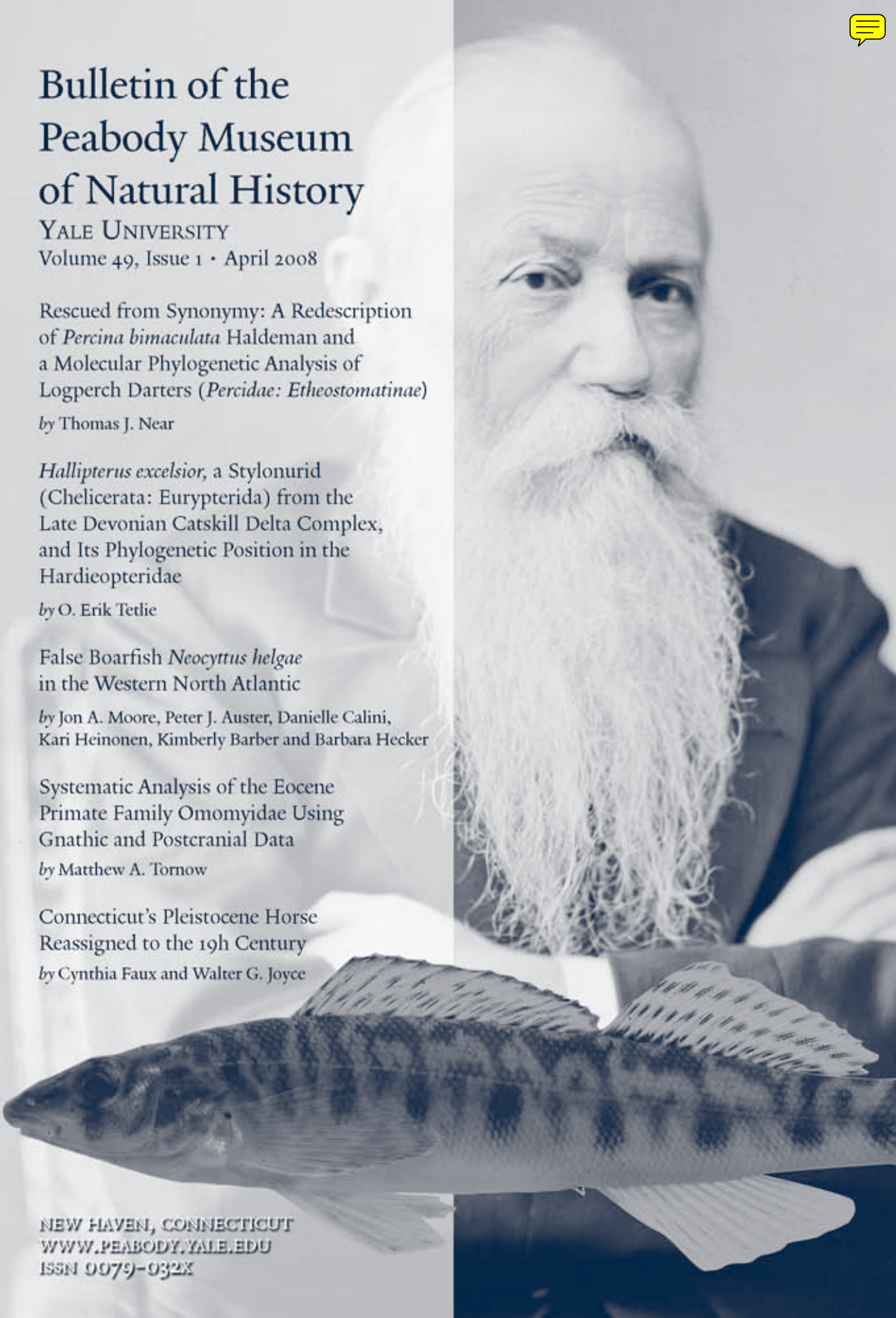
Bulletin of the Peabody Museum of Natural History

YALE UNIVERSITY
Volume 49, Issue 1 • April 2008



NEW HAVEN, CONNECTICUT
WWW.PEABODY.YALE.EDU
ISSN 0079-032X

Rescued from Synonymy: A Redescription of *Percina bimaculata* Haldeman and a Molecular Phylogenetic Analysis of Logperch Darters (Percidae: Etheostomatinae)

Thomas J. Near

Department of Ecology and Evolutionary Biology, Osborn Memorial Labs,
P. O. Box 208106, Yale University, New Haven CT 06520-8106 USA

Peabody Museum of Natural History, Yale University,
P. O. Box 208118, New Haven, Connecticut 06520-8118 USA
— *email:* thomas.near@yale.edu

Abstract

Percina nebulosa and *Percina bimaculata* have been considered synonyms of *P. caprodes* for over 130 years. The taxonomic history of *P. nebulosa* is complicated by the fact that the name is preoccupied by *Perca nebulosa* Rafinesque. *Percina bimaculata* Haldeman is the available and appropriate name for this species, and the Chesapeake Logperch is the proposed common name. Recent phylogenetic analyses of mitochondrial DNA gene sequences support the hypothesis that *P. bimaculata* is a distinct species; however, a morphological comparison between *P. bimaculata* and other logperch darter species has never been published. An examination of morphological characters and a new molecular phylogeny of both mitochondrial and nuclear gene sequence data support the recognition of *P. bimaculata* as a distinct species most closely related to *P. kathae* and *P. austroperca*. Historically, *P. bimaculata* was distributed in the lower Susquehanna River Basin of Pennsylvania and Maryland and the middle to lower Potomac River Basin of Maryland, Virginia and the District of Columbia, USA. The species has not been recorded from the Potomac Basin since the 1930s and is currently found only in the lower Susquehanna River Basin. The restricted geographic distribution and extirpation from the Potomac Basin indicates that *P. bimaculata* is an imperiled species and may warrant protection under the Endangered Species Act of 1973. The molecular phylogeny also indicates that populations recognized as *P. caprodes* sampled from the upper Mississippi River Basin in Illinois, Wisconsin and Minnesota are not closely related to *P. caprodes* populations sampled from the Ohio, Tennessee, White and Hudson river drainages.

Keywords

Nuclear gene phylogeny, darter, Potomac, Susquehanna, cryptic species, meristic, morphometric, species description, Teleostei.

Introduction

Darters (Etheostomatinae) are a clade of approximately 225 species of freshwater teleost fishes that are endemic to eastern North America. Page's (1983) monographic treatment of darter diversity recognized 129 species. The addition of 100 species to the recognized diversity of darters since the mid-1980s has come about through the description of new species and the elevation of previously recognized subspecies. The Chesapeake Logperch provides an example of a darter species long relegated to obscurity as a synonym of another darter species, despite being a distinct evolutionary lineage that is imperiled and extirpated from much of its documented geographic distribution.

Haldeman (1842) described the Chesapeake Logperch as *Perca* (*Percina*) *nebulosa* from the Susquehanna River in Pennsylvania, USA, and two years later (Haldeman 1844) described a second logperch species from the Susquehanna

Table 1. Collection data and GenBank® accession information for specimens used in molecular phylogenetic analyses (Benson et al. 2007). *Abbreviations:* ANSP, Academy of Natural Sciences, Philadelphia; CUMZ, Cornell Museum of Vertebrate Zoology; INHS, Illinois Natural History Survey; UAIC, University of Alabama Ichthyological Collection; USNM, Unites States National Museum; UT, University of Tennessee Research Collection of Fishes; YFTC, Yale Fish Tissue Collection; YPM, Yale Peabody Museum of Natural History.

Species	Collection locality	Museum voucher	YFTC	GenBank® (*cytb*, ND2, S7)
Percina austroperca (A)	Big Escambia Creek, Escambia Co., Alabama	UAIC 9993.19	129	AF386546, AY770846, EU379106
Percina austroperca (B)	Escambia River, Escambia Co., Florida	INHS 38433	220	AF386547, AY770847, EU379107
Percina bimaculata (A)	Conowingo Creek, Cecil Co., Maryland	No voucher	2311	AY770843, AY770856, EU379108
Percina bimaculata (B)	Conowingo Creek, Cecil Co., Maryland	YPM 17016	10960	EU379092, EU379077, EU379109
Percina burtoni (A)	Spring Creek, Polk Co., Tennessee	UAIC 9819.17	164	AY770840, AY770848, EU379110
Percina burtoni (B)	Buffalo River, Wayne Co., Tennessee	INHS 38531	335	AF386554, EU379078, EU379111
Percina caprodes (C)	Lake Wawasee, Kosciusko Co., Indiana	INHS 68983	349	AF386550, AY770849, EU379112
Percina caprodes (D)	Big Piney Fork, Sharp Co., Arkansas	INHS 41160	396	AY770841, AY770850, EU094728
Percina caprodes (BC)	Little River, Blount Co., Tennessee	UT 91.6797	3320	EU379093, EU379079, EU379121
Percina caprodes (EA)	Schoharie Creek, Schoharie Co., New York	YPM 17492	11179	EU379094, EU379080, EU379122
Percina caprodes (EB)	Schoharie Creek, Schoharie Co., New York	YPM 17492	11180	EU379095, EU379081, EU379123
Percina cf. *caprodes* (P)	Illinois River, Putnam Co., Illinois	INHS 38502	228	EU379096, EU379082, EU379113
Percina cf. *caprodes* (S)	St. Croix River, Chisago Co., Minnesota	INHS 40658	267	EU379097, EU379083, EU379114
Percina cf. *caprodes* (T)	Lake Andrusia, Beltrami Co., Minnesota	INHS 39509	276	EU379098, EU379084, EU379115
Percina cf. *caprodes* (U)	Lake Andrusia, Beltrami Co., Minnesota	INHS 39509	277	EU379099, EU379085, EU379116
Percina cf. *caprodes* (V)	Lake Andrusia, Beltrami Co., Minnesota	INHS 39509	278	EU379100, EU379086, EU379117
Percina cf. *caprodes* (AJ)	Mississippi River, Jo Daviess Co., Illinois	INHS 43064	514	EU379101, EU379087, EU379118
Percina cf. *caprodes* (AR)	Jump River, Rusk Co., Wisconsin	INHS 47046	1167	EU379102, EU379088, EU379119
Percina cf. *caprodes* (AS)	Wisconsin River, Sauk Co., Wisconsin	INHS 47440	1183	EU379103, EU379089, EU379120
Percina carbonaria (A)	Colorado River, Travis Co., Texas	UAIC 11412.18	309	AF386553, AY770851, EU379124
Percina carbonaria (B)	Guadalupe River, Kerr Co., Texas	UT 91.6926	4987	EU381042, EU381043, EU379125
Percina fulvitaenia (A)	Maries River, Osage Co., Missouri	YPM 15606	8144	EU379104, EU379090, EU379126
Percina fulvitaenia (C)	Fourche La Fave River, Perry Co., Arkansas	INHS 54009	1469	EU379105, EU379091, EU379127
Percina jenkinsi (A)	Conasauga River, Whitfield/Murray Co., Georgia	UAIC 11680.01	160	AF386555, AY770852, EU379128

Continued

Table 1 continued.

Species	Collection locality	Museum voucher	YFTC	GenBank® (cyt*b*, ND2, S7)
Percina kathae (A)	Conasauga River, Bradley Co., Tennessee	INHS 41653	439	AY770842, AY770853, EU379129
Percina kathae (C)	Hilabee Creek, Tallapoosa Co., Alabama	INHS 38632	166	AF386549, AY770854, EU379130
Percina macrolepida (A)	South Fork of San Gabriel River, Williamson Co., Texas	UAIC 11681.01	188	AF386552, AY770855, EU379131
Percina rex (A)	Roanoke River, Roanoke Co., Virginia	UAIC 7932.15	147	AF386556, AY770857, EU379132
Percina suttkusi (A)	Bogue Chitto River, Washington Parrish, Louisiana	UAIC 10466.12	159	AF386551, AY770858, EU379133
Percina peltata (A)	South Anna River, Louisa/Goochland Co., Virginia	UAIC 9825.11	132	AF386595, AY770845, EU379134
Percina roanoka (A)	Blackwater River, Franklin Co., Virginia	INHS 64359	76	AF386597, AY225722, EU094726

River in Pennsylvania, *Percina bimaculata.* Both *P. nebulosa* and *P. bimaculata* have been considered synonyms of the Logperch, *Percina caprodes* (Rafinesque) for over 130 years (Jordan 1877a; Fowler 1945; Collette and Knapp 1966; Page 1983). Complicating the taxonomy of *P. nebulosa* is that *Perca* (*Percina*) *nebulosa* Haldeman is a homonym of *Perca nebulosa* Rafinesque (1814), thus *Percina bimaculata* Haldeman is the available and appropriate name for the Chesapeake Logperch. Subsequent phylogenetic analysis of mtDNA gene sequences and unpublished morphological data supported the recognition of *Percina bimaculata* as a distinct species and not a synonym of *P. caprodes* (Near and Benard 2004).

The type locality of *P. nebulosa* and *P. bimaculata* is the Susquehanna River in Pennsylvania (Haldeman 1842; Mombert 1869), and the current distribution of the species is the lower Susquehanna River of Maryland and Pennsylvania, USA (Lee 1976; Lee et al. 1976; Thompson 1980; Lee et al. 1981; Jenkins and Burkhead 1994; Rohde et al. 1994). In addition to the Susquehanna River, logperch populations historically referred to as *P. caprode*s are found in disjunct regions on the central Atlantic Slope in the Potomac and Hudson drainages (Thompson 1980; Smith 1985; Jenkins and Burkhead 1994; Starnes 2002). Jenkins and Burkhead (1994) hypothesized that the Potomac River populations are closely related to those found in the Susquehanna; however, the Chesapeake Logperch has not been collected in the Potomac River since 1938 and is considered extirpated (Lee et al. 1981, 1984; Jenkins and Burkhead 1994; Starnes 2002). Logperch populations in Atlantic Slope drainages have long been considered *P. c. caprodes* or *P. c. semifasciata.* Using meristic and morphometic data, Jenkins and Burkhead (1994) concluded that logperch populations in the Potomac and Susquehanna were the same taxon, and R. E. Jenkins later stated through a personal communication that these populations may represent a distinct taxon (Starnes 2002). The only published information on the morphology of the Chesapeake Logperch is found in the original species descriptions of *Perca* (*Percina*) *nebulosa* and *Percina bimaculata* (Haldeman 1842, 1844).

In this study, the nomenclature of the Chesapeake Logperch is investigated, with the conclusion that the available name *Percina bimaculata* Haldeman is the appropriate scientific name for this species, and *P. bimaculata* is redescribed with information from morphological characters commonly used to diagnose and differentiate logperch species (Stevenson 1971; Morris and Page 1981; Thompson 1985, 1995, 1997a, 1997b). In addition, the phylogenetic relationships among the 11 recognized logperch species are investigated through analyses of nuclear and mitochon-

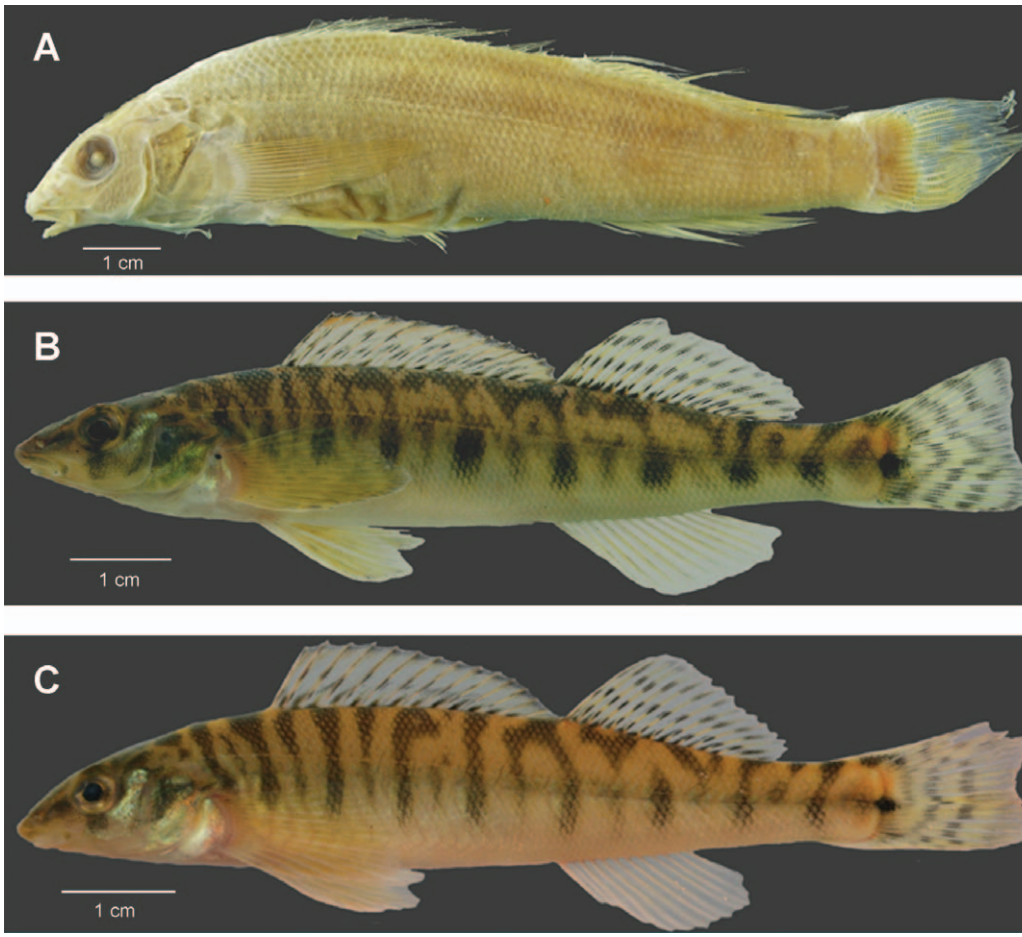


FIGURE 1. **A.** *Percina nebulosa* holotype specimen (ANSP 22652), 109.4 mm standard length (SL) male, Susquehanna River, Pennsylvania, USA. **B.** *Percina bimaculata* YPM 17016, YFTC 10967, 85.5 mm SL male, Conowingo Creek, Cecil Co., Maryland, USA. **C.** *Percina bimaculata* YPM 16748, YFTC 9740, 74.6 mm SL female, Conowingo Creek, Cecil Co., Maryland, USA.

drial DNA sequences. Morphological diagnosis supports the conclusion that *P. bimaculata* is a distinct species and does not represent a geographically disjunct population of *P. caprodes*. The molecular phylogenies provide important insight into the relationships of *P. bimaculata* and indicate the existence of multiple clades masquerading as *P. caprodes*.

Materials and Methods

Specimens for morphological analyses were obtained from field collections and collection records were gathered from museum research collections. Institutional abbreviations follow Leviton et al. (1985) and Leviton and Gibbs (1988), except CUMZ refers to the Cornell Museum of Vertebrate Zoology and YFTC to the Yale Fish Tissue Collection. Meristic data and morphometric measurements were made as outlined in Hubbs and Lagler (1958) and Page (1974, 1981), except that the number of transverse scales were counted as described in Page (1983). Terminology for body pigmentation features follows Moenkhaus (1894), Stevenson (1971) and Morris and Page (1981). Specifically, regular vertical bars on the side of the body are those that are "relatively straight, even-edged and discrete" (Morris and Page 1981:96). Irregular bars are crooked, have edges that are not straight, and often connect with other bars. The number of whole and half vertical bars were counted from the occiput to the

hypural plate (Morris and Page 1981). Standard length (SL) and 17 other straight-line body measurements were taken on specimens with a SL greater than 55 mm using a needle point Paleo-Tech™ Hillson-FitzGerald dental caliper (http://www.paleo-tech.com).

Phylogenetic relationships among logperch species were estimated using DNA sequences from a nuclear gene (S7 ribosomal protein intron 1) and two mitochondrial encoded genes, cytochrome *b* (cyt*b*) and NADH subunit 2 (ND2). Genomic DNA was isolated from frozen or ethanol-fixed fin tissue using standard phenol–chloroform extraction followed by ethanol precipitation or using a protocol outlined in the Qiagen DNeasy® tissue kit (http://www1.qiagen.com/Products/). Extracted DNA was used as the template for the polymerase chain reaction technique (PCR) to amplify each target gene region with primer sequences reported in Chow and Hazama (1998), Near et al. (2000) and Kocher et al. (1995). Cycling conditions for PCR followed those used in Page et al. (2003). Amplification products resulting from successful PCR were prepared for sequencing with Qiagen QIAquick kits (http://www1.qiagen.com/Products/) or by digesting with 1.0 unit of Exonuclease I and shrimp alkaline phosphatase and incubated for 15 min at 37 °C and 20 min at 80 °C. Treated PCR products were used as the template for DNA sequencing done by the DNA Analysis Facility on Science Hill at Yale University or Yale's W. M. Keck Foundation Biotechnology Resource Laboratory. Contiguous sequences were assembled from individual sequencing reactions using the computer program Sequencher™, v. 4.5 (Gene Codes Corp. 2005). Gene sequences collected from *Percina peltata* and *P. roanoka* were used as outgroups in the phylogenetic analyses (Table 1).

The alignment of the cyt*b* and ND2 DNA sequences was done by eye, guided by the inferred amino acid sequences. The computer program MUSCLE was used to align the S7 ribosomal protein intron 1 DNA sequences (Edgar 2004). Partitioned mixed-model Bayesian analyses were used to generate phylogenetic trees from the aligned DNA sequences. The combined mtDNA and nuclear gene alignments, and the separate mtDNA and nuclear gene alignments were analyzed. Four data partitions were identified: three codon positions for the mtDNA protein coding genes and a single partition for the nuclear S7 intron. The optimal molecular evolutionary model for each partition was determined using Akaike Information Criteria in the computer program Modeltest, v. 3.0 (Posada and Crandall 1998, 2001, 2005). The optimal models were assigned to the appropriate data partitions in the computer program MrBayes 3.1 (Ronquist and Huelsenbeck 2003, 2005), and run for 10.0×10^6 generations with the burn-in period determined by graphically tracking the maximum likelihood scores to identify the generation where it reached a plateau. Trees and parameter values sampled before the burn-in were discarded. A Bayesian posterior probability greater than or equal to 0.95 was considered significant.

Taxonomy

Percina bimaculata Haldeman, 1844
Figure 1, Tables 3–10
Chesapeake Logperch, proposed common name

Percina bimaculata. Haldeman 1844:157 (meristic data, original description).

Perca (*Percina*) *nebulosa* (preoccupied by *Perca nebulosa* Rafinesque, 1814). Haldeman 1842:330 (meristic data on type specimen, species description).

Perca nebulosa. DeKay 1842:7 (meristic data on type specimen, distribution in Susquehanna); Jackson 1860:381 (distribution in Susquehanna).

Etheostoma nebulosa. Storer 1846:271 (meristic data on type specimen, distribution in Susquehanna).

Etheostoma bimaculata. Storer 1846:272 (meristic data, distribution in Susquehanna)

Percina nebulosa. Girard 1859:66 (distribution); Near and Benard 2004:2799-2800, figs. 1, 2, 3 (species status, distribution, phylogenetic relationships); Neely and George 2006:392 (distribution in Susquehanna).

Pileoma nebulosa. Vaillant 1873:51-52 (meristic data on type specimen, distribution in Susquehanna).

Pileoma bimaculata. Vaillant 1873:52 (meristic data, distribution in Susquehanna).

Percina caprodes. Jordan 1876:224 (synonymy); Uhler and Lugger 1876:114 (distribution in Potomac); Jordan 1877a:17 (synonymy); 1877b:312 (synonymy); Bean 1880:100 (distribution in Potomac); Jordan 1882:970-971 (synonymy); Jordan and Gilbert 1882:499-500 (synonymy); Boulenger 1895:57-58 (synonymy); Jordan and Evermann 1896–1900:1026-1027 (synonymy); Smith and Bean 1899:186 (distribution in Potomac); Fowler 1906:521 (synonymy, distribution in Maryland, status of type); Fowler 1907:18 (synonymy); Truitt et al. 1929:80 (distribution in Maryland); Jordan et al. 1930:282-283 (distribution, synonymy); Mansueti 1964:37 (distribution in Maryland); Stevenson 1971:66 (synonymy); Denoncourt and Cooper 1975:123 (distribution in

Table 2. Museum records of *Percina bimaculata* collections. Asterisks indicate specimens for which meristic data were provided by R. E. Jenkins. *Abbreviations:* ANSP, Academy of Natural Sciences, Philadelphia; CUMZ, Cornell Museum of Vertebrate Zoology; NCSM, North Carolina State Museum; USNM, Unites States National Museum; YPM, Yale Peabody Museum of Natural History.

Catalog number	Collecting date	Collecting locality	Number of specimens	Latitude, longitude
ANSP 22652	Prior to 1842	Susquehanna River, Pennsylvania	1	No data
USNM 9731	No data	Potomac River, Virginia	6	No data
USMN 1195 *	1855	Potomac River at Georgetown, District of Columbia	1	38°54′2.19″N, 77° 3′33.50″W
USNM 69745 *	June 1892	Potomac River above Long Branch, District of Columbia	1	38°50′25.40″N, 77° 1′51.20″W
USNM 68171 *	19 March 1898	Potomac River at Jackson Creek, Westmoreland Co., Virginia	1	38°6′22.03″N, 76°35′53.07″W
USNM 70715 *	9 June 1908	Potomac River, District of Columbia	1	No data
USNM 85400 *	2 July 1912	Potomac River at Bryan Point, Prince Georges Co., Maryland	1	38°41′43.22″N, 77° 3′58.28″W
USNM 85399 *	7 November 1912	Potomac River at Bryan Point, Prince Georges Co., Maryland	1	38°41′43.22″N, 77° 3′58.28″W
USNM 85729	10, 11 November 1912	Potomac River at Bryan Point, Prince Georges Co., Maryland	1	38°41′43.22″N, 77° 3′58.28″W
USNM 66329 *	6, 7 May 1919	Potomac River at Chain Bridge, District of Columbia	3	38°55′47.42″N, 77°06′58.57″W
USNM 89530 *	13 April 1930	Potomac River at Chain Bridge, District of Columbia	1	38°55′47.42″N, 77°06′58.57″W
UMMZ 158976 *	19 June 1949	Winters Run, 9 miles SW of Aberdeen, Harford Co., Maryland	6	39°26′15.92″N, 76°18′4.23″W
CUMZ 23465 *	14 August 1950	Northeast River, 2 miles N Havre Point, Cecil Co., Maryland	6	39°35’56.04″N, 75°56′46.31″W
CUMV 58388	5 July 1966	Susquehanna River 200 yards upstream from Fishing Creek, Lancaster Co., Pennsylvania	1	39°47′30.80″N, 76°16′4.11″W
CUMV 57855	7 July 1966	Susquehanna River 200 yards upstream from Fishing Creek, Lancaster Co., Pennsylvania	1	39°47′30.80″N, 76°16′4.11″W
CUMV 57499	10 July 1966	Fishing Creek, Lancaster Co., Pennsylvania	1	No data
CUMV 59545	9 August 1966	Susquehanna River 75 yards downstream from mouth of Fishing Creek, Lancaster Co., Pennsylvania	1	39°47′26.52″N, 76°15′56.01″W
CUMV 57833	10 August 1966	Susquehanna River, 200 feet off mouth, Peters Creek, Lancaster Co., Pennsylvania	1	39°45′22.86″N, 76°14′7.57″W
CUMV 58329	16 August 1966	Fishing Creek, Lancaster Co., Pennsylvania	1	39°47′29.49″N, 76°15′53.78″W
CUMV 57540	September 1966	Susquehanna River 230 yards out from mouth of Fishing Creek, Lancaster Co., Pennsylvania	1	39°47′25.39″N, 76°16′1.84″W
CUMV 57160	13 October 1966	Peach Bottom East, Lancaster Co., Pennsylvania	1	39°45′26.89″N, 76°14′11.27″W
CUMV 58496	27 March 1967	Fishing Creek, Lancaster Co., Pennsylvania	5	39°47′29.49″N, 76°15′53.78″W
CUMV 59629	13 May 1967	Fishing Creek, Lancaster Co., Pennsylvania	1	39°47′29.49″N, 76°15′53.78″W
CUMV 61155	1 June 1967	Muddy Creek, York Co., Pennsylvania	1	39°47′25.28″N, 76°17′56.84″W

Continued

Table 2 continued.

Catalog number	Collecting date	Collecting locality	Number of specimens	Latitude, longitude
CUMV 60296	11 July 1967	Peach Bottom Beach, Lancaster Co., Pennsylvania	4	39°45′26.89″N, 76°14′11.27″W
NCSM 8613	8 December 1967	Susquehanna River above Conowingo Creek, Cecil Co., Maryland	1	39°40′55.92″N, 76°11′49.92″W
YPM 15768	22 December 2006	Conowingo Creek, Cecil Co., Maryland	2	39°41′8.60″N, 76°11′37.07″W
YPM 16748	7 July 2007	Conowingo Creek, Cecil Co., Maryland	26	39°41′8.60″N, 76°11′37.07″W
YPM 17016	18 August 2007	Conowingo Creek, Cecil Co., Maryland	34	39°41′8.60″N, 76°11′37.07″W

Susquehanna); Lee et al. 1976:209 (distribution in Maryland); Lee et al. 1981:5, 6, 8 (distribution in Susquehanna and Potomac); Lee et al. 1984: figs. 2d, 10, 302 (distribution in Susquehanna and Potomac, illustration of specimen, distribution map); Page 1983:50 (synonymy, distribution); Rohde et al. 1994:198-200 (distribution); Starnes 2002:284, 315 (distribution in Potomac).

Etheostoma caprodes. Moenkhaus 1894:656 (synonymy).

Percina caprodes caprodes. Fowler 1945:134, fig. 202 (synonymy, distribution, illustration of *P. nebulosa* type specimen); Lee 1976:153, 156 (distribution in Potomac); Lee 1977:20 (distribution in Potomac).

Percina (*Percina*) *caprodes semifasciata.* Bailey and Gosline 1955:13, 36 (distribution, vertebral counts); Collette and Knapp 1966:56-57, 76 (synonymy, distribution, status of type); Böhlke 1984:138-139 (status of type).

Percina caprodes semifasciata. Jenkins et al. 1972:92-93 (distribution, relationship between Susquehanna and Potomac populations); Lee 1976:156, 157 (distribution in Susquehanna, illustration of a specimen); Lee 1977:19, 20 (distribution in Susquehanna, photograph of a specimen); Thompson 1980:719-720 (distribution, illustration of a specimen); Hocutt et al. 1986:171, 200 (distribution, relationship and origin of Susquehanna and Potomac populations); Jenkins and Burkhead 1994:790-791, map 162 (distribution); Thompson 1997a:2 (synonymy).

Type material. Haldeman (1844) described *Percina bimaculata* from the Susquehanna River in Pennsylvania. The type specimen (USNM 1405) is lost (Collette and Knapp 1966), but the specimen record indicates that it was collected at Columbia, Pennsylvania, USA, in Lancaster County. In accordance with recommendations presented in Article 75 of the International Code of Zoological Nomenclature (ICZN 1999), I decline to designate a neotype specimen, because the present investigation will clear up taxonomic confusion about *P. bimaculata*. Haldeman (1842) described *Perca* (*Percina*) *nebulosa* from the Susquehanna River in Pennsylvania; however, specific locality data are absent. Fowler (1906, 1945), Collette and Knapp (1966) and Böhlke (1984) listed ANSP 22652 as the type specimen. The type is a male with the SL measuring 109.4 mm (Figure 1A); other authors report the SL as 110 mm (Collette and Knapp 1966). Given the status of the *P. bimaculata* type specimen, the similarity of the *P. nebulosa* and *P. bimaculata* descriptions, and the brevity of both descriptions, they are both reproduced in their entirety. Haldeman's (1842:330) description of *P. nebulosa* reads:

> Perca (Percina) *nebulosa*. Body slender, slightly compressed; head and mouth small; dorsal fins separated; lateral line straight; scales small, and strongly serrated; tail truncated; pectoral fins very long; branchiostegous rays six. Yellowish brown, with irregular dark transverse bands. The fin rays are D 14+15: P 14: V 7: A 11: C 18. Length five and a half inches.

Two years later Haldeman (1844:157) described *P. bimaculata* with many features similar to thoses mentioned in the *P. nebulosa* description:

> Dr. Storer read extracts from a letter of Mr. S. S. Haldeman, as follows:—"I have a third undescribed species of Percina, from the Susquehanna, which may be characterized as follows.… P. bimaculata. Light yellow, sides transversely and irregularly branded with black, and dorsal fins clouded with brown, a distinct black spot at the extremity of the lateral line. Slender, lateral line sub-rectilinear, above the middle; ten or twelve irregular transverse bands upon the back and side; rays of second dorsal and caudal fins crossed by bands of dark brown. D. 15 — 15 : P. 13 : V.6 : A 11 : C 17. The length of the pectoral fins deserves mention as a generic character."

Material examined. Many museum records of *P. bimaculata* (Table 2) were unavailable for study because they were on loan to other researchers; however, R. E. Jenkins generously provided meristic data from most of the Potomac River collections (see Table 2).

Susquehanna River System—*Pennsylvania:* ANSP 22652 (1) Susquehanna River, specimen lacking detailed locality information. *Maryland:* Cecil County: YPM 15768 (2), Conowingo Creek at first riffle/cataract upstream of mouth (lat 39°41′8.60″N, long 76°11′37.07″W), 22 December 2006; YPM 16748 (26), same locality, 7 July 2007; YPM 17016 (34), same locality, 18 August 2007.

Etymology. The name *bimaculata* is Latin for "two spots," perhaps referring to the distinct caudal spot present on each

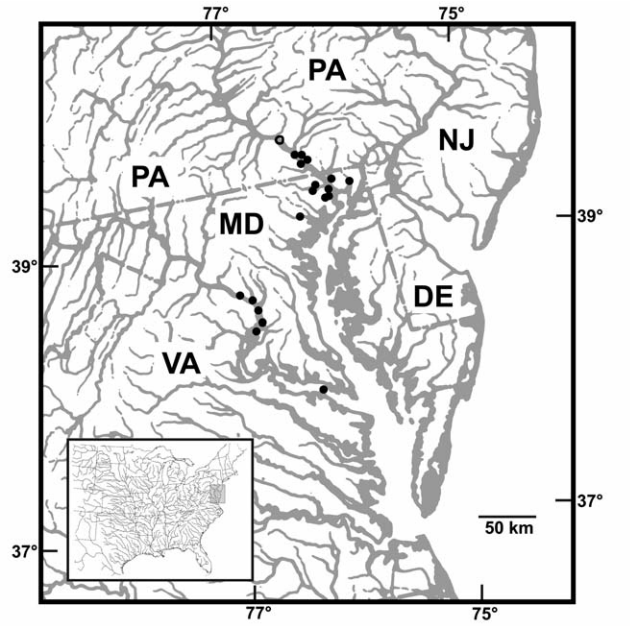


FIGURE 2. Localities where *Percina bimaculata* have been collected or observed. The open circle indicates the type locality.

side of the body. The proposed common name, Chesapeake Logperch, refers to the geographic region occupied by the species.

Diagnosis. A species in the *Percina caprodes* clade, as designated by Near (2002) and diagnosed morphologically by Page (1974). Specific characters include a conical snout that projects beyond the upper jaw and a large interorbital width. The *P. caprodes* clade contains *P. austroperca* Thompson, *P. bimaculata* Haldeman, *P. burtoni* Fowler, *P. caprodes* (Rafinesque), *P. carbonaria* (Baird and Girard), *P. fulvitaenia* Morris and Page, *P. jenkinsi* Thompson, *P. kathae* Thompson, *P. macrolepida* Stevenson, *P. rex* (Jordan and Evermann) and *P. suttksi* Thompson. *Percina bimaculata* is distinguished from all other species in the *Percina caprodes* clade by the following combination of characteristics: usually 7 to 11 irregular shaped lateral bars that extend down from the dorsum past the lateral line; lateral bars crossing the middle extent of the lateral line often anastomose on the mid-dorsum; narrow and faint orange-yellow submarginal band in the first dorsal fin of males and present but often diffuse in females (see Figure 1B, C); nape of adults naked; breast naked except for modified breast scales (Page 1976); supraoccipital and prepectoral naked, and no prepectoral blotch.

Percina c. caprodes has many more regular lateral bars (usually 19 or 20), higher scale counts, and narrow clear submarginal band in the first dorsal fin without orange-yellow color (Morris and Page 1981; Etnier and Starnes 1993). *P. c. semifasciata,* with which *P. bimaculata* (as *P. nebulosa*) had been considered a synonym, has a higher number of regular lateral bars (usually 20) and no submarginal orange-yellow band in the first dorsal fin (Morris and Page 1981). *Percina austroperca* has an entirely scaled nape, more than 12 regular lateral bars (half and whole bars), and higher scale and dorsal fin element counts (Thompson 1995; Boschung and Mayden 2004). *Percina burtoni* has a scaled prepectoral area, higher scale and fin element counts, and mid-lateral pigmentation of 7 to 9 round or oval blotches (Etnier and Starnes 1993; Jenkins and Burkhead 1994). *Percina carbonaria* has higher scale counts and more than 15 regular lateral bars (Morris and Page 1981). *Percina fulvitaenia* has an entirely scaled nape, a broad orange band in the first dorsal fin of adult males, higher scale counts, and usually 20 regular lateral pigment bars (Morris and Page 1981; Thompson 1997b). *Percina jenkinsi* lacks any coloration in the first dorsal fin, has higher scale and fin element counts, and an unscaled nape (Thompson 1985). *Percina kathae* has an entirely scaled nape, supraocipital, breast and prepectoral regions, higher scale counts, and more than 12 regular lateral pigment bars (Etnier and Starnes 1993; Thompson 1997a; Boschung and Mayden 2004). *Percina macrolepida* has no color pigmentation in the first dorsal fin, scales on the nape, supraocipital and breast regions, and more than 12 long narrow regular lateral pigment bars (Stevenson 1971). *Percina rex* has scales on the prepectoral region, higher scale counts, and lateral pigmentation consisting of short vertical bars centered below the lateral line and not extending over the dorsum (Jordan 1889; Morris and Page 1981; Jenkins and Burkhead 1994). *Percina suttkusi* has scales on the nape and prepectoral regions, slightly higher scale counts, and more than 12 regular lateral pigment bars (Thompson 1997b).

Description. A large darter species, it reaches a maximum size of 109 mm SL with an elongate body, but robust when compared to other species in the *Percina caprodes* clade. Fleshy

snout that overhangs the upper jaw and a broad frenum. The top of the head is broad and concave. Six branchiostegal rays with narrowly connected branchiostegal membranes. Cheek and opercle scaled. Nape, supraoccipital and prepectoral regions, and breast unscaled. A single midventral row of 16 to 28 modified scales in males. The midventral line in adult females is unscaled from the point posterior to the bases of the pelvic fins. Number of lateral line scales (pored and unpored) 67 to 82 (with a mean of 75.31; standard deviation is 3.38), 12 to 15 scales below the lateral line (usually 12 to 14), 2 anal-fin spines, 17 branched caudal-fin rays, 12 to 14 pectoral-fin rays (usually 13 to 14); see Tables 3 through 9 for frequency distributions of other scale and fin element counts. See Table 10 for proportional body measurements for the *P. nebulosa* holotype, adult male, and adult female *P. bimaculata* specimens.

With the exception of the first dorsal fin, the coloration and pigmentation differ slightly among males, females and juveniles. Information on pigmentation of breeding males is unavailable. The sides and dorsum have a light yellow-orange color and the belly has a hue of off-white or cream-yellow. Between the occiput and hypural plate there are usually 7 to 11 dark brown to black irregularly shaped vertical bars that extend over the dorsum. Towards the posterior of the body the vertical bars often are expanded below the lateral line, forming blotches that are usually connected to the bars. These blotches are more prominent in larger adult males (see Figure 1B). Pigmentation on the dorsum includes dark brown to black irregularly shaped bars that cross the dorsal mid-line. There are four dark dorsal saddles, similar to the "night saddles" described in *P. kathae* (Thompson 1997a). The four dark saddles are wider than the intervening lateral bars that cross the mid-line of the dorsum. The first saddle is immediately anterior to the origin of the first dorsal fin; the second saddle is located at the junction between the first and second dorsal fins; the third saddle is immediately posterior to the second dorsal fin; and the fourth saddle is posterior and close to the third saddle. A large black spot is present on the caudal fin base. The head is dark with diffuse pigment dorsally, and light ventrally. Black diffuse pigmentation forms preorbital and suboccular bars (see Figure 1B, C).

Pectoral, pelvic and anal fins have a clear light yellow-orange color and lack pigment in females. In males, the pectoral fin has a diffuse submarginal band of black pigmentation with a band of white color distally and the pelvic fins have diffuse dark pigmentation toward the distal edge. Second dorsal and caudal fins cream-yellow color with three to five bands formed by concentrations of black pigmentation on the fin rays. First dorsal fin with thin black distal band, narrow submarginal band of faint orange-yellow color that is more diffuse in females, and basal portion with irregular black pigmentation on the fin rays and membranes (see Figure 1B).

Sexual dimorphism is present in two of the proportional measurements examined. Mean values for males were significantly larger for snout length and anal fin length. No significant differences were detected among the other 12 measured characters (see Table 10).

Distribution. Specimens of *P. bimaculata* have been collected in the lower Susquehanna River basin in Pennsylvania and Maryland, USA. The Maryland Biological Stream Survey has determined that populations of *P. bimaculata* are present in Conowingo, Deer, Broad and Octoraro creeks. The species has also been collected in Winters Run and the Northeast River, which drain into the upper portion of the Chesapeake Bay in Maryland (see Figure 2 and Table 2). Before the 1930s, the species was present in the middle to lower Potomac River basin and was most frequently collected in the District of Columbia (see Figure 2 and Table 2). One of the more curious museum records for *P. bimaculata* is USNM 68171, a collection from March 1898 with "Jackson C. Virginia" as the only available locality data. Jackson Creek in Westmoreland County, Virginia, USA, drains into the lower portion of the Potomac and is the southernmost collection locality plotted in Figure 2.

Habitat. There is no published information on the habitat of *P. bimaculata*; however, all known collection records are from large river habitats or near the mouth of tributaries that drain into large rivers. It is assumed that the habitat preferences of *P. bimaculata* will be similar to that reported for other logperch darter species (Page 1983; Etnier and Starnes 1993; Jenkins and Burkhead 1994; Boschung and Mayden 2004).

Neely and George (2006) reported on a population of *P. bimaculata* in Conowingo Creek, Cecil County, Maryland, at the first riffle approximately 0.25 km upstream of the mouth where Conowingo Creek enters the Susquehanna River. The riffle has a steep gradient and is composed of large and small boulders with a bedrock substrate. *Percina bimaculata* specimens were found primarily in the runs and flowing pools, often associated with areas that contained large rocks and boulders.

Species captured with *P. bimaculata* at Conowingo Creek were Clupeidae: *Dorosoma cepedianum* (Lesueur); Cyprinidae: *Cyprinella analostana* Girard, *Luxilus cornutus* (Mitchill), *Nocomis micropogon* (Cope), *Notropis hudsonius* (Clinton), *Notropis procne* (Cope), *Notropis rubellus* (Agassiz), *Pimephales notatus* (Rafinesque), and *Rhinichthys atratulus* (Hermann); Catostomidae: *Hypentelium nigricans* (Lesueur) and *Moxostoma macrolepidotum* (Lesueur); Ictaluridae: *Ictalurus punctatus* (Rafinesque); Centrarchidae: *Ambloplites rupestris* (Rafinesque), *Lepomis macrochirus* Rafinesque, *Micropterus dolomieu* Lacepède and *Micropterus salmoides* (Lacepède); Percidae: *Etheostoma blennioides* Rafinesque, *Etheostoma olmstedi* Storer, *Etheostoma zonale* (Cope), *Percina peltata* (Stauffer), and *Sander vitreus* (Mitchill).

Molecular phylogeny. The mtDNA cyt*b* gene was 1140 base pairs (bp) and the ND2 gene was 1047 bp in all of the sampled specimens. The alignment of these gene regions did not require the insertion of any gaps. The aligned nuclear encoded S7 intron 1 was 524 bp, and all of the inferred indels occurred in four separate blocks that ranged from 2 to 9 bp. All but one of these blocks represented differences between logperch species, and *P. bimaculata, P. austroperca* and *P. caprodes* (*sans* upper Mississippi River Drainage populations) each had a unique indel block.

The phylogeny resulting from the Bayesian analysis of the S7 intron was mostly unresolved with the only node representing the most recent common ancestor of all logperches and the most recent common ancestor for several of the intraspecific nodes supported with significant posterior probabilities (tree not shown). Despite the lack of resolution in the nuclear gene

TABLE 3. Counts of pored lateral line scales in *Percina bimaculata.* The count for the *Percina nebulosa* holotype specimen is underlined. *Abbreviations:* N, number of specimens; SD, standard deviation.

	Number of pored lateral line scales																		
	66	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**74**	**75**	**76**	**77**	**78**	**79**	**80**	**81**	**N**	**Mean**	**SD**
Percina bimaculata Susquehanna	1	1	1	3	2	5	4	7	7	9	6	5	4	5		2	62	74.27	3.35
Percina bimaculata Potomac								2		2	1	1	3		1		10	76.30	2.31

TABLE 4. Counts of transverse scale rows in *Percina bimaculata.* The count for the *Percina nebulosa* holotype specimen is underlined. *Abbreviations:* N, number of specimens; SD, standard deviation.

	Number of transverse scales							
	21	**22**	**23**	**24**	**25**	**N**	**Mean**	**SD**
Percina bimaculata	3	28	23	7	1	62	22.60	0.82

TABLE 5. Counts of caudal-peduncle scale rows in *Percina bimaculata.* The count for the *Percina nebulosa* holotype specimen is underlined. *Abbreviations:* N, number of specimens; SD, standard deviation.

	Caudal peduncle scales									
	25	**26**	**27**	**28**	**29**	**30**	**31**	**N**	**Mean**	**SD**
Percina bimaculata Susquehanna	3	15	24	16	2	2		62	27.08	1.06
Percina bimaculata Potomac			1	1	3	1	1	7	29.00	1.29

TABLE 6. Counts of scales above the lateral line in *Percina bimaculata.* The count for the *Percina nebulosa* holotype specimen is underlined. *Abbreviations:* N, number of specimens; SD, standard deviation.

	Scales above lateral line					
	7	**8**	**9**	**N**	**Mean**	**SD**
Percina bimaculata Susquehanna	10	37	15	62	8.09	0.64
Percina bimaculata Potomac	2	6	2	10	8.00	0.67

TABLE 7. Counts of anal fin rays in *Percina bimaculata.* The count for the *Percina nebulosa* holotype specimen is underlined. *Abbreviations:* N, number of specimens; SD, standard deviation.

	Anal fin rays					
	9	**10**	**11**	**N**	**Mean**	**SD**
Percina bimaculata Susquehanna	2	41	19	62	10.27	0.52
Percina bimaculata Potomac	1	3	3	7	10.29	0.76

Table 8. Counts of dorsal fin spines in *Percina bimaculata*. The count for the *Percina nebulosa* holotype specimen is underlined. *Abbreviations:* N, number of specimens; SD, standard deviation.

	Dorsal fin spines					
	13	**14**	**15**	**N**	**Mean**	**SD**
Percina bimaculata Susquehanna	25	31	5	61	13.65	0.66
Percina bimaculata Potomac	2	4	1	7	13.29	0.69

Table 9. Counts of dorsal fin rays in *Percina bimaculata*. The count for the *Percina nebulosa* holotype specimen is underlined. *Abbreviations:* N, number of specimens; SD, standard deviation.

	Dorsal fin spines					
	14	**15**	**16**	**N**	**Mean**	**SD**
Percina bimaculata Susquehanna	14	37	11	62	14.95	0.64
Percina bimaculata Potomac	2	5	—	7	14.71	0.49

tree, no combination of *P. bimaculata* and *P. caprodes* was found as a clade in this phylogeny.

The phylogeny resulting from the combined mtDNA and S7 partitioned Bayesian analysis was very similar to the Bayesian mtDNA phylogeny (see Figure 3). As in a previous study using cyt*b* and ND2 (Near and Benard 2004), *P. bimaculata* (as *P. nebulosa*) was the sister species to a clade containing *P. austroperca* and *P. kathae,* and this node was supported with a significant Bayesian posterior probability (see Figure 3). Populations of *P. caprodes* sampled from the upper Mississippi River Basin in Illinois, Wisconsin and Minnesota formed a clade with a significant Bayesian posterior; however, this clade was not closely related to a clade of *P. caprodes* populations sampled from the Ohio, Tennessee, White and Hudson river drainages. These two clades of *P. caprodes* are separated on the phylogeny by three nodes, and two of these nodes are supported with a significant Bayesian posterior probability (see Figure 3).

Discussion

The logperches are a clade that has seen a dynamic and increasingly informed concept of species diversity in the group. From the late 19th century to 1971, two species were recognized (*Percina caprodes* and *P. rex*), and the increase to 11 recognized species over the past 30 years has come from both original species descriptions and taxonomic elevation of former synonyms or subspecies of *P. caprodes.* Knowledge of species diversity in the logperch clade is key to a more complete understanding of the biodiversity and biogeography of North American freshwater fishes, because the group has been the subject of several evolutionary studies. For instance, logperches were a component of a comparative phylogeographic study to investigate the importance of life history parameters on migration and gene flow (Turner et al. 1996); time-calibrated phylogenies of logperch species were used to investigate patterns of lineage diversification in the context of allopatric speciation (Near and Benard 2004); and an imperiled logperch species was the focus of a thorough phylogeographic analysis (George et al. 2006).

Although no type specimen is available for *P. bimaculata,* Haldeman (1844:157) described, quite precisely, the characteristic pigmentation of *P. bimaculata* as consisting of "irregular transverse bands upon the back and side" and a distinct black spot on the base of the caudal fin (see Figure 1B, C). Also, his meristic characters are consistent with those observed in specimens examined for the present study (see Tables 3–9). Considering the precise and accurate description of *P. bimaculata* provided by Haldeman (1844), there is no credible doubt that his communication refers to the Chesapeake Logperch, and no other ray-finned fish species in freshwater habitats of the Chesapeake Basin fits this description. Accordingly, there is no need to designate a neotype specimen (see Taxonomy, above, for elaboration).

Perhaps the most compelling evidence for the recognition of *P. bimaculata* as a distinct species comes from the results of the molecular phyloge-

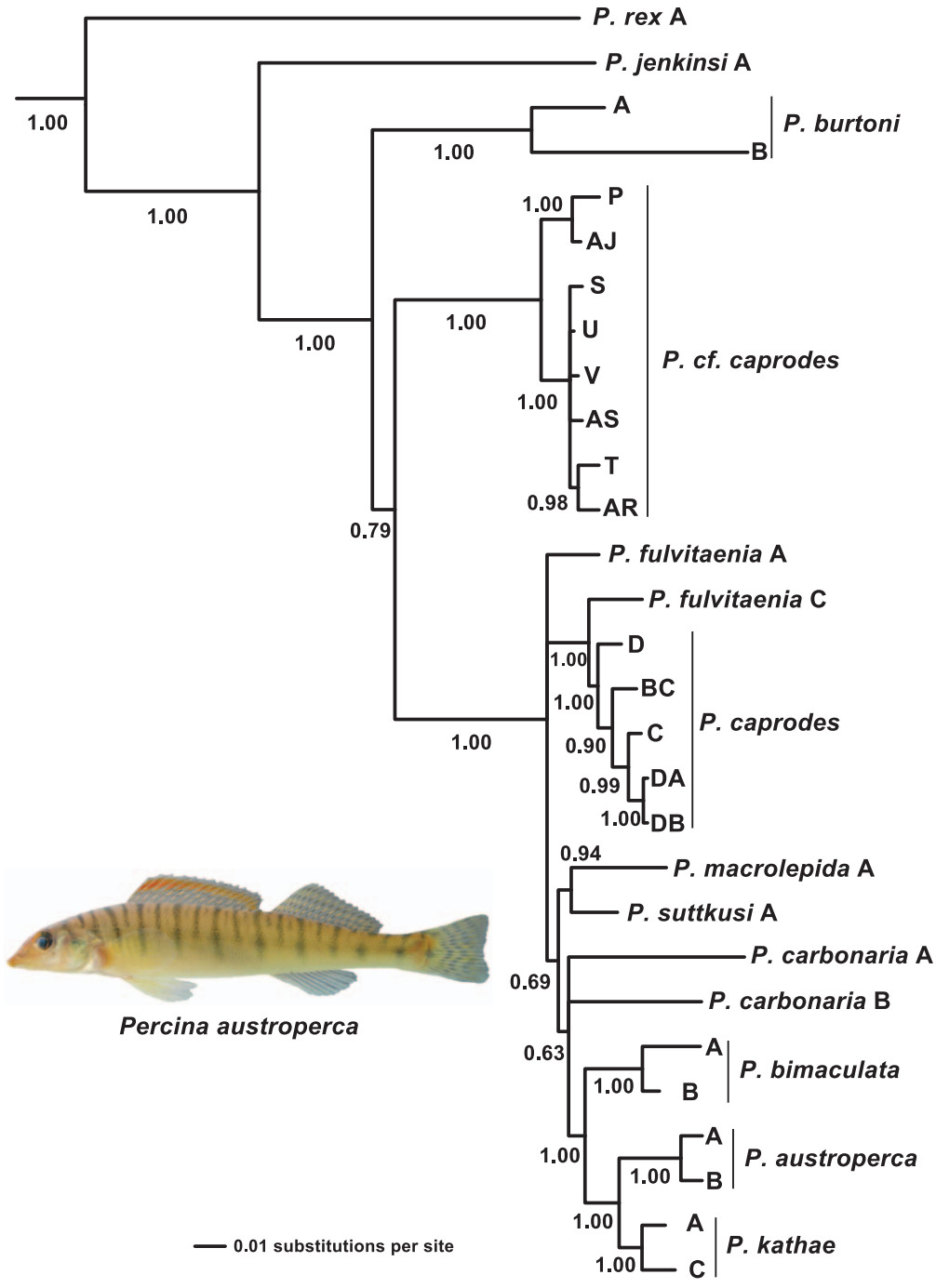


FIGURE 3. Phylogeny of logperches based on a combined-data partitioned Bayesian analysis of the mitochondrial cytochrome *b* and ND2 genes, and the nuclear encoded S7 ribosomal protein intron 1. Numbers at nodes are Bayesian posterior probabilities.

Table 10. Range of standard lengths and proportional measurements of the *Percina bimaculata* and *Percina nebulosa* holotype specimens, expressed as ratios of standard length, and t-test results (t) comparing male (not including holotype) and female specimens; significant p-values (*P*) are in bold.

		Males (14)		Females (10)			
Measurement (mm)	**Holotype**	**Mean**	**Range**	**Mean**	**Range**	**t**	***P***
Standard length	109.4	75.0	56.8–89.8	75.1	60.0–93.9	NA	NA
Head length	0.230	0.254	0.243–0.270	0.252	0.242–0.258	0.604	0.552
Head width	0.122	0.117	0.101–0.129	0.115	0.105–0.133	0.604	0.552
Snout length	0.079	0.074	0.064–0.087	0.069	0.061–0.078	2.152	**0.043**
Body depth	0.180	0.160	0.147–0.171	0.157	0.146–0.175	0.755	0.459
Predorsal length	0.341	0.318	0.301–0.333	0.316	0.301–.0329	0.502	0.621
Interorbital width	0.053	0.054	0.049–0.064	0.055	0.048–0.061	0.594	0.559
Gape width	0.053	0.054	0.046–0.065	0.055	0.048–0.060	0.523	0.606
Caudal–peduncle depth	0.089	0.082	0.077–0.088	0.080	0.077–0.085	1.610	0.122
Pectoral fin length	0.249	0.229	0.216–0.247	0.227	0.211–0.245	0.483	0.634
Second dorsal fin length	0.305	0.279	0.262–0.304	0.266	0.229–0.297	1.556	0.134
First dorsal fin base length	0.301	0.298	0.260–0.319	0.304	0.287–0.322	0.551	0.589
Second dorsal fin base length	0.189	0.229	0.206–0.242	0.216	0.196–0.228	1.743	0.095
Anal fin length	0.291	0.255	0.232–0.272	0.238	0.203–0.273	2.603	**0.016**
Pelvic fin length	0.207	0.229	0.216–0.247	0.227	0.211–0.245	0.427	0.674

netic analyses, in which taxa previously classified as *P. caprodes* (*P. bimaculata* and *P.* cf. *caprodes*) do not form monophyletic groups in the mitochondrial and nuclear gene trees (see Figure 3). In addition to these molecular phylogenetic results, examination of traditional morphological characters in *P. bimaculata* specimens reveals that they are distinct from *P. caprodes* or any other logperch species. There is broad overlap in meristic traits among many logperch species; however, a combination of meristic characters, patterns of squamation and unique pigmentation patterns provide an ample diagnosis for *P. bimaculata*.

Percina bimaculata is one of two darter species endemic to the Chesapeake Basin. The other species is *Etheostoma sellare* (Radcliffe and Welsh), the Maryland Darter, that historically was present in tributaries of the lower Susquehanna River (Knapp et al. 1963; Knapp 1976). The species has not been observed since 1989 and may be extinct (Neely et al. 2003). The historical occurrence of *P. bimaculata* in the Potomac and Susquehanna rivers and the shared distribution of two cyprinid species, *Campostoma anomalum* (Rafinesque) and *Notropis buccattus* (Cope), are consistent with a pattern that could have resulted from instances of downstream dispersal at a time when there could have been a connection between the lower Potomac and lower Susquehanna, or movement of fish populations between the two river systems could have been facilitated by stream capture between upper portions of the Potomac and Susquehanna basins (Lee 1976). Support for the hypothesis that conditions favoring dispersal among Chesapeake Basin tributaries have been present in the past comes from analysis of allozyme variation in the sculpin *Cottus caeruleomentum* that resulted in monophyly of the sampled Chesapeake Basin populations, including the Potomac and Susquehanna rivers (Kinziger et al. 2000).

There are valid concerns for the conservation of *P. bimaculata*. The species has not been collected in the Potomac River since the 1930s (see Figure 2 and Table 2), and Lee et al. (1984) state that the species has not been observed in the Potomac since 1938. This contrasts sharply with Smith and Bean's (1899:186) statement that the species is common "in gravely streams" that flow through the District of Columbia. The species has been sporadically collected in tributaries and the main stem of the lower Susquehanna River in

Maryland and Pennsylvania. The species, regarded as *P. caprodes,* has a conservation status of threatened in Maryland, but no conservation status in Pennsylvania or Virginia. In fact, the species is not recorded, even as *P. caprodes,* in Cooper's (1983) distributional study of Pennsylvania fishes. The lack of a sustained concern for the extirpation of *P. bimaculata* from the Potomac River and limited action from state and federal agencies are clearly the result of the species being considered a synonym of *P. caprodes* for over 130 years. *Percina bimaculata* is appropriately regarded as a species driven to obscurity by a taxonomic oversight. This status had removed the species from the working lexicon of ichthyologists and evolutionary biologists working with the diverse North American freshwater fish fauna, as well as appropriate governmental agencies that can initiate important protection and conservation measures. Given the restricted distribution of the species (see Figure 2) and the apparent extirpation from a substantial portion of its historical distribution, *P. bimaculata* would be a worthy candidate for protection under the United States Endangered Species Act of 1973.

Acknowledgments

Gregory Watkins-Cowell (Yale Peabody Museum of Natural History), Charles Dardia (Cornell University Museum of Vertebrates), Doug Nelson (University of Michigan Museum of Zoology) and Jeffery Williams (United States National Museum) provided assistance with museum collections. Robert E. Jenkins shared unpublished data. Christen M. Bossu, Rose L. Carlson, B. Jacob Kendrick, Evan M. McCartney-Melstead and Allison M. Near assisted with field work. Sally H. Pallatto assisted with the distribution map and Lawrence F. Gall provided editorial assistance. B. Jacob Kendrick coordinated collection of DNA sequence data. Bruce H. Bauer, G. R. Dinkins, David A. Etnier, Phillip R. Hollingsworth, Benjamin P. Keck, Lawrence M. Page and Wayne C. Starnes provided valuable discussion, advice and comments on earlier versions of the manuscript. Gerald R. Smith and three anonymous reviewers shared comments and suggestions that greatly improved the manuscript. The Division of Vertebrate Zoology at the Peabody Museum of Natural History, Yale University, and the National Science Foundation (DEB-0716155) supported this work.

Received 29 October 2007; revised and accepted 7 January 2008.

Literature Cited

Bailey, R. M. and W. A. Gosline. 1955. Variation and systematic significance of vertebral counts in the American fishes of the family Percidae. Miscellaneous Publications of the Museum of Zoology University of Michigan 93:1-44.

Bean, T. H. 1880. Check-list of duplicates of North American fishes distributed by the Smithsonian Institution in behalf of the United States National Museum, 1877–1880. Proceedings of the United States National Museum 3:75-116.

Benson, D. A., I. Karsch-Mizrachi, D. J. Lipman, J. Ostell and D. L. Wheeler. 2007 Jan. GenBank. Nucleic Acids Research 35:D21–D25. Published online 2006 December 5. doi: 10.1093/nar/gkl986.

Böhlke, E. B. 1984. Catalog of type specimens in the ichthyological collection of the Academy of Natural Sciences of Philadelphia. Academy of Natural Sciences of Philadelphia Special Publication 14:1-246.

Boschung, H. T. Jr. and R. L. Mayden. 2004. Fishes of Alabama. Washington, DC: Smithsonian Books. 736 pp.

Boulenger, G. A. 1895. Catalogue of the perciform fishes in the British Museum. London: Taylor and Francis. 394 pp.

Chow, S. and K. Hazama. 1998. Universal PCR primers for S7 ribosomal protein genes in fish. Molecular Ecology 7: 1255-1256.

Collette, B. B. and L. W. Knapp. 1966. Catalog of type specimens of the darters (Pisces, Percidae, Etheostomatini). Proceedings of the United States National Museum 119:1-88.

Cooper, E. L. 1983. Fishes of Pennsylvania and the Northeastern United States. University Park, PA: Pennsylvania State University Press. 243 pp.

DeKay, J. E. 1842. Natural History of New York. Part I, Zoology: Reptiles and Fishes. Albany, NY: W. & A. White and J. Visscher. 535 pp.

Denoncourt, R. F. and E. L. Cooper. 1975. A review of the literature and checklist of fishes of the Susquehanna River drainage above Conowingo Dam. Proceedings of the Pennsylvania Academy of Science 49:121-125.

Edgar, R. C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32(5):1792-1797. Available from: http://www.drive5.com/muscle/

Etnier, D. A. and W. C. Starnes. 1993. The Fishes of Tennessee. Knoxville, TN: University of Tennessee Press. 681 pp.

Fowler, H. W. 1906. Some new and little-known percoid fishes. Proceedings of the Academy of Natural Science Philadelphia 58:510-528.

—1907. Records of Pennsylvania fishes. American Naturalist 41:5-21.

—1945. A study of the fishes of the southern Piedmont and Coastal Plain. Monographs of the Academy of Natural Science of Philadelphia 7:1-408.

Gene Codes Corp. 2005. Sequencher [computer program]. Version 4.5. Ann Arbor, MI: Gene Codes Corporation. Available from: http://www.genecodes.com/

George, A. L., D. A. Neely and R. L. Mayden. 2006. Conservation genetics of an imperiled riverine fish from Eastern North America, the Blotchside Logperch, *Percina burtoni* (Teleostei: Percidae). Copeia 2006:585-594.

Girard, C. 1859. Ichthyological notices, 5-27. Proceedings of the Academy of Natural Science Philadelphia 11:56-68.

Haldeman, S. S. 1842. Description of two new species of the genus *Perca,* from the Susquehanna River. Proceedings of the Academy of Natural Science Philadelphia 8:330.

—1844. [*Percina bimaculata,* n. sp. from the Susquehanna]. Proceedings of the Boston Society of Natural History 1:157.

Hocutt, C. H., R. E. Jenkins and J. R. Stauffer Jr. 1986. Zoogeography of the fishes of the Central Appalachians and Central Atlantic Coastal Plain. In: C. H. Hocutt and E. O. Wiley, eds. The Zoogeography of North American Freshwater Fishes. New York: Wiley. pp. 161-211.

Hubbs, C. L. and K. F. Lagler. 1958. Fishes of the Great Lakes Region. Ann Arbor, MI: University of Michigan. 213 pp.

[ICZN] International Commission on Zoological Nomenclature. 1999. International Code of Zoological Nomenclature, 4th ed. London: The Natural History Museum, International Trust for Zoological Nomenclature. 306 pp.

Jackson, R. M. S. 1860. The Mountain. Philadelphia: Lippincott. 632 pp.

Jenkins, R. E. and N. M. Burkhead. 1994. Freshwater Fishes of Virginia. Bethesda: American Fisheries Society. 983 pp.

Jenkins, R. E., E. A. Lachner and F. J. Schwartz. 1972. Fishes of the Central Appalachian drainages: their distribution and dispersal. In: P. C. Holt, ed. The Distributional History of the Biota of the Southern Appalachians. Part 3, Vertebrates. Blacksburg, VA: Virginia Polytechnic Institute and State University. pp. 43-117. (Research Division Monograph 4).

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. Chicago: Jansen, McClurg. 342 pp.

—1877a. Contributions to North American ichthyology. II, Notes on Cottidae, Etheostomatidae, Percidae, Centrarchidae, Aphredoderidae, Umbridae, Esocidae, Dorysomatidae, and Cyprinidae with revisions of genera and descriptions of new or little known species. Bulletin of the United States National Museum 9:1-53.

—1877b. A partial synopsis of the fishes of upper Georgia. Annals of the New York Lyceum of Natural History 11:307-369.

—1882. Report on the fishes of Ohio. Geological Survey of Ohio 4:738-1002.

—1889. Descriptions of fourteen species of fresh-water fishes collected by the U.S. Fish Commission in the summer of 1888. Proceedings of the United States National Museum 11:351-362.

Jordan, D. S. and B. W. Evermann. 1896–1900. 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. Bulletin of the United States National Museum 47(1-4):1-3136.

Jordan, D. S., B. W. Evermann and H. W. Clark. 1930. Check list of the fishes and fish-like vertebrates of North and Middle America north of the northern boundary of Venezuela and Columbia. Appendix X to the Report of the United States Commission of Fish and Fisheries for 1928. Washington, DC: Government Printing Office. 670 pp.

Jordan, D. S. and C. H. Gilbert. 1882. Synopsis of the Fishes of North America. Bulletin of the United States National Museum 16:1-1018. (Smithsonian Miscellaneous Collections 24, 1883).

Kinziger, A. P., R. L. Raesly and D. A. Neely. 2000. New species of *Cottus* (Teleostei: Cottidae) from the middle Atlantic eastern United States. Copeia 2000:1007-1018.

Knapp, L. W. 1976. Redescription, relationships and status of the Maryland darter, *Etheostoma sellare* (Radcliffe and Welsh), an endangered species. Proceedings of the Biological Society of Washington 89:99-117.

Knapp, L. W., W. J. Richards, R. V. Miller and N. R. Foster. 1963. Rediscovery of the percid fish *Etheostoma sellare* (Radcliffe and Welch). Copeia 1963:455.

Kocher, T. D., J. A. Conroy, K. R. McKaye, J. J. R. Stauffer and S. F. Lockwook. 1995. Evolution of NADH dehydrogenase subunit 2 in East African cichlid fish. Molecular Phylogenetics and Evolution 4:420-432.

Lee, D. S. 1976. Aquatic zoogeography of Maryland. Atlantic Naturalist 31:147-158.

—1977. The darters of Maryland. Maryland Conservationist 53:18-23.

Lee, D. S., A. Norden, C. R. Gilbert and R. Franz. 1976. A list of the freshwater fishes of Maryland and Delaware. Chesapeake Science 17:205-211.

Lee, D. S., S. P. Platania, C. R. Gilbert, R. Franz and A. Norden. 1981. A revised list of freshwater fishes of Maryland and Delaware. Southeastern Fishes Council Proceedings 3:1-10.

Lee, D. S., S. P. Platania, A. W. Norden, C. R. Gilbert and R. Franz. 1984. Endangered, threatened, and extirpated freshwater fishes of Maryland. In: A. W. Norden, D. C. Forester and G. H. Fenwick, eds. Threatened and Endangered Plants and Animals of Maryland. Annapolis, MD: Maryland Department of Natural Resources. pp. 287-328.

Leviton, A. E. and R. H. Gibbs Jr. 1988. Standards in herpetology and ichthyology. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Supplement no. 1: additions and corrections. Copeia 1988(1):280-282.

Leviton, A. E., R. H. Gibbs Jr., E. Heal and C. E. Dawson. 1985. Standards in herpetology and ichthyology: part 1, standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985(3): 802-832.

Mansueti, R. J. 1964. Eggs, larvae, and young of the white perch, *Roccus americanus,* with comments on its ecology in the estuary. Chesapeake Science 5:3-45.

Moenkhaus, W. J. 1894. Variation of North American fishes. I. The variation of *Etheostoma caprodes* Rafinesque. American Naturalist 28:641-660.

Mombert, J. I. 1869. An Authentic History of Lancaster County in the State of Pennsylvania. Lancaster, PA: J. E. Barr. 617 pp.

Morris, M. A. and L. M. Page. 1981. Variation in western logperches (Pisces: Percidae) with description of a new subspecies from the Ozarks. Copeia 1981:95-108.

[NCBI] National Center for Biotechnology Information. 2007. GenBank® [online database]. Bethesda, MD: National Library of Medicine, National Center for Biotechnology Information. Available at: http://www.ncbi.nlm.nih.gov/Genbank/

Near, T. J. 2002. Phylogenetic relationships of *Percina* (Percidae: Etheostomatinae). Copeia 2002:1-14.

Near, T. J. and M. F. Benard. 2004. Rapid allopatric speciation in logperch darters (Percidae: *Percina*). Evolution 58:2798-2808.

Near, T. J., J. C. Porterfield and L. M. Page. 2000. Evolution of cytochrome *b* and the molecular systematics of *Ammocrypta* (Percidae: Etheostomatinae). Copeia 2000: 701-711.

Neely, D. A. and A. L. George. 2006. Range extensions and rapid dispersal of *Etheostoma blennioides* (Teleostei: Percidae) in the Susquehanna River drainage. Northeastern Naturalist 13:391-402.

Neely, D. A., A. E. Hunter and R. L. Mayden. 2003. Threatened fishes of the world: *Etheostoma sellare* (Radcliffe & Welsh) 1913 (Percidae). Environmental Biology of Fishes 67:340.

Page, L. M. 1974. The subgenera of *Percina*. Copeia 1974: 66-86.

—1976. The modified midventral scales of *Percina* (Osteichthyes; Percidae). Journal of Morphology 148:255-264.

—1981. The genera and subgenera of darters (Percidae, Etheostomatini). Occasional Papers of the Museum of Natural History the University of Kansas 90:1-69.

—1983. Handbook of Darters. Neptune City, NJ: T. F. H. Publications. 271 pp.

Page, L. M., M. Hardman and T. J. Near. 2003. Phylogenetic relationships of barcheek darters (Percidae: Etheostoma, subgenus *Catonotus*) with descriptions of two new species. Copeia 2003:512-530.

Posada, D. and K. A. Crandall. 1998. Modeltest: testing the model of DNA substitution. Bioinformatics 14:817-818.

—2001. Selecting the best-fit model of nucleotide substitution. Systematic Biology 50:580-601.

—2005. Modeltest [computer program]. Version 3.7. Vigo, Spain: Distributed by the authors. Available from: http://darwin.uvigo.es/software/modeltest.html

Rafinesque, C. S. 1814. Précis des découvertes et travaux somiologiques. Palerme: Published by the author. 55 pp.

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

Ronquist, F. and J. P. Huelsenbeck. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572-1574.

—2005. MrBayes: Bayesian Analysis of Phylogeny [computer program]. Version 3.1. Talahassee, FL: Florida State University. Available from: http://mrbayes.csit.fsu.edu/

Smith, C. L. 1985. The inland fishes of New York State. Albany, NY: New York State Department of Environmental Conservation. 522 pp.

Smith, H. M. and B. A. Bean. 1899. List of fishes known to inhabit the waters of the District of Columbia and vicinity. Bulletin of the United States Fish Commission 18:179-187.

Starnes, W. C. 2002. Current diversity, historical analysis, and biotic integrity of fishes in the lower Potomac basin in the vicinity of Plummers Island, Maryland — Contribution to the natural history of Plummers Island, Maryland XXVII. Proceedings of the Biological Society of Washington 115:273-320.

Stevenson, M. M. 1971. *Percina macrolepida* (Pisces, Percidae, Etheostomatinae), a new percid fish of the subgenus *Percina* from Texas. Southwestern Naturalist 16:65-83.

Storer, J. E. 1846. A synopsis of the fishes of North America. Memoirs of the American Academy of Arts and Sciences 2: 253-550.

Thompson, B. A. 1980. *Percina caprodes,* logperch. In: D. S. Lee, C. R. Gilbert, C. H. Hocutt, et al., eds. Atlas of North American Freshwater Fishes. Raleigh, NC: North Carolina State Museum. pp. 719-720.

—1985. *Percina jenkinsi,* a new species of logperch (Pisces, Percidae) from the Conasauga River, Tennessee and Georgia. Occasional Papers of the Museum of Zoology Louisiana State University 61:1-23.

—1995. *Percina austroperca*: a new species of logperch (Percidae, subgenus *Percina*) from the Choctawhatchee and Escambia Rivers in Alabama and Florida. Occasional Papers of the Museum of Natural Science Louisiana State University 69:1-19.

—1997a. *Percina kathae,* a new logperch endemic to the Mobile Basin in Mississippi, Alabama, Georgia, and Tennessee (Percidae, Etheostomatini). Occasional Papers of the Museum of Natural Science Louisiana State University 73:1-34.

—1997b. *Percina suttkusi,* a new species of logperch (subgenus *Percina*) from Louisiana, Mississippi, and Alabama (Perciformes, Percidae, Etheostomatini). Occasional Papers of the Museum of Natural Science Louisiana State University 72:1-27.

Truitt, R. V., B. A. Bean and H. W. Fowler. 1929. The fishes of Maryland. Maryland Conservation Bulletin 3:1-120.

Turner, T. F., J. C. Trexler, D. N. Kuhn and H. W. Robison. 1996. Life-history variation and comparative phylogeography of darters (Pisces: Percidae) from the North American central highlands. Evolution 50:2023-2036.

Uhler, P. R. and O. Lugger. 1876. List of the fishes of Maryland. Report of the Commissioners of Fisheries of Maryland 1876:67-176.

Vaillant, L. 1873. Recherches sur les poissons des eaux douces de l'Amerique septentrionale. Nouvelles Archives du Museum Natural Paris 9:1-154.