notogramma*, *P. pantherina*, and *P. peltata*). Three characters the restricted *Alvordius* shares with the subgenus *Cottogaster* are: strongly developed ventral scales; enlarged mid-breast scale present on males (often lacking in *Imostoma*); and lateral body blotches quadrate to oblong rather than deep diamond-shaped or narrow vertical bars. We suggest that *P. c. crassa* and *P. c. roanoka* or *P. crassa* and *P. roanoka* as proposed by Mayden and Page (1979), do not belong in *Alvordius*. Whether the two subspecies or species belong with *Ericosma* (Bailey and Gosline, 1955) or elsewhere is beyond the scope of this paper.

CONSERVATION STATUS: There has been an increasing concern in recent years with regards to the status of our native freshwater fishes. Trautman (1957) was the first author to remark on diminishing populations of *Percina copelandi*. He reported large populations along the south shore of Lake Erie in Ohio, especially around Bass Islands during the early 1900s but by the mid-1900s these populations were greatly reduced. Maher (1970) listed *P. copelandi* as rare or endangered in Ontario. Miller (1972) listed *P.*

copelandi as rare in Kentucky and West Virginia. Comiskey and Etnier (1972) listed *P. copelandi* as uncommon in Big South Fork Cumberland system in Tennessee. Cloutman and Olmsted (1974) reported *P. copelandi* to be common in the lower part of Cossatat River in southwestern Arkansas. Gilbert and Burgess (1980) suggested that *P. copelandi* was extirpated from lower Tennessee River. Burr (1980) reported *P. copelandi* uncommon in upper Green, upper Cumberland (below the falls), upper Kentucky, middle Licking, and upper Big Sandy rivers in Kentucky. Jenkins and Musick (1980) recommended "Special Concern" status for *P. copelandi* in Virginia. Trautman (1981) repeated his analysis of 1957. Branson, et al. (1981) considered *P. copelandi* as a species of "Special Concern" in Kentucky. Warren (1981) reported several new Kentucky records for *P. copelandi*, however he repeated the "Special Concern" status suggested by Branson, et al. Burr and Warren (1986) designated *P. copelandi* as a species of "Special Concern" in Kentucky but recommended delisting. McAllister, et al. (1985) and Coad (1987) suggested *P. copelandi* as a candidate for rare or threatened status in Canada. Johnson (1987) listed *P. copelandi* as a species of "Special Concern" in Kentucky and Province of Quebec and legal protection in Michigan and Ohio. Etnier and Starnes (1991) recommended protected status for *P. copelandi* in Tennessee. Burkhead al. Jenkins (1991) continued the recommendation of "Special Concern" status for *P. copelandi* in Virginia. Campbell (1992) proposed placement of *P. copelandi* in "Vulnerable" status in Canadian waters. Etnier (1994) reported that there were no recent collections of *P. copelandi* from French Broad River system or Tennessee River system below Knoxville since the 1940's and also the recent absence from areas in the Clinch and Powell rivers in Tennessee where it had been common. We agree with Etnier's (1994) postulations about population fluctuations and also the high degree of uncertainty with regards to recovery after a period of seeming disappearance of a species. The continued separation and fragmentation of the small remnant populations by impoundments and stream deterioration decrease the likelihood of recovery.

Deacon, et al. (1979) placed Pearl channel darter (=*Percina aurora*) in "Threatened category, subcategory (1)", "present and threatened habitat destruction in Louisiana and Mississippi." Gilbert and Burgess (1980) noted the undescribed species (=*P. aurora*) of the Pearl and Pascagoula river drainages in Mississippi as extremely rare and bordering on extinction. Williams, et al. (1989) repeated the Deacon, et al. (1979) placement of the Pearl channel darter (=*P. aurora*) in the "Threatened" category in Louisiana and Mississippi.

Our collection records of *P. aurora* from Strong River, tributary to Pearl River, Simpson County, Mississippi extend from April 1958 to July 1971, thereafter none was collected. Our records of *P. aurora* from the Pearl River drainage in Lawrence County, Mississippi extend from November 1960 to August 1973, thereafter none was collected. The absence of *P. aurora* from this 20 mile section of the Pearl River in Lawrence County after 1973 is alarming because we continued to make 32 collections a year in the same section of the river from 1973 through 1992. Records of *P. aurora* from the Pearl River drainage in Marion County, Mississippi extend from October 1950 to October 1968. We made no recent attempts to collect *P. aurora* in the Marion County area. Our records of *P. aurora* from Pearl River drainage in Pearl River County, Mississippi extend from April 1963 through October 1972, thereafter none was collected. During the period from 1972 to 1994 no fewer than 24 and as many as 32 fish samples per year were taken from this same section of the Pearl River in Pearl River County without capture of any *P. aurora*. Our records of *P. aurora* from the Pearl River drainage in St. Tammany Parish, Louisiana extend from September 1963 to October 1971. Sampling efforts in the St. Tammany Parish area have been less intense than in the Pearl River County area, but have been nearly continuous from 1971 through 1993. We believe that a natural recovery of *P. aurora* in the Pearl River drainage is highly unlikely. We attribute the possible extinction of *P. aurora* in the Pearl River drainage to increased disturbance and destruction of its habitat. The removal of riparian vegetation and cultivation of extensive areas along the immediate bank of the river has led to excessive rapid runoff, bank erosion, scouring of the main channel and deposition of silt when flood waters receed. Some gravel beds have been buried under sand and silt deposits. Certainly continued clearance of riparian vegetation and/or dredging of main channel or tributaries will lessen the chance of natural recovery of *Percina aurora*.

Our sampling efforts in the Pascagoula River drainage in Mississippi have been infrequent in comparison to our efforts in the Pearl River drainage. Excluding the USNM 129182 series collected in May 1933, our records of *P. aurora* extend from August 1958 to April 1987. Additional specimens (from as late as August 1990) are at the University of Southern Mississippi (USM). We are unaware of a preferred spawning site for *P. aurora* in the Pascagoula River drainage such as formerly existed at the Strong River rapids in Simpson County, Mississippi.

There seems to be a viable population of *Percina brevicauda* in the Cahaba River system; our most recent collections were obtained in 1982. Maurice F. Mettee's (GSA) most recent collection of *P. brevicauda* from type locality was 8 July 1993 and 8 September 1993 from Cahaba River at Booth Ford. However the small, isolated populations in the Coosa and Black Warrior river systems plus the potential threatened destruction of habitat in these two river systems and also in the Cahaba River system has evoked concern about the future of the species.

Ramsey, et al. (1980) after a census of populations of *Percina* sp. (cf. *copelandi*), (=*Percina brevicauda*) concluded that the species continued to be environmentally sensitive since the 1979 survey. Ramsey, et al. (1984) in reference to *Percina* sp. cf. *copelandi* (=*P. brevicauda*) placed it in category (ExLd) (Range Extensive, Locally

Common, population trend decreasing). Williams, et al. (1989) placed Alabama channel darter, *Percina (Cottogaster)* sp. (=*P. brevicauda*) in category (T1) (Threatened, nature of threat = present or threatened destruction, modification, or curtailment of its habitat or range).

Thus all remaining populations of the three species (*Percina copelandi, P. aurora, P. brevicauda*) should be carefully monitored and in a few places immediate action must be taken to slow or stop habitat destruction to prevent further extirpation of the species.

Acknowledgements

Study materials for the analysis of the subpopulations of *Percina copelandi* were primarily received on loan from the following institutions in 1976. Reeve M. Bailey (UMMZ) sent many lots that represented the geographical breadth and included a list of their entire holdings. Eugene C. Beckham (CU), then the collection manager, loaned several series from west of the Mississippi River. Herbert T. Boschung (UAIC) also loaned several series from west of the Mississippi River. Branley A. Branson (EKU) loaned many series from Kentucky. Ted M. Cavender (OSUM) loaned a selection of series from various parts of Ohio. Frank B. Cross (KU) sent most of their large series that represented the widest distribution in the waters of Kansas, and he included a listing of their entire holdings from Kansas, Arkansas, and Oklahoma. Neil H. Douglas (NLU) loaned many series from Arkansas and Oklahoma. David A. Etnier (UT) loaned many series from Tennessee and several series from west of the Mississippi River. Ernest A. Lachner and Stanley H. Weitzman (USNM) made available early historical material as well as some more recent collections from west of the Mississippi River. Karl F. Liem and Karsten Hartel (MCZ) made available some relatively recent collections from Vermont. Larry M. Page (INHS) loaned several series from Tennessee and west of the Mississippi River. We are indebted to the above named individuals and their institutions for the loans and for extensive distributional data.

Most of the *Percina aurora* specimens were collected by Tulane University (TU) personnel. A few series were loaned by Neil H. Douglas (NLU), one lot by David A. Etnier (UT), and one lot on loan from National Museum (USNM) through the courtesy of Ernest A. Lachner. Several recently collected series from the Pascagoula River drainage were loaned by Stephen T. Ross (USM). A complete listing of Tulane University personnel who helped collect *P. aurora* during the 20 plus years would be rather extensive and so we limit our listing to those who collected a few to many specimens. Glenn H. Clemmer, the late Gerald E. Gunning, John S. Ramsey, Dawn Remington, and Jayson S. Suttkus helped collect many specimens. Susan Anderson, Myrna Andersson, Clyde D. Barbour, Katherine Carter, John H. Caruso, Robert C. Cashner, Betsy Grover, Robert Heath, Roy Irwin, Clyde Jones, Jill Jordan, David D. Norriss, Jonathan Shaeffer, C. Lavett Smith, Jan M. Suttkus, and Marilyn Warkentin each participated in the collection of a few series. We extend our deep appreciation to all of these individuals.

We received some critical historical and geographical series of *Percina brevicauda* from various institutions. We are grateful to Herbert T. Boschung and James D. Williams (UAIC) for the early loan of series from the Cahaba and Black Warrior river systems, to Ernest A. Lachner (USNM) for specimens from the Black Warrior River at Tuscaloosa, Alabama, to Maurice F. Mettee for allowing access to some recently collected series from the Cahaba River system, to John S. Ramsey (AUM) for the loan of material from the Black Warrior, Cahaba, and Coosa river systems, and to Donald C. Scott (UGAMNH) for the loan of preimpoundment specimens from the Coosa River in Alabama. We would like to thank individually those who helped collect much of the materials used in our study: Ann Black, Richard D. Caldwell, Robert C. Cashner, Glenn H. Clemmer, William M. Howell, Maurice F. Mettee, David L. Nieland, Tom Timmons, R.K. Wallace, Werner Wieland, and James D. Williams. Also we extend our thanks to J. Malcolm Pierson for the use of his records for the Cahaba River system.

We thank Reeve M. Bailey for reidentification of materials formerly housed at Indiana University (IU), now cataloged at University of Michigan, Museum of Zoology (UMMZ).

We are grateful to Jeanne Robinson Suttkus for the black and white photos (Figures 1–3). Too, we thank J. Malcolm Pierson for the use of a color slide of a nuptial male, *Percina brevicauda*, and we thank Jayson S. Suttkus for the color photograph of the type locality of *Percina aurora*.

We extend our deep appreciation to Dr. Reeve M. Bailey and Dr. David A. Etnier for their thorough reviews and their numerous suggestions for the improvement of the manuscript.

Literature Cited

Agassiz, L. 1850. Lake Superior: its physical character, vegetation, and animals, compared with those of other similar regions. With a narrative of the tour, by J. Elliott Cabot. Boston. 428pp.

Bailey, R. M. 1951. A check-list of the fishes of Iowa, with keys for identification. 187–238. *In*: Iowa fish and fishing. Iowa State Cons. Comm., Des Moines.

Bailey, R. M. and D. A. Etnier. 1988. Comments on the subgenera of darters (Percidae) with descriptions of two new species of *Etheostoma (Ulocentra)* from southeastern United States. Misc. Publ. Mus. Zool. Univ. Mich. No. 175: 48pp, color Pl.

Bailey, R. M. and W. A. Gosline. 1955. Variation and systematic significance of vertebral counts in the American fishes of the family Percidae. Misc. Publ. Mus. Zool. Univ. Mich. No. 93: 44pp.

Bailey, R. M., J. E. Fitch, E. S. Herald, E. A. Lachner, C. C. Lindsey, C. R. Robins, and W. B. Scott. 1970. A list of common and scientific names of fishes from the United States and Canada. 3rd. edition Amer. Fisheries Soc., Special Publ. No. 6: 149pp.

Bailey, R. M., E. A. Lachner, C. C. Lindsey, C. R. Robins, P. M. Roedel, W. B. Scott, L. P. Woods. 1960. A list of common and scientific names of fishes from the United States and Canada. Amer. Fisheries Soc., Special Publ. No. 2: 102pp.

Bailey, R. M., H. E. Winn, and C. L. Smith. 1954. Fishes from the Escambia River, Alabama and Florida, with ecologic and taxonomic notes. Proc. Acad. Nat. Sci. Phila. 106: 109–164.

Bangham, R. V. and G. W. Hunter, III. 1939. Studies on fish parasites of Lake Erie. Distribution studies. Zoologica: New York Zoological Soc. 24, No. 27: 385–448.

Barclay, L. A., Jr. and W. M. Howell. 1973. Ichthyofauna of the Locust Fork of the Black Warrior River system of Alabama. J. Alabama Acad. Sci. 44(1): 120–146.

Bean, T. H. 1903. Catalogue of the fishes of New York. New York State Mus. Bull. 60 (Zoology 9) (Univ. State of New York, Bull. 278): 784pp.

Blair, A. P. 1959. Distribution of the darters. (Percidae, Etheostomatinae) of northeastern Oklahoma. Southwestern Naturalist. 4(1): 1–13.

Blatchley, W. S. 1938. The fishes of Indiana with descriptions, notes on habits and distribution in the state. Nature Publishing Co., Indianapolis, 121pp.

Boschung, H. T. 1992. Catalog of freshwater and marine fishes of Alabama. Alabama Mus. Nat. Hist. Bull. No. 14: 266pp.

Boulenger, G. A. 1895. Catalogue of the fishes in the British Museum. Catalogue of the perciform fishes in the British Museum. Second edition. 1. *i–xix* + 1–394, Pls. 1–15.

Branson, B. A. 1967. Fishes of the Neosho River system in Oklahoma. Amer. Midl. Nat. 78(1): 126–154.

Branson, B. A., D. F. Harker, Jr., J. M. Baskin, M. E. Medley, D. L. Batch, M. L. Warren, Jr., W. H. Davis, W. C. Hontcooper, B. Monroe, Jr., L. R. Phillippe, and P. Cupp. 1981. Endangered, threatened, and rare animals and plants of Kentucky. Trans. Kentucky Acad. Sci., 42(3–4): 77–89.

Branson, B. A. and G. U. Ulrikson. 1967. Morphology and histology of the branchial apparatus in percid fishes of the genera *Percina*, *Etheostoma*,and*Ammocrypta* (Percidae: Percinae:Etheostomatini). Trans. Amer. Microsc. Soc. 86(4): 371–389.

Buchanan, T. M. 1973. Key to the fishes of Arkansas. Arkansas Game and Fish Comm., Little Rock, 68pp.

Burkhead, N. M. and R. E. Jenkins. 1991. Fishes. 321–409. *In*: Virginia's endangered species. McDonald and Woodward Publishing Co., Blacksburg.

Burr, B. M. 1980. A distributional checklist of fishes of Kentucky. Brimleyana, No. 3: 53–84.

Burr, B. M. and L. M. Page. 1985. Zoogeography of fishes of the lower Ohio - upper Mississippi basin. Chap. 9: 287–324. *In*: The zoogeography of North American freshwater fishes. John Wiley and Sons, New York.

Burr, B. M. and M. L. Warren, Jr. 1986. A distributional atlas of Kentucky fishes. Kentucky Nature Preserves Comm., Scientific and Tech. Series No. 4: 398pp.

Campbell, R. R. 1992. Rare and endangered fishes and marine mammals of Canada: COSEWIC fish and marine mammal subcommittee status reports VIII. Canadian Field-Naturalist, 106(1): 1–6.

Clarke, R. F., J. Brenkelman, and T. F. Andrews. 1958. An annotated check list of the vertebrates of Lyon County, Kansas. Trans. Kansas Acad. Sci. 61(2): 165–194.

Clay, W. M. 1975. The fishes of Kentucky. Kentucky Dept. Fish and Wildlife Resources, Frankfort, 416pp.

Cloutman, D. G. and L. L. Olmsted. 1974. A survey of the fishes of the Cossatat River in southwestern Arkansas. Southwestern Nat. 19(3): 257–266.

Cloutman, D. G. and L. L. Olmsted. 1976. The fishes of Washington County, Arkansas. Arkansas Water Research Center Publ. No. 39: 109pp.

Coad, B. W. 1987. Checklist of the fishes of the Ottawa District. Trail and Landscape 21(1): 1–60.

Coburn, M. M. and J. I. Gaglione. 1992. A comparative study of percid scales (Teleostei: Perciformes). Copeia, 1992(4): 986–1001.

Collette, B. B. 1965. Systematic significance of breeding tubercles in fishes of the family Percidae. Proc. U. S. Natl. Mus. 117(3518): 567–614.

Collette, B. B. and L. W. Knapp. 1967. Catalog of type specimens of the darters (Pisces, Percidae, Etheostomatini). Proc. U. S. Natl. Mus. (1966)119 (3550): 1–88.

Comiskey, C. E. and D. A. Etnier. 1972. Fishes of the Big South Fork of the Cumberland River. J. Tennessee Acad. Sci. 47(4): 140–145.

Conger, A. C. 1920. A key to Michigan vertebrates, except birds. Zoological Dept., Teacher-Training Dept., Michigan Agricultural College, East Lansing, 76pp.

Cooper, E. L. 1983. Fishes of Pennsylvania and the northeastern United States. Pennsylvania State Univ. Press, University Park, 243pp.

Cope, E. D. 1868. On the distribution of freshwater fishes in the Alleghany Region of southwestern Virginia. J. Acad. Nat. Sci. Phila., New Series Vol. 6, part 3:207–277.

Cross, F. B. 1967. Handbook of fishes of Kansas. Univ. Kansas Mus. Nat. Hist. Misc. Publ. No. 45: 357pp., color Pls. 1–4.

Cross, F. B. and J. T. Collins. 1975. Fishes in Kansas. Univ. Kansas Mus. Nat. Hist. Public Education Series, No. 3: 189pp.

Cross, F. B., R. L. Mayden, and J. D. Stewart. 1985. Fishes in the western Mississippi basin (Missouri, Arkansas and Red rivers). Chap. 11: 363–412. *In*: The zoogeography of North American freshwater fishes. John Wiley and Sons, New York.

Cross, F. B. and G. A. Moore. 1952. The fishes of the Poteau River, Oklahoma and Arkansas. Amer. Midl. Nat. 47(2): 396–412.

Deacon, J. E. 1961. Fish populations, following a drought, in the Neosho and Marais des Cygnes rivers of Kansas. Univ. Kansas Publ., Mus. Nat. Hist., 13(9): 359–427.

Deacon, J. E., G. Kobetich, J. D. Williams, S. Contreras, and other members of the endangered species committee of the Amer. Fish. Soc. 1979. Fishes of North America endangered, threat-

ened, or of special concern: 1979. Fisheries, 4(2): 29–44.

DeKay, J. E. 1842. Zoology of New York; or the New York fauna; comprising detailed descriptions of all the animals hetherto observed within the state of New York, with brief notices of those occasionally found near its borders... *In*:Natural History of New York. Part IV. Fishes 415 pp., Pls. 1–79.

Denoncourt, R. F. 1976. Sexual dimorphism and geographic variation in the bronze darter, *Percina palmaris* (Pisces: Percidae). Copeia, 1976(1): 54–59.

Douglas, N. H. 1974. Freshwater fishes of Louisiana. Claitor's Publishing Division, Baton Rouge, 443pp.

Dymond, J. R. 1922. A provisional list of the fishes of Lake Erie. Univ. Toronto Studies, Biol. Ser., No. 20 (Publ. Ont. Fish. Res. Lab., No. 4): 55–73.

Eschmeyer, W. N. and R. M. Bailey. 1990. Genera of recent fishes, Part 1, 7–433. *In*: Catalog of the genera of recent fishes. California Acad. Sci., San Francisco.

Etnier, D. A. 1976. *Percina (Imostoma) tanasi*, a new percid fish from the Little Tennessee River, Tennessee. Proc. Biol. Soc. Washington. 88(44): 469–488.

Etnier, D. A. 1994. Our southeastern fishes - what have we lost and what are we likely to lose. Proc. Southeastern Fishes Council. No. 29: 5–9.

Etnier, D. A. and W. C. Starnes. 1991. An analysis of Tennessee's jeopardized fish taxa. J. Tennessee Acad. Sci. 66(4): 129–133.

Etnier, D. A. and W. C. Starnes. 1994. The fishes of Tennessee. Univ. Tennessee Press, Knoxville, 681 pp.

Evermann, B. W. 1902. List of species of fishes known to occur in the Great Lakes or their connecting waters. Bull. U. S. Fish Comm. (1901)21: 95–96.

Evermann, B. W. 1918. The fishes of Kentucky and Tennessee: a distributional catalogue of the known species. Bull. Bur. Fish. (1915–16)35 (858): 295–368.

Evermann, B. W. and S. F. Hildebrand. 1916. Notes on the fishes of east Tennessee. Bull. U. S. Bur. Fish. (1914)34: 431–451.

Evermann, B. W. and W. C. Kendall. 1895. A list of the species of fishes known from vicinity of Neosho, Missouri. Bull. U. S. Fish Comm. (1894)14: 469–472.

Evermann, B. W. and W. C. Kendall. 1898. Descriptions of new or little-known genera and species of fishes from the United States. Bull. U.S. Fish Comm. (1897)17 (art. 5): 125–133, Pls. 6–9.

Facey, D. E. and G. W. LaBar, 1989. A survey of the fishes of Vermont waters of the southern Lake Champlain basin. Vermont Fish Wildlife Dept. Tech. Rep. No. 7: 61pp.

Fish, M. P. 1932. Contributions to the early life histories of sixty-two species of fishes from Lake Erie and its tributary waters. Bull. U. S. Bur. Fish. 47(10) (1931–33): 292–398.

Garman, H. 1894. A preliminary list of vertebrate animals of Kentucky. Bull. Essex Inst. 26 (1, 2, 3): 1–63.

Gerking, S. D. 1945. Distribution of the fishes of Indiana. Invest. Indiana Lakes and streams. 3, No. 1: 1–137.

Gilbert, C. R. and G. H. Burgess. 1980. *Percina copelandi* (Jordan), channel darter. Page 721 *In*: D. S. Lee et al. eds. Atlas of North American freshwater fishes. North Carolina State Mus. Nat. Hist., Raleigh, 854pp.

Gilbert, C. R. and S. J. Walsh. 1991. Provenance and disposition of fish specimens appearing in color plates of Kuehne and Barbour's book, The American Darters. Proc. Southeastern Fishes Council, No. 24: 12–19.

Gilbert, C. H. 1891. Report of explorations made in Alabama during 1889, with notes on the fishes of the Tennessee, Alabama, and Escambia rivers. Bull. U. S. Fish Comm. (1889) 9: 132–160.

Greeley, J. R. 1929. Fishes of the Erie-Niagara watershed: 150–179, color Pls. 1–8. *In*: A biological survey of the Erie-Niagara system. Suppl. 18th Ann. Rep. New York State Cons. Dept. (1928).

Greeley, J. R. 1930. Fishes of the Lake Champlain watershed: 44–87, color Pls. 1–16. *In*: A biological survey of the Champlain watershed. Suppl. 19th Ann. Rep. New York State Cons. Dept. (1929).

Greeley, J. R. and S. C. Bishop. 1932. Fishes of the area, with annotated list: 54–92, color Pls. 1–12. *In*: A biological survey of the Oswegatchie and Black river systems, including also the lesser tributary streams of the upper St. Lawrence River and of northeastern Lake Ontario. Suppl. 21st Ann. Rep. (1931).

Greeley, J. R. 1934. Fishes of the Raquette watershed, with annotated list: 53–108, color Pls. 1–12. *In*: A biological survey of the Raquette watershed. Suppl. 23rd Ann. Rep. (1933).

Greeley, J. R. and C. W. Greene. 1931. Fishes of the area with annotated list: 44–94, color Pls. 1–12. *In*: A biological survey of the St. Lawrence watershed, including the Grass, St. Regis, Salmon, Chateugay systems and the St. Lawrence between Ogdensburg and the International Boundary. Suppl. 20th Ann. Rep. New York State Cons. Dept. (1930).

Hay, O. P. 1894. The lampreys and fishes of Indiana. Indiana Dept. Geo. and Nat. Resources. 19th Annual Report: 147–296.

Henshall, J. A. 1889. Contributions to the ichthyology of Ohio. No. 2. J. Cincinnati Soc. Nat. Hist. 11: 122–126.

Hocutt, C. H., R. E. Jenkins, and J. R. Stauffer, Jr. 1985. Zoogeography of the fishes of the central Appalachians and central Atlantic coastal plain. Chap. 6: 161–211. *In*: The zoogeography of North American freshwater fishes. John Wiley and Sons, New York.

Hoffman, G. L. 1970. Parasites of North American freshwater fishes. Univ. California Press, Los Angeles, 486pp.

Hubbs, C. L. 1926. A check-list of the fishes of the Great Lakes and tributary waters, with nomenclatorial notes and analytical keys. Misc. Pub. Mus. Zool. Univ. Michigan, No. 15: 1–77, Pls. 1–4.

Hubbs, C. L. 1930. Further additions and corrections to the list of the fishes of the Great Lakes and tributary waters. Papers Michigan Acad. Sci., Arts and Letters (1929)11: 425–436.

Hubbs, C. L. 1955. Hybridization between fish species in nature. Syst. Zool. 4(1): 1–20.

Hubbs, C. L. and C. W. Greene. 1928. Further notes on the fishes

of the Great Lakes and tributary waters. Papers Michigan Acad. Sci., Arts and Letters (1927)8: 371–392.

Hubbs, C. L. and K. F. Lagler. 1939. Keys for the identification of the fishes of the Great Lakes and tributary waters. Ann Arbor, 37 pp. (published by the authors).

Hubbs, C. L. and K. F. Lagler. 1941. Guide to the fishes of the Great Lakes and tributary waters. Bull. Cranbrook Inst. Sci., No. 18: 1–100.

Hubbs, C. L. and K. F. Lagler. 1947. Fishes of the Great Lakes region. Bull. Cranbrook Inst. Sci. No. 26: 1–109. 26 color Pls.

Hubbs, C. L. and K. F. Lagler. 1958. Fishes of the Great Lakes region. Bull. Cranbrook Inst. Sci. No. 26: 1–213, color Pls 1–44.

Hubbs, C. L. and A. I. Ortenburger. 1929. Fishes collected in Oklahoma and Arkansas in 1927. Pub. Univ. Oklahoma Biol. Surv. 1(3): 47–112. Pls, 1–13.

Hubbs, C. and C. Bryan. 1975. Ontogenetic rates and tolerances of the channel darter, *Hadropterus copelandi*. Texas J. Sci. 26(3 and 4): 623–625.

Jenkins, R. E. 1976. A list of undescribed freshwater fish species of Continental United States and Canada, with additions to the 1970 checklist. Copeia, 1976(3): 642–644.

Jenkins, R. E. and N. M. Burkhead. 1994. Freshwater fishes of Virginia. Amer. Fish. Soc., Bethesda, 1079pp.

Jenkins, R. E., E. A. Lachner, and F. J. Schwartz. 1972. Fishes of the central Appalachian drainages: their distribution and dispersal. 43–117. *In*: The distributional history of the biota of the southern Appalachians. Part III: Vertebrates. Virginia Polytech. Inst. State Univ. Res. Div. Mongr. 4, Blacksburg.

Jenkins, R. E. and J. A. Musick. 1980. Freshwater and marine fishes, 319–373. *In*: D. W. Linzey, Ed., Endangered and threatened plants and animals of Virginia. Virginia Polytech. Inst. St. Univ., Blacksburg.

Johnson, J. E. 1987. Protected fishes of the United States and Canada. Amer. Fish. Soc., Bethesda, 42pp.

Jordan, D. S. 1876. Manual of the vertebrates of the northern United States including the district east of the Mississippi River, and north of North Carolina and Tennessee, exclusive of marine species (1st ed.). Jansen, McClurg and Co., Chicago, 342pp.

Jordan, D. S. 1877a. On the fishes of northern Indiana. Proc. Acad. Nat. Sci. Phila. 1877: 42–82.

Jordan, D. S. 1877b. A partial synopsis of the fishes of upper Georgia, with supplementary papers on fishes of Tennessee, Kentucky, and Indiana. Ann. Lyc. Nat. Hist. New York 11(no. 11–12) (29): 307–377.

Jordan, D. S. 1877c. Contributions to North American ichthyology based primarily on the collections of the United States National Museum. No. 2. A. - Notes on Cottidae, Etheostomatidae, Percidae, Centrarchidae, Aphododeridae, Umbridae, Esocidae, Dorysomatidae, Cyprinidae, Catostomidae, and Hyodontidae, with revisions of the genera and descriptions of new or little known species. Bull. U. S. Natl. Mus. No. 10: 5–68.

Jordan, D. S. 1878a. Manual of the vertebrates of the northern United States, including the district east of the Mississippi River and north of North Carolina and Tennessee, exclusive of marine species. (2nd ed.) Jansen, McClurg and Co., Chicago, 407pp.

Jordan, D. S. 1878b. A catalogue of fishes of the fresh waters of North America. Bull. U. S. Geol. Geogr. Surv. Terr. 4(no. 2, art. 18): 407–442.

Jordan, D. S. 1878c. A catalogue of the fishes of Illinois. Illinois State Laboratory of Natural History. Bull. 1(2): 37–70.

Jordan, D. S. 1880. Manual of the vertebrates of the northern United States, including the district east of the Mississippi River, and north of North Carolina and Tennessee, exclusive of marine species. (3rd ed. Jansen, McClurg and Co., Chicago, 407pp.

Jordan, D. S. 1882. Report on the fishes of Ohio. Rep. Geol. Surv. Ohio 4: 737–1002.

Jordan, D. S. 1884. Manual of the vertebrates.... (4th ed., same as 3rd ed.)

Jordan, D. S. 1885. A catalogue of the fishes known to inhabit the waters of North America, north of the Tropic of Cancer, with notes on the species discovered in 1883 and 1884. Rep. U. S. Fish Comm. 13: 789–973; also issued as an extract from the Annual Rep. of the Commissioner of Fish and Fisheries for 1884 with different pagination (1–185).

Jordan, D. S. 1888. A manual of the vertebrate animals of the northern United States, including the district north and east of the Ozark Mountains, south of the Laurentian Hills, north of the southern boundary of Virginia, and east of the Missouri River, inclusive of marine species. (5th ed.) McClurg and Co., Chicago, 357pp.

Jordan, D. S. 1890. Report of explorations made during the summer and autumn of 1888, in the Alleghany region of Virginia, North Carolina and Tennessee, and in western Indiana, with an account of the fishes found in each of the river basins of those regions. Bull. U. S. Fish Comm. 8: 97–173.

Jordan, D. S. 1899. A manual of the vertebrate animals of the northern United States, including the district north and east of the Ozark Mountains, south of the Laurentian Hills, north of the southern boundary of Virginia, and east of the Missouri River, inclusive of marine species. (8th ed.) McClurg and Co., Chicago, 397pp.

Jordan, D. S. 1904. A manual of the vertebrate animals, ... (9th ed., same as 8th ed.)

Jordan, D. S. 1910. A manual of the vertebrate animals, ... (10th ed., same as 8th ed.).

Jordan, D. S. 1914. A manual of the vertebrate animals, ... (11th ed., same as 8th ed.).

Jordan, D. S. 1916. A manual of the vertebrate animals, ... (12th ed., same as 8th ed.).

Jordan, D. S. 1919. The genera of fishes and a classification of fishes, Part III, from Guenther to Gill, 1859–1880, twenty-two years, with the accepted type of each. A contribution to the stability of scientific nomenclature. Leland Stanford Jr. Univ. Publ., Univ. Ser. No. 39: 285–410, (index, *i–xv*.).

Jordan, D. S. 1929. Manual of the vertebrate animals of the northeastern United States, inclusive of marine species. (13th

ed.) World Book Co., New York, 446pp.

Jordan, D. S. and A. W. Brayton. 1878. Contribution to North American ichthyology, based primarily on the collections of the United States National Museum. III. A. On the distribution of the fishes of the Alleghany region of South Carolina, Georgia, and Tennessee, with descriptions of new or little known species. Bull. U. S. Natl. Mus. No. 12: 3–95.

Jordan, D. S. and H. E. Copeland. 1877. Check list of the fishes of the fresh waters of North America. Bull. Buffalo Soc. Nat. Sci. 3: 133–164. (see bottom p. 137, 145, 153, 161, December, 1876).

Jordan, D. S. and C. H. Eigenmann. 1886. Notes on skeletons of Etheostomatinae. Proc. U. S. Natl. Mus. 8: 68–72.

Jordan, D. S. and B. W. Evermann. 1896a. A check list of the fishes and fish-like vertebrates of North and Middle America. Rep. U. S. Fish Comm. 21 (1895) Append. 5: 207–584.

Jordan, D. S. and B. W. Evermann. 1896b. The fishes of North and Middle America: a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the isthmus of Panama. Part I. Bull. U. S. Natl. Mus. No. 47: 1240pp.

Jordan, D. S. and B. W. Evermann. 1898. The fishes of North and Middle America: a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the isthmus of Panama. Part III. Bull. U. S. Natl. Mus. No. 47: 2183a–3136.

Jordan, D. S. and B. W. Evermann. 1900. The fishes of North and Middle America: a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the isthmus of Panama, Part IV. Bull. U. S. Natl. Mus. No. 47: 3137–3313, Pls. 1–392.

Jordan, D. S., B. W. Evermann, and H. W. Clark. 1930. Check list of the fishes and fishlike vertebrates of North and Middle America north of the northern boundary of Venezuela and Columbia. Rep. U. S. Comm. Fish. (1928) Pt. 2: 670pp.

Jordan, D. S. and C. H. Gilbert. 1877. On the genera of North American fresh-water fishes. Proc. Acad. Nat. Sci. Phila. 1877: 83–104.

Jordan, D. S. and C. H. Gilbert. 1883. Synopsis of the fishes of North America. Bull. U. S. Natl. Mus. No. 16: 1018pp. [for publication date see: Jordan's (1884) Preface to 4th ed., Manual of the vertebrates; (1885:1, "issued to the public about April 1, 1883"); and (1888) Preface to 5th ed., Manual of the vertebrate annimals].

Jordan, D. S. and C. H. Gilbert. 1886. List of fishes collected in Arkansas, Indian Territory, and Texas, in September, 1884, with notes and descriptions. Proc. U. S. Natl. Mus. 9: 1–25.

Kirsch, P. H. 1893. Notes on a collection of fishes from the southern tributaries of the Cumberland River in Kentucky and Tennessee. Bull. U. S. Fish Comm. (1891)11: 259–268.

Kirsch, P. H. 1895. A report upon investigations in the Maumee River basin during the summer of 1893. Bull. U. S. Fish Comm. (1894)14: 315–337.

Kuehne, E. R. 1939. A guide to the fishes of Tennessee and the mid-south. Division of Game and Fish, Tennessee Dept. Conservation, Nashville, 124pp.

Kuehne, R. A. and R. W. Barbour, 1983. The American darters. Univ. Press of Kentucky, Lexington, 177pp.

Lang, J. W. 1967. Geohydrologic summary of the Pearl River Basin. Water Resources Division, U.S. Geol. Surv. Open-file Report, 44pp.

Lee, D. S., C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAllister and J. R. Stauffer, Jr. 1980 (eds.). Atlas of North American Freshwater Fishes. North Carolina State Mus. Nat. Hist. Raleigh, 854pp.

Legendre, V. 1954. The freshwater fishes, volume 1. key to game and commercial fishes of the Province of Quebec. Canad. Soc. Ecology and Quebec Game and Fisheries Dept. 1–180.

Maher, F. P. 1970. Extinct, rare and endangered fishes in Ontario. Ontario Fish and Wildlife Review. 9(1–2): 9–20.

Mayden, R. L. 1987. Historical ecology and North American Highland fishes: A research program in community ecology. Art. 26: 210–222. *In*: Community and evolutionary ecology of North American stream fishes. W. J. Matthews and D. C. Heins (eds.). Univ. Oklahoma Press, Norman.

Mayden, R. L. and L. M. Page. 1979. Systematics of *Percina roanoka* and *P. crassa*, with comparisons to *P. peltata* and *P. notogramma*. Copeia, 1979(3): 413–426.

McAllister, D. E. and B. W. Coad. 1974. Fishes of Canada's National Capital Region. Misc. Special Publ. 24: 200pp.

McAllister, D. E., B. J. Parker and P. M. McKee. 1985. Rare, endangered and extinct fishes in Canada. Syllogeus, No. 54: 192pp.

McCormick, L. M. 1892. A descriptive list of the fishes of Lorain County, Ohio. Bull. Publ. by Oberlin College, No. 2:1–33.

Meek, S. E. 1891. Report of explorations made in Missouri and Arkansas during 1889, with an account of the fishes observed in each of the river basins examined. Bull. U. S. Fish Comm. 9: 115–141.

Meek, S. E. 1895. Report of investigations respecting the fishes of Arkansas conducted during 1891, 1892, and 1893, with a synopsis of previous explorations in the same state. Bull. U. S. Fish Comm. (1894)14: 67–94.

Metcalf, A. L. 1959. Fishes of Chautauqua, Cowley and Elk counties, Kansas. Univ. Kansas Publ. Mus. Nat. Hist. 11(6): 345–400, Pls. 9–10.

Mettee, M. F. 1978. The fishes of the Birmingham-Jefferson county region of Alabama with ecologic and taxonomic notes. Geol. Surv. Alabama Bull. No. 115: 182pp.

Mettee, M. F., P. E. O'Neil, J. M. Pierson and R. D. Suttkus. 1989a. Fishes of the Black Warrior River system in Alabama Geol. Surv. Alabama Bull. no. 133: 201pp.

Mettee, M. F., P. E. O'Neil, J. M. Pierson and R. D. Suttkus. 1989b. Fishes of the western Mobile River basin in Alabama and Mississippi. Atlas No. 24: 170 pp.

Miller, R. R. 1972. Threatened freshwater fishes of the United States. Trans. Amer. Fish. Soc., 1972(2): 239–252.

Miller, J. R. and H. W. Robison. 1973. The fishes of Oklahoma. Oklahoma State Univ. Mus. Nat. and Cultural Hist. Series No. 1, 246pp.

Moore, G. A. 1957. Fishes, Part II, 22–165. *In*: Vertebrates of the United States. 2nd edition. McGraw-Hill Book Co., Inc., New York.

Moore, G. A. 1968. Fishes, Part II, 22–165. *In*: Vertebrates of the United States. 2nd edition. McGraw-Hill Book Co., Inc., New York.

Nash, C. W. 1908. Check list of the fishes of Ontario. 7–122, Pls. 1–32. *In*: Ontario Dept. of Education, Toronto.

New, J. G. 1966. Reproductive behavior of the shield darter, *Percina peltata*, in New York. Copeia, 1966(1): 20–28.

Olmsted, L. L. , G. D. Hickman and D. G. Cloutman. 1972. A survey of the fishes of the Mulberry River, Arkansas. Arkansas Water Resources Research Center Publ. No. 10: 20pp.

Osburn, R. C. 1901. The fishes of Ohio. Ohio State Acad. Sci., Special Paper No. 4: 1–105.

Osburn, R. C., E. L. Wickliff and M. B. Trautman. 1930. A revised list of the fishes of Ohio. 30(3): 169–176.

Page, L. M. 1974. The subgenera of *Percina* (Percidae: Etheostomatini). Copeia, 1974(1): 66–86.

Page, L. M. 1976. The modified midventral scales of *Percina* (Osteichthyes; Percidae). J. Morph. 148(2): 255–264.

Page, L. M. 1977. The lateralis system of darters (Etheostomatini). Copeia, 1977(3): 472–475.

Page, L. M. 1981. The genera and subgenera of darters (Percidae, Etheostomatini). Occ. Pap. Mus. Nat. Hist., Univ. Kansas. No. 90: 69pp.

Page, L. M. 1983. Handbook of darters. TFH Publications, Inc. Ltd. Neptune City, 271pp.

Page, L. M. and B. M. Burr. 1991. A field guide to freshwater fishes, North America, north of Mexico. Houghton Mifflin Co., Boston, 432pp.

Page, L. M. and D. L. Swofford. 1984. Morphological correlates of ecological specialization in darters. Environmental Biology Fishes 11(2): 139–159.

Page, L. M. and G. S. Whitt. 1973a. Lactate dehydrogenase isozymes, malate dehydrogenase isozymes and tetrazolium oxidase mobilities of darters (Etheostomatini). Comp. Biochem. Physiol., 44B: 611–623.

Page, L. M. and G. S. Whitt. 1973b. Lactate dehydrogenase isozymes of darters and the inclusiveness of the genus *Percina*. Illinois Nat. Hist. Surv. Biol. Notes, 82: 1–7.

Pflieger, W. L. 1971. A distributional study of Missouri fishes. Univ. Kansas Publ. Mus. Nat. Hist., 20(3): 225–570.

Pflieger, W. L. 1975. The fishes of Missouri. Missouri Dept. Conservation, Jefferson City, 343pp.

Pierson, J. M., W. M. Howell, R. A. Stiles, M. F. Mettee, P. E. O'Neil, R. D. Suttkus, and J. S. Ramsey. 1989. Fishes of the Cahaba River system in Alabama. Geol. Surv. Alabama Bull. No. 134: 183pp.

Putnam, F. W. 1863. List of the fishes sent by the museum to different institutions, in exchange for other specimens, with annotations. Bull. Mus. Comp. Zool. 1(art. 1): 2–16.

Ramsey, J. S., H. T. Boschung, W. M. Howell, T. S. Jandebeur, M. F. Mettee, P. E. O'Neil, J. M. Pierson, W. C. Reeves, R. A. Stiles, and W. Wieland. 1984. Freshwater fishes; 1–14 *In*: Vertebrate Wildlife of Alabama. Alabama Agricultural Experiment Station, Auburn Univ., Auburn.

Ramsey, J. S., W. Wieland, R. K. Wallace and T. J. Timmons. 1980. Sampling rare fishes in the Cahaba River, Alabama. A. S. B. Bull. 27(2): 58.

Robins, C. R., R. M. Bailey, C. E. Bond, J. R. Brooker, E. H. Lachner, R. N. Lea, and W. B. Scott. 1980. A list of common and scientific names of fishes from the United States and Canada. 4th. edition Amer. Fish. Soc., Special Publ. No. 12: 174pp.

Robins, C. R., R. M. Bailey, C. E. Bond, J. R. Brooker, E. A. Lachner, R. N. Lea, and W. B. Scott. 1991. Common and scientific names of fishes from the United States and Canada. 5th. edition Amer. Fish. Soc. Special Publ. No. 20: 183pp.

Robison, H. W. and T. M. Buchanan. 1988. Fishes of Arkansas. Univ. Arkansas Press, Fayetteville, 536pp.

Rohde, F. C., R. G. Arndt, D. G. Lindquist, and J. F. Parnell. 1994. Freshwater fishes of the Carolinas, Virginia, Maryland, and Delware. Univ. North Carolina Press, Chapel Hill, 222pp.

Ross, S. T., D. C. Heins and J. W. Burris. 1992. Fishes of Okatoma Creek, a free-flowing stream in south-central Mississippi. Proc. Southeastern Fishes Council, No. 26: 2–10.

Schelske, C. L. 1957. An ecological study of the fishes of the Fall and Verdigris rivers in Wilson and Montgomery counties, Kansas, March 1954 to February 1955. Emporia State Research Studies (Graduate Publ. Kansas State Teachers College, Emporia) 5, No. 3: 31–56.

Scott, D. M. 1955. Additional records of two fishes, *Erimyzon sucetta kennerlyi* and *Hadropterus copelandi*, from southern Ontario, Canada. Copeia, 1955(2): 151.

Scott, W. B. 1963. A review of the changes in the fish fauna of Ontario. 1963. Trans. Royal Canadian Inst. 34, Pt. II: 111–125.

Scott, W. B. and E. J. Crossman. 1969. Checklist of Canadian freshwater fishes with keys for identification. Life Sci. Misc. Publ. Royal Ontario Mus., 104pp.

Scott, W. B. and E. J. Crossman. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Canada. 184: 966pp.

Seehorn, M. E. 1975. Fishes of southeastern national forests. Proc. 29th Ann. Conf. Southeastern Assoc. Fish and Wildlife Agencies, 10–27.

Simons, A. M. 1992. Phylogenetic relationships of the *Boleosoma* species group (Percidae: *Etheostoma*):268–292. *In*: R. L. Mayden (ed.), Systematics, historical ecology and North American freshwater fishes, Stanford University Press.

Smith, C. L. 1985. The inland fishes of New York state. New York State Dept. Environmental Conservation, Albany, 522pp.

Smith-Vaniz, W. F. 1968. Freshwater fishes of Alabama. Auburn Univ. Agricultural Experiment Sta., Auburn, 211pp.

Starnes, W. C., D. A. Etnier, L. B. Starnes and N. H. Douglas. 1977. Zoogeographic implications of the rediscovery of the percid genus *Ammocrypta* in the Tennessee River drainage.

Copeia. 1977(4): 783–786.

Starnes, W. C. and D. A. Etnier. 1985. Drainage evolution and fish biogeography of the Tennessee and Cumberland rivers drainage realm. Chap. 10: 325–361. *In*: The zoogeography of North American freshwater fishes. John Wiley and Sons, New York.

Suttkus, R. D. 1985. Identification of the percid, *Ioa vigil* Hay. Copeia, 1985(1): 225–227.

Suttkus, R. D. and J. S. Ramsey. 1967. *Percina aurolineata*, a new percid fish from the Alabama River system and a discussion of ecology, distribution, and hybridization of darters of the subgenus *Hadropterus*. Tulane Stud. Zool. 13(4): 129–145.

Swift, C. C., C. R. Gilbert, S. A. Bortone, G. H. Burgess, R. W. Yerger. 1986. Zoogeography of the freshwater fishes of the southeastern United States: Savannah River to Lake Pontchartrain. Chap. 7: 213–265. *In*: The zoogeography of North American freshwater fishes. John Wiley and Sons, New York.

Thompson, B. A. and K. E. Hartel. 1994. Hybridization between *Percina copelandi* and *P. caprodes semifasciata* with a review of hybridization in Percina. A. S. B. Bull. 41(2): 132.

Thompson, Z. 1853. Appendix to: Natural history of Vermont. Burlington, 224pp.

Trautman, M. B. 1957. The fishes of Ohio, with illustrated keys. Ohio State Univ. Press, Columbus, 683pp.

Trautman, M. B. 1981. The fishes of Ohio, with illustrated keys. Revised edition. Ohio State Univ. Press, Columbus, 782pp.

Turner, C. L. 1921. Food of the common Ohio darters. Ohio J. Sci. 22(2): 41–62.

Underhill, J. C. 1985. The fish fauna of the Laurentian Great Lakes, the St. Lawrence lowlands, Newfoundland and Labrador. Chap. 4: 105–136. *In*: The zoogeography of North American freshwater fishes. John Wiley and Sons, New York.

Wallus, R. and N. H. Douglas. 1973. Ichthyofauna of Strong River, south-central Mississippi. Proc. Louisiana Acad. Sci. 36: 111–122.

Warren, M. L. 1981. New distributional records of eastern Kentucky fishes. Brimleyana No. 6: 129–140.

Welter, W. A. 1938. A list of the fishes of the Licking River drainage in eastern Kentucky. Copeia, 1938, (2): 64–68.

Werner, R. G. 1980. Freshwater fishes of New York state, a field guide. Syracuse Univ. Press, Syracuse, 186pp.

Williams, J. E., J. E. Johnson, D. A. Hendrickson, S. Contreras–Balderas, J. D. Williams, M. Navarro–Mendoza, D. E. McAllister, and J. E. Deacon. 1989. Fishes of North America endangered, threatened, or of special concern. Fisheries, 1989. 14(6): 2–20.

Winn, H. E. 1953. Breeding habits of the percid fish *Hadropterus copelandi* in Michigan. Copeia, 1953(1): 26–30.

Winn, H. E. 1958a. Observations on the reproductive habits of darters (Pisces-Percidae). Amer. Midl. Nat. 59, (1): 190–212.

Winn, H. E. 1958b. Comparative reproductive behavior and ecology of fourteen species of darters (Pisces-Percidae). Ecological Monographs. 28(2): 155–191.

Woolman, A. J. 1892. Report of an examination of the rivers of Kentucky, with lists of the fishes obtained. Bull. U. S. Fish Comm. (1890)10: 249–288, Pl. 51.

Table 1. Comparison of type specimens of nominal species of subgenus *Cottogaster* (= *Percina copelandi*).

	USNM 20143, Lectotype *Rheocrypta copelandi*	USNM 197796, Paralectotype *Rheocrypta copelandi*	USNM 23461, Paralectotype *Rheocrypta copelandi*	USNM 1314, Lectotype *Cottogaster putnami*	USNM 198000, Paralectotype *Cottogaster putnami*	USNM 198000, Paralectotype *Cottogaster putnami*	USNM 47531, Holotype *Ulocentra gilberti*	USNM 125373, Paratype *Ulocentra gilberti*	USNM 48781, Holotype *Cottogaster cheneyi*	USNM 48782, Paratype *Cottogaster cheneyi*	USNM 48782, Paratype *Cottogaster cheneyi*	USNM 48782, Paratype *Cottogaster cheneyi*	USNM 48782, Paratype *Cottogaster cheneyi*	USNM 126978, Paratype *Cottogaster cheneyi*	USNM 126978, Paratype *Cottogaster cheneyi*	USNM 126978, Paratype *Cottogaster cheneyi*	USNM 126978, Paratype *Cottogaster cheneyi*
Sex	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
SL (mm)	42.9	43.2	43.9	45.6	48.5	45.3	37.8	35.8	50.5	47.0	40.8	40.1	38.7	47.4	41.8	41.3	38.3
Dorsal fins	XI–12	XI–12	XI–12	XI–12	–	–	IX–11	IX–11	XI–12	XII–12	XII–12	XI–13	XI–12	X–11	X–13	XI–12	IX+13
Anal fin	II, 9	II, 9	II, 8	II, 8	II, 9	II, 9	II, 8	II, 7	II, 8	II, 8	II, 8	II, 8	II, 9	II, 8	II, 9	II, 8	II, 9
Pectoral fin	13—14	14—15	13—12	14—14	–	–	14—	–	14—14	–	–	–	–	15—	–	–	–
Lateral line scales	54	55	51	48	47	47	49	51	52	52	50	51	48	50	46	55	49
Transverse scale rows	13	14	13	13	14	13	14	14	14	15	14	13	11	13	12	13	13
Caudal peduncle scale rows	17	17	16	16	16	16	15	15	16	17	16	16	16	16	18	17	16
Branchiostegal rays	6—6	6—6	6—6	6—6	6—6	6—6	5—5	6—6	6—6	6—6	6—6	6—6	6—6	6—6	6—6	6—6	6—6
Modified belly scales	8	10	5	6	8	6	8	8	6	0	0	8	6	0	0	0	1
Nape squamation	2 scales	3 scales	33%	2 scales	25%	naked	100%	90%	1 scale	33%	25%	1 scale	2 scales	naked	4 scales	25%	50%
Cheek squamation	1 scale	naked	50%	naked	naked	naked	100%	100%	naked	naked	naked	naked	naked	naked	naked	naked	naked
Opercle squamation	100%	33%	33%	100%	100%	3 scales	100%	100%	33%	100%	100%	50%	4 scales	3 scales	100%	90%	75%
Premaxillary frenum	absent	absent	absent	narrow	absent	absent	absent	absent	absent	narrow	narrow	narrow	narrow	narrow	narrow	narrow	narrow

Table 2. Frequency distribution of lateral line scales in the species of *Percina*, subgenus *Cottogaster*.

	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	N	$\bar{x}$	S.D.
P. copelandi																													
Great Lakes	1	–	1	9	16	28	45	67	60	64	38	38	26	17	9	4	2										425	50.4	2.7
Ohio R.		1	1	2	11	16	16	23	26	30	12	9	12	2	4	3											168	50.1	2.7
Cumberland R.				1	4	5	8	13	18	19	12	9	9	3	4												105	50.8	2.4
Tennessee R.			1	–	1	1	2	4	3	7	13	14	6	4	1	–	1										58	51.9	2.4
Arkansas R.							1	1	1	5	6	17	26	27	26	18	11	8	7	3	–	1					158	55.4	2.4
Little Missouri R.												2	4	4	8	7	7	5	3	3	1	2	1				47	57.6	2.7
Caddo R.									1	–	1	–	–	2	3	2	9	4	9	3	4	1	1				40	58.7	2.7
Ouachita R.												2	2	2	4	4	4	2	3	2	1	1					27	57.5	2.7
Saline R.											2	2	1	2	6	10	3	1	2	–	–	–	1				30	56.6	2.4
Red R.												1	5	2	4	9	8	11	13	13	14	13	11	6	7	2	119	60.8	3.2
P. aurora																													
Pearl R.									3	4	8	11	26	21	31	18	19	5	5	4							155	55.6	2.3
Pascagoula R.													1	–	4	4	5	3	2	2							21	57.8	1.7
P. brevicauda																													
Coosa R.									1	–	2	4	2	–	2	2	1										14	54.1	2.3
Cahaba R.									1	–	1	3	2	10	9	9	11	25	15	8	8	4	1	4	1		112	58.7	2.9
Warrior R.										3	–	1	4	5	4	2	7	5	4	3	6			1			45	57.7	3.3

Table 3. Frequency distribution of transverse scale rows in species of *Percina*, subgenus *Cottogaster*.

	11	12	13	14	15	16	17	18	19	20	21	22	N	$\bar{x}$	S.D.
P. copelandi															
Great Lakes	4	108	157	103	34	7							413	13.2	1.0
Ohio R.	6	40	68	40	8	4							166	13.1	1.0
Cumberland R.		1	14	21	22	12	2						72	14.5	1.1
Tennessee R.		5	25	22	6								58	13.5	0.8
Arkansas R.		1	1	14	49	48	35	7	3				158	15.8	1.1
Little Missouri R.				4	13	13	13	4					47	16.0	1.1
Caddo R.				2	5	20	16	7					50	16.4	0.9
Ouachita R.				2	8	8	4	4	1				27	16.1	1.3
Saline R.			1	2	7	10	9	1					30	15.9	1.1
Red R.				1	4	13	26	34	17	2	–	1	98	17.6	1.2
P. aurora															
Pearl R.					2	12	43	56	32	8	2		155	17.9	1.1
Pascagoula R.							10	6	5				21	17.8	0.8
P. brevicauda															
Coosa R.						4	6	3	1				14	17.1	0.9
Cahaba R.					3	18	32	44	19	8	1	1	126	17.7	1.2
Warrior R.					6	13	13	11	1	1			45	16.8	1.1

Table 4. Frequency distribution of number of scales around caudal peduncle in species of *Percina*, subgenus *Cottogaster*.

	13	14	15	16	17	18	19	20	21	22	23	N	$\bar{x}$	S.D.
P. copelandi														
Great Lakes	2	8	79	265	58	13						425	16.0	0.7
Ohio R.	4	6	50	86	18	4						168	15.7	0.8
Cumberland R.			3	14	25	19	9	2				72	17.3	1.1
Tennessee R.		3	11	23	17	4						58	16.1	0.9
Arkansas R.				9	34	35	56	18	5	–	1	158	18.4	1.2
Little Missouri R.					15	11	19	2				47	18.2	0.9
Caddo R.					13	13	18	5	1			50	18.4	1.0
Ouachita R.					3	12	9	3				27	18.4	0.8
Saline R.						2	8	15	5			30	17.8	0.8
Red R.					2	13	45	21	15	2		98	19.4	1.0
P. aurora														
Pearl R.							27	68	49	8	3	155	20.3	0.8
Pascagoula R.							2	5	8	4	2	21	20.9	1.1
P. brevicauda														
Coosa R.						3	4	4	3			14	19.5	1.0
Cahaba R.					2	9	53	34	22	3	1	124	19.6	1.0
Warrior R.					1	3	27	9	4	1		45	19.3	0.9

Table 5. Frequency distribution of dorsal fin ray counts in species of *Percina*, subgenus *Cottogaster*.

	Dorsal spines									Dorsal soft rays								
	9	10	11	12	13	14	N	$\bar{x}$	S.D.	9	10	11	12	13	14	N	$\bar{x}$	S.D.
P. copelandi																		
Great Lakes	4	140	234	22	2		402	10.7	0.6		1	110	218	73	1	403	11.9	0.6
Ohio R.	2	94	69	1			166	10.4	0.5		3	96	66	1		166	11.4	0.5
Cumberland R.	13	46	7				66	9.9	0.5		7	53	6			66	11.0	0.4
Tennessee R.	8	42	8				58	10.0	0.5	2	18	36	2			58	10.6	0.6
Arkansas R.		2	57	94			157	11.6	0.5		3	53	92	9		157	11.7	0.6
Little Missouri R.		2	34	10	–	1	47	11.2	0.6			7	27	12	1	47	12.1	0.6
Caddo R.		8	31	10	–	1	50	11.1	0.6			19	26	5		50	11.7	0.6
Ouachita R.		4	20	3			27	11.0	0.5			15	10	2		27	11.5	0.6
Saline R.		2	21	7			30	11.2	0.5			8	22			30	11.6	0.4
Red R.		1	35	58	–	4	98	11.7	0.5			31	61	6		98	11.7	0.5
P.. aurora																		
Pearl R.		32	113	9			154	10.8	0.4			9	92	52	1	154	12.3	0.5
Pascagoula R.	1	5	14	1			21	10.7	0.6			4	13	4		21	12.0	0.6
P. brevicauda																		
Coosa R.			13	1			14	11.1	0.2			8	6			14	11.4	0.5
Cahaba R.		11	86	27			124	11.1	0.5		8	80	35	1		124	11.2	0.5
Warrior R.		8	29	8			45	11.0	0.6		2	24	16	3		45	11.4	0.6

Table 6. Frequency distribution of anal and pectoral fin ray counts in species of *Percina*, subgenus *Cottogaster*.

	Anal spines				Anal soft rays								Left pectoral rays						
	0	1	2	3	6	7	8	9	10	N	$\bar{x}$	S.D.	12	13	14	15	N	$\bar{x}$	S.D.
P. copelandi																			
Great Lakes			412	2		43	246	116	9	414	8.2	0.6	1	84	211	34	330	13.8	0.6
Ohio R.		2	164		1	33	115	17		166	7.9	0.5	3	57	97	5	162	13.6	0.5
Cumberland R.			66			11	49	6		66	7.9	0.5		44	22		66	13.3	0.4
Tennessee R.		1	55	2	1	18	39			58	7.6	0.5	1	31	22	2	56	13.4	0.6
Arkansas R.	1	6	150	1		20	116	22		158	8.1	1.4		66	88	3	157	13.6	0.5
Little Missouri R.		1	46			3	23	20	1	47	8.4	0.6	1	37	9		47	13.2	0.4
Caddo R.		3	47			4	33	12	1	50	8.2	0.6	6	37	7		50	13.0	0.5
Ouachita R.		2	24	1		6	18	3		27	7.8	0.5	2	22	3		27	13.0	0.4
Saline R.			29	1		6	21	3		30	7.9	0.5	4	22	4		30	13.0	0.5
Red R.		2	96			15	70	13		98	8.0	0.5	1	26	67	4	98	13.7	0.5
P. aurora																			
Pearl R.			147	7		3	82	67	2	154	8.4	0.5	2	33	112	8	155	13.8	0.5
Pascagoula R.		1	20			2	15	4		21	8.1	0.5	1	8	11	1	21	13.6	0.6
P. brevicauda																			
Coosa R.			14			4	10			14	7.7	0.4	1	10	3		14	13.1	0.5
Cahaba R.		2	122		1	15	94	14		124	8.0	0.5	8	69	17		94	13.1	0.5
Warrior R.			44	1		11	31	3		45	7.8	0.5	1	34	10		45	13.2	0.4

Table 7. Frequency distribution of number of vertebrae and number of branchiostegal rays in species of *Percina*, subgenus *Cottogaster*.

	Vertebrae									Branchiostegal rays							
	36	37	38	39	40	41	N	$\bar{x}$	S.D.	5—5	5—6	6—5	6—6	6—7	7—6	7—7	N
P. copelandi																	
Great Lakes		9	148	162	14	1	334	38.6	0.6	4	4	8	253	2	–	1	272
Ohio R.		7	96	33			136	38.2	0.5		4	2	138	2	1	1	148
Cumberland R.			23	21			44	38.5	0.5			4	66	–	1	1	72
Tennessee R.			13	5			18	38.3	0.4		2	–	40	1	1	2	46
Arkansas R.			29	106	26		161	39.0	0.5	3	3	1	131	11	5	4	158
Little Missouri R.		1	54	14	1		70	38.2	0.5		2	–	45				47
Caddo R.	1	10	39	10			60	38.0	0.6	3	1	5	41				50
Ouachita R.		8	31	11			50	38.1	0.6	2	1	–	23				26
Saline R.		2	21	11			34	38.3	0.5	1	–	1	25	1	1	1	30
Red R.*		2	15	64	34		115	39.1	0.6		1	–	91	2	1	2	97
P. aurora																	
Pearl R.			24	99	7	1	131	38.9	0.5	3	1	3	144	1	1	1	154
Pascagoula R.			1	21	1		23	39.0	0.3		1	–	20				21
P. brevicauda																	
Coosa R.		1	1				2	37.5			2	–	12				14
Cahaba R.	1	33	50	8			92	37.7	0.6		2	2	88	1	1		94
Warrior R.		5	14	5			24	38.0	0.6				37	2	1		40

* one specimen has 5—7 branchiostegal rays

Table 8. Frequency distribution of number of gill rakers on first left arch in species of *Percina*, subgenus *Cottogaster*.

	9	10	11	12	13	14	15	16	17	N	$\bar{x}$	S.D.
P. copelandi												
Great Lakes		2	14	50	46	18	9			139	12.6	1.1
Ohio R.			8	37	29	13				87	12.5	0.8
Cumberland R.			1	12	20	20	5			58	13.3	0.9
Tennessee R.				4	3	8	5			20	13.7	1.0
Arkansas R.			3	28	60	21	8			120	12.9	1.2
Little Missouri R.			1	9	11	3	1			25	12.8	0.8
Caddo R.			4	16	4	1				25	12.1	0.7
Ouachita R.	1	–	9	8	6	1				25	11.8	1.0
Saline R.			1	20	18	8				47	12.7	0.7
Red R.			4	24	42	13	4			87	12.9	0.8
P. aurora												
Pearl R.			1	6	28	25	16	3	1	80	13.8	1.0
Pascagoula R.					8	9	3	1		21	13.8	0.8
P. brevicauda												
Coosa R.			3	3	6	1	1			14	12.6	1.1
Cahaba R.			3	20	35	28	3	2		91	13.1	0.9
Warrior R.			3	16	13	5	1	2		40	12.8	1.1

Table 9. Frequency distribution of number of modified belly scales on males of species of *Percina*, subgenus *Cottogaster*.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	N	$\bar{x}$	S.D.
P. copelandi																			
Great Lakes		2	8	29	58	67	62	39	7	3							275	6.1	1.5
Ohio R.				5	6	12	21	15	4	6	1						70	7.1	1.6
Cumberland R.					2	5	8	7	6	4	3	–	1				36	8.1	1.8
Tennessee R.						2	5	5	2	2							16	7.8	1.2
Arkansas R.			2	3	8	20	15	17	19	9	3	3	1				100	7.6	2.0
Little Missouri R.			1	–	1	2	12	12	14	7	3	3	1				56	8.5	1.8
Caddo R.			1	–	3	7	15	25	57	48	36	22	10	2	3	1	230	9.7	1.9
Ouachita R.				1	1	5	11	27	30	15	5	7	3	1			106	8.9	1.7
Saline R.						1	6	6	7	11	6	3					40	9.3	1.6
Red R.				1	2	5	5	13	19	7	8	5					65	8.8	1.8
P. aurora																			
Pearl R.					2	22	26	30	24	5							109	7.6	1.2
Pascagoula R.						1	3	–	2	1	1						8	8.2	1.7
P. brevicauda																			
Coosa R.									2	–	2	3					7	10.8	1.3
Cahaba R.			1	1	5	9	18	23	18	17	13	6					111	8.5	1.9
Warrior R.	1	–	–	–	–	2	4	2	4	3	2	1	1				20	8.5	2.6

Table 10. Modified belly scales in females of species of *Percina*, subgenus *Cottogaster*.

	Total number of females	Number modified scales	Percent without	Number with modified scales	Range in number of modified scales	$\bar{x}$ number modified scales per specimen
P. copelandi						
Great Lakes	119	101	84.9	18	1–5	2.3
Ohio R.	59	52	88.1	7	1–4	1.6
Cumberland R.	25	16	64.0	9	1–5	2.3
Tennessee R.	11	10	90.9	1		2.0
Arkansas R.	50	28	56.0	22	1–6	2.0
Little Missouri R.	59	40	67.8	19	1–4	2.2
Caddo R.	51	24	47.1	27	1–7	3.7
Ouachita R.	44	30	68.2	14	1–6	3.1
Saline R.	10	5	50.0	5	2–4	3.0
Red R.	23	16	69.6	7	1–5	2.1
P. aurora						
Pearl R.	58	37	63.8	21	1–6	2.6
P. brevicauda						
Cahaba R.	77	69	89.6	8	1–5	2.6

Table 11. Frequency distribution of number of marginal spines on the modified ventral scales in males of *Percina*, subgenus *Cottogaster*.

	Number of Specimens	Number* of modified scales	Number of spines per modified scale																				$\bar{x}$ spines per modified scale	S.D.
			0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20		
P. copelandi																									
Arkansas R.	25	253				22	40	62	55	42	20	7	2	2	–	1								5.7	1.6
Caddo R.	25	283	1	2	12	56	71	73	38	18	8	2	–	–	1	1								4.6	1.6
P. aurora																									
Pearl R.	25	250			1	3	6	15	26	43	48	34	25	16	11	11	4	2	2	1	–	–	2	8.5	2.7
P. brevicauda																									
Cahaba R.	25	289	1	5	53	85	51	50	21	16	4	2	1											3.9	1.6

* inclusive of breast and interpelvic modified scales.

Table 12. Frequency distribution of number of pores in infraorbital (INF) and preoperculomandibular (POM) canals in species of *Percina*, subgenus *Cottogaster*.

	INF								POM						
	6	7	8	9	10	N	$\bar{x}$	S.D.	8	9	10	11	N	$\bar{x}$	S.D.
P. copelandi															
Great Lakes		3	67	4	1	75	8.0	0.3	1	9	65		75	9.8	0.3
Ohio R.		1	43	5	1	50	8.1	0.4		5	44	1	50	9.9	0.3
Cumberland R.		1	25	24	4	54	8.6	0.6			53	1	54	10.0	0.1
Tennessee R.			37	5	1	43	8.2	0.4		7	36		43	9.8	0.3
Arkansas R.		1	46	3		50	8.0	0.2			45	5	50	10.1	0.3
Little Missouri R.		1	44	4	1	50	8.1	0.4		4	45	1	50	9.9	0.3
Caddo R.	2	13	30	5		50	7.8	0.6		3	41	6	50	10.1	0.4
Ouachita R.		1	42	7		50	8.1	0.3		1	45	4	50	10.1	0.3
Saline R.		1	44	9		54	8.1	0.4		1	53		54	10.0	0.1
Red R.			60	3		63	8.0	0.2		2	60	1	63	10.0	0.2
P. aurora															
Pearl R.		3	46	2	1	52	8.0	0.4		2	49	1	52	10.0	0.2
Pascagoula R.		1	20			21	7.9	0.2		2	19		21	9.9	0.3
P. brevicauda															
Coosa R.			7	5	2	14	8.6	0.7		2	12		14	9.8	0.3
Cahaba R.		1	59	1		61	8.0	0.1		1	59	1	61	10.0	0.1
Warrior R.		1	33	6		40	8.1	0.4		1	38	1	40	10.0	0.2

Table 13. Frequency distribution of squamation of cheek of species of *Percina*, subgenus *Cottogaster*.

	Naked	1–4 Scales	25% to 50%	66% to 100%
P. copelandi				
Great Lakes	313	10		
Ohio R.	124	21	18	3
Cumberland R.	6		39	27
Tennessee R.		1	23	34
Arkansas R.			24	134
Little Missouri R.	6	15	19	7
Caddo R.	6		24	17
Ouachita R.	2		13	12
Saline R.	4		18	12
Red R.	1	1	48	47
P. aurora				
Pearl R.		2	1	107
Pascagoula R.			1	20
P. brevicauda				
Coosa R.	13		1	
Cahaba R.	94			
Warrior R.	44	1		

Table 14. Frequency distribution of squamation of opercle of species of *Percina*, subgenus *Cottogaster*.

	Naked	1–4 Scales	25% to 50%	66% to 100%
P. copelandi				
Great Lakes	3	17	153	150
Ohio R.	1	1	44	120
Cumberland R.			10	62
Tennessee R.			1	57
Arkansas R.			5	153
Little Missouri R.				22
Caddo R.			6	69
Ouachita R.			1	23
Saline R.			3	30
Red R.			5	87
P. aurora				
Pearl R.				110
Pascagoula R.				21
P. brevicauda				
Coosa R.			4	10
Cahaba R.	2	4	52	36
Warrior R.	1	1	15	28

Table 15. Frequency distribution of squamation of nape of species of *Percina*, subgenus *Cottogaster*.

	Naked	1–4 Scales	25% to 50%	66% to 100%
P. copelandi				
Great Lakes	25	67	294	46
Ohio R.	10	30	117	6
Cumberland R.	1	3	45	23
Tennessee R.			2	56
Arkansas R.		6	89	63
Little Missouri R.	4	13	27	3
Caddo R.	5	14	29	2
Ouachita R.	3	7	15	2
Saline R.	2	9	21	2
Red R.	6	26	51	15
P. aurora				
Pearl R.	105	3		
Pascagoula R.	19	2		
P. brevicauda				
Coosa R.	4	4	6	
Cahaba R.	28	25	35	4
Warrior R.	10	12	21	2

Table 16. Development of premaxillary frenum in species of *Percina*, subgenus *Cottogaster*.

	None	Intermediate	Frenum	N
P. copelandi				
Great Lakes	79	37	66	182
Ohio R.	97	21	43	161
Cumberland R.	48	9	4	61
Tennessee R.	55	2	1	58
Arkansas R.	61	60	29	150
Little Missouri R.	59	23	18	100
Caddo R.	71	19	10	100
Ouachita R.	64	22	15	101
Saline R.	18	16	3	37
Red R.	27	31	12	70
P. aurora				
Pearl R.	42	22	23	87
Pascagoula R.	16	3	2	21
P. brevicauda				
Coosa R.	9	2	3	14
Cahaba R.	87	4		91
Warrior R.	36	7	2	45

Table 17. Measurements in thousandths of standard length for males of species of *Percina*, subgenus *Cottogaster*.

	P. copelandi (N=25) Ohio River system			*P. copelandi* (N=25) Red and Ouachita River systems			*P. aurora* (N=25) Pearl River system				*P. brevicauda* (N = 27) Cahaba River system			
	Range	$\bar{x}$	S.D.	Range	$\bar{x}$	S.D.	Holotype	Range	$\bar{x}$	S.D.	Holotype	Range	$\bar{x}$	S.D.
Standard length (mm)	37.2–44.0	40.3	2.3	37.5–51.3	45.5	3.0	59.7	51.4–61.0	55.8	2.2	45.8	37.1–46.9	43.3	2.7
Head length	231–264	250	8.5	234–280	253	13.6	270	242–267	255	6.4	255	243–274	260	8.0
Head depth	136–157	149	6.0	130–169	152	9.9	146	135–156	145	5.6	153	145–158	150	3.6
Body depth	142–175	162	8.7	144–192	170	11.5	164	147–179	160	8.9	179	152–181	164	6.4
Body width	121–158	144	9.7	112–154	139	10.9	149	128–152	139	6.0	157	133–154	144	5.2
Caudal peduncle length	207–243	224	7.3	205–244	222	10.4	214	205–241	225	9.9	244	207–246	225	12.3
Caudal peduncle depth	74–89	80	3.3	71–91	84	4.7	90	75–91	84	3.7	94	76–95	85	4.5
Snout length	52–75	65	5.6	53–76	64	6.3	75	60–72	66	3.7	74	64–77	72	3.3
Orbit length	52–73	64	5.0	49–67	60	5.4	65	58–71	64	2.9	68	59–70	66	2.8
Longest dorsal spine	93–121	109	6.7	84–122	102	9.1	115	104–125	118	5.7	100	88–111	99	5.8
Longest dorsal soft ray	106–143	124	10.9	114–145	128	9.4	151	120–149	135	7.5	131	119–139	125	4.9
Longest anal soft ray	100–149	126	11.5	112–150	134	11.2	134	109–146	127	8.8	127	107–146	124	8.8
Caudal fin length	158–198	182	11.4	155–202	177	10.6	196	172–198	187	7.3	159	141–205	180	15.7
Pectoral fin length	210–285	250	17.7	197–253	229	14.6	258	214–257	233	10.4	207	188–242	218	12.6
Pelvic fin length	181–216	202	8.5	186–225	206	10.5	204	174–215	195	11.7	192	179–223	201	10.9
Interorbital width	35–50	43	3.7	34–50	42	3.9	45	36–48	42	3.4	48	35–48	41	3.5
Upper jaw length	60–82	68	5.1	67–87	76	5.3	87	75–90	80	4.5	83	64–83	74	4.7

Table 18. Measurements in thousandths of standard length for females of species of *Percina*, subgenus *Cottogaster*.

	P. copelandi (N=10) Ohio River system			*P. copelandi* (N=10) Red and Ouachita systems			*P. aurora* (N=10) Pearl River system			*P. brevicauda* (N = 10) Cahaba River system		
	Range	$\bar{x}$	S.D.	Range	$\bar{x}$	S.D.	Range	$\bar{x}$	S.D.	Range	$\bar{x}$	S.D.
Standard length (mm)	37.2–44.2	40.5	2.3	39.2–46.1	41.8	2.0	49.1–57.5	53.4	2.7	36.7–44.1	41.7	2.2
Head length	236–265	251	8.8	237–263	256	7.9	246–266	256	6.7	242–267	257	7.6
Head depth	139–161	152	7.5	133–163	145	9.6	128–149	142	7.2	142–158	148	5.0
Body depth	159–186	173	9.0	153–206	170	17.1	153–188	171	12.0	160–204	180	12.7
Body width	140–161	150	7.0	135–162	148	10.5	133–143	138	3.9	140–172	155	10.3
Caudal peduncle length	206–246	221	11.8	189–243	216	17.2	209–240	228	9.3	212–257	232	12.6
Caudal peduncle depth	76–85	81	3.0	74–89	80	4.7	77–91	84	4.3	80–90	85	2.7
Snout length	53–75	65	7.4	61–67	65	2.0	57–73	68	5.2	60–72	66	3.6
Orbit length	54–73	64	6.8	58–70	65	4.2	61–71	67	3.0	65–72	68	2.4
Longest dorsal spine	90–110	101	6.9	79–108	94	8.8	109–123	116	4.8	81–102	94	7.1
Longest dorsal soft ray	100–138	126	13.0	88–126	114	12.5	111–136	126	9.0	111–122	115	3.5
Longest anal soft ray	102–148	131	13.3	81–139	120	16.0	111–143	127	9.5	103–136	116	11.4
Caudal fin length	165–206	188	13.3	167–193	176	8.6	167–198	186	10.9	143–199	170	20.0
Pectoral fin length	220–283	257	24.1	194–261	219	18.2	203–242	229	10.9	196–238	214	12.2
Pelvic fin length	182–230	205	14.9	177–216	195	9.9	178–203	191	7.9	175–224	195	14.3
Interorbital width	37–50	43	4.0	38–46	43	2.2	36–48	42	3.7	35–49	42	4.4
Upper jaw length	53–77	64	7.7	70–85	76	4.1	71–86	81	4.5	71–77	74	2.1

Table 19. Means of 16 body measurements, expressed in thousandths of standard length, for *Percina aurora*, *P. brevicauda*, and two populations of *P. copelandi*. Bold type denotes means that were significantly different among species/population multiple-range-test comparisons within sexes. Asterisks denote significant sexual dimorphism in favor of the denoted sex in within species/population comparisons.

	Percina copelandi Ohio River Dr.		*Percina copelandi* Red River Dr.		*P. aurora* Pearl River Dr.		*P. brevicauda* Alabama River Dr.			
Body measurement	Males (25)	Females (10)	Males (25)	Females (10)	Males (26)	Females (10)	Males	(N)	Females	(N)
Head length	250	251	253	256	255	256	259	36	257	28
Head Depth	149	152	152	145	145	142	**151**	28	149	10
Body depth	162	173*	**170**	170	160	171*	165	28	180*	10
Body width	144	150	139	148	139	**138**	145	28	155	10
Caudal peduncle length	224	221	222	216	225	228	226	28	232	10
Caudal peduncle depth	**80**	81	84*	80	84	84	85	36	83	21
Snout length	65	65	64	65	66	68	**72***	28	66	10
Orbit length	64	64	**60**	65*	64	67	66	28	68	10
Interorbital width	43	43	42	43	42	42	42	28	42	10
Upper jaw length	**68**	**64**	77	76	**80**	81	75	28	74	10
Longest dorsal spine	**109***	**101**	**102***	**94**	**118**	**116**	**96***	41	92	19
Longest dorsal ray	124	126	128*	114	**135***	**126**	124	43	**114**	20
longest anal ray	126	131	**134***	120	127	127	125*	42	117	20
Caudal fin length	182	188	177	176	187	186	173	60	170	34
Pectoral fin length	**250**	**257**	229	219	233	229	**217**	60	217	34
Pelvic fin length	**202**	205	206*	195	195	191	**196**	60	192	34

Table 20. Comparison of nuptial males of *Percina copelandi*, *P. aurora*, and *P. brevicauda*.

Character	*P. copelandi*	*P. aurora*	*P. brevicauda*
Spinous dorsal fin			
Marginal edging	thin edging, moderately dark	thin edging, dusky	thin edging, dark
Intermediate pale space	distinct, moderately broad	distinct, moderately to very broad	narrow anteriorly, partially to completely obliterated by extensions of basal pigmentation in posterior part of fin
Basal band	moderately broad and dark	moderately broad, anterior blotches dark, the rest dusky	moderately to very broad, very dark
Lateral blotches (centered along lateral line)	frequently oblong in shape in populations east of Mississippi River; ovoid or quadrate blotches common in southwestern populations	range from ovoid to quadrate to oblong in shape	range from ovoid to quadrate to oblong in shape
Confluent; forming a continuous band	occasional specimen	none observed	occasional specimen
Second dorsal fin length vs. anal fin length	anal fin slightly longer in half (26 of 50) of Little and Caddo river specimens	anal fin slightly longer in 18 of 51 specimens from Pearl River	anal fin slightly longer in 18 of 51 specimens from Cahaba River
Venter pigmentation	moderately dark	dusky	moderately to densely pigmented
Tubercular ridges on pelvic and anal fin rays	present, moderately developed	absent	present, well developed
Tubercles	occasionally present, weakly developed	none observed	occasionally present, weakly developed
Modified ventral scales	small rounded or oval elongate	small to large, broadly rounded	small rounded or oval elongate
Scales along anal fin and ventral surface of caudal peduncle	with enlarged ctenii in some specimens	with enlarged ctenii in some specimens	none observed with enlarged ctenii
Number of marginal spines on modified ventral scales	mean = 5.7, Arkansas R. mean = 4.6, Caddo R.	mean = 8.5	mean = 3.9
Squamation of cheek	naked to covered with scales	typically covered with scales	typically naked
Squamation of opercle	partially to covered with scales	typically covered with large ctenoid scales	partially to covered with scales
Squamation of nape	naked to partially covered with scales, naked strip narrow when present	typically naked, naked strip relatively wide	naked to partially covered with scales, naked strip narrow when present

Table 21. Fin measurements in thousandths of standard length for males of five species of *Percina*.

	P. copelandi (N=50) Little and Caddo river systems			*P. aurora* (N=51) Pearl River system			*P. brevicauda* (N=51) Cahaba River system			*P. shumardi* (N=50) Pearl River system			*P. vigil* (N=50) Pearl River system		
	Range	$\bar{x}$	S.D.	Range	$\bar{x}$	S.D.	Range	$\bar{x}$	S.D.	Range	$\bar{x}$	S.D.	Range	$\bar{x}$	S.D.
Standard length (mm)	37.3–46.9	40.8	2.4	49.9–64.2	56.2	3.0	37.5–46.7	41.8	2.3	47.6–82.8	58.1	6.4	42.8–57.5	50.0	3.4
Second dorsal fin length	233–289	258	13.0	251–294	272	10.2	231–273	249	9.0	275–351	312	18.8	279–336	314	12.8
Anal fin length	236–290	260	13.2	234–300	268	12.3	226–275	247	9.9	280–425	368	30.3	338–417	372	19.9

Occasional Papers Tulane University Museum of Natural History
(Back Issues)

1. The humbpack chub, Gila cypha, in the Grand Canyon area of the Colorado River. Royal D. Suttkus and Glenn H. Clemmer, November 1977, 30 pp. $3.00

2. Mammals of the riparian region of the Colorado River in the Grand Canyon area of Arizona. Royal D. Suttkus, Glenn H. Clemmer, and Clyde Jones, September 1978, 23 pp. $3.00

3. Distributional checklist of the mammals along the Colorado River in the Grand Canyon. Clyde Jones, Glenn H. Clemmer, Royal D. Suttkus and Richard D. Curnow, November 1982, 15 pp. $3.00

4. Two new darters, *Percina* (*Cottogaster*), from the southeastern United States, with a review of the subgenus. Royal D. Suttkus, Bruce A. Thompson and Henry L. Bart, Jr., December 1994, 46 pp. $5.00

Instructions for Authors

Manuscripts dealing with biological aspects of natural history (taxonomy, systematics, biogeograghy, ecology, and environmental biology) will be considered for publication in the *Occasional Papers*. Please review this carefully, and consult recent issues of the *Occasional Papers* and the *Council of Biology Editors style manual* (5th Edition) for examples of format and style. Manuscripts should be double-spaced throughout and printed in clear type on 8 1/2 by 11 inch paper with one inch margins. Manuscripts should be arranged as follows: title, authors(s) and address(es), abstract, and text, with headings for major sections (Introduction, Methods, Results, Discussion, Acknowledgments, Literature Cited) in mixed case and bold type, and subsection headings in italics with only the first letter of the first word capitalized. Use italics and bold face as appropriate; do not use underlines in the manuscript to indicate italic or bold type. A style sheet with formats for taxonomic descriptions, literature citations and other exampls should be requested from the Editor. Follow text with appendices, figure legends, figures, and tables with table headings. Tables may be printed in landscape format on 8 1/2 by 14 inch paper. Send clear copies of figures; retain originals until the manuscript is accepted for publication. Submit three copies of the manuscript to:

The Editor, *Occasional Papers*
Tulane University Museum of Natural History
Belle Chasse, LA 70037

The Editor will seek two to three reviews. Manuscripts will be judged based on scientific merit.

Page layout and production of camera-ready copy of the *Occasional Papers* is performed at the Tulane University Museum of Natural History using desktop publishing software. Once accepted for publication, manuscripts should be submitted on standard 3.5 or 5.25 inch DOS or Macintosh-compatible floppy diskettes, in addition to a revised printed copy. Most major word-processing software formats are acceptable. Original figures should be submitted at this time, although PICT, TIFF or EPS image files on floppy diskettes are also acceptable formats for figures. Please contact the Editor to discuss issues of software compatibility. Original art will be returned.

Authors with grants or institutional resources are encouraged to pay page charges which are currently estimated at $100 per page.