1983

Systematics, Redescription, and Geographic Variation of the Blackside Darter, Percina Maculata (Pisces; Percidae).

Eugene Clifton Beckham III

Louisiana State University and Agricultural & Mechanical College

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Beckham, Eugene Clifton, III

SYSTEMATICS, REDescription, AND GEOGRAPHIC VARIATION OF THE BLACKSIDE DARTER, PERCINA MACULATA (PISCES; PERCIDAE)

The Louisiana State University and Agricultural and Mechanical Col. Ph.D. 1983

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SYSTEMATICS, REDESCRIPTION, AND GEOGRAPHIC VARIATION OF THE BLACKSIDE DARTER, PERCINA MACULATA (PISCES; PERCIDAE)

A Dissertation

Submitted to the Graduate Faculty of the Louisiana State University and Agricultural and Mechanical College in partial fulfillment of the requirements for the degree of Doctor of Philosophy in The Department of Zoology and Physiology

by

Eugene C. Beckham, III
B.S., University of Alabama, 1970
M.S., University of Alabama, 1973
May 1983
DEDICATION

To my parents, Mr. and Mrs. E. C. Beckham, Jr., for their continued support and encouragement over the years.
ACKNOWLEDGEMENTS

I would like to thank Dr. J. M. Fitzsimons, who served as my major professor, for his encouragement and assistance during my studies at Louisiana State University, and also to express my appreciation to the other members of my doctoral committee for their advice and suggestions regarding my research.

The following persons loaned specimens for this study: Reeve Bailey, University of Michigan (UMMZ); Herbert Boschung, University of Alabama (UAIC); Branley Branson, Eastern Kentucky University (EKU); Ed Brothers, Cornell University (CU); Robert Cashner, University of New Orleans (UNO); Ted Cavender, Ohio State University (OSU); Earl Crossman, Royal Ontario Museum (ROM); Neil Douglas, Northeastern Louisiana University (NLU); Mike Fitzsimons, Louisiana State University (LSU); Carter Gilbert, University of Florida (UF); Larry Page, Illinois Natural History Survey (INHS); Donn Rosen, American Museum of Natural History (AMNH); Frank Schwartz, University of North Carolina Institute of Marine Science (UNC); Royal Suttkus, Tulane University (TU); and Ralph Yerger, Florida State University (FSU).
In addition to those above I wish to thank the following people for their assistance during the course of this project: Ron Boudreaux, Albert Doucette, Kirk Easley, Charles Hocutt, Mike Howell, Bob Jenkins, Jeff Korth, Scott Mettee, Jay Stauffer, Ben Wall, Jim Williams, and Bruce Thompson. Lastly, a special note of thanks to my wife, Esther, for her inspiration, encouragement, and support during this project.
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ABSTRACT

A systematic study of the North American percid fish Percina (Alvordius) maculata (Girard) was undertaken to determine the extent and pattern of geographic variation, subspeciation and sexual dimorphism. A brief nomenclatorial history is presented, the species is redescribed, and variation, distribution, habitat, and subgeneric relationships are discussed.

Other than dorsal fin pigmentation, absence of modified midventral scales in females, and limited intrapopulational sexual dimorphism in a few morphometric characters, no variation in most of the thirty-nine characters examined is present between males and females. Morphometrics exhibited no pattern of geographic variation; however, meristic characters revealed a major trend in geographic variation. Lateral-line, transverse, caudal peduncle, and modified midventral scales exhibited clinal variation with highest counts in the southern part and lowest counts in the northern-most part of the range of P. maculata. Less variable characters showed this trend to a slight degree or not at all. The reverse trend, higher counts in the north and lower in the south, appeared in dorsal and anal fin-ray
counts.

*P. maculata* is distributed in the Mobile Bay, Pearl River, Lake Pontchartrain, and Calcasieu River drainages of the Gulf slope, the lower and upper Mississippi River drainages, the Ohio River, the Great Lakes system, and the Red River of the North of the Hudson Bay drainage. This species is an inhabitant of clear streams with sand and gravel bottoms and is typically associated with the margins of stream pools.

Within the subgenus *Alvordius*, *P. maculata* is most closely related to *P. pantherina* as interpreted from meristics, pigmentation patterns, and zoogeography.
Hubbs and Raney (1939) referred to *P. maculata* as "probably a complex of subspecies" when alluding to the variation within the species over its entire range. Therefore, with the extensive distribution of *P. maculata* and its limited systematic treatment in the literature, the present study was undertaken in order to more clearly define the species, assess the limits and extent of geographic variation, and to determine if, indeed, this "complex of subspecies" does exist.

**Distribution and Habitat.**—The blackside darter is distributed in the eastern half of North America in four major drainage systems (the Mobile Bay, the Mississippi River, the Great Lakes, and the Hudson Bay drainages) and three minor drainage systems of the Gulf slope (the Calcasieu River, Lake Pontchartrain, and Pearl River drainages).

Within the Mobile Bay drainage, *Percina maculata* is found prevalently in the upper Tombigbee and Black Warrior River, both above and below the fall line; however, its distribution in the eastern tributaries is generally restricted to habitats at or below the fall line in the Alabama, Cahaba, and Tallapoosa rivers. Its occurrence
above the Fall Line in the Warrior system, but not in the Coosa or Tallapoosa drainages, may be the result of two independent invasions of the Mobile basin from the lower Mississippi-Pearl in the west and from the Tennessee in the north.

The Gulf slope drainage distribution of *P. maculata* is unique among darters. Four other darter species (*Etheostoma chlorosomum, E. fusiforme, E. proeliare,* and *Percina sciara*) are found in the combination of Mobile basin, Pearl River, Lake Pontchartrain, and Calcasieu River, but their distributions include other drainages within the Gulf slope (Lee et al., 1980).

The most extensive distribution of *P. maculata* is in the Mississippi River drainage. Although the species ranges both east and west of the river proper, it occurs predominantly in the eastern tributaries of the Mississippi River with the Ohio River basin exhibiting the highest concentration of site records. Although collection records reveal a virtually ubiquitous distribution in Illinois, Indiana, and Ohio for the blackside darter, recent surveys indicate a decline in its actual range within the area due to pollution and stream degradation (Larimore and Smith, 1963; Smith, 1971). *P. maculata* is sparsely distributed in the southern tributaries of the Ohio River with a very patchy distribution within the
The records for *P. maculata* in the Tennessee River system of Georgia (Dahlberg and Scott, 1971: 46) are in error and are actually based on specimens of *P. evides*. The validity of the single record from Virginia (listed in material examined), although the specimens are good *maculata*, has been questioned based on a possible mix-up in locality data (R.E. Jenkins, pers. comm.).

*P. maculata* is found in all of the Great Lakes drainage systems except Lake Superior. Distribution in Lake Ontario is limited to tributaries along the southern shores in New York and Ontario, whereas lakes Erie, St. Clair, and Michigan exhibit a circumferential distribution by *P. maculata*. Tributaries along the eastern and western shores of Lake Huron contain *P. maculata*; however, its northern shore does not.

In the expansive Hudson Bay drainage, *P. maculata* is found only within the Nelson River basin. It ranges primarily in the Red River of the North drainage within this system in Minnesota and the Dakotas of the United States and extreme southeastern Saskatchewan and southwestern Manitoba of Canada. The most northerly record of the blackside darter is from the lower Saskatchewan River in western Manitoba.

A distribution map delimiting the range of *Percina maculata* is figured in Beckham and Platania (1983).
The blackside darter inhabits moderate sized streams with a moderate gradient and prefers the edges of pools with some current or small pools associated with riffles (Trautman, 1957). *P. maculata* has been reported to occur in both sluggish water (Scott, 1954) and swift streams (Greeley, 1927). Thomas (1970) and Trautman (1957) indicated a variable preference for bottom type with sand and gravel being predominant, but with reference to individuals having been taken over mud bottoms, rock or rubble and occasionally associated with brush, logs, or tree roots under cut-banks. Winn (1958) discussed habitat preference in relation to the reproductive habits of *P. maculata*.

Trautman (1957) stated that in Ohio usually fewer than three individuals per collection site were taken in 1925-50 surveys. In samples examined for the present study, an average of 3.34 individuals per collection were found for the Ohio River drainage as a whole. Much variation in this statistic is exhibited for the remaining drainage systems: Gulf slope (1.83), lower Mississippi River (2.52), upper Mississippi River (7.15), Great Lakes (11.89), and Hudson Bay (10.67). Of these, the Hudson Bay drainage collections may show more bias than the others due to small sample size and selection of material for examination based on size of collection; however, the largest number of specimens per
lot from the Great Lakes may represent a habitat difference between drainage systems. Some of the unusually large series collected, e.g. from Lake Huron, may reflect substantially larger, i.e. wider, yet relatively shallow rivers offering more suitable habitat, thus sustaining a larger population of *P. maculata* than many of the moderate to large creeks in other drainages.

**Taxonomic history.**— The blackside darter was originally described as *Alvordius maculatus* by Charles Girard (1859a) from specimens collected by Benjamin Alvord at Fort Gratiot, Michigan. Subsequently, in the same volume, Girard (1859b) described *Hadropterus maculatus* from the Potomac River drainage. When these two forms were later considered congeneric, the Atlantic coast *maculatus* became a junior homonym due to preoccupation by *A. maculatus*. The species from the Potomac was re-described as *Hadropterus notogrammus* by Raney and Hubbs (1948). Cope and Jordan (in Jordan, 1877) described *Alvordius aspro* as a replacement name for a figure (but not a description) labeled *Etheostoma blennioides* from the Ohio River drainage in a publication by Kirtland (1841). The latter name was preoccupied; however, Cope and Jordan's replacement name, listed by Boulenger (1895) as *Percina aspro* but subsequently consigned
along with *Alvordius maculatus* to the genus *Hadropterus* by Jordan and Evermann (1896), was deemed a synonym of *Hadropterus maculatus* by Hubbs (1926). *Etheostoma aspro*, another synonym of the blackside darter, was referred to by Eigenmann and Eigenmann (1892) in a list of fishes from Ontario. The use of *Etheostoma* was not justified by the authors, and there is no other reference to this usage elsewhere. This omission is perhaps due to the tendency of some early ichthyologists to synonymize all darters into one genus, whereas other relegated the various species to genera discernable by very tenuous characters; e.g., Jordan et al. (1930) divided the darters into 31 genera. Darter nomenclature was given a more stable foundation by Bailey (1951) as he divided the existing species into four genera: *Ammocrypta*, *Etheostoma*, *Hadropterus* (including *H. maculatus*), and *Percina*. Bailey (in Bailey et al., 1954) reduced the number of darter genera to three with the inclusion of *Hadropterus* in *Percina* and defined the blackside darter as *Percina maculata* (Girard). Recently these three genera and their subgeneric divisions have been examined extensively by Page (1974; 1981) and Williams (1975).

Since the original description, virtually no systematic account of *Percina maculata* has been published. Hubbs and Raney (1939) and Raney and Hubbs (1948) used what they considered to be *maculata* for limited comparison in original
descriptions of P. oxyrhyncha and P. notogramma, respectively. The comparison, however, was actually with P. gymnocephala, long considered to be P. maculata, but shown recently to be a distinct species endemic to the New River drainage (Beckham, 1980). Moore and Reeves (1955) compared P. pantherina with P. maculata in their description of the leopard darter. Richards and Knapp (1964) used limited P. maculata material for subgeneric comparisons in their treatment of the subgenus Hadropterus. Page (1976) used counts of P. maculata modified midventral scales for comparison with other Percina and used a series from a single locality for comparing all species of Percina to discern subgeneric divisions (Page, 1974).

METHODS AND MATERIALS

Over 1500 specimens of Percina maculata were examined from all major drainage systems within its range, and counts and measurements were made on approximately 1000 of these specimens for this study. To reduce allometric bias, only adult specimens greater than 45 mm SL were used for measurements. Counts were made from specimens over 38 mm SL.

Counts and measurements, other than those noted, were made as described in Hubbs and Lagler (1964). The number of transverse scale rows was taken from the origin of the
second dorsal fin down and back to the anal fin, as proposed in Raney and Suttkus (1964). Head-canal pore counts were made following the methods of Hubbs and Cannon (1935). Only major lateral blotches were counted from the first full blotch posterior to the pectoral fin base back to, and including, the blotch ending at the hypural plate. Small blotches occasionally formed at the juncture of two major confluent blotches were discounted. Dorsal blotches were counted only on the left side of a mid-dorsal line because blotches on either side of the dorsal fins were occasionally asymmetrically distributed and could result in different counts on each side.

Thirty-nine characters were examined on specimens from the six major drainage divisions and analyzed to determine trends in variation. Some characters were used extensively, and others were used sparingly or disregarded if little variation was found. Variation was analyzed to note differences between localities and between sexes. The characters included lateral line, transverse, caudal peduncle, and modified mid-ventral scales, dorsal and anal spines; dorsal, anal, caudal, and pectoral fin rays; branchiostegal rays, cranial pores; opercular, nape, and cheek squamation; lateral and dorsal blotches; lengths of the head, orbit, snout, snout to first dorsal, snout to second dorsal, snout to anal, snout to pelvic, snout to junction gill membrane, caudal peduncle, first dorsal base, second dorsal base, anal base, longest dorsal spine,
longest dorsal ray, longest anal ray, pectoral, pelvic and upper jaw; body and upper jaw widths; and body and caudal peduncle depths.

A one-way classification analysis of variance (Sokal and Rohlf, 1969) was used to compare sample means. A stepwise discriminant functions analysis was performed on the six groups (major drainage systems) of darter specimens. Variables in the analysis were dorsal spines, dorsal rays, anal rays, lateral line scales, transverse scales, caudal peduncle scales, midventral scales, dorsal blotches, and lateral blotches.

Material examined.-- Numbers of specimens of *P. maculata* are in parentheses. Institutional abbreviations are identified in acknowledgments. Complete locality data may be obtained from the author on request.

Mobile Bay drainage. Alabama: Blount Co., UAIC 2512 (3), 3304 (3); Bullock Co., UAIC 1484 (1); Chilton Co., UAIC 4683.08 (2), 4706.15 (1); Clarke Co., UAIC 2318 (1); Fayette Co., UAIC 1581 (1), 4518 (1), 4525 (1), 4530 (3), 4541 (2), 4550 (1), 4552 (8), 4557 (1), 4558 (11), 4564 (1), 4571 (1), 4576 (2); Greene Co., UAIC 694 (1), 2487 (3), 2849 (3); Jefferson Co., UAIC 1932 (1), 2518 (2), 3311 (1), 3316 (3), 3324 (1); Lowndes Co., UMMZ 111240 (1); Macon Co.,
UAIC 1368 (1), 1477 (1), 1480 (1); Marengo Co., UAIC 428 (2); Pickens Co., UAIC 1891 (1), 2022 (1), 4408.17 (2), 4411.20 (2); Sumter Co., CU 15554 (7); Tuscaloosa Co., UAIC 1062 (1), 1292 (1), 2093 (1), 2800 (2), 3534 (1). Mississippi: Clay Co., UAIC 4324.13 (1); Itawamba Co., UAIC 2293 (2), 4407.17 (1); Kemper Co., UAIC 2159 (1); Lee Co., UAIC 4307.16 (1); Lowndes Co., UAIC 4357.26 (1); Monroe Co., UAIC 4361.19 (1), 4432.22 (3); Wilkinson Co., UAIC 1272 (1).

Pearl River drainage. Louisiana: Washington Par., TU 105471 (1), 111571 (2). Mississippi: Copiah Co., NLU 6773 (3); Leake Co., NLU 47813 (4); Marion Co., TU 15176 (1); Neshoba Co., NLU 47746 (1); Simpson Co., TU 30881 (1), 56617 (1).

Lower Mississippi River drainage. Arkansas: Arkansas Co., TU 2230 (1); Bradley Co., TU 92971 (2); Crawford Co., TU 86325 (1); Drew Co., NLU 33123 (2); Independence Co., TU 49972 (2); Johnson Co., TU 93240 (1); Lawrence Co., FSU 14404 (1); Nevada Co., NLU 47957 (2); Saline Co., TU 70282 (1); Sevier Co., NLU 29379 (1); Van Buren Co., NLU 42878 (2); Yell Co., TU 15566 (19), 38716 (2). Kentucky: Carlisle Co., FSU 9002 (3). Louisiana: Jackson Par., NLU 5877 (3); Lincoln Par., NLU 45253 (1); Livingston Par., LSU 1866 (2); Union Par., NLU 12773 (2), 12823 (9), 35128 (2), 35194 (7), 39204 (1), 44050 (2), 44701 (1), uncat. (5). Mississippi: Amite
Co., TU 75639 (1), UNO 436 (1), 978 (1), 996 (1), 1718 (2), 1740 (2); Choctaw Co., FSU 10555 (1), TU 79987 (2); Claiborne Co., TU 91256 (2), 91339 (1); Copiah Co., FSU 10737 (1), TU 84121 (6), 85992 (4), 91495 (1), 103746 (3); Hinds Co., TU 91109 (2), 91134 (2); Holmes Co., TU 88224 (1); Lafayette Co., TU 57191 (2); Lincoln Co., TU 78735 (1), 78818 (1), 85943 (1); Union Co., FSU 10618 (1). Missouri: New Madrid Co., INHS 75549 (3). Tennessee: Hardeman Co., CU 52595 (1), UF 16519 (2).

Upper Mississippi River drainage. Illinois: Bureau Co., INHS 12689 (1); Coles Co., INHS 19058 (8); Iroquois Co., INHS 7208 (1); Jackson Co., INHS 22592 (7), 22660 (1); Kankakee Co., INHS 5356 (4), 5614 (4), 5630 (6); Livingston Co., INHS 6827 (1); Logan Co., INHS 18645 (1); Marshall Co., INHS 10482 (6); Mason Co., INHS 14528 (2), 25700 (1); McDonough Co., INHS 14730 (5); McLean Co., INHS 21148 (6), 21247 (1); Morgan Co., INHS 16278 (3); Moultrie Co., INHS 8863 (7); Piatt Co., INHS 8541 (10); Scott Co., INHS 10259 (1); Tazewell Co., INHS 14942 (9), 14965 (9); Will Co., INHS 4872 (11), 5101 (10); Woodford Co., INHS 10930 (14). Iowa: Greene Co., UMMZ 146848 (1). Kansas: Douglas Co., UAIC 1634 (1). Minnesota: Clearwater Co., FSU 13307 (7); Steele Co., UF 8721 (1). Missouri: Lincoln Co., INHS 75548 (2). Wisconsin: Green Lake Co., UMMZ 73788 (26); Marathon Co.,
Ohio River drainage. Alabama: Colbert Co., UAIC 2085 (1); Limestone Co., UMMZ uncat. (1). Illinois: Clark Co., INHS 2837 (17); Clay Co., INHS 7972 (2); Coles Co., INHS 18856 (2); Crawford Co., INHS 11571 (1); Cumberland Co., INHS 26902 (3); Douglas Co., INHS 8282 (4); Edwards Co., INHS 7154 (8); Effingham Co., INHS 7662 (1); Jasper Co., INHS 9613 (1), 9638 (10); Johnson Co., INHS 2181 (2); Lawrence Co., INHS 9336 (3); Pope Co., INHS 1350 (6), 1468 (4); Vermilion Co., INHS 12198 (2); White Co., INHS 9359 (1). Indiana: Warrick Co., INHS 75542 (2). Kentucky: Calloway Co., TU 53466 (1); Clark Co., EKU 100 (1); Clay Co., EKU 556 (2), 562 (2), 563 (3), 565 (1), 570 (11), 572 (1), 593 (2), 596 (3), 606 (2), 608 (3), 610 (1), 780 (2), UF 10069 (3), 15304 (1); Elliott Co., CU 64085 (10); Estill Co., EKU 50 (2); Greenup Co., EKU 137 (6); Jackson Co., EKU 435 (2), 576 (3); Knox Co., UF 9996 (3); Leslie Co., EKU 305 (1), 550 (1), 552 (2), UF 10047 (4); Lincoln Co., EKU 340 (1), 342 (6), 387 (1), 400 (6), 411 (2), 429 (2), CU 37477 (5); Livingston Co., INHS 75545 (1), 75546 (4); Marshall Co., CU 25667 (8); Montgomery Co., INHS 75544 (1); Owen Co., EKU 485 (2); Owsley Co., EKU 566 (1), 589 (1), 600 (2); Pike Co., EKU 59 (2); Powell Co., EKU 19 (2),
47 (2), 55 (4), 105 (1), 128 (2); Rockcastle Co., EKU 355 (1); Washington Co., INHS 75543 (1); Wolfe Co., EKU 44 (2).

New York: Cattaraugus Co., CU 4672 (8), 4689 (3), 8592 (3), 8615 (18), 8646 (2), 8731 (1), 19942 (1), 43072 (1), 44635 (1), 44669 (1), 44670 (1), 44681 (3), 62645 (3); Chautauqua Co., CU 4675 (5), 46926 (1). Ohio: Pickaway Co., CU 32961 (3), 42051 (2), 46382 (6); Pike Co., CU 42221 (1); Wayne Co., OSU 2221 (9). Pennsylvania: Beaver Co., CU 3520 (2), 40706 (2); Butler Co., CU 6537 (3); Crawford Co., CU 40022 (1); Erie Co., CU 40920 (1); Greene Co., CU 40152 (1); Lawrence Co., CU 39932 (1), 40542 (1), 40762 (1); McKean Co., CU 10710 (2), 39894 (2), 40582 (1), 40777 (3); Mercer Co., CU 3762 (1), 4157 (2), 6410 (8), 7812 (4), 8236 (3), 34732 (1), 39935 (2), 40225 (2), 40382 (6), 40494 (4), 45540 (6); Potter Co., CU 22979 (4); Venango Co., CU 7854 (1); Warren Co., CU 62784 (8). Tennessee: Anderson Co., CU 19147 (2); Cambell Co., NLU 47434 (13); Fentress Co., CU 30762 (2); Montgomery Co., CU 23188 (2); Roane Co., UMMZ 104366 (1); Stewart Co., CU 23222 (2), 47857 (3); Sumner Co., UF 22319 (1); (Powell River), UMMZ 187255 (1). Virginia: Smyth Co., UMMZ 119678 (3). West Virginia: Cabell Co., UNC 6921 (3); Kanawha Co., CU 4979 (1), 4991 (1); Lincoln Co., CU 14791 (51); Tyler Co., UNC 6951 (1).

Great Lakes drainage. Michigan: Alpena Co., UMMZ
Percina maculata (Girard)

Blackside darter

Figs. 1, 2, and 3

Types.—Two syntypes (USNM 1346) from Fort Gratiot on Lake Huron, on which Girard's original description was based, are
listed in the USNM catalog as having been thrown away and efforts to find them have proven unsuccessful (Collette and Knapp, 1966). Because no subspecific categories are proposed, no neotype is designated herein, since no "exceptional circumstances . . . for solving a complex zoological problem . . . in the interest of stability of nomenclature" (Stoll, 1964: Art. 75a.) exists for P. maculata.

**Diagnosis.**—A species of the genus Percina, subgenus Alvordius (diagnosed by Page, 1974), distinguished from other known species of the subgenus by the following combination of characters: spinous dorsal fin with proximal concentration of melanophores on first 2 - 4 interradial membranes; distinct basicaudal spot; 5 - 8 (usually 6 or 7) round to oval, moderately to broadly connected, dark brown lateral blotches; 6 - 12 (usually 8 - 11) rectangular, irregular, dark brown dorsal blotches along midline; nape with embedded scales posteriorly, opercles fully scaled, cheeks scaled or with at least a few embedded scales; chin and branchiostegal membranes immaculate or with uniformly distributed melanophores; no bright breeding colors; 40 - 44 (usually 42 or 43) vertebrae; only males with modified midventral scales.

Pigmentation pattern (Fig. 1) separates P. maculata from all other species in Alvordius. P. maculata is
distinct from *P. crassa* and *P. roanoka* of the Atlantic coast drainages in having a higher number of lateral line and caudal peduncle scales, but differs from *P. macrocephala* and *P. pantherina* of the Mississippi River basin in having a lower number of lateral line and caudal peduncle scales. *P. maculata* differs from *P. gyrocephala* in head squamation and number of vertebrae, and differs from *P. peltata* and *P. notogramma* from the Atlantic coast drainages in having modally higher scale counts. *P. gyrocephala* and *P. macrocephala* females have modified midventral scales present, whereas *P. maculata* females do not.

**Description.** — *P. maculata* is a moderate sized species of the subgenus *Alvordius* and attains a maximum size of 84 mm SL.

Premaxillary frenum well developed; branchiostegal membranes separate; branchiostegal rays 6-6 (rarely with 5 or 7 on either or both sides); cephalic sensory canal system without interruptions: a single coronal pore, supratemporal canal with three pores, supraorbital canal with four pores, infraorbital canal with eight pores, preoperculo-mandibular canal with 10 pores.
Dorsal spines 12 to 17 (usually 13 to 15); dorsal rays 10 to 15 (usually 12 or 13); anal spines 2 (rarely 1 or 3); anal rays 7 to 11 (usually 8 or 9); pectoral fin rays 11 to 16 (usually 13 or 14); caudal rays modally 17 (occasionally 15 or 16, rarely 14). Total vertebrae 40 to 44 (usually 42 or 43). Breeding tubercles absent.

Cheeks typically scaled, or with at least some embedded scales. Opercles fully scaled. Nape squamation typically embedded scales on posterior 25%, but occasionally naked or partially embedded scales up to 75% of area. Breast usually naked. Midventral row of modified scales well developed and present in males. Lateral line straight, complete (rarely 1 to 3 unpored scales) with 53 to 79 (usually 60 to 71) scales. Transverse scales 13 to 22 (usually 15 to 19). Caudal peduncle scales 18 to 29 (usually 20 to 26).

Proportional measurements, expressed as thousandths of the standard length, range as follows: head length, 246 - 293; orbit diameter, 49 - 82; snout length, 56 - 81; snout to first dorsal, 325 - 364; snout to second dorsal, 625 - 676; snout to anal, 622 - 674; snout to pelvic, 215 - 321; snout to junction gill membrane, 96 - 146; body depth, 137 - 202; body width, 119 - 158; caudal peduncle length, 197 - 247; caudal peduncle depth, 74 - 96; first dorsal base, 223 - 337; second dorsal base, 140 - 203; anal base, 118 - 183; longest dorsal spine, 84 - 139; longest dorsal
ray, 90 - 135; longest anal ray, 103 - 155; pectoral length, 184 - 243; pelvic length, 152 - 213; upper jaw length, 63 - 91; upper jaw width, 7 - 13.

Pigmentation pattern (Fig. 1) consists of a series of slightly to broadly confluent, horizontally ovate to round, dark brown lateral blotches, numbering usually 6 or 7. There are typically 8 to 11 irregularly rectangular dark brown dorsal blotches, the anteriormost of which is often irregularly splotched with light areas. An irregular, wavy or broken, dark band extends along the mid-dorsolateral surface between the lateral and dorsal blotches producing two irregular light bands between the former and the latter, and forming, to a greater or lesser degree, a reticulated pattern along the upper body area.

The ventrolateral body and venter are typically cream colored to light tan and are usually immaculate or occasionally covered with uniformly spaced melanophores giving the region a dusky appearance. The head is dark above the ventral margin of the eye with the snout having a mottled appearance. A narrow, dark band of pigment extends from the anterior edge of the eye to the tip of the snout onto the premaxillary frenum. Dark pigment extends from this point back along the upper jaw to a distance of one third to three quarters of its full length. A narrow, dark bar is present on the orbit above the pupil, and a dark subocular bar extends
down and slightly back from the eye to the ventral margin of the preopercle. The chin and branchiostegal membranes are immaculate or with uniformly distributed melanophores giving the area a dusky appearance. A concentration of melanophores is usually present just anterior to the base of the pectoral fins. A distinct basicaudal spot, usually darker than the lateral blotches, is typically present; however, occasionally this pigmentation will be sufficiently broad and diffuse to form a blotch.

The dorsal fins exhibit sexual dimorphism in pigmentation patterns. Both males and females typically exhibit a proximal concentration of melanophores forming a dark blotch at the corner of the spinous dorsal fin in the anterior two to four interradial membranes. Males have some concentration of pigment forming a proximal dark band on the remaining interradial membranes. Another concentration of melanophores is located along the distal margin of the first dorsal and forms a dusky band along the border. Uniformly distributed pigment between these bands is often present and gives the entire fin a dark, dusky appearance. The second dorsal of males has a column of melanophores extending along the posterior half of each interradial membrane from the base to the point of branching of the rays. The membranes surrounding the branched ends are uniformly
pigmented to form a dusky proximal band. In females a fainter series of proximal and distal bands are present in the first dorsal, but the interradial membrane just posterior to each spine has a vertical series of 3 or 4 dark lines forming a series of bands made of vertical dashed lines. The second dorsal of females has a similar pattern with a series of bands formed by 4 or 5 dusky patches vertically oriented in each interradial membrane.

The anal fin is either immaculate or has an overall dusky appearance with the rays being slightly outlined with melanophores. Occasionally a narrow, single band of melanophores is associated with the center of each ray. Series of 4 or 5 patches of melanophores along each caudal ray, but not in the membranes, give the caudal fins a series of 4 or 5 (occasionally 3 or 6) dark, vertical bands. In larger adults the bands may be obscure and the caudal fin may be dusky in appearance. The pectoral fins have 4 to 6 pale bands formed by concentrations of melanophores in patches along the rays. The pelvic fins may appear immaculate or dusky but do not have pigment arranged in bands. Petravicz (1938) noted sexual dimorphism in the shape of the pelvic fins.

VARIATION

Sexual and geographic variation were found in both the
meristic and morphometric data (Figs. 4 through 9). Some slight sexual dimorphism appeared in the morphometric data, but none was indicated in the meristic characters. Sexual dimorphism occurred in one of the six major drainage divisions for longest dorsal spine and ray and first dorsal base, and in two of the six drainages for snout length, body and caudal peduncle depths, and second dorsal and anal fin bases. However, when data from the six drainages were combined for each measurement, the sexual differences disappeared, as the range of values tended to overlap broadly.

Comparison of ranges and means between drainage systems for individual proportional measurements indicated no geographic variation.

Meristic data exhibited pronounced clinal variation in those characters with relatively high variability, i.e. broad ranges. The major trend was for counts to decrease from south to north as seen for lateral line, transverse, caudal peduncle, and modified midventral scale counts as well as for lateral and dorsal blotches (Figs. 4 through 9). Ontogenetic variation in modified midventral scales of *P. maculata* was discussed by Page (1976). A difference in meristic characters between Great Lakes and Hudson Bay populations had been noted by Scott and Crossman (1973). The number of dorsal spines exhibited this south-north decrease to a
lesser degree (Fig. 10); however, the reverse trend, a south-north increase, was observed for those characters with a relatively low variability, i.e. narrow range, specifically dorsal and anal ray counts (Figs. 11 and 12).

The major clinal trend mentioned above showed the highest counts above the fall line in the Mobile Bay and lower Mississippi River drainages. Counts were slightly lower than these within the same drainages below the fall line (including the separate Gulf slope drainages). Counts were lower still above the fall line in the upper Mississippi River and Ohio River systems, and these two drainages exhibited similar tendencies in that counts of meristic characters in the upper reaches of these basins were lower than those nearer the mouth. Within the Great Lakes drainage, counts were slightly lower than in the adjacent, aforementioned systems, and there was even a moderate trend toward decreasing lateral line scale counts from eastern to western lakes. *P. maculata* from the Hudson Bay drainage exhibited the lowest counts of meristic characters. These were somewhat lower than those of the adjacent Great Lakes and upper Mississippi River drainages.

The number of anal spines showed almost no variation (98.82% of the specimens with 2 spines, 0.64% with 1, and 0.54% with 3). Nape, cheek, and opercular squamation showed some slight variation, but this was independent of geographic
region or sex (Fig. 13). Virtually no variation in the number of head pores (one specimen had 6, rather than 8, infraorbital pores) was found in \textit{P. maculata}, which has been shown to be the case for all species of \textit{Percina} (Page, 1977).

Numbers of lateral and dorsal blotches varied clinally (Figs. 8 and 9), whereas the actual pigmentation patterns showed a variety of forms within individual drainages (Fig. 2). Dorsal-fin pigmentation exhibited sexual dimorphism (Fig. 1). Some individual and interpopulational variation in body pattern may be due to habitat substrate. Many specimens from below the fall line typically have a greater number of, thus smaller, dorsal and lateral blotches, and more finely delineated dorso-lateral markings in association with sand, silt, and fine gravel bottoms, whereas in more northerly streams coarser, darker gravel and rocks may initiate a darker, bolder pattern in many specimens. Mathur (1973) discussed melanophore response to background coloration in \textit{Percina nigrofasciata}, in which body and fins became darker or lighter depending on the substrate. A similar response in \textit{P. maculata} is of obvious advantage and likely has led to the establishment of these patterns.

The environment can play an important role in the expression of variation in both meristic and morphometric characters in fishes. Environmentally induced variation has generally been discussed in relation to an increase in
elements of particular characters from south to north, which indicates a correlation between cooler water temperatures and higher meristic values (Barlow, 1961; Gordon, 1957). The effects of environmental factors on numbers of vertebrae in percid fishes, for example, was discussed by Bailey and Gosline (1955). *Menidia beryllina* exhibited clinal variation in characters responding to a gradient of environmental factors between salt marsh and inland freshwater habitats along the Gulf coast (Chernoff et al., 1981). That meristic characters may show opposite clinal trends in a single species has been shown by Bryan (1969) for *Micropterus*. Resh et al. (1976) indicated a reverse cline for vertebral number in *Notropis atherinoides* of the Ohio River opposite to the clinal variation reported by Bailey and Allum (1962) for that species in the upper Mississippi River and Great Lakes drainages. Typically this reverse cline (south–north decrease) is found only in fishes with the more common trend of meristic variation (south–north increase) (Barlow, 1961). As noted above, *P. maculata* exhibited both the typical clinal trend and the reverse trend, but with the latter being more pronounced in its expression.

These clinal trends were tested within and between the six major drainage systems occupied by populations of *P. maculata*. Analysis of variance indicated a significant
difference between at least two sample means for the majority of meristic characters examined. Data for *P. maculata* were further examined beyond the ANOVA to determine where the differences were occurring and whether the differences were the result of breaks between drainages or due primarily to the geographic extremes. The nine meristic characters exhibiting most variation were examined by the stepwise discriminant functions analysis.

The results of this analysis indicated that transverse scale counts were the most reliable of the characters in discriminating populations of *Percina maculata*. Each successive step added the following sequence of characters: dorsal blotches, caudal peduncle scales, lateral blotches, lateral line scales, dorsal spines, dorsal rays, midventral scales, and anal rays. For the classification generated, individual group covariance matrices were used. The classification results indicated an overall 53.59% of the grouped cases being correctly identified. Individually the Hudson Bay samples were correctly identified in 82.4% of the cases, the Great Lakes samples, 80.6%, the Ohio River samples, 15.7%, the Upper Mississippi samples, 39.8%, the Lower Mississippi samples, 67.4%, and the Gulf Slope samples, 64.0%. This inability to demarcate populations indicates the high variability of meristic characters in the Ohio and upper
Mississippi River drainages and the difficulty of assigning specimens from these regions to a specific population classification. The scatterplot generated from the discriminant functions analysis is depicted as cluster outlines in Figure 14. This visual assessment of the drainage grouping of the discriminant functions clearly shows the broadly overlapping nature of these populations of *P. maculata*. The only two drainage systems exhibiting no overlap are the Hudson Bay and Gulf Slope (Fig. 14: cluster outlines 1 and 6), which are the most widely separated geographically. The outlines, although densely clustered, implicitly depict clinality. Thus by inspection of the relative positions of sample means in Figures 4 through 12 plus analysis of geographic variation between the drainages as depicted in Figure 14, the clinal nature of variation for *P. maculata* emerges.

Vandermeer (1966) found similarly significant F values in analysis of variance of meristic characters for the widely distributed cyprinid fish, *Pimephales promelas*. However, his determination of clinal patterns of variation in the then recognized subspecies of *P. promelas* led him to the conclusion that the use of these taxonomic designations should be discontinued. There are many other references which have based taxonomic decisions on the presence of clinal variation; for example, *Menidia audens* was placed in synonymy with *M. beryllina* by Chernoff et al. (1981) based
on the discovery of clinal patterns in meristic characters. Page and Smith (1976) referred *Etheostoma cumberlandicum* to the synonymy of *E. kennicotti* based on the clinal variation exhibited by five meristic characters in this species of darter.

*Percina maculata* has an expansive distribution relative to *E. kennicotti*. Only two other darter species, *E. nigrum* and *P. caprodes*, have distribution patterns covering as wide a geographic area as *P. maculata*. These two species have been divided into subspecies; however, their taxonomic status is currently in a state of flux. Cole (1967) merely listed the three known subspecies of *E. nigrum* and intimated a fourth but did not give data on which the designations had been based. The validity of one of these subspecies has been questioned based on the polymorphic nature of the species and the intergradation zone not conforming to that of basic subspecific patterns (Underhill, 1963). Thompson (1980) outlined the distribution of *P. caprodes* and briefly discussed the recognized subspecies and forms within the complex which he deems to be distinct species. Morris and Page (1981) described a new subspecies of *P. caprodes* and elevated *P. carbonaria* to a full species. Their meristic data indicated some clinal trends in *P. caprodes*; however, they dealt with color pattern differences which aided in the definition of subspecific groups.
Subspecies are not recognized in this study of *Percina maculata*. Geographic variation in meristic characters is clinal and pigmentation patterns vary over the entire range such that no combination of the two sufficiently separates populations. Separation of the blackside darter into subspecies would be totally subjective because much of the variation is of a non-concordant clinal pattern for the various characters and could not be justified on the basis of conventional systematic methods for subspecific determination as outlined by Mayr (1969). Also there is no zone of intergradation which conforms to the relatively narrow geographic area for subspecific designation as proposed by Bailey et al. (1954.)

RELATIONSHIPS

In his treatment of the subgenera of *Percina*, Page (1974) proposed a phylogeny of the subgenus *Alvordius* based on phenograms generated from 45 characters measured on all species within the subgenus that were recognized at the time. Subsequently, Page (1981) presented phenograms and cladograms including relationships of *Alvordius* in his study of all darter subgenera based on 52 characters. The results of these clusterings indicate that *P. maculata*, *P. macrocephala*,
and *P. pantherina* are closely related and that they represent the most primitive members of *Alvordius*. *P. maculata* is most closely related to *P. pantherina* in five different phenograms generated by Page (1974) based on different character groupings with males, females, and both sexes together. Page (1981) indicated a close relationship between *P. maculata* and *P. pantherina* for one phenogram, but found *P. macrocephala* to be more closely related to *P. maculata* in another phenogram and in one cladogram that represented members of the genus *Percina*. Most data used in the comparison of species in *Alvordius* were made up of meristic, morphometric, and pigmentation characters. These comparisons clearly show that, although the three species in question are related, *P. maculata* and *P. pantherina* show a closer relationship to each other than either does with *P. macrocephala*. Moore and Reeves (1955) proposed a closer relationship between *P. pantherina* and *P. maculata* based on the presence of scaled cheeks and opercles in these two species. *P. macrocephala* has naked cheeks and opercles. Page (1978) concurred with this assessment of relationships between these three species in his treatment of *P. macrocephala*.

The more complete description of *P. maculata* afforded by my study corroborates the relationship inferred by Page (1974; 1978; 1981) and Moore and Reeves (1955).
Zoogeography is an important consideration in the relationship of these species. All three species occur in the Mississippi River basin; however, *P. pantherina* is allopatric to *P. maculata* (and *P. macrocephala*). The allopatry exhibited by *P. maculata* and *P. pantherina* may represent a more recent divergence of the two species than that indicated by the overlap in distribution of *P. maculata* and *P. macrocephala*.

Another possible relative of *P. maculata* is an undescribed species from the Mobile Bay drainage. Its closest extant relative in the subgenus should be more clearly defined subsequent to its description. *Percina maculata* and *P. gymnocephala* may have shared a common ancestor, but the latter species has been shown by Beckham (1980) to have a closer kinship to Atlantic coast members of *Alvordius*. 
LITERATURE CITED


Fig. 1. Adult male (A) and female (B) *Percina maculata*. Composite drawing based on UMMZ 194283, Great Lakes drainage.
Fig. 2. Variation in lateral and dorsal pigmentation patterns exhibited by *P. maculata*.
Fig. 3. Distribution of drainage localities for *P. maculata* material used in meristic character analysis. Letters correspond to those in Figs. 4, 5, and 6.
Fig. 4. Variation in the number of lateral line scales in populations of *P. maculata*. The letters correspond to sites depicted in Fig. 3. The diagrams represent the sample range (base line), the mean (center triangle), one standard deviation on either side of the mean (outer limits of open triangle), and two standard errors on either side of the mean (black rectangle).
Fig. 5. Variation in the number of transverse scales in populations of *P. maculata*. See legend for Fig. 4 for explanation of diagrams.
Fig. 6. Variation in the number of caudal peduncle scales in populations of P. maculata. See legend for Fig. 4 for explanation of diagram.
CAUDAL PEDUNCLE SCALES

LATITUDE

CAUDAL PEDUNCLE SCALES

A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
Fig. 7. Variation in the number of modified midventral scales on males in populations of *P. maculata*. Drainage designations are Hudson Bay (HB), Great Lakes (GL), Ohio River (OH), upper Mississippi River, (UM), lower Mississippi River (LM), and Gulf slope (GS). See legend for Fig. 4 for explanation of diagrams.
Fig. 8. Variation in the number of lateral blotches in populations of *P. maculata*. See legends for Figs. 4 and 7 for explanation of diagrams and drainage designations, respectively.
Fig. 9. Variation in the number of dorsal blotches in populations of \textit{P. maculata}. See legends for Figs. 4 and 7 for explanation of diagrams and drainage designations, respectively.
Fig. 10. Variation in the number of dorsal spines in populations of P. maculata. See legends for Figs. 4 and 7 for explanation of diagrams and drainage designations, respectively.
Fig. 11. Variation in the number of dorsal rays in populations of *P. maculata*. See legends for Figs. 4 and 7 for explanation of diagrams and drainage designations, respectively.
Fig. 12. Variation in the number of anal rays in populations of *P. maculata*. See legends for Figs. 4 and 7 for explanation of diagrams and drainage designations, respectively.
Fig. 13. Percent squamation (black portion of circles) of cheek, opercle, and nape regions of *P. maculata* in the six drainage divisions of its range. Within each drainage the left circle represents average percent of cheek covered with scales, center circle represents average percent of opercle covered with scales, and right circle represents average percent of nape covered with scales.
Fig. 14. Cluster outline representing the major drainage division scores plotted on the first two principal component axes. Percent of variance for the two discriminant functions totals 86.58%. (1 = Hudson Bay; 2 = Great Lakes; 3 = Ohio River; 4 = Upper Mississippi River; 5 = Lower Mississippi River; 6 = Gulf Slope.)
DISCRIMINANT FUNCTION 1

DISCRIMINANT FUNCTION 2
VITA

Eugene Clifton Beckham III was born on February 14, 1948 in Birmingham, Alabama. He was graduated from University Military School of Mobile, Alabama in 1966. He received both his Bachelor of Science degree in 1970 and his Master of Science degree in 1973 from the University of Alabama. From 1974 through 1976 he was employed by Cornell University as an Associate Curator for their Herpetological and Ichthyological collections. He then accepted the position of Associate Curator of Fishes at Tulane University and remained there until 1979. He served as field assistant to Dr. Charles Fugler on an expedition to Bolivia, South America, during the summer of 1979 before returning to school full time at Louisiana State University to pursue his doctoral degree. In 1982 he accepted the position of State Parks Naturalist with the Louisiana Office of State Parks. He is married to the former Esther Boykin of Leroy, Alabama, and they reside in Baton Rouge, Louisiana.
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Major Field: Zoology

Title of Thesis: Systematics, Redescription, and Geographic Variation of the Blackside darter, Percina maculata (Pisces; Percidae)

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Date of Examination:

April 21, 1983