ALABAMA MUSEUM of Natural History

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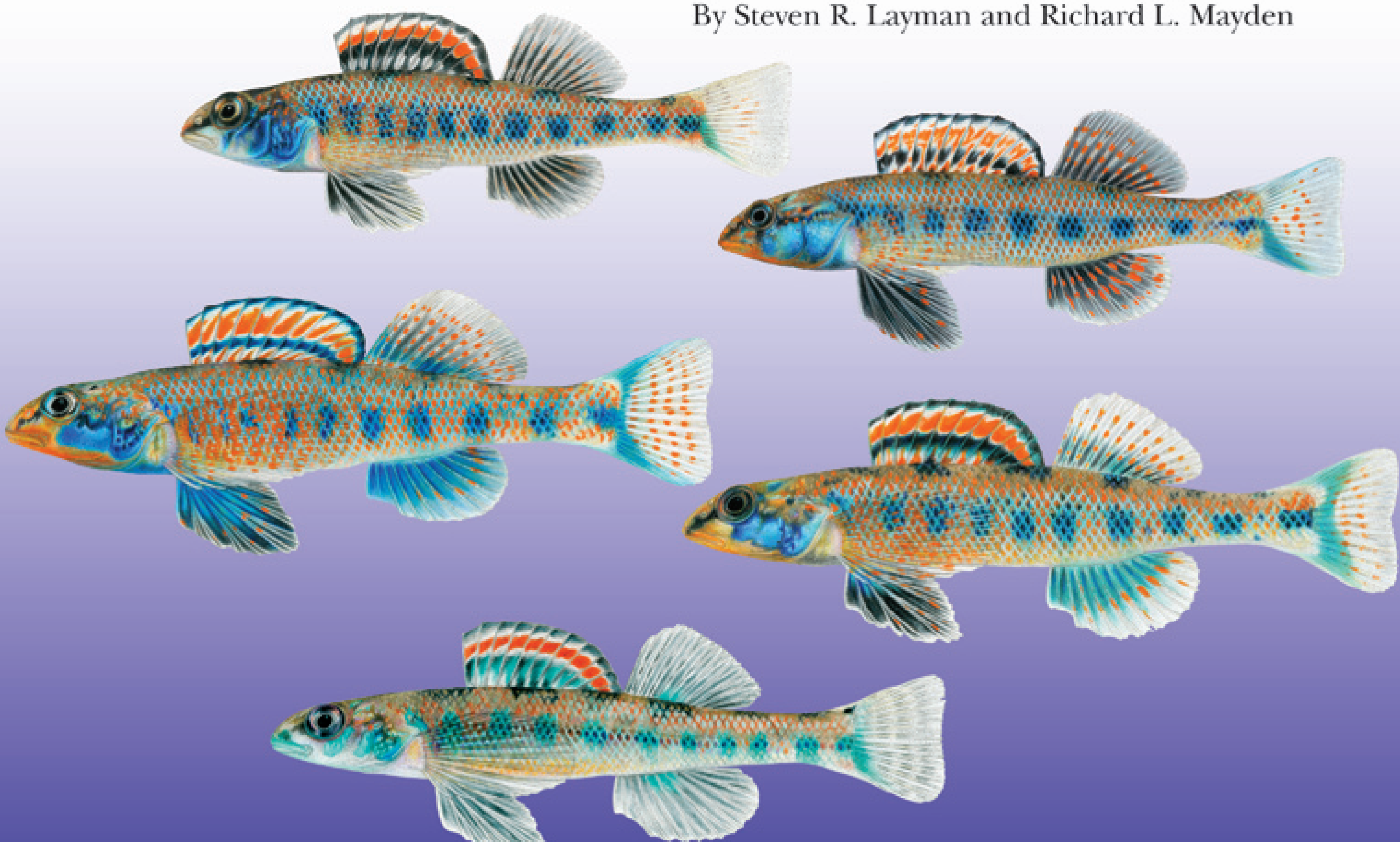

BULLETIN
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Morphological Diversity and Phylogenetics of the Darter Subgenus *Doration* (Percidae: *Etheostoma)*, with Descriptions of Five New Species

STEVEN R. LAYMAN
Geosyntec Consultants
1255 Roberts Blvd NW
Kennesaw, GA 30144 USA
slayman@geosyntec.com

RICHARD L. MAYDEN
Department of Biology
3507 Laclede Ave
Saint Louis University
St. Louis, MO 63103 USA
maydenrl@slu.edu

ABSTRACT

The evolutionary diversity and phylogenetic relationships of darters of the subgenus *Doration* were investigated using variation in morphology and male breeding colors. A revision of the subgenus is presented, with redescriptions of *Etheostoma stigmaeum*, *E. jessiae*, *E. meadiae*, descriptions of five new species, distributional data, comparisons, and a key to the species. Along with *E. akatulo*, a total of nine species are recognized in the subgenus. New species are described, including *E. obama* from the Duck River system, *E. gore* from the Cumberland River drainage, *E. jimmycarter* from the Green River drainage, *E. teddyroosevelt* from the Arkansas and upper White river drainages of the Ozark Highlands, and *E. clinton* from the upper Ouachita River system of the Ouachita Highlands. Evidence was found that specimens from Little Bear Creek, Alabama, represent pure *E. jessiae* rather than hybrids with *E. stigmaeum* from adjacent Bear Creek. Patterns of morphological and allozyme variation suggested possible introgressive hybridization between *E. jessiae* and *E. meadiae* in the Clinch River system. Phylogenetic relationships were evaluated using 34 discrete breeding color, morphological, and behavioral characters. *Doration* was supported as a monophyletic group with *E. akatulo* sister to a clade containing all other species in the subgenus. Relationships were well resolved, with the exception of a trichotomy involving new species from the Duck and Cumberland rivers and the ancestor of a clade of new species from the Green and Arkansas/White rivers.
Key Words: darters, Percidae, *Etheostoma*, *Doration*, new species, phylogenetic relationships

INTRODUCTION

Species diversity and phylogenetic relationships of darters of the subgenus *Doration* of *Etheostoma* are poorly known. *Doration* was resurrected as a subgenus by Cole (1967) to include the nominal species *Etheostoma stigmaeum* and *E. jessiae*, former members of subgenus *Boleosoma* (Bailey and Gosline, 1955). Cole (1967) diagnosed the subgenus on the basis of the elongate, tubular, genital papilla of breeding females and the development of male nuptial tubercles on pelvic and anal fin rays and ventral body scales. Howell (1968) examined meristic variation in *Doration*

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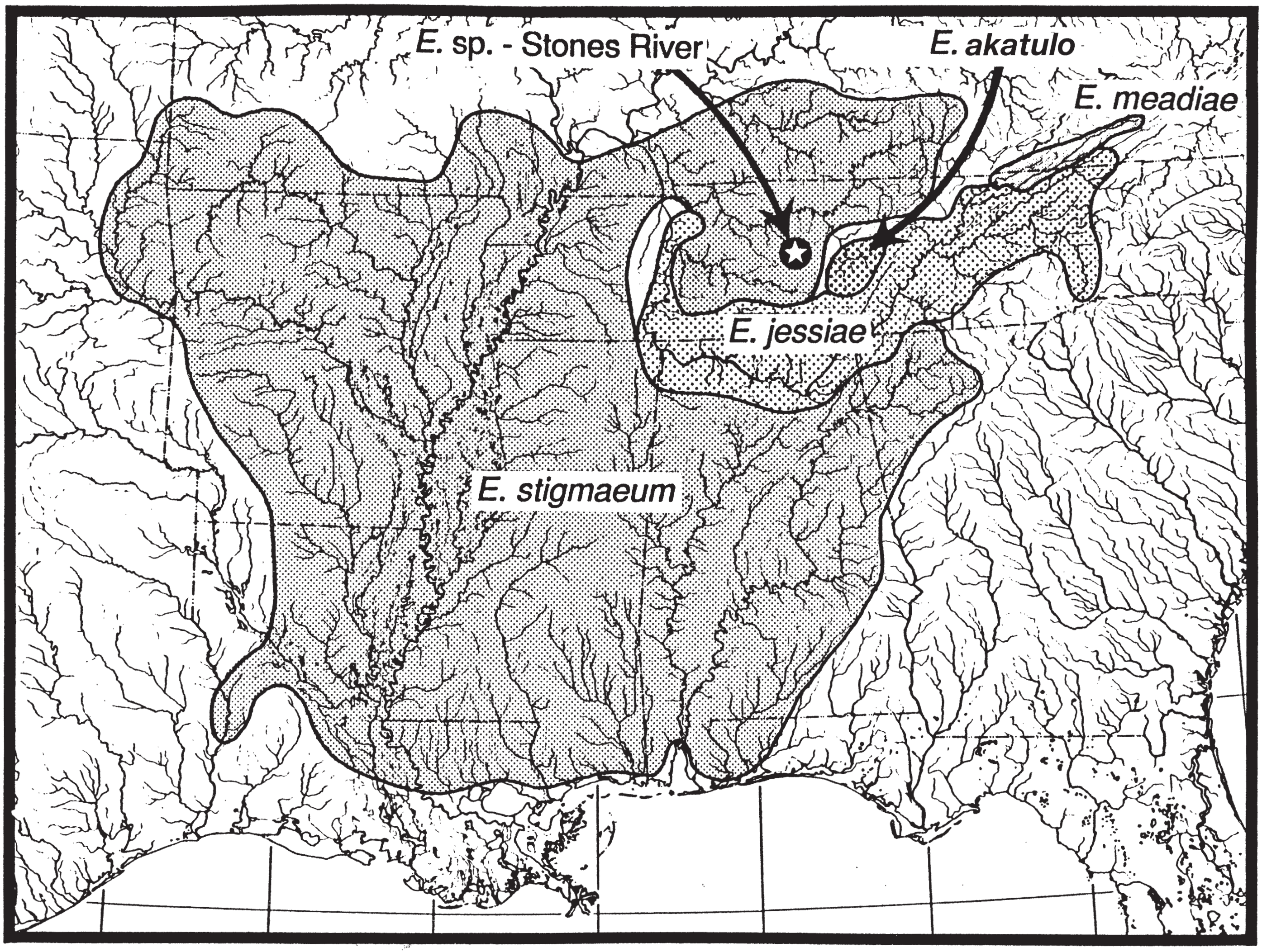

Fig. 1. Distribution of five taxonomic forms of *Doration* recognized by Howell (1980a, 1980b, 1980c) as distinct species. Map provided by Division of Fishes, University of Michigan Museum of Zoology and used with permission.

and treated the subgenus as the single polytypic species *E. stigmaeum*, consisting of three subspecies; however, others continued to recognize *E. jessiae* as a separate species (Bailey et al., 1970; Robins et al., 1980). In reassessing the status of apparent intergrades and considering evidence suggesting reproductive isolation between two sympatric forms, Howell (1980a, 1980b, 1980c) later recognized five distinct species (Fig. 1) (cited by Etnier and Starnes, 1994, as pers. comm. with Howell). These included: 1) *E. stigmaeum*, occurring from Gulf Coastal drainages, up the lower Mississippi River Basin, west into the Arkansas and White river drainages, and east into the lower Tennessee, Cumberland, and Green river drainages; 2) *E. jessiae*, endemic to the Tennessee River drainage; 3) *E. meadiae* of the upper Clinch and Powell rivers in the upper Tennessee River drainage; 4) a species endemic to Caney Fork River of the Cumberland River drainage, since described as *E. akatulo* by Layman and Mayden (2009); and 5) an undescribed *E. jessiae*-like species known only from a single collection from Stones River in the Cumberland River drainage. Most authorities continue to either recognize only *E. stigmaeum* and *E. jessiae* as species (Page, 1983; Robins et al., 1991; Mayden et al., 1992) or treat all taxa as subspecies of *E. stigmaeum* (Etnier and Starnes, 1994; Jenkins and Burkhead, 1994).

Howell's (1968) study was based mainly on preserved museum specimens. While he described male breeding coloration in Mobile Basin specimens (Howell and Boschung, 1966), his color descriptions of other *Doration* taxa (Howell, 1968) suggest he did not have fresh breeding material from throughout the range of the subgenus. Color descriptions and plates in Kuehne and Barbour (1983), Page (1983), Robison and Buchanan (1988), Burkhead and Jenkins (1991), and other sources indicate remarkable geographic variation in breeding coloration among taxa, especially within the widespread nominal form *E.*

stigmaeum. A thorough reassessment of the systematics of the subgenus using additional characters, including breeding coloration, is clearly needed.

Doration is also of special interest due to its wide distribution in highland regions east and west of the Mississippi River, and in lowland regions of the Gulf Coastal Plain and Mississippi Embayment (Fig. 1). *Doration* offers enormous potential for exploring evolutionary and biogeographic questions and the history of these regions. This paper investigates evolutionary species diversity in *Doration*, describes new species, and infers the phylogenetic relationships of species of *Doration* using characters associated with variation in morphology and breeding colors. Geographic coverage encompasses the entire range of the group and includes several regions from which specimens were unavailable to Howell (1968). A subgeneric revision is presented, with redescriptions of three nominal species and descriptions of five new species, bringing to nine the total number of species in the subgenus.

MATERIALS AND METHODS

Meristic and Morphometric Variation

Meristic data were gathered from 3,049 specimens, including 585 specimens used in the description of *Etheostoma akatulo* (Layman and Mayden 2009). Scale and fin-ray counts followed Hubbs and Lagler (1974), with the following exceptions. Transverse scales were counted from the origin of the anal fin anterodorsally to the spinous dorsal fin (Page, 1983). Cheek, nape, opercle, and belly squamation were estimated to the nearest 10%, with regions defined in Layman and Mayden (2009). Meristic counts characterized as usual occurred with a frequency of 90% or more. Morphometric data were based on 326 specimens, including 134 specimens from Layman and Mayden (2009). Twenty-eight measurements were made under a dissecting microscope using digital calipers and followed Hubbs and Lagler (1974), with the following exceptions. Body width was measured between the dorsal insertions of the pectoral fins. Trans-pelvic width was the distance between the outer bases of the pelvic spines (Bailey and Etnier, 1988). Caudal peduncle depth was measured between the dorsal and ventral insertions of the caudal fin and approximated least depth. Additional landmark-based truss measurements, taken to characterize more fully body shape (Bookstein et al., 1985), are the same as those presented in Layman and Mayden (2009).

Means of meristic counts and morphometric proportions within species were tested for sexual dimorphism using a Student's t-test. Multivariate analysis of meristic and morphometric variation among species was conducted using principal component analysis. For the meristic data, principal components were obtained from a correlation matrix; sexes were combined. The morphometric data were evaluated using sheared principal component analysis to remove the effects of size, with principal components factored from a covariance matrix of log-transformed variables (Humphries et al., 1981; Bookstein et al., 1985; program by D. L. Swofford, modified by M. L. Warren, Jr.). Sexes were analyzed separately due to significant dimorphism in body proportions. Statistical analyses were performed using SAS 5.18 and 6.07 (SAS Institute Inc., 1985, 1990).

Color descriptions and comparisons were based on original color notes and photographs of live and freshly preserved breeding specimens collected from 65 localities throughout the range of *Doration* (Fig. 2). Detailed color notes were recorded in the field for 135 adult specimens, including 100 breeding males. Adult specimens (205) were photographed, including 152 nuptial males. Photographs of preserved specimens were taken moments after fixation in strong formalin in a portable camera box designed by Page and Cummings (1984). Live specimens were photographed in daylight in a small water-filled glass tank; fish were held in position by a movable glass plate. Color comparisons were also based on color plates and/or literature accounts in Cross (1967), Page (1983), Kuehne and Barbour (1983), Johnson (1987), Robison and Buchanan (1988), and Burkhead and Jenkins (1991), and color notes and photographs provided by colleagues. Counts of lateral blotches or bars were made from the humeral area to the caudal peduncle and do not include the basicaudal bar in breeding males. Institutional abbreviations follow Leviton et al. (1985) as modified by Leviton and Gibbs (1988).

The following drainage units are used to simplify the presentation of meristic data. Eastern Gulf Coast refers to the Perdido, Escambia, and Blackwater rivers in Alabama and the Florida panhandle. Central Gulf Coast refers to the Escatawpa River, Pascagoula River, Pearl River, and Lake Pontchartrain systems in Alabama, Mississippi, and Louisiana. Eastern tributaries of the lower Mississippi Embayment include the Homochitto, Bayou Pierre, Big Black, and Yazoo river systems in Mississippi. Eastern tributaries of the upper Mississippi Embayment include the Hatchie and Clarks rivers in Tennessee and Kentucky. Western tributaries of the upper Mississippi Embayment include the Castor River, St. Francis River and adjacent lowland drainage ditches, Black River, lower White River, and Little Red River in Missouri and Arkansas. Western tributaries of the lower Mississippi Embayment include the Ouachita River and Red River-Atchafalaya River systems in Arkansas and Louisiana. Lower and middle Tennessee River refers to tributary systems from Paint Rock River downstream to Whiteoak Creek in Alabama and Tennessee (not including Duck River). Upper Tennessee River refers to tributary systems upstream of, and including, Sequatchie River in Tennessee and Virginia. Middle Cumberland River refers to tributaries upstream of Caney Fork River and downstream of Cumberland Falls in Tennessee and Kentucky. Lower Cumberland River refers to those downstream of Caney Fork River in Tennessee.

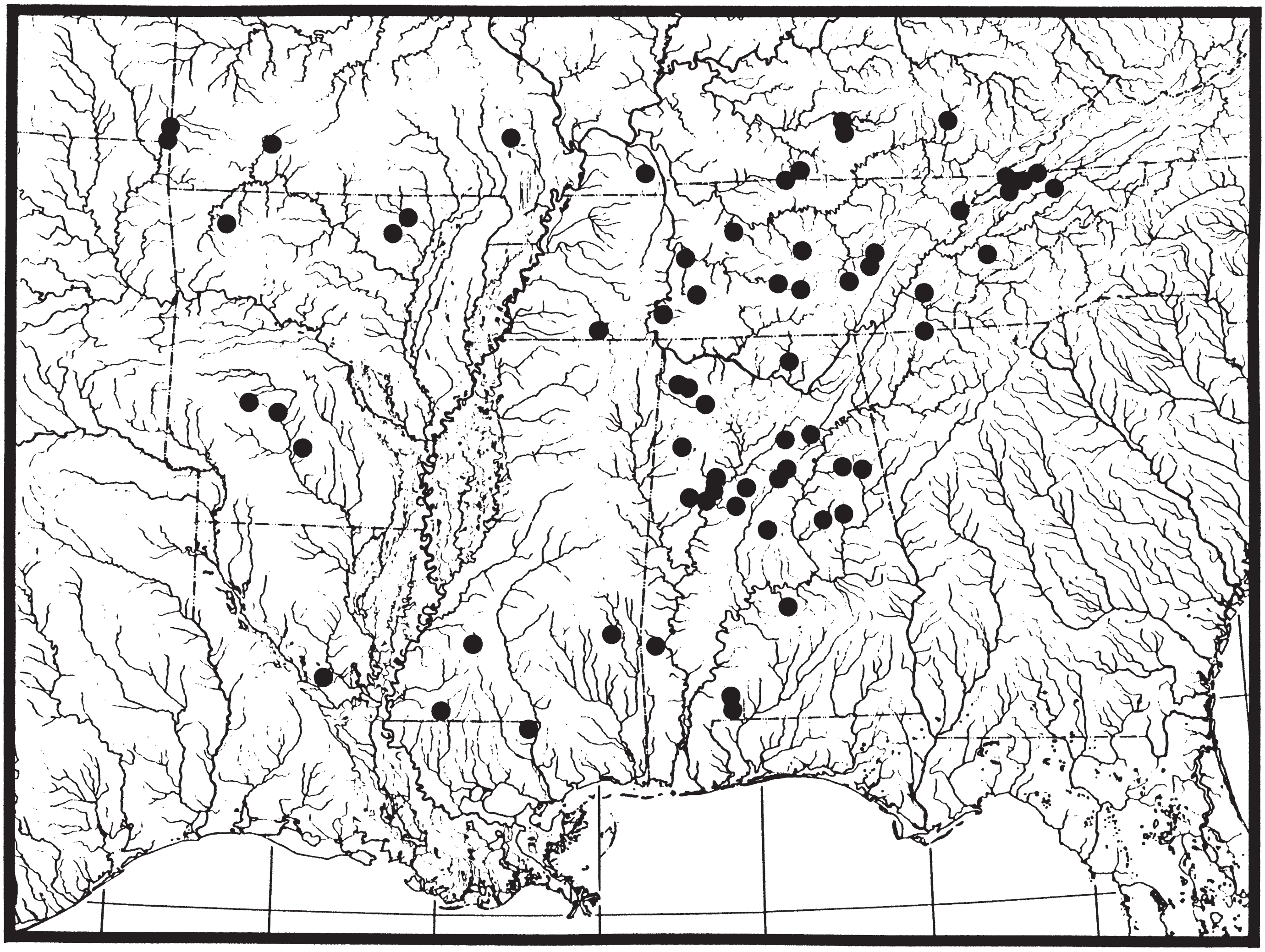

Fig. 2. Localities (65) at which color notes or photographs were taken of breeding males of *Doration* from 1990-93. Map provided by Division of Fishes, University of Michigan Museum of Zoology and used with permission.

Phylogenetic Analyses

Phylogenetic relationships were inferred under the principle of maximum parsimony (Hennig, 1966; Wiley, 1981) using outgroup comparison (Watrous and Wheeler, 1981; Maddison, et al., 1984). Discrete character variation among nine ingroup and four outgroup taxa was analyzed using the computer program PAUP, version 3.1.1 (Swofford, 1993). The branch-and-bound algorithm was used to find all optimal (minimum-length) and near-optimal trees. Bootstrap analysis (Felsenstein, 1985) was performed using the branch-and-bound option (1000 replicates) to estimate the degree of support for monophyletic groups found in optimal trees.

Outgroup taxa used in the analyses were *E.* (*Vaillantia*) *chlorosoma*, *E.* (*Boleosoma*) *nigrum*, *E.* (*Oligocephalus*) *caeruleum*, and *E.* (*Etheostoma*) *euzonum*. Subgenera *Vaillantia* and *Boleosoma* are considered to be closely related to *Doration* based on the phylogenetic hypothesis of Page (1985), in which *Doration* is sister to a clade containing *Vaillantia*, *Boleosoma*, and *Ioa*. Bailey and Etnier (1988) also provisionally associate *Doration* with a *Boleosoma* group containing *Vaillantia, Boleosoma*, and *Ioa*. In a phylogenetic analysis of a *Boleosoma* group including the subgenera *Vaillantia, Boleosoma, Ioa,* and *Ammocrypta*, Simons (1992) used *Doration* as an outgroup based on a shared osteological character indicating possible close relationship. Howell (1968) and Bailey and Etnier (1988) suggested a possible relationship between *Doration* and *Oligocephalus*, generally regarded as a more derived subgenus than those in the *Boleosoma* group; hence, *E. caeruleum* was selected as an outgroup. *Etheostoma euzonum* was also used as an outgroup to represent the *Etheostoma* group (subgenera *Etheostoma* and *Ulocentra/Nanostoma*), which is typically placed in a phyletic position just below the *Boleosoma* group (Page, 1983; Kuehne and Barbour, 1983; Bailey and Etnier, 1988).

Thirty-four discretely coded characters were used in the analyses, including 15 breeding color characters, 17 external morphological and nonbreeding pigmentation characters, and 2 behavioral characters. Characters were included that might be informative with respect to the largely unresolved relationships of the outgroups. Given the phylogenetic evidence above suggesting that *E. chlorosoma* and *E. nigrum* are more closely related to *Doration* than *E. caeruleum* or *E. euzonum*, trees were rooted using *E. caeruleum* and *E. euzonum*. This tested the monophyly of *Doration* by essentially treating *E. chlorosoma* and *E. nigrum* as part of an enlarged ingroup.

Breeding male color patterns provided a rich source of characters for inferring ingroup relationships. Although variation in color patterns was observed intraspecifically, character states were defined conservatively to include the range of variation observed within each species. Unfortunately, breeding color characters pose difficulties for polarization because ingroup character states are often not shared by outgroup taxa. In these situations polarity decisions cannot be reached, and the analysis relies heavily on the distribution of derived states for other characters that can be polarized unequivocally. These characters may ultimately drive the polarity of initially unpolarized characters in achieving a globally parsimonious tree topology.

The characters used in the phylogenetic analyses are described in Appendix A and the data matrix appears in Appendix B. Scale and fin ray counts were generally avoided as characters because overlapping frequency distributions among the ingroup species make discrete character coding particularly difficult. Character states for the outgroups were obtained from Page (1981, 1983), Page and Cordes (1983), Kuehne and Barbour (1983), Bart and Cashner (1986), and Cole (1957). Two phylogenetic analyses were performed. The first analysis treated all multistate characters as unordered to avoid assumptions regarding character evolution (unordered analysis). The second analysis treated multistate characters 7 and 12 as ordered, based on reasoning provided in Appendix A, and all other multistate characters as unordered (mixed analysis). Character state reconstructions for minimum-length trees used both ACCTRAN and DELTRAN optimization schemes (Swofford and Maddison, 1987).

All presidential photographs are public domain from the Clinton and Carter libraries or the Library of Congress.

SPECIES CONCEPTS

Herein, new species of darters of the genus *Etheostoma* are described. Many species of darters of the genera *Percina, Etheostoma, Ammocrypta,* and *Crystallaria* are commonly described and diagnosed on the basis of morphometric, meristic, and coloration differences from close relatives, as well as such seemingly minor differences between species as observed in alterations in the lateralis system (body and head) and secondary sexual color patterns in their fins that may only be present for a few weeks of the year in breeding adults.

Our theoretical concept, of species as natural kind, is the Evolutionary Species Concept, as outlined by Wiley (1978) and later modified by Wiley and Mayden (2000a, b, c) and further elaborated on by Mayden (1997, 1999, 2002). Thus, we hypothesize that species are independent evolutionary lineages. As our surrogate nominal-kind definitions of a species that we employed in the discovery and descriptions of new species as independent lineages we employed multiple operational species concepts, most notably the Phylogenetic Species Concept, the Morphological Species Concept, and, given the diagnosability of these species on the basis of allozyme variation (Layman, 1994) the Genetic Species Concept.

TAXONOMIC DESCRIPTIONS

Subgenus *Doration* Jordan

Doration Jordan, 1929:156 (new genus, type species *Boleosoma stigmaeum* Jordan).

Diagnosis.—Member of genus *Etheostoma* as diagnosed by Page (1981) and modified by Simons (1991, 1992). Breeding male distinguished by: iridescent blue or blue-green pigment on operculum, cheek, and suborbital bar; lateral series of 7–11 iridescent blue or blue-green bars or blotches extending from humeral area to caudal peduncle; blue or blue-green bar on base of caudal fin. Breeding male spinous dorsal fin with black, blue, or blue-green marginal and submedial bands; red to orange medial band. Medial caudal fin base with two small, vertically aligned, closely spaced dark spots, most conspicuous in juveniles and nonbreeding adults (obscure on breeding male). Dorsum with 6 dark brown quadrate to hourglass-shaped saddles. Breeding males often with tubercles on ventral body scales and/or pelvic and anal fin rays. Breeding female genital papilla a long conical tube. Branchiostegal rays modally 6; membranes usually narrowly connected.

Description.—Meristic and morphometric data for all taxa appear in Tables 1 through 12. Lateral line complete or incomplete; lateral scale rows 38–65. Pored lateral-line scales 20–55; unpored scales 0–28. Transverse scale rows 9–19. Scale rows below lateral line 5–10. Scale rows above lateral line 3–8. Caudal peduncle scale rows 12–22. Cheek and nape naked to fully scaled. Opercle and belly scaled. Breast naked; prepectoral area occasionally with a few scales. Dorsal fin spines 9–14; dorsal fin soft rays 8–14. Principal caudal fin rays 12–18. Anal fin spines 2; anal fin soft rays 5–11. Pectoral fin rays 11–16. Branchiostegal rays 6; membranes narrowly to moderately connected. Frenum present or absent. Vomerine teeth present; palatine teeth present or absent. Infraorbital canal uninterrupted with 8 pores. Supratemporal canal usually uninterrupted with 3 pores. Preoperculomandibular pores 9 or 10. Lateral canal pores 5, supraorbital canal pores 4, coronal pore single. Vertebrae 38–42 (Bailey and Gosline, 1955). Maximum size 35–65 mm standard length (SL), adult males typically averaging larger than females.

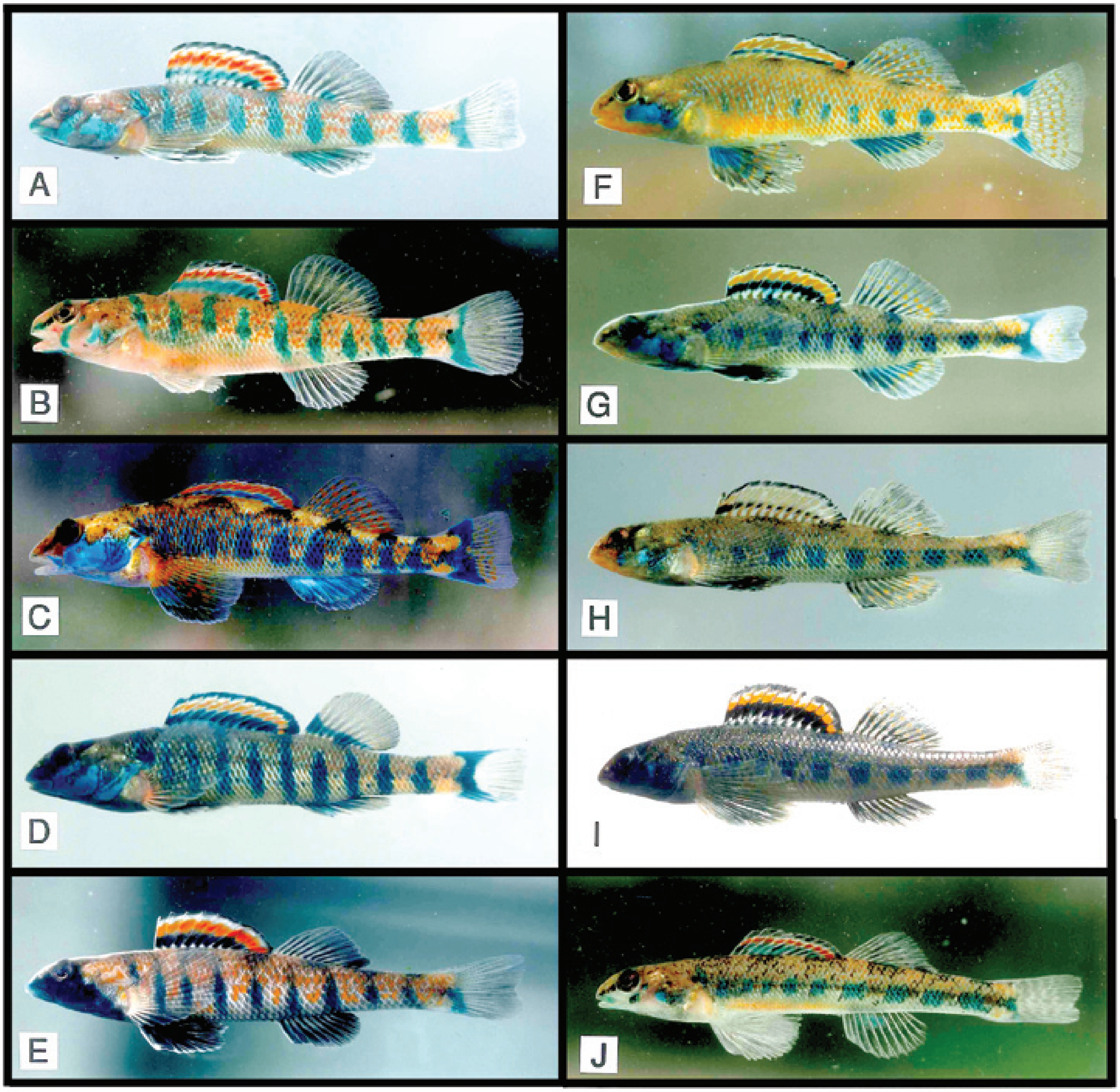

Fig. 3. Photographs of breeding males of species of *Doration*. (A) *Etheostoma stigmaeum* (Jordan, 1877), UAIC 10791.01, 44 mm SL, Hurricane Creek at US Hwy 11, Tuscaloosa County, Alabama, 5 April 1993. (B) *E. stigmaeum*, UAIC 10310.11, 48 mm SL, Big Creek at old blockaded bridge, 5.3 air km NW Pollock, Grant Parish, Louisiana, 20 March 1992. (C) *E. jessiae* (Jordan and Brayton, 1878), UAIC 10372.01, 59 mm SL, Little Bear Creek at AL Hwy 187, 8.0 km S Belgreen, Franklin County, Alabama, 14 March 1992. (D) *E. meadiae* (Jordan and Evermann, 1898), UAIC 10706.01, 51 mm SL, Blackwater Creek at TN Hwy 70, 0.5 km S Virginia line, Hancock County, Tennessee, 1 April 1993. (E) *E. akatulo* (Layman and Mayden), 2009, UAIC 10382.02, holotype, 45.5 mm SL, Collins River between mouths of Scott and Hillis creeks, 1.6 air km SE Irving College, Warren County, Tennessee, 11 April 1992. (F) *E. obama* (Mayden and Layman), UAIC 10319.09, 46 mm SL, Buffalo River at Cuba Landing Rd. (200 m upstream of bridge), Humphreys County, Tennessee, 28 March 1992. (G) *E. gore* (Layman and Mayden), UAIC 10707.01, holotype, 40.3 mm SL, Turnbull Creek 0.8 km W Kingston Springs on co. rd., Cheatham County, Tennessee, 25 April 1993. (H) *E. jimmycarter* (Layman and Mayden), UAIC 10708.01, 47.1 mm SL, Trammel Fork at Old State Rd., 1.6 km NNE Red Hill, Allen County, Kentucky, 25 April 1993. (I) *E. teddyroosevelt* (Layman and Mayden), UAIC 10460.21, holotype, 40.7 mm SL, Spring River at KS Hwy 96, Cherokee County, Kansas, 24 March 1991. (J) *E. Clinton* (Mayden and Layman), UAIC 10302.05, holotype, 33.7 mm SL, Caddo River at AR Hwy 182, 3.2 km N Amity, Clark County, Arkansas, 4 April 1992.

Nonbreeding coloration.—Nonbreeding males and females exhibit little dimorphism in coloration, except as noted. Base color of upper body tan or straw to olivaceous; small melanophores along scale edges, imparting overall sand-grained appearance. Dorsum with 6 dark brown quadrate to hourglass-shaped saddles. First saddle located anterior to spinous dorsal fin; second saddle just anterior to middle of spinous dorsal fin; third saddle at posterior end of spinous dorsal fin; fourth saddle at middle of soft dorsal fin; fifth saddle posterior to soft dorsal fin; sixth saddle at dorsal insertion of caudal fin. Sides with usually 8–10 (7–11) quadrate blotches extending from lateral line ventrad 2–3 scale rows, formed by crosshatching of dark pigment along scale edges (W-, V-, and X-shaped markings); blotches may have tinge of blue. Dark X-markings may also occur between lateral blotches in line with ventral edges. Sides and upper body also with many smaller scattered dark brown markings. A dusky blotch may also be present on body just anterior to caudal fin base. Medial base of caudal fin with two small vertically aligned, closely spaced dark spots, sometimes appearing fused or obscured by dusky pigment; most distinct in juveniles and nonbreeding adults. Lower body light straw to white; males may be lightly dusky. Head dark above and light below, with dark preorbital bars extending onto lip but not meeting at midline, dark suborbital bar or spot, and dark postorbital spot. Tinge of blue on operculum and preoperculum.

Male spinous dorsal fin with faint dusky marginal band, narrow clear submarginal band, red to orange medial band, dusky submedial band (with hint of blue in some species), and clear basal band with dusky areas in posterior portions of membranes. Female spinous dorsal fin mostly clear, with narrow red-orange or orange medial band; spines with scattered dark pigment. Male and female soft dorsal fin membranes clear; rays with 2–4 brown dashes. Caudal fin membranes clear; rays with 4–5 brown dashes. Anal fin membranes clear; rays with faint dusky streaks. Pelvic fin membranes mostly clear; rays with a few dark dashes or specks. Pectoral fins mostly clear; rays with yellow-orange hue basally; rays with a few dark dashes or specks.

Breeding coloration.—Breeding males (Fig. 3) with lateral blotches becoming iridescent blue or blue-green, quadrate or vertically elongate; blue or blue-green bar developing on base of caudal fin. Sides with scattered red to orange spots and X-markings; scales between lateral blotches outlined in powder blue. Iridescent blue or blue-green on operculum, pre-operculum, and cheek; present or absent on lips and mid-gular area. Base color of face gray, tangerine orange, or entirely blue. Body dusky overall. Genital papilla a small dusky or pale conical flap.

Spinous dorsal fin with distinctive banding coloration: thin black, blue, or blue-green marginal band; narrow white submarginal band; wide red to orange medial band; wide black, blue, or blue-green submedial band; clear basal band with black or orange pigment in posterior portions of membranes. Second dorsal, caudal, anal, and pectoral fins with or without bright orange spots. Second dorsal and anal fins with or without basal blue or blue-green pigment.

Breeding females much more subdued, developing only hint of male breeding coloration. Genital papilla a long pale conical tube.

Tuberculation.—Breeding males may develop tubercles or tubercular ridges on pelvic and anal fin rays. Pelvic spine with overall thickened epidermis; rays 1–3 with narrow epidermal ridges on ventral surfaces, covering distal half to entire length. Rays 3–5 with broken ridges and/or small tubercles on medial-distal ventral surfaces. Anal spines and rays with narrow ridges and/or distinct rounded tubercles, usually on distal half to four-fifths; may be more weakly developed posteriorly. Ridge surfaces may contain keratin and possibly function as breeding tubercles.

Nuptial males may also develop crescent-shaped, mound-like, or rounded to pointy tubercles along posterior edges of ventral body scales. At maximum development, tubercles on belly scales, scales above anal fin base, and ventral caudal peduncle scales; development typically weakest on latter two regions. Variations on this basic pattern of tubercle distribution and form are described under species accounts.

Habitat.—Species of *Doration* are found in clear, medium to large sized creeks and small rivers of moderate gradient. All species occupy similar habitats. Adults and juveniles occur in slow to moderate current over mixtures of sand, gravel, and occasionally silt, typically just downstream of riffles, in moderate runs, gentle riffles, or along margins of pools. In early spring breeding adults occupy gravelly runs and shallow riffles with moderately swift current where spawning presumably occurs. Winn (1958a, 1958b) observed spawning behavior in aquarium-held adults of the newly described species *E. jimmycarter* from the Green River. The male mounts the female in a horizontal position, the two vibrate, and eggs are deposited in gravel. Based on the collection of nuptial males and gravid females, spawning probably begins as early as February in southern populations and terminates by late May or June in northern populations.

Comparisons.—*Doration* is morphologically most similar to subgenera *Vaillantia* and *Boleosoma*. Species of all three subgenera possess 6 dorsal saddles and lateral blotches formed by X-markings, and all were once classified in subgenus *Boleosoma* (Bailey and Gosline, 1955). Species of *Doration* differ from those of *Vaillantia* and *Boleosoma* in breeding males having bright iridescent blue or blue-green lateral body and head coloration (versus lacking in *Vaillantia* and *Boleosoma*; *E. davisoni* with light green iridescence); breeding males having black, blue, or blue-green bands separated by a bright red to orange band in the spinous dorsal fin (vs. lacking); breeding males often developing tubercles on ventral body scales (vs. lacking); and breeding females having a long tubular genital papilla (vs. rugose, spatulate in *Vaillantia* and flat, bifurcate in *Boleosoma*). Species of *Doration* differ further in developing a pair of small dark spots on the base of the caudal fin (may be obscured in breeding males), a character also recognized by Douglas (1974) in *E. stigmaeum*. This pair of spots is a highly useful field character in distinguishing juveniles and small adults of *Doration* from sympatric *E. nigrum* or *E. chlorosoma*, which develop a single irregular blotch. However, it is not useful in separating *E. stigmaeum* from *E. davisoni*, a species that also possesses two small basicaudal spots.

Species of *Doration* differ further from those of *Vaillantia* and *Boleosoma* in consistently having two anal spines (vs. 1 in some species). They differ further from species of *Boleosoma* in breeding males developing tubercles on pelvic and anal fin rays. They differ further from species of *Vaillantia* in preorbital bars not meeting at midline.

Key To Species Of *Doration*

1. Premaxillary frenum present .... Go to 2
   Premaxillary frenum absent .... Go to 3
2. Anal fin soft rays modally 9; cheek squamation 10–30%, usually 1–18 scales on upper cheek; caudal peduncle scales usually 17 or more; principal caudal fin rays 15 .... *Etheostoma jessiae*
   Anal fin soft rays modally 8; cheek naked, occasionally with 1–3 scales behind eye; caudal peduncle scales usually 16; principal caudal fin rays often 16–17 .... *Etheostoma meadiae*
3. Lateral line complete; cheeks fully scaled or nearly so; breeding male with continuous blue mask of pigment covering lower face, snout, and underside of head .... *Etheostoma akatulo*
   Lateral line usually incomplete, or if complete, cheeks naked or nearly so; breeding male with blue pigment on head but not as continuous mask......................... Go to 4
4. Unpored lateral scales usually 0–7 (0–13); principal caudal fin rays usually 16–17 (70% of specimens) .... *Etheostoma meadiae*
   Unpored lateral scales usually >10 (0–28); principal caudal fin rays 15... Go to 5
5. Palatine teeth present (>85% of specimens); nape naked to fully scaled; breeding male soft dorsal and caudal fins lacking bright orange spots .... Go to 6
   Palatine teeth absent (>70% of specimens); nape fully scaled or nearly so; breeding male soft dorsal and caudal fins with discrete, often bright, orange spots .... Go to 7
6. Preoperculomandibular pores 10 (>75% of specimens); anal fin soft rays modally 8; breeding male lacking thin dusky midlateral stripe running through lateral blue-green bars .... *Etheostoma stigmaeum*
   Preoperculomandibular pores 9 (>90% of specimens); anal fin soft rays modally 9; breeding male with thin dusky midlateral stripe running through lateral blue-green blotches .... *Etheostoma clinton*
7. Breeding male with base color of face gray with milky blue sheen, spinous dorsal fin lacking bright orange in basal band; scales below lateral line modally 7; transverse scales modally 13 .... *Etheostoma teddyroosevelt*
   Breeding male with base color of face tangerine orange, spinous dorsal fin with bright orange in basal band; scales below lateral line modally 6; transverse scales modally 12 .... Go to 8
8. Breeding male spinous dorsal fin with black submedial band, interrupted by orange streaks in posterior portions of membranes; breeding male soft dorsal and anal fins lacking basal blue pigment .... *Etheostoma jimmycarter*
   Breeding male spinous dorsal fin with blue in submedial band, uninterrupted by orange streaks; breeding male soft dorsal and anal fins with basal blue pigment .... Go to 9
9. Pectoral fin rays modally 15; scales above lateral line modally 5; cheek squamation 10–30%, usually 2–15 scales on upper cheek; soft dorsal rays modally 12; breeding male anal fin lacking orange spots or with weak orange spots at distal edge of basal blue band... ....*Etheostoma obama*
   Pectoral fin rays modally 14; scales above lateral line modally 4; cheek naked or nearly so, with usually 0–5 scales behind eye; soft dorsal rays modally 11; breeding male anal fin with orange spots, usually 1–2 per ray ....*Etheostoma gore*

***Etheostoma stigmaeum* (Jordan)**
Speckled Darter
Figs. 3, 4

Boleosoma stigmaeum Jordan, 1877:311 (original description from small tributaries of Etowah and Oostanaula rivers near Rome, Floyd County, Georgia); Bailey et al., 1954: 142 (designation of lectotype); Collette and Knapp, 1966: 19 (location of lectotype and paralectotypes).

Ulocentra stigmaea: Jordan and Brayton, 1878:45,82 (recorded from Alabama River basin; also known from Louisiana); Jordan and Gilbert, 1883:495 (description; distributed from Georgia to Louisiana); Jordan and Evermann, 1896:1047–1048 (description; distributed from Tennessee and Arkansas to Georgia and Louisiana); Fowler, 1907:522, fig. 5 (figure of syntype); Jordan, Evermann, and Clark, 1930:287 (distributed from Tennessee and Arkansas to Georgia and Louisiana); Fowler, 1945:37, 354–355, 369 (description; recorded from Alabama and Mississippi river basins).

Poecilichthys saxatilis Hay, 1881:495 (original description from tributary of Chickasawha River at Enterprise, Clarke County, Mississippi); Jordan and Gilbert, 1883:515–516 (description; known from Chickasawha River, Mississippi); Bailey et al., 1954:142 (synonym of *E. stigmaeum*); Collette and Knapp, 1966 (location of holotype; synonym of *E.* (*Boleosoma*) *stigmaeum*).

Etheostoma (*Etheostoma*) *saxatile*: Gilbert, 1888:57–58 (description; found in Black Warrior River, Alabama, and Saline and Ouachita rivers, Arkansas).

Etheostoma saxatile: Jordan, 1890:133 (distributed from Tennessee to Arkansas and south); Gilbert, 1891:150 (synonym of *E. stigmaeum*).

Etheostoma stigmaeum: Gilbert, 1891: 150, 155, 157 (Escambia, Alabama, and Pascagoula rivers included in range; also known from Arkansas); Bailey et al., 1954: 143 (Gulf tributaries and Mississippi Basin included in range); Cole, 1967:28–29 (removed from subgenus *Boleosoma* and placed in subgenus *Doration*); Howell, 1980c:697 (in part; systematics; distribution and habitat; biology); Page, 1983:26, 81, 238, plate 19A (in part; description; range; natural history; systematics; key; photo of breeding male from Opintoloco Cr., Alabama); Kuehne and Barbour, 1983:16, 66, 101–102, plate 13 (in part; description; distribution; natural history; systematics; key; photo of breeding male from Cottondale Cr., Tuscaloosa County, Alabama (Gilbert and Walsh, 1991)).

Doration stigmaeum: Jordan, 1929:156 (new genus: type, *Boleosoma stigmaeum* Jordan; description; distributed from Kentucky to Georgia and Alabama).

Etheostoma (*Boleosoma*) *stigmaeum*: Bailey and Gosline, 1955:15, 26, 38 (vertebral counts for specimens from Missouri, Mississippi, Alabama, and Florida); Collette, 1965:586–587 (description of breeding tubercles for specimens from Mobile Basin, Escambia River, and Bogue Chitto River); Collette and Knapp, 1966: 19 (taxonomic status of nominal species *Boleosoma stigmaeum*); Howell and Boschung, 1966:510–514 (natural intersubgeneric hybrid with *E.* (*Oligocephalus*) *whipplii artesiae*).

Etheostoma stigmaeum stigmaeum: Burkhead and Jenkins, 1991:386 (in part; found in lower Ohio and Mississippi river basins and adjacent drainages of Gulf of Mexico; not known from Virginia); Etnier and Starnes, 1994:533–537 (in part; biology; distribution and status; systematics; key; photo of nuptial male from Conasauga River, Tennessee); Jenkins and Burkhead, 1994:838 (widespread, but inhabits only lower portion of Tennessee drainage).

Nominal species *Etheostoma stigmaeum* was treated by Howell (1968) as a wide ranging subspecies, occurring from Gulf Coast drainages, up the lower Mississippi River Basin, west into the Arkansas and White rivers in the Ozark Highlands, and east into the Tennessee (Duck River and Bear Creek systems), Cumberland, and Green River drainages. Characters used to diagnose the taxon were lack of a frenum, usually less than 50% squamation of the cheek, and low counts of pored lateral-line scales. Two races were recognized on the basis of meristic differentiation, a widespread "typical race" and a Cumberland-Green River race, with one or both populations of the latter race having higher modal counts of anal soft rays (9 versus 8 in the typical race), pectoral rays (15 vs. 14), and dorsal spines (12–13 vs. 11). With respect to these characters, the Green River population was noted as being closer to nominal form *E. jessiae* than the typical race of nominal *E. stigmaeum*. Howell (1968) further noted that breeding males of the Cumberland-Green River race resemble those of nominal *E. jessiae* in having orange "blocks" of pigment on the fins and orange pigment in the base of the spinous dorsal fin.

This study indicates that nominal *E. stigmaeum*, as conceived by Howell (1968), actually represents a complex of six species. Four species are recognized from Howell's typical race, including widespread but newly restricted *E. stigmaeum*, a new species from the Arkansas and upper White rivers, a new species endemic to upper Ouachita River above the Fall Line, and a new species endemic to Duck River of the Tennessee drainage. Only ten specimens of the latter two species were available to Howell (1968). Howell's Cumberland-Green River race is recognized as two new species endemic to each of those drainages. New species from the Arkansas/upper White, Duck, Cumberland, and Green rivers all develop orange spots on the second dorsal and caudal fins, as in *E. jessiae*. *Etheostoma stigmaeum*, as redescribed below, remains the most widely distributed species of *Doration* but is herein restricted to Mobile Basin and other Gulf Coast systems, the Mississippi Embayment and highland tributaries thereof in northeastern Arkansas and southeastern Missouri, and Bear Creek of the Tennessee drainage.

Lectotype.–ANSP 20645, male, 39 mm SL, Etowah River, tributary of Coosa River near Rome, Floyd County, Georgia, summer 1876, D. S. Jordan and C. H. Gilbert; selected by Bailey et al. (1954:142).

Paralectotypes.–ANSP 20646 (3; 36–39 mm SL) (original numbers ANSP 20646–48), same data as lectotype; one syntype figured by Fowler (1907:fig. 5).

Diagnosis.—A member of the subgenus *Doration*. Breeding male distinguished by: spinous dorsal fin with blue or blue-green marginal and submedial bands, red-orange medial band, basal band lacking bright orange pigment; soft dorsal, caudal, and pectoral fins lacking distinct orange spots on rays; soft dorsal and anal fins with blue or blue-green in base of fin; face and lower head gray with blue or blue-green on operculum, preoperculum, suborbital bar, cheek, lips, and mid-gular region; vertically

Figure 4. ***Etheostoma stigmaeum*** **(Jordan, 1877). Caddo R. at US Hwy 67, 5.9 km N Arkadelphia (Ouachita River system), Clark County, Arkansas, 4 April 1992. UAIC 10379.01; male, 46 mm SL. Drawing by Joseph R. Tomelleri (americanfishes.com). Copyrighted by Joseph R. Tomelleri. Used with permission.**

elongate lateral blue or blue-green bars; basicaudal blue or blue-green bar extending from dorsal to ventral margin of caudal fin. Frenum absent. Lateral line incomplete, unpored scales modally >10. Cheek partially scaled. Palatine teeth present. Dorsal fin spines modally 11; dorsal soft rays modally 11. Anal fin soft rays modally 8. Pectoral fin rays modally 14. Principal caudal fin rays modally 15. Caudal peduncle scales modally 16. Preoperculomandibular canal pores modally 10.

Description.—Males average larger than females; largest male 48.9 mm SL, largest female 42.4 mm SL. In populations from four drainages, sexes exhibit significant dimorphism ($P<0.05$) in five to 13 body proportions (Table 12), with males almost always having larger values.

Counts for selected meristic variables in 1225 total specimens appear in Tables 1 through 10. Lateral line incomplete; lateral scale rows 38–56 scales, usually 41–51. Unpored lateral scales 0–26, usually 8–19. Transverse scale rows usually 11–15 (9–17). Scale rows below lateral line modally 6–7 (5–10). Scale rows above lateral line modally 4–5 (3–6). Caudal peduncle scale rows usually 14–18 (12–20), modally 16. Cheek squamation highly variable, usually 10–70%; usually 1–22 scales on cheek (0–37). Nape squamation highly variable, usually 20–100% (0–100). Opercle squamation 30% (1 specimen), 40 (1), 50 (2), 60 (4), 70 (24), 80 (83), 90 (524), or 100 (586); $\overline{x}$ = 93.5, SD = 7.81. Belly squamation 40% (1), 50 (2), 60 (5), 70 (36), 80 (99), 90 (322), or 100 (760); $\overline{x}$ = 94.6, SD = 8.32. Breast usually naked. Vertebrae 38–41 (Bailey and Gosline, 1955).

Dorsal fin spines modally 11 (9–13). Dorsal fin soft rays modally 11 (8–13). Principal caudal fin rays 13(1 specimen), 14 (29), 15 (1079), 16 (101), or 17 (15); $\overline{x}$ = 15.1, SD = 0.39. Anal fin spines 2; anal fin soft rays modally 8 (6–9). Pectoral fin rays modally 14 (12–15). Branchiostegal rays 6, rarely 5 or 7; membranes narrowly connected.

Frenum absent in 1206 (98%) of 1225 specimens. Vomerine teeth present; palatine teeth present in 1068 (87%) of 1225 specimens. Infraorbital canal uninterrupted with 6 (6 specimens), 7 (138), 8 (1001), 9 (75), or 10 (5) $\overline{x}$ pores; $\overline{x}$ = 7.9, SD = 0.46. Preoperculomandibular canal pores modally 10 (8–12). Supratemporal canal usually uninterrupted with 3 pores. Lateral canal pores 5, supraorbital canal pores 4, coronal pore single.

Significant differences ($P<0.05$) in mean counts between 608 males and 617 females were found in four meristic variables. Soft dorsal ray count higher in males (11.0) than females (10.9), principal caudal fin ray count higher in males (15.1) than females (15.0), anal ray count higher in males (8.1) than females (8.0), and pored lateral-line scale count higher in males (33.7) than females (33.2).

Breeding male coloration.—Spinous dorsal fin with thin gray to blue-green marginal band, with blue-green most prominent posteriorly; narrow white submarginal band; wide red-orange medial band; wide blue-green submedial band, sometimes with narrow pale zone between it and red-orange band above; narrow clear basal band with dark triangular areas in posterior portions of membranes along spines. Soft dorsal fin membranes dark gray to black basally, dusky distally; rays with scattered dark pigment; medial-distal portions of posterior rays sometimes with faint yellow-orange or gold tinge (but no distinct orange spots). Soft dorsal fin with blue-green blotch in middle base of fin just above fourth dorsal saddle, appearing to 'bleed" onto fin from saddle; peak males also with submedial blue-green in anterior two or three membranes, and sometimes extending posteriorly as faint horizontal band. Caudal fin membranes clear basally to lightly dusky distally; rays with tiny melanophores, sometimes forming dashes. Vertical blue-green bar on base of caudal fin extending from dorsal to ventral edge of fin and posteriorly along edges up to one-half or three-fourths the length of the fin; usually extending farther posteriad along ventral margin; dorsal portion of bar may be more weakly developed. Medial base of caudal fin with two dark basicaudal spots (may be obscured by blue-green basicaudal bar). Anal fin dark gray or dusky distally, bright blue-green basally; medial-distal portions of some rays may have faint yellow-orange or gold tinge (but no distinct orange spots). Pelvic fins dark gray with blue-green at bases of medial rays. Pectoral fin membranes clear to lightly dusky; rays with faint orange-yellow wash at base of fin.

Base color of cheeks, snout, underside of head, and breast dark gray. Iridescent blue-green on operculum, preoperculum, suborbital bar, anterior preorbital bar, lips, and mid-gular area. Lateral belly yellow or orange-yellow; medial belly gray. Base color of upper body straw to olivaceous. Sides with usually 8–10 vertical iridescent blue-green bars, several of these typically connecting dorsolaterally with saddles in the form of wishbones. Posterior bars may encircle caudal peduncle either ventrally or dorsally (at fifth and sixth saddles). Dusky spot or smudge often present on body just anterior of basicaudal spots. Scales between lateral bars outlined in powder blue and forming crosshatched pattern. Sides with red-orange spots and X-markings between lateral bars and extending to dorsum, often quite bright. Dorsolateral area also with many small scattered dark markings. Dorsum with 6 quadrate saddles, slightly constricted medially. Body dusky overall. Color plates of breeding males are also presented by Kuehne and Barbour (1983) and Page (1983).

Tuberculation.—As noted by Collette (1965), fin tubercles are usually more developed than ventral body scale tubercles. Pelvic fins with mostly narrow low ridges on rays 1–3 and weak broken ridges and small individual tubercles on medial-distal portions of rays 3–5. Anal fin spines and anterior rays with mostly tubercular ridges, grading into broken ridges and individual rounded tubercles on posterior rays; smaller individuals tend to show greater development of rounded tubercles. Larger individuals occasionally develop tubercles on ventral body scales. At maximum development tubercles may occur on up to 8 midventral scale rows on the posterior two-thirds of the belly, 1–2 scale rows above anal fin base, and 3–5 midventral scale rows on caudal peduncle. Well-developed tubercles have been noted on specimens collected from 31 January (Bogue Chitto, Pike County, Mississippi) to 22 May (Middle Fork Clarks River, Calloway County, Kentucky), with weak tubercles detected as late as 9 June (Stamp Creek, Bartow County, Georgia).

Variation.—Modal fin ray counts are fairly consistent throughout the range of *E. stigmaeum*, but there is considerable geographic variation in scale counts, degree of squamation, body size and shape, and breeding coloration. Specimens from eastern Gulf Coast systems have the lowest mean count of lateral scales and the lowest modal counts of transverse and caudal peduncle scales (Tables 1, 3, and 5). Specimens from Mobile Basin have the highest mean counts of transverse scales and scales below and above the lateral line (Tables 3 and 4); those from Coosa River (n = 131) of the Mobile Basin have the highest mean number of lateral scales (49.6). Within the Mobile Basin, specimens from upper Tombigbee (n = 60) and lower Tombigbee (n = 58) rivers have lower modal counts of lateral scales (43–45), transverse scales (12), and scales above (4) and below (6–7 or 6) the lateral line than any other populations. The similarity of these counts to those in specimens from Bear Creek of the Tennessee River drainage (Tables 1, 3, and 4) lend further support to the hypothesis that a portion of the Bear Creek system was captured from the adjacent upper Tombigbee River system (Wall, 1968; Starnes and Etnier, 1986). Also within Mobile Basin, specimens from the Black Warrior River system (n = 60) have the lowest modal cheek squamation (0%), lowest modal nape squamation (10%), and lowest modal counts of pectoral fin rays (13) (compare with Tables 6, 7, and 9). In eastern and western tributaries of the upper Mississippi Embayment, 24–33% of specimens have prepectoral scales versus 10% or less in all other populations. Additional breakdown of meristic data by river system is provided by Howell (1968).

Maximum adult size is greatest in the Coosa and Tallapoosa river systems of Mobile Basin. Specimens from Coosa River commonly exceed 45 mm SL, the largest specimen being a 48.9–mm SL male (n = 131); the largest specimen from Tallapoosa River (n = 60) was a 46.0–mm SL male. Maximum size in all other drainages ranges from about 39 to 45 mm SL. Proportional measurements from four drainages (Table 12) indicate that specimens from Coosa River also tend to have a longer snout and upper jaw, shorter soft dorsal fin, and a deeper caudal peduncle.

Breeding coloration varies mainly in the amount of blue-green pigment in the base of the anal fin. Breeding males from Mobile Basin typically have a wide blue-green basal band at peak development. Those from eastern and central Gulf Coast systems and much of the western Mississippi Embayment often have only a hint of blue-green in the base of the fin. Hues of blue-green coloration vary from turquoise blue to almost green, but no clear geographic trends have been identified.

Distribution.—*Etheostoma stigmaeum* occurs in Gulf Coast drainages from Pensacola Bay in Florida and Alabama west to the Red-Atchafalaya and Sabine river systems in Louisiana (Fig. 5), but excluding the Mermentau and Calcasieu rivers (Douglas, 1974). Contrary to the species account in Kuehne and Barbour (1983), it does occur in Escambia River in Alabama and Florida as well as Pond Creek, a tributary of Blackwater River just to the east in the Florida panhandle. The species is distributed north up the Mississippi River Embayment to western Kentucky and southeastern Missouri. West of the Mississippi River

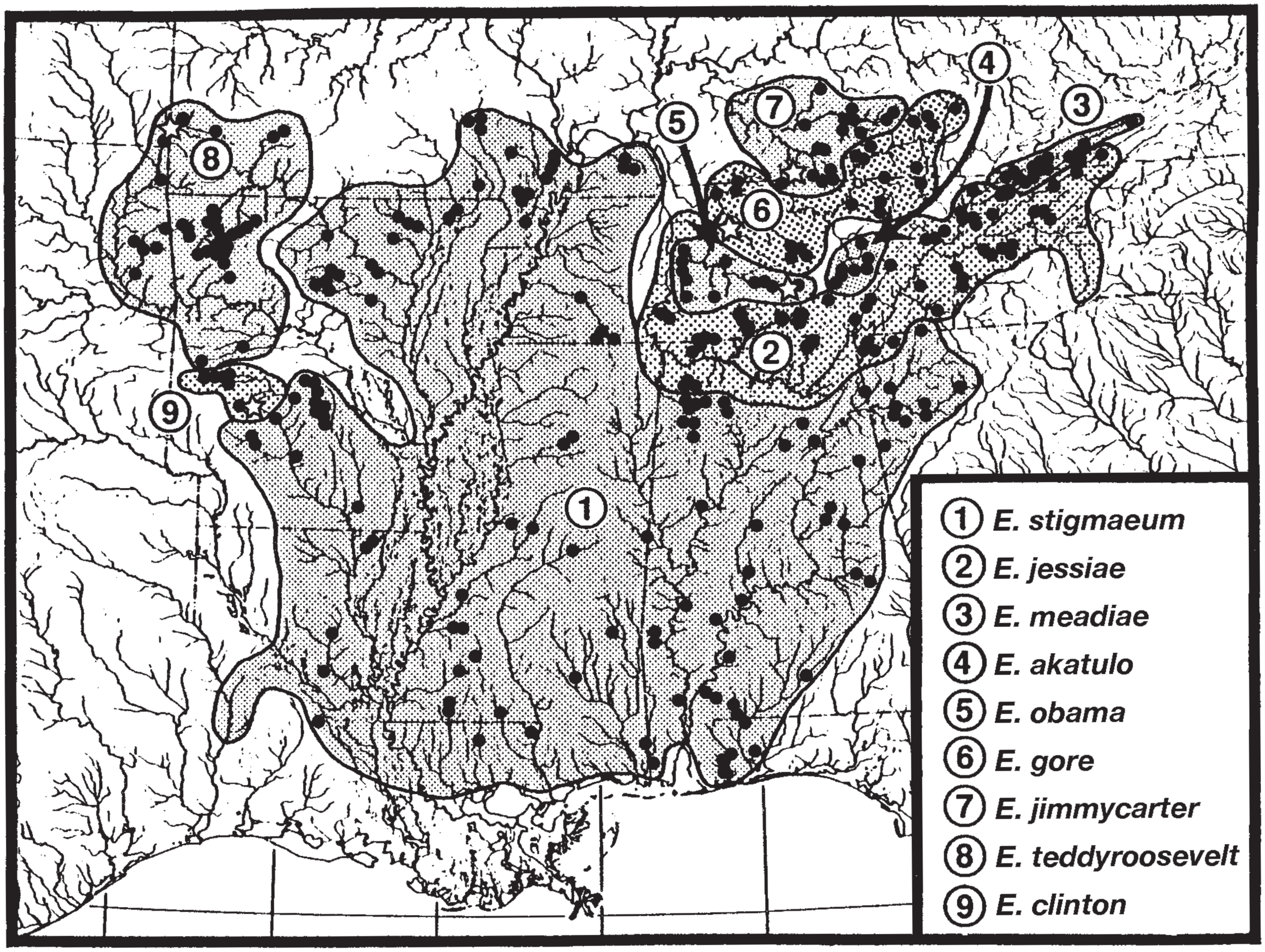

Figure 5. Distribution of nine species of *Doration*. Type localities of the five new species are indicated by stars. Stars and dots show localities of material examined. Some dots represent more than one locality. Species are identified in legend on map. Map provided by Division of Fishes, University of Michigan Museum of Zoology and used with permission.

it occurs in the Ouachita River below the Fall Line, lower White River as far upstream as (and including) Buffalo River, Little Red River, Black River, St. Francis River, Castor River, and lowland drainage ditches of southeastern Missouri. To the east *E. stigmaeum* occurs in direct tributaries of the Mississippi River from southeastern Louisiana to the Hatchie River in southwestern Tennessee. In the Tennessee drainage it occurs in Clarks River and Jonathan Creek in western Kentucky, and Bear Creek in northwestern Alabama.

Records of *E. stigmaeum* from the Sabine River system in Louisiana could not be verified. The five lots examined were misidentified specimens of either *E. chlorosoma* (NLU 14752,57493,57497; UT 91.1377) or *E. whipplei* (NLU 56431). The single lot examined by Howell (1968; NLU 4439, formerly NLSC 4439) could not be located but was presumably identified correctly, as all five specimens possessed 2 anal spines, ruling out the likelihood that they could have been *E. chlorosoma* (1 anal spine).

Comments.—Howell's (1968) original concept of *E. stigmaeum* as a polytypic species was largely based on his interpretation of a small contact zone between nominal *E. stigmaeum* and *E. jessiae* in the Bear Creek system of the Tennessee River drainage in northwestern Alabama. Six of 12 specimens he examined from Little Bear Creek possessed a frenum, which he considered the most distinctive character separating *E. stigmaeum* (frenum absent) and *E. jessiae* (frenum present). He therefore concluded that these were intergrades, and as such, provided evidence of incomplete reproductive isolation between the two taxa. However, our analysis of meristic, breeding color, and allozyme data discussed below under "CONTACT ZONES" indicates that the Little Bear Creek population actually represents "pure" *E. jessiae.*

Etheostoma jessiae (Jordan and Brayton)
Blueside Darter
Figs. 3, 6

Poecilichthys jessiae Jordan and Brayton in Jordan, 1878:227, and in Jordan and Brayton, 1878:59 (description from Chickamauga River at Ringgold, Georgia); Jordan, 1880:227 (description; distributed in Tennessee River); Jordan and Gilbert, 1883:518–519 (description; known from Chickamauga River, Georgia); Jordan, 1884:227 (description; distributed in Tennessee River; Kuhne, 1939:92 (known from Tennessee); Fowler, 1945:39, 251 (distributed in Alabama, Tennessee, and Sabine rivers, based in part on misidentifications).

Etheostoma (*Etheostoma*) *saxatile*: Gilbert, 1888:57–58 (description; distribution includes tributaries of Clinch River near Clinton, Tennessee).

Etheostoma jessiae: Jordan, 1890: 133 (description; distributed from Tennessee to Wabash Valley, Illinois and east Texas, based in part on misidentifications); Jordan and Evermann, 1896:1084 (description; distributed from Indiana to Iowa and south to Mississippi and Texas, based largely on confusion with *E. asprigene* and *E. swaini*); Evermann, 1918:317, 319, 359, 364, 368 (identification of species reported as *P. jessiae* by Jordan and Brayton (1878) from Chickamauga River at Ringgold, Georgia); Cole, 1967:28–29 (removed from subgenus *Boleosoma* and placed in subgenus *Doration*); Howell, 1980a:656 (systematics, distribution, habitat, biology); Page, 1983:26, 80, 238, plates 18G and 18H (description; range; natural history; key; photos of breeding male and female from Little Pigeon River, Sevier County, Tennessee); Kuehne and Barbour, 1983:16, 100, plate 13 (description; distribution; natural history; photo of breeding male from West Branch Shoal Cr., Lawrence County, Tennessee (Gilbert and Walsh, 1991)).

Etheostoma stigmaeum: Gilbert, 1891:150, 152 (Tennessee River drainage included in range; recorded from Cypress Creek, Florence, and Big Nance Creek, Courtland, Alabama).

Ulocentra stigmaea: Evermann and Hildebrand, 1916:449–450 (recorded from Ball Creek, tributary of Big Sycamore Creek near Tazewell, Tennessee, and Arnwine Spring Creek near Athens, Tennessee; compared with specimens from Wolf and Obeys rivers; two forms represented); Evermann, 1918:320, 321, 326, 356, 367 (identification of species recorded as *E.* (*Etheostoma*) *saxatile* by Gilbert (1888) from tributaries of Clinch River near Clinton, Tennessee; identification of species recorded as *E. stigmaeum* by Gilbert (1891) from Cypress and Big Nance creeks, Alabama; identification of species recorded as *E. saxatile* by Gilbert and Swain, 1884, unpublished, from Bull Run at Hershells, Tennessee, and Clinch River at Clinton, Tennessee).

Oligocephalus jessiae: Jordan et al., 1930:291 (distributed from southern Illinois to Georgia and Mississippi, based in part on misidentifications).

Etheostoma (*Boleosoma*) *jessiae*: Bailey and Gosline, 1955: 15, 38 (vertebral counts); Collette, 1965:570, 583, 585–586, 608 (description of breeding tubercles; systematics); Collette and Knapp, 1966:63, figure 4 (location of type material of nominal species *Poecilichthys jessiae* unknown; figure of possible syntype).

Etheostoma stigmaeum jessiae: Burkhead and Jenkins, 1991:385–387 (description; Virginia distribution and status; habitat; life history; recommendations); Etnier and Starnes, 1994:533–537 (biology; distribution and status; systematics; key; photo of female from Little River, Tennessee); Jenkins and Burkhead, 1994:838–840 (systematics; description; biology; habitat; distribution).

Syntypes.—Number and dispostion unknown, Chickamauga River at Ringgold, Georgia, summer 1877, D. S. Jordan and A. W. Brayton, assisted by C. H. Gilbert and a party of students from Butler University (Jordan and Brayton, 1878). Jordan and Brayton (1878) described the species from "Several specimens, each about two inches long, ... " Collette and Knapp (1966:63, fig. 4) failed to locate any type material but found a drawing by Ernest Copeland in the files of the USNM Division of Fishes labeled "*Poecilichthys jessiae*, Chickamauga River, Ga," They reproduced the drawing, believing that it probably represents one of the lost syntypes.

Two papers describing this species were published in the same year, but that of Jordan (1878) apparently preceded, or was intended to precede, by date that of Jordan and Brayton (1878). The latter paper references the former and indicates species authorship as Jordan and Brayton, rather than providing the notation "sp. nov." Robins et al. (1991:89) cited Jordan (1878) as the original description, pointing to an error in Jordan and Evermann (1896:1085), which gives the publication date for the species as 1877. The paper by Jordan and Brayton (1878) provides a more detailed description and includes provenance of the type specimens, information lacking in Jordan (1878). In fact, Jordan and Evermann (1896:1085) duplicate the account from Jordan and Brayton (1878) as the "original description of *Poecilichthys jessiae*." We have been unable to determine which of the 1878 papers was actually published first that year.

Diagnosis.—A member of the subgenus *Doration*. Breeding male distinguished by: spinous dorsal fin with blue marginal and submedial bands, orange medial band, basal band with bright orange pigment; soft dorsal, caudal, and pectoral fins with bright orange spots on rays; soft dorsal and anal fins with blue in base of fin; face and lower head gray with blue on operculum, preoperculum, suborbital bar, and lips (but not mid-gular region); vertically elongate lateral blue bars; basicaudal blue bar

Figure 6. ***Etheostoma jessiae*** **(Jordan and Brayton, 1878). Coal Creek along Tennessee Hwy 116, 2.1 air km SW Lake City, Morgan Co., Tennessee, 12 April 1992. UAIC 10380.01; male, 53 mm SL. Drawing by Joseph R. Tomelleri (americanfishes.com). Copyright by Joseph R. Tomelleri. Used with permission.**

extending from dorsal to ventral margin of caudal fin. Frenum usually present. Lateral line incomplete, unpored scales modally 8. Cheek partially scaled. Palatine teeth present. Dorsal fin spines modally 12–13; dorsal soft rays modally 12. Anal fin soft rays modally 9. Pectoral fin rays modally 14–15. Principal caudal fin rays modally 15. Caudal peduncle scales modally 17–18. Preoperculomandibular canal pores modally 10.

Description.—Males average larger than females; largest male 64.6 mm SL, largest female 56.1 mm SL. Sexes exhibit significant dimorphism ($P<0.05$) in 10 of 18 body proportions (Table 12), with males having longer head, snout, and upper jaw, larger spinous dorsal, anal, and pelvic fins, and deeper and wider body.

Meristic counts in 575 total specimens appear in Tables 1 through 11. Lateral line typically incomplete; lateral scale rows 41–60, usually 46–55. Unpored lateral scales 0–23, usually 1–14. Transverse scale rows usually 13–16 (11–19). Scale rows below lateral line modally 7–8 (6–10). Scale rows above lateral line modally 5–6 (4–8). Caudal peduncle scale rows usually 16–19 (14–22), modally 17–18. Cheek squamation modally 20%; usually 1–18 scales on upper cheek (0–38). Nape squamation usually 100% (70–100). Opercle squamation 10% (1 specimen), 20 (2), 30 (4), 40 (8), 50 (13), 60 (31), 70 (82), 80 (178), 90 (222), or 100 (34); $\overline{x}$ = 80.6, SD = 13.38. Belly fully scaled. Breast usually naked. Vertebrae 40–42 (Bailey and Gosline, 1955).

Dorsal fin spines modally 12–13 (10–14). Dorsal fin soft rays modally 12 (10–14). Principal caudal fin rays 12 (1 specimen), 13 (1), 14 (17), 15 (485), 16 (64), or 17 (7); $\overline{x}$ = 15.1, SD = 0.45. Anal fin spines 2; anal fin soft rays modally 9 (7–10). Pectoral fin rays modally 14–15 (13–16). Branchiostegal rays 6, rarely 5 or 7; membranes narrowly to moderately connected.

Narrow to broad frenum present in 507 (88%) of 575 specimens. Vomerine teeth present; palatine teeth present in 439 (76%) of 575 specimens. Infraorbital canal uninterrupted with 7 (32 specimens), 8 (484), 9 (54), 10 (4), or 11 (1) pores; $\overline{x}$ = 8.1, SD = 0.44. Preoperculomandibular canal pores modally 10 (8–11). Supratemporal canal usually uninterrupted with 3 pores. Lateral canal pores 5, supraorbital canal pores 4, coronal pore single.

Significant differences ($P<0.05$) in mean counts between 295 males and 280 females were found in two meristic variables. Unpored lateral-line scale counts higher in females (8.5) than males (7.4), and scales below lateral line higher in males (7.6) than females (7.4).

Breeding male coloration.—Spinous dorsal fin with thin gray to blue marginal band, with blue most developed in posterior third of fin; narrow white to clear submarginal band; wide orange medial band; wide blue submedial band with narrow irregular pale zone between it and orange band above; narrow clear basal band with prominent orange triangular areas in posterior portions of membranes along spines. Soft dorsal fin membranes dark gray; rays with 3–5 distinct bright orange spots. Soft dorsal fin with blue blotch in middle base of fin just above fourth dorsal saddle (at rays 5–7) and submedial blue pigment in anterior two or three membranes; the latter sometimes extending posteriorly to blotch at middle base of fin as horizontal band. Caudal fin membranes clear to dusky; rays with 3–4 distinct bright orange spots. Vertical blue bar on base of caudal fin extending from dorsal to ventral edge of fin and posteriorly along edges up to one-half the length of the fin; dorsal portion of bar may be more weakly developed. Anal fin dark gray distally, bright blue basally. Pelvic fins dark gray to black with blue in medial base; rays with scattered faint orange spots. Pectoral fin membranes clear to lightly dusky, rays with 5–6 distinct bright orange spots.

Base color of cheeks, snout, lips, underside of head, and breast dark gray to black. Iridescent blue on operculum, preoperculum, and suborbital bar; no blue on midgular area. Lateral belly yellow; medial belly gray. Base color of upper body straw to olivaceous or gray. Sides with usually 9–10 (8–11) vertical iridescent blue bars. Scales between lateral bars outlined in powder blue. Sides with orange markings along scale edges between lateral bars and extending to dorsum; orange becoming brighter posteriorly on caudal peduncle. Dorsolateral area also with many small dark brown and blue markings. Dorsum with 6 prominent dark brown or gray hourglass-shaped saddles. Johnson (1987) provides a color plate of a live breeding male photographed by W. N. Roston. Color plates are also provided by Page (1983) and Kuehne and Barbour (1983).

Tuberculation.—Pelvic and anal fin tuberculation primarily consists of epidermal ridges, which are often well developed. Pelvic rays 3–5 and last few anal rays occasionally with broken ridges and only rarely with a few individual distinct tubercles. As also noted by Collette (1965), ventral body scale tubercles are often well developed. At maximum development, tubercles may occur on 2 midventral scale rows behind pelvic fin bases, 11 midventral scale rows at mid-belly, 9 midventral scale rows at anus, 1–4 scale rows above anal fin, and 5–6 midventral scale rows on caudal peduncle. Well-developed tubercles have been noted on specimens collected from 3 February (Elk River, Grundy County, Tennessee) to 9 May (Lick Creek, Greene County, Tennessee), with weak tubercles detected as early as 26 January (Spring Creek, Polk County, Tennessee) and as late as 21 May (Factory Creek, Lawrence County, Tennessee).

Variation.—The most notable morphological character exhibiting geographic variation is the premaxillary frenum. Eighty-eight percent of all specimens examined (n = 575) possessed a narrow to broad frenum. In the upper Tennessee drainage, including the Clinch River system both above and below Norris Dam, this proportion is 86–98% (n = 405). In contrast, 76.5% of specimens (n = 170) from the lower and middle Tennessee drainage, including Little Bear Creek, have a usually narrow to moderate frenum. Howell (1968; 1980a) treated specimens from Little Bear Creek as intergrades or hybrids between *E. jessiae* and *E. stigmaeum* (from adjacent Bear Creek) because only six of 12 available specimens (50%) possessed a frenum. However, examination of 49 specimens from Little Bear Creek found that 69% of specimens possess a frenum. A few other populations of *E. jessiae* in the middle Tennessee drainage exhibit similar frequencies of individuals possessing a frenum but there is no clear geographic cline suggestive of a hybrid or intergrade zone. Moving up the Tennessee River from Bear Creek, proportions of specimens with a frenum are 100% in Cypress Creek (n = 10), 73% in Shoal Creek (n = 26), 100% in Bluewater Creek (n = 10), 88% in Elk River (n = 16), 65% in Paint Rock River (n = 23), and 73% in Sequatchie River (n = 26). An alternative explanation to Howell's (1968) hypothesis of hybridization, one that is supported by additional meristic, breeding color, and allozymic data discussed below under "CONTACT ZONES," is that the polymorphic condition of the frenum has been retained from the ancestor of *E. jessiae*.

Specimens of *E. jessiae* from the French Broad River system have higher scale counts than any other populations examined. Mean counts (and ranges) for 60 specimens were 53.4 (46–60) lateral scales, 15.5 (13–19) transverse scales, 8.1 (7–10) scales below the lateral line, 6.2 (5–8) scales above the lateral line, and 18.9 (16–22) caudal peduncle scales (compare with Tables 1, 3, 4, and 5). This observation led to the determination that the single record of *E. jessiae* from Stones River of the Cumberland drainage (CU 46558), thought by Howell (1980a) to represent an undescribed species similar to *E. jessiae*, was based erroneously on specimens of *E. jessiae* from Little Pigeon River of the French Broad River system (Layman, 1994). The largest specimen of *E. jessiae* is also from the French Broad River system: a 64.6–mm SL male from the Nolichucky River system (UT 91.1209). Elsewhere maximum adult size is about 57 mm SL.

Modal pectoral fin ray counts in *E. jessiae* are 15 throughout the Tennessee drainage, with the exception of Clinch River populations, where the mode is 14. This shift may due to introgressive hybridization with *E. meadiae* (Etnier and Starnes, 1994), which also has a mode of 14 and occurs farther upstream in the Clinch River system (see "CONTACT ZONES" below).

Distribution.—*Etheostoma jessiae* is endemic to the Tennessee River Drainage, occurring from White Oak Creek, Houston and Humphreys counties, Tennessee, upstream, but not including Duck River, through Alabama and Tennessee into the French Broad River in North Carolina and the Holston River in Virginia (Fig. 5). In the Bear Creek system of Alabama, *E. jessiae* occurs only in the Little Bear Creek tributary system and is parapatric with *E. stigmaeum*, which is restricted to upper Bear Creek and its tributaries; the two species have not been taken together. The historic range of *E. jessiae* extends upstream in the Clinch and lower Powell rivers to at least three tributaries of Norris Reservoir, including (Fig. 7): Cove Creek, downstream of the Clinch and Powell rivers confluence; a "pond opposite Doak's Dam" (UMMZ 103591), presumably in the Davis Creek system of the lower Powell River (possibly in the Davis Creek embayment); and Big Sycamore Creek, a tributary of the Clinch River in the upper end of the reservoir. The species was last collected in Cove and Davis creeks in 1936–37, shortly after completion of Norris Dam, and may no longer occur there due to impoundment of habitat. *Etheostoma jessiae* is parapatric with *E. meadiae*, which occurs upstream of Norris Reservoir in the Clinch and Powell rivers. Specimens from Possum Creek (CU 68500) and Cove Creek (UMMZ 130756) of North Fork Holston River, Scott County, Virginia, were verified as *E. jessiae*; Jenkins and Burkhead (1994) had

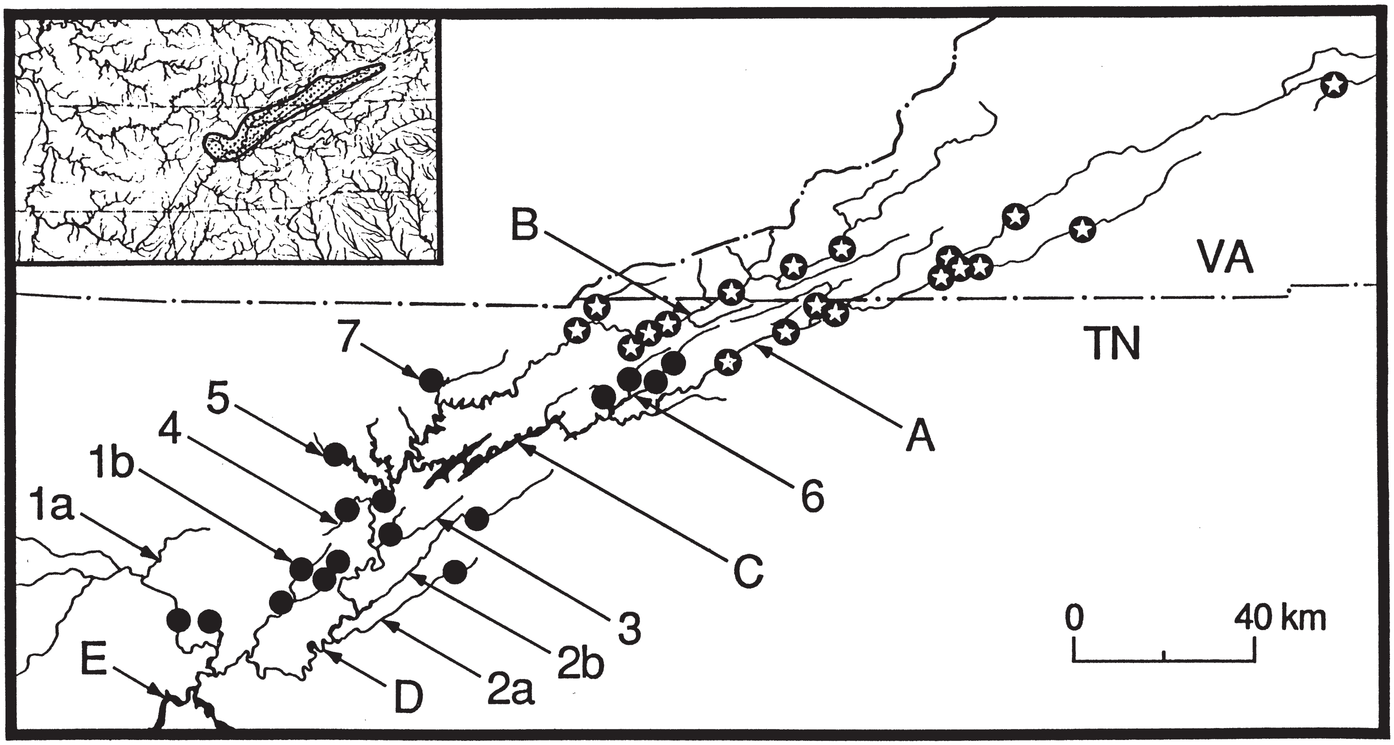

Figure 7. Distribution of *Etheostoma jessiae* (solid dots) and *E. meadiae* (dots with stars) in the Clinch and Powell rivers of the upper Tennessee River drainage. Dots indicate localities of materials examined; some represent more than one locality. Streams are: A—upper Clinch River; B—Powell River; C—Norris Reservoir; D—lower Clinch River; E—Tennessee River (Watts Bar Reservoir); 1a—Emory River; 1b—Poplar Creek; 2a—Beaver Creek; 2b—Bull Run Creek; 3—Hinds Creek; 4—Coal Creek; 5—Cove Creek; 6—Big Sycamore Creek; 7—pond opposite Doak's dam (Davis Creek).

noted possible problems with the identifications of these specimens. Three specimens from Mills River and South Fork Mills River of the French Broad River system in Henderson County, North Carolina, the only records of the species from that state, were not examined but were verified by W. M. Howell (Menhinick et al., 1974): the specimens (originally cataloged at Duke University) could not be located (W. M. Palmer, pers. comm.).

Etheostoma meadiae (Jordan and Evermann)
Bluespar Darter
Figs. 3, 8

Ulocentra meadiae Jordan and Evermann, 1898:2852 (original description from Indian Creek, basin of Powell River, Cumberland Gap, Tennessee); Jordan and Evermann, 1900:fig. 447 (figure); Evermann and Hildebrand, 1916:450 (known from Indian Creek, tributary of Powell River near Cumberland Gap); Evermann, 1918:330, 331, 356, 365, 367 (known from Indian Creek, tributary of Powell River near Cumberland Gap).

Etheostoma stigmaeum: Gilbert, 1891:150 (Tennessee River drainage included in range); Page, 1983:81, 238 (upper Clinch and Powell rivers included in distribution).

Imostoma meadiae: Jordan et al., 1930:286 (known from Indian Creek, Powell River basin, eastern Tennessee).

Doration meadiae: Kuhne, 1939:92 (known from Tennessee).

Ulocentra mediae: Fowler, 1945:251 (compared with *Poecilichthys hopkinsi*; species epithet misspelled).

Cottogaster mediae: Fowler, 1945:37 (distributed in Tennessee River drainage; species epithet misspelled).

Etheostoma (*Boleosoma*) *jessiae*: Collette and Knapp, 1966:72 (senior synonym of nominal species *Ulocentra meadiae*; location of types of *U. meadiae*).

Etheostoma meadiae: Howell, 1980b:666 (previously considered intergrade population; distributed in upper Powell and Clinch river systems, Virginia and Tennessee; habitat, biology); Mayden et al., 1992:859 (nominal species warranting additional study to determine taxonomic status).

Etheostoma stigmaeum meadiae: Burkhead and Jenkins, 1991:386–387, plate 149 (breeding male color description and plate; Virginia distribution); Etnier and Starnes, 1994:534–537 (biology; distribution and status; systematics; key); Jenkins and Burkhead, 1994: 838–840, fish 290–291, plate 28 (systematics; description; breeding male coloration; biology; habitat; distribution; halftone photos; breeding male color plate).

Etheostoma meadiae (Jordan and Evermann) was resurrected by Howell (1980b), who found the name available for a distinctive form of *Doration* from the upper Clinch and Powell rivers in the upper Tennessee drainage. Howell (1968) had earlier treated these populations as intergrades between what he considered nominal *E. stigmaeum* from the Cumberland drainage (described as a new species below) and nominal *E. jessiae*. He based this assessment on the observation that 53% of specimens possessed a frenum, which he considered the most distinctive character separating the taxa, and present-day drainage patterns suggestive of stream capture between the Cumberland and Powell rivers.

Examination of additional specimens later convinced Howell (1980b) that these apparent intergrades actually represent a distinct taxon (Etnier and Starnes, 1994). His recognition of *E. meadiae* and all other taxa of *Doration* as distinct species (Howell, 1980a, 1980b, 1980c) was bolstered by the apparent reproductive isolation of sympatric forms of *E. stigmaeum* and *E. jessiae* in the Stones River of the Cumberland drainage (Etnier and Starnes, 1994, in pers. comm. with Howell). Howell's (1980a, 1980b, 1980c) conclusions were not accompanied by supporting data. Consequently, *E. meadiae* has failed to gain recognition as a species. Furthermore, the single record of *E. jessiae* from the Stones River has been shown to be invalid, having resulted from an error in cataloging specimens from Little Pigeon River in the Tennessee River drainage (Layman, 1994).

Etheostoma meadiae is currently treated as a subspecies or race of a polytypic *E. stigmaeum* by Etnier and Starnes (1994). Jenkins and Burkhead (1994) also treat it as a subspecies but hold out the possibility of it being an intergrade. Starnes and Etnier (1986) pointed to the lack of evidence for a major stream capture between the Cumberland and Powell rivers, weakening support for Howell's intergradation hypothesis (Etnier and Starnes, 1994). Patterns of nuptial male coloration are also inconsistent with intergradation. Males of both supposed parental taxa develop orange pigment in the base of the spinous dorsal fin and bright orange spots on the soft dorsal, caudal, and pectoral fins. These features are lacking in *E. meadiae*.

Morphological and breeding color data gathered in this study indicate that *E. meadiae* warrants recognition as a distinct species. Moreover, the phylogenetic hypothesis generated using these data suggests that *E. meadiae* and *E. jessiae* are not even sister taxa. *Etheostoma meadiae* is treated herein as a distinct species restricted to the upper Clinch and Powell rivers upstream of Norris Reservoir in Tennessee and Virginia.

Holotype.—USNM 48903, male, 46 mm SL, Indian Creek, tributary of Powell River, Cumberland Gap, Tennessee, 17 October 1893, R. R. Gurley. The holotype is figured in Jordan and Evermann (1900:fig. 447).

Paratypes.—USNM 125623, male, 46 mm SL, same data as holotype, original number BF 711 (U. S. Bureau of Fisheries). According to Collette and Knapp (1966), the third type was apparently sent to Stanford University, but it was not listed among the types there by Bohlke (1953); they were unable to locate it.

Figure 8. *Etheostoma meadiae* (Jordan and Evermann, 1898). Blackwater Creek at TN Hwy 70, 0.5 km S Virginia line, Hancock County, Tennessee, 1 April 1993. UAIC 10706.01; male, 51 mm SL. Drawing by Joseph R. Tomelleri (americanfishes.com). Copyrighted by Joseph R. Tomelleri. Used with permission.

Diagnosis.—A member of the subgenus *Doration*. Breeding male distinguished by: spinous dorsal fin with blue marginal and submedial bands, orange medial band, basal band lacking bright orange pigment; soft dorsal, caudal, and pectoral fins lacking discrete orange spots on rays (although diffuse yellow-orange streaks and dashes may be present); soft dorsal and anal fins with blue in base of fin; face and lower head gray with profuse blue on operculum, preoperculum, cheeks, suborbital bar, ventrolateral head, and lips (but not mid-gular region); vertically elongate lateral blue bars; basicaudal blue bar extending from dorsal to ventral margin of caudal fin. Frenum present or absent. Lateral line usually incomplete with <8 unpored scales ($\bar{x}$ = 4.1). Cheeks usually naked. Palatine teeth usually absent, present in 33% of specimens. Dorsal fin spines modally 12; dorsal soft rays modally 11–12. Anal fin soft rays modally 8. Pectoral fin rays modally 14. Principal caudal fin rays modally 17. Caudal peduncle scales modally 16. Preoperculomandibular canal pores modally 10.

Description.—Largest male 54.5 mm SL, largest female 49.5 mm SL. Sexes exhibit significant dimorphism ($P<0.05$) in nine of 18 body proportions (Table 12), with males having longer upper jaw, larger fins, deeper body, and greater trans-pelvic width.

Meristic counts in 181 total specimens appear in Tables 1 through 11. Lateral line incomplete, occasionally complete; lateral scale rows 41–53 scales, usually 43–51. Unpored lateral scales usually 0–7 (0–13); 17% of specimens with complete lateral line. Transverse scale rows usually 12–15 (11–16). Scale rows below lateral line modally 6 (5–8). Scale rows above lateral line modally 6 (4–7). Caudal peduncle scale rows modally 16 (13–18). Cheek squamation modally 0% (0– 40); usually no more than 1–3 scales behind eye (0–5). Nape squamation modally 80– 90% (20–100). Opercle squamation 50% (1 specimen), 60 (5), 70 (5), 80 (32), 90 (106), or 100 (32); $\bar{x}$ = 88.4, SD = 8.83. Belly fully scaled. Breast usually naked.

Dorsal fin spines modally 12 (10–14). Dorsal fin soft rays modally 11–12 (9– 12). Principal caudal fin rays usually 15–17 (12–17), modally 17 (Table 11). Anal fin spines 2; anal fin soft rays modally 8 (7–9). Pectoral fin rays modally 14 (13–15). Branchiostegal rays 6, rarely 5 or 7; membranes narrowly to moderately connected.

Narrow to moderate frenum present in 106 (59%) of 181 specimens. Vomerine teeth present; palatine teeth present in 59 (33%) of 181 specimens. Infraorbital canal uninterrupted with 6 (1 specimen), 7 (14), 8 (149), 9 (15), or 10 (2) pores; $\bar{x}$ = 8.0, SD = 0.48. Preoperculomandibular canal pores modally 10 (7– 11). Supratemporal canal usually uninterrupted with 3 pores. Lateral canal pores 5, supraorbital canal pores 4, coronal pore single. No significant differences were found in mean meristic counts between 95 males and 86 females.

Breeding male coloration.—Spinous dorsal fin with narrow blue marginal band; narrow white to clear submarginal band; wide bright orange medial band; wide blue submedial band with narrow pale zone between it and orange band above; narrow clear basal band with dark pigment in posterior portions of membranes along spines. Soft dorsal fin membranes dark gray basally, dusky distally; medial-distal portions of rays with 2–3 diffuse yellow-orange dashes or streaks (no distinct bright orange spots as in *E. jessiae*). Soft dorsal fin with blue blotch in middle base of fin just above fourth dorsal saddle (at rays 6–8) and submedial blue pigment in anterior two or three membranes; the latter sometimes extending posteriorly to blotch at middle base of fin as horizontal band. Caudal fin membranes clear to dusky; rays with diffuse yellow-orange dashes but lacking distinct orange spots. Wide vertical blue bar on base of caudal fin extending from dorsal to ventral edge and extending posteriad along entire lengths of ventral and dorsal edges of fin. Anal fin dark gray distally, bright blue basally; distal portions of last 2–3 rays with faint orange-yellow dashes or streaks. Pelvic fins dark gray to black. Pectoral fin clear to lightly dusky, with faint salmon-orange in base of rays; peak males sometimes with blue on proximal bases of dorsal 2–3 pectoral fin rays.

Base color of face, snout, underside of head, and breast dark gray to black. Bright iridescent blue on operculum, preoperculum, suborbital bar, postorbital spot, cheek, lips, preorbital bar, and ventrolateral surface of head; blue nearly continuous in coverage but with intervening dark gray areas on cheek and underside of head; gular area dark gray to black. Lateral belly yellow; medial belly gray. Base color of upper body straw to dark olivaceous. Sides with usually 9–10 vertical iridescent blue bars, several connecting dorsally with saddles; posterior two bars may extend ventrally around caudal peduncle. Scales between lateral bars outlined in powder blue and forming crosshatched pattern. Lateral scales with diffuse dark orange pigment. Dorsolateral area with many small scattered dark markings. Dorsum with 6 dark saddles, irregular in shape and sometimes with blue pigment. Burkhead and Jenkins (1991) also provide a detailed description of *E. meadiae* nuptial males and a color plate under their account of *E. stigmaeum jessiae*.

Tuberculation.—Pelvic fin rays and anal fin spines and rays often have well developed tubercular ridges. Pelvic rays 4–5 may have weaker broken ridges. Rounded to crescent-shaped tubercles are typically well developed on ventral body scales. At maximum development, tubercles may occur on 2 midventral scale rows behind pelvic fin bases, 7 midventral scale rows at mid-belly, 7 midventral scale rows at anus, 1–3 scale rows above anal fin, and 3–5 midventral scale rows on caudal peduncle. Tuberculate males have been noted in collections from 1 April (Blackwater Creek, Hancock County, Tennessee) to 13 May (Copper Creek, Scott County, Virginia).

Figure 9. *Etheostoma akatulo* Layman and Mayden, 2009. Collins River between mouths of Scott and Hillis creeks, 1.6 air km SE Irving College, Warren County, Tennessee, 11 April 1992. UAIC 10382.02; holotype, male, 45.5 mm SL. Drawing by Joseph R. Tomelleri (americanfishes.com). Copyrighted by Joseph R. Tomelleri. Used with permission.

Variation.—The disjunct Powell and Clinch River populations vary mainly in the proportion of individuals possessing a frenum and counts of dorsal fin soft rays. Thirty-seven percent of specimens from Powell River have a usually narrow frenum, while 67% of those from Clinch River have a usually narrow or moderate frenum. Mean soft dorsal ray counts are 11.1 in Powell River and 11.5 in Clinch River.

Distribution.—*Etheostoma meadiae* occurs only in the Powell and Clinch River systems of the Tennessee River drainage upstream of Norris Reservoir in Tennessee and Virginia (Figs. 5 and 7). Populations in the two river systems are isolated by Norris Reservoir, with *E. jessiae* occurring in intervening tributaries of Norris Reservoir (Fig. 7). The two species are distributed parapatrically.

Etheostoma akatulo Layman and Mayden
Bluemask Darter
Figs. 3, 9

Etheostoma akatulo was diagnosed and described by Layman and Mayden (2009). It is endemic to the upper Caney Fork River system of the Cumberland River drainage, Tennessee. Meristic counts for 203 total specimens are summarized in Tables 1 through 10. This rare species presently occurs in only four isolated tributaries of Great Falls Reservoir in the eastern Highland Rim physiographic province, including Collins River, Rocky River, Cane Creek, and upper Caney Fork River (Fig. 5); it formerly occurred in the Calfkiller River.

Etheostoma obama Mayden and Layman, New species
Spangled Darter
Figs. 3, 10

Figure 10. *Etheostoma obama*, new species Mayden and Layman. Buffalo River at Cuba Landing Rd. (200 m upstream of bridge), Humphreys County, Tennessee, 28 March 1992. UAIC 10319.09; male, 46 mm SL. Drawing by Joseph R. Tomelleri (americanfishes.com). Copyrighted by Joseph R. Tomelleri. Used with permission.

Synonymy

Etheostoma stigmaeum: Gilbert, 1891:150 (Tennessee River drainage included in range); Howell, 1980c:697 (Duck River system included in distribution map); Page, 1983:81, 238 (Duck River system included in distribution map); Kuehne and Barbour, 1983:101 (Duck River system included in range map);

Etheostoma stigmaeum stigmaeum: Etnier and Starnes, 1994:534 (Duck and Buffalo river systems included in distribution).

Holotype.—UAIC 10337.29, breeding male, 42.7 mm SL, Duck River below dam at TN Hwy 64/US Hwy 231 in Shelbyville, Bedford County, Tennessee, 13 April 1991, S. R. Layman and A. M. Simons.

Paratypes.—UAIC 10337.27 (30; 26.1–43.4 mm SL), USNM 328259 (6; 33.0–42.6), same data as holotype; UT 91.1538 (22; 31.5–41.9), Duck R. at end of unnumbered co. rd., 4.0 air km SE Chapel Hill, Marshall County, Tennessee, 23 March 1978, Beets, N. M. Burkhead, J. L Harris, J. Louton, D. L Nieland, and M. G. Ryon; NLU 52970 (3; 41.7–43.5), Duck R. at Hooper Island, river km 259, Maury County, Tennessee, 23 June 1979, J. Feeman, C. Saylor, et al.; UAIC 9874.32 (33; 33.1–46.0), SIUC 22876 (5; 36.8–45.4), TU 167869 (5; 34.9–41.8), UF 100288 (5; 34.1–42.9), UMMZ 225160 (5; 35.5–45.1), Buffalo R. at mouth of Grinders Cr. and TN Hwy 99, Lewis County,

Figure 11. Barack Hussein Obama II, 44th President of the United States of America

Tennessee, 26 May 1990, S. R. Layman, R. M. Wood, and B. R. Kuhajda; INHS 79399 (13; 29.1–37.9) same locality data as preceding collection, 14 April 1978, L. M. Page and R. L. Mayden; UAIC 10319.09 (6; 32.7–45.9), Buffalo R. at Cuba Landing Rd. (200 m upstream of bridge), Humphreys County, Tennessee, 28 March 1992, S. R. Layman and C. M. Bertram.

Diagnosis.—A member of the subgenus *Doration*. Breeding male distinguished by: spinous dorsal fin with blue marginal and submedial bands, orange medial band, basal band with bright orange pigment; soft dorsal, caudal, and pectoral fins with distinct bright orange spots on rays; soft dorsal and anal fins with blue in base of fin; anal fin sometimes with orange spots or streaks on rays; face and lower head tangerine orange with blue on operculum, preoperculum, cheek, and suborbital bar (not on lips and mid-gular region); quadrate lateral blue blotches extending ventrad from lateral line scale row; basicaudal blue bar extending from dorsal to ventral margin of caudal fin. Frenum absent. Lateral line incomplete, unpored scales modally >10 (12). Cheek partially scaled. Palatine teeth usually absent; present in 29% of specimens. Dorsal fin spines modally 12–13; dorsal soft rays modally 12. Anal fin soft rays modally 9. Pectoral fin rays modally 15. Principal caudal fin rays modally 15. Caudal peduncle scales modally 16. Preoperculomandibular canal pores modally 10. Allozyme products of sIdh-A locus characterized by relative mobilities b, e, and g (Layman, 1994).

Description.—Males average larger than females; largest male 48.3 mm SL, largest female 42.9 mm SL. Sexes exhibit significant dimorphism ($P<0.05$) in 11 of 18 body proportions (Table 12), with males having longer head and upper jaw, larger fins, and deeper and wider body.

Meristic counts in 185 specimens appear in Tables 1 through 10. Lateral line incomplete; lateral scale rows 40–52, usually 44–50. Unpored lateral scales 7–27, usually 8–19. Transverse scale rows usually 12–14 (11–15), modally 12. Scale rows below lateral line modally 6 (5–8). Scale rows above lateral line modally 5 (4–6). Caudal peduncle scale rows usually 16–18 (15–20), modally 16. Cheek squamation usually 0–40% (0–70), modally 20%; usually 2–15 scales on upper cheek (0–37). Nape squamation usually 80–100% (40–100). Opercle squamation 0% (1 specimen), 40 (2), 50 (2), 60 (9), 70 (6), 80 (30), 90 (111), or 100 (24); $\overline{x}$ = 86.1, SD = 12.64. Belly fully scaled. Breast usually naked.

Dorsal fin spines modally 12–13 (10–14). Dorsal fin soft rays usually 11–12 (10–13), modally 12. Principal caudal fin rays 12 (2 specimens), 13 (1), 14 (13), 15 (149), or 16 (20); $\overline{x}$ = 15.0, SD = 0.55. Anal fin spines 2; anal fin soft rays modally 9 (8–11). Pectoral fin rays modally 15 (13–16). Branchiostegal rays 6, rarely 5 or 7; membranes narrowly to moderately connected.

Frenum absent in 177 (96%) of 185 specimens. Vomerine teeth present; palatine teeth present in 54 (29%) of 185 specimens. Infraorbital canal uninterrupted with 7 (21 specimens), 8 (151), 9 (11), or 10 (2) pores; $\overline{x}$ = 8.0, SD = 0.47. Preoperculomandibular canal pores modally 10 (8–11). Supratemporal canal usually uninterrupted with 3 pores. Lateral canal pores 5, supraorbital canal pores 4, coronal pore single.

Significant differences ($P<0.05$) in mean counts between 98 males and 87 females were found in two meristic variables. Mean principal caudal fin ray count higher in males (15.1) than females (14.9), and mean anal ray count higher in males (9.1) than females (8.8).

Breeding male coloration.—Spinous dorsal fin with thin gray to blue marginal band, blue concentrated posteriorly; narrow white to clear submarginal band; wide bright orange medial band; wide blue submedial band, with narrow pale zone between it and orange band above; narrow clear basal band with bright orange triangular areas in posterior portions of membranes along spines. Soft dorsal fin membranes dark gray basally, dusky distally; rays with 3–5 bright orange spots. Soft dorsal fin with blue area in middle base of fin just above fourth dorsal saddle and submedial blue blotch in anterior membranes. Caudal fin membranes clear basally to dusky in distal portion; rays with 3–5 prominent orange spots. Vertical blue bar on base of caudal fin extending from dorsal to ventral edge and posteriorly along edges up to one-half the length of the fin; dorsal portion may be more weakly developed. Anal fin dark gray to black distally, blue in basal three-fourths of fin; an orange streak or spot may occur on posterior 2–3 rays at distal margin of the blue basal band. Pelvic fins dark gray to black, bright blue basally; rays with faint orange spots. Pectoral fin membranes clear to lightly dusky; rays with bright orange spots for most of their lengths.

Base color of cheeks, snout, lips, and underside of head tangerine orange. Prominent iridescent blue on operculum, preoperculum, and suborbital bar. In peak males, iridescent blue extends from operculum anteriorly across cheek to beneath eye, forming solid blue bar that contrasts sharply with bright orange lower face and underside of head. No blue on lips, snout, or mid-gular area. Breast black, sometimes with iridescent blue on anterior portion. Lateral belly yellow-orange; medial belly dark gray to black. Base color of upper body straw to olivaceous. Sides with 8–10 quadrate blue bars, extending from lateral line ventrad 2–3 scale rows. Posterior two bars may encircle caudal peduncle ventrally. Scales between lateral bars with powder blue along edges, forming crosshatched pattern. Sides with profuse bright orange spots and markings between lateral blotches and extending to dorsum; orange particularly conspicuous on caudal peduncle. Dorsolateral area also with scattered dark gray and brown markings. Dorsum with 6 dark saddles, medially constricted, sometimes irregularly shaped; blue from lateral bars may span some saddles.

Tuberculation.—Pelvic fins with mostly narrow low ridges on rays 1–3 and weak broken ridges and small individual tubercles on medial-distal portions of rays 3–5. Anal fin spines and anterior rays usually with tubercular ridges, grading into broken ridges and individual rounded tubercles on posterior rays; smaller individuals tend to develop short ridges and rounded tubercles on most rays. Ventral body scale tubercles typically not as well developed, occurring on up to 4 midventral scale rows on posterior half of belly. Tuberculate males have been found in collections from 7 March to 20 May (Duck River, Marshall and Bedford counties, Tennessee).

Distribution.—This species is endemic to the Duck and Buffalo Rivers of the Tennessee River drainage, Tennessee (Fig. 5). In the Duck River it occurs below Normandy Dam in the Nashville Basin and western Highland Rim downstream past the confluence of Buffalo River to the backwaters of Kentucky Lake. It occurs in the Buffalo River, located wholly on the western Highland Rim, from upper reaches downstream to its mouth. *Etheostoma obama* is distributed parapatrically with *E. jessiae*, which occurs in Tennessee River tributaries upstream, and in at least one tributary downstream (Whiteoak Creek), of Duck River.

Etymology.—The common name spangled darter refers to the bright orange spots adorning the body and fins of breeding males. The species epithet is a noun in apposition that honors President Barack Obama (Fig. 11), the 44th President of the United States of America, and his environmental leadership and commitment during challenging economic times in the areas of clean energy, energy efficiency, environmental protection and humanitarian efforts globally, and especially for the people of the United States.

Comments.—Only five specimens from the Duck River system were available to Howell (1968), and presumably because they lacked a frenum he treated them as nominal *E. stigmaeum*. Etnier and Starnes (1994) examined 46 additional specimens from the system and reported modal counts of dorsal fin spines, dorsal fin soft rays, anal fin rays, and pectoral fin rays that are closer to those of *E. jessiae*. They suggested possible intergradation between nominal *E. stigmaeum*, invading from the Cumberland River (recognized herein as a new species), and *E. jessiae*. Examination of 185 specimens, observations of breeding colors in the upper and lower reaches of the system, and survey of allozyme variation (Layman, 1994) indicate that the population from the Duck River system is distinguishable and diagnosable as a species. The phylogenetic hypothesis presented below suggests that meristic similarities between *E. obama* and *E. jessiae* may best be explained by more recent common ancestry of *E. obama* with *E. jessiae* than with nominal *E. stigmaeum*.

Etheostoma gore Layman and Mayden, New species
Cumberland Darter
Figs. 3, 12

Figure 12. *Etheostoma gore,* new species Layman and Mayden. Turnbull Creek 0.8 km W Kingston Springs on co. rd., Cheatham County, Tennessee, 25 April 1993. UAIC 10707.02; male, 40.3 mm SL. Drawing by Joseph R. Tomelleri (americanfishes.com). Copyrighted by Joseph R. Tomelleri. Used with permission.

Synonymy

Etheostoma stigmaeum: Gilbert, 1891:150 (Cumberland River drainage included in range); Kirsch, 1893:262, 265, 268 (recorded from Smith Fork of lower Caney Fork River, Obeys River, Eagle Creek, Wolf River, Willis Creek and four tributaries of Big South Fork of the Cumberland River); Bailey et al., 1954:143 (Cumberland drainage included in range); Comiskey and Etnier, 1972:143 (reported from Big South Fork of the Cumberland River): Clay, 1975:361–362 (Cumberland drainage, Kentucky, included in distribution); Howell, 1980c:697 (Cumberland drainage included in distribution): Page, 1983:81,238 (Cumberland drainage included in distribution); Kuehne and Barbour, 1983:101, plate 13 (Cumberland drainage included in range; photo of breeding male from North Fork Rockcastle River, Jackson County, Kentucky (Gilbert and Walsh, 1991)); Burr and Warren, 1986:322 (Cumberland drainage included in distribution).

Ulocentra stigmaea: Evermann, 1918:330, 356, 367 (identification of species recorded as *E. stigmaeum* by Kirsch (1893) from the Cumberland River; reported from Stones River near Nashville, Gilbert and Swain, 1884, collectors).

Etheostoma stigmaeum stigmaeum: Etnier and Starnes, 1994:534 (Cumberland drainage, excluding Caney Fork, included in distribution).

Holotype.—UAIC 10707.02, breeding male, 40.3 mm SL, Turnbull Creek 0.8 km W Kingston Springs on co. rd.,

Figure 13. Albert Arnold "Al" Gore, Jr., 45th Vice-President of the United States of America. Courtesy : William J. Clinton Presidential Library.

Cheatham County, Tennessee, 25 April 1993, S. R. Layman and E. B. Jones.

Paratypes.—UAIC 10707.01 (14; 33.6–38.9 mm SL), same data as holotype; UAIC 9863.26 (19; 29.8–37.9), USNM 328260 (4; 34.0–38.8), UT 91.4452 (4; 35.3–40.5), SIUC 22877 (4; 35.9–37.3), same locality data as holotype, 21 May 1990, S. R. Layman, B. R. Kuhajda, and R. M. Wood; UMMZ 175059 (10; 29.7–37.8), Red R. on state rd. just SE Keysburg, Kentucky, Robertson County, Tennessee, 21 June 1957, C. R. Gilbert and F. A. Gilbert; CU 37282 (12; 33.5–42.8), East Fork Stones R. at US Hwy 231, 9.6 km N Murfreesboro, Rutherford County, Tennessee, 26 March 1961, W. J. Richards, N. R. Foster, and L. W. Knapp; INHS 87340 (4; 37.4–39.4), East Fork Stones R. 1.6 km NW Readyville, Rutherford County, Tennessee, 6 May 1981, M. E. Retzer and L. M. Page.

Diagnosis.—A member of the subgenus *Doration*. Breeding male distinguished by: spinous dorsal fin with blue marginal and submedial bands, orange medial band, basal band with bright orange pigment; soft dorsal, caudal, and pectoral fins with distinct bright orange spots on rays; soft dorsal and anal fins with blue in base of fin; anal fin with distinct orange spots on rays; face and lower head tangerine orange with blue on operculum, preoperculum, cheek, and suborbital bar (not on lips and mid-gular region); quadrate lateral blue blotches extending ventrad from lateral line scale row; basicaudal blue bar extending from dorsal to ventral margin of caudal fin. Frenum absent. Lateral line incomplete, unpored scales modally>10 (11). Cheek naked or nearly naked. Palatine teeth absent. Dorsal fin spines modally 12; dorsal soft rays modally 11. Anal fin soft rays modally 8–9. Pectoral fin rays modally 14. Principal caudal fin rays modally 15. Caudal peduncle scales modally 16. Preoperculomandibular canal pores modally 10. Locus sIdh-A fixed for allele f (Layman, 1994).

Description.—Males average larger than females; largest male 42.8 mm SL, largest female 41.2 mm SL. Sexes exhibit significant dimorphism (P<0.05) in 12 of 18 body proportions (Table 12), with males having longer head and upper jaw, taller spinous dorsal fin, larger anal, pelvic, and pectoral fins, and deeper and wider body. Females have greater distance between spinous dorsal and soft dorsal fin origins.

Meristic counts in 195 total specimens appear in Tables 1 through 10. Lateral line incomplete; lateral scale rows 40–53, usually 42–50. Unpored lateral scales 5–28, usually 8–18. Transverse scale rows usually 12–14 (10–15), modally 12. Scale rows below lateral line usually 6–7 (5–9), modally 6. Scale rows above lateral line usually 4–5 (3–6), modally 4. Caudal peduncle scale rows usually 14–17 (13–18), modally 16. Cheek squamation usually 0–20% (0–40), modally 0%; usually no more than 5 scales behind eye (0–10). Nape squamation usually 70–100% (30–100). Opercle squamation 20% (1 specimen), 50 (2), 60 (7), 70 (12), 80 (37), 90 (92), or 100 (44); $\overline{x}$ = 87.3, SD = 11.55. Belly fully scaled. Breast naked.

Dorsal fin spines usually 11–12 (10–14), modally 12. Dorsal fin soft rays usually 11–12 (10–13), modally 11. Principal caudal fin rays 14 (3 specimens), 15 (167), 16 (21), 17 (3), or 18 (1); $\overline{x}$ = 15.1, SD = 0.46. Anal fin spines 2; anal fin soft rays modally 8–9 (5–10). Pectoral fin rays modally 14 (13–15). Branchiostegal rays 6, rarely 5 or 7; membranes narrowly to moderately connected.

Frenum absent in all 195 specimens. Vomerine teeth present; palatine teeth absent in 185 (95%) of 195 specimens. Infraorbital canal uninterrupted with 6 (1 specimen), 7 (9), 8 (171), 9 (13), or 10 (1) pores; $\overline{x}$ = 8.0, SD = 0.39. Preoperculomandibular canal pores modally 10 (8–11). Supratemporal canal uninterrupted with 3 pores, rarely interrupted. Lateral canal pores 5, supraorbital canal pores 4, coronal pore single.

Significant differences (P<0.05) in mean counts between 105 total males and 90 total females were found in two meristic variables. Mean dorsal spine count higher in males (11.8) than females (11.6), and mean anal ray count higher in males (8.6) than females (8.4).

Breeding male coloration.—Spinous dorsal fin with thin black and blue marginal band; narrow white to clear submarginal band; wide bright orange medial band; wide blue to black submedial band; narrow clear basal band with orange triangles in posterior portions of membranes along spines. Soft dorsal fin dark gray basally to dusky distally; rays with 2–4 distinct bright orange spots. Caudal fin membranes dusky; rays with 1–3 bright orange spots alternating with dusky dashes. Vertical blue bar on base of caudal fin extending from dorsal to ventral edge and posteriorly along edges of fin; dorsal portion may be more weakly developed in smaller males. Two small dark basicaudal spots may be obscured by basicaudal blue band. Anal fin dark gray distally, blue basally; rays with orange spots or streaks at distal edge of blue band. Pelvic fins dark gray to black with blue in base of fin; distal portions of rays with small orange streaks or spots. Pectoral fin membranes clear to lightly dusky; rays with 3–5 bright orange spots.

Base color of cheeks, snout, lips, and underside of head bright tangerine orange. Iridescent blue on operculum, preoperculum, and suborbital bar; this pigment continuous across cheek in larger specimens, contrasting sharply with orange lower head; no blue on lips, snout, or mid-gular area. Breast dark gray to black. Lateral belly yellowish; medial belly gray. Base color of upper body straw to olivaceous. Sides with usually 8–9 iridescent blue quadrate blotches, extending from lateral line ventrad 2–3 scale rows. Dusky smudge or spot often present on body just anterior of basicaudal spots. Scales between lateral blotches outlined in powder blue, forming crosshatched pattern. Sides with small orange spots and X-markings between lateral bars and extending to dorsum; orange is particularly prominent on caudal peduncle. Dorsolateral area also with many small scattered dark markings. Dorsum with 6 dark hourglass-shaped saddles. A color plate of the breeding male of this species also appears in Kuehne and Barbour (1983).

Tuberculation.—Pelvic fins with usually narrow low ridges on rays 1–3 and small rounded tubercles on medial-distal portions of rays 3–5. Anal fin spines and rays 1–2 or 1–4 usually with tubercular ridges; all other rays dominated by distinct rounded tubercles. Tubercles may also develop on ventral body scales. At maximum development, rounded to crescent-shaped tubercles occur on up to 7 midventral scale rows on posterior two-thirds of belly, 1–2 scale rows above anal fin base, and 3- 4 midventral scale rows on caudal peduncle. Tuberculate males have been found in collections from 15 March (Rockcastle River, Rockcastle County, Kentucky) to 24 May (East Fork Stones River, Rutherford County, Tennessee), with weak tubercles detected as late as 13 June (Buck Creek, Pulaski County, Tennessee).

Distribution.—*Etheostoma gore* occurs in the Cumberland River drainage below Cumberland Falls from Rockcastle River in Kentucky downstream to Red River in Kentucky and Tennessee (Fig. 5). It appears to be absent from Caney Fork River, a major southern tributary in Middle Tennessee, but specimens of *E. stigmaeum* reported by Kirsch (1893) from lower Caney Fork River (disposition unknown) probably represented this species rather than *E. akatulo*, which is endemic to the system above Great Falls (Layman et al., 1993; Layman and Mayden, 2009). *Etheostoma gore* was once thought to have been sympatric in East Fork Stones River with an undescribed *E. jessiae*-like form (Howell, 1968; 1980a), but the single record of the latter was shown to be invalid as a result of a cataloging error (Layman, 1994).

Etymology.— The common name Cumberland darter refers to the species' endemic distribution in the Cumberland River drainage. The species epithet is a noun in apposition that honors Al Gore, the 45th Vice President of the United States of America (Fig. 13), serving with President Bill Clinton, and his environmental vision, commitment, and accomplishments throughout decades of public service and his role in educating the public and raising awareness on the issue of global climate change.

Etheostoma jimmycarter Layman and Mayden, New species
Bluegrass Darter
Figs. 3, 14

Figure 14. *Etheostoma jimmycarter*, new species Layman and Mayden. Little Barren R. at KY Hwy 70, Sulphur Well, Metcalfe County, Kentucky. 15 March 1990. UAIC 9852.14; male, 47 mm SL. Drawing by Joseph R. Tomelleri (americanfishes.com). Copyrighted by Joseph R. Tomelleri. Used with permission.

Synonymy

Etheostoma stigmaeum: Woolman, 1892:260, 288 (reported from Big Barren River, Drake Creek, Little Barren River, and Green River, Kentucky); Bailey et al., 1954:143 (Green River drainage included in range); Bailey and Gosline, 1955:15, 26, 38 (vertebral counts for specimens from Peters Creek, Barren River system, Kentucky); Collette, 1965:586–587 (description of breeding tubercles includes specimens from East Fork Barren and Green rivers, Kentucky); Clay, 1975:361–362 (Green River drainage included in distribution); Howell, 1980c:697 (Green River drainage included in distribution); Page, 1981:9, 10, 12, 15, 33, 47, 53, 58, 63, 68 (specimens from Barren River, Kentucky used in phenetic and cladistic analyses of darter subgenera; morphological characters); Page, 1983:81, 238, plate 19B (Green River drainage included in distribution map; photo of female from West Fork Drakes Creek, Sumner County, Tennessee); Kuehne and Barbour, 1983:101 (Green River drainage included in distribution); Burr and Warren, 1986:322 (Green River drainage included in distribution).

Ulocentra stigmaea: Evermann, 1918:356,367 (identification of species reported as *E. stigmaeum* by Woolman (1892) from Green River Basin, Kentucky).

Etheostoma (*Doration*) *saxatile*: Winn, 1958a:191–192, 197, 209 (reproductive habits); Winn, 1958b:156, 159, 160–161, 164–165, 167–170, 172–173, 176–177, 179–180, 182, 185–188 (reproductive habits; systematic significance).

Figure 15. James Earl "Jimmy" Carter, Jr., the 39th President of the United States of America

Etheostoma stigmaeum stigmaeum: Etnier and Starnes, 1994:534 (Barren and Green river systems included in distribution).

Holotype.—UAIC 10708.01, breeding male, 47.1 mm SL, Trammel Fork at Old State Rd., 1.6 km NNE Red Hill, Allen County, Kentucky, 25 April 1993, S. R. Layman and E. B. Jones.

Paratypes.—UAIC 10708.02 (34; 31.3–41.6 mm SL), SIUC 22878 (10; 32.6–46.5), same data as holotype; UAIC 9853.19 (46; 31.5–44.1), INHS 32134 (10; 32.8–42.3), UF 100289 (10; 35.9–43.5), USNM 328261 (10; 33.5–43.5), same locality data as holotype, 16 March 1990, S. R. Layman, R. L. Mayden, B. R. Kuhajda, and R. M. Wood; NLU 18876 (32; 29.2–51.8), Trammel Fk. 32 km E Franklin on KY Hwy 100, Allen County, Kentucky, 9 April 1971, B. Wallus and D. Wallus; TU 81925 (23; 27.7–41.8), UT 91.780 (45; 30.0–44.8), Middle Fork Drakes Cr. 1.2 km upstream of KY Hwy 265, 4.3 km SE Gold City, Allen County, Kentucky, 14 April 1973, Etnier, Hoyt, Oakberg, Taylor, Thompson, Stiles; UMMZ 165344 (38; 28.7–47.7), East Fork Barren R. 8.0 km NW Tompkinsville, Monroe County, Kentucky, 6 April 1953, R. M. Bailey, D. Bailey, H. E. Winn, J. Keleher.

Diagnosis.—A member of the subgenus *Doration*. Breeding male distinguished by: spinous dorsal fin with black marginal band, orange medial band, black submedial band interrupted by vertical orange streaks extending from medial band above to basal band, basal band with bright orange pigment; soft dorsal, caudal, and pectoral fins with distinct bright orange spots on rays; soft dorsal and anal fins lacking blue pigment; anal fin with many distinct orange spots on rays; face and lower head tangerine orange with blue on operculum, preoperculum, cheek, and suborbital bar (not on lips and mid-gular region); quadrate lateral blue blotches extending ventrad from lateral line scale row; blue wedge on ventral half of caudal fin base but not developed dorsally. Frenum absent. Lateral line incomplete, unpored scales modally >10 (14). Cheek usually naked. Palatine teeth absent. Dorsal fin spines modally 12–13; dorsal soft rays modally 11. Anal fin soft rays modally 8. Pectoral fin rays modally 15. Principal caudal fin rays modally 15. Caudal peduncle scales modally 16. Preoperculomandibular canal pores modally 10.

Description.—Males average larger than females; largest male 49.0 mm SL, largest female 46.5 mm SL. Sexes exhibit significant dimorphism ($P<0.05$) in eight of 18 body proportions (Table 12), with males having longer head and upper jaw, larger spinous dorsal, anal, and pelvic fins, deeper body, and greater trans-pelvic width.

Meristic counts in 209 specimens appear in Tables 1 through 10. Lateral line incomplete; lateral scale rows 40–51, usually 42–49. Unpored lateral scales 9–24, usually 11–19. Transverse scale rows usually 11–14 (10–16), modally 12. Scale rows below lateral line modally 6 (5–8). Scale rows above lateral line 4–6, modally 5. Caudal peduncle scale rows usually 14–16 (13–18), modally 16. Cheek squamation 0–20%, modally 0%; usually no more than 4 scales behind eye (0–9). Nape squamation usually 80–100% (40–100). Opercle squamation 20% (1 specimen), 50 (2), 60 (5), 70 (14), 80 (27), 90 (126), or 100 (34); $\overline{x}$ = 87.6, SD = 10.53. Belly fully scaled. Breast usually naked. Vertebrae 40–42 (Bailey and Gosline, 1955).

Dorsal fin spines modally 12–13 (11–14). Dorsal fin soft rays usually 11–12 (10–13), modally 11. Principal caudal fin rays 14 (3 specimens), 15 (170), 16 (28), or 17 (8); $\overline{x}$ = 15.2, SD = 0.51. Anal fin spines 2; anal fin soft rays usually 8–9 (7–9), modally 8. Pectoral fin rays usually 14–15 (13–16), modally 15. Branchiostegal rays 6, rarely 5 or 7; membranes narrowly to moderately connected.

Frenum absent in 204 (98%) of 209 specimens. Vomerine teeth present; palatine teeth absent in 202 (97%) of 209 specimens. Infraorbital canal uninterrupted with 7 (10 specimens), 8 (179), or 9 (20) pores; $\overline{x}$ = 8.0, SD = 0.38. Preoperculomandibular canal pores modally 10 (8–11). Supratemporal canal usually uninterrupted with 3 pores. Lateral canal pores 5, supraorbital canal pores 4, coronal pore single.

A significant difference ($P<0.05$) in mean infraorbital canal pore counts between 103 males and 106 females was found. Males have higher count (8.1) than females (8.0).

Breeding male coloration.—Spinous dorsal fin with thin gray to black marginal band; wide orange medial band; black submedial band with orange extending through posterior portions of membranes from band above into base of fin; clear basal band with vertical orange streaks in posterior portions of membranes. Soft dorsal fin membranes dark gray to black; rays with 2–4 distinct bright orange spots. Caudal fin membranes clear to lightly dusky; rays with 2–3 bright orange spots. Blue bar or wedge on base of caudal fin extending ventroposteriorly from two small dark spots at medial fin base (sometimes obscured by blue and dusky pigment) to ventral edge of fin; may be hint of dorsal blue wedge in larger peak males, but never fully developed. Anal fin dark gray to black; typically 2 (1–3) bright orange spots per ray in distal 2/3 of fin. Pelvic fins dusky gray to black; rays with orange spots or faint streaks. Pectoral fin membranes clear to lightly dusky; rays with 2–4 distinct orange spots or dashes.

Base color of cheeks, snout, lips, and underside of head tangerine orange. Iridescent blue on operculum, preoperculum, and suborbital bar. Breast dark gray to black. Lateral belly orange-yellow; medial belly gray. Base color of upper body straw to olivaceous. Sides with 8–10 iridescent blue quadrate lateral blotches, extending from lateral line ventrad 2–3 scale rows. Dusky to blue smudge or spot often present just anterior of basicaudal spots. Scales between lateral blotches outlined in powder blue. Sides with scattered orange spots and X-markings between lateral blotches and extending to dorsum; orange prominent on caudal peduncle. Sides and dorsolateral area also with scattered dark markings. Dorsum with 6 dark brown or black saddles, somewhat hourglass-shaped.

Tuberculation.—Pelvic fins with mostly narrow low ridges on rays 1–3 and weak broken ridges and rounded tubercles on medial-distal portions of rays 3–5. Anal fin spines and anterior rays usually with tubercular ridges, giving way to broken ridges and individual rounded tubercles on posterior rays; some specimens with rounded tubercles on all rays. Posterior belly scales occasionally with weak tubercles, observed on up to 3 midventral scale rows. Winn (1958b) also reported tubercles from the pelvic and anal fins. Tuberculate males have been taken in collections from 10 March (tributary of Russell Creek, Adair County, Kentucky) to 24 May (Little Barren River, Green County, Kentucky).

Distribution.— *Etheostoma jimmycarter* is endemic to the Green River drainage of Kentucky and Tennessee, occurring mainly in the Highland Rim physiographic province (Fig. 5). It is distributed widely in the upper Barren and upper Green rivers, and is also found in the upper Rough River, a tributary of lower Green River (Burr and Warren, 1986). Specimens from Rough River have not been examined.

Etymology.— The name bluegrass darter refers to the range of the species lying mostly within Kentucky, nicknamed the "Bluegrass State." The species epithet is a noun in apposition that honors President Jimmy Carter (Fig. 15), the 39th President of the United States of America, and his environmental leadership and accomplishments in the areas of national energy policy and wilderness protection, and his life-long commitment to social justice and basic human rights.

Etheostoma teddyroosevelt Layman and Mayden, New species
Highland Darter
Figs. 3, 16

Figure 16. *Etheostoma teddyroosevelt*, new species Layman and Mayden. Shoal Creek at KS Hwy 26 at Schermerhorn Park, 3.2 km S Galena, Cherokee County, Kansas, 24 March 1991. UAIC 10072.15; male, 47 mm SL. Drawing by Joseph R. Tomelleri (americanfishes.com). Copyrighted by Joseph R. Tomelleri. Used with permission.

Synonymy

Etheostoma stigmaeum: Bailey et al., 1954:143 (eastern Oklahoma and southern Missouri included in range); Bailey and Gosline, 1955:15, 26, 38 (vertebral counts for specimens from Illinois River, Oklahoma); Cross and Minckley, 1958:104, 107–108 (reported from Shoal Creek and Spring River, Kansas; description; nuptial coloration; habitat); Collette, 1965:586–587 (description of breeding tubercles includes specimens from Spring River, Kansas); Cross, 1967: 303–304 (distributed in Spring River and Shoal Creek, Kansas; description; male breeding coloration; habitat; figure); Branson, Triplett, and Hartmann, 1969:457, 467 (common in the Neosho River system; possibly entered Neosho River via headwater exchange from White River); Miller and Robison, 1973:214–215 (northeastern Oklahoma included in distribution; description; halftone plate); Pflieger, 1975:309–310 (southwestern Ozarks included in distribution); Howell, 1980c:697 (Arkansas and upper White river drainages included in distribution map); Page, 1983:81, 238 (Arkansas and upper White river drainages included in distribution map); Kuehne and Barbour, 1983:101 (Arkansas and upper White river drainages included in range map); Robison and Buchanan, 1988:441–442 (Arkansas and upper White River drainages included in distribution map; photo of breeding male from upper White River drainage, Missouri (W. N. Roston, pers. comm.)).

Figure 17. Theodore "Teddy" Roosevelt, the 26th President of the United States of America

Etheostoma saxatile: Metcalfe, 1959:393 (Spring River, Kansas as westernmost record of species).

Etheostoma stigmaeum stigmaeum: Etnier and Starnes, 1994:534 (Arkansas and White river systems of southwestern Missouri included in range).

Holotype.—UAIC 10460.21, breeding male, 40.7 mm SL, Spring River at KS Hwy 96, Cherokee County, Kansas, 24 March 1991, S. R. Layman, B. R. Kuhajda, A. M. Simons, R. M. Wood.

Paratypes.—UAIC 10460.16 (5; 32.0–42.6 mm SL), USNM 328262 (4; 34.8–43.4), UT 91.4453 (4; 35.1–42.9), same data as holotype; KU 3597 (9; 34.1–36.8), same locality data as holotype, 7 April 1956, F. B. Cross and class; UAIC 10072.15 (7; 29.1–42.1), INHS 32135 (4; 34.9–43.2), SIUC 22879 (4; 34.9–42.1), Shoal Cr. at KS Hwy 26 at Schermerhorn Park, 3.2 km S Galena, Cherokee County, Kansas; TU 92739 (3; 31.5– 38.9), Clear Cr. at Savoy, tributary to Illinois R., below dam, Washington County, Arkansas, 9 May 1970, Strawn and Galloway; NLU 48970 (6; 29.8–42.2), Illinois R. at US Hwy 62, Cherokee County, Oklahoma, 28 November 1981, G. Varney, K. Kessler, E. Grissom, and J. Wise; UMMZ 137865 (19; 32.6–39.9), Illinois R. near mouth of Swimmer's Cr., Sequoyah County, Oklahoma, 12 April 1941, Oklahoma A&M University Field Class.

Diagnosis.—A member of the subgenus *Doration*. Breeding male distinguished by: spinous dorsal fin with black marginal and submedial bands, orange medial band, basal band lacking bright orange pigment; soft dorsal, caudal, and pectoral fins with subdued but usually discrete orange spots on rays; soft dorsal and anal fins lacking blue pigment; anal fin with subdued orange spots on rays; face and lower head dark gray with milky blue sheen; deep blue on operculum, preoperculum, cheek, and suborbital bar (not on lips and mid-gular region); quadrate lateral blue blotches extending ventrad from lateral line scale row; blue wedge on ventral half of caudal fin base but not developed dorsally. Frenum absent. Lateral line incomplete, unpored scales modally >10 (16). Cheek usually naked. Palatine teeth usually absent; present in 16% of specimens. Dorsal fin spines modally 11–12; dorsal soft rays modally 11. Anal fin soft rays modally 8. Pectoral fin rays modally 14. Principal caudal fin rays modally 15. Caudal peduncle scales modally 16. Preoperculomandibular canal pores modally 10.

Description.—Males average larger than females; largest male 43.4 mm SL, largest female 41.5 mm SL. Sexes exhibit significant dimorphism ($P<0.05$) in eight of 18 body proportions (Table 12), with males having longer head, snout, and upper jaw, deeper caudal peduncle, larger anal and pelvic fins, and greater trans-pelvic width. Females have greater distance between spinous and soft dorsal fin origins.

Meristic counts in 172 total specimens appear in Tables 1 through 10. Lateral line incomplete; lateral scale rows 41–56, usually 45–51. Unpored lateral scales 9–22, usually 12–19. Transverse scale rows usually 12–15 (11–17), modally 13. Scale rows below lateral line modally 7 (5–10). Scale rows above lateral line modally 5 (4–6). Caudal peduncle scale rows usually 15–17 (14–19), modally 16. Cheek squamation usually 0% (0–30); usually no more than 2 scales behind eye (0– 15). Nape squamation usually 50–100% (10–100). Opercle squamation 10% (1 specimen), 30 (1), 40 (1), 50 (3), 60 (6), 70 (14), 80 (38), 90 (81), or 100 (27); $\overline{x}$ = 84.9, SD = 13.31. Belly squamation 80% (1), 90 (4), or 100 (167); $\overline{x}$ = 99.7, SD = 2.13. Breast usually naked. Vertebrae 39–41 (Bailey and Gosline, 1955).

Dorsal fin spines usually 11–12 (10–13). Dorsal fin soft rays usually 11–12 (10– 13), modally 11. Principal caudal fin rays 14 (2 specimens), 15 (123), 16 (39), or 17 (8); $\overline{x}$ = 15.3, SD = 0.58. Anal fin spines 2; anal fin soft rays modally 8 (7–10). Pectoral fin rays 13–15, modally 14. Branchiostegal rays 6, rarely 5 or 7; membranes narrowly to moderately connected. Frenum absent in 168 (98%) of 172 specimens. Vomerine teeth present; palatine teeth absent in 145 (84%) of 172 specimens. Infraorbital canal uninterrupted with 6 (2 specimens), 7 (25), 8 (132), or 9 (13); $\overline{x}$ = 7.9, SD = 0.51. Preoperculomandibular canal pores modally 10 (8–11). Supratemporal canal usually uninterrupted with 3 pores. Lateral canal pores 5, supraorbital canal pores 4, coronal pore single. No significant differences were found in mean meristic counts between 98 males and 74 females.

Breeding male coloration.—Spinous dorsal fin with thin dusky to black marginal band; narrow white to clear submarginal band; wide bright orange medial band; wide black submedial band; clear basal band with black pigment extending vertically through posterior portions of membranes from submedial band to base of fin. Soft dorsal fin membranes dark gray to black basally, dusky distally; rays with 2–3 small distinct, somewhat subdued orange spots alternating with dark gray dashes. Caudal fin membranes clear to dusky; rays with alternating dusky and orange dashes or spots, about 2 orange spots per ray, most prominent in medial portions. Base of caudal fin with blue-green bar or wedge extending ventroposteriorly from two small dark spots on medial base of fin (sometimes obscured by dusky or blue pigment) to ventral edge of fin. Anal fin membranes dark gray to black basally, dusky distally; rays with 2–4 subdued orange spots on medial-distal portions. Orange spots on the anal fin are most evident in pre-breeding males, becoming suffused with melanophores at peak nuptial development. Pelvic fin membranes dark gray to black; rays with orange tinge on distal portions. Pectoral fin membranes mostly clear; rays with faint orange-yellow spots or dashes.

Base color of cheek, lateral snout, and underside of head dark gray with overall milky blue sheen. Tangerine orange, often pale, on tip of snout and medial upper lip between preorbital bars. Iridescent deep blue pigment on operculum, preoperculum, and suborbital bar. Breast dark gray. Belly and lower sides gray. Upper body dark straw to olivaceous or gray. Sides with 8–10 iridescent deep blue quadrate blotches extending from lateral line ventrad 2–4 scale rows. Smaller dark spot or blotch often present on body just anterior of basicaudal spots. Lower sides with powder blue iridescence along scale edges. Sides with orange coloration on scales between lateral blotches and extending to dorsum. Dorsolateral area also with scattered dark black and blue markings. Dorsum with 6 dark gray to black saddles, slightly constricted medially. Body often quite dark. Cross (1967) also provides a detailed description of nuptial male coloration.

Tuberculation.—Pelvic fins with mostly narrow low ridges on rays 1–3 and weak broken ridges and rounded tubercles on medial-distal portions of rays 3–5. Anal fin spines and anterior rays usually with tubercular ridges, giving way to broken ridges and individual rounded tubercles on posterior rays; some specimens with rounded tubercles on all rays. Posterior one-third to two-thirds of belly occasionally with oblong to crescent-shaped tubercles, occurring on up to 6 midventral scale rows (Collette, 1965). Cross (1967) also noted tubercles on the pelvic and anal fins. Tuberculate males have been taken in collections from 24 March (Spring River, Cherokee County, Kansas) to 22 May (King's River, Madison County, Arkansas).

Variation.—Specimens from the Arkansas River (n = 103) and upper White River (n = 69) vary mainly in nape squamation and the frequency of palatine teeth. Nape squamation is usually 90–100% (60–100) in Arkansas River specimens but varies widely in those from upper White River (10–100%). Palatine teeth are present in only 7% of Arkansas River specimens but occur in 29% of upper White River specimens.

Distribution.—*Etheostoma teddyroosevelt* occurs in the Arkansas and upper White river drainages on the Ozark Plateau of Missouri, Arkansas, extreme southeastern Kansas, and northeastern Oklahoma (Fig. 5). In the Arkansas River it occurs mainly in northern tributary systems from the Neosho River system downstream to Illinois Bayou. The species is also found in the Petit Jean and Fourche La Fave river systems, southern tributaries along the northern edge of the Ouachita Mountains. In the White River drainage, the species occurs upstream of Bull Shoals Dam.

Etymology.— The common name highland darter reflects the high fidelity of this species to streams draining the Ozark Highlands. The species epithet is a noun in apposition that honors President Theodore Roosevelt, the 26th President of the United States of America (Fig. 17), and his enduring legacy in environmental conservation and stewardship, including the designation of vast areas as national forests, wildlife refuges, national monuments, and national parks, and his efforts to forge the American Museum of Natural History, New York.

Etheostoma clinton Mayden and Layman, New species
Beaded Darter
Figs. 3, 18

Figure 18. *Etheostoma clinton*, new species Mayden and Layman. Caddo River at Arkansas Hwy 182, 3.2 km N Amity, Clark County, Arkansas, 4 April 1992. UAIC 10302.09, holotype, 33.7 mm SL. Drawing by Joseph R. Tomelleri (americanfishes.com). Copyrighted by Joseph R. Tomelleri. Used with permission.

Synonymy

Etheostoma stigmaeum: Meek, 1891:139 (scarce in Ouachita, South Fork Ouachita, and Caddo rivers); Dewey and Moen, 1978:42 (reported as uncommon in Caddo River); Harris and Douglas, 1978:58 (reported from the mountain province of the Ouachita River); Howell, 1980c:697 (upper Ouachita River included in distribution map); Page, 1983:81, 238 (upper Ouachita and upper Caddo rivers included in distribution map); Kuehne and Barbour, 1983:101 (Ouachita highland area included in range map); Robison and Buchanan, 1988:442 (upper Ouachita and upper Caddo rivers included in distribution map).

Etheostoma stigmaeum stigmaeum: Etnier and Starnes, 1994:534 (Ouachita highland area included in range).

Holotype.—UAIC 10302.09, breeding male, 33.7 mm SL, Caddo River at AR Hwy 182, 3.2 km N Amity, Clark County, Arkansas, 4 April 1992, S. R. Layman and M. A. Layman.

Paratypes.—UAIC 10302.05 (4; 28.4–32.8 mm SL), same data as holotype; NLU 18733 (40; 26.5–34.3), UMMZ 225161 (6; 27.6–32.3), USNM 328263 (6; 29.1–31.3), same locality data as holotype, 3 April 1971, D. Fruge, J. Lindley, H. Wimberly, D. Hill, J. Mulina, P. Hambrick, and T. Guidroz; UT 91.1497 (5; 27.0–31.6), Ouachita R. at McGuire Public Access Area, 3.2 km S AR Hwy 88, Polk County, Arkansas, 27 December 1978, J. L. Harris; UAIC 10063.13 (2; 29.5–29.8), Ouachita R. downstream of Co. Rd. 67 and at Mill Cr., 1.6 km S Cherry Hill, Polk County, Arkansas, 28 March 1991, S. R. Layman, B. R. Kuhajda, A. M. Simons, and R. M. Wood; NLU 58202 (27; 25.7–30.8),

Figure 19. William Jefferson "Bill" Clinton, the 42nd President of the United States of America

Ouachita R. and tributary bridge on graded rd., 0.8 km S AR Hwy 88 and 1.6 km E Pine Ridge, T2S, R27W, S9, Montgomery County, Arkansas, 8 November 1985, J. Herrock and J. Halk; UT 91.1553 (5; 26.4– 31.7), South Fork Ouachita R. at AR Hwy 379, ca. 4.0 rd. km W Mount Ida, Montgomery County, Arkansas, 1 April 1978, J. L. Harris, D. L. Nieland, and M. G. Ryon.

Diagnosis.—A member of the subgenus *Doration*. Breeding male distinguished by: spinous dorsal fin with blue-green marginal and submedial bands, red-orange medial band, basal band lacking bright orange pigment; soft dorsal, caudal, and pectoral fins lacking distinct orange spots on rays; soft dorsal and anal fins with blue-green in base of fin; face and lower head gray with blue or blue-green on operculum, preoperculum, suborbital bar, lips, and mid-gular region; quadrate lateral blue-green blotches with narrow continuous midlateral band of melanophores running through blotches; blue-green wedge on ventral half of caudal fin base but not developed dorsally. Frenum absent. Lateral line incomplete, unpored scales modally >10 (14). Cheek usually naked. Palatine teeth present. Dorsal fin spines modally 11; dorsal soft rays modally 11. Anal fin soft rays modally 9. Pectoral fin rays modally 13–14. Principal caudal fin rays modally 15. Caudal peduncle scales modally 16. Preoperculomandibular canal pores modally 9.

Description.—Largest male 34.6 mm SL, largest female 34.1 mm SL. Sexes exhibit significant dimorphism ($P<0.05$) in seven of 18 body proportions (Table 12), with males having longer upper jaw, taller spinous dorsal fin, and larger soft dorsal, anal, and pelvic fins. Females have greater distance between spinous and soft dorsal fin origins.

Meristic counts in 104 specimens appear in Tables 1 through 10. Lateral line incomplete; lateral scale rows 45–57, usually 46–53. Unpored lateral scales 11– 28, usually 11–21. Transverse scale rows usually 12–15 (11–16), modally 13–14. Scale rows below lateral line usually 6–8 (6–9), modally 8. Scale rows above lateral line usually 4–5 (3–6), modally 4. Caudal peduncle scale rows usually 15–18 (15–19), modally 16. Cheek squamation usually 0–20% (0–80), modally 0%; usually no more than 8 scales on cheek (0–28). Nape squamation highly variable, usually 0–60% (0–100). Opercle squamation 60% (1 specimen), 70 (4), 80 (25), 90 (64), or 100 (10); $\overline{x}$ = 87.5, SD = 7.21. Belly squamation 50% (1), 60 (3), 70 (13), 80 (30), 90 (46), or 100 (11); $\overline{x}$ = 84.4, SD = 10.03. Breast naked.

Dorsal fin spines modally 11 (10–13). Dorsal fin soft rays modally 11 (10–13). Principal caudal fin rays 13 (1 specimen), 14 (3), 15 (85), 16 (10), or 17 (5); $\overline{x}$ = 15.1, SD = 0.58. Anal fin spines 2; anal fin soft rays modally 9 (7–10). Pectoral fin rays modally 13–14 (11–16). Branchiostegal rays 6, rarely 5 or 7; membranes narrowly connected.

Frenum absent in 100 (96%) of 104 specimens. Vomerine teeth present; palatine teeth present in all 104 specimens. Infraorbital canal uninterrupted with 7 (21 specimens), 8 (79), or 9 (4) pores; $\overline{x}$ = 7.8, SD = 0.46. Preoperculomandibular canal pores modally 9 (8–10). Supratemporal canal usually uninterrupted with 3 pores. Lateral canal pores 5, supraorbital canal pores 4, coronal pore single.

A significant difference ($P<0.05$) in mean pored lateral-line scale counts between 51 males and 53 females was found. Males with higher count (34.1) than females (32.7).

Breeding male coloration.—Spinous dorsal fin with thin dusky gray to blue-green marginal band, with blue-green occurring posteriorly; narrow white submarginal band; moderately wide red to red-orange medial band; broad blue-green submedial band extending nearly to base of fin, sometimes with dusky zone between it and red-orange band above; narrow clear basal zone with dark pigment in posterior portions of membranes, or dusky throughout. Soft dorsal fin membranes dark gray to black basally, dusky distally; rays with alternating dark and pale dashes, 2–4 pale dashes per ray. Soft dorsal fin with blue-green blotch in middle base of fin just above fourth dorsal saddle (between rays 5–8). Caudal fin membranes clear to lightly dusky; rays with alternating dusky and pale dashes, forming 3–5 irregular pale vertical bands on fin. Base of caudal fin with blue-green bar or wedge extending ventroposteriorly from two small dark spots on medial base of fin (may be obscured by dusky and blue-green pigment) to ventral edge of fin and posteriorly along edge to one-fourth the length of the fin; blue-green may be most intense at medial base of fin. Anal fin dusky gray to black with blue-green pigment basally. Pelvic fin membranes dusky gray; rays with wash of iridescent yellow. Pectoral fin membranes clear to lightly dusky; rays with orange-yellow wash at base of fin.

Base color of cheeks, snout, underside of head, and breast dusky gray; breast typically darker. Iridescent blue-green on operculum, preoperculum, postorbital spot, suborbital bar, lips, and mid-gular area: preorbital bar dark. Lateral belly yellow-orange; medial belly gray. Base color of upper body straw to olivaceous. Sides with usually 9–11 iridescent turquoise blue or blue-green quadrate blotches, typically extending from lateral line scale row ventrad 2–4 scale rows. Narrow midlateral dusky band of pigment extending from humeral area to caudal fin base, consisting of tiny melanophores. Anteriorly along the pored scales of the lateral-line series these tiny melanophores usually occur on one, and occasionally two, scale rows below the pores. Posteriorly along the unpored scales melanophore coverage expands dorsally to include the entire exposed field of the lateral-line scale row; a somewhat wider dusky expansion may occur just anterior to the caudal fin base. Scales between lateral blue-green blotches outlined in powder blue, forming vague crosshatched pattern. Sides with small red-orange X-markings and spots between lateral blotches and extending to dorsum; markings not very prominent. Dorsolateral area also with many small scattered dark markings. Dorsum with 6 dark quadrate saddles, not medially constricted; first saddle may appear less discrete due to incomplete scalation of nape.

Additional coloration notes.—In preservative, as the blue-green pigment of breeding males fades, the series of quadrate lateral blotches becomes difficult to distinguish from the midlateral dusky band. Hence, preserved breeding males may appear to have a continuous wide band along the sides rather than individual blotches. The narrow dusky midlateral band is also present in breeding females but tends to be less wide and less consistent in continuity than in males; the lateral blotches are discernible in life or preservative.

Tuberculation.—Pelvic fins with weak rounded tubercles on medial-distal portions of rays 1–4. Anal fin typically with distinct rounded to conical tubercles on all rays and occasionally the second anal spine. Posterior two-thirds of belly occasionally with minute rounded tubercles, occurring on up to 8 midventral scale rows. Tuberculate males have been taken between 25 March and 4 April from Caddo River, Montgomery and Clark counties, Arkansas.

Variation.— The disjunct populations of the upper Ouachita and upper Caddo rivers vary in several meristic features. Specimens from upper Ouachita River (n = 57) have modally 14 pectoral rays versus 13 in those from upper Caddo River (n = 47). Specimens from Caddo River tend to have higher scale counts, with modally 14–15 transverse scales (versus 12–13 in Ouachita River), modally 8 scales below the lateral line (vs. 6–7), modally 5 scales above the lateral line (vs. 4), and modally 17 caudal peduncle scales (vs. 16).

Distribution.—*Etheostoma clinton* is known only from the upper Caddo and upper Ouachita rivers upstream of the Fall Line in the Ouachita Mountains province of Arkansas (Figs. 5 and 20). In the Caddo River it is found upstream of DeGray Reservoir. In the Ouachita River it occurs upstream of Lake Ouachita in the upper Ouachita and South Fork Ouachita rivers. The species may also occur in tributaries of lakes Hamilton and Catherine, which are situated above the Fall Line. Harris and Douglas (1978) surveyed several tributaries of these impoundments but did not collect the species (then known as *E. stigmaeum*). Robison and Buchanan (1988) show one record of *E. stigmaeum* from Little Mazarn Creek, a tributary to Lake Hamilton, but we

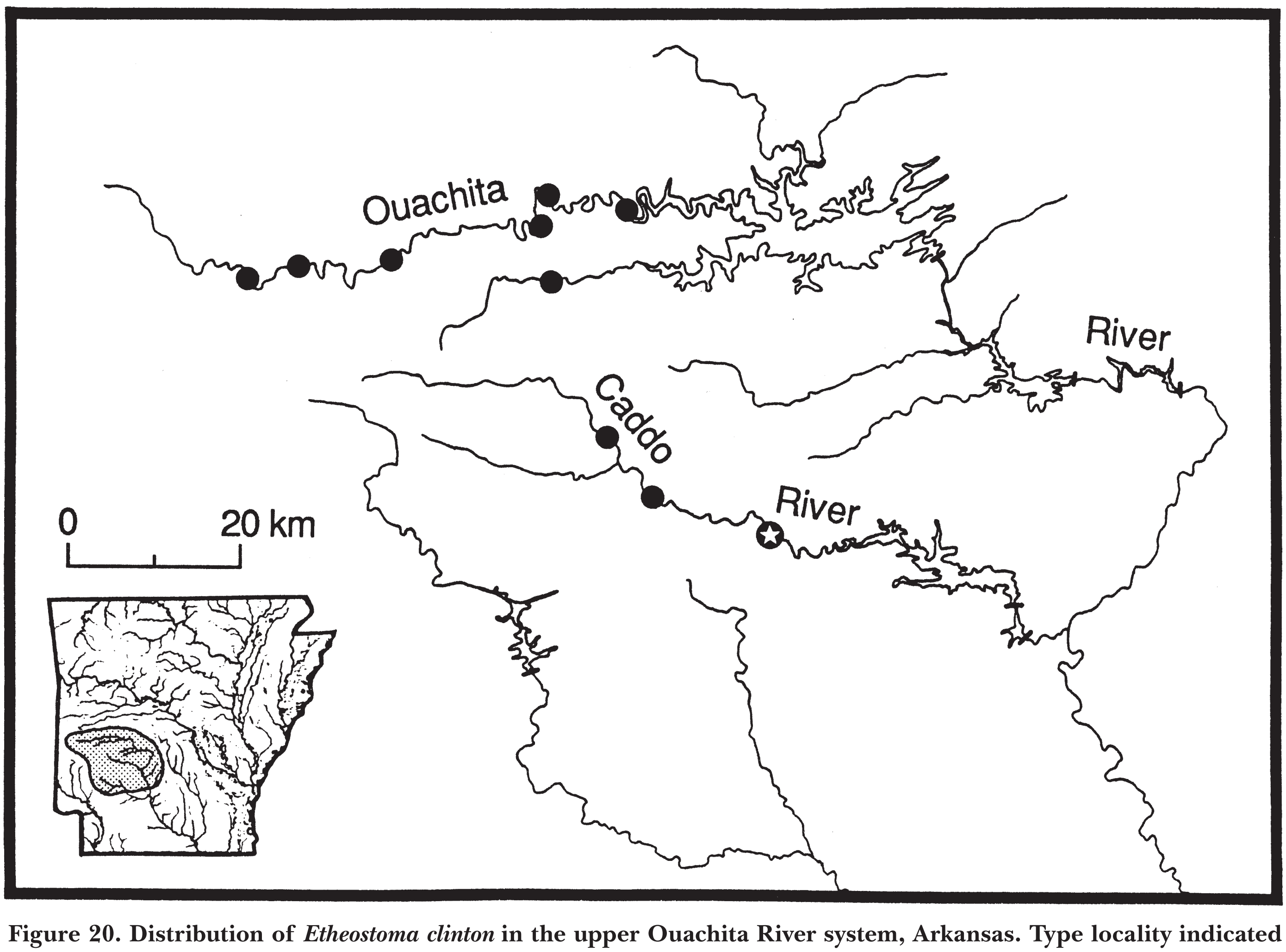

Figure 20. Distribution of *Etheostoma clinton* in the upper Ouachita River system, Arkansas. Type locality indicated by dot with star.

have not examined the material to determine if it represents the new species. The occurrence of *E. pallididorsum* in a nearby tributary of Lake Hamilton (Robison, 1974) suggests that the Little Mazarn Creek record may indeed represent *E. clinton* because the overall ranges of these two species are highly congruent (Mayden, 1985; Robison and Buchanan, 1988), but this needs to be confirmed.

Populations of *E. clinton* from the upper Caddo and upper Ouachita rivers are isolated from each other by several man-made impoundments and the intervening Coastal Plain portion of the Ouachita River system (including lower Caddo River), which is occupied by *E. stigmaeum*. *Etheostoma clinton* has a small and nearly identical distribution with that of *Noturus taylori*, with the exception that the latter is also known from the headwaters of the Little Missouri River system (Robison and Harris, 1978). Several other fish species endemic to this region also have largely overlapping distributions with that of *E. clinton* (Mayden, 1985). A status survey is needed to more clearly define the distribution of *E. clinton*, particularly in tributaries of the main rivers and impoundments, and should include the upper Little Missouri River system above Lake Greeson.

Etymology.— The name beaded darter refers to the distinctive midlateral dusky band that runs through the turquoise blue blotches, suggesting a string of beads. The species epithet is a noun in apposition that honors President Bill Clinton, the 42nd President of the United States of America (Fig. 19), and his lasting environmental accomplishments in creating and expanding national monuments, preserving millions of acres of wilderness areas, his leadership and commitment during challenging economic times, and his continued commitment to global humanitarian issues and needs and peace.

COMPARISONS

Meristics and breeding colors.—Meristic and breeding color comparisons are provided in Table 13 and Figure 3. *Etheostoma akatulo* is highly distinctive, differing from all other species in usually having a complete lateral line, fully or nearly fully scaled cheeks, and breeding males with bright cobalt or royal blue pigment continuously covering the lower face, and soft dorsal and anal fins lacking orange and blue pigment. *Etheostoma jessiae* is the only species consistently having a frenum, although its presence is more variable in some systems of the middle Tennessee drainage; a frenum is present in 37–67% of specimens of *E. meadiae*. *Etheostoma jessiae* has the highest counts of lateral, caudal peduncle, and transverse scales of all species and attains the greatest maximum size. The species differs further from *E. stigmaeum*, *E. meadiae*, *E. akatulo*, and *E. clinton* in breeding males having distinct, bright orange spots on the second dorsal, caudal, and pectoral fin rays, and having bright orange pigment in the base of the spinous dorsal fin. *Etheostoma jessiae* differs further from *E. stigmaeum* in having modally 12–13 dorsal spines (versus 11 in *E. stigmaeum*), modally 12 dorsal soft rays (vs. 11), modally 9 soft anal rays (vs. 8), modally 14–15 pectoral rays (vs. 14), modally 7–8 scales below the lateral line (vs. 6–7), modally 5–6 scales above the lateral line (vs. 4–5), usually 1–14 unpored lateral-line scales (vs. 8–19), and a more completely and consistently scaled nape. Breeding males of *E. jessiae* differ further from those of *E. stigmaeum* in lacking blue pigment on the mid-gular region.

In addition to characters described above, *Etheostoma jessiae* differs from *E. meadiae* in having modally 9 anal rays (vs. 8 in *E. meadiae*), modally 7–8 scales below the lateral line (vs. 6), modally 14–15 pectoral rays (vs. 14), modally 15 principal caudal rays (vs. 16–17), usually 1–14 unpored lateral-line scales (vs. 0–7), partly scaled cheeks (vs. usually naked), and palatine teeth usually present (vs. present in only 33% of specimens). The nape is more completely and consistently scaled in *E. jessiae* than *E. meadiae*.

Etheostoma jessiae is similar to *E. obama*, *E. gore*, and *E. jimmycarter* in breeding males having orange spots on the soft dorsal, caudal, and pectoral fin rays, and orange pigment in the base of the spinous dorsal fin. *Etheostoma jessiae* differs from these three species in breeding males having the base color of the face and underside of the head gray (versus tangerine orange), blue pigment typically present on the lips (vs. absent), and orange spots lacking on the anal fin (vs. present or sometimes present). Additionally, *E. jessiae* has higher counts of scale rows below and above the lateral line.

Etheostoma jimmycarter differs from *E. obama* and *E. gore* in breeding males having a black submedial band in the spinous dorsal fin (vs. blue), soft dorsal and anal fins lacking blue pigment in the base, and the basicaudal blue bar mainly developed ventrally, not extending to the dorsal margin of the caudal fin. *Etheostoma obama* differs from *E. gore* in having modally 15 pectoral rays (vs. 14 in *E. gore*), modally 12 soft dorsal rays (vs. 11), modally 5 scales above the lateral line (vs. 4), partly scaled cheeks (vs. usually naked), and palatine teeth present in 29% of specimens (vs. palatine teeth absent). Breeding males of *E. obama* differ from those of *E. gore* in often lacking orange spots on the anal fin. These two species are very similar in morphology and breeding colors; however, patterns of allozyme variation suggest that no gene flow is occurring between them. The two species, each represented by two population samples, have no alleles in common at the sIdh-A locus (Layman, 1994). In addition, the occurrence of unique derived alleles in both samples of *E. gore* (Mpi-Aa and Pk-Bd) and the occurrence of a unique derived allele in the Duck River sample of *E. obama* (Pnp-Ae) suggest that the species are maintaining separate identities and are pursuing their own evolutionary tendencies and fates (Wiley, 1978).

Etheostoma stigmaeum differs from *E. meadiae* in having usually 8–19 unpored lateral-line scales (vs. 0–7 in *E. meadiae*), partly scaled cheeks (vs. cheeks usually naked), palatine teeth present (vs. palatine teeth present in only 33 % of specimens), modally 11 dorsal spines (vs. 12), modally 4–5 scales above the lateral line (vs. 6), and modally 15 principal caudal rays (vs. 16–17). Although many aspects of breeding coloration are similar, *E. stigmaeum* differs further from *E. meadiae* in having blue-green pigment on the mid-gular region.

Etheostoma stigmaeum differs from *E. obama*, *E. gore*, and *E. jimmycarter* in having modally 11 dorsal spines (vs. 12–13) and palatine teeth usually present (vs. usually absent or present in only 29% of specimens). Breeding males of *E. stigmaeum* differ from those of the other three species in having soft dorsal, caudal, and pectoral fins lacking orange spots, the base of the spinous dorsal fin lacking orange pigment, the base color of the face and underside of head gray (vs. tangerine orange), and the lateral blotches vertically elongate (vs. quadrate).

Etheostoma clinton is distinguished from all other species of *Doration* by having 9 preoperculomandibular pores (vs. 10 in all other species), smallest maximum adult size (<38 mm vs. usually >40 mm SL), and breeding males having a narrow midlateral band of melanophores connecting the series of blue-green blotches. It is most similar to *E. stigmaeum* in overall appearance but differs further from that species in having modally 9 anal soft rays (vs. 8), modally 13–14 pectoral rays (vs. 14), usually naked or nearly naked cheeks (vs. usually partly scaled), and a higher mean count of lateral scales (49.9 vs. 46.4).

Etheostoma teddyroosevelt is similar to *E. obama*, *E. gore*, and *E. jimmycarter* in that breeding males have distinct orange spots on the second dorsal, caudal, and anal fins; however, in *E. teddyroosevelt* they are more subdued and occasionally obscured by melanophores. *Etheostoma teddyroosevelt* differs from these three species in having breeding males lacking orange pigment in the base of the spinous dorsal fin and having the base color of the face gray (vs. tangerine orange), and in having modally 7 scales below the lateral line (vs. 6). It differs further from *E. obama* and *E. gore* in breeding males having black marginal and submedial bands in the spinous dorsal fin (vs. blue), soft dorsal and anal fins lacking blue pigment, and the basicaudal blue bar mainly developed ventrally. It differs further from *E. jimmycarter* in having modally 14 pectoral rays (vs. 15), a higher mean count of lateral scales (48.1 vs. 45.4), and breeding males with a solid black submedial black band (vs. interrupted with vertical orange streaks).

Etheostoma teddyroosevelt differs from *E. stigmaeum* and *E. clinton* in breeding males having black marginal and submedial bands in the spinous dorsal fin (vs. blue-green), deep blue lateral blotches (vs. blue-green), orange spots on the soft dorsal, caudal, and anal fins (vs. lacking), and in lacking blue pigment on the lips and mid-gular region (vs. present). It differs further from these two species in usually lacking palatine teeth (although present in up to 29% of upper White River specimens) and having a more completely and consistently scaled nape. *Etheostoma teddyroosevelt* differs further from *E. clinton* in having a fully scaled belly (vs. incompletely scaled anteriorly) and differs further from *E. stigmaeum* in having usually naked cheeks (vs. partly scaled).

Principal component analysis of 17 meristic variables in 3,049 specimens shows a high degree of overlap among the nine species of *Doration* (Fig. 21). This, in part, illustrates why the systematics of the group has been so poorly understood without fuller knowledge of breeding color variation. The analysis does not incorporate data on the frenum or palatine teeth, characters that are also useful in distinguishing species. *Etheostoma stigmaeum*, the geographically most widespread species, encompasses the greatest amount of meristic variation, both along principal component one (PC-I) and PC-II (Fig. 21). The PC-I axis provides nearly complete separation between *E. jessiae* and *E. akatulo*. Variables loading most heavily on PC-I include transverse scales, caudal peduncle scales, scales above and below the lateral line, and lateral scales (Table 14). Other variables loading heavily are several fin ray counts and opercle, nape, and cheek squamation. The PC-II axis provides little distinction between species from the Tennessee (*E. jessiae*, *E. meadiae*, *E. obama*), Cumberland (*E. akatulo* and *E. gore*), and Green (*E. jimmycarter*) river drainages but largley polarizes this group from *E. clinton* (Fig. 21). The plot completely separates both *E. jessiae* and *E. akatulo* from *E. clinton*. Variables with the highest loadings on PC-II are nape and belly squamation (Table 14). Others loading heavily include scales below the lateral line, unpored lateral scales, anal fin rays, pectoral fin rays, transverse scales, dorsal fin spines, and cheek squamation. The greatest overlap occurs between *E. meadiae*, *E. obama*, *E. gore*, and *E. jimmycarter* (Fig. 21).

Morphometrics.—Comparison of proportional measurements in Table 12 and in Layman and Mayden (2009) reveals that *E. jessiae* has a longer snout than any other species of *Doration*. In addition, *E. jessiae* has relatively greater head length, predorsal length, upper jaw length, and soft dorsal fin base length than most other species. *Etheostoma meadiae* has a moderate snout but shares with *E. jessiae* a relatively long head, predorsum, and upper jaw. It differs from *E. jessiae* and most other species in having a deeper body at the spinous and soft dorsal fin origins, deeper and shorter caudal peduncle, wider body, and greater anal spine length. *Etheostoma stigmaeum* from the Coosa River also has a moderately produced snout, long upper jaw, deep body at the soft dorsal fin origin, and deep caudal peduncle. *Etheostoma teddyroosevelt* is also relatively robust, with greater body width and body depth at the spinous dorsal fin origin than all other species except *E. meadiae*.

Etheostoma obama has proportionally larger fins than most other species of *Doration* as indicated by mean measurements of spinous dorsal fin origin to soft dorsal fin origin, dorsal spine length, soft dorsal fin base length, anal fin base length, and pectoral and pelvic fin lengths (Table 12; Layman and Mayden, 2009: table 1). *Etheostoma gore* has

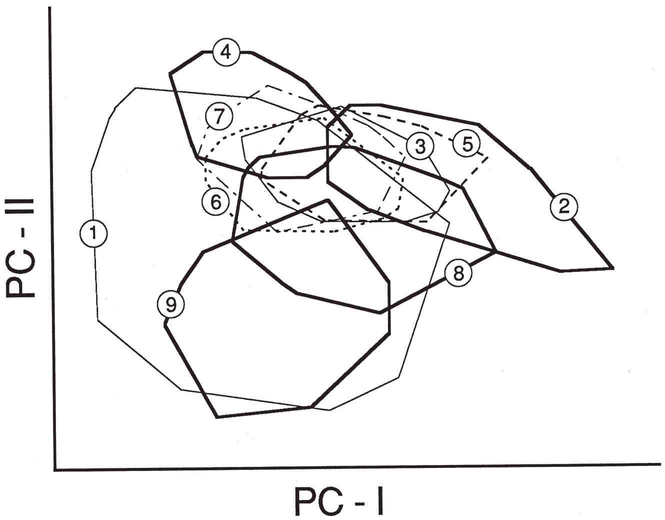

Figure 21. Plot of meristic principal component one (PC-1) and PC-II for nine species of *Doration.* Polygons bound all individuals of: 1—E*theostoma stigmaeum;* 2—E. j*essiae;* 3—*E. meadiae;* 4—*E. akatulo;* 5—*E. obama;* 6—*E. gore;* 7—*E. jimmycarter;* 8—*E. teddyroosevelt;* 9—*E. clinton.*

a large spinous dorsal fin, and it and *E. jimmycarter* have relatively long pectoral and pelvic fins. *Etheostoma akatulo* is a slender species of *Doration* with a moderate snout, narrow body depth at the spinous dorsal fin origin, long and narrow caudal peduncle, narrow trans-pelvic width, and short pectoral and pelvic fins. Within *Doration*, the diminutive *E. clinton* has the shortest snout, narrowest body depth at the spinous and soft dorsal fin origins, shortest distance between the spinous and soft dorsal fin origins, narrowest trans-pelvic width, and narrowest body.

Sheared principal component analysis of 28 morphometric variables reveals substantial overlap among males of species of *Doration* in overall body form and fin size, but several species can be distinguished from one another on this basis. The plot of sheared PC-II against sheared PC-III completely or nearly completely separates *E. jessiae* from all other species except *E. akatulo*, with which it overlaps only moderately (Fig. 22A). Most notably, *E. jessiae* separates completely from *E. meadiae* and *E. obama*, parapatric neighbors in the Tennessee River drainage. All or most of this separation occurs along sheared PC-II. Variables loading heavily on this axis are first anal spine length, snout length, and distance from the midline at least interorbital width to the snout (Table 15). Nearly complete separation is also obtained between *E. meadiae* and *E. stigmaeum* from the Coosa River along sheared PC-II (Fig. 22A). Sheared PC-III completely separates *E. teddyroosevelt* from all other species except *E. stigmaeum* (Fig. 22A). Variables accounting for the most variance on this axis include three body depth measurements, first anal spine length, anal fin base length, and snout length (Table 15). The plot nearly separates *E. meadiae* and *E. akatulo* (Fig. 22A). In addition, *E. clinton* separates almost completely from *E. stigmaeum* of the Ouachita River (Fig. 22B); these samples are from geographically close localities in the Ouachita River system above and below the Fall Line, respectively. Among populations of *E. stigmaeum*, the least overlap occurs between the Ouachita and Coosa rivers, the geographically most distant samples (Fig. 22B).

The plot of sheared PC-II versus sheared PC-III for female measurements (Fig. 23, Table 15) reveals similar trends in shape differentiation as observed in males, with *E. jessiae* completely separated from *E. meadiae*, *E. obama*,

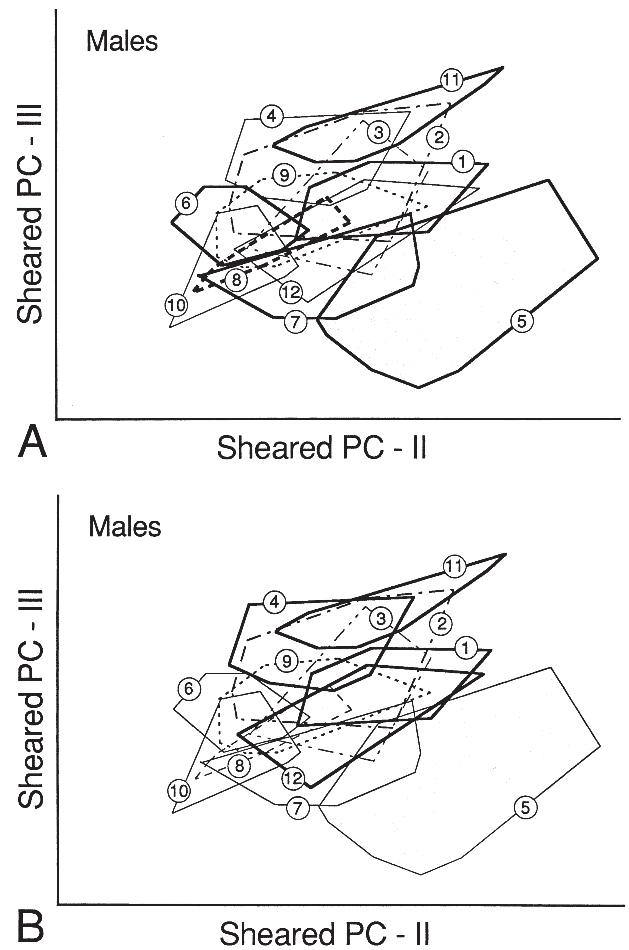

Figure 22. Plot of morphometric sheared principal component two (PC-II) and sheared PC-III for males of nine species of *Doration.* (A) and (B) are the same but highlight different sets of polygons to facilitate interpretation. Polygons bound all individuals of: 1—*Etheostoma stigmaeum,* Coosa River (Mobile Basin); 2—*E. stigmaeum,* Pearl River (central Gulf Coast); 3—*E. stigmaeum,* Clarks River (upper Mississippi Embayment); 4—*E. stigmaeum,* Ouachita River (lower Mississippi Embayment); 5—*E. jessiae;* 6—*E. meadiae;* 7—*E. akatulo;* 8—*E. obama;* 9—*E. gore;* 10—*E. jimmycarter;* 11—E. *teddyroosevelt;* 12—*E. clinton.*

E. jimmycarter, *E. teddyroosevelt*, and *E. clinton*. Both *E. meadiae* and *E. jimmycarter* separate completely or nearly completely from *E. stigmaeum*, *E. akatulo*, and *E. clinton*. Unlike the male analysis, females of *E. clinton* broadly overlap those of *E. stigmaeum* from Ouachita River, *E. jimmycarter* partly overlaps *E. teddyroosevelt*, and *E. teddyroosevelt* partly overlaps *E. clinton* (Fig. 23). Variables loading heavily on sheared PC-II include first anal spine length, upper jaw length, snout length, and distance from the midline at least interorbital width to the snout (Table 15). Those loading most heavily on sheared PC-III are first anal spine length, anal fin base length, snout length, and two measures of body depth.

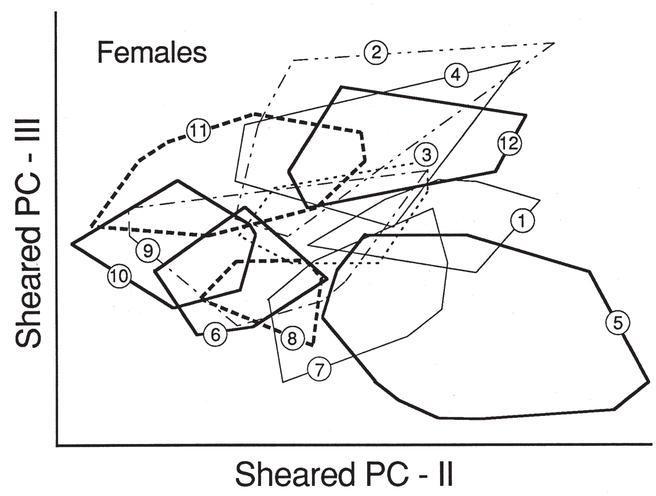

Figure 23. Plot of morphometric sheared principal component two (PC-II) and sheared PC-III for females of nine species of *Doration*. Polygons bound all individuals of: 1—*Etheostoma stigmaeum*, Coosa River (Mobile Basin); 2—*E. stigmaeum*, Pearl River (central Gulf Coast); 3—*E. stigmaeum*, Clarks River (upper Mississippi Embayment); 5—*E. jessiae;* 6—*E. meadiae;* 7—*E. akatulo;* 8—*E. obama;* 9—*E. gore;* 10—*E. jimmycarter;* 11—*E. teddyroosevelt;* 12—*E. clinton*.

CONTACT ZONES

Bear Creek system, Alabama.—Howell (1968; 1980a) treated specimens from Little Bear Creek in the Bear Creek system of Alabama (Tennessee River drainage) as intergrades or hybrids between *E. jessiae* and *E. stigmaeum*. *Etheostoma stigmaeum* occurs in adjacent Bear Creek, having presumably entered the system via stream capture from the upper Tombigbee River system (Wall, 1968; Starnes and Etnier, 1986). Howell based his assessment on the observation that six of 12 available specimens (50%) possessed a frenum, which he considered the most distinctive character separating the two taxa. However, meristic, breeding color, and allozyme data all indicate that Little Bear Creek contains "pure" *E. jessiae* and this "apparent zone of intergradation" (Wiley, 1981) does not involve gene flow between *E. stigmaeum* from Bear Creek and *E. jessiae*. This conclusion is discussed below.

First, it has been shown above with a larger sample size (n = 49) that actually about 69% of specimens from Little Bear Creek possess a frenum. This frequency is comparable to that observed in geographically proximate populations of *E. jessiae* from Shoal Creek, Paint Rock River, and Sequatchie River; however, there is no clear pattern of clinal variation, as several intervening populations exhibit frenum frequencies of 100%. Second, in comparing meristic frequencies between Little Bear Creek specimens, *E. jessiae*, and 54 specimens of *E. stigmaeum* from Bear Creek, counts for Little Bear Creek are highly consistent with those of *E. jessiae*. This is true for counts of lateral scales, unpored lateral scales, transverse scales, scales below and above the lateral line, caudal peduncle scales, dorsal spines, dorsal soft rays, anal soft rays, pectoral rays, and nape squamation, distributions of which are diagnostic for the two species (Tables 1 through 5, and Tables 7 through 9). No meristic counts examined exhibit intermediacy that would support a hybridization hypothesis. Principal component analysis of 16 meristic variables in *E. jessiae* shows that Little Bear Creek specimens are typical for the species, broadly overlapping all other populations on the plot of PC- I versus PC-II (Fig. 24; Table 16). Third, breeding coloration (Fig. 3) and maximum size (56 mm SL) of Little Bear Creek males are typical of *E. jessiae*. Breeding coloration of *E. stigmaeum* males observed from Bear Creek is typical for that species (Fig. 3), and maximum size is only about 42 mm SL. Finally, patterns of allozyme variation presented in (Layman, 1994) indicate that *E. stigmaeum* and *E. jessiae* from the Bear Creek system are not hybridizing. At four diagnostic loci between *E. stigmaeum* from Bear Creek and *E. jessiae*, all Little Bear Creek specimens (n = 10) possessed only *E. jessiae* alleles; no individuals were heterozygous for alleles from both species.

There is no convincing evidence that *E. stigmaeum* and *E. jessiae* have hybridized in the Bear Creek system. The species occur parapatrically in the system, with their distributions separated by a gap that Wall (1968) attributes to lack of suitable sand and gravel substrates. This study suggests that the polymorphic condition of the frenum in populations of *E. jessiae* from Little Bear Creek and other rivers in the southern bend of the Tennessee River represents residual geographic variation left from the ancestor of *E. jessiae*, perhaps maintained by chance or local selection (Wiley, 1981). Furthermore, even if hybridization had occurred, it would have little bearing on decisions concerning the species status of these taxa, since the phylogeny presented below suggests that they are not sister taxa.

Clinch River system, Tennessee.—*Etheostoma jessiae* and *E. meadiae* occur parapatrically in the Clinch and Powell rivers (Fig. 7). Meristic and breeding color data indicate that *E. jessiae* occurs both downstream of Norris Dam and

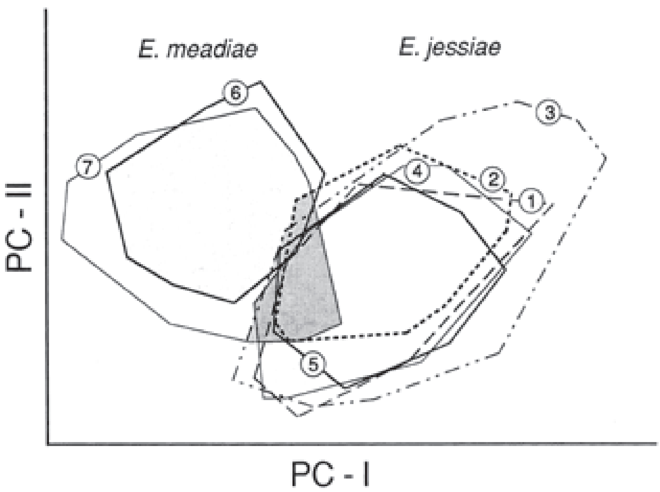

Figure 24. Plot of meristic principal component one (PC-I) and PC-II for *Etheostoma jessiae* and *E. meadiae*. Polygons bound all individuals of: 1—*E. jessiae*, lower and middle Tennessee River drainage; 2—*E. jessiae*, Little Bear Creek, Alabama; 3—*E. jessiae*, upper Tennessee River drainage exclusive of Clinch River; 4—*E. jessiae*, Clinch River downstream of Norris Dam; 5—*E. jessiae*, Clinch-Powell river upstream of Norris Dam; 6—*E. meadiae*, Powell River; 7—*E. meadiae*, Clinch River. Overlap between the two species is indicated by shading.

in at least three tributaries of Norris Reservoir. The tributaries include Cove Creek downstream of the confluence of the two rivers, Davis Creek (pond opposite Doak's Dam) in the lower Powell River, and Big Sycamore Creek in the Clinch River upstream of the Powell River confluence. Several diagnostic meristic features show distinct shifts in modes between these populations of *E. jessiae* and populations of *E. meadiae* in the upper Powell and Clinch rivers. These include counts of lateral scales, unpored lateral scales, caudal peduncle scales, transverse scales, scales below the lateral line, anal soft rays, and estimates of cheek and nape squamation (Tables 1 through 7). In addition, clear shifts occur in counts of principal caudal fin rays and the proportions of individuals having a frenum and palatine teeth as shown by stream system in Table 11 (see also Fig. 7).

Meristic variation between *E. jessiae* and *E. meadiae* was further evaluated using principal component analysis. The plot of PC-I versus PC-II for 16 meristic variables (Fig. 24) shows nearly complete separation of all populations of *E. jessiae* from *E. meadiae* of the upper Powell River, and provides major separation between *E. jessiae* and *E. meadiae* of the upper Clinch River. Populations of *E. jessiae* from the Clinch River system both above and below Norris Dam broadly overlap all other populations of *E. jessiae* and are distinct from *E. meadiae*. Separation between *E. jessiae* and *E. meadiae* occurs along PC-I, which is most strongly correlated with counts of transverse scales, caudal peduncle scales, scales below the lateral line, and scales in lateral series, estimates of nape and cheek squamation, and counts of caudal and anal fin rays (Table 16). In addition, breeding males observed from Big Sycamore Creek above Norris Dam and Coal Creek below Norris Dam consistently possessed bright orange spots on the soft dorsal, caudal, and pectoral fins, and bright orange pigment in the base of the spinous dorsal fin. These aspects of coloration are typical of *E. jessiae* but not *E. meadiae*.

Etnier and Starnes (1994) hypothesized that tributaries of Norris Reservoir and Clinch River below Norris Dam contain apparent intergrades or introgressed hybrids between *E. jessiae* and *E. meadiae*. The morphological analysis above strongly supports recognition of these populations as *E. jessiae*. Only counts of pectoral fin rays suggest possible introgression of these populations by *E. meadiae*. Like *E. meadiae*, Clinch River populations of *E. jessiae* modally have 14 pectoral rays, compared to 15 in most other *E. jessiae* populations. Alternatively, this apparent shift in *E. jessiae* may represent residual geographic variation that was present in the species' ancestor. A large proportion of *E. jessiae* specimens throughout the remainder of the upper Tennessee drainage possesses 14 pectoral rays (Table 9), and Etnier and Starnes (1994) noted that the modal count was also 14 in the Little Tennessee River system.

Patterns of allozyme variation, presented in Layman and Mayden (ms), provide stronger evidence for introgression of *E. jessiae* populations by *E. meadiae* in the Clinch River system. At the single diagnostic locus between the taxa, populations identified as *E. jessiae* from Coal Creek (n= 10), located just downstream of Norris Dam, and Big Sycamore Creek (n= 16), tributary to Norris Reservoir, contained individuals homozygous for alleles of *E. jessiae* and individuals heterozygous for alleles of both species. The Coal Creek population also contained two individuals that were homozygous for the allele of *E. meadiae*. Whether these specimens represent pure *E. meadiae* versus F2 or backcross classes cannot be determined without additional genetic markers.

Although allozyme evidence suggests that introgressive hybridization may have occurred between *E. jessiae* and *E. meadiae*, the data are ambiguous. Neither species exhibits unique derived alleles at this locus, and thus, the presence of the *E. meadiae* allele in the two *E. jessiae* populations could also be explained as a retained ancestral polymorphism. Nevertheless, the abutting distributions of these two species (Fig. 7) leave little doubt that they have had ample opportunity to hybridize in the past. Given the hypothesized phylogeny below in which these two species are not considered to be sister taxa, these encounters may represent cases of secondary contact. If so, they have little bearing on decisions regarding the species status of these taxa.

PHYLOGENETIC RELATIONSHIPS

Phylogenetic hypothesis

Phylogenetic analyses using both the unordered and mixed unordered-ordered character sets produced the same three minimum-length trees with a length of 60 steps and a consistency index of 0.683 (CI; Kluge and Farris, 1969) (uninformative characters excluded). The retention index was 0.776 in the unordered analysis and 0.787 in the mixed analysis (RI; Farris, 1989). The least resolved of the minimum-length trees, which also represents the strict consensus tree, is shown in Figure 25. All three trees support the monophyly of *Doration* with *E. akatulo* sister to a clade containing all other species in the subgenus. A pattern of asymmetrical branching proceeds up the tree with *E. clinton*, *E. stigmaeum*, *E. meadiae*, and *E. jessiae*. *Etheostoma jessiae* is sister to a clade containing *E. obama*, *E gore*, *E. jimmycarter*, and *E. teddyroosevelt*. The other two minimum-length trees differ only in the resolution of the trichotomy involving this latter clade. One tree places *E. gore* as sister to the *E. jimmycarter-E. teddyroosevelt* clade, and the other tree unites *E. obama* and *E. gore* as sister to the *E. jimmycarter-E. teddyroosevelt* clade. As the more conservative estimate of relationships, the less highly resolved tree is presented as the preferred phylogenetic hypothesis (Fig. 25).

The monophyly of *Doration* is supported by ten derived character states (Fig. 25). Breeding males of the ancestor of this clade are hypothesized to have possessed a series of 7–11 vertically elongate blue bars, scattered red-orange markings on the sides, iridescent blue or blue-green pigment on the opercles, cheeks, lips, and mid-gular area, a spinous dorsal fin with dusky to black marginal and submedial bands and red-orange medial band, and a ventrally-developed blue-green basicaudal bar. The ancestor also possessed a pair of small dark spots on the medial caudal fin base and modally 11–13 dorsal spines.

Within *Doration*, *E. akatulo* is sister to a clade containing all other species in the subgenus. This latter clade is united by three derived features of male breeding coloration: blue or blue-green marginal and submedial bands in the spinous dorsal fin, blue or blue-green pigment in the base of the soft dorsal fin, and blue or blue-green pigment in the base of the anal fin. *Etheostoma akatulo* is characterized by three homoplasious autapomorphies: a complete lateral line, fully scaled cheeks, and loss of palatine teeth. The complete lateral line is interpreted in this optimization as a reversal, but an equally parsimonious reconstruction allows for parallel derivation of an incomplete lateral line in *E. caeruleum*, *E. chlorosoma*, and the ancestor of the clade sister to *E. akatulo*. Derivation of fully scaled cheeks in *E. akatulo* is an instance of parallel evolution of the same state in the ancestor of the *E. obama-E. gore-E. jimmycarter-E. teddyroosevelt* clade, and the loss of palatine teeth is a parallel transformation with that in *E. chlorosoma*.

Monophyly of the clade containing *E. stigmaeum*, *E. meadiae*, *E. jessiae*, *E. obama*, *E. gore*, *E. jimmycarter*, and *E. teddyroosevelt* is supported by a single character, a vertical blue or blue-green basicaudal bar in nuptial males that extends from the dorsal to the ventral margin of the caudal fin. *Etheostoma clinton*, sister to this clade, exhibits quadrate lateral blotches in breeding males and 9 preoperculomandibular pores as autapomorphies. Both states represent instances of parallel development, the former with the ancestor of the *E. obama-E. gore-E. jimmycarter-E. teddyroosevelt* clade, and the latter with *E. nigrum*.

The clade containing *E. meadiae*, *E. jessiae*, *E. obama*, *E. gore*, *E. jimmycarter*, and *E. teddyroosevelt* is united by the absence of blue or blue-green pigment on the gular area

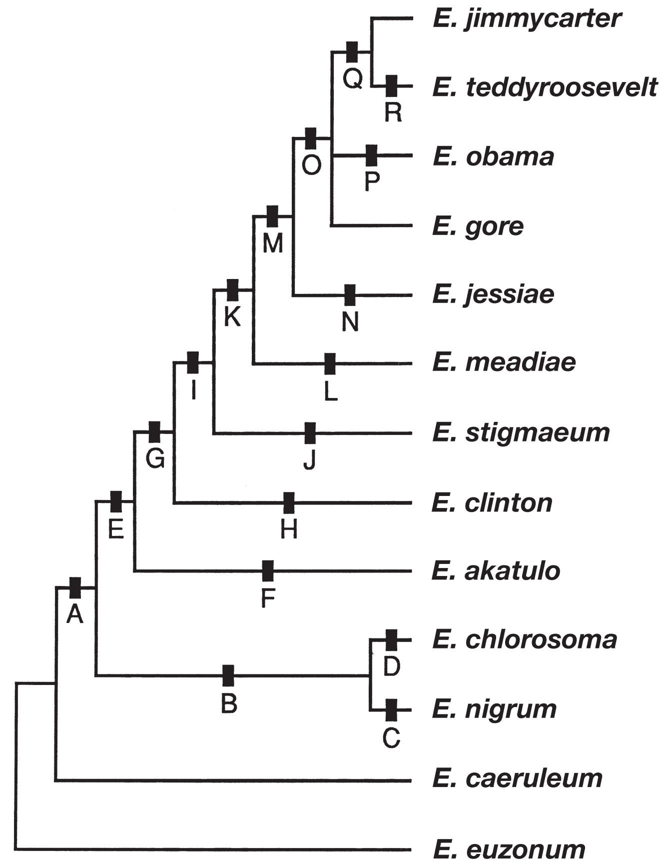

Figure 25. Hypothesized phylogeny of species of the subgenus *Doration*. This is one of three minimum-length trees and also represents the strict consensus tree. Derived character states supporting each of the lettered branches are: A) 17(1), 19(1), 22(1), 34(1); B) 16(1), 25(1), 26(1), 30(1), 34(2); C) 17(0)*, 23(0)*, 27(1)*; D) 28(0)*, 29(0)*; E) 1(1), 2(1), 3(1), 4(1), 5(1), 7(1), 8(1), 12(1), 20(1), 32(1); F) 23(0)*, 24(1)*, 28(0)*; G) 7(2), 10(1), 13(1); H) 1(2)*, 27(1)*; I) 12(2); J) 28(1)*; K) 5(0)*, 8(2); L) 22(0,1)*, 24(0,1)*; M) 9(1), 11(1), 15(1); N) 22(0)*, 28(1)*; O) 1(2)*, 4(0)*, 6(1), 14(2), 24(1)*; P) 14(1), 28(1)*; Q) 7(1)*, 10(0)*, 12(1)*, 13(0)*; R) 6(0)*, 9(0)*. See Appendix A for character descriptions and Appendix B for data matrix. Homoplasious transformations indicated by asterisks.

of breeding males, a reversal, and development of a true orange medial band (in life) in the spinous dorsal fin of breeding males. This group is sister to *E. stigmaeum*, which is characterized by partly scaled cheeks, a case of parallel development with *E. jessiae* and *E. obama*.

Etheostoma meadiae is sister to a clade containing *E. jessiae*, *E. obama*, *E. gore*, *E. jimmycarter*, and *E. teddyroosevelt*. Monophyly of the latter group is supported by the unique derivation of three male breeding color features: orange pigment in the base of the spinous dorsal fin, orange spots on the second dorsal and caudal fin rays, and orange spots on the pectoral fin rays.

Etheostoma meadiae is distinguished by polymorphic conditions of the frenum and palatine teeth. Because PAUP does not assign polymorphic states to internal nodes, both polymorphic conditions are optimized as having arisen through anagenesis in *E. meadiae* rather than in an ancestor. In the case of the frenum, its appearance in *E. meadiae* is interpreted as a reversal. The only other species of *Doration* possessing a frenum is *E. jessiae*, for which this state is also interpreted as a reversal. This optimization of the frenum on the phylogenetic tree (Fig. 25) requires three steps, because PAUP assigns a cost of one step to all transformations between unordered character states, even when occurring between fixed and polymorphic states. However, if generalized parsimony (Swofford and Olsen, 1990) is adopted for this character, in which transformations between fixed states are assigned a cost of two steps and those between fixed and polymorphic states a cost of one step, then an equally parsimonious reconstruction is possible. The polymorphic state could have arisen in the ancestor of the *E. meadiae-E. jessiae-E. obama-E. gore-E. jimmycarter-E. teddyroosevelt* clade, with fixation to presence of a frenum occurring in *E. jessiae* and fixation to absence of a frenum occurring in the ancestor of the *E. obama-E. gore-E. jimmycarter-E. teddyroosevelt* clade. This alternative reconstruction is consistent with present-day patterns of polymorphism observed in *E. jessiae*, in that the frenum apparently has not reached complete fixation in several populations of the middle Tennessee drainage, including Little Bear Creek.

The polymorphic condition of palatine teeth in *E. meadiae* is optimized in the present tree (Fig. 25) as a convergence with *E. obama*. However, using a generalized parsimony approach as described above, a more parsimonious reconstruction (one step shorter) allows for development of a polymorphic state in the ancestor of *E. meadiae*, presence of palatine teeth becoming fixed in *E. jessiae*, and absence of teeth becoming fixed in the ancestor of an *E. gore-E. jimmycarter-E. teddyroosevelt* clade, with *E. obama* retaining the pleisiomorphic polymorphic condition. This reconstruction supports the minimum-length tree that resolves *E. gore* as sister to the *E. jimmycarter-E. teddyroosevelt* clade.

Etheostoma jessiae is sister to a clade containing *E. obama*, *E. gore*, *E. jimmycarter*, and *E. teddyroosevelt*. In addition to presence of a frenum, *E. jessiae* is distinguished by partly scaled cheeks, a parallel transformation with those in *E. stigmaeum* and *E. obama*. Monophyly of the *E. obama-E. gore-E. jimmycarter-E. teddyroosevelt* clade is supported by five synapomorphies: breeding males with tangerine orange pigment on the face and underside of the head;

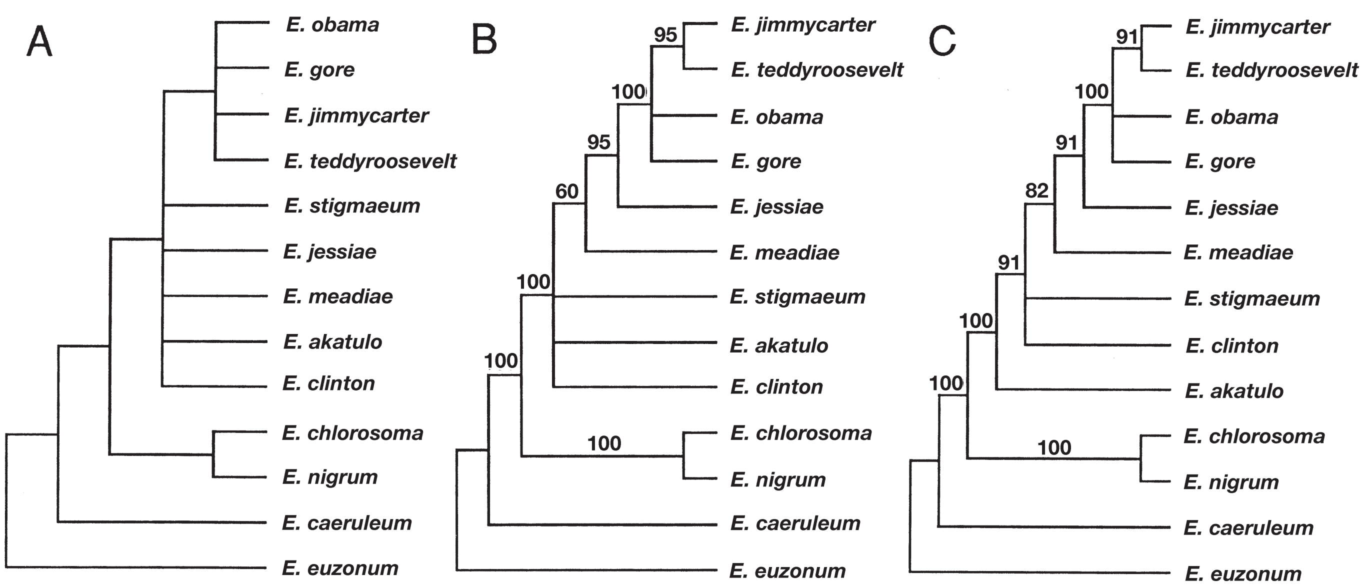

Figure 26. Consensus trees for minimum-length trees plus all trees one step longer. (A) Strict consensus and (B) majority-rule consensus of 20 trees from unordered analysis. (C) Majority-rule consensus of 11 trees from mixed unordered-ordered analysis. Numbers above branches in (B) and (C) represent percentages of trees supporting a given clade.

breeding males with orange spots on the anal fin; breeding males with quadrate lateral blotches (parallelism with *E. clinton*); breeding males with no blue pigment on the lips (reversal); and loss of palatine teeth (parallelism with *E. akatulo*). Within this clade, *E. jimmycarter* and *E. teddyroosevelt* are united by four features of nuptial male coloration, all reversals, including black marginal and submedial bands in the spinous dorsal fin, no blue pigment in the soft dorsal fin, a ventrally-developed blue-green basicaudal bar, and no blue pigment in the anal fin. *Etheostoma teddyroosevelt* exhibits two reversals as autapomorphies, loss of orange pigment on the face and loss of orange pigment in the base of the spinous dorsal fin. *Etheostoma obama* is characterized by three autapomorphic character states: restriction of orange spots in the anal fin of breeding males to the posteromedial portion of the fin, development of partly scaled cheeks, and polymorphism in the occurrence of palatine teeth.

The relationships of *E. obama*, *E. gore*, and the *E. jimmycarter-E. teddyroosevelt* clade are unresolved in the minimum-length tree presented in Figure 25. In one of the other two minimum-length trees, a sister relationship between *E. obama* and *E. gore* is supported by the development of orange pigment on the face, which is interpreted as a parallelism with the same transformation in *E. jimmycarter*. However, this character state reconstruction is ambiguous, occurring only under DELTRAN optimization. The third minimum length tree places *E. gore* as sister to the *E. jimmycarter-E. teddyroosevelt* clade. This relationship is supported by the more extensive development of orange spots in the anal fin of nuptial males; transformation to this state occurs under both optimization schemes but from different ancestral states. An *E. gore-E. jimmycarter-E. teddyroosevelt* clade is also supported by the derivation of naked cheeks, a parallel reversal with that in *E. meadiae*, but this occurs only under ACCTRAN optimization. Under DELTRAN optimization the clade is also supported by the absence of palatine teeth; this transformation shifts down the tree to the ancestor of the *E. obama-E. gore-E. jimmycarter-E. teddyroosevelt* clade under ACCTRAN. Additional characters are clearly needed to more confidently resolve the relationships of these species.

Evaluation of support.—The degree of support for the hypothesis of phylogenetic relationships (Fig. 25) was further evaluated by generating the strict and majority rule consensus trees for the minimum-length trees (60 steps) plus all trees that are one step longer. Twenty trees ≤61 steps were found in the unordered analysis and eleven were found in the mixed analysis. The strict consensus trees for the two analyses are identical (Fig. 26A), depict-

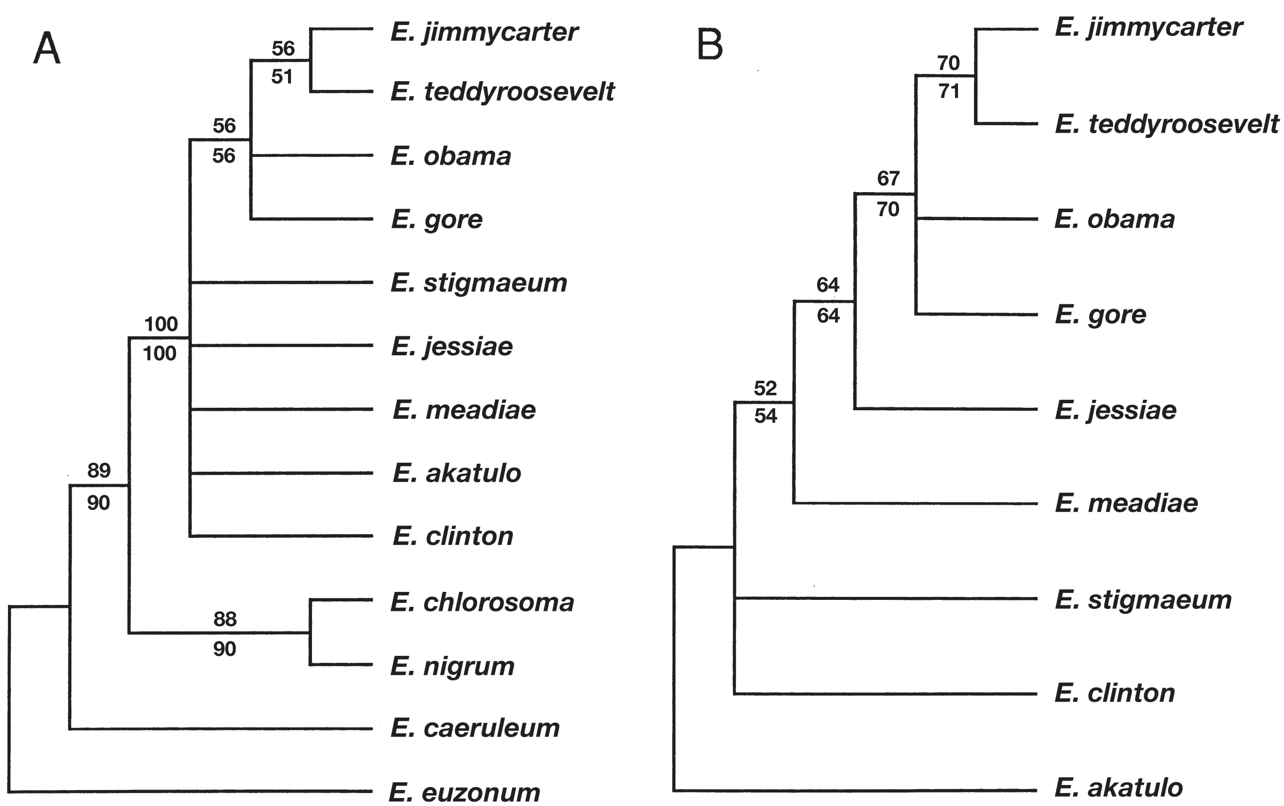

Figure 27. Bootstrap majority-rule consensus trees. (A) Full data set analysis. (B) Functional-outgroup data set analysis. Numbers above and below branches represent percentages of bootstrap replicates supporting the clade in the unordered and mixed unordered-ordered analysis, respectively.

ing a monophyletic *Doration* and an unresolved clade containing *E. obama*, *E. gore*, *E. jimmycarter*, and *E. teddyroosevelt*. The majority-rule consensus tree for the unordered analysis (Fig. 26B) indicates that 95% of the trees $\leq$61 steps place *E. jimmycarter* sister to *E. teddyroosevelt*, and 60% place *E. meadiae* sister to *E. jessiae* plus the *E. obama-E. gore-E. jimmycarter-E. teddyroosevelt* clade. In the mixed analysis (Fig. 26C) 82% of the trees support the *E. meadiae-E. jessiae-E. obama-E. gore-E. jimmycarter-E. teddyroosevelt* clade and 91% also place *E. akatulo* sister to a clade containing all other species of *Doration*. Thus, the ordering of characters 7 and 12 strengthens the position of *E. akatulo* as the basal species in the subgenus.

Bootstrapping of the unordered and mixed unordered-ordered data sets yielded majority-rule consensus trees with identical topologies and only slightly different proportions of replicates supporting the recovered clades (Fig. 27A). Strong support is indicated for the monophyly of *Doration* (100%) but only moderate support for the *E. obama-E. gore-E. jimmycarter-E. teddyroosevelt* clade (56%) and *E. jimmycarter-E. teddyroosevelt* clade (51–56%). The low bootstrap proportions (<50%) for the four other ingroup clades found in the minimum-length trees (Fig. 25) may be due to the relatively low character to taxon ratio of 2.6 and moderately high levels of homoplasy (Sanderson, 1989). In a data set exhibiting no homoplasy, at least three characters are required to support a monophyletic group at a bootstrap proportion of 95% (Felsenstein, 1985). In the minimum-length tree shown in Figure 25, only one character supports the *E. stigmaeum* clade and two characters support the *E. meadiae* clade. Interestingly, Hillis and Bull (1993) tested bootstrapping of parsimony analyses under a wide variety of conditions and found that bootstrap proportions provide highly conservative estimates of accuracy, with values above 50% often much lower than the actual probability that the corresponding clade is correct.

Another consideration in the performance of bootstrapping is the distribution of characters in the original data set. Since many of the characters are only informative with respect to the monophyly of *Doration* (ten characters support this clade) and the relationships of the outgroups, sampling with replacement will continue to generate the same relatively high proportion of characters that contribute only to the relationships between *Doration* and the outgroups. To examine the effect of eliminating this bias, analyses were performed using *E. akatulo* as a functional outgroup and all other species of *Doration* as the functional ingroup (Watrous and Wheeler, 1981); uninformative characters were excluded. Both unordered and mixed unordered-ordered analyses generated the same three most-parsimonious trees (length = 31 steps; CI = 0.677; RI = 0.722). Their topologies are identical to the ingroup portions of the most-parsimonious trees found in the original analyses. However, bootstrap proportions are 11–20 percentage points higher for the same clades supported in the original bootstraps (Fig. 27B). In addition, moderate support is indicated for the *E. jessiae-E. obama-E. gore-E. jimmycarter-E. teddyroosevelt* clade (64%), and the *E. meadiae-E. jessiae-E. obama-E. gore-E. jimmycarter-E. teddyroosevelt* clade (52–54%).

Monophyly and relationships of *Doration* relative to other darter species or groups using genetic data provided additional information as to the phylogenetic position of species of Doration. Wood and Mayden (1997) used allozyme variation to examine relationships. In their analysis *E. stigmaeum* (*Doration*) was resolved in a clade composed of a basal paraphyletic group of species of *Oligocephalus* but in a terminal sister-group relationship to a clade composed of *E. cinereum* (*Allohistium*) and *E. coosae* (*Nanostoma*) (fig. 1). When darter species were constrained as a monophyletic group relative to outgroups, *E. stigmaeum* (*Doration*), along with a number of species *Etheostoma*, was resolved in polytomus relationships (fig. 2). In their most parsimonious resolution of relationships using FREQPAS and allele frequencies, *E. stigmaeum* (*Doration*) formed the sister group to *Ioa* plus *Boleosoma*. Lang and Mayden (2007), using phylogenetic analysis of both mitochondrial ND2 and nuclear S7 sequences resolved *Etheostoma jessiae* (*Doration*) as the sister group to *E. chlorosoma* (*Vaillantia*), a relationship also resolved by Sloss et al. (2004). Most recently, Near et al. (2011) resolved a clade described as *Maydenichthys* Near and Keck inclusive of *Doration* as a well supported sister to the monophyleticgroup *Vaillantia*.

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MATERIAL EXAMINED

See Layman and Mayden (2009) for all material of *E. akatulo* examined.

Etheostoma stigmaeum.—Mobile Basin. Coosa River system, Tennessee. Polk County: UAIC 9861.16 (10), Conasauga R. ca. 1.6 river km upstream US Hwy 411 at large island along co. rd. Bradley County: CU 69879 (10), Conasauga R. at TN Hwy 74 and downstream of bridge for 0.4 km. Coosa River system, Georgia. Floyd County: UMMZ 168823 (6), Little Armuchee Cr. at US Hwy 27, Crystal Springs, 7.2 km NW Armuchee; UMMZ 88269 (1), Spring Cr. at Spring Creek, ca. 16 km SE Rome; ANSP 20645 (1; lectotype), Etowah R. near Rome; ANSP 20646 (3; paralectotypes), Etowah R. near Rome. Chattooga County: UGAMNH 1180 (1), Armuchee Cr. at US Hwy 27 near Gore. Dawson County: UGAMNH 2040 (1), Yellow Cr. from Co. Rd. 157 to confluence with Etowah R. Bartow County: UGAMNH 37 (2), Stamp Cr. above upper bridge; INHS 75090 (1), Stamp Cr. 6.4 km SE White; UAIC 10116.07 (12), Stamp Cr. at GA Hwy 20; UGAMNH 16 (7), Allatoona Cr. 3.2 km from mouth; UGAMNH 100 (5), Allatoona Cr. lower section. Paulding County: UF 80126 (7), 84743 (5), UAIC 10103.12 (11), Raccoon Cr. at Braswell Mountain Road, 6.0 km NE Braswell at powerline. Coosa River system, Alabama. Cherokee County: TU 26070 (13), trib. to Chattooga R. ca. 4.8 km ENE Chesterfield. Etowah County: UAIC 9821.09 (20), Little Canoe Cr. 5.3 km NNE Steele ca. 1.3 km upstream US Hwy 11. Calhoun County: TU 68587 (20), Shoal Cr. 3.7 km E White Plains. Clay County: UAIC 8532.13 (5), Hatchet Cr. 11.5 km WNW Millerville at Co. Rd. 7. Coosa County: UAIC 10044.08 (5), Hatchet Cr. at US Hwy 280. Tallapoosa River system, Georgia. Haralson County: UGAMNH 2142 (20), Tallapoosa R. 8.3 air km WNW Buchanan. Tallapoosa River system, Alabama. Tallapoosa County: UAIC 9815.03 (4), UAIC 10043.07 (16), Hillabee Cr. at AL Hwy 22,10.1 km NE Alexander City. Macon County: UAIC 1477.22 (7), Opintolocco Cr. 4.8 km E Tuskegee on Co. Rd. 26; INHS 78764 (10), East Opintolocco Cr. 4.8 km SE Tuskegee; AUM 6565 (3), Uphapee Cr. 5.6 air km N Tuskegee at 1-85. Alabama River tributaries, Alabama. Dallas County: AUM 7970 (16), Big Swamp Cr. 12.5 air km SE Orrville, T14N, R9E, S3; UAIC 2393 (4), Big Swamp Cr. ca. 3.2 km E Tasso, T14N, R9E, S3. Wilcox County: TU 44512 (20), Turkey Cr. 1.6 km S Kimbrough at AL Hwy 5. Monroe County: TU 44449 (20), Flat Cr. 13.8 km NW Monroeville at AL Hwy 41; UAIC 9705.13 (5), Little R. 5.3 km SSE Uriah at AL Hwy 21, Escambia County line. Escambia County: TU 99951 (11), Little R. at Co. Rd. 1, 12.6 km NW McCullough. Cahaba River system, Alabama. Bibb County: UAIC 5604.27 (20), Little Cahaba R. at Bulldog Bend. Dallas County: UAIC 9610.17 (10), Oakmulgee Cr. ca. 4.8 km W Summerfield, ca. 0.8 km below AL Hwy 219; UAIC 9611.12 (10), Oakmulgee Cr. ca. 5.3 km WSW Summerfield, T18N, Rl0E, S29. Black Warrior River system, Alabama. Etowah County: UAIC 3307 (12), Little Cove Cr., T11S, R3E, S12. Blount County: UAIC 2512 (8), Little Warrior R. at AL Hwy 79, 16 km N Jefferson County line. Winston County: UAIC 4111.07 (9), Sipsey Fork at Low Pressure Bridge, ca. 6.4 km E AL Hwy 195, ca. 8.8 km NNE Double Springs; UAIC 4329.16 (11), Sipsey Fork at Sipsey Fork Recreation Area. Tuscaloosa County: UAIC 8332.06 (11), UAIC 8334.08 (6), UAIC 9857.09 (3), Mill Cr. at US Hwy 82, Northport. Upper Tombigbee River system, Alabama. Marion County: TU 40510 (17), trib. to Buttahatchie R. at US Hwy 278,0.6 km W AL Hwy 129 jct.; UAIC 4315.24 (3), Williams Cr. at US Hwy 43, Hamilton, TI0S, RI4W, S35; UAIC 4316.19 (16), UAIC 10371.01 (4), Luxapalila Cr. at US Hwy 43, Winfield. Sumter County: TU 48924 (20), Noxubee R. at AL Hwy 17, 7.0 km NW Geiger. Lower Tombigbee River tributaries, Alabama. Marengo County: TU 60933 (20), Beaver Cr. 19.0 km SW Linden at AL Hwy 69. Choctaw County: TU 56991 (10), Souwilpa Cr. 6.2 km S Gilbertown at AL Hwy 17; TU 57009 (10), Bogueloosa Cr. 1.3 km N Toxey at AL Hwy 17. Washington County: UAIC 1088 (16), UAIC 2498 (2), Bilbo Cr. at US Hwy 43, 4.5 km S McIntosh. Tennessee River drainage. Bear Creek system, Alabama. Franklin County: UAIC 5968.12 (11), UAIC 10336.02 (13), Bear Cr. at Co. Rd. 93, 3.6 km NE Posey Mill, T8S, Rl0W, S23/24; UAIC 2323 (3), Little Bear Cr. ca. 4.8 km SE Phil Campbell at Burdeshaw Bridge, T8S, R11W, S34; UAlC 1777 (3), Little Bear Cr. below Batestown Bridge, T8S, R11W, S26; UAIC 1797 (1), Bear Cr. between Price's Bridge and mouth of Whitehead Spring Branch, T8S, R12W, S32; UAIC 2194 (1), Bear Cr. ca. 4.0 km NE Hodges, ca. 61 m downstream of Scott Bridge, T8S, R13W, S15. Winston County: UAIC 2322 (10), Bear Cr. ca. 6.4 km N Haleyville, T9S, R11 W, S7. Marion County: UAIC 1886 (9), Bear Cr. 1.6 km W Bear Creek community on AL Hwy 172, T9S, R11W, S17; UAIC 1795 (3), Bear Cr. ca. 4.8 km E Hackleburg at AL Hwy 172, T9S, R12W, S11. Eastern Gulf Coast systems. Pensacola Bay system, Alabama. Covington County: UAIC 4506.17 (3), trib. to Conecuh R. 2.4 km from Gantt. Escambia County: UAIC 10374.01 (7), Big Escambia Cr. at first bridge N I–65, 3.8 km NW Barnett Crossroads; UAIC 10283.06 (15), Big Escambia Cr. 9.6 km NW Flomaton just downstream of powerline and pipeline crossing, T1N, R7E, S11. Pensacola Bay system, Florida. Santa Rosa County: TU 56722 (20), Pond Cr. 3.2 km SW Milton at US Hwy 90; UF 75442 (3), Escambia R. ca. 1.6 km upstream FL Hwy 4, 2.7 km E Century, Escambia County line; UF 75376 (5), Escambia R. at FL Hwy 4, 2.7 km E Century, Escambia County line; UF 75365 (1), Escambia R. below FL Hwy 4, above Look and Tremble Oxbow. Perdido River system, Alabama. Baldwin County: TU 56700 (1), trib. to Styx R. 16 km W Florida state line at I-10; TU 87833 (16), Blackwater R. 1.8 km S US Hwy 90, 5.8 km SW Seminole. Perdido River system, Florida. Escambia County: TU 92066 (8), TU 98521 (1), TU 115961 (2), Perdido R. at FL Hwy 184, Muscogee. Central Gulf Coast systems. Pascagoula River system, Mississippi. Clarke County: UAIC 1583 (11), UAIC 10050.17 (7), Shubuta Cr. at US Hwy 11, 9.6 km S Pachuta. Jones County: TU 56151 (20), Leaf R. just below I-59,3.2 km W Moselle. George County: UAIC 4058 (6), Escatawpa R., T3S, R5W, S2/3. Pascagoula River system, Alabama. Mobile County: TU 100953 (11), Franklin Cr. at US Hwy 90, 0.8 km E Mississippi state line. Pearl River system, Mississippi. Leake

County: TU 128164 (8), TU 128234 (2), Pearl R. at Edinburg, MS Hwy 16. Copiah County: TU 56819 (10), trib. to Pearl R. at MS Hwy 27, 8.8 km NW Georgetown. Simpson County: TU 56071 (20), Strong R. at MS Hwy 28,3.2 km W Pinola. Pike County: TU 43129 (20), Bogue Chitto at US Hwy 98,15.2 km E McComb. Pearl River system, Louisiana. Washington Parish: TU 17464 (7), UAIC 10066.12 (13), Pushepatapa Cr. at LA Hwy 21,0.3 km S Varnado. Lake Ponchartrain system, Louisiana. Tangipahoa Parish: TU 116611 (20), East Fork Big Cr. at LA Hwy 1054, 7.8 km ENE Arcola. Lake Ponchartrain system, Mississippi. Amite County: UAIC 10373.01 (4), trib. of West Fork Amite River at MS Hwy 567, 7.2 air km N Liberty; TU 76067 (16), West Fork Amite R. at MS Hwy 48,5.1 km SW Liberty. Lower Mississippi Embayment, eastern tributaries. Homochitto River system, Mississippi. Lincoln County: TU 66522 (20), Homochitto R. at MS Hwy 550, 8.0 km E Union Church. Bayou Pierre system, Mississippi. Copiah County: UAIC 10320.07 (3), trib. to Bayou Pierre 1.6 km S Glancy, 12.0 air km SW Hazelhurst; TU 93642 (8), Bayou Pierre at second bend below MS Hwy 18, 1.3 km below bridge. Claiborne County: TU 91167 (9), Bayou Pierre 0.6 km N Carlisle Post Office. Big Black River system, Mississippi. Attala County: TU 138972 (16), Long Cr. 1.1 km S McAdams. Warren County: UAIC 246 (13), Clear Cr. 16 km E Vicksburg, 0.8 km N US Hwy 80. Yazoo River system, Mississippi. Calhoun County: TU 156228 (2), Lucknuck Cr. at MS Hwy 9; TU 156253 (8), McGill Cr. at MS Hwy 9, 5.9 km SW Pontotoc County line. Holmes County: TU 146272 (20), Williams Cr., T14N, R2E, S7. Upper Mississippi Embayment, eastern tributaries. Hatchie River system, Tennessee. McNairy County: UT 91.530, part 1 of 2 (1), Boles Cr. at co. rd., 4.8 km S TN Hwy 57; UT 91.530, part 2 of 2 (1), Mosses Cr. on Rose Creek Rd., 2.1 km N TN Hwy 57,4.0 km ENE Pocahontas. Hardeman County: CU 65770 (6), Spring Cr. above and below second bridge on TN Hwy 125 S Bolivar; UT 91.529 (16), Spring Cr. at Co. Rd. 8158; UAIC 10375.01 (1), Spring Cr. at co. rd., 7.0 air km E Saulsbury. Haywood County: UAIC 10298.27 (3), Hatchie R. at Big Eddy, 17.4 air km SE Brownsville at E end Hatchie National Wildlife Refuge. Clarks River system, Kentucky. Calloway County: UAIC 9866.18 (20), Middle Fork Clarks R. at Martin Chapel Rd., ca. 2.4 km upstream KY Hwy 121 near Murray; TU 53465 (6), East Fork Clarks R. 2.7 km S Murray; SIUC 326 (1), SIUC 12540 (1), West Fork Clarks R. 1.6 km E Coldwater at KY Hwy 121. Graves County: SIUC 11797 (1), old channel West Forks Clark R., 3.2 km W Clear Springs. Upper Mississippi Embayment, western tributaries. Castor River system, Missouri. Bollinger County: KU 9279 (9), Castor R. 9.6 km W Zalma, T29N,. R8E, S28; UAIC 10342.15 (6), Castor R. at Co. Rd. 736 (Gipsey Bridge). St. Francis River system, Missouri. Madison County: TU 74549 (14), St. Francis R. at Co. Rd. C bridge, 13.3 km NW jct. US Hwy 67 and Co. Rd. N, T31N, R5E, S11. Wayne County: SIUC 12537 (4), St. Francis R. 4.8 km NW Silva. Iron County: Big Creek 2.4 km SE Annapolis. Scott County: KU 9232 (1), Ditch 1, 3.2 km E Vanduser, T27N, R13E, S16; INHS 81727 (1), canal 1.6 km W Grant City. Stoddard County: INHS 81737 (1), Ditch No.1, Badersville. New Madrid County: INHS 81165 (1), Jones Ditch Canal 7.2 km E Gideon; INHS 81136 (3), Main Ditch District No.1, 4.0 km E Morehouse; INHS 76782 (4), drainage ditch 1.6 km E Malden; KU 9422 (1), ditch 4.0 km W Matthews, T24N, R13E, S3. Pemiscot County: KU 9592 (1), Main Ditch 4.8 km W Hayti, TI9N, RI2E, S31. Black River system, Missouri. Butler County: UMMZ 139675 (3), Cane Cr. at confluence with Ten Mile Cr., 8.0 km W Poplar Bluff. Black River system, Arkansas. Clay County: TU 66007 (10), Current R. 7.2 km NW Success along AR Hwy 211. Randolph County: TU 59738 (7), Current R. 0.5 km NW Biggers; TU 54622 (3), Current R. at US Hwy 67, 12.8 km ENE Pocahontas; NLU 41964 (3), Spring R. at Ravenden access near Ravenden; NLU 44321 (4), Spring R. at island near gravel pit, T18N, R1W, S31. Sharp County: UAIC 10376.01 (5), Spring R. at Hardy, Hardy Beach Access, just off of AR Hwy 342; NLU 42089 (8), Spring R. at Williford access; UAIC 10378.01 (10), Strawberry R. at US Hwy 167, 3.2 km N Evening Shade. White River system, Arkansas. Marion County: TU 79889 (1), Buffalo R. 0.8 km upstream Bush Cr., T17N, R15W, Sl1; NLU 24915 (1), Buffalo R., state park, T17N, RI5W, S34. Baxter County: TU 51237 (1), Buffalo R., second riffle above mouth. Independence County: NLU 14111 (2), NLU 16215 (2), White R. ca. 24 km NW Batesville, ca. 0.4 km S Lock and Dam No.3; NLU 14193 (1), White R. at Lock and Dam No.3; NLU 29224 (2), NLU 49076 (11), White R. below Lock and Dam No.1, Batesville. Little Red River system, Arkansas. Van Buren County: KU 9840 (1), Choctaw Cr., T10N, R14W, S15, and Dry Fk., T10N, R14W, S10; INHS 81088 (1), South Fork Little Red R. 14.4 km SW Clinton; NLU 48727 (1), Archey Cr. 1.6 km N Clinton, T11N, R14W, S10. Stone County: NLU 28937 (1), Middle Fork Little Red R. ca. 7.2 km NW Arlberg, T31N, R13W, S23. Van Buren County: UT 91.987, Middle Fork Little Red R. at AR Hwy 9 above Shirley. Cleburne County: NLU 52715 (5), Big Cr. 1.6 km down co. rd. off AR Hwy 110, 3.2 km N Pangburn. Lower Mississippi Embayment, western tributaries. Ouachita River system, Arkansas. Hot Spring County: NLU 67242 (5), Ouachita R. below Remmel Dam, above and below Stone Quarry Cr., 8.0 km W I-30, T3S, R17W, S29. Clark County: UT 91.3360 (1), Caddo R. at I-30; NLU 58836 (4), UAIC 10379.01 (2), Caddo R. at US Hwy 67, 5.9 km N Arkadelphia; NLU 58816 (20), Caddo R. at mouth (Ouachita R.). Ouachita County: UAIC 10062.20 (2), TU 45702 (6), Tulip Cr. at AR Hwy 7,24.0 km N Camden. Pike County: NLU 52546 (7), Antoine R. 1.6 km S Antoine, T8S, R23W, S25. Nevada County: NLU 47956 (3), Brushy Cr. 1.6 km N Prescott on US Hwy 67, left on paved rd. 12.8 km, T9S, R22W, S28. Garland County: NLU 48699 (1), South Fork Saline R. at co. rd. 0.4 km E off AR Hwy 5, 4.8 km E Fountain Lake. Saline County: NLU 15388 (11), South Fork Saline R. 4.8 km W Benton, T1S, R15W, S28;

NLU 38590 (8), South Fork Saline R. at co. rd. 1.6 km E Nance. Grant County: NLU 16928 (1), Saline R. at AR Hwy 229,4.8 km N Poyen; NLU 15186 (4), Saline R. at US Hwy 270,8.0 km W Prattsville; NLU 16946 (5), Saline R. at Jenkins Ferry State Park, AR Hwy 46, 6.4 km E Leola. Bradley County: NLU 54006 (20), Saline R., "Moors Mill," 9.6 km S Johnsville, T16S, R9W, S26. Ouachita River system, Louisiana. Morehouse Parish: NLU 59633 (5), Bayou Bartholomew 6.4 km below LA Hwy 139 bridge; NLU 63652 (15), Bayou Bartholomew 0.4 km W LA Hwy 2 bridge, 0.2 km W US Hwy 165 jct., T21N, R5E, S28. Red River-Atchafalaya River system, Louisiana. LaSalle Parish: NLU 58504 (10), Castor Cr. 30 m S LA Hwy 124 spillway, 3.2 km W Olla. Grant Parish: UAIC 10310.11 (13), Big Cr. at old blockaded bridge, 5.3 air km NW Pollock (access from S side); TU 37282 (7), Big Cr. at LA Hwy 8, Fishville. Rapides Parish: NLU 49173 (10), Spring Cr. 2.4 km N Glenmora.

Etheostoma jessiae.—Lower and middle Tennessee River drainage, Tennessee. Houston County: TU 14670 (2), Whiteoak Cr. at Hwy 13,13.6 km S jct. Hwys. 13 and 49. Humphreys County: UT 91.1040 (1), Whiteoak Cr. at continuation of Houston Co. Rd. 6365; UAIC 9864.16 (5), Whiteoak Cr. at Pennywinkle Rd., 0.8 km W Tennessee Ridge Rd. near Houston County line. Hardin County: UT 91.2789 (8), UAIC 10335.03 (10), Alexander Br. at bridge between TN Hwy 128 and Co. Rd. 8230, trib. to Indian Cr.; UT 91.685 (3), Indian Cr. at US Hwy 64; UT 91.2566 (6), Indian Cr. river km 6.4–16.0 and 17.6–32.0. Wayne County: CU 64701 (15), Butler Cr.3.6 km E Pleasant Springs Church. Lawrence County: UAIC 4773.18 (5), Factory Cr. at bridge 1.9 km SW Westpoint; UAIC 4775.11 (4), Factory Cr. at ford 2.9 km W Westpoint; UAIC 2505 (10), Bluewater Cr. ca. 2.4 km SE Loretto. Lincoln County: CU 46607 (4), Elk R. ca. 19.2 air km WSW Winchester on secondary rd; UT 91.1587 (1), Elk R. at US Hwy 231/US Hwy 431, Fayetteville. Franklin County: UAIC 4003 (4), Elk R. at Garner Ford, 3.0 km S Beech Hill, 1.6 km W Tims Ford Dam. Grundy County: UAIC 2835 (3), Elk R. at Elk Head. Giles County: UAIC 2704.10 (1), Richland Cr. ca. 5.0 km W Elkton; UT 91.3697 (3), Richland Cr. km 51.2,7.2 air km NW Pulaski. Lower and middle Tennessee River drainage, Alabama. Lauderdale County: UAIC 4817.19 (10), Little Cypress Cr., T1S, R11W, S33; CU 54801 (2), Little Butler Cr. at Pruitton. Jackson County: CU 64702 (17), Hurricane Cr. 5.3 km NE Freedom Baptist Church, Estill Fork; UAIC 7123.20 (7), Estill Fk. near Bostick Hill Church at dirt rd. ford, T2S, R4E, S2. Little Bear Creek system, Alabama. Franklin County: TU 40546 (16), Little Bear Cr. 0.4 km above AL Hwy 187; UAIC 10372.01 (2), UAIC 10461.09 (4), AUM 8779 (1), Little Bear Cr. at AL Hwy 187, 8.0 km S Belgreen; UAIC 1884 (1), UAIC 1918 (3), UAIC 10309.09 (7), Little Bear Cr. at AL Hwy 24, just below Jordan's Mill; AUM 9724 (2), Little Bear Cr., river km 4.8 and 24.0; AUM 4126 (3), Cedar Cr. at km 33.6, 1.3 air km N White Oak, T6S, R14W, S10; UAIC 2420 (3), Spring Cliff Br., trib. to Cedar Cr., 3.2 km N Spruce Pine, T7S, R11 W, S30; UAIC 1782 (1), Little Bear Cr., T7S, R12W, S29; UAIC 1780 (1), Little Bear Cr. at rd. crossing, T8S, RI2W, S7; AUM 9440 (3), Little Bear Cr. 8.5 air km SW Belgreen, Co. Rd. 27; AUM 9464 (2), Little Bear Cr. at Carpenter's Bridge, 5.8 air km SSW Guinn Cross Roads. Upper Tennessee River drainage, Tennessee (excluding Clinch River). Sequatchie County: UAIC 10110.15 (6), Sequatchie R. at Old State Hwy 28, just E Dunlap; TU 33462 (2), Sequatchie R. 5.4 km S Dunlap, US Hwy 127; UAIC 2779 (2), Sequatchie R. ca. 2.4 km ESE Dunlap. Marion County: UT 91.2133 (1), Sequatchie R. ca. 0.4 km above mouth of Little Sequatchie R.; UAIC 8995.01 (2), Sequatchie R. ca. 0.8 km above mouth of Little Sequatchie R.; UT 91.2326 (2), Sequatchie R. river km 14.9–16.2; UT 91.3662 (5), Sequatchie R. river km 11.4. Bledsoe County: UAIC 2775 (4), INHS 77089 (2), Sequatchie R. ca. 1.6 km SE Ninemile. Polk County: UAIC 9819.15 (7), UAIC 10040.13 (5), UAIC 10071.17 (3), UT 91.2432 (1), Spring Cr. at bridge on unnamed gravel rd., 5.3 air km N Reliance, access from TN Hwy 315; UT 91.4095 (2), Spring Cr. at "Watercamp," near mouth. McMinn County: USNM 70646 (2), Arnwine Cr., Athens. Monroe County: UAIC 4148.18 (2), Little Tennessee R. at US Hwy 411, SW Knoxville; UAIC 8971.02 (2), Citico Cr. at Citico bridge; UT 91.308 (6), Citico Cr. 1.6 km above mouth; UT 91.2321 (3), Citico Cr. 7.2 air km SSE Citico Beach; UT 91.2835 (1), Citico Cr. 5.8 km above last iron bridge on Mountain Settlement Rd. Blount County: CU 67581 (7), UAIC 8591.12 (10), UAIC 9845.01 (3), Little R. at US Hwy 411; CU 65046 (2), Little R. below Melrose Mill Dam; CU 65171 (2), Little R. ca. 0.5 km above Wildwood Bridge on Wildwood Rd.; CU 65203 (1), Little R. at river km 34.4; CU 65213 (1), Little R. at river km 33.6. Sevier County: CU 52716 (1), East Fork Little Pigeon R. at US Hwy 411, 8.0 km E Sevierville; CU 55070 (1), West Prong Little Pigeon R. at bridge just E US Hwy 441,0.3 km S US Hwy 441 bridge at Pigeon Forge; CU 38184 (7), Little Pigeon R. at roadside park 3.2 km E Sevierville on US Hwy 411; CU 41884 (18), Walden Cr., trib. to West Prong Little Pigeon R., 5.0 air km SW Pine Grove; CU 46624 (3), Cove Cr., trib. to Walden Cr., 18.6 km NE Townsend; CU 72044 (2), Walden Cr. Greene County: UT 91.770 (15), Nolichucky R. below first bridge above Meadows Cr., and Meadow Cr. 0.4 km upstream of mouth; UT 91.4190 (8), Lick Cr. at TN Hwy 348, 8.3 air km E of its mouth. Hamblen County: UT 91.1209 (5), Bent Cr., trib. to Nolichucky R. Knox County: UT 91.3984 (20), Flat Cr. below confluence with Little Flat Cr. on Idumea Rd. Hawkins County: UT 91.3713 (8), Beech Cr. along Tunnel Hill Rd., 0.8 rd. km N Webster Valley Rd. Sullivan County: UT 91.4169 (2), Horse Cr. at TN Hwy 92,7.7 air km SSW Kingsport. Upper Tennessee River drainage, Georgia. Dade County: UT 91.2114 (6), Lookout Cr., 8.0 stream km S Trenton, below old mill dam; UGAMNH 1488 (6), Lookout Cr., 1.6 km S Trenton; UGAMNH 1487 (1), Lookout Cr. 4.8 km S Trenton; UAIC 1690 (1), Lookout Cr. near Trenton, below old mill dam. Walker County: TU 34964 (19), West Chickamauga Cr. at GA Hwy 143,2.1 km W jct. GA Hwy 341; UAIC 1821 (3), West Chickamauga Cr. at GA Hwy 143 S Pond Springs. Catoosa County: UT 91.2726 (8), South Chickamauga Cr. ca. 1.6 km SE Ringgold at L&N RR bridge along GA Hwy 3. Upper Tennessee River drainage, Virginia. Scott County: UMMZ 130756 (1), Cove Cr., near Bristol, along US Hwy 58, ca. 3.2 road km below point where road leaves Cove Cr.; CU 68S00 (2), Possum Cr. at Hwy 713 bridge S Cleveland School, 4.8 air km SW Gate City. Clinch River system downstream of Norris Dam, Tennessee. Morgan County: UT 91.110 (12), Emory R. at Oakdale; INHS 83043 (4), Bitter Cr. 4.8 km ESE Oakdale. Anderson County: CU 52088 (1), trib to Brushy Cr. near Spessard Mills, 5.8 km W Clinton; CU 52943 (1), Brushy Fk., trib, to Poplar Cr., 8.0 km WSW Clinton, 3.8 km NNW Elza Gate, Oak Ridge; CU 44028 (2), Poplar Cr. 5.1 km NE Oliver Springs; CU 19151 (11), Poplar Cr. near Oliver Springs, Brown Cr., Brushy Fk.; UT 91.89 (3), in part, Brushy Fk.; TU 29093 (20), Hinds Cr. ca. 9.6 km SW Norris; UT 91.1280 (4), Buffalo Cr., trib. to Clinch R. at I-75; UMMZ 103676 (4), Clinch R. below bridge; UMMZ 159179 (2), Clinch R. 1.6 km below Norris Dam; UT 91.89 (4), in part, Coal Cr.; UAIC 10380.01 (18), Coal Cr. along TN Hwy 116, 2.1 air km SW Lake City; UT 91.2251 (6), Coal Cr. below Briceville; UT 91.2252 (12), Coal Cr. at river km 7.7, above Lake City. Knox County: UT 91.692 (13), UT 91.1264 (3), Beaver Cr. at US Hwy 441, Halls Crossroads. Union County: UT 91.3368 (9), Bull Run Cr. at first bridge above TN Hwy 33. Clinch River system upstream of Norris Dam, Tennessee. Campbell County: UMMZ 113588 (19), Cove Cr. below Caryville Dam; UMMZ 104177 (1), Cove Cr.; UMMZ 103591 (10), Pond opposite Doak's Dam. Claiborne County: USNM 70644 (2), USNM 70645 (9), Ball Cr., Tazewell. UMMZ 96903 (1), Little Sycamore Cr., not far from Tazewell; UAIC 9838.11 (19), Big Sycamore Cr. at Buck Lick Rd., ca. 0.4 km SE TN Hwy 33, ca. 4.8 km upstream Norris Reservoir; CU 49709 (5), Big Sycamore Cr. 5.9 km E jct. of TN Hwy 33 and US Hwy 25 at Howardton Church.

Etheostoma meadiae.—Powell River system, Tennessee. Claiborne County: UMMZ 158372 (10), CU 48256 (6), UT 91.4183 (1), Powell R. 4.8 km SE Harrogate at US Hwy 25E; UF 17188 (1), Powell R. at US Hwy 25E and four other sites to 3.7 km above bridge, 4.8 km S Harrogate; UT 91.55 (3), Russell Cr. at Powell R.; UF 9853 (3), Powell R. 15.2 km NE Tazewell, near Hoop; UT 91.2247 (5), UCT 91.2249 (5), UT 91.2250 (2), UAIC 9840.23 (7), Powell R. at Buchanan Ford, access via Yeary Rd. from TN Hwy 345 at Hopewell Church; USNM 048903 (1; holotype), USNM 125623 (1; paratype), Indian Cr., Cumberland Gap, Tennessee, Powell River system, Virginia. Lee County: UT 91.2253 (3), Powell R. at Fletcher Ford, river km 187.7; UAIC 7951.19 (1), Powell R. at VA Hwy 70,1.6 km S Bowling; UMMZ 103443 (2), Powell R. at mouth of Station Cr. on US Hwy 58 E Jonesville. Clinch River system, Tennessee. Hancock County: UT 91.3948 (6), Clinch R. km 275.7, Swan Island, 8.8 air km SW Sneedville; UT 91.1266 (6), UT 91.2129 (20), UAIC 8880.04 (8), Clinch R. at Frost Ford, ca. 6.4 km above Sneedville; UAIC 9855.14 (6), UAIC 10705.01 (6), Panther Cr. at Jimmie Brooks Rd., just off of TN Hwy 33, 5.6 km E Sneedville; UAIC 10706.01 (7), Blackwater Cr. at TN Hwy 70, 0.5 km S Virginia line; CU 46433 (1), CU 46434 (11), Clinch R. 0.5 km downstream TN Hwy 70, Kyles Ford; UAIC 8986.09 (9), Clinch R. at Kyles Ford, ca. 16 km ENE Sneedville. Clinch River system, Virginia. Lee County: CU 52785 (1), Blackwater Cr. at VA Hwy 70 and Co. Rd. 600 bridge, ca. 12.8 air km N Kyles Ford. Scott County: UAIC 7942.20 (2), Clinch R. 0.4 km downstream of US Hwy 23/58; CU 62669 (3), CU 62919 (1), CU 63130 (2), CU 63502 (3), CU 64129 (2), CU 52159 (1), Copper Cr. 0.4 km above mouth on Co. Rd. 627, 2.0 air km S Clinchport; CU 52134 (2), Copper Cr. from mouth to 0.6 km upstream, off Co. Rd. 627, 2.0 air km S Clinchport; UT 91.1926 (2), Copper Cr. at VA Hwy 71, ca. 2.4 air km SSW Nickelsville; CU 62845 (2), Copper Cr. 4.0 km above mouth on Co. Rd. 627, 5.4 air km ESE Clinchport; TU 71971 (15), Copper Cr. 2.4 km NE Speers Ferry; TU 69268 (4), Copper Cr. at ford, 4.0 km NE Speers Ferry; CU 63476 (1), Clinch R. above Hwy 35/Hwy 58 bridge, 1.6 km S Clinchport; UAIC 10484.19 (1), Clinch R. 0.4 km downstream US Hwy 23/58; UT 91.2255 (2), Clinch R. just above Hwy 71 at Fort Blackmore, river km 364.0. Tazewell County: VPI 2690 (14), Indian Cr. at jct. Hwy 627 and Hwy 630.

Etheostoma obama.—Duck River system, Tennessee. Humphreys County: UT 91.832 (3), Duck R. at mouth of Hurricane Cr.: UT 91.856 (3), Buffalo R. (the “whirl”) 2.1 river km above mouth, at access to private home, gravel shoals and island. Hickman County: UT 91.1292 (2), Lick Cr. ca. 1.6 km NW Primm Springs at low water bridge. Maury County: NLU 50667 (2), Duck R. 0.5 air km E I-65 at mouth of Dewberry Br. Marshall County: UAIC 6395.11 (23), Duck R. ca. 3.2 km upstream US Hwy 31A. Bedford County: UT 91.747 (1), Sinking Cr. N TN Hwy 64; UAIC 10039.21 (4), Flat Cr. at TN Hwy 64, ca. 1.9 km SW Shelbyville; UAIC 2534 (5), Flat Cr. 0.3 km S Shelbyville on US Hwy 231; UT 91.1599 (16), Duck R. at end of unnumbered co. rd., 9.1 air km NW Shelbyville, 3.2 air km NW Elbethel; UAIC 9862.15 (8), Duck R. below dam at TN Hwy 64/US Hwy 231 in Shelbyville; UT 91.739 (9), Garrison Cr. Perry County: NLU 56575 (1), Cane Cr. at TN Hwy 50, ca. 4.8 km E Beardstown. Wayne County: NLU 28797 (10), Buffalo R. at TN Hwy 13, ca. 2.4 km SE Flatwoods. Lewis County: UT 91.3973 (1), Buffalo R. 3.5 air km below TN Hwy 13; UAIC 10462.15 (14), Buffalo R. at mouth of Grinders Cr. and TN Hwy 99.

Etheostoma gore.—Cumberland River drainage, Tennessee. Robertson County: CU 22168 (2), Sulphur Cr. at TN Hwy 76, 8.0 km S Adams; UT 91.4066 (1), Sulphur Fork Cr. 0.8 km above TN Hwy 76. Montgomery County: CU 23301 (1), Yellow Cr. at old bridge, 0.8 km off of TN Hwy 13, S

Clarksville and 16.8 km N jct. TN Hwy 13 and TN Hwy 48. Rutherford County: UT 91.2237 (1), Middle Fork Stones R. at "County Farm Ford," ca. 0.8 km SSE Murfreesboro; CU 42008 (2), CU 51527 (1), INHS 84130 (1), TU 19506 (1), UAIC 9865.19 (13), UT 91.708 (2), East Fork Stones R. at US Hwy 231, just below dam at Walterhill, 10.4 km N Murfreesboro; NLU 15742 (3), East Fork Stones R. 3.2 km S Lacassa. Jackson County: UT 91.276 (2), Roaring R. just off TN Hwy 135, at old bridge 4.8 km SE Gainesboro; KU 11539 (12), Roaring R. at TN Hwy 135, 23.7 km NNW Cookeville. Overton County: KU 11514 (4), West Fork Obey R. 8.0 km E Alpine; AUM 11022 (1), West Fork Obey R. at TN Hwy 85, 2.1 km SSE Allred; INHS 58232 (3), Cowan Br. at TN Hwy 52, 4.8 km E Alpine. Pickett County: UT 91.196 (5), Wolf R. bridge N Byrdstown-Forbus Rd., 2.4 km E Byrdstown. Scott County: UT 91.426 (10), Station Camp Cr. at mouth, and 0.8 km above mouth. Cumberland River drainage, Kentucky. Cumberland County: INHS 63055 (1), Marrowbone Cr. 3.2 km W Burkesville, Hwy 691; UMMZ 154639 (3), Marrowbone Cr. at mouth of Farris Fork, 1.2 km E Marrowbone; SIUC 4016 (3), Crocus Cr. ca. 3.2 km NNW Bakerton. Pulaski County: UF 15405 (8), Fishing Cr. at KY Hwy 635, 9.6 km WNW Science Hill; INHS 78871 (4), Buck Cr. 6.4 km W Bandy; SIUC 7584 (6), Buck Cr. at KY Hwy 1677, 3.3 km N US Hwy 80; SIUC 13245 (4), Buck Cr. ca. 4.8 stream km downstream KY Hwy 1012 bridge. Wayne County: TU 74586 (20), Little South Fork Cumberland River at Parmleysville, 19.2 air km SE Monticello. Rockcastle County: UAIC 9851.08 (23), Rockcastle R. along KY Hwy 89, ca. 2.7 km NE KY Hwy490.

Etheostoma jimmycarter.—Green River drainage, Kentucky, Monroe County: SIUC 3948 (4), East Fork Barren R. at KY Hwy 63, 6.4 km NW Tompkinsville. Allen County: SIUC 37 (2), Long Cr. 1.6 km SW Amos; SIUC 78 (2), Long Cr. 2.4 km SE Amos. Barren County: UMMZ 165401 (10), Fallen Timber Cr. at KY Hwy 63, 9.6 km SE Glasgow; INHS 77938 (10), Skaggs Cr. 3.2 km N Roseville. Casey County: UMMZ 165267 (10), Green R. at Yosemite, KY Hwy 198; UMMZ 169473 (4), branch of Trace Fk. at KY Hwy 910, just S Phil. Taylor County: KU 11626 (4), Big Pitman Cr. at KY Hwy 210, 11.8 km NW Campbellsville. Green County: UMMZ 165302 (8), SIUC 1101 (2), Green R. at Greensburg; UAIC 10521.01 (16), Little Barren R. at KY Hwy 88, 16.0 air km W Greensburg. Adair County: UAIC 6495.15 (6), trib. to Russell Cr. at KY Hwy 80, ca. 7.0 air km W Russell Springs; UAIC 7157.13 (14), Russell Cr. at KY Hwy 80, Metcalfe County: UAIC 9852.14 (6), Little Barren R. at KY Hwy 70, Sulphur Well Larue County: UMMZ 165432 (10), South Fork Nolin R. at Buffalo; INHS 78479 (8), Walters Cr. 6.4 km N Magnolia. Edmonson County: SIUC 18977 (1), Green R. at river km 319.0, upstream end of island, ca. 14 km ENE Brownsville. Green River drainage, Tennessee. Clay County: UT 91.117 (2), Big Trace Cr. at Hermitage Springs; UT 91.393, in part (6), Big Trace Cr. at Tennessee-Kentucky line; UT 91.393, in part (1), Salt Lick Cr. at Co. Rd. 6138, 1.3 km from Kentucky line; UT 91.1311 (1), Salt Lick Cr. at Bethany Rd. Sumner County: UAIC 9870.12 (19), UT 91.876, in part (11), West Fork Drakes Cr. at Coker Ford Rd., ca. 1.6 km E Mitchellville; UT 91.876, in part (4), West Fork Drakes Cr. at mouth of Caney Cr.

Etheostoma teddyroosevelt.—Arkansas River drainage, Missouri. Lawrence County: KU 6511 (5), Spring R. at MO Hwy 97; KU 10793 (1), Spring R. 9.6 km E La Russel, T28N, R28W, S13. Jasper County: UAIC 10711.30 (1), Spring R. at Co. Rd. D at Quaker Mill Park, just SW Purcell. Arkansas River drainage, Kansas. Cherokee County: KU 11409 (1), KU 18443 (1), KU 16088 (4), Shoal Cr. at KS Hwy 26, Schermerhorn Park, 3.2 km S Galena. Arkansas River drainage, Oklahoma. Delaware County: UMMZ 103187 (4), Elk R. at Turkey Ford, trib. of Grand R. Cherokee County: UMMZ 210571 (3), Fourteen Mile Cr. Adair County: KU 2425 (2), Illinois R. at US Hwy 59; UMMZ 127177 (4), Barren Fork Cr., trib. of Illinois R., near Proctor. Arkansas River drainage, Arkansas. Washington County: UT 91.1833 (3), Illinois R. at ford above end of gravel rd., 10.1 rd. km W US Hwy 71; KU 6333 (2), Illinois R. at Moffit, 17.6 km SW Fayetteville; UMMZ 170924 (2), Illinois R. at AR Hwy 68,24.0 km W Springdale. Johnson County: UAIC 10305.14 (2), Mulberry R. at AR Hwy 103, 0.8 km S AR Hwy 215 jct. Scott County: KU 3546 (1), Mill Cr., trib. to Fourche La Fave R., at US Hwy 71, 6.4 km S Boles. Yell County: TU 93495 (3), Fourche La Fave R. at bridge 3.2 km S Briggsville. Upper White River drainage, Arkansas. Washington County: UT 91.1576 (6), West Fork White R. at unnumbered rd. crossing off US Hwy 71, ca. 22.4 rd. km S Fayetteville; TU 16568 (1), White R. at AR Hwy 68,12.8 km E Springdale; TU 47038 (1), White R. from AR Hwy 68 to 2.4 km upstream; TU 46961 (2), White R. from bridge W Sulphur City to 2.4 km upstream; TU 46972 (2), White R. from ford N Durham to 2.8 km upstream; UAIC 10355.11 (3), Richland Cr. 0.4 km downstream Co. Rd. 79 (first bridge upstream AR Hwy 45); TU 50065 (8), Richland Cr. from confluence with Mill Br. to 61 m downstream, 12.8 km E Fayetteville; TU 50574 (9), Richland Cr. just below 0.8 km above Hwy 71 bridge, T16N, R28W, S18. Benton County: TU 50588 (1), White R. at Eden's Ford to 0.8 km downstream, TI9N, R29W, S34; TU 50419 (3), War Eagle Cr. from bridge to 2.4 km upstream, 0.8 km SW War Eagle. Madison County: TU 46992 (2), White R. from bridge at Patrick to 1.6 km downstream; TU 49778 (5), War Eagle Cr. from AR Hwy 68 bridge to 2.4 km upstream, NE Huntsville, T17N, R26W, S24; UAIC 10325.08 (12), War Eagle Cr. at US Hwy 412 (formerly AR Hwy 68); UT 91.1014 (10), King's R. at AR Hwy 68. Carroll County: INHS 86836 (1), Osage Cr. at AR Hwy 68, 1.6 km NW Osage. Upper White River drainage, Missouri. Webster County: UAIC 10317.12 (1), James R. at MO Hwy KK; KU 10821 (1), James R. 9.6 km S Marshfield, T29N, R18W, S3. Greene County: KU 7885 (1), James R. at Hwy M-125, 9.6 km S Strafford.

Etheostoma clinton.—Upper Ouachita River system, Arkansas. Polk County: NLU 35232 (1), UT 91.1382 (4), Ouachita R. at McGuire Public Access Area, 3.2 km S AR Hwy 88 between Ink and Cherry Hill; NLU 58149 (10), NLU 59452 (1), Ouachita R. and Mill Cr. just downstream of Co. Rd. 67, 1.6 km S Cherry Hill. Montgomery County: NLU 34707 (1), NLU 34922 (2), Ouachita R. 1.6 km S AR Hwy 88, just E Pine Ridge, T2S, R27W, S9; NLU 34531 (1), Ouachita R. at US Hwy 270, Rocky Shoals, T1S, R25W, S31; NLU 34933 (3), Ouachita R. at US Hwy 270, Rocky Shoals, T1S, R25W, S32; NLU 38580 (7), Ouachita R. at AR Hwy 88, Rocky Shoals; NLU 58422 (2), Ouachita R. at AR Hwy 298, ca. 1.6 km S Sims, T1S, R25W, S20; NLU 34918 (4), Ouachita R. at Clifton's Camp, ca. 2.9 km S AR Hwy 88 and 4.8 km SW Washita, T1S, R24W, S29. Upper Caddo River system, Arkansas. Montgomery County: NLU 15868 (3), NLU 57893 (1), NLU 58925 (7), Caddo R. at jct. AR Hwy 240 and AR Hwy 8, T4S, R24W, S19. Pike County: UT 91.947 (2), Caddo R. at US Hwy 70. Clark County: NLU 18358 (2), NLU 20674 (2), NLU 20706 (1), NLU 28201 (3), NLU 34012 (1), Caddo R. at AR Hwy 182, 3.2 km N Amity.

TABLE 1. LATERAL SCALE ROW COUNTS IN SPECIES OF *DORATION*. Values for holotypes are in boldface.

	Lateral Scale Rows													
	38	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**
Etheostoma stigmaeum														
Mobile Basin		3	3	9	19	32	32	34	49	57	43	66	47	39
Bear Cr. (Tennessee R.)		3	-	3	4	8	14	8	3	6	3	2		
Eastern Gulf coast systems	2	2	10	14	15	8	16	10	3	2				
Central Gulf Coast systems	1	1	3	6	10	26	18	29	25	22	15	5	3	1
Lower Miss. Embayment, eastern tributaries		2	1	8	11	14	19	16	12	5	9	2		
Upper Miss. Embayment, eastern tributaries					2	2	3	6	12	4	11	4	10	1
Upper Miss. Embayment, western tributaries					2	2	13	14	19	23	18	17	13	7
Lower Miss. Embayment, western tributaries					1	5	15	12	23	30	17	30	7	8
Etheostoma jessiae														
Lower and middle Tennessee R.							2	-	3	5	12	20	30	16
Little Bear Cr.								1	-	1	7	9	11	7
Upper Tennessee R. (excluding Clinch R.)					1	-	3	3	10	13	12	18	30	35
Clinch R. downstream of Norris Dam						1	-	7	6	11	15	27	22	16
Clinch/Powell R. upstream of Norris Dam				1	2	-	-	1	4	3	5	6	11	9
Etheostoma meadiae														
Upper Powell River					3	3	7	7	9	3	4	5	3	5
Upper Clinch River				1	4	7	8	20	21	15	20	8	15	5
Etheostoma akatulo		1	1	1	12	25	28	47	33	25	17	8	4	1
Etheostoma obama			1	-	4	6	**20**	21	32	32	28	25	10	5
Etheostoma gore														
Middle Cumberland R.			2	1	6	11	13	19	17	18	10	5	3	3
Lower Cumberland R.					3	4	8	10	17	15	13	**8**	6	-
Etheostoma jimmycarter			1	4	17	18	40	37	28	25	18	**16**	4	1
Etheostoma teddyroosevelt														
Arkansas R.				1	-	2	4	9	13	21	**13**	17	8	8
Upper White R.						1	-	4	9	11	7	16	9	10
Etheostoma clinton								2	5	8	14	13	23	14

TABLE 1. (Continued)

	Lateral Scale Rows											
	52	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**	**n**	**Mean**	**SD**
Etheostoma stigmaeum												
Mobile Basin	27	13	4	4	4					485	47.5	3.30
Bear Cr. (Tennessee R.)										54	44.3	2.36
Eastern Gulf coast systems										82	42.5	2.05
Central Gulf Coast systems										165	45.0	2.35
Lower Miss. Embayment, eastern tributaries										99	44.3	2.24
Upper Miss. Embayment, eastern tributaries	1	-	1							57	47.2	2.49
Upper Miss. Embayment, western tributaries	2	2								132	47.3	2.31
Lower Miss. Embayment, western tributaries	3									151	47.2	2.17
Etheostoma jessiae												
Lower and middle Tennessee R.	15	7	6	3	1	1				121	50.3	2.27
Little Bear Cr.	3	8	-	2						49	50.3	2.08
Upper Tennessee R. (excluding Clinch R.)	19	27	16	16	10	5	2	-	1	221	51.2	3.11
Clinch R. downstream of Norris Dam	14	5	3	1	-	1				129	49.4	2.34
Clinch/Powell R. upstream of Norris Dam	5	3	4	1						55	49.6	3.00
Etheostoma meadiae												
Upper Powell River										49	46.4	2.65
Upper Clinch River	4	4								132	47.0	2.67
Etheostoma akatulo										203	45.3	2.04
Etheostoma obama	1									185	46.7	2.15
Etheostoma gore												
Middle Cumberland R.	-	1								109	45.7	2.41
Lower Cumberland R.	2									86	46.6	2.18
Etheostoma jimmycarter										209	45.4	2.20
Etheostoma teddyroosevelt												
Arkansas R.	5	1	-	-	1					103	47.8	2.43
Upper White R.	2									69	48.4	2.00
Etheostoma clinton	**12**	7	2	3	-	1				104	49.9	2.31

TABLE 2. UNPORED LATERAL SCALE ROW COUNTS IN SPECIES OF *DORATION*. Values for holotypes are in boldface.

	Unpored Lateral Scale Rows													
	0	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
Etheostoma stigmaeum														
Mobile Basin						1	-	1	3	7	27	55	74	66
Bear Cr. (Tennessee R.)											3	5	13	10
Eastern Gulf coast systems								2	11	15	18	19	10	-
Central Gulf Coast systems								2	1	14	17	33	35	32
Lower Miss. Embayment, eastern tributaries	1	-	-	1	2	5	3	11	10	15	12	15	11	5
Upper Miss. Embayment, eastern tributaries										1	2	8	4	8
Upper Miss. Embayment, western tributaries											12	22	18	19
Lower Miss. Embayment, western tributaries								1	3	10	14	24	29	22
Etheostoma jessiae														
Lower and middle Tennessee R.		3	4	5	16	7	13	16	17	10	14	5	4	2
Little Bear Cr.	1	7	3	5	5	5	4	5	5	4	3	1	-	-
Upper Tennessee R. (excluding Clinch R.)	5	2	12	9	9	21	22	23	23	22	16	14	16	4
Clinch R. downstream of Norris Dam	2	3	3	-	10	7	10	18	21	9	6	5	9	4
Clinch/Powell R. upstream of Norris Dam	2	-	2	2	4	3	6	4	6	10	3	5	1	1
Etheostoma meadiae														
Upper Powell River	10	4	2	8	5	10	6	3	1					
Upper Clinch River	20	7	8	15	17	19	19	11	6	5	2	2	-	1
Etheostoma akatulo	180	15	3	4	-	-	-	-	1					
Etheostoma obama								3	8	12	13	13	25	19
Etheostoma gore														
Middle Cumberland R.						1	2	3	-	5	15	17	13	14
Lower Cumberland R.							2	2	8	12	16	16	9	9
Etheostoma jimmycarter										2	5	13	15	22
Etheostoma teddyroosevelt														
Arkansas R.										1	1	2	8	**5**
Upper White R.													3	6
Etheostoma clinton												7	4	**9**

TABLE 2. (Continued)

	Unpored Lateral Scale Rows													
	14	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**
Etheostoma stigmaeum														
Mobile Basin	74	53	37	30	15	16	9	6	7	2	-	1	1	
Bear Cr. (Tennessee R.)	6	5	6	4	1	-	-	-	1					
Eastern Gulf coast systems	4	3												
Central Gulf Coast systems	15	10	3	1	1	-	1							
Lower Miss. Embayment, eastern tributaries	5	2	-	1										
Upper Miss. Embayment, eastern tributaries	9	5	10	2	4	3	-	1						
Upper Miss. Embayment, western tributaries	20	12	8	10	3	5	2	1						
Lower Miss. Embayment, western tributaries	15	13	6	6	2	3	2	1						
Etheostoma jessiae														
Lower and middle Tennessee R.	1	2	1	1										
Little Bear Cr.	-	1												
Upper Tennessee R. (excluding Clinch R.)	5	2	7	3	4	1	-	-	-	1				
Clinch R. downstream of Norris Dam	6	3	3	4	3	1	2							
Clinch/Powell R. upstream of Norris Dam	1	2	1	1	-	-	-	1						
Etheostoma meadiae														
Upper Powell River														
Upper Clinch River														
Etheostoma akatulo														
Etheostoma obama	16	15	**24**	7	8	7	3	2	5	-	-	4	-	1
Etheostoma gore														
Middle Cumberland R.	7	7	6	5	6	3	2	1	1	-	-	-	-	-
Lower Cumberland R.	**5**	4	1	2										
Etheostoma jimmycarter	33	26	27	24	9	**20**	5	4	2	1	1			
Etheostoma teddyroosevelt														
Arkansas R.	10	12	14	19	11	11	5	2	2					
Upper White R.	11	9	13	5	13	5	2	2						
Etheostoma clinton	14	13	10	10	7	8	6	6	2	5	1	1	-	-

TABLE 2. (Continued)

	Unpored Lateral Scale Rows			
	28	n	Mean	SD
Etheostoma stigmaeum				
Mobile Basin		485	14.0	2.98
Bear Cr. (Tennessee R.)		54	13.6	2.34
Eastern Gulf coast systems		82	10.3	1.81
Central Gulf Coast systems		165	12.0	1.99
Lower Miss. Embayment, eastern tributaries		99	9.5	2.88
Upper Miss. Embayment, eastern tributaries		57	14.3	2.67
Upper Miss. Embayment, western tributaries		132	13.6	2.60
Lower Miss. Embayment, western tributaries		151	12.7	2.64
Etheostoma jessiae				
Lower and middle Tennessee R.		121	7.3	3.23
Little Bear Cr.		49	5.4	3.31
Upper Tennessee R. (excluding Clinch R.)		221	8.2	4.15
Clinch R. downstream of Norris Dam		129	8.9	4.39
Clinch/Powell R. upstream of Norris Dam		55	8.2	4.13
Etheostoma meadiae				
Upper Powell River		49	3.4	2.38
Upper Clinch River		132	4.3	2.87
Etheostoma akatulo		203	0.2	0.77
Etheostoma obama		185	14.0	3.92
Etheostoma gore				
Middle Cumberland R.	1	109	13.0	3.68
Lower Cumberland R.		86	10.9	2.35
Etheostoma jimmycarter		209	15.2	2.85
Etheostoma teddyroosevelt				
Arkansas R.		103	16.1	2.66
Upper White R.		69	16.0	3.58
Etheostoma clinton	1	104	16.6	3.58

TABLE 3. TRANSVERSE SCALE ROW COUNTS IN SPECIES OF *DORATION*. Values for holotypes are in boldface.

	Transverse scale rows												
	9	10	11	12	13	14	15	16	17	18	19	n	Mean	SD
Etheostoma stigmaeum														
Mobile Basin		2	32	104	129	121	78	17	2			485	13.3	1.30
Bear Cr. (Tennessee R.)		4	14	20	13	3						54	11.9	1.02
Eastern Gulf coast systems	1	20	24	22	14	1						82	11.4	1.11
Central Gulf Coast systems		7	17	85	48	7	1					165	12.2	0.87
Lower Miss. Embayment, eastern tributaries			4	47	22	17	9					99	12.8	1.07
Upper Miss. Embayment, eastern tributaries		6	6	28	13	2	2					57	12.1	1.11
Upper Miss. Embayment, western tributaries		2	10	65	31	21	3					132	12.5	0.98
Lower Miss. Embayment, western tributaries		5	9	51	57	21	7	1				151	12.7	1.08
Etheostoma jessiae														
Lower and middle Tennessee R.				12	23	54	23	8	1			121	14.0	1.06
Little Bear Cr.					10	16	15	8				49	14.4	1.00
Upper Tennessee R. (excluding Clinch R.)			1	7	30	66	56	43	13	4	1	221	14.7	1.34
Clinch R. downstream of Norris Dam				4	26	44	43	10	2			129	14.3	1.02
Clinch/Powell R. upstream of Norris Dam				1	10	18	18	8				55	14.4	1.01
Etheostoma meadiae														
Upper Powell River			1	12	16	12	8					49	13.3	1.08
Upper Clinch River			1	35	40	40	14	2				132	13.3	1.04
Etheostoma akatulo		10	29	107	42	15						203	12.1	0.91
Etheostoma obama			11	83	62	**25**	4					185	12.6	0.87
Etheostoma gore														
Middle Cumberland R.		1	12	51	33	11	1					109	12.4	0.88
Lower Cumberland R.			4	38	26	**17**	1					86	12.7	0.88
Etheostoma jimmycarter		9	25	**108**	50	15	1	1				209	12.2	0.95
Etheostoma teddyroosevelt														
Arkansas R.			1	17	**49**	23	10	2	1			103	13.3	1.02
Upper White R.			1	12	26	19	9	2				69	13.4	1.06
Etheostoma clinton			3	24	28	**29**	16	4				104	13.4	1.20

TABLE 4. COUNTS OF SCALE ROWS BELOW AND SCALE ROWS ABOVE LATERAL LINE IN SPECIES OF *DORATION*. Values for holotypes are in boldface.

	Scale rows below lateral line								
	5	**6**	**7**	**8**	**9**	**10**	**n**	**Mean**	**SD**
Etheostoma stigmaeum									
Mobile Basin	16	140	207	101	19	2	485	6.9	0.91
Bear Cr. (Tennessee R.)	8	27	17	2			54	6.2	0.75
Eastern Gulf coast systems	22	37	21	2			82	6.0	0.79
Central Gulf Coast systems	9	98	50	8			165	6.3	0.66
Lower Miss. Embayment, eastern tributaries	3	49	28	16	3		99	6.7	0.89
Upper Miss. Embayment, eastern tributaries	8	31	14	4			57	6.2	0.79
Upper Miss. Embayment, western tributaries	9	66	43	14			132	6.5	0.78
Lower Miss. Embayment, western tributaries	7	58	68	16	2		151	6.7	0.78
Etheostoma jessiae									
Lower and middle Tennessee R.		18	66	30	7		121	7.2	0.77
Little Bear Cr.		2	19	21	7		49	7.7	0.77
Upper Tennessee R. (excluding Clinch R.)		20	85	80	31	5	221	7.6	0.91
Clinch R. downstream of Norris Dam		16	50	53	10		129	7.4	0.81
Clinch/Powell R. upstream of Norris Dam		6	22	25	2		55	7.4	0.74
Etheostoma meadiae									
Upper Powell River	1	23	18	7			49	6.6	0.76
Upper Clinch River	1	66	47	18			132	6.6	0.73
Etheostoma akatulo	15	135	49	4			203	6.2	0.59
Etheostoma obama	2	116	**59**	8			185	6.4	0.59
Etheostoma gore									
Middle Cumberland R.	2	61	42	4			109	6.4	0.60
Lower Cumberland R.	2	44	**36**	3	1		86	6.5	0.66
Etheostoma jimmycarter	34	**129**	41	5			209	6.1	0.67
Etheostoma teddyroosevelt									
Arkansas R.	1	21	**52**	23	5	1	103	7.1	0.86
Upper White R.	1	17	35	12	4		69	7.0	0.85
Etheostoma clinton		29	31	**38**	6		104	7.2	0.92

TABLE 4. (Continued)

	Scale rows above lateral line								
	3	**4**	**5**	**6**	**7**	**8**	**n**	**Mean**	**SD**
Etheostoma stigmaeum									
Mobile Basin	4	150	270	61			485	4.8	0.65
Bear Cr. (Tennessee R.)		34	19	1			54	4.4	0.53
Eastern Gulf coast systems	10	52	19	1			82	4.1	0.62
Central Gulf Coast systems	12	100	52	1			165	4.3	0.59
Lower Miss. Embayment, eastern tributaries	1	41	52	5			99	4.6	0.60
Upper Miss. Embayment, eastern tributaries	3	46	8				57	4.1	0.43
Upper Miss. Embayment, western tributaries	3	85	43	1			132	4.3	0.53
Lower Miss. Embayment, western tributaries	7	95	48	1			151	4.3	0.56
Etheostoma jessiae									
Lower and middle Tennessee R.		5	60	55	1		121	5.4	0.59
Little Bear Cr.			17	29	3		49	5.7	0.58
Upper Tennessee R. (excluding Clinch R.)		2	63	121	34	1	221	5.9	0.69
Clinch R. downstream of Norris Dam		1	46	74	8		129	5.7	0.60
Clinch/Powell R. upstream of Norris Dam		2	29	21	3		55	5.5	0.66
Etheostoma meadiae									
Upper Powell River			14	31	4		49	5.8	0.58
Upper Clinch River		3	55	65	9		132	5.6	0.65
Etheostoma akatulo	2	113	82	6			203	4.5	0.57
Etheostoma obama		48	**117**	20			185	4.8	0.59
Etheostoma gore									
Middle Cumberland R.	5	60	42	2			109	4.4	0.61
Lower Cumberland R.	2	43	**40**	1			86	4.5	0.57
Etheostoma jimmycarter		52	**138**	19			209	4.8	0.56
Etheostoma teddyroosevelt									
Arkansas R.		15	**78**	10			103	5.0	0.49
Upper White R.		8	50	11			69	5.0	0.53
Etheostoma clinton	4	**54**	44	2			104	4.4	0.60

TABLE 5. CAUDAL PEDUNCLE SCALE ROW COUNTS IN SPECIES OF *DORATION*. Values for holotypes are in boldface.

	Caudal peduncle scale rows													
	12	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**n**	**Mean**	**SD**
Etheostoma stigmaeum														
Mobile Basin		11	29	77	188	127	45	7	1			485	16.2	1.17
Bear Cr. (Tennessee R.)	2	4	12	16	18	1	1					54	14.9	1.20
Eastern Gulf coast systems	3	18	28	28	4	1						82	14.2	1.00
Central Gulf Coast systems		4	11	79	60	10	1					165	15.4	0.82
Lower Miss. Embayment, eastern tributaries			2	24	41	26	6					99	16.1	0.91
Upper Miss. Embayment, eastern tributaries			1	16	29	8	3					57	15.9	0.84
Upper Miss. Embayment, western tributaries		2	9	36	55	26	3	1				132	15.8	1.00
Lower Miss. Embayment, western tributaries			2	17	76	35	18	2	1			151	16.4	0.97
Etheostoma jessiae														
Lower and middle Tennessee R.				2	24	31	53	9	2			121	17.4	1.00
Little Bear Cr.					12	16	17	4				49	17.3	0.93
Upper Tennessee R. (excluding Clinch R.)			1	3	23	50	68	43	26	5	2	221	18.0	1.36
Clinch R. downstream of Norris Dam			1	5	29	40	43	9	1	-	1	129	17.2	1.14
Clinch/Powell R. upstream of Norris Dam				2	17	20	11	4	1			55	17.0	1.06
Etheostoma meadiae														
Upper Powell River				3	30	11	5					49	16.4	0.76
Upper Clinch River		1	4	23	86	16	2					132	15.9	0.73
Etheostoma akatulo	1	10	31	89	54	16	2					203	15.2	1.02
Etheostoma obama				7	79	62	**32**	3	2			185	16.7	0.92
Etheostoma gore														
Middle Cumberland R.		1	15	29	56	6	2					109	15.5	0.90
Lower Cumberland R.		1	5	18	41	**14**	7					86	16.0	1.02
Etheostoma jimmycarter		6	27	34	**134**	6	2					209	15.5	0.89
Etheostoma teddyroosevelt														
Arkansas R.			1	19	**49**	24	9	1				103	16.2	0.92
Upper White R.			2	14	35	17	1					69	16.0	0.80
Etheostoma clinton				11	45	**35**	10	3				104	16.5	0.91

TABLE 6. PERCENT CHEEK SQUAMATION IN SPECIES OF *DORATION*. Values for holotypes are in boldface.

	Percent cheek squamation													
	0	**10**	**20**	**30**	**40**	**50**	**60**	**70**	**80**	**90**	**100**	**n**	**Mean**	**SD**
Etheostoma stigmaeum														
Mobile Basin	33	54	152	113	47	35	23	21	6	1		485	28.9	18.04
Bear Cr. (Tennessee R.)	2	16	18	17	1							54	19.8	9.21
Eastern Gulf coast systems			1	6	17	23	14	14	7			82	53.8	14.54
Central Gulf Coast systems	1	9	36	73	28	16	2					165	30.5	10.78
Lower Miss. Embayment, eastern tributaries			1	5	8	12	28	23	12	10		99	63.0	16.19
Upper Miss. Embayment, eastern tributaries			3	12	10	6	7	12	5	2		57	51.9	19.59
Upper Miss. Embayment, western tributaries		2	7	18	19	20	39	18	7	2		132	51.5	17.23
Lower Miss. Embayment, western tributaries		4	19	25	34	28	21	14	5	1		151	44.1	17.41
Etheostoma jessiae														
Lower and middle Tennessee R.	11	36	45	23	5	-	1					121	18.3	10.62
Little Bear Cr.	2	10	28	9								49	19.0	7.43
Upper Tennessee R. (excluding Clinch R.)	2	32	105	67	10	4	1					221	23.0	9.01
Clinch R. downstream of Norris Dam	10	31	58	19	8	1	2					129	19.6	11.28
Clinch/Powell R. upstream of Norris Dam	2	11	24	14	4							55	21.3	9.44
Etheostoma meadiae														
Upper Powell River	46	1	2									49	1.0	4.21
Upper Clinch River	121	10	-	-	1							132	1.1	4.33
Etheostoma akatulo					2	5	2	6	29	62	97	203	91.0	12.11
Etheostoma obama	**11**	32	82	49	10	-	-	1				185	21.1	10.10
Etheostoma gore														
Middle Cumberland R.	72	28	8	1								109	4.3	6.72
Lower Cumberland R.	43	**30**	12	-	1							86	6.7	8.04
Etheostoma jimmycarter	**146**	44	19									209	3.9	6.50
Etheostoma teddyroosevelt														
Arkansas R.	**91**	10	1	1								103	1.5	4.52
Upper White R.	68	1										69	0.1	1.20
Etheostoma clinton	50	28	16	**7**	1	-	-	-	2			104	9.7	13.97

TABLE 7. PERCENT NAPE SQUAMATION IN SPECIES OF *DORATION*. Values for holotypes are in boldface.

	Percent nape squamation													
	0	**10**	**20**	**30**	**40**	**50**	**60**	**70**	**80**	**90**	**100**	**n**	**Mean**	**SD**
Etheostoma stigmaeum														
Mobile Basin	21	51	56	75	57	49	42	64	37	23	10	485	44.6	26.15
Bear Cr. (Tennessee R.)			9	14	13	8	4	4	2			54	40.7	16.35
Eastern Gulf coast systems			1	1	2	2	1	6	17	32	20	82	84.8	16.27
Central Gulf Coast systems	1	3	13	18	18	11	16	30	21	11	23	165	61.4	26.39
Lower Miss. Embayment, eastern tributaries			3	7	7	13	9	23	30	6	1	99	64.5	18.75
Upper Miss. Embayment, eastern tributaries					1	3	4	9	16	11	13	57	81.2	15.24
Upper Miss. Embayment, western tributaries		2	1	2	1	9	5	22	24	45	21	132	79.5	18.57
Lower Miss. Embayment, western tributaries		6	11	17	8	12	12	22	32	28	3	151	61.9	25.40
Etheostoma jessiae														
Lower and middle Tennessee R.									4	16	101	121	98.0	4.76
Little Bear Cr.								1	3	3	42	49	97.6	6.62
Upper Tennessee R. (excluding Clinch R.)									2	7	212	221	99.5	2.56
Clinch R. downstream of Norris Dam									3	11	115	129	98.7	4.03
Clinch/Powell R. upstream of Norris Dam									1	3	51	55	99.1	3.48
Etheostoma meadiae														
Upper Powell River				2	2	3	4	7	11	15	5	49	76.5	18.32
Upper Clinch River			1	1	3	11	11	22	39	35	9	132	76.4	15.83
Etheostoma akatulo					2	3	12	41	26	35	84	203	86.0	14.87
Etheostoma obama					1	1	**2**	4	14	36	127	185	94.9	9.67
Etheostoma gore														
Middle Cumberland R.				1	1	3	10	15	35	32	12	109	80.3	13.71
Lower Cumberland R.								3	16	37	**30**	86	90.9	8.21
Etheostoma jimmycarter					1	1	2	7	16	33	**149**	209	95.0	9.81
Etheostoma teddyroosevelt														
Arkansas R.							1	4	3	13	**82**	103	96.6	7.99
Upper White R.		1	3	5	8	3	3	6	13	9	18	69	71.6	26.77
Etheostoma clinton	9	18	24	19	10	9	6	**6**	2	-	1	104	30.0	21.41

TABLE 8. DORSAL FIN SPINE AND SOFT RAY COUNTS IN SPECIES OF *DORATION*. Values for holotypes are in boldface.

	Doral fin spines								
	9	**10**	**11**	**12**	**13**	**14**	**n**	**Mean**	**SD**
Etheostoma stigmaeum									
Mobile Basin	1	41	304	132	7		485	11.2	0.62
Bear Cr. (Tennessee R.)		1	32	21			54	11.4	0.52
Eastern Gulf coast systems		3	50	29			82	11.3	0.54
Central Gulf Coast systems		10	106	49			165	11.2	0.55
Lower Miss. Embayment, eastern tributaries		22	67	10			99	10.9	0.56
Upper Miss. Embayment, eastern tributaries		6	36	15			57	11.2	0.59
Upper Miss. Embayment, western tributaries	1	25	68	38			132	11.1	0.71
Lower Miss. Embayment, western tributaries		24	92	33	2		151	11.1	0.65
Etheostoma jessiae									
Lower and middle Tennessee R.			1	52	68		121	12.6	0.52
Little Bear Cr.			2	20	27		49	12.5	0.58
Upper Tennessee R. (excluding Clinch R.)		2	16	111	89	3	221	12.3	0.67
Clinch R. downstream of Norris Dam			5	55	64	5	129	12.5	0.64
Clinch/Powell R. upstream of Norris Dam			4	28	23		55	12.3	0.62
Etheostoma meadiae									
Upper Powell River			7	29	13		49	12.1	0.63
Upper Clinch River		1	26	88	16	1	132	11.9	0.61
Etheostoma akatulo		10	93	92	8		203	11.5	0.66
Etheostoma obama		1	6	83	**83**	12	185	12.5	0.69
Etheostoma gore									
Middle Cumberland R.			34	71	3	1	109	11.7	0.56
Lower Cumberland R.		1	**30**	52	2	1	86	11.7	0.60
Etheostoma jimmycarter			8	94	**92**	15	209	12.5	0.69
Etheostoma teddyroosevelt									
Arkansas R.		1	**42**	53	7		103	11.6	0.62
Upper White R.		1	34	29	5		69	11.6	0.65
Etheostoma clinton		21	**59**	23	1		104	11.0	0.68

TABLE 8. (Continued)

	Dorsal fin soft rays									
	8	**9**	**10**	**11**	**12**	**13**	**14**	**n**	**Mean**	**SD**
Etheostoma stigmaeum										
Mobile Basin			94	313	78			485	11.0	0.60
Bear Cr. (Tennessee R.)			18	34	2			54	10.7	0.54
Eastern Gulf coast systems			24	55	3			82	10.7	0.52
Central Gulf Coast systems	1		68	91	5			165	10.6	0.58
Lower Miss. Embayment, eastern tributaries			20	72	7			99	10.9	0.51
Upper Miss. Embayment, eastern tributaries			7	30	20			57	11.2	0.66
Upper Miss. Embayment, western tributaries		1	25	78	28			132	11.0	0.66
Lower Miss. Embayment, western tributaries			10	99	39	3		151	11.2	0.59
Etheostoma jessiae										
Lower and middle Tennessee R.				17	95	9		121	11.9	0.46
Little Bear Cr.				11	34	4		49	11.9	0.54
Upper Tennessee R. (excluding Clinch R.)			2	45	148	26		221	11.9	0.59
Clinch R. downstream of Norris Dam				37	86	6		129	11.8	0.53
Clinch/Powell R. upstream of Norris Dam			1	13	36	4	1	55	11.8	0.66
Etheostoma meadiae										
Upper Powell River		1	4	32	12			49	11.1	0.63
Upper Clinch River			2	61	69			132	11.5	0.53
Etheostoma akatulo			25	142	36			203	11.1	0.55
Etheostoma obama			1	81	**97**	6		185	11.6	0.57
Etheostoma gore										
Middle Cumberland R.			4	64	40	1		109	11.3	0.57
Lower Cumberland R.			5	**61**	20			86	11.2	0.51
Etheostoma jimmycarter			10	**128**	68	3		209	11.3	0.58
Etheostoma teddyroosevelt										
Arkansas R.			4	**58**	40	1		103	11.4	0.58
Upper White R.			6	44	19			69	11.2	0.58
Etheostoma clinton			27	**67**	8	2		104	10.9	0.63

TABLE 9. ANAL FIN SOFT RAY AND LEFT PECTORAL FIN RAY COUNTS IN SPECIES OF *DORATION*. Values for holotypes are in boldface.

	Anal fin soft rays								
	5-6	**7**	**8**	**9**	**10**	**11**	**n**	**Mean**	**SD**
Etheostoma stigmaeum									
Mobile Basin		57	334	94			485	8.1	0.55
Bear Cr. (Tennessee R.)		2	44	8			54	8.1	0.42
Eastern Gulf Coast systems		19	61	2			82	7.8	0.46
Central Gulf Coast systems		39	117	9			165	7.8	0.51
Lower Miss. Embayment, eastern tributaries		22	71	6			99	7.8	0.51
Upper Miss. Embayment, eastern tributaries		2	38	17			57	8.3	0.52
Upper Miss. Embayment, western tributaries		14	94	24			132	8.1	0.53
Lower Miss. Embayment, western tributaries	1	8	111	31			151	8.1	0.52
Etheostoma jessiae									
Lower and middle Tennessee R.		2	28	83	8		121	8.8	0.57
Little Bear Cr.		1	17	30	1		49	8.6	0.57
Upper Tennessee R. (excluding Clinch R.)		1	48	151	21		221	8.9	0.56
Clinch R. downstream of Norris Dam			41	80	8		129	8.7	0.56
Clinch/Powell R. upstream of Norris Dam			16	34	5		55	8.8	0.59
Etheostoma meadiae									
Upper Powell River		6	35	8			49	8.0	0.54
Upper Clinch River		4	89	39			132	8.3	0.51
Etheostoma akatulo		19	160	24			203	8.0	0.46
Etheostoma obama			38	**119**	27	1	185	9.0	0.61
Etheostoma gore									
Middle Cumberland R.		1	56	50	2		109	8.5	0.55
Lower Cumberland R.	1	2	41	**40**	2		86	8.5	0.70
Etheostoma jimmycarter		6	**120**	83			209	8.4	0.54
Etheostoma teddyroosevelt									
Arkansas R.		7	**63**	32	1		103	8.3	0.59
Upper White R.		2	56	11			69	8.1	0.42
Etheostoma clinton		1	36	**62**	5		104	8.7	0.58

TABLE 9 (Continued)

	Left pectoral fin rays								
	11	12	13	14	15	16	n	Mean	SD
Etheostoma stigmaeum									
Mobile Basin		5	110	328	42		485	13.8	0.57
Bear Cr. (Tennessee R.)				33	21		54	14.4	0.49
Eastern Gulf Coast systems			23	58	1		82	13.7	0.47
Central Gulf Coast systems			33	125	7		165	13.8	0.47
Lower Miss. Embayment, eastern tributaries			27	66	6		99	13.8	0.54
Upper Miss. Embayment, eastern tributaries			7	42	8		57	14.0	0.52
Upper Miss. Embayment, western tributaries			35	76	21		132	13.9	0.65
Lower Miss. Embayment, western tributaries		2	44	90	15		151	13.8	0.63
Etheostoma jessiae									
Lower and middle Tennessee R.				17	87	17	121	15.0	0.53
Little Bear Cr.				6	39	4	49	15.0	0.45
Upper Tennessee R. (excluding Clinch R.)			3	90	122	6	221	14.6	0.57
Clinch R. downstream of Norris Dam			1	87	41		129	14.3	0.48
Clinch/Powell R. upstream of Norris Dam				41	14		55	14.3	0.44
Etheostoma meadiae									
Upper Powell River			1	31	17		49	14.3	0.52
Upper Clinch River			10	92	30		132	14.2	0.53
Etheostoma akatulo			3	81	119		203	14.6	0.53
Etheostoma obama			5	67	**109**	4	185	14.6	0.58
Etheostoma gore									
Middle Cumberland R.			3	74	32		109	14.3	0.50
Lower Cumberland R.			8	**70**	8		86	14.0	0.43
Etheostoma jimmycarter			1	88	**116**	4	209	14.6	0.54
Etheostoma teddyroosevelt									
Arkansas R.			5	**78**	20		103	14.1	0.47
Upper White R.			3	55	11		69	14.1	0.44
Etheostoma clinton	1	1	**51**	48	2	1	104	13.5	0.65

TABLE 10. LEFT PREOPERCULOMANDIBULAR CANAL PORE COUNTS IN SPECIES OF *DORATION*. Values for holotypes are in boldface.

	Left preoperculomandibular canal pores							
	7-8	**9**	**10**	**11**	**12**	**n**	**Mean**	**SD**
Etheostoma stigmaeum	3	129	1060	32	1	1225	9.9	0.37
Etheostoma jessiae	2	38	525	10		575	9.9	0.31
Etheostoma meadiae	1	12	164	4		181	9.9	0.37
Etheostoma akatulo	1	28	169	5		203	9.9	0.41
Etheostoma obama	1	31	**151**	2		185	9.8	0.42
Etheostoma gore	4	28	**161**	2		195	9.8	0.45
Etheostoma jimmycarter	1	38	166	**4**		209	9.8	0.44
Etheostoma teddyroosevelt	3	47	**118**	4		172	9.7	0.54
Etheostoma clinton	1	**95**	8			104	9.1	0.29

TABLE 11. PRINCIPAL CAUDAL FIN RAY COUNTS AND FREQUENCIES OF INDIVIDUALS WITH A FRENUM AND PALATINE TEETH IN *ETHEOSTOMA JESSIAE* FROM THE UPPER TENNESSEE RIVER AND *E. MEADIAE*. Numbered localities are shown in Figure 7.

		Principal caudal fin rays								Frenum present		Palatine teeth present	
	n	**12**	**13**	**14**	**15**	**16**	**17**	**Mean**	**SD**	**No.**	**%**	**No.**	**%**
Etheostoma jessiae													
Upper Tennessee R. (excluding Clinch R.)	221	1	-	4	186	27	3	15.1	0.47	204	92.3	185	83.7
Clinch R. downstream of Norris Dam													
1. Emory R. and Poplar Cr.	34			1	30	3		15.1	0.34	32	94.1	24	70.6
2. Beaver Cr. And Bull Run Cr.	25		1	2	21	1		14.9	0.53	25	100.0	22	88.0
3. Hinds Cr.	24			3	16	4	1	15.1	0.68	24	100.0	23	95.8
4. Coal Cr. and nearby Clinch R.	46			3	37	4	2	15.1	0.57	45	97.8	37	80.4
Clinch/Powell R. upstream of Norris Dam													
5. Cove Cr.	20				12	8		15.4	0.50	19	95.0	16	80.0
6. Big Sycamore Cr.	25				23	2		15.1	0.28	20	80.0	16	64.0
7. Pond opposite Doak's Dam (Powell R.)	10				10			15.0	0.00	8	80.0	8	80.0
Etheostoma meadiae													
Upper Powell River	49				9	10	30	16.4	0.79	18	36.7	18	36.7
Upper Clinch River	132	1	2	1	36	43	49	16.0	0.97	88	66.7	41	31.4

TABLE 12. MEASUREMENTS IN THOUSANDTHS OF STANDARD LENGTH FOR SPECIES OF *DORATION*.
Measurements for *E. akatulo* appear in Layman and Mayden (2009). D1 = spinous dorsal fin origin; D2 = soft dorsal fin origin; P2 = lateral pelvic fin insertion; A = anal fin origin. Asterisks indicate significant differences between sexes (P<0.05).

Etheostoma stigmaeum	Males (n = 10)			Females (n = 10)		
Coosa River	**Mean**	**Range**	**SD**	**Mean**	**Range**	**SD**
Standard length (mm)	42.0	37.4-48.6	3.4	38.7	33.9-42.0	2.8
Head length	282*	273-296	7.3	274	265-291	7.5
Snout length	82*	75-91	4.7	75	67-86	4.8
Predorsal length	350*	342-359	6.1	343	334-353	6.8
Orbit length	68	62-75	3.8	68	66-71	1.7
Upper jaw length	86*	77-93	4.2	79	73-84	3.5
D1 to P2 body depth	185*	167-210	12.4	172	160-180	5.6
D1 to D2	295	280-308	7.5	291	276-303	8.4
6th dorsal spine length	122*	114-132	6.5	112	105-119	5.2
D2 to A body depth	162*	149-175	8.0	142	130-148	5.3
Soft dorsal fin base length	159	152-178	8.4	158	149-168	6.9
Caudal peduncle length	243*	231-256	7.3	251	240-265	8.1
Caudal peduncle depth	97*	88-104	4.7	90	84-96	3.8
Anal fin base length	130*	118-139	6.6	112	102-120	5.6
1st anal spine length	69	60-81	7.7	64	58-75	5.6
Pectoral fin length	266	241-283	14.2	267	257-287	9.0
Pelvic fin length	226*	213-242	8.4	211	183-223	11.9
Trans-pelvic width	78*	74-83	3.0	73	66-78	4.4
Body width	129*	117-140	6.2	123	116-130	4.5

Etheostoma stigmaeum	Males (n = 10)			Females (n = 10)		
Pearl River	**Mean**	**Range**	**SD**	**Mean**	Range	SD
Standard length (mm)	37.0	29.9–42.8	4.0	36.2	32.0–40.1	2.7
Head length	273	263–283	6.8	268	258–275	6.2
Snout length	73	65–78	4.5	68	62–77	5.6
Predorsal length	341	327–354	9.7	344	331–362	9.2
Orbit length	67	61–72	2.9	68	64–72	2.4
Upper jaw length	77	72–83	3.2	76	71–83	4.2
D1 to P2 body depth	183	157–205	17.0	193	177–208	10.5

TABLE 12 (Continued)

D1 to D2	292	278–311	11.3	296	282–310	8.8
6th dorsal spine length	127*	119–133	4.2	114	104–121	5.7
D2 to A body depth	159	144–171	9.2	153	140–161	7.1
Soft dorsal fin base length	163	151–177	8.3	161	149–175	7.1
Caudal peduncle length	249	241–270	8.8	251	234–267	11.3
Caudal peduncle depth	92*	84–97	3.7	88	84–92	2.4
Anal fin base length	133*	124–151	9.1	112	94–126	10.8
1st anal spine length	72*	58–84	8.5	63	50–74	8.1
Pectoral fin length	265	247–282	10.2	264	249–280	10.2
Pelvic fin length	217*	185–229	12.3	200	190–210	7.1
Trans–pelvic width	76*	72–79	2.3	72	67–78	3.2
Body width	133	118–148	9.3	132	120–142	8.4

Etheostoma stigmaeum	Males (n = 10)			Females (n = 10)		
Clarks River	Mean	Range	SD	Mean	Range	SD
Standard length (mm)	38.7	31.8–42.9	3.5	36.7	33.4–39.8	2.3
Head length	281*	264–291	7.8	271	258–281	6.6
Snout length	76*	70–83	4.7	70	64–76	3.0
Predorsal length	350	338–366	8.4	347	339–355	5.7
Orbit length	69	65–75	3.1	68	63–72	3.1
Upper jaw length	80*	72–85	3.5	74	69–83	4.3
D1 to P2 body depth	184	163–214	14.9	189	177–200	
D1 to D2	284	262–300	11.1	293	277–319	
6th dorsal spine length	124*	116–132	5.2	114	107–120	
D2 to A body depth	148*	133–169	11.2	138	129–147	
Soft dorsal fin base length	169	155–184	8.9	164	156–174	
Caudal peduncle length	248	235–259	8.3	248	239–259	
Caudal peduncle depth	87*	80–97	4.6	82	78–89	
Anal fin base length	142*	129–159	9.3	120	108–133	
1st anal spine length	72	61–83	6.9	66	57–78	
Pectoral fin length	279	253–302	13.1	271	253–294	
Pelvic fin length	238*	223–257	11.1	211	196–224	
Trans–pelvic width	78	70–83	4.7	75	71–81	
Body width	130	119–153	9.8	127	119–137	

TABLE 12 (Continued)

Etheostoma stigmaeum	Males (n = 10)			Females (n = 10)		
Ouachita River	Mean	Range	SD	Mean	Range	SD
Standard length (mm)	34.7	31.4–42.3	3.5	34.3	31.2–37.4	1.7
Head length	277	265–291	8.4	277	264–285	7.2
Snout length	71	66–77	3.2	72	63–78	4.9
Predorsal length	340	313–364	14.9	347	331–358	8.9
Orbit length	69	60–77	5.2	69	61–73	3.5
Upper jaw length	78	72–84	4.2	76	66–81	4.5
D1 to P2 body depth	181*	169–196	9.3	196	183–214	8.7
D1 to D2	299	270–321	14.5	290	282–299	6.1
6th dorsal spine length	123*	104–149	12.1	114	104–123	5.3
D2 to A body depth	162	149–177	8.1	157	147–164	4.7
Soft dorsal fin base length	163	146–172	7.9	164	149–182	10.9
Caudal peduncle length	248	230–259	10.2	248	225–260	10.2
Caudal peduncle depth	92	88–99	3.7	88	84–96	4.0
Anal fin base length	128*	113–142	8.7	112	92–137	14.4
1st anal spine length	73*	64–86	6.8	61	51–67	5.6
Pectoral fin length	269	243–301	18.4	269	248–286	14.0
Pelvic fin length	228*	214–251	10.6	207	183–226	11.0
Trans–pelvic width	74	67–80	4.0	73	66–79	4.0
Body width	130	123–139	5.6	135	122–147	8.5

Etheostoma jessiae	Males (n = 30)			Females (n = 30)		
Tennessee River	Mean	Range	SD	Mean	Range	SD
Standard length (mm)	46.4	32.8–57.7	6.4	43.1	30.7–51.7	5.8
Head length	290*	273–310	8.9	285	263–303	10.0
Snout length	88*	79–101	6.0	83	72–94	5.5
Predorsal length	354	332–373	10.2	352	333–367	9.4
Orbit length	65	58–75	3.7	65	57–76	4.5
Upper jaw length	86*	76–96	4.9	83	71–94	5.5
D1 to P2 body depth	180	159–203	12.2	178	160–210	12.7
D1 to D2	300	268–326	14.8	305	275–346	15.8

TABLE 12 (Continued)

6th dorsal spine length	119*	100–139	9.4	108	92–122	7.9
D2 to A body depth	146*	133–163	8.0	139	128–154	5.9
Soft dorsal fin base length	170	155–186	6.9	167	150–183	8.3
Caudal peduncle length	222	191–238	10.0	219	204–243	9.1
Caudal peduncle depth	83	73–94	5.2	81	72–89	4.3
Anal fin base length	145*	129–170	10.5	133	118–151	7.8
1st anal spine length	71*	53–85	8.1	64	50–75	5.8
Pectoral fin length	270	233–296	12.9	266	234–303	17.9
Pelvic fin length	222*	194–249	3.8	208	184–230	10.3
Trans–pelvic width	75*	67–81	4.0	71	64–79	3.9
Body width	134*	120–153	7.7	129	111–147	8.5

Etheostoma meadiae	Males (n = 12)			Females (n = 12)		
Clinch and Powell rivers	**Mean**	**Range**	**SD**	**Mean**	**Range**	**SD**
Standard length (mm)	43.1	34.8–47.6	4.1	40.8	32.5–46.3	4.1
Head length	287	273–304	9.6	281	275–289	5.4
Snout length	79	73–86	4.2	76	71–87	4.3
Predorsal length	352	337–365	9.1	355	346–368	6.9
Orbit length	68	w63–78	4.4	67	62–72	2.6
Upper jaw length	84 *	73–94	6.4	78	72–84	3.9
D1 to P2 body depth	199	186–219	11.3	196	188–208	6.6
D1 to D2	314	297–336	11.2	316	299–331	10.1
6th dorsal spine length	124*	114–132	6.6	112	94–121	7.1
D2 to A body depth	168*	155–195	11.8	156	142–171	8.9
Soft dorsal fin base length	165*	154–172	5.7	157	144–171	8.7
Caudal peduncle length	222	214–235	7.1	226	210–236	7.1
Caudal peduncle depth	95*	84–107	6.0	89	80–100	6.2
Anal fin base length	143*	126–161	9.1	124	112–139	7.2
1st anal spine length	90*	80–106	8.1	83	71–93	5.6
Pectoral fin length	284	259–319	16.7	282	251–302	12.8
Pelvic fin length	232*	214–249	10.8	222	211–233	6.7
Trans–pelvic width	79*	68–93	6.9	73	67–78	3.8
Body width	141	131–165	9.2	139	130–149	6.1

TABLE 12 (Continued)

Etheostoma obama	**Males (n = 10)**			**Females (n = 10)**		
Duck River	**Mean**	**Range**	**SD**	**Mean**	**Range**	**SD**
Standard length (mm)	39.8	36.1–43.4	2.8	35.6	31.4–39.1	2.1
Head length	276*	270–284	4.6	267	252–277	8.4
Snout length	76	70–82	4.1	72	64–77	4.1
Predorsal length	340	330–348	5.0	337	326–353	7.6
Orbit length	68	64–71	2.6	67	62–73	3.8
Upper jaw length	78*	75–82	2.4	71	69–76	2.2
D1 to P2 body depth	185	176–191	4.9	183	171–201	8.2
D1 to D2	318	308–336	10.0	321	311–332	7.4
6th dorsal spine length	131*	119–147	10.1	117	107–125	5.9
D2 to A body depth	157*	149–162	3.7	140	121–151	7.9
Soft dorsal fin base length	172	161–180	5.8	166	146–180	9.3
Caudal peduncle length	233	223–248	7.6	232	209–253	12.5
Caudal peduncle depth	85*	82–91	3.2	80	74–83	2.8
Anal fin base length	157*	141–166	8.5	134	124–148	7.3
1st anal spine length	75*	65–86	6.6	69	63–75	3.7
Pectoral fin length	308*	287–329	12.2	290	272–319	13.0
Pelvic fin length	250*	237–262	8.4	227	217–241	8.8
Trans–pelvic width	76*	70–81	3.5	71	68–77	3.2
Body width	135*	129–141	4.1	127	117–135	6.4

Etheostoma gore	**Males (n = 20)**			**Females (n = 20)**		
lower Cumberland River	**Mean**	**Range**	**SD**	**Mean**	**Range**	**SD**
Standard length (mm)	38.1	34.4–42.3	2.1	36.3	33.0–40.0	2.1
Head length	265*	254–282	7.2	258	241–274	7.0
Snout length	73	66–80	3.8	70	61–79	4.4
Predorsal length	339	327–353	8.8	337	318–351	7.9
Orbit length	65	59–71	3.8	63	59–71	3.0
Upper jaw length	71*	64–76	3.3	68	61–73	3.1
D1 to P2 body depth	175	156–190	9.7	180	154–208	12.5

TABLE 12 (Continued)

D1 to D2	300*	286–318	7.4	306	287–329	10.7
6th dorsal spine length	117*	105–126	5.5	106	94–119	7.6
D2 to A body depth	154*	141–165	7.3	145	135–155	6.5
Soft dorsal fin base length	165	148–191	8.7	160	142–176	9.2
Caudal peduncle length	239	221–256	9.8	241	219–263	11.6
Caudal peduncle depth	85*	76–93	4.4	80	72–87	3.6
Anal fin base length	141*	126–155	7.5	126	94–142	12.5
1st anal spine length	76*	55–83	6.9	67	59–77	4.7
Pectoral fin length	293*	263–316	17.6	279	254–307	11.7
Pelvic fin length	235*	208–263	14.3	217	198–239	10.5
Trans–pelvic width	76*	69–85	5.1	71	62–79	4.5
Body width	127*	116–141	5.7	123	117–136	5.1

Etheostoma jimmycarter	Males (n = 12)			Females (n = 12)		
Barren River	Mean	Range	SD	Mean	Range	SD
Standard length (mm)	43.4	35.9–51.8	4.0	38.6	33.0–41.5	2.6
Head length	271*	262–281	6.2	262	256–274	5.4
Snout length	76	69–86	5.9	72	65–79	4.3
Predorsal length	333	319–345	8.0	330	319–343	6.7
Orbit length	62	59–68	3.0	64	60–70	3.1
Upper jaw length	77*	74–83	2.5	70	66–73	2.5
D1 to P2 body depth	181	165–197	11.0	189	178–199	7.1
D1 to D2	316	302–326	8.0	319	299–339	11.4
6th dorsal spine length	128*	115–138	8.2	116	104–139	11.0
D2 to A body depth	153*	140–166	7.6	147	140–156	5.8
Soft dorsal fin base length	158	144–181	10.3	154	142–166	7.0
Caudal peduncle length	237	227–257	8.6	243	223–252	7.5
Caudal peduncle depth	84	78–92	4.0	83	78–90	3.7
Anal fin base length	145*	131–161	10.1	124	112–136	7.5
1st anal spine length	82*	76–93	4.9	72	65–79	4.5
Pectoral fin length	295	275–316	13.2	291	271–308	11.7
Pelvic fin length	238*	223–257	8.1	226	201–243	11.3
Trans–pelvic width	77*	71–83	3.3	73	68–78	3.1
Body width	133	116–140	7.0	130	120–143	7.0

TABLE 12 (Continued)

Etheostoma teddyroosevelt	Males (n = 10)			Females (n = 10)		
middle Arkansas River	**Mean**	**Range**	**SD**	**Mean**	**Range**	**SD**
Standard length (mm)	39.1	31.9–43.1	3.9	36.4	30.9–40.0	3.4
Head length	268*	259–276	5.8	261	249–269	5.9
Snout length	73*	63–81	5.4	68	62–75	4.4
Predorsal length	339	328–354	9.6	335	319–350	9.8
Orbit length	63	57–70	4.0	64	61–70	3.5
Upper jaw length	72*	65–77	4.4	67	63–75	3.9
D1 to P2 body depth	191	172–212	13.6	199	181–215	9.8
D1 to D2	296*	273–317	11.9	311	292–332	14.5
6th dorsal spine length	109	95–123	7.8	109	97–118	7.1
D2 to A body depth	160	152–170	7.3	154	144–170	7.6
Soft dorsal fin base length	164	153–179	7.5	158	145–170	7.9
Caudal peduncle length	247	231–263	9.9	244	222–264	15.7
Caudal peduncle depth	87*	81–92	4.2	81	76–87	3.3
Anal fin base length	137*	123–146	7.3	128	114–140	8.0
1st anal spine length	65	54–72	6.8	62	48–73	8.1
Pectoral fin length	278	258–299	12.5	269	254–280	9.4
Pelvic fin length	222*	207–238	9.8	212	191–227	10.9
Trans–pelvic width	79*	73–84	4.2	73	65–81	4.3
Body width	140	129–155	8.0	135	123–147	8.4

Etheostoma clinton	Males (n = 12)			Females (n = 12)		
Caddo and Ouachita rivers	**Mean**	**Range**	**SD**	**Mean**	**Range**	**SD**
Standard length (mm)	30.9	28.0–34.2	1.9	30.9	28.7–33.9	**1.6**
Head length	272	259–284	7.3	270	255–285	**8.9**
Snout length	64	60–69	3.0	64	56–72	**4.4**
Predorsal length	344	331–354	8.0	344	330–356	**6.9**
Orbit length	66	59–70	3.2	66	62–72	**2.8**
Upper jaw length	73*	71–76	1.5	70	65–76	**2.8**

TABLE 12 (Continued)

D1 to P2 body depth	153	140–165	7.2	171	136–187	14.5
D1 to D2	280*	260–287	8.2	290	264–309	13.2
6th dorsal spine length	113*	102–128	8.4	101	93–110	6.2
D2 to A body depth	134	126–145	5.7	135	122–143	6.4
Soft dorsal fin base length	156*	145–175	9.1	148	134–170	8.8
Caudal peduncle length	238	222–247	6.7	240	216–257	12.0
Caudal peduncle depth	84	73–90	5.5	82	77–89	3.2
Anal fin base length	140*	126–151	6.6	115	102–122	6.5
1st anal spine length	66*	51–81	7.3	60	54–69	4.3
Pectoral fin length	262	243–279	10.9	259	230–278	14.2
Pelvic fin length	225*	202–241	11.8	209	180–226	13.7
Trans–pelvic width	64	55–71	4.9	63	60–67	2.1
Body width	111	103–119	4.7	117	101–130	8.4

TABLE 13. CHARACTERS USEFUL IN DISTINGUISHING SPECIES OF *DORATION*. Color characters are for breeding males.

Character	*E. stigmaeum*	*E. jessiae*	*E. meadiae*	*E. akatulo*	*E. obama*
Frenum	absent	present	present/absent	absent	absent
Mean lateral scale rows	46.4	50.4	46.9	45.3	46.7
Mean unpored lateral scales	12.9	7.9	4.1	0.2	14.0
Mean % cheek squamation	38.5	20.7	1.0	91.0	21.1
Modal caudal peduncle scales	14-16	17-18	16	15	16
Modal transverse scales	11-13	14-15	13-14	12	12
Modal scales below lateral line	6-7	7-8	6	6	6
Modal scales above lateral line	4-5	5-6	6	4	5
Modal dorsal spines	11	12-13	12	11-12	12-13
Modal soft dorsal rays	11	12	11-12	11	12
Modal principal caudal rays	15	15	17	15	15
Modal soft anal rays	8	9	8	8	9
Modal pectoral rays	14	14-15	14	15	15
Palatine teeth	present	present	absent/present	absent	absent/present
Preoperculomandibular pores	10	10	10	10	10
Maximum size (mm SL)	48.9	64.6	54.5	48.0	48.3
Face coloration	gray w/blue-green	gray w/blue	gray w/blue	entirely blue	orange w/blue
Blue on lips	present	present	present	present	absent
Blue on mid-gular area	present	absent	absent	present	absent
Orange spots on soft dorsal and caudal fin rays	absent	present	absent	absent	present
Blue in base of soft dorsal and anal fin	present	present	present	absent	present
Spinous dorsal fin marginal and submedial bands	blue-green	blue	blue	black	blue
Spinous dorsal fin medial band	red-orange	orange	orange	red-orange	orange
Orange in spinous dorsal fin basal band	absent	present	absent	absent	present
Basicaudal bar development	dorsal/ventral	dorsal/ventral	dorsal/ventral	dorsal/ventral	dorsal/ventral
Orange spots on anal fin rays	absent	absent	absent	absent	absent/present
Lateral blue blotches	elongate	elongate	elongate	elongate	quadrate

TABLE 13 (Continued)

Character	*E. gore*	*E. jimmycarter*	*E. teddyroosevelt*	*E. clinton*
Frenum	absent	absent	absent	absent
Mean lateral scale rows	46.1	45.4	48.1	49.9
Mean unpored lateral scales	12.1	15.2	16.1	16.6
Mean % cheek squamation	5.4	3.9	0.9	9.7
Modal caudal peduncle scales	16	16	16	16
Modal transverse scales	12	12	13	13-14
Modal scales below lateral line	6	6	7	8
Modal scales above lateral line	4	5	5	4
Modal dorsal spines	12	12-13	11-12	11
Modal soft dorsal rays	11	11	11	11
Modal principal caudal rays	15	15	15	15
Modal soft anal rays	8-9	8	8	9
Modal pectoral rays	14	15	14	13-14
Palatine teeth	absent	absent	usually absent	present
Preoperculomandibular pores	10	10	10	9
Maximum size (mm SL)	42.8	49.0	43.4	34.6
Face coloration	orange w/blue	orange w/blue	gray w/blue	gray w/blue-green
Blue on lips	absent	absent	absent	present
Blue on mid-gular area	absent	absent	absent	present
Orange spots on soft dorsal and caudal fin rays	present	present	present (faint)	absent
Blue in base of soft dorsal and anal fin	present	absent	absent	present
Spinous dorsal fin marginal and submedial bands	blue	black	black	blue-green
Spinous dorsal fin medial band	orange	orange	orange	red-orange
Orange in spinous dorsal fin basal band	present	present	absent	absent
Basicaudal bar development	dorsal/ventral	ventral	ventral	ventral
Orange spots on anal fin rays	present	present	present (faint)	absent
Lateral blue blotches	quadrate	quadrate	quadrate	quadrate

TABLE 14. PRINCIPAL COMPONENT LOADINGS FOR 17 MERISTIC VARIABLES IN 3,049 SPECIMENS OF *DORATION*.

	Principal component	
Variable	**I**	**II**
Dorsal fin spines	0.540	0.325
Dorsal fin rays	0.586	0.235
Principal caudal fin rays	0.086	0.130
Anal fin rays	0.554	0.100
Pectoral fin rays	0.415	0.454
Lateral scale rows	0.599	-0.266
Unpored lateral scale rows	-0.131	-0.459
Transverse scale rows	0.752	-0.418
Scale rows below lateral line	0.629	-0.461
Scale rows above lateral line	0.705	-0.028
Caudal peduncle scale rows	0.722	-0.290
Percent cheek squamation	-0.363	0.320
Percent nape squamation	0.415	0.724
Percent belly squamation	0.315	0.682
Percent opercle squamation	-0.435	0.127
Infraorbital canal pores	0.128	0.069
Preoperculomandibular canal pores	0.061	0.210

TABLE 15. SHEARED PRINCIPAL COMPONENT (PC) LOADINGS FOR 28 MORPHOMETRIC MEASUREMENTS IN 326 SPECIMENS OF *DORATION*. D1 = spinous dorsal fin origin; D2 = soft dorsal fin origin; IOW = midline at least interobital width; P2 = lateral pelvic fin insertion; A = anal fin origin.

	Males (n = 163)			Females (n = 163)		
		Sheared PC			Sheared PC	
Measurement	Size	II	III	Size	II	III
Standard length	0.166	0.053	-0.087	0.176	0.018	-0.013
Head length	0.168	0.150	-0.130	0.176	0.205	-0.071
Snout length	0.203	0.353	-0.251	0.207	0.357	-0.284
Orbit length	0.153	0.067	0.032	0.175	0.141	0.073
Upper jaw length	0.213	0.214	-0.175	0.222	0.370	-0.062
Predorsal length	0.178	0.139	-0.066	0.181	0.136	-0.003
D1 to occiput	0.204	0.114	-0.022	0.204	0.131	0.134
Occiput to snout	0.168	0.154	-0.101	0.173	0.177	-0.118
Occiput to IOW	0.160	0.053	0.066	0.156	0.061	0.045
IOW to snout	0.187	0.274	-0.192	0.190	0.274	-0.223
P2 to snout	0.170	0.086	-0.069	0.175	0.192	-0.079
Occiput to P2	0.210	-0.008	0.180	0.203	-0.057	0.105
D1 to P2	0.231	-0.034	0.380	0.228	-0.230	0.271
D1 to D2	0.184	-0.094	-0.093	0.187	-0.188	-0.040
D1 to A	0.193	-0.027	0.045	0.208	-0.127	0.082
P2 to A	0.181	0.051	-0.021	0.202	-0.058	0.074
D2 to P2	0.188	-0.049	-0.008	0.193	-0.143	0.042
D2 to A	0.219	-0.107	0.395	0.212	-0.148	0.272
Soft dorsal fin base length	0.171	0.091	-0.084	0.195	0.019	-0.093
Caudal peduncle depth	0.195	-0.052	0.381	0.192	-0.003	0.244
Caudal peduncle length	0.147	0.055	0.017	0.164	-0.028	0.180
Anal fin base length	0.194	-0.068	-0.275	0.154	-0.196	-0.492
1st anal spine length	0.183	-0.708	-0.374	0.148	-0.484	-0.493
Petoral fin length	0.189	-0.147	0.002	0.186	-0.139	-0.039
Pelvic fin length	0.182	-0.184	-0.030	0.170	-0.149	-0.072
Trans-pelvic width	0.221	-0.097	0.188	0.209	-0.050	0.113
6th dorsal spine length	0.188	-0.218	-0.167	0.151	-0.100	-0.030
Body width	0.214	-0.005	0.210	0.219	-0.100	0.157

TABLE 16. PRINCIPAL COMPONENT LOADINGS FOR 16 MERISTIC VARIABLES IN 756 SPECIMENS OF *ETHEOSTOMA JESSIAE* AND *E. MEADIAE*. Belly squamation did not vary and was omitted from the analysis.

Variable	Principal component I	Principal component II
Dorsal fin spines	0.201	-0.305
Dorsal fin rays	0.416	-0.344
Principal caudal fin rays	-0.541	0.354
Anal fin rays	0.515	-0.329
Pectoral fin rays	0.329	-0.136
Lateral scale rows	0.601	-0.144
Unpored lateral scale rows	0.354	-0.371
Transverse scale rows	0.732	0.545
Scale rows below lateral line	0.716	0.482
Scale rows above lateral line	0.275	0.620
Caudal peduncle scale rows	0.731	0.249
Percent cheek squamation	0.683	-0.050
Percent nape squamation	0.684	-0.280
Percent opercle squamation	-0.180	0.322
Infraorbital canal pores	0.125	0.120
Preoperculomandibular canal pores	0.008	-0.001

LITERATURE CITED

Bailey, R. M., and D. A. Etnier. 1988. Comments on the subgenera of darters (Percidae) with descriptions of two new species of *Etheostoma (Ulocentra)* from southeastern United States. Miscellaneous Publications Museum of Zoology, University of Michigan 175.

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 Museum of Zoology, University of Michigan 93.

Bailey, R. M., H. E. Winn, and C. L. Smith. 1954. Fishes from the Escambia River, Alabama and Florida, with ecologic and taxonomic notes. Proceedings of the Academy of Natural Sciences, Philadelphia 106:109–164.

Bailey, R. M., J. E. Fitch, E. S. Herald, E. A. Lachner, C. C. Lindsey, C. R. Robins, and W. B. Scott. 1970. A list of common and scientific names of fishes from the United States and Canada. American Fisheries Society Special Publication 6.

Bart, H. L., Jr., and R. C. Cashner. 1986. Geographic variation in Gulf Slope populations of the bluntnose darter, *Etheostoma chlorosomum* (Hay). Tulane Studies of Zoology and Botany 25:151–170.

Bohlke, J. E. 1953. A catalogue of the type specimens of recent fishes in the Natural History Museum of Stanford University. Stanford Ichthyological Bulletin 5:1–168.

Bookstein, F. L., B. Chernoff, R. L. Elder, J. M. Humphries, Jr., G. R. Smith, and R. E. Strauss. 1985. Morphometries in evolutionary biology. Academy of Natural Sciences, Philadelphia, Special Publication 15.

Branson, B. A., J. Triplett, and R. Hartmann. 1969. A partial biological survey of the Spring River drainage in Kansas, Oklahoma and Missouri. Part II: the fishes. Transactions Kansas Academy of Sciences 72:429–472.

Burkhead, N. M., and R. E. Jenkins. 1991. Fishes, p. 321–409, plates 124–156. *In*: Virginia's endangered species. K. Terwilliger (coordinator). McDonald and Woodward Publishing Company, Blacksburg, Virginia.

Burr, B. M., and M. L. Warren, Jr. 1986. A distributional atlas of Kentucky fishes. Kentucky Nature Preserves Comm., Scientific Technical Series 4.

Clay, W. M. 1975. The fishes of Kentucky. Kentucky Department of Fish and Wildlife Research, Frankfort.

Cole, C. F. 1957. The taxonomy of the percid fishes of the genus *Etheostoma*, subgenus *Boleosoma*, of eastern United States. Unpublished. Ph.D. dissertation, Cornell University, Ithaca, New York.

Cole, C. F. 1967. A study of the eastern johnny darter, *Etheostoma olmstedi* Storer (Teleostei, Percidae). Chesapeake Science 8:28–51.

Collette, B. B. 1965. Systematic significance of breeding tubercles in fishes of the family Percidae. Proceedings of the United States National Museum 117:567–614.

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 (3550):1–88.

Comiskey, C. E., and D. A. Etnier. 1972. Fishes of the Big South Fork of the Cumberland River. Journal Tennessee Academy of Sciences 47:140–145.

Cross, F. B. 1967. Handbook of fishes of Kansas. University of Kansas Museum of Natural History, Museum of Natural History Publication 45.

Cross, F. B., and W. L. Minckley. 1958. New records of four fishes from Kansas. Transactions Kansas Academy of Sciences 61:104–108.

Dewey, M. R., and T. E. Moen. 1978. Fishes of the Caddo River, Arkansas after impoundment of DeGray Lake. Proceedings of the Arkansas Academy of Sciences 32:39–42.

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

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

Evermann, B. W. 1918. The fishes of Kentucky and Tennessee: a distributional catalogue of the known species. Bulletin United States Bureau of Fisheries XXXV 1915–1916: 293–368.

Evermann, B. W., and S. F. Hildebrand. 1916. Notes on the fishes of east Tennessee. Bulletin United States Bureau of Fisheries XXXIV 1914:431–452.

Farris, J. S. 1989. The retention index and the rescaled consistency index. Cladistics 5:417–419.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783–791.

Fowler, H. W. 1907. Some new and little-known percoid fishes. Proceedings of the Academy of Natural Sciences, Philadelphia 58:510–528.

Fowler, H. W. 1945. A study of the fishes of the southern Piedmont and Coastal Plain. Academy of Natural Sciences, Monograph 7.

Gilbert, C. H. 1888. Descriptions of new and little known etheostomoids. Proceedings of the United States National Museum 10:47–64.

Gilbert, C. H. 1891. Report of explorations made in Alabama during 1889, with notes on the fishes of the Tennessee, Alabama, and Escambia rivers. Bulletin of the United States Fisheries Commission IX, for 1889:143–159.

Gilbert, C. R., and S. J. Walsh. 1991. Provenance and disposition of fish specimens appearing in color plates of Kuehne and Barbour's book, "The American Darters." Proceedings of the Southeastern Fishes Council 24:12–19.

Harris, J. L., and N. H. Douglas. 1978. Fishes of the mountain province section of the Ouachita River. Proceedings of the Arkansas Academy of Sciences 32:55–59.

Hay, O. P. 1881. On a collection of fishes from eastern Mississippi. Proceedings of the United States National Museum 3:488–515.

Hennig, W. 1966. Phylogenetic systematics. University of Illinois Press, Urbana, Illinois.

Hillis, D. M., and J. J. Bull. 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. Systematic Biology 42:182–192.

Howell, W. M. 1968. Taxonomy and distribution of the percid fish, *Etheostoma stigmaeum* (Jordan), with the validation and redescription of *Etheostoma davisoni* Hay. Unpublished Ph.D., dissertation, University of Alabama, Tuscaloosa.

Howell, W. M. 1980a. *Etheostoma jessiae* (Jordan and Brayton), blueside darter, p. 656. *In*: Atlas of North American freshwater fishes. D. S. Lee, C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAllister, and J. R. Stauffer, Jr. (eds.). North Carolina State Museum Natural History, Raleigh, North Carolina.

Howell, W. M. 1980b. *Etheostoma meadiae* (Jordan and Evermann), p. 666. *In*: Atlas of North American freshwater fishes. D. S. Lee, C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAllister, and J. R. Stauffer, Jr. (eds.). North Carolina State Museum Natural History, Raleigh, North Carolina.

Howell, W. M. 1980c. *Etheostoma stigmaeum* (Jordan), speckled darter, p. 697. *In*: Atlas of North American freshwater fishes. D..S. Lee, C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAllister, and J. R. Stauffer, Jr. (eds.). North Carolina State Museum Natural History, Raleigh, North Carolina.

Howell, W. M., and H. T. Boschung. 1966. A natural hybrid darter, *Etheostoma whipplii artesiae* X *Etheostoma stigmaeum* (Pisces, Percidae). American Midland Naturalist 76:510–514.

Hubbs, C. L., and K. F. Lagler. 1974. Fishes of the Great Lakes region. University of Michigan Press, Ann Arbor.

Humphries, J. M., Jr., F. L. Bookstein, B. Chernoff, G. R. Smith, R. L. Elder, and S. G. Poss. 1981. Multivariate discrimination by shape in relation to size. Systematic Zoology 30:291–308.

Jenkins, R. E., and N. M. Burkhead. 1994. Freshwater fishes of Virginia. American Fisheries Society, Bethesda, Maryland.

Johnson, J. E. 1987. Protected fishes of the United States and Canada. American Fisheries Society, Bethesda, Maryland.

Jordan, D. S. 1877. A partial synopsis of the fishes of upper Georgia. Annuals of the Lyceum of Natural History of New York XI:307–377.

Jordan, D. S. 1878. 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, second edition. Jansen, McClurg and Company, Chicago.

Jordan, D. S. 1880. Manual of the vertebrates of the northern United States, including the district east of the Mississippi River, and north of North Carolina and Tennessee, exclusive of marine species, third edition. Jansen, McClurg and Company, Chicago.

Jordan, D. S. 1884. 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, fourth edition. Jansen, McClurg and Company, Chicago.

Jordan, D. S. 1890. A manual of the vertebrate animals of the northern United States including the district north and east of the Ozark Mountains, south of the Laurentian Hills, north of the southern boundary of Virginia, and east of the Missouri River, fifth edition. A. C. McClurg and Company, Chicago.

Jordan, D. S. 1929. Manual of the vertebrate animals of the northeastern United States inclusive of marine species, thirteenth edition. World Book Co., Yonkers–on–Hudson, New York.

Jordan, D. S., and A. W. Brayton. 1878. Contributions to North American ichthyology, based primarily on the collections of the United States National Museum. III. A – On the distribution of the fishes of the Alleghany region of South Carolina, Georgia, and Tennessee, with descriptions of new or little known species. Bulletin of the United States National Museum 12.1–95.

Jordan, D. S., and B. W. Evermann. 1896. The fishes of North and Middle America: a descriptive catalogue of the species of fishlike vertebrates found in the waters of North America, north of the Isthmus of Panama. Bulletin of the United States National Museum 47, Part 1.

Jordan, D. S., and B. W. Evermann. 1898. The fishes of North and Middle America: a descriptive catalogue of the species of fishlike vertebrates found in the waters of North America, north of the Isthmus of Panama. Bulletin of the United States National Museum 47, Part 3.

Jordan, D. S., and B. W. Evermann. 1900. The fishes of North and Middle America: a descriptive catalogue of the species of fishlike vertebrates found in the waters of North America, north of the Isthmus of Panama. Bulletin of the United States National Museum 47, Part 4.

Jordan, D. S., and C. H. Gilbert. 1883. Synopsis of the fishes of North America. Smithsonian Miscellaneous Collection XXIV, Bulletin of the United States National Museum 16.

Jordan, D. S., B. W. Evermann, and H. W. Clark. 1930. Check list of the fishes and fishlike vertebrates of North and Middle America north of the northern boundary of Venezuela and Colombia. Report of the United States Commisison of Fisheries for 1928, Part II.

Kirsch, P. H. 1893. Notes on a collection of fishes from the southern tributaries of the Cumberland River in Kentucky and Tennessee. Bulletin of the United States Fisheries Commission XI for 1891:259–268.

Kluge, A. G., and J. S. Farris. 1969. Quantitative phyletics and the evolution of anurans. Systematic Zoology 18:1–32.

Kuehne, R. A., and R. W. Barbour. 1983. The American darters. University Press Kentucky, Lexington.

Kuhne, E. R. 1939. A guide to the fishes of Tennessee and the mid-South. Tennessee Department of Conservation, Nashville.

Lang, N. J., and R. L. Mayden. 2007. Systematics of the subgenus *Oligocephalus* (Teleostei: Percidae: *Etheostoma*) with complete subgeneric sampling of the genus *Etheostoma*. Molecular Phylogenetics and Evolution 43:605–615.

Layman, S.R. 1994. Phylogenetic systematics and biogeography of darters of the subgenus *Doration* (Percidae: *Etheostoma*). Unpublished Ph.D., dissertation, University of Alabama, Tuscaloosa.

Layman, S.R., and R. L. Mayden. 2009. A new species of the darter subgenus *Doration* (Percidae: *Etheostoma*) from the Caney Fork River system, Tennessee. Copeia 2009:157–170.

Layman, S. R., A. M. Simons, and R. M. Wood. 1993. Status of the dirty darter, *Etheostoma olivaceum*, and bluemask darter, *Etheostoma* (*Doration*) sp., with notes on fishes of the Caney Fork River system, Tennessee. Journal Tennessee Academy of Sciences 68(2):65–70.

Leviton, A. E., and R. H. Gibbs, Jr. 1988. Standards in herpetology and ichthyology. Standard symbolic codes for institution resource collections in herpetology and ichthyology. Supplement No.1: additions and corrections. Copeia 1988:280–282.

Leviton, A. E., R. H. Gibbs, Jr., E. Heal, and C. E. Dawson. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985:802–832.

Maddison, W. P., M. J. Donoghue, and D. R. Maddison. 1984. Outgroup analysis and parsimony. Systematic Zoology 33:83–103.

Mayden, R. L. 1985. Biogeography of Ouachita Highland fishes. Southwestern Naturalist 30:195–211.

Mayden, R. L. 1997. A hierarchy of species concepts: the denouement in the saga of the species problem, p. 381–424. *In*: Species: The Units of Biodiversity. Claridge, M.F., Dawah, H.A. and Wilson, M.R. (eds). Chapman and Hall Ltd., London.

Mayden, R. L. 1999. Consilience and a hierarchy of species concepts: Advances towards closure on the species puzzle. Journal of Nematology 31:95–116

Mayden, R. L. 2002. On biological species, species concepts, and individuation in the natural world. Fish and Fisheries 2:1–26.

Mayden, R. L., B. M. Burr, L. M. Page, and R. R. Miller. 1992.

The native freshwater fishes of North America, p. 827–863. *In*: Systematics, historical ecology, and North American freshwater fishes. R. L. Mayden (ed.). Stanford University Press, Stanford, California.

Meek, S. E. 1891. Report of explorations made in Missouri and Arkansas during 1889, with an account of the fishes observed in each of the river basins examined. Bulletin of the United States Fisheries Commission IX for 1889:113–141.

Menhinick, E. F., T. M. Burton, and J. R. Bailey. 1974. An annotated checklist of the freshwater fishes of North Carolina. Journal of the Elisha Mitchell Scientific Society 90:24–50.

Metcalf, A. L. 1959. Fishes of Chautauqua, Cowley and Elk counties, Kansas. Miscellaneous Publications, University of Kansas Museum of Natural History 11:345–400.

Miller, R. J., and H. W. Robison. 1973. Fishes of Oklahoma. Oklahoma State University Press, Stillwater.

Near, T. J., C. M. Bossu, G. S. Bradburd, R. L. Carlson, R. C. Harrington, P. R. Hollingsworth, B. J. Keck, and D. A. Etneir. 2011. Phylogeny and Temporal Diversification of Darters (Percidae: Etheostomatinae). Systematic Biology 60:565–595.

Page, L. M. 1981. The genera and subgenera of darters (Percidae, Etheostomatini). Occasional Papers Museum of Natural History, University of Kansas 90.

Page, L. M. 1983. Handbook of darters. TFH Publications, Neptune City, New Jersey.

Page, L. M. 1985. Evolution of reproductive behaviors in percid fishes. Bulletin Illinois Natural History Survey 33:275–295.

Page, L. M., and L. E. Cordes. 1983. Variation and systematics of *Etheostoma euzonum*, the Arkansas saddled darter (Pisces: Percidae). Copeia 1983:1042–1050.

Page, L. M., and K. S. Cummings. 1984. A portable camera box for photographing small fishes. Environmental Biology of Fishes 11:160.

Pflieger, W. L. 1975. The fishes of Missouri. Missouri Department of Conservation

Robins, C. R., R. M. Bailey, C. E. Bond, J. R. Brooker, E. A. Lachner, R. N. Lea, and W. B. Scott. 1980. A list of common and scientific names of fishes from the United States and Canada, 4th ed. American Fisheries Society Special Publication 12.

Robins, C. R., R. M. Bailey, C. E. Bond, J. R. Brooker, E. A. Lachner, R. N. Lea, and W. B. Scott. 1991. Common and scientific names of fishes from the United States and Canada, 5th ed. American Fisheries Society Special Publication 20.

Robison, H. W. 1974. An additional population of *Etheostoma pallididorsum* Distler and Metcalf in Arkansas. American Midland Naturalist 91:478–479.

Robison, H. W., and T. M. Buchanan. 1988. Fishes of Arkansas. University of Arkansas Press, Fayetteville.

Robison, H. W., and J. L. Harris. 1978. Notes on the habitat and zoogeography of *Noturus taylori* (Pisces: Ictaluridae). Copeia 1978:548–550.

Sanderson, M. J. 1989. Confidence limits on phylogenies: the bootstrap revisited. Cladistics 5:113–129.

SAS Institute Inc. 1985. SAS user's guide: statistics, version 5 edition. SAS Institute Inc., Cary, North Carolina.

SAS Institute Inc. 1990. SAS procedures guide, version 6, third edition. SAS Institute Inc., Cary, North Carolina.

Simons, A. M. 1991. Phylogenetic relationships of the crystal darter, *Crystallaria asprella* (Teleostei: Percidae). Copeia 1991:927–936.

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

Sloss, B. L., N. Billington and B. M. Burr. 2004. A molecular phylogeny of the Percidae (Teleostei, Perciformes) based on mitochondrial DNA sequence. Mol. Phylogenet. Evol. 32, 545–562.

Starnes, W. C., and D. A. Etnier. 1986. Drainage evolution and fish biogeography of the Tennessee and Cumberland Rivers drainage realm, p. 325–362. *In*: The zoogeography of North American freshwater fishes. C. H. Hocutt and E. O. Wiley (eds.). John Wiley & Sons, New York.

Swofford, D. L. 1993. PAUP: phylogenetic analysis using parsimony, version 3.1. Computer program distributed by Illinois Natural History Survey, Champaign.

Swofford, D. L., and W. P. Maddison. 1987. Reconstructing ancestral states under Wagner parsimony. Mathematical Bioscience 87:199–229.

Swofford, D. L., and G. J. Olsen. 1990. Phylogeny reconstruction, p. 411–501. *In*: Molecular systematics. D. M. Hillis and C. Moritz (eds.). Sinauer Associates, Inc., Sunderland, Massachusetts.

Wall, B. R. 1968. Studies on the fishes of the Bear Creek drainage of the Tennessee River system. Unpubl. M.S. thesis, University of Alabama, Tuscaloosa.

Watrous, L. E., and Q. D. Wheeler. 1981. The outgroup comparison method of character analysis. Systematic Zoology 30:1–11.

Wiley, E. O. 1978. The evolutionary species concept reconsidered. Systematic Zoology 27:17–26.

Wiley, E. O. 1981. Phylogenetics, the theory and practice of phylogenetic systematics. John Wiley and Sons, Inc., New York.

Wiley, E. O., and R. L. Mayden. 2000a. The evolutionary species concept, p. 70–89. *In*: Species Concepts and Phylogenetic Theory: A Debate (Q. D. Wheeler and R. Meier, eds.) Columbia University Press, New York, New York.

Wiley, E. O., and R. L. Mayden. 2000b. Comments on Alternative species concepts, p. 146–158. *In*: Species Concepts and Phylogenetic Theory: A Debate (Q. D. Wheeler and R. Meier, eds.) Columbia University Press, New York, New York.

Wiley, E. O., and R. L. Mayden. 2000c. A reply to our critics, p. 198–208. *In*: Species Concepts and Phylogenetic Theory: A Debate (Q. D. Wheeler and R. Meier, eds.) Columbia University Press, New York, New York.

Winn, H. E. 1958a. Observations on the reproductive habits of darters (Pisces-Percidae). American Midland Naturalist 59:190–212.

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

Wood, R. M., and R. L. Mayden. 1997. Phylogenetic relationships among selected darter subgenera (Teleostei: Percidae) as inferred from analysis of allozymes. Copeia 1997:265–274.

Woolman, A. J. 1892. Report of an examination of the rivers of Kentucky, with lists of the fishes obtained. Bulletin United States Fisheries Commission X, for 1890:249–288.

APPENDIX A. CHARACTER DESCRIPTIONS

1. Breeding male lateral body banding pattern: 0 = no series of 7-11 blue or blue-green vertically aligned bars or quadrate blotches; 1 = series of 7-11 vertically elongate blue or blue-green bars, typically extending above lateral line scale row; 2 = series of 7-11 quadrate blue blotches, usually not extending above lateral line scale row. The blue bars of the outgroup *Etheostoma caeruleum*, which are obliquely aligned and number up to 14, are not considered homologous.

2. Breeding male lateral body coloration: 0 = no scattered red-orange spots or irregular markings on midlateral and dorsolateral areas; 1 = scattered red-orange spots or irregular markings on midlateral and dorsolateral areas. The lateral red pigment in *E. caeruleum* tends to be concentrated on the lower sides and is more consistent in distribution, typically covering the central exposed portions of scales; this condition is not considered homologous.

3. Breeding male lateral head coloration: 0 = no bright iridescent blue or blue-green pigment on the opercle and cheek; 1 = bright iridescent blue or blue-green pigment on the opercle and cheek. The blue pigment in *E. caeruleum* typically lacks the iridescent quality of the blue/blue-green in species of *Doration* and is not considered homologous on the basis of the criterion of special similarity (Wiley, 1981).

4. Breeding male lip coloration: 0 = blue or blue-green pigment absent; 1 = blue or blue-green pigment usually present on a portion of the lips.

5. Breeding male gular area: 0 = no blue or blue-green pigment present; 1 = blue or blue-green pigment present as medial bar or completely covering area.

6. Breeding male base color of anterior face and underside of head: 0 = without tangerine orange pigment; 1 = covered with tangerine orange pigment. The orange-red pigment on the underside of the head of *E. caeruleum* does not extend onto the anterior face and is not considered homologous.

7. Breeding male first dorsal fin pattern: 0 = no distinct marginal and submedial bands of the same color; 1 = dusky to black marginal and submedial bands; 2 = blue or blue-green marginal and submedial bands. In species of *Doration* (ingroup) the marginal and submedial bands are always the same color (blue or blue-green in marginal band may be restricted to posterior membranes) and are assumed to be coupled. This character can be ordered based on the observation that melanization often accompanies blue/blue-green pigment in these bands, and in males entering reproductive condition the bands are dusky to black before blue/blue-green appears.

8. Breeding male first dorsal fin medial zone: 0 = no distinct medially-restricted red or orange band; 1 = medial band red or red-orange in life; 2 = medial band true orange in life.

9. Breeding male first dorsal fin basal zone: 0 = no bright orange triangles or streaks in posterior portions of membranes; 1 = bright orange triangles or streaks in posterior portions of membranes.

10. Breeding male second dorsal fin membranes: 0 = no blue or blue-green pigment in base of fin above fourth dorsal saddle; 1 = blue or blue-green in base of fin above fourth dorsal saddle (often accompanied by blue/blue-green spot or submedial band across anterior membranes).

11. Breeding male second dorsal and caudal fin rays: 0 = no discrete orange spots (may be suffused with pale orange or yellow); 1 = discrete, often bright orange spots. In *E. teddyroosevelt* these spots are small and tend to be paler on the caudal fin, but they are usually discrete.

12. Breeding male caudal fin base at peak development: 0 = no blue or blue-green bar; 1 = blue or blue-green bar extending from medial caudal fin base to ventral margin of caudal fin; 2 = blue or blue-green vertical bar extending from dorsal to ventral margins of caudal fin. This character can be ordered based on the observation that males developing character state 2 pass through a stage in which the bar first develops ventrally (state 1).

13. Breeding male anal fin membranes: 0 = no blue or blue-green pigment in base of fin: 1 = blue or blue-green pigment, often forming broad band, in base of fin.

14. Breeding male anal fin rays: 0 = no discrete orange spots; 1 = discrete orange spots restricted to posteromedial portion of fin, usually only one per ray; 2 = discrete orange spots throughout fin, usually two or three per ray. In *E. teddyroosevelt*, the orange spots are often pale but discrete and may be most discernible in males that have not yet reached peak development; melanization of the fin at peak development can obscure these spots.

15. Breeding male pectoral fin rays: 0 = no discrete orange spots along entire lengths of rays (pale yellow-orange spots may be concentrated near base of fin); 1 = discrete, often bright orange spots along entire lengths of rays. In *E. teddyroosevelt*, the orange spots tend to be pale.

16. Breeding tubercles on ventral body scales: 0 = present; 1 = absent.

17. Breeding tubercles on anal and pelvic fin rays: 0 = absent; 1 = present.

18. Structure of breeding female genital papilla: 0 = conical, tubular; 1 = flat, bifurcate; 2 = rugose, spatulate.

19. Non-breeding male and female midlateral body pattern: 0 = no blotches formed by X-, V-, or W-shaped markings; 1 = blotches formed by X-, V-, or W-shaped markings.

20. Non-breeding male and female caudal fin base: 0 = no pair of vertically aligned small dark spots at insertion of medial rays; 1 = pair of vertically aligned small dark spots at insertion of medial rays (on scales sheathing base of rays, not on musculature; in breeding males often obscured by nuptial coloration).

21. Number of dorsal saddles: 0 = 6 to 10; 1 = 4; 2 = 6.

22. Frenum: 0 = present (65-100% individuals); 1 = absent (90-100% individuals).

23. Lateral line: 0 = complete; 1 = incomplete.

24. Palatine teeth: 0 = present (75-100% individuals); 1 = absent (75-100% individuals).

25. Infraorbital canal: 0 = uninterrupted; 1 = interrupted.

26. Supratemporal canal: 0 = uninterrupted; 1 = interrupted.

27. Preoperculomandibular pores: 0 = 10; 1 = 9.

28. Cheek squamation: 0 = fully scaled; 1 = partly scaled; 2 = naked or nearly so.

29. Breast squamation: 0 = scaled; 1 = unscaled.

30. Number of anal fin spines: 0 = 2; 1 = 1.

31. Modal (mean) number of anal fin soft rays: 0 = 10 (10.0); 1 = 7-9 (7.5-9.0); 2 = 6-7 (6.7).

32. Modal (mean) number of dorsal fin spines: 0 = 13 (13.0); 1 = 11-13 (10.9-12.6); 2 = 8-10 (<10.0).

33. Mode of egg deposition: 0 = burying; 1 = attaching; 2 = clustering. Egg burying is assumed for all species of *Doration* based on Winn's (1958a, 1958b) observations of this behavior in *E. jimmycarter*. Egg burying is also assumed for *E. euzonum* based on reports cited by Page (1983) for closely related *E. variatum* and *E. tetrazonum*.

34. Habitat: 0 = swift, gravel/rubble riffles; 1 = slow to moderate current over sand or gravel; 2 = slow current over sand, mud, or silt.

APPENDIX B. DATA MATRIX USED IN PHYLOGENETIC ANALYSIS. See Appendix A for description of characters and character states.
OG = outgroup.

	Character																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Etheostoma stigmaeum	1	1	1	1	1	0	2	1	0	1	0	2	1	0	0	0	1
Etheostoma jessiae	1	1	1	1	0	0	2	2	1	1	1	2	1	0	1	0	1
Etheostoma meadiae	1	1	1	1	0	0	2	2	0	1	0	2	1	0	0	0	1
Etheostoma akatulo	1	1	1	1	1	0	1	1	0	0	0	1	0	0	0	0	1
Etheostoma obama	2	1	1	0	0	1	2	2	1	1	1	2	1	1	1	0	1
Etheostoma gore	2	1	1	0	0	1	2	2	1	1	1	2	1	2	1	0	1
Etheostoma jimmycarter	2	1	1	0	0	1	1	2	1	0	1	1	0	2	1	0	1
Etheostoma teddyroosevelt	2	1	1	0	0	0	1	2	0	0	1	1	0	2	1	0	1
Etheostoma clinton	2	1	1	1	1	0	2	1	0	1	0	1	1	0	0	0	1
Etheostoma chlorosoma (OG)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Etheostoma nigrum (OG)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Etheostoma euzonum (OG)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Etheostoma caeruleum (OG)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	Character																
	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Etheostoma stigmaeum	0	1	1	2	1	1	0	0	0	0	1	1	0	1	1	0	1
Etheostoma jessiae	0	1	1	2	0	1	0	0	0	0	1	1	0	1	1	0	1
Etheostoma meadiae	0	1	1	2	0,1	1	0,1	0	0	0	2	1	0	1	1	0	1
Etheostoma akatulo	0	1	1	2	1	0	1	0	0	0	0	1	0	1	1	0	1
Etheostoma obama	0	1	1	2	1	1	0,1	0	0	0	1	1	0	1	1	0	1
Etheostoma gore	0	1	1	2	1	1	1	0	0	0	2	1	0	1	1	0	1
Etheostoma jimmycarter	0	1	1	2	1	1	1	0	0	0	2	1	0	1	1	0	1
Etheostoma teddyroosevelt	0	1	1	2	1	1	1	0	0	0	2	1	0	1	1	0	1
Etheostoma clinton	0	1	1	2	1	1	0	0	0	1	2	1	0	1	1	0	1
Etheostoma chlorosoma (OG)	2	1	0	2	1	1	0	1	1	0	0	0	1	1	2	1	2
Etheostoma nigrum (OG)	1	1	0	2	1	0	0	1	1	1	2	1	1	1	2	2	2
Etheostoma euzonum (OG)	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0
Etheostoma caeruleum (OG)	0	0	0	0	0	1	0	0	0	0	2	1	0	2	2	0	0

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24. The Whitesburg Bridge Site, Ma^{V}10. William S. Webb and D. L. DeJarnette. 44 pp., illus., 1948. Out of Print
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