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A new species of *Percina* (Perciformes: Percidae) from the Apalachicola River drainage, southeastern United States

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Abstract

Percina crypta, the Halloween Darter, is described as a new species endemic to the Chattahoochee and Flint River systems in Georgia and Alabama. *Percina crypta* differs from sympatric *Percina nigrofasciata* in having narrowly separated dorsal saddles (inter-saddle spaces typically less than or equal to saddle width, compared to frequently wider than saddle width in *P. nigrofasciata*), in usually possessing a single modified scale between the pelvic bases (compared to two or more in *P. nigrofasciata*), and in having dark wide bands on pectoral-fin rays (versus pectoral fin clear, or with irregular dark marks or weak tessellations on fin rays in *P. nigrofasciata*). Phylogenetic relationships of *P. crypta* to other species of *Percina* are obscure. *Percina crypta* occurs in shoal and riffle habitats in the Chattahoochee and Flint River mainstems and in a few tributary systems, with the known extant range comprising four disjunct areas separated by mainstem impoundments and altered river reaches.

Key words: *Percina crypta*, *Percina nigrofasciata*, Chattahoochee River, Flint River, Halloween Darter, Blackbanded Darter

Introduction

Historically, only a single species of the genus *Percina*, *P. nigrofasciata* (Agassiz), has been reported from the Apalachicola River drainage, Georgia, Alabama and Florida, USA. Herein we describe a new species of *Percina*, endemic to the Chattahoochee and Flint River systems of the Apalachicola River drainage. The new species is sympatric with *P. nigrofasciata*, which it cryptically resembles and with which it is often collected.

Percina nigrofasciata, the Blackbanded Darter, occurs in Atlantic Coast drainages from the Edisto River in South Carolina to peninsular Florida and on the eastern Gulf Coast from the Suwannee River westward to Thompson Creek, an eastern tributary of the Mississippi River, in Mississippi and Louisiana (Crawford 1956; Guillory 1976). Across its range, *P. nigrofasciata* occurs in a variety of flowing-water habitats including small tributaries and larger rivers in the Blue Ridge, Piedmont and Coastal Plain physiographic provinces (Crawford 1956; Boschung & Mayden 2004). The species also is notably variable in pigmentation, particularly in the number and elongation of the vertical lateral bars that give the species its common name.

Noting variability in appearances and habitats occupied, Ronald W. Crawford examined geographic variation in meristic and morphometric characters of *P. nigrofasciata* in the 1950's. Crawford (1956) recognized two subspecies: *P. nigrofasciata raneyi*, restricted to the Savannah River drainage above the Fall Line, Georgia and South Carolina, and *P. nigrofasciata nigrofasciata*, regarded as eight geographic races based on modal

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variation in meristics and body proportions. Crawford synonymized *P. nigrofasciata westfalli*, a subspecies described by Henry W. Fowler (Fowler 1942) from the St. Johns River drainage in Florida, for lack of diagnostic differences in counts or measurements from other populations. However, Crawford's "races" of *P. nigrofasciata nigrofasciata* broadly overlapped in most counts and measurements. Crawford did not note consistent differences in pigmentation among specimens from different systems, although he did describe males from the "Apalachicola Bay race" as often having more block-shaped lateral bars.

Ichthyologists have since noted that *P. nigrofasciata* in the Apalachicola River drainage often have more blocky lateral markings compared to specimens from other drainages (David A. Etnier, personal communication). We (MCF and BJF) first encountered *P. crypta* in 1990 in Ichawaynochaway Creek, a tributary of the lower Flint River, Georgia. Although confident that we were collecting two *Percina* species while in the stream, including one with atypical orange color in the dorsal fins, we were initially unable to sort preserved specimens into groups with coherent morphological differences. After placing prenuptial males and females of both forms in an 1800-L circulating laboratory tank, we observed frequent social interactions between males and females in pairs, and noted that interacting individuals shared one of two patterns of dorsal pigmentation. We subsequently sorted collected specimens according to relative width of the dorsal saddles, and this allowed us to identify a suite of diagnostic characters separating the two species. Substantial variation in the pigmentation and shape of lateral bars among *P. nigrofasciata* individuals, even of the same sex and similar size, has likely confounded discovery of *P. crypta* and allowed the new species to remain virtually obscure.

Material and methods

Institutional abbreviations follow Leviton *et al.* (1985) and Leviton and Gibbs (1988), except for Georgia Museum of Natural History (GMNH). We examined collections of *Percina* from the Apalachicola River drainage accessioned at Auburn University (AUM), Cornell University (CU), Florida Museum of Natural History, University of Florida (UF), Georgia Museum of Natural History, Illinois Natural History Survey (INHS), Tulane University (TU), University of Alabama (UAIC), University of Tennessee (UT), and the National Museum of Natural History (USNM) for specimens of *P. crypta*. Locations (n=734; Fig. 1) for all examined collections and occurrences of *P. crypta* were geo-referenced using USGS 7.5 minute quad maps and entered into a Geographic Information System maintained by GMNH at the University of Georgia.

Counts and measurements followed Hubbs and Lagler (1958) except for the following. Transverse-body scales were counted from the origin of the anal fin diagonally upward to the base of the first-dorsal fin. Body depth was measured at origin of the first-dorsal fin. Body width was measured at the widest part of the body. Transpelvic width was measured across the outer bases of the pelvic spines (Suttkus & Etnier 1991). Mandible-gill membrane distance was measured from the tip of the mandible to the union of the branchiostegal membranes (Richards & Knapp 1964). Vertebral counts, including the urostyle, were made from cleared and stained specimens. Measurements were made with electronic needle-point calipers and recorded to the nearest 0.01 mm. Terms and definitions of pigmentation patterns are from Jenkins and Burkhead (1994); unless stated otherwise, pigment descriptions refer to melanophore patterns.

Meristic and proportional measurements were summarized for specimens from four geographically separated portions of the species' range (Fig. 1): upper Chattahoochee River (upstream from Lake Lanier, Georgia); Uchee Creek (counts only), an Alabama tributary to the middle Chattahoochee River; the upper Flint River system (Georgia, upstream from the Fall Line), and the lower Flint River system in the Coastal Plain of Georgia (and downstream from Lake Blackshear, a Flint River impoundment). For comparison, we summarized counts for specimens of *P. nigrofasciata* from the lower Flint River system, and also examined count frequencies reported by Crawford (1956) for the Apalachicola (including the Chattahoochee) and Flint systems.

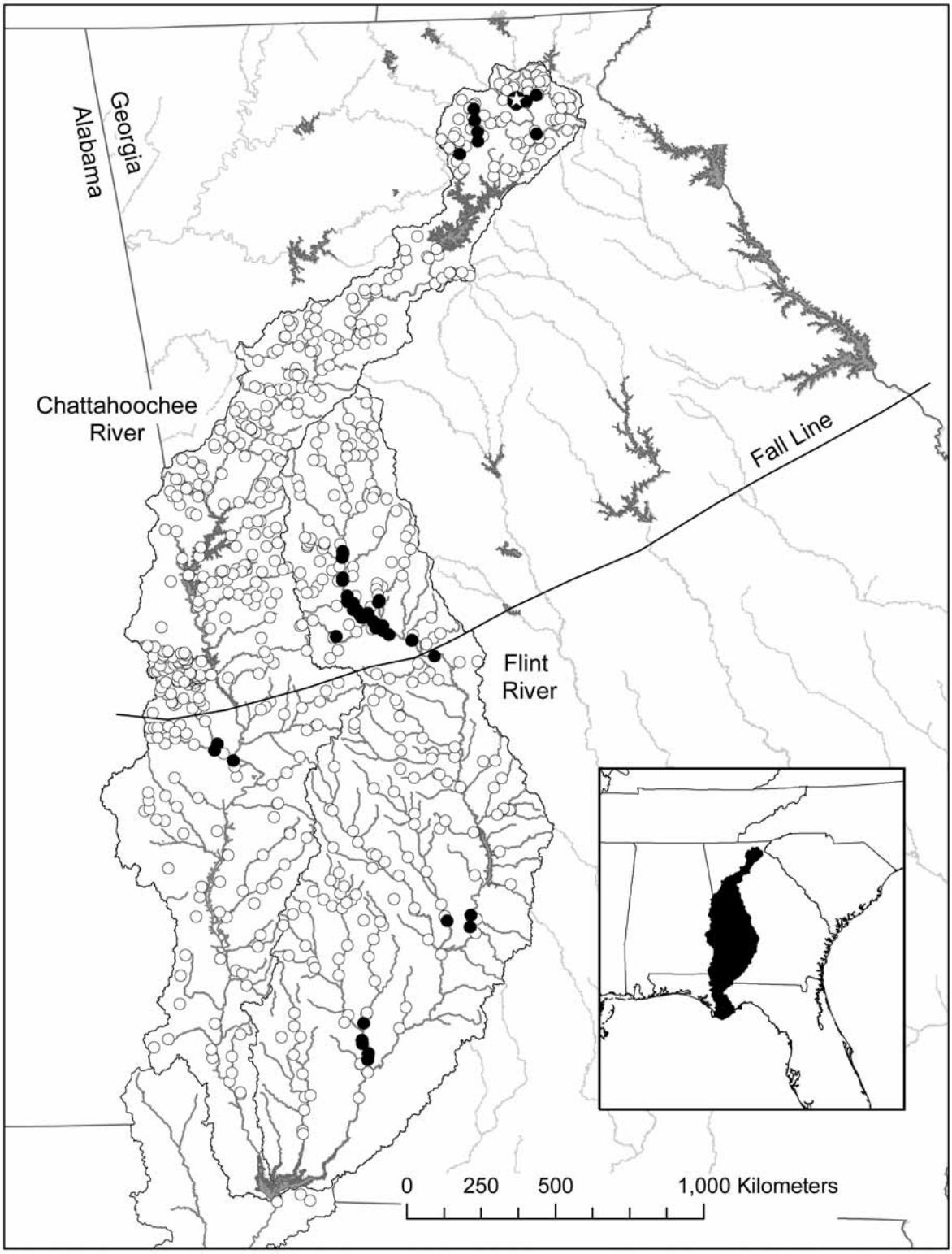

FIGURE 1. Distribution of *Percina crypta* (closed circles), Chattahoochee and Flint River systems, Apalachicola River drainage (inset), USA. Type locality indicated with a star. Circles indicate examined collections of *Percina*. *Percina nigrofasciata* is known from all plotted localities; *P. crypta* has been found only at the localities marked with closed circles.

We analyzed morphometric variation among specimens of *P. crypta* from the upper Chattahoochee River and the two portions of the Flint River system, and *P. nigrofasciata* from the lower Flint River system, using

sheared principal components analysis (Humphries *et al.* 1981) in SAS system software (program by D. Swofford; Bookstein *et al.* 1985). Data for males and females were analyzed separately. Scores on the second and third sheared principal components, which represent shape factors free from influence of size, were plotted for individual specimens and inspected for multivariate differences among *P. crypta* corresponding to geographic area, and between *P. crypta* and *P. nigrofasciata*. Measurements are standard length (SL) unless otherwise noted.

***Percina crypta*, Freeman, Freeman & Burkhead, new species**
Halloween Darter
(Fig. 2A and 2B)

Holotype. GMNH 21606, male, 69.7 mm SL, Georgia, White County, Chattahoochee River at GA Hwy 17/75 at Nacoochee, Georgia (Nora Mill), 11.1 air km NNE Cleveland, 17 May 1994, B. J. Freeman, J. Devivo, J. W. Garrett, M. J. Zieg, R. E. Jenkins, J. S. Boyce, L. M. Hartle, M. Flood.

Paratopotypes. GMNH 21610 (18; 48–73 mm), Collected with the holotype. GMNH 21578 (11; 52–72 mm), 5 April 2000; TU 200399 (4; 55–66 mm) same data as GMNH 21578; USNM 393568 (4, 58–64 mm) same data as GMNH 21578.

Paratypes. Georgia: Lumpkin County: GMNH 21607 (1; 58 mm) Chestatee River at and alongside GA Hwy 60, 3.7 km S of Dahlonega, 30 October 1996; GMNH 21602 (106; 29–76 mm) Chestatee River at County Route 41, 8.8 km E of Dahlonega, 13 November 1996; UAIC 15066.01 (5, 41–74 mm) same data as GMNH 21602; AUM 47715 (5, 46–58 mm) same data as GMNH 21602; UT 91.7859 (5, 40–69 mm) same data as GMNH 21602; GMNH 21603 (21; 26–85 mm) Chestatee River upstream of County Route 190, 10.3 km NE of Dahlonega, 13 November 1996; UF 172181 (4, 39–72 mm) same data as GMNH 21603; CU 94240 (4, 39–66 mm) same data as GMNH 21603; GMNH 21604 (3; 47–64 mm) Chestatee River at Turners Corner, junction of US Hwys19 and 129, 14.8 km NE of Dahlonega, 16 November 1996; GMNH 21605 (11; 49–65 mm) Chestatee River at County Route134, 16 November 1996;. **White/Habersham counties:** GMNH 21580 (11; 30–68 mm) Chattahoochee River at GA Hwy 115, 14 September 1996; GMNH 21596 (7; 33–42 mm) Chattahoochee River between GA Hwys 115 and 384, 13 October 1996; GMNH 21608 (56, 37–82 mm) Chattahoochee River 1.6 km downstream GA Hwy 115, 24 October 1963. **White County:** GMNH 21588 (6; 52–65 mm) Sautee Creek at GA Hwy 255, 14 September 1996.

Additional material examined (nontypes).

Upper Flint River system, Georgia: Meriwether/Pike counties: AUM 6635 (12) Flint River, 6.4 km ESE of Gay, hardtop road, 18 March 1971. AUM 24790 (1) Flint River between Flat Shoals and GA Hwy 18 (R.M. 280), W of Molena, 21 June 1984. **Meriwether/Upson counties:** AUM 24799 (319) Flint River 17.1 km WNW of Thomaston at Pleasant Valley (R.M. 270), 13 June 1984. **Upson County:** AUM 6959 (11) Potato Creek at State Rt. 36, 11 September 1971; TU 27520 (25) same locality, 23 April 1962; GMNH 21554 (92) Potato Creek between GA Hwys 74 and 36, 4.3 km W of Thomaston, 25 June 1994; GMNH 21553 (11) same locality, 27 May 1994. **Upson/Talbot counties:** GMNH 22061 (2) Flint River at Sprewell Bluff State Park, 15 km W of Thomaston, 1 July 2002; AUM 6903 (7) Flint River at Adam's Island, 3.4 km W of mouth of Potato Creek, 13.7 km SSW of Thomaston, 17 June 1971; AUM 24802 (3) Flint River 12.9 km SSW of Thomaston, 1.6 km below Pobiddy Bridge, 20 June 1984; AUM 6882 (7) Flint River at Pasley Shoal, 14.5 km W of Thomaston, 16 June 1971; AUM 17272 (4) Flint River ca. 5 km below GA Hwy 36, 9.2 km E of Pleasant Hill, 25 June 1978; AUM 24789 (269) Flint River 11.7 km WSW of Thomaston, above GA Hwy 36 (R.M. 260), 12 June 1984; AUM 6966 (4) Flint River, 10 km SW of Thomaston, GA Hwy 36, 14 September 1971; GMNH 21555 (4) Flint River at Big Lazer WMA, 28 April 1995. **Talbot County:** GMNH 21556 (14) Lazer Creek at GA Hwy 36, 17 September 2001. **Taylor/Upson counties:** AUM 24815 (1) Flint River 18.5 km SSE

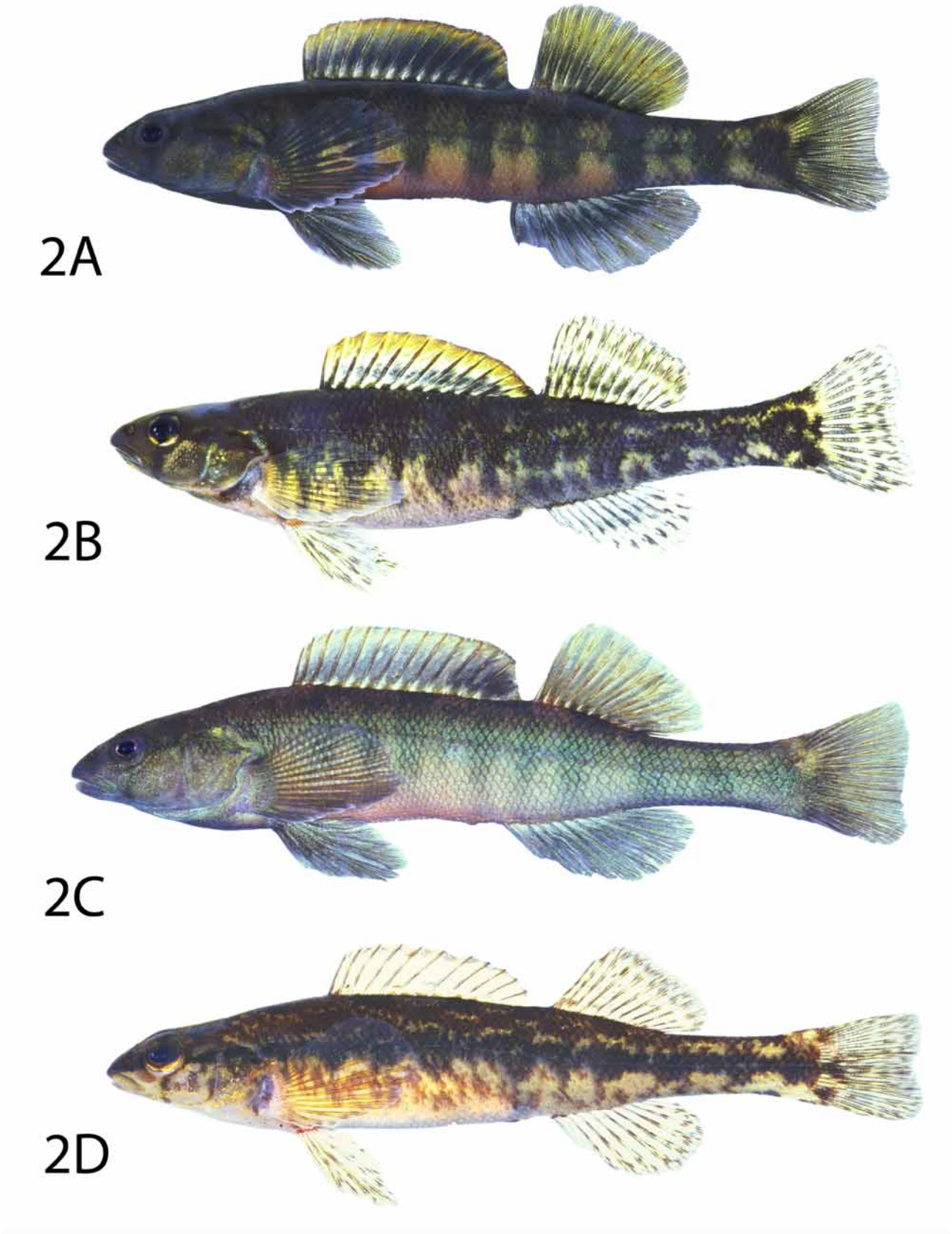

FIGURE 2. Nuptial adults of *Percina crypta* and *Percina nigrofasciata*. A: *P. crypta* male, 68 mm SL; B: *P. crypta* female, 65 mm SL; C: *P. nigrofasciata* male, 77 mm SL; D: *P. nigrofasciata* female, 66 mm SL. Chattahoochee River at GA Hwy 17/75 at Nacoochee, White County, Georgia, 5 April 2000; except *P. crypta* female: Chickasawhatchee Creek (Lower Flint River system) at GA Hwy 37, Baker County, Georgia, 3 April 2000. Photos by NMB.

of Thomaston, 2.4 and 10.5 km above US Hwy 80 (R.M. 240), 26 June 1984; **Taylor/Crawford counties:** AUM 24829 (1) Flint River 21.2 km NNW of Reynolds, 3.2 km above GA Hwy 128 (RM 230), 19 June 1984.

Lower Flint River system, Georgia: Baker County: GMNH 13418 (24) Ichawaynochaway Creek immediately downstream of dam at upstream boundary of J. E. Jones Ecological Research Center Property, 18 October 1990; GMNH 21568 (4) same locality, 7 January 2000; GMNH 21569 (2) & GMNH 21570 (2) same locality, 16 June 2000; GMNH 13430 (2) Ichawaynochaway Creek 4 km N GA Hwy 91, 16 October 1990; GMNH 13470 (17) Ichawaynochaway Creek downstream from County Route 25, 0.3 km NE of GA Hwy 91 crossing, 18 October 1990; GMNH 13483 (7) Ichawaynochaway Creek, first shoal immediately upstream from GA Hwy 200 crossing, 19 October 1990; GMNH 14174 (3) same locality, 6 December 1991; GMNH 14225 (34) Chickasawhatchee Creek at GA Hwy 37, 5 December 1991; GMNH 14250 (17) same locality, 7 May 1992; GMNH 14275 (15) same locality, 18 May 1992; GMNH 21567 (8) same locality, 26 April 1995; GMNH 21572 (1) same locality, 3 April 2000; GMNH 14262 (2) Ichawaynochaway Creek between dam at upstream boundary of J. E. Jones Ecological Research Center Property and GA Hwy 200, 8 April 1992. **Lee County:** AUM 12348 (4) Muckalee Creek, 6.1 km SE of Leesburg, Beverly Acres, 1 October 1973. **Lee/Worth counties:** GMNH 21576 (12) Flint River about 1 km upstream from GA Hwy 32, near mouth of Philema Branch, 24 May 2004.

Chattahoochee River system, Georgia: Lumpkin County: GMNH 22055 (2) Chestatee River at County Route134, 16 November 1996.

Chattahoochee River system, Alabama: Russell County: AUM 698 (1) Uchee Creek at AL Hwy 165, 1 September 1967; GMNH 21557 (4) same locality, 22 April 1989; INHS 64577 (2) same locality, 18 March 1989; GMNH 21559 (1) same locality, 30 July 1991; GMNH 21561 (5) same locality, 31 October 1997; GMNH 21565 (11) same locality, 22 November 1996; AUM 1516 (1) Uchee Creek 16.1 km SW of Phoenix City, vicinity of US Hwy 431, 4 November 1968; GMNH 21564 (3) same locality, 22 November 1996; GMNH 21563 (1) Little Uchee Creek at US Hwy 431, 23 November 1996.

Diagnosis. *Percina crypta* differs from all other described species of *Percina* in possessing the following combination of characters: branchiostegal membranes slightly connected; preopercular margin non-serrate; premaxillary frenum well-developed; rectangular dorsal saddles usually seven, closely spaced; snout subconical, subocular bar prominent; and first-dorsal fin with yellow-orange to orange submarginal band in nuptial males and females. Nuptial males lack discrete tubercles, but exhibit tubercular ridges on the anal-fin rays and ventrally on pelvic rays. Lateral blotches rectangular, forming discrete blocks or bars, sometimes conjoined with dorsal saddles and tapering ventrally. Caudal-fin base with three vertically aligned spots or dashes that enclose two pale areas, middle mark may conjoin with small blotch at caudal base.

Percina crypta is most readily distinguished from sympatric *P. nigrofasciata* in having narrowly separated dark dorsal saddles, pale inter-saddle width usually less than or rarely equal to saddle width versus pale inter-saddle width usually greater than saddle width; width of last two dorsal saddles always greater than pale inter-saddle space versus width of last two dorsal saddles always less than inter-saddle space (Fig. 3); usually a single modified scale between the pelvic bases versus two or more scales; and pectoral-fin rays strongly banded versus fins clear or pectoral rays lightly tessellated. Lateral pigmentation highly variable in *P. nigrofasciata*; lateral blotches may conjoin with dorsal saddles in large adults and frequently taper ventrally onto lower side; subocular bar variably present; and nuptial males may develop a pale submarginal yellow wash suffused with pale iridescent green in the first-dorsal fin.

Description. *Percina crypta* is moderately large and robust with a terete body (males are larger than females, maximum size approximately 101 mm versus 85 mm SL); snout subconical, mouth subterminal; dorsal fins large, spinous-dorsal fin distinctly separate from soft-dorsal fin (more so in males than in females); caudal fin emarginate, lobes rounded; anal fin in nuptial males larger than second dorsal fin. Frequency distributions of scale and fin-ray counts of *P. crypta* are given in Tables 1–6; proportional measurements are summarized in Table 7. Lateral line complete with 50–68 scales, usually 55–65 (mean=59.3, S.D. =2.80, n=188);

pored scales on caudal fin 0 (116 specimens), 1 (68) or 2 (7); and transverse-scale rows 14–23, averaging approximately one scale row less in females (mean=18.7, S.D. =1.42; n=104) than males (mean=20.3, S.D. =1.44, n=86). Scale rows above lateral line 5–8 in females and 6–9 in males. Scale rows below lateral line 8–14, usually 11 in females and 12 in males. Caudal-peduncle scale rows 16–25, usually 19–24, approximately one scale row less in females (mean=20.7, S.D. =1.49, n=103) than males (mean=22.0, S.D. =1.38, n=87). Dorsal spines 11–15, usually 11–13; dorsal rays 10–12; anal-fin spines 2; anal rays 7–10, usually 8–9; pectoral-fin rays 12–15, usually 12–14. Branchiostegal rays 6–6 in 94% of examined specimens (ES). Modified midventral scales on belly 8–17 (mean=12.1, S.D. =1.69, n=87) in males; 15% of females (n=104) have 1–10 modified scales on belly. Modified scales between pelvic fin bases number 0 (1 specimen), 1 (155; 62% of males and 95% of females), 2 (35), or 3 (2). Infraorbital pores 7–9, modally 8 (49 of 55 ES); preoperculomandubular pores 9–11, modally 10 (44 of 53 ES). Vertebrae 41–42 (n=6).

Squamation variable on nape, opercle and cheek, scales usually fully or partially embedded, less frequently fully scaled or naked; breast naked in most females (64 of 65 ES), naked or with partially embedded scales in males; anterior abdomen naked in females, usually naked in males (42 of 50 ES).

Coloration in alcohol. Head countershaded and body disruptively colored with varied dark markings over pale background. Head dorsum dark in adults, snout and interorbital area dusky or darkish in juveniles; dark to black pre- and postorbital bars, former not encircling snout and latter extending across preopercle and opercle (nearly contiguous with dark midlateral stripe) forming boundary between dark upper half and pale lower half of head; skin encircling eyes dark in adults and dusky in juveniles; suborbital bar black (adults) to darkish (juveniles, small adults); upper jaw pale to dusky at angle and dark distally, tip of upper jaw and snout dark in adults, pale in juveniles; lower jaw pale at angle, tip and chin dusky; branchiostegal rays and gular area pale to dusky, sometimes with patchy dark stippling; cheek sometimes pale, usually dusky or with patchy stippling in adults, pale in juveniles; opercle darkish, ventral portion pale to dusky, margin usually dark (pale in juveniles). Body ground color pale; dorsum with seven dark rectangular saddles, first saddle entirely anterior to spinous dorsal and last saddle overlying caudal peduncle. Inter-saddle spaces usually marked with scattered dark crescents (exposed scale edges pigmented) to uniform crescent maculation in adults, dusky or flecked in juveniles. Widths of dorsal saddles nearly always greater than widths of inter-saddle spaces on nape and mid-dorsum; always greater than inter-saddle space widths on peduncle (Fig. 3). Dorsolateral body with crisscross pattern formed by darkly pigmented, alternating anterior and posterior oblique scale rows; crisscross marks narrow or reduced to oblique rows of crescents or flecks in juveniles. Side conspicuously marked with 7 to 13 dark to black bars or angular blotches; bars or blotches superimpose narrow dark midlateral stripe, extending from cleithral area to caudal base; midlateral stripe less pronounced in juveniles (blotches more separated) or obscure in dark specimens; lower edges of bars or blotches dusky or darkish, sometimes tapering ventrally in females. Ventrolateral area often with dark scrawl marks, small blotches, or large flecks between bars in females, versus dusky and usually unmarked in males. Venter flecked or with patchy stippling in females versus dusky, immaculate in males; both sexes with dark midventral line (dark peritoneum visible through naked integument). Dark saddles and lateral bars may be contiguous or virtually obscured in very dark specimens.

Dorsal fin typically dusky in males and with medial dusky band in females. Second-dorsal fin dusky with light, distal band. Anal fin dusky (in males) or with a distal light colored band (females). Pelvic fins dusky in males and heavily speckled in females. Pectoral-fin rays pigmented along their length to form one or two light bands in the medial portion of the fin. Caudal fin dusky with an irregular medial band and two light-colored spots that separate three vertically aligned dark spots at base of fin.

Coloration in life. A nuptial male and female *P. crypta* are depicted in Figure 2. In males, head dark blue-gray to black with gold to green iridescent specks concentrated on cheek and opercle, specks less dense on posterior maxilla, below snout, and above black postorbital bar; eye dark, ventral edge orbit sometimes lightly stippled with gold-green iridescence flecks, preorbital bar black, lower jaw and chin black with bluish cast.

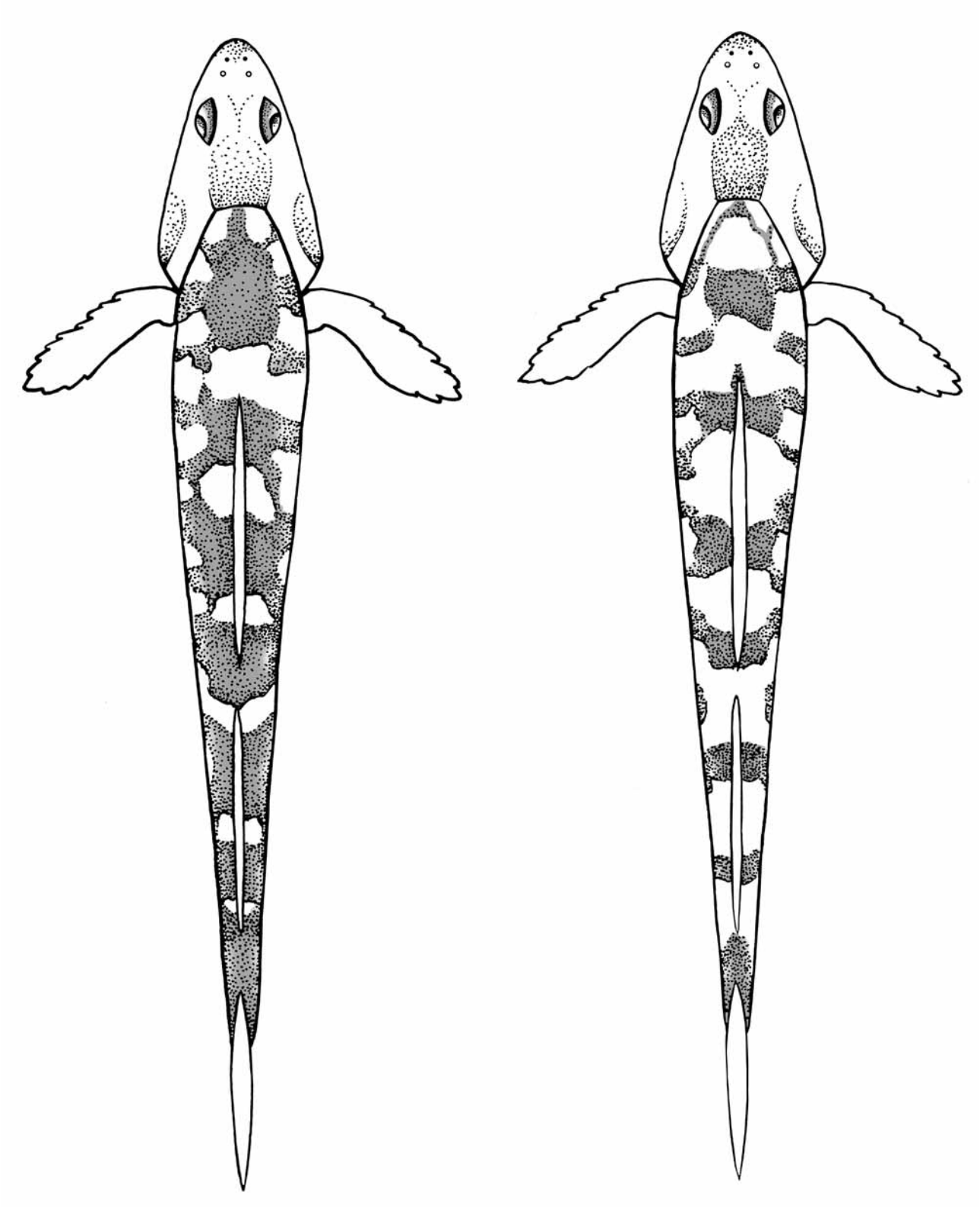

FIGURE 3. Dorsal saddle pigmentation differences between *Percina crypta* (left) and *Percina nigrofasciata* (right); note diagnostic difference in widths of pale inter-saddle spaces between *P. crypta* (usually less than saddle width) versus *P. nigrofasciata* (usually greater than saddle width). Illustration by Bricelyn H. Strauch based on photographs of dorsally oriented live specimens from the type locality, and preserved specimens from GMNH 14225 (Lower Flint River system).

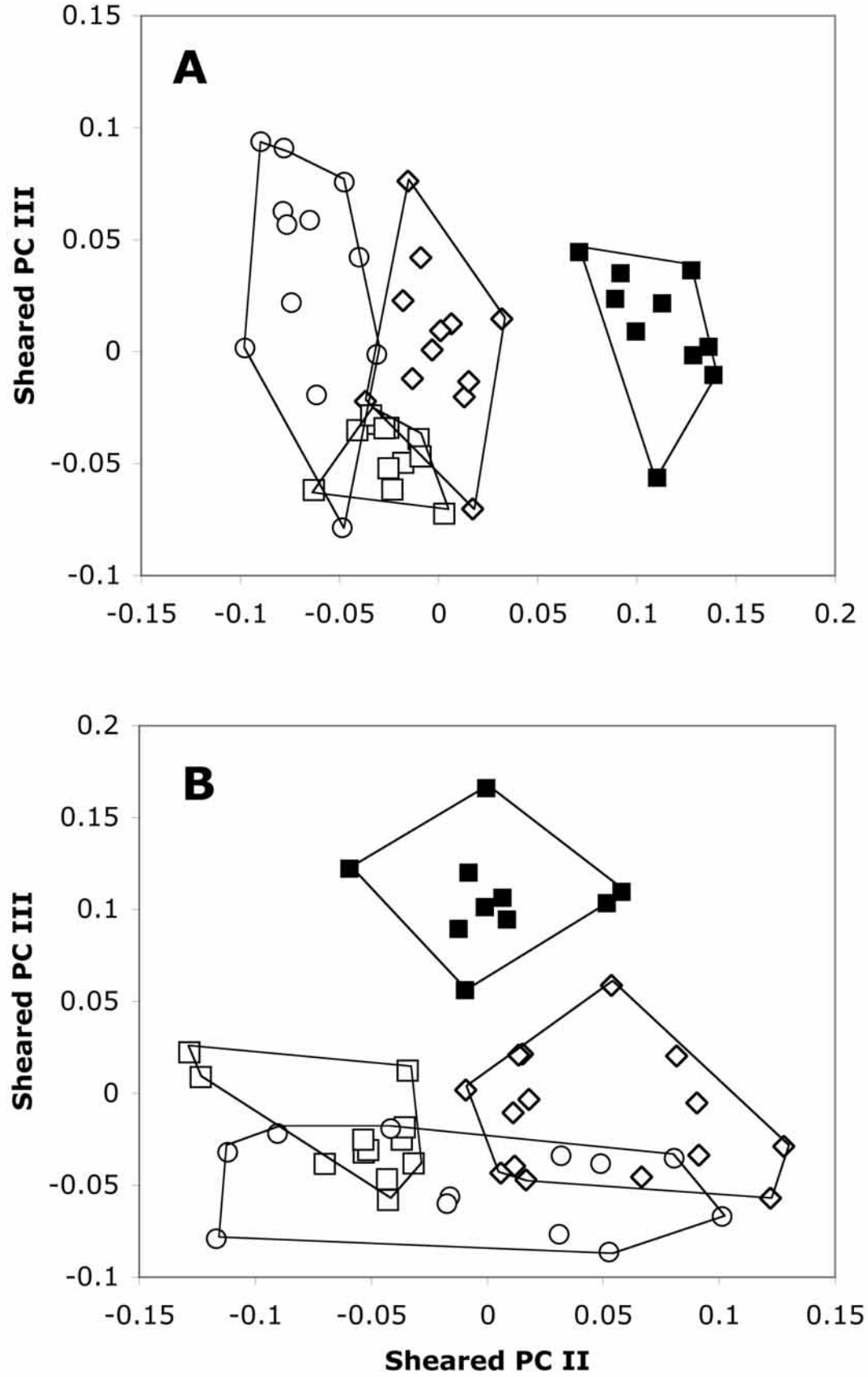

FIGURE 4. Sheared principal components analysis of morphometric variation among *Percina crypta* from the upper Chattahoochee River system (open circles), the upper Flint River system (open squares), and the lower Flint River system (open diamonds), and *Percina nigrofasciata* from the lower Flint River system (filled squares). Males (n=46, A) and females (n=49, B) were analyzed and plotted separately.

Lateral bars black to olive-black, suffused with iridescent green sheen; background straw to pale orange; entire side stippled with minute gold, orange, green, and lime iridescent specks. Dorsum black (saddles obscure) or black saddles evident, inter-saddle spaces amber to orange, lacking iridescent specks; breast gray-black, abdomen amber, sometimes with ventral pink tinge. In females, head dorsum dark olive-black; snout medium olive-black, sometimes with median yellow to amber mark; cheek and opercle variable, medium olive-black with yellow crescent marks (over scales), or with pale yellow mottling and stippling; iridescent gold to green specks concentrated on opercle, over cleithrum, and just above opercle spine. Eye black with yellow to amber edges, along ventral margin, divided by midventral black mark; suborbital bar obscure or black, preorbital bar obscure or black, postorbital bar black. Upper and lower jaws olive-black to pale yellow, dappled with olive-black specks and marks. Lateral bars olive-black, conjoined by small blotches and dark marks; bars taper ventrally and contrasted with pale yellow-green abdomen to pink tinged venter; lower side and abdomen speckled with olive-black marks on scales and blotches or marks on lower peduncle; lateral bars on upper side variegated by irregular pale yellow marks. Entire side with minute to tiny iridescent gold, orange, green, and lime specks, most evident when contrasted against lateral bars. Dorsal saddles dark olive-black or black, inter-saddle spaces pale yellow to amber with black flecks or crescent marks.

In males, first-dorsal fin with distinct olive-yellow to orange marginal band that becomes submarginal posteriorly, distally bounded by diffuse olive-black edge; basal interspinous membranes black, except for small clear window behind spine base of the third to penultimate spines. Second-dorsal fin with diffuse olive-black margin (rays yellow), wide yellow-green wash in distal third of fin (rays amber at first branch), and remaining base of fin and rays dusky black. Caudal-fin membranes dusky black with olive yellow rays, caudal base with two light yellow-olive areas. Anal fin dusky black, darkest in basal third of fin; rays with prominent apparently keratinized blue-gray ridges. Pelvic fins dusky black to olive at fin tip, ventral rays thickened and blue-gray along leading edge; pectoral-fin membranes clear, rays dusky black; rays with thickened blue-gray edges along leading and distal margins of lower fin. In females, median fins are distinctly banded. First-dorsal fin has yellow-orange marginal band that becomes submarginal posteriorly, bounded by olive-black distal edge; basal pigmentation consists of clear, dusky black, and clear irregular bands. Second-dorsal fin has irregular dusky olive and olive-black marks and clear areas on membranes and rays in distal third of fin, an uneven clear band in mid-fin, and variegated clear and dusky black pigmentation in basal third of fin. Caudal fin with alternating olive-black and clear banding on rays, membranes clear to slightly dusky along ray edges; distal ray tips black edged, with submarginal clear and olive-black bands, medial clear band, and basal third of fin rays olive-black; caudal base with two light yellow areas separated by upper, medial, and lower black marks. Anal fin with dusky green-olive pigment in basal third of membranes, rays with alternating olive-black and clear banding; clear submarginal band present in longest rays and medially across fin. Pelvic fins with yellow-olive banding on rays, leading ventral ray thickened; pelvic fin banded yellow and olive-black on rays, membrane yellow, except for clear ventral edge.

Geographic Variation and Comparison to *P. nigrofasciata*. Meristic variation among populations of *P. crypta* from the lower Flint River, upper Flint River, upper Chattahoochee River and Uchee Creek systems entail differences in central tendency of scale and fin-ray counts, although count distributions broadly overlap among populations for all variables (Tables 1–6). Uchee Creek specimens average about one to two fewer lateral-line, transverse and caudal-peduncle-scale rows than upper Flint River specimens. Specimens from the upper Chattahoochee modally have 13 dorsal spines compared to 12 in the other three populations (Table 5). Count distributions also overlap between *P. crypta* and *P. nigrofasciata* from the lower Flint River system, although *P. nigrofasciata* average two to four fewer lateral-line scales (Table 1), and modally have nine anal rays compared to eight in *P. crypta* (Table 6). Lateral-line scale counts reported by Crawford (1956) for *P. nigrofasciata* from Apalachicola (including the Chattahoochee River system) and Flint populations also tend lower (averages = 55.3 and 54.4, respectively) than counts reported here for *P. crypta*. Crawford (1956) also reports a modal count of nine anal rays in *P. nigrofasciata*. Other counts reported by Crawford (scales above

and below the lateral line, scale rows around the caudal peduncle, dorsal-fin spines and rays) for *P. nigrofasciata* broadly overlap with counts for *P. crypta*.

TABLE 1. Frequency distribution of lateral-line scales for *Percina crypta* from four portions of the species range: Chattahoochee River system upstream from Lake Lanier (Upper Chattahoochee); Uchee Creek (an Alabama tributary to the middle portion of the Chattahoochee River); the Flint River system above (Upper Flint) and below (Lower Flint) the Fall Line, and for *P. nigrofasciata* from the Lower Flint. Numeric value for the holotype is in boldface.

Lateral-Line Scales	50	51	52	53	54	55	56	57	**58**	59	60	61	62	63	64	65	66	68	n	Mean
P. crypta																				
Upper Chattahoochee						3	3	6	7	6	7	5	5	2	1	3			48	59.5
Uchee Creek	1		1		1	5	1	2	4	5	2			4		1			27	58.0
Upper Flint			1		1	1	5	4	11	14	15	9	6	7	2	2	1		79	59.7
Lower Flint						1	4	5	4	4	6	2	6	1				1	34	59.3
P. nigrofasciata																				
Lower Flint	1	1		2	2	6	5	3	6	3	1								30	56.0

TABLE 2. Frequency distribution of scale counts above and below the lateral line for *Percina crypta* from four portions of the species range, as described in Table 1, and for *P. nigrofasciata* from the lower Flint River system. Numeric value for the holotype is in boldface.

	Scales Above Lateral Line							Scales Below Lateral Line								
	5	6	7	**8**	9	n	Mean	8	9	10	11	12	**13**	14	n	Mean
P. crypta																
Upper Chattahoochee		13	29	5	2	49	6.9		5	6	17	15	5		48	11.2
Uchee Creek	2	17	4			23	6.1	1	1	8	7	9	1		27	10.9
Upper Flint		23	48	10		81	6.8		5	11	27	18	15	5	81	11.5
Lower Flint	1	9	24	2		36	6.8		4	8	15	8	1		36	10.8
P. nigrofasciata																
Lower Flint		14	16			30	6.5	1	2	11	8	4	4		30	10.8

Morphometric analysis shows some differentiation among *P. crypta* specimens from the upper Flint River, lower Flint River and upper Chattahoochee River systems, based on a sheared PCA of the 22 variables listed in Table 7 (Fig. 4, Table 8). Males from all three populations overlap on both sheared principal components (Fig. 4A), although specimens from the upper Flint River system tend toward shorter pectoral and pelvic fins (PC III; Tables 7 and 8). Additionally, males from the lower Flint River system tend toward greater orbit length and greater gill-mandible length than in males from the upper Chattahoochee River system (PC II; Fig. 4A). Females from the two Flint River populations separate primarily on the basis of body depth, head depth, and length of longest dorsal spine and anal spine (PC II; Fig. 4B). Females from both Flint River system populations overlap on both principal components with females from the upper Chattahoochee River system (Fig. 4B). For all individual variables, measurement ranges broadly overlap among populations (Table 7). We have not discerned any characters that are diagnostic of *P. crypta* from the separated portions of its range.

Percina crypta from all three examined populations separate from *P. nigrofasciata* from the lower Flint River system in the multivariate space defined by the sheared PCA (Fig. 4). The measured *P. nigrofasciata* have greater inter-orbital width (average, range of proportional measurement: males, 47, 42–50; females 46,

44–48) than *P. crypta* (38–41; Table 7). *Percina nigrofasciata* also tends toward lesser caudal peduncle depth (males 86, 82–89; females 81, 77–86), and greater gill-mandible distance (males 142, 132–159; females 145, 122–166). Male *P. nigrofasciata* additionally separate from male *P. crypta* on the basis of greater orbit length (66, 61–70; PCII, Fig. 4A). Female *P. nigrofasciata* additionally separate from female *P. crypta* in having lesser body depth (172, 161–184) and greater snout length (69, 64–76; PCIII, Fig. 4B).

TABLE 3. Frequency distribution of transverse-scale rows for *Percina crypta* from four portions of the species range, as described in Table 1, and for *P. nigrofasciata* from the lower Flint River system. Numeric value for the holotype is in boldface.

	Scale Rows											
	14	15	16	17	18	19	20	21	**22**	23	n	Mean
P. crypta												
Upper Chattahoochee			2	3	5	10	12	13	2	1	48	19.6
Uchee Creek	1		1	6	5	7	6	1			27	18.4
Upper Flint			3	3	8	25	13	13	10	6	81	19.9
Lower Flint				6	6	14	7	3			36	18.9
P. nigrofasciata												
Lower Flint	1		1	2	10	9	4	3			30	18.6

TABLE 4. Frequency distribution of caudal-peduncle-scale rows for *Percina crypta* from four portions of the species range, as described in Table 1, and for *P. nigrofasciata* from the lower Flint River system. Numeric value for the holotype is in boldface.

	Scale Rows											
	16	17	18	19	20	21	22	**23**	24	25	n	Mean
P. crypta												
Upper Chattahoochee	1		1	4	13	18	5	5	2		49	20.8
Uchee Creek		2	3	9	4	8	1				27	19.6
Upper Flint				4	3	22	17	26	6	2	80	22.0
Lower Flint					5	15	9	5	2		36	21.6
P. nigrofasciata												
Lower Flint				3	4	13	7	2	1		30	21.1

TABLE 5. Frequency distribution of dorsal-fin ray counts for *Percina crypta* from four portions of the species range, as described in Table 1, and for *P. nigrofasciata* from the lower Flint River system. Numeric values for the holotype are in boldface.

	Dorsal Spines							Dorsal Rays				
	11	12	**13**	14	15	n	Mean	10	11	**12**	n	Mean
P. crypta												
Upper Chattahoochee		13	34	2		49	12.8	4	35	10	49	11.1
Uchee Creek	9	17	1			27	11.7	2	24	1	27	11.0
Upper Flint	6	51	23		1	81	12.2	16	59	6	81	10.9
Lower Flint	3	27	6			36	12.1	7	27	2	36	10.9
P. nigrofasciata												
Lower Flint	2	20	6	2		30	12.3	2	24	4	30	11.1

TABLE 6. Frequency distribution of anal-fin and left pectoral-fin ray counts for *Percina crypta* from four portions of the species range, as described in Table 1, and for *P. nigrofasciata* from the lower Flint River system. Numeric values for the holotype are in boldface.

	Anal Rays						Left Pectoral Rays					
	7	8	**9**	10	n	Mean	12	13	**14**	15	n	Mean
P. crypta												
Upper Chattahoochee	2	36	11		49	8.2		7	40	2	49	13.9
Uchee Creek		17	9	1	27	8.4		13	14		27	13.5
Upper Flint	1	56	23	1	81	8.3	3	40	38		81	13.4
Lower Flint		28	8		36	8.2	2	20	14		36	13.3
P. nigrofasciata												
Lower Flint		7	21	2	30	8.8		5	23	2	30	13.9

TABLE 7. Standard length and proportional measurements for *Percina crypta* from three portions of the native range: Chattahoochee River system upstream from Lake Lanier (Chattahoochee), and the Flint River system above (Upper Flint) and below (Lower Flint) the Fall Line. Measurements (except SL) are expressed in thousandths of standard length.

		Chattahoochee (n=24)			Upper Flint (n=24)			Lower Flint (n=27)		
	Holotype	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD
Standard length	70	53–81			52–74			47–80		
Head length	252	240–277	256	7.7	246–273	258	6.5	241–272	258	7.0
Body depth	203	175–222	197	13.4	185–220	202	9.8	164–213	188	11.9
Head depth	180	142–183	160	9.2	146–171	160	6.3	125–179	149	12.3
Predorsal length	313	298–343	322	9.7	314–341	329	8.7	310–352	326	9.4
Snout length	63	56–71	63	3.5	59–69	64	2.2	58–70	64	3.7
Upper–jaw length	76	69–78	74	2.4	67–78	71	3.2	66–79	72	3.4
Orbit length	57	50–66	58	5.2	51–65	60	4.0	58–71	64	3.4
Interorbital width	41	32–45	38	3.4	37–45	41	2.0	38–48	41	2.4
Caudal-peduncle length	235	201–243	231	8.8	226–249	236	5.8	225–263	243	9.9
Caudal-peduncle depth	105	90–107	98	4.0	94–111	101	4.3	86–109	99	5.6
Transpelvic width	84	74–90	84	3.3	73–89	79	3.6	77–89	84	3.2
Pectoral-fin length	239	229–268	254	10.4	208–242	222	9.0	185–265	229	16.6
Pelvic-fin length	195	179–222	202	10.4	179–207	195	8.2	174–237	208	15.8
First-dorsal-fin-base length	336	280–342	319	14.6	283–326	305	9.6	280–330	309	10.6
Longest dorsal spine	116	102–131	113	6.5	93–113	103	5.7	103–138	115	8.6
Second-dorsal-fin-base length	183	159–193	173	9.1	147–186	163	9.0	152–191	169	10.1
Longest dorsal ray	145	133–156	148	6.3	135–156	146	5.8	132–168	150	9.3
Anal-fin-base length	183	138–183	160	15.4	128–182	154	14.2	133–180	158	13.6
First-anal-fin-spine length	60	56–85	71	7.1	53–82	71	6.1	62–90	73	7.1
Longest anal-fin ray	140	124–163	150	8.7	145–163	153	4.7	135–183	157	10.4
Mandible-gill membrane distance	132	106–156	124	13.0	121–157	135	9.2	114–154	132	12.1

TABLE 8. Sheared principal component loadings for analysis of morphometric variables for *P. crypta* from the upper Chattahoochee River (n=12 females, 12 males), upper Flint River system (n=12 males, 12 females) and lower Flint River system (n=12 males, 15 females), and *P. nigrofasciata* from the lower Flint River system (n=10 males, 10 females)

	Males		Females	
Variable	Sheared PC II	Sheared PC III	Sheared PC II	Sheared PC III
Standard length	-0.01	-0.03	-0.02	0.01
Head length	0.05	0.01	-0.09	0.10
Body depth	-0.21	-0.29	-0.38	-0.35
Head depth	-0.30	-0.22	-0.46	-0.17
Predorsal length	0.12	-0.02	-0.07	0.09
Snout length	0.20	-0.10	-0.07	0.33
Upper-jaw length	0.13	0.10	-0.09	0.15
Orbit length	0.35	0.06	-0.06	0.27
Interorbital width	0.52	0.04	0.11	0.40
Caudal-peduncle length	0.14	0.04	0.10	-0.01
Caudal-peduncle depth	-0.38	-0.26	-0.09	-0.43
Transpelvic width	-0.14	0.07	-0.02	-0.14
Pectoral-fin length	-0.21	0.56	0.09	-0.13
Pelvic-fin length	0.00	0.30	0.25	-0.13
First-dorsal-fin-base length	-0.01	0.08	-0.08	-0.01
Longest dorsal spine	0.08	0.25	0.37	0.00
Second-dorsal-fin-base length	-0.16	0.16	0.05	0.04
Longest dorsal ray	-0.05	0.05	0.15	-0.01
Anal-fin-base length	-0.14	-0.13	0.06	0.01
First-anal-fin-spine length	0.01	-0.03	0.53	-0.27
Longest anal-fin ray	0.05	0.08	0.16	0.11
Mandible-gill membrane distance	0.32	-0.50	-0.18	0.34

Comparisons. *Percina crypta* possesses characters that would variously align it with species in the subgenera *Ericosma*, *Hadropterus*, and *Alvordius* as diagnosed by Page (1974) and as described by Boschung and Mayden (2004). *Percina crypta* resembles *P. palmaris* in pigmentation, but differs from the subgenus *Ericosma* in lacking tubercles, having the lateral bars usually not conjoined across the dorsum, and in the first-dorsal fin of breeding males with a dark basal band, not entirely orange. *Percina crypta* differs from members of the subgenus *Hadropterus* in having narrowly connected branchiostegal membranes (versus moderately connected), nuptial coloration, pored scales on the caudal fin normally 0 to 1 (usually 0, versus 0 to 6), and in lacking distinct serrae on the preopercular margin. *Percina crypta* differs from the species of the subgenus *Alvordius* in usually possessing a narrow connection between the branchiostegal membranes (frequently separate in *Alvordius*), and in having an orange submarginal band in the first dorsal fin (bright colors usually lacking in *Alvordius*). Recent analysis using gene sequence data (Near 2002) provides evidence that the subgenera *Ericosma*, *Hadropterus*, and *Alvordius* are not monophyletic. The same analysis (Near 2002) has supported monophyly in five of the six remaining *Percina* subgenera. *Percina crypta* lacks the apomorphic characters defining four of these subgenera; an elongated anal fin in males of the subgenus *Imostoma*; a caudal keel and lack of modified scales along the belly midline in male *Odontopholis*; an elongated snout in *Swainia* (which also has a moderate connection between the branchiostegal membranes); a bulbous, conical snout in *Percina* s.s. (Page 1974; Near 2002). *Percina crypta* differs from species in the subgenus *Cottogaster* as diagnosed by

Suttkus *et al.* (1994) in large size, possession of a broad premaxillary frenum, and in having a connection between the branchiostegal membranes. *Percina crypta* differs from the single species (*P. aurantiaca*) assigned to the subgenus *Hypohomus* in a number of characters, including possessing a row of modified scales on the midline of the belly.

Distribution. *Percina crypta* is endemic to the Apalachicola River drainage, where the species occurs in the Flint River system, Georgia, and the Chattahoochee River system, Alabama and Georgia (Fig. 1). Within the Flint River system, the species is known from the Flint River mainstem above and below the Fall Line (the boundary between Piedmont and Coastal Plain physiographic provinces), and in at least four tributary stream systems (Lazer Creek and Potato Creek, in the Piedmont province, and Muckalee Creek and the Ichawaynochaway Creek system in the Coastal Plain province). Within the Chattahoochee River system, *P. crypta* is known from two broadly separated areas, the upper portion of the system in Georgia, including the mainstem Chattahoochee River, Chestatee River, and Sautee Creek (all upstream from Lake Lanier and in the Blue Ridge province), and from the Uchee Creek system, an Alabama tributary that enters the Chattahoochee River in the Fall Line Hills district of the upper Coastal Plain (Couch *et al.* 1996).

We hypothesize that *P. crypta* historically occurred more widely in the Chattahoochee River mainstem, prior to the construction of 13 dams on the river beginning in the mid-nineteenth century (Couch *et al.* 1996). The construction of Buford Dam, which began operating in 1959, likely eliminated habitat for *P. crypta* in the Chattahoochee and Chestatee mainstems in what is now Lake Lanier, and modified the thermal and hydrologic regime in the Chattahoochee River downstream from the dam (Collier *et al.* 1996; Couch *et al.* 1996). Pollutants originating in the Atlanta metropolitan area have also altered water quality in the Chattahoochee downstream from Buford Dam (Couch *et al.* 1996). Shoal habitat (rocky areas that are relatively shallow with swift velocities at base-flow discharges) exists in this reach of the river; however, habitat quality for many species is impaired by altered water quality and hydrologic conditions.

Percina crypta may also have historically occurred more widely in the Coastal Plain portion of the system, prior to the removal of rock shoals from the Chattahoochee and Flint rivers. Navigation surveys conducted in 1871 and 1872 (U.S. Congress 1874) list numerous rock shoals as impediments to navigation by steamboats in the Coastal Plain portions of both rivers. A subsequent report (U.S. Congress 1910) documents efforts during the late 1800's and early 1900's to remove rock shoals, along with snags, logs and boulders, to improve navigability for steamboats in the lower portions of the Chattahoochee and Flint rivers. Channel modifications involving removing rock and "cutting through rock reefs" may have removed habitat for *P. crypta*. Currently, populations of *P. crypta* are known from shoals in the Flint River mainstem and larger tributary streams below the Fall Line (Fig. 1), and the species likely also historically occurred in similar habitat in the lower Chattahoochee River prior to channel improvements for navigation. We have relatively fewer collection records from the lower Flint and Chattahoochee river mainstems (Fig.1), and it is possible that future efforts will locate additional extant populations of *P. crypta* if appropriate habitats persist in these river reaches. We have no records of *P. crypta* from the Apalachicola River, formed by the confluence of the Chattahoochee and Flint rivers. We hypothesize that the species has never occurred far downstream into the Apalachicola River, where shoal habitat is restricted to the upstream-most portion of the channel.

Habitat and ecology. *Percina crypta* inhabits relatively swiftly flowing areas over bedrock or a mixture of coarse (boulder to gravel) bed sediments (Hill 1996; Marcinek 2003). The species is frequently associated with the aquatic macrophyte *Podostemum ceratophyllum* (Marcinek 2003). All of our observations of *P. crypta* have been in shoal habitats, which contrasts markedly with the broader range of stream habitats (pools, runs and riffles) occupied by the co-occurring congener *P. nigrofasciata*.

Hill (1996) studied life history aspects of *P. crypta* in the upper Flint River system. *Percina crypta* in this population consumed aquatic insect larvae, including Diptera, Ephemeroptera and Trichoptera. Spawning occurred during April and May, based on observations of gonad condition, when mean monthly water

temperatures were 18 to 20° C. Individuals reached sexual maturity at age one or two; maximum observed age was estimated at three years based on otolith examination.

Percina crypta occurs commonly and abundantly in shoals of the upper Flint River, above the Fall Line, where the species often outnumbers *P. nigrofasciata* in catch data (Marcinek 2003; GMNH records). This does not appear to apply to populations in the lower Flint system or in the Chattahoochee system, where known localities are fewer and *P. crypta* are generally outnumbered by *P. nigrofasciata* in collections. Frequently associated species include *Cyprinella callitaenia* in the upper Flint system, *C. venusta*, *Luxilus zonistius* in the upper Chattahoochee system, *Ameiurus brunneus*, *Noturus leptacanthus*, *Micropterus cataractae*, *Lepomis auritus*, *Etheostoma swaini* in the lower Flint and Uchee Creek systems, and *P. nigrofasciata*.

Conservation status. *Percina crypta* is considered vulnerable by Warren *et al.* (2000) and Jelks *et al.* (2008). Within Alabama, *P. crypta* is considered a species of highest conservation concern (Johnston & Kuhajda 2002), and the species is listed as threatened under the State of Georgia Endangered Wildlife Act. *Percina crypta* is considered imperiled primarily because of its fragmented distribution within a range limited to two river systems. As discussed above, *P. crypta* may have been extirpated from a major portion of the species' historic range in the Chattahoochee River mainstem as a result of dam construction and operation, and channel modification to support navigation. The status of the *P. crypta* population in the Uchee Creek system is uncertain; this population is isolated from all others by mainstem dams on the Chattahoochee River upstream and downstream of the mouth of Uchee Creek. Distribution of *P. crypta* in the Flint River system is also fragmented by two mainstem dams located below the Fall Line. Upstream from these dams, shoals in the Piedmont portion of the upper Flint River mainstem appear to support the largest populations of *P. crypta*.

Present threats to the persistence of *P. crypta* primarily consist of effects of urban growth on stream hydrology and water quality, particularly in the north Georgia mountains and in the vicinity of the Atlanta Metropolitan area. The Flint River headwaters originate in Atlanta, and population growth in the upper Flint River system is expected to place increasing demands on the river system for water supply and waste assimilation. Similarly, population growth in the Blue Ridge province of North Georgia will affect water availability and quality in the Chattahoochee River headwaters.

Etymology. From the Greek root *crypt*, meaning hidden or concealed, in reference to the close similarity in appearance between *P. crypta* and the co-occurring congener, *P. nigrofasciata*. The common name refers to the striking black and orange coloration of nuptial individuals, colors associated with the Western celebration of Halloween (a Celtic festival adopted by the Roman Catholic Church as the eve of All Saints Day).

Discussion

Percina crypta exemplifies hidden biological diversity, as a species that has until recently gone undetected in a relatively well-studied region. The southeastern U.S. harbors an incompletely known but presumably high level of cryptic aquatic biodiversity, especially in the form of distinct evolutionary lineages within wide-ranging polytypic species (Burkhead *et al.* 1997; Warren *et al.* 2000; Boschung & Mayden 2004). In the case of *P. crypta*, cryptic diversity has existed as an undiagnosed species in sympatry with a morphologically similar congener, also not uncommon in southeastern fishes. Examples include *Etheostoma brevirostrum* with *E. coosae*, and *P. jenkinsi* with *P. kathae* in the Coosa River system, and the undescribed Sicklefin Redhorse, *Moxostoma* sp. (Warren *et al.* 2000), with two additional *Moxostoma* species in the Hiwassee River system. Discovery of hidden biodiversity is of inherent value in terms of knowing what exists, and also informs our understanding of the ecology and evolutionary history of the systems involved.

Historically, the shoal fauna of the Chattahoochee and Flint river systems has been understood to include a single, common and often abundant, species of *Percina*. This has been in marked contrast to percid diversity in rivers of the Coosa and Tallapoosa systems, to the immediate west, where three to six *Percina* species may

occur syntopically (i.e., *P. palmaris* and *P. kathae* with *P. smithvanizi* in the upper Tallapoosa River system, and with *P. nigrofasciata, P. kusha, P. antesella,* and *P. lenticula* in the upper Coosa River system). We now confirm that at least two *Percina* species, the Blackbanded Darter and the Halloween Darter occur syntopically in portions of the Chattahoochee and Flint rivers. As noted above, phylogenetic relationships of *P. crypta* to other species of *Percina* are obscure. Resolving phylogenetic relationships of *P. crypta*, and among *Percina* species generally, awaits additional analyses, and should shed substantial light on the biogeographic history of the genus.

Material examined for counts and measurements of *Percina nigrofasciata*

Georgia: Baker County: GMNH 13415 (3) Ichawaynochaway Creek immediately downstream of dam at upstream boundary of J. E. Jones Ecological Research Center Property, 18 October 1990; GMNH 14224 (20) Chickasawhatchee Creek at GA Hwy 37, 5 December 1991; GMNH 22060 (7) Ichawaynochaway Creek, first shoal immediately upstream from GA Hwy 200 crossing, 6 December 1991.

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References

Bookstein, F.L., Chernoff, B., Elder, R.L., Humphries Jr., J.M., Smith, G.R. & Strauss, R.E. (1985) *Morphometrics in Evolutionary Biology.* Academy of Natural Sciences Special Publication 15, Philadelphia, Pennsylvania, 277 pp.

Boschung, H.T., Jr. & Mayden, R.L. (2004) *Fishes of Alabama*. Smithsonian Books, Washington, DC, 736 pp.

Burkhead, N.M., Walsh, S.J., Freeman, B.J. & Williams J.D. (1997) Status and restoration of the Etowah River, an imperiled southern Appalachian ecosystem. *In*: Benz, G.W. & Collins, D.E. (Eds.), *Aquatic Fauna in Peril: the Southeastern Perspective*. Southeast Aquatic Research Institute, Special Publication 1, Decatur, Georgia, pp. 375–444.

Collier, M., Webb, R.H. & Schmidt, J.C. (1996) *Dams and rivers: primer on the downstream effects of dams.* USGS Circular 1126. U.S. Geological Survey, Tucson, Arizona.

Couch, C.A., Hopkins, E.H. & Hardy, P.S. (1996) *Influences of environmental settings on aquatic ecosystems in the Apalachicola-Chattahoochee-Flint river basin.* Water-Resources Investigations Report 95-4278, U.S. Geological Survey, National Water-Quality Assessment Program, Atlanta, Georgia.

Crawford, R.W. (1956) A study of the distribution and taxonomy of the percid fish *Percina nigrofasciata* (Agassiz). *Tulane Studies in Zoology,* 4, 1–55.

Fowler, H.W. (1942) Descriptions of six new fresh-water fishes (Cyprinidae and Percidae) from the southeastern United States. *Notulae Naturae,* 107,1–11.

Guillory, Sr., V. (1976) Apparent absence of *Percina nigrofasciata* from the Mississippi Valley. *Copeia,* 1976, 804–805.

Hill, P.L. (1996) *Habitat use and life history of the Halloween darter, Percina sp., in the upper Flint River system, Geor-*

gia. Master of Science thesis, Auburn University, Auburn, Alabama. 45 pp.
Hubbs, C.L. & Lagler, K.F. (1958) Fishes of the Great Lakes region. 2nd edition. *Cranbrook Intitute Science Bulletin*, 26, 1–213.
Humphries, J.M., Bookstein, F.L., Chernoff, B., Smith, G.R., Elder, R.L. & Poss, S.G. (1981) Multivariate discrimination by shape in relation to size. *Systematic Zoology*, 30, 291–308.
Jelks, H.L., Walsh, S.J., Burkhead, N.M., Contreras-Balderas, S., Díaz-Pardo, E., Hendrickson, D.A., Lyons, J., Mandrak, N.E., McCormick, F., Nelson, J.S., Platania, S.P., Porter, B.A., Renaud, C.B., Schmitter-Soto, J.J., Taylor, E.B. & Warren, Jr., M.L. (2008) Conservation status of imperiled North American freshwater and diadromous fishes. *Fisheries*, 33, 372–407.
Jenkins, R.E. & Burkhead, N.M. (1994) *Freshwater Fishes of Virginia*. American Fisheries Society, Bethesda, Maryland, 1079 pp.
Johnston, C.E. & Kuhajda, B.R. (2002) Halloween darter *Percina* sp. *In*: Mirachi, R.E., Garner, J.T., Mettee, M.F. & O'Neil, P.E. (Eds.), *Alabama Wildlife. Vol. 2. Imperiled Aquatic Mollusks and Fishes*. The University of Alabama, Tuscaloosa, Alabama, pp. 201–202.
Leviton, A.E. & Gibbs, Jr., R.H. (1988) Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Supplement No. 1: additions and comments. *Copeia*, 1988, 280–282.
Leviton, A.E., Gibbs, Jr., R.H., Heal, E. & Dawson, C.E. (1985) Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia*, 1985, 802–832.
Marcinek, P.A. (2003) *Variation of fish assemblages and species abundances in the upper Flint River shoals, Georgia*. Master of Science thesis, University of Georgia, Athens, Georgia, 75 pp.
Near, T.J. (2002) Phylogenetic relationships of *Percina* (Percidae: Etheostomatinae). *Copeia*, 2002,1–14.
Page, L.M. (1974) The subgenera of *Percina* (Percidae: Etheostomatini). *Copeia*, 1974, 66–86.
Richards, W.J. & Knapp, L.W. (1964) *Percina lenticula*, a new percid fish, with a redescription of the sugenus *Hadropterus*. *Copeia*, 1964, 690–701.
Suttkus, R.D. & Etnier, D.A. (1991) *Etheostoma tallapoosae* and *E. brevirostrum*, two new darters, subgenus *Ulocentra*, from the Alabama River drainage. *Tulane Studies in Zoology and Botany*, 28,1–24.
Suttkus, R.D., Thompson, B.A. & Bart, Jr., H. L. (1994) Two new darters, *Percina* (*Cottogaster*), from the southeastern United States, with a review of the subgenus. *Occasional Papers Tulane University Museum of Natural History*, 4, 1–46.
U.S. Congress (1874) *Ex. Doc. No. 65, A Report of the Survey of the Flint and Chattahoochee in Florida*. United States House of Representatives, Washington, D.C.
U.S. Congress (1910) *Report No. 527, Report on the River and Harbor Bill by the Committee on Commerce, United States Senate*. Government Printing Office, Washington, D.C.
Warren, Jr., M.L., Burr, B.M., Walsh, S.J., Bart Jr., H.L., Cashner, R.C., Etnier, D.A., Freeman, B.J., Kuhajda, B.R., Mayden, R.L., Robison, H.W., Ross, S.T. & Starnes,W.C. (2000) Diversity, distribution, and conservation status of the native freshwater fishes of the southern United States. *Fisheries*, 25(10), 7–29.