SYSTEMATIC REVIEW OF SUBGENUS *FUSCATELUM* OF *ETHEOSTOMA* WITH DESCRIPTION OF A NEW SPECIES FROM THE UPPER BLACK WARRIOR RIVER SYSTEM, ALABAMA

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Abstract

The subgenus *Fuscatelum* was thought to contain a single, widespread, lowland species, the goldstripe darter, *Etheostoma parvipinne*. However, comparison of populations from throughout the goldstripe darter's reported range has revealed that populations in the upper Black Warrior River system represent a new species. The new species has lower scales counts than the goldstripe darter, lacks the distinctive gold stripe, and has a less intensive pattern of brown pigmentation along its sides. There are concerns about the conservation status of the new species, because only three rather widely separated populations are known, and the species cannot be reliably taken in any of these areas. In addition to describing the new species, we redescribe the goldstripe darter and review morphological attributes of subgenus *Fuscatelum*.

Introduction

The goldstripe darter, *Etheostoma parvipinne* Gilbert and Swain, inhabits small, vegetated Coastal Plain streams across a broad area of the Gulf and extreme lower Atlantic slopes. Maps of the distribution of this species show the species occurring well above the Fall Line only in the Black Warrior River system in Alabama (Rohde, 1980; Page, 1983, Figure 1). Careful study of these populations has revealed that they represent a distinct species.

In this paper we describe the new species, redescribe *E. parvipinne* based on material from throughout its geographic range, and review morphological attributes and systematics of subgenus *Fuscatelum*.

Materials and Methods

Material used in this study was obtained from fish collections at Auburn University (AUM), Geological Survey of Alabama (GSA), Southern Illinois University (SIU), Tulane University Museum of Natural History (TU), University of Alabama (UAIC), and the University of Texas Memorial Museum (TNHC). Paratypes of the new species were deposited at Academy of Natural Sciences, Philadelphia (ANSP), Illinois Natural History Survey (INHS), University of Alabama, University of Florida

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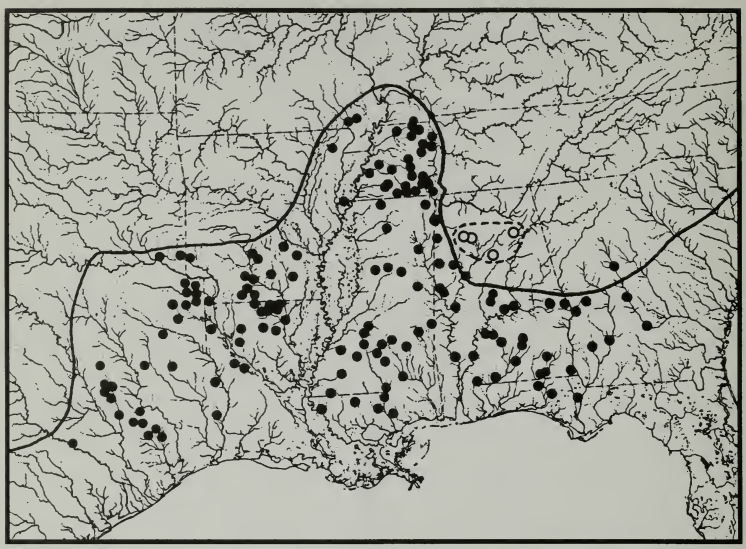

Figure 1. Map of the distribution of darters in subgenus *Fuscatelum* in relation to the Fall Line (heavy line). Open circles within dashed line represents known populations of *E. phytophilum* in the upper Black Warrior River system of Alabama. Solid circles mostly below the Fall Line show the distribution of *E. parvipinne*. (Map modified from Richards, 1963).

(UF), University of Michigan (UMMZ), and the United States National Museum of Natural History (USNM).

Counts and measurements follow Hubbs and Lagler (1958) except that transverse body scales were counted from the origin of the anal fin diagonally upward to the base of the spinous dorsal fin, and only branched rays in the caudal fin were counted. The great range in variation of lateral-line and pored lateral-line scale counts made it difficult to format the tables to fit on a page. Data for these counts are reported in two-scale intervals simply to reduce the width of Tables 1 and 2. Thus, counts of 38 and 39 in Table 1 are tabulated under "38–39", and so on. Vertebral counts were made from radiographs of 20 specimens from a Tombigbee River system population of *E. parvipinne* (TU 76977), and 27 specimens from the Turkey Creek (AUM 27017) and Clear Creek (TU 162757) populations of the new species.

Data for 15 body measurements, including standard length (SL), were gathered for samples of 17 males and 13 females from the lower Black Warrior population of *Etheostoma parvipinne* (GSA 6848.06, GSA 6855.06, GSA 7204.09, GSA 7249.08, GSA 7384.11, GSA 7993.11 and TU 168007, all Tuscaloosa Co., AL) and 15 males and 15 females from Turkey and Clear Creek populations of *E. phytophilum* (AUM 18747,

AUM 21148, AUM 21155, AUM 27017, TU 163757, TU 176230 and Holotype, TU 187503). Measurements were made with needle point calipers to the nearest 0.1 mm. Data for 14 of the body measurements were converted to ratios of standard length. The ratios were arcsine transformed to normalize ratio distributions. The transformed ratios were subjected to ANOVA to test for differences between sexes within species, and between species within each sex.

The arcsine-transformed mensural data were also subjected to principal components analysis (PCA) to characterize shape differences between the two species. PCA was performed on the covariance matrix because the data were not standardized. All statistical analyses were performed on a personal computer with Microsoft Excel 97 and Statistical Analysis System (SAS) Inc., software. Names used for species associates of the new species follow Robins et al. (1991).

Subgenus ***Fuscatelum***, Page, 1981

Type Species: *Etheostoma parvipinne* Gilbert and Swain (in Gilbert, 1887).

Diagnosis: Subgenus *Fuscatelum*, as diagnosed by Page (1981), is distinguished by the absence of bright breeding colors (red, blue, green or yellow) on body or fins, presence of a frenum, and presence of tubercles on the anal fin of breeding males (Page, 1981). As pointed out by Shaw (1996), the combination of these characters distinguishes *E. parvipinne* from all other *Etheostoma* except *E. fusiforme*. The addition of caudal peduncle depth/SL ratio greater than 0.11 (vs. less than 0.11 in *E. fusiforme*) distinguishes *Fuscatelum* from all *Etheostoma* inclusive of *E. fusiforme*.

Description: The following is a summary of the morphological characteristics of subgenus *Fuscatelum*, based on the new species and all populations of *E. parvipinne* examined in this study. For completeness, some of this description is repeated in the species accounts below.

Lateral line is straight and nearly (91–98%) complete. The nape, cheek, opercle, prepectoral area, breast and anterior belly are fully scaled (cheek scales sometimes partially embedded). A broad premaxillary frenum is always present. Branchiostegal membrane is moderately to broadly connected across the isthmus.

The head is brown dorsally with an even darker brown horizontal stripe running on either side from top of opercle through eye, across snout and onto upper jaw. A thick dark brown subocular bar extends down onto underside of the head. Side and underside of head below lateral stripe light yellow-brown to whitish-yellow with only a scattering of melanophores. Lower jaw and chin also light yellow-brown to whitish-yellow with darker brown edging or flecking. Opercle brown; humeral spot weakly developed. Brown pigment on body diffuse, giving the sides a more or less continuous brown cast, or producing a dense mottling of brown that dissipates dorsally and ventrally. When most intense, the brown pigment forms a series of 8–10 irregular dashes or blotches along the side of body, which may be extended into a series of vertical bars. Dorsum darker than ventrum but lighter than sides.

Medial fins have dark brown pigment forming a varying number of wavy bands. The bands are most numerous on the caudal fin and least developed on the anal fin.

Most of the pigment forming the bands is along the edges of fin rays. Fin membranes adjacent to the bands have only a scattering of melanophores, making the bands appear interrupted. The base of the caudal fin has two to four dark brown spots of varying intensity. Paired fins lack pigment in non-breeding individuals.

Breeding males differ from the above pattern mainly in having black melanophores scattered over all of the body and fins (least so on the pectoral), giving the body a dusky cast. Black pigment is concentrated on the anterior interradial membrane of the spinous dorsal fin in mature males, producing a distinct blotch. The rest of the first dorsal fin is dusky except for a white (pigmentless) strip along the distal margin. The soft dorsal, anal, pelvic and (less so) pectoral fins also develop black melanophores on the interradial membranes, making the fins appear dusky. Breeding tubercles develop only on anal soft rays of nuptial males. Female genital papillae are bulbous at the base and extended into a tube distally. Papillae of males very short and tubular, though wider at base than at tip.

As mentioned above, the caudal peduncle in subgenus *Fuscatelum* is relatively deep (more than 0.118 when expressed as a proportion of standard length), most like the situation in subgenera *Catonotus* and *Nothonotus* (Page 1981, Brooks 1993). The snout is very short (0.054–0.58 of standard length for both *E. parvipinne* and *E. phytophilum*). In this regard, subgenus *Fuscatelum* is most like subgenus *Boleichthys* (*sensu* Page, 1981). Pectoral fin length (0.205–0.224 of standard length) and soft dorsal fin base length (0.14 of standard length) are short relative to other *Etheostoma* (Page, 1981; Brooks, 1993). In this regard subgenus *Fuscatelum* is most like *E. exile* (subgenus *Boleichthys*, *sensu* Page, 1981; subgenus *Oligocephalus*, *sensu* Bailey and Etnier, 1988). Finally, the caudal fin is relatively long (0.212–0.229 of standard length), similar to the condition in subgenera *Boleichthys*, *Boleosoma*, *Catonotus*, *Psychromaster*, *Villora*, and *Ozarka*.

Systematics: *Etheostoma parvipinne* has been traditionally allied to darters in subgenus *Oligocephalus*. Richards (1963) concluded that *E. parvipinne* formed a natural group with *E. fricksium* and *E. mariae*, then also classified in subgenus *Oligocephalus*. Richards (1963) speculated that *E. parvipinne* was derived from an *E. fricksium*-like prototype through advancements such as reduction in dorsal fin color and interruption of the supratemporal canal. Page (1981) removed *E. parvipinne* from subgenus *Oligocephalus*, and established for it the subgenus *Fuscatelum* to emphasize its lack of bright breeding colors. Page (1981) considered *Fuscatelum* to be part of a highly evolved group of darters, which included members of the subgenera *Nothonotus*, *Belophlox* (*E. fricksium* and *E. mariae*), *Ozarka* (*E. punctulatum* and allies), *Oligocephalus*, *Catonotus*, and perhaps *Villora* (*E. edwini*). Bailey and Etnier (1988) commented that *Fuscatelum* shares a number of traits with subgenus *Ozarka*, including tuberculate anal fin, a distinctively depigmented nape, and late winter habits which suggested reproduction in "temporarily flooded fields" as seen in subgenus *Ozarka*.

No consistent hypothesis of relationships has emerged from three phylogenetic analyses involving subgenus *Fuscatelum* (Shaw, 1996; Wood and Mayden, 1997; Turner, 1997). Shaw (1996) analyzed 141 osteological, external morphological, and behavioral characters for 82 species of darters (genera *Crystallaria*, *Ammocrypta*, *Percina*, *Etheostoma*) and three Eurasian percids. In this analysis, *Fuscatelum* (*E. parvipinne*)

was sister to all other *Etheostoma* (76 species representing all traditionally allied subgenera, except *Ioa*), suggesting that *Fuscatelum* is the most ancestral subgenus in genus *Etheostoma*.

Wood and Mayden (1997) analyzed allozyme variation at 32 presumptive gene loci for 26 species of darters (genera *Crystallaria*, *Ammocrypta*, *Percina*, and *Etheostoma*) and three other percids. The most parsimonious solution was a tree based on allozyme frequencies with a topological constraint among outgroups consistent with previously published work. Subgenus *Fuscatelum* (*E. parvipinne*) occupied a more derived position in this phylogeny than in the analysis by Shaw (1996), and was sister to a group consisting of *Ozarka* (*E. cragini*)+ *Catonotus* (*E. flabellare* + *E. crossopterum*). This group was sister in turn to subgenus *Boleichthys* (*E. gracile* + *E. microperca*). Subgenus *Belophlox* was not represented in the analysis.

Turner (1997) analyzed sequence data from the mitochondrial DNA control region. Again, subgenus *Fuscatelum* (*E. parvipinne*) was more derived than in the analysis by Shaw (1996). It was most closely related to subgenus *Villora* in the most parsimonious topology, and was in a group of darters—together with representatives of the subgenera *Belophlox* (*E. mariae*), *Boleichthys* (*E. exile*, *E. gracile*), *Ozarka* (*E. pallididorsum*), *Villora* (*E. edwini*), and *Oligocephalus* (in part)—which lacked a tandem repeat at the proline tRNA end of the control region.

Fuscatelum shares a depigmented lateral line and a similar pattern of blotches or dashes along the side (most like *E. mariae* in this regard) with darters in subgenus *Belophlox* (Richards, 1963). The spinous dorsal fin of breeding males of *E. parvipinne* and *E. phytophilum* has a clear to milky-white marginal band with black pigment concentrated in the anterior interradial membranes, a situation most like that seen in *E. mariae* of subgenus *Belophlox* (Richards, 1963) and in some *Nothonotus*, but without the other band(s) of color seen in the spinous dorsal fin in these groups. Shaw (1996) mistakenly coded the spinous dorsal fin marginal band color as black in *Fuscatelum* (state 3), rather than opaque/tan/milky-yellow (state 4), as interpreted for *E. mariae*, members of *Nothonotus* and *E. blennioides*. She attributed character state 0 (marginal band clear) to *E. fricksium*, when in fact the margin of the spinous dorsal in breeding males of this species is clear to opaque-white with a stippling of black melanophores.

Etheostoma phytophilum, new species
Rush Darter
Figure 2a, b

Etheostoma parvipinne. Mettee 1978:144 (account, Fishes of the Birmingham-Jefferson County region of Alabama with ecological and taxonomic notes); Rohde 1980:680 (distribution, in part); Page 1983:245 (distribution, in part); Kuehne and Barbour 1983:141 (distribution, in part); Mettee et al. 1989a:181 (distribution, in part); Mettee et al. 1989b:144 (distribution, in part—Atlas); Page and Burr 1991:413 (distribution, in part—Map 359); Mettee et al. 1996:654–655 (distribution, in part, reference to distinct form in Turkey Creek system, Jefferson Co.).

HOLOTYPE: TU 187503: Spring run trib. to trib. to Turkey Creek along Alabama

Highway 79, Pinson, Jefferson Co, AL, 1 April 1994, H. Bart, J. Buckley and C. Gradney, collectors.

PARATOPOTYPES: TU 176230 (3, collected with holotype); AUM 18747 (1), 11 March 1979; AUM 21155 (2), 8 July 1979; AUM 27017 (17, distributed as follows: AUM 27017 (5), ANSP 177501 (2), INHS 48900 (2), UAIC 1295.01 (2), UF 110739 (2), UMMZ 234787 (2), USNM 351328 (2)) 6 November 1990; UAIC 11064.01(2), 17 April 1994.

OTHER PARATYPES: AUM 21148 (1): AL, Jefferson Co., Penny's Spring, 8 July 1979; TU 60078 (1): AL, Jefferson Co., Turkey Creek , 20 October 1969.

ADDITIONAL MATERIAL EXAMINED, NOT DESIGNATED AS TYPES: Wildcat Branch, trib. to Clear Creek, Winston Co., AL: AUM 27031 (11), 27 November 1990; TU 162757 (10), 11 April 1992; TU 167887 (2), 26 February 1993; TU 167895 (3), 27 February 1993; UAIC 10645.01 (in part 16), 25 February 1993; Cove Spring, Etowah Co., AL: UAIC 4139.04 (1), 4 May 1975.

DIAGNOSIS: *Etheostoma phytophilum* is a member of subgenus *Fuscatelum* as diagnosed herein and by Page (1981). It differs from the only other species in the subgenus, *E. parvipinne*, in usually having 47 or fewer lateral line scales (lateral line scales usually 48 or higher in *E. parvipinne*), usually 13 or fewer transverse scales (tranverse scales usually 14 or higher in *E. parvipinne*), and 22 or fewer caudal peduncle circumferential scales (caudal penduncle scales usually 23 or higher in *E. parvipinne*). Lateral line not distinctly depigmented at any stage (lateral line distinctly depigmented, especially anteriorly, in female and non-breeding *E. parvipinne*).

DESCRIPTION: *Etheostoma phytophilum* is a moderate-sized species of *Etheostoma*: the average size of the 68 specimens examined in this study (none less than 30 mm SL) is 40.22 mm SL; the largest known specimen is a 58 mm SL female. Lateral line with 39–51 scales (usually 47 or fewer) of which 32–50 are pored (Tables 1 and 2). Transverse scales 10–14, (usually 13 or fewer, Table 3). Caudal peduncle circumferential scales 18–22, usually 21 (Table 4). Only 10 of 68 *E. phytophilum* examined (15%) had more than 47 lateral line scales, only 2 of 68 (3%) had more than13 transverse scales, and none had more than 22 caudal peduncle scales. The combination of lateral line scales 47 or fewer, transverse scales 13 or fewer, and caudal peduncle scales fewer than 22, was seen in only 25 of 376 specimens (6.7%) of *E. parvipinne* examined from through the species' geographic range.

First dorsal fin has 8 to 11 (usually 10) spines and is entirely separate from the second dorsal fin, which has 9–13 (usually 10–11) soft rays (Tables 5 and 6). The right side pectoral fin has 14–16 (usually 15) rays (Table 7). The pelvic fin always has one spine and six rays. The anal fin almost always has two spines (although one may be reduced) and 7 to 10 (usually 9) soft rays (Table 8). The caudal fin has 11–15 (usually 13) branched rays (13–15 principal rays, Table 9). Vertebrae number 35–37 ($\bar{x}$ = 36.4).

Cephalic lateralis system is as follows: lateral canal complete with 5 pores, supratemporal canal incomplete with two pores; supraorbital canal complete with four pores; a coronal pore is usually present; infraorbital canal complete with 5–10 (usu-

Figure 2. a) *Etheostoma phytophilum*, holotype (TU 187503), breeding male, 44 mm SL, spring run in the Turkey Creek system; b) *E. phytophilum*, breeding male, 43 mm SL, Wildcat Branch trib to Clear Creek (TU 167895).

ally 8) pores (Table 10); preoperculomandibular canal complete with 9–12 (usually 10) pores (Table 11).

Color in life khaki (light yellowish brown) to golden brown, with a pattern of darker gray-brown pigment overlaying a yellowish to golden ground color. Head gray-brown dorsally with a dark brown stripe running horizontally from top of opercle, through eye, across snout, and onto upper jaw. A dark brown vertical bar runs below eye to underside of the head. Brown pigment on body diffuse, giving the sides a brown cast or producing a dense mottling of brown that dissipates dorsally and ventrally. At its most intense, the brown pigment forms a series of 8–10 irregular dashes along the side of body. Dorsum darker than ventrum but lighter than sides.

Even at its most intense, the brown pigment on the sides of the rush darter is seldom as intense as in the goldstripe darter, and mid lateral dashes are never drawn into vertical bars, as frequently seen in breeding males of *E. parvipinne*. The distinct gold stripe typical of *E. parvipinne* is never well developed in *E. phytophilum*. Only a very narrow strip may be depigmented along the anterior portion of the lateral line, above the midlateral dashes.

Brown pigment occurs at intervals along the edges of fin rays in median fins, producing a varying number of wavy bands. Fin membranes adjacent to the bands have a scattering of melanophores that make the bands appear interrupted. The base

of the caudal fin has two to four dark brown spots of varying intensity. Paired fins lack pigment in non-breeding individuals.

Breeding males of *E. phytophilum* have black melanophores scattered over all of the body and fins (least so on the pectoral fin), making the body appear dusky. A concentration of black melanophores forms on anterior interradial membranes of the spinous dorsal fin in mature males, producing a distinct blotch. The rest of the first dorsal fin is dusky except for a white (pigmentless) strip along the distal margin. The soft dorsal, anal, pelvic and (less so) pectoral fins also develop a dusky appearance due to the presence of black melanophores on interradial membranes. Breeding tubercles develop only on anal soft rays of nuptial males, female genital papillae are bulbous at the base and extended into a tube distally, and genital papillae of males are short and tubular, though wider at base than at tip.

Variation: The population in the Clear Creek system has slightly higher average counts of lateral line and pored lateral line scales than the Turkey Creek population. The Clear Creek population also has higher modal counts of right pectoral (16) and branched caudal fin rays (14) than the Turkey Creek population (modes of 14 or 15, and 13, respectively). Dorsal soft rays are modally lower in the Clear Creek population (10) than in the Turkey Creek population (11 or 12). None of the differences is statistically significant. In the Clear Creek system population, breeding males tend to have more mottling on the lower sides than in males from the Turkey Creek population. Clear Creek breeding males also develop a yellowish cast in the spinous and soft dorsal, pectoral and caudal fins (Figure 2b). We collected only two males in high reproductive stage in the Turkey Creek system (the holotype and a paratype form the same collection), and neither of them had yellow pigment in the fins. An older March-collected specimen was too faded to discern fin coloration. The Cove Creek population cannot be adequately compared because it is represented by a single specimen.

Distribution: *Etheostoma phytophilum* is endemic to upland portions (Appalachian Plateau and Valley and Ridge provinces) of the Black Warrior River system in Alabama. Only three rather widely separated populations are known (Figures 1 and 3): one in streams in the Clear Creek system, a tributary of the Sipsey Fork of the Black Warrior River in Bankhead National Forest; one in springs tributary to Turkey Creek north of Birmingham, AL; and one in a spring around Little Cove Creek near Gadsden, AL (a single specimen known from this location). The latter two streams are tributary to the Locust Fork of the Black Warrior River. Considering the area of the upper Black Warrior River system over which *E. phytophilum* occurs (Figure 3), and the large number of springs in this area, it would seem likely that other populations exist. The sampling locations depicted in Figure 3 give the impression that the upper Black Warrior Basin has been extensively sampled. However, the vast majority of the sampling locations are on streams larger than those that support *E. phytophilum*. Small streams and spring runs in the upper Black Warrior system need to be surveyed to determine the full extent of the rush darter's distribution.

Habitat and Biology: *Etheostoma phytophilum* is an uncommon species that is

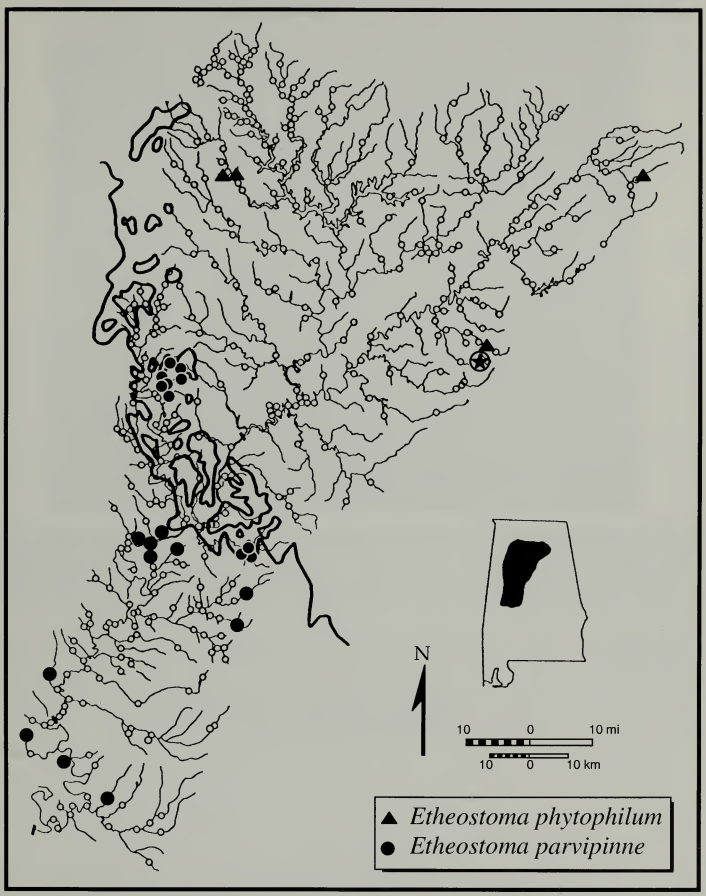

Figure 3. Map of the Black Warrior River system in Alabama, showing collection sites (open circles) and the distributions of *Etheostoma parvipinne* (solid circles), *E. phytophilum* (solid triangles, with circled star representing the type locality) in relation to the Fall Line (heavy broken line). Map modified from Mette et al. (1989a).

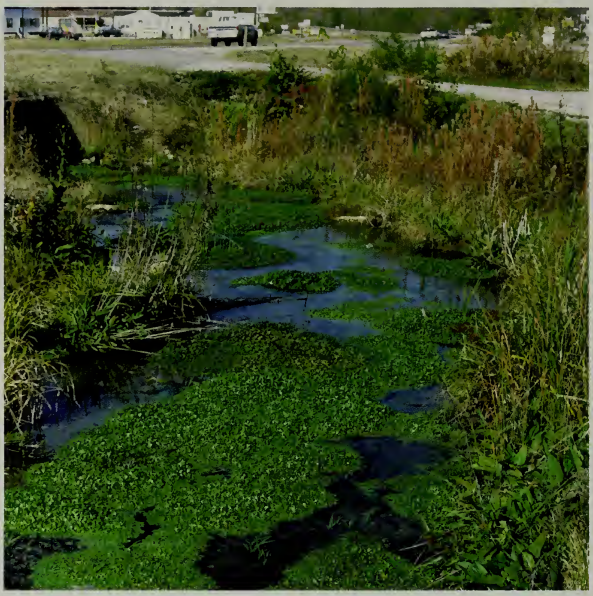

Figure 4. Type locality of *Etheostoma phytophilum*, showing the proximity to Alabama Highway 79. Note the abundant stream-side vegetation (prefered habitat of the rush darter) and the evidence of spring influence (watercress in mid channel).

usually taken in low numbers (fewer than 10 specimens). We have had the most success collecting the species from the root masses of emergent vegetation in very shallow water along the margin of small spring-fed streams (Figure 4). Vegetation types include rushes (*Juncus* spp.), dock (*Rumex* spp.), and a variety of unidentified grasses (Gramineae). Although water along the margins of these streams is shallow, it is typically clear, cool and flowing. The rush darter is never taken in the thick growths of water cress found both along the sides and at mid-channel in spring runs in the Turkey Creek system. The two streams in the Clear Creek system (Sipsey Fork of the Black Warrior) where rush darters have been collected appear to be less spring-influenced than streams in the Locust Fork, and the streamside vegetation is thick, tall and dominated by rushes and grasses. Cove Spring in Etowah Co., AL, where a single rush darter was collected, flows into a reach of Cove Creek which is impounded by beaver. Lower reaches of Cove Spring Run appear to offer good habitat, but are difficult to access and sample effectively.

Males taken in March and April are tuberculate and exhibit dusky breeding pigmentation. Females collected in March and early April have enlarged ovaries

with large ripening oocytes. Spawning and other aspects of life history are presently unknown.

In the Turkey Creek system, species associates of the rush darter include *Campostoma oligolepis*, *Cyprinella callistia*, *Luxilus chrysocephalus*, *Semotilus atromaculatus*, *Lepomis cyanellus*, *Etheostoma whipplei artesiae* and *Cottus carolinae*. In the Clear Creek system, species associates include *Ichthyomyzon gagei*, *Campostoma oligolepis*, *Luxilus chrysocephalus*, *Nocomis leptocephalus*, *Notropis baileyi*, *Semotilus thoreauianus*, *Erimyzon oblongus*, *Lepomis cyanellus*, and *Percina nigrofasciata*.

Concerns about the conservation status of *E. phytophilum* are increasing because of its sporadic occurrence in streams in the Clear Creek and Turkey Creek systems, increasing threats to habitat quality in the latter, and our inability to collect the species in Cove Spring. The species is known from three locations in the Turkey Creek system, but cannot be reliably collected at any of these locations. The type locality is a spring run that forms part of the road side drainage system along Alabama Highway 79, southwest of Pinson, AL. The stream has been modified extensively and receives runoff from several business. Mainly because of the spring influence, upper reaches of the spring run continue to offer what appears to be favorable habitat. Specimens of *E. phytophilum* have also been taken in a spring north of Pinson on two occasions (a total of two specimens, only one of which is archived). The watercress darter *E. nuchale* was introduced into this spring by W. Mike Howell in 1988 to reduce a then looming threat of extinction of this species due to destruction of its native habitat (Mettee et al., 1989a). The watercress darter appears to be doing well in the spring; the rush darter is rare.

Etymology: The name *phytophilum* is derived from the Greek words phytum, meaning plant or vegetation, and philo meaning to love or loving, and is in reference to the preference of this species for emergent vegetation along stream margins. The vernacular name, rush darter, is suggested because rushes (*Juncus* spp.) are an obvious component of the stream side vegetation in streams inhabited by *E. phytophilum*.

Etheostoma parvipinne Gilbert and Swain
Goldstripe Darter

Etheostoma (*Etheostoma*) *parvipinne* Gilbert and Swain in Gilbert, 1887:59–60 (original description).

Etheostoma squamiceps Bollman, 1886:464–465; Escambia River at Flomaton. Gilbert, 1891:156,159 (Alabama records: Little Escambia River; 1 mile south of Pollard; Sandy Creek, 3 miles east of Evergreen), and Escambia River system. Jordan and Evermann, 1896: 1096 (in part, incorrectly synonymized *E. parvipinne* in *E. squamiceps*).

Claricola squamiceps Jordan et al., 1930: 292 (in part, incorrectly synonymized *E. parvipinne* in *C. squamiceps*).

Poecilichthys parvipinnis. Hubbs and Black, 1941: 9 (validation, not a synonym of *P. squamiceps*). Moore and Cross, 1950: 145–146 (confirmation of Hubbs and Black's, 1941 validation; comparison with *P. squamiceps*; characters; distribution). Moore and Rigny, 1952: 7.

HOLOTYPE: USNM 36716, male 43.0 mm SL, small spring branch tributary to the Black Warrior at Tuscaloosa, AL, summer 1884, C.H. Gilbert and J. Swain, collectors.

MATERIAL EXAMINED:Colorado River Dr.: TNHC 23901 (6): TX, Bastrop Co., Alum Creek; TNHC uncataloged (8): TX, Bastrop Co., Alum Creek. Brazos River Dr.: TNHC 11436 (1): TX, Leon Co., Long Hollow Creek. San Jacinto River Dr.: TNHC 1205 (13): TX, Montgomery Co., Trib. to Peach Creek; TNHC 1346 (1): TX, Polk Co., Trib. to Trinity River; TNHC 2614 (1): TX, Polk Co., Morgan Creek; TNHC 2722 (1): TX, Polk Co., Bluff Creek; TNHC 2749 (13): TX, Walker Co., Gum Branch; TU 74010 (1): TX, Montgomery Co., Stewart Creek. Sabine River Dr.: TNHC 1523 (1): TX, Smith Co., Trib. to Harris Creek; TNHC 2455 (1): TX, Anderson Co., Copperas Creek; TU 60256 (3): LA, Beauregard Par., Hoosier Creek; TU 86888 (1): TX, Newton Co., Big Cow Creek; TU 86935 (2): LA, Beauregard Par., Anacoco River; TU 103251 (5): TX, Tyler Co., Drakes Branch. Red River Dr.: TNHC 2454 (3): TX, Morris Co., Boggy Creek; TNHC 3654 (8): TX, Upshur Co., Trib. to Big Cypress Bayou; TNHC 3928 (11): TX, Bowie Co., Caney Creek; TNHC 12381 (1): TX, Upshur Co., Jones Creek. Obion River Dr.: SIU 3335 (16): TN, Weakley Co., Old Knob Creek; SIU 4126 (14): TN, Weakley Co., Old Knob Creek. Tennessee River Dr.: TU 87968 (1): MS, Alcorn Co., Sevenmile Creek; TU 88014 (5): MS, Tishomingo Co., Little Yellow Creek; TU 88580 (7): MS, Tishomingo Co., Little Yellow Creek; TU 88656 (1): MS, Tishomingo Co., Caney Creek; TU 88666 (4): TN, McNairy Co., Trib. to Tennessee River; TU 88689 (1): TN, McNairy Co., Owl Creek; TU 89326 (1): TN, Hardeman Co., Hatchie River; TU 153375 (2): MS, Tippah Co., Hatchie River. Lower Mississippi River: TU 33049 (2): MS, Lafayette Co., Trib. to Yacona River; TU 55713 (1): MS, Jefferson Co., North Fork Coles Creek; TU 56552 (1): MS, Wilkinson Co., Little Buffalo Creek; TU 57952 (1): MS, Wilkinson Co., Little Buffalo River; TU 61654 (4): MS, Wilkinson Co., Buffalo Bayou; TU 64850 (2): MS, Copiah Co., Bayou Pierre; TU 67983 (8): MS, Lincoln Co., Homochitto River; TU 68014 (2): MS, Lincoln Co., Homochitto River; TU 68060 (1): MS, Lincoln Co., Homochitto River; TU 69003 (1): LA, West Feliciana Par., Thompson Creek; TU 75460 (1): MS, Hinds Co., Big Black River; TU 78730 (1): MS, Lincoln Co., Homochitto River; TU 84066 (1): MS, Copiah Co., Homochitto River; TU 91107 (1): MS, Hinds Co., Tallahala Creek; TU 91201 (4): MS, Copiah Co., Foster Creek; TU 124195 (1): MS, Lincoln Co., Homochitto River. Pearl River Dr.: TU 17652 (3): MS, Marion Co., Pearl River; TU 26537 (1): MS, Marion Co., Harvey Creek; TU 26601 (1): LA, St. Tammany Par., Talley's Creek; TU 28920 (1): MS, Marion Co., Trib. to Pearl River; TU 36048 (2): LA, Washington Par., Talisheek Creek; TU 50186 (1): LA, Washington Par., Pearl River; TU 53615 (1): MS, Simpson Co., Strong River; TU 54389 (2): MS, Simpson Co., Strong River; TU 55521 (2): MS, Simpson Co., Strong River; TU 56069 (4): MS, Simpson Co., Strong River; TU 56489 (1): MS, Simpson Co., Strong River; TU 56611 (2): MS, Simpson Co., Strong River; TU 57437 (1): LA, Washington Par., Pearl River; TU 58215 (3): MS, Simpson Co., Strong River; TU 59264 (2): MS, Simpson Co., Strong River; TU 62465 (1): MS, Simpson Co., Strong River; TU 64472 (1): MS, Simpson Co., Strong River; TU 170514 (1): MS, Lincoln Co., Fair River. Pascagoula River Dr.: TU 4284 (19): MS, Jasper Co., Minnows Inc. Hatchery; TU 55480 (1): MS, Covington Co., Okatoma Creek; TU 56653 (1): MS, Jones Co., Leaf River; TU 66040 (2): MS, Jones Co., Leaf River. Tombigbee River/lower Black Warrior: AUM 19506 (1): AL, Greene Co., Gainesville Lake; GSA 6607.05 (3): AL, Tuscaloosa Co., Little Tyro Creek; GSA 6619.03 (2): AL, Tuscaloosa Co., Little Tyro Creek; GSA 6848.06 (10): AL, Tuscaloosa Co., Little Tyro Creek; GSA 6855.06 (8): AL, Tuscaloosa Co., Little Tyro Creek; GSA 7000.07 (2): AL, Tuscaloosa Co., Little Tyro Creek; GSA 7204.09 (2): AL, Tuscaloosa Co., Little Tyro Creek; GSA 7249.08 (3): AL, Tuscaloosa Co., Kepple Creek; GSA 7384.11 (7): AL, Tuscaloosa Co., Kepple Creek; GSA 7393.11 (7): AL, Tuscaloosa Co., Kepple Creek; GSA 7496.14 (2): AL, Hale Co., German Creek; GSA 7560.11 (2): AL, Greene Co.,

Minter Creek; TU 76977 (36): AL, Greene Co., Needham Creek; UAIC 1541.01 (7): AL, Tuscaloosa Co., seepage pool. Alabama River: AUM 6791 (5): AL, Lee Co., Trib. to Choctafaula Creek; AUM 10885 (8): AL, Macon Co., Sandy Creek; AUM 19968 (1): AL, Macon Co., Opintloco Creek; AUM 23151 (1): AL, Lowndes Co., temporary pond; AUM 27682 (1): AL, Lowndes Co., Dry Cedar Creek; TU 35057 (11): AL, Dallas Co., Oakmulgee Creek; TU 35142 (1): AL, Dallas Co., Pine Flat Creek; TU 70675 (1): AL, Wilcox Co., Alabama River; TU 163142 (1): AL, Wilcox Co., Alabama River. Perdido River Dr.: TU 23980 (1): AL, Escambia Co., Brushy Creek. Escambia River Dr.: AUM 20999 (4): AL, Covington Co., Blue Spring. Choctawhatchee River Dr.: AUM 4693 (30): AL, Barbour Co., Easterling Fish Hatchery. Apalachicola River Dr.: AUM 1285 (1): AL, Russell Co., Snake Creek; AUM 2850 (19): AL, Lee Co., Trib. to Flake Creek; AUM 9266 (1): AL, Lee Co., Flake Creek; AUM 10749 (3): AL, Lee Co., Trib. to Little Uchee Creek; AUM 10815 (3): AL, Lee Co., White's Creek; AUM 13373 (1): AL, Russell Co., Padgett Branch; AUM 15153 (1): AL, Lee Co., Trib. to Little Uchee Creek; AUM 24067 (1): AL, Lee Co., Trib. to Uchee Creek. Altamaha River Dr.: Uncataloged (1): GA, Butts Co., Plymale Creek; AUM 10370 (5): GA, Ben Hill Co., Merritts Pond; AUM 14212 (1): GA, Dekalb Co., Swift Creek.

DIAGNOSIS: A species of subgenus *Fuscatelum*, as diagnosed herein and by Page (1981), differing from the only other recognized species in the subgenus, *E. phytophilum*, in usually having 48 or more lateral line scales (lateral line scales usually 47 or lower in *E. phytophilum*), 14 or more transverse scales (tranverse scales usually 13 or lower in *E. phytophilum*), and 23 or more caudal peduncle circumferential scales (caudal penduncle scales usually 22 or lower in *E. phytophilum*). The lateral line in females and non-breeding males is distinctly depigmented, especially anteriorly (not distinctly depigmented in *E. phytophilum*.).

DESCRIPTION: *E. parvipinne* is a moderate-sized species of genus *Etheostoma*, similar in size to *E. phytophilum*: the average size of 376 specimens examined in this study (none less than 30 mm SL) is 38.78 mm SL; maximum size, 55 mm SL. Lateral line scales 42–66 (usually 48 or more, Table 1), of which 33 to 61 are pored (Table 2); transverse scale rows 11 to 18 (usually 14 or more, Table 3); caudal peduncle circumferential scales 20–30 (usually 23 or more, Table 4). The combination of 48 or more lateral line scales, 14 or more transverse scales, and 23 or more caudal peduncle scales characterizes 93% of the specimens of *E. parvipinne* examined. Nape, cheeks, opercle, prepectoral area, breast and anterior belly fully scaled (scales sometimes partly embedded). First dorsal fin with 7 to 14 (usually 9 or 10) spines (Table 5); second dorsal fin with 9 to 13 (usually 10 or 11) soft rays (Table 6); right pectoral rays 13 to 17, (usually 15 or 16, Table 7); pelvic fin invariant with one spine and 5 soft rays; anal fin with two spines (one sometimes reduced) and 7 to 10 (usually 8 or 9) soft rays (Table 8); caudal fin with 10–16 branched rays (12–16 principal rays, Table 9). Vertebrae 34–38.

Etheostoma parvipinne is nearly identical to *E. phytophilum* in characters of the lateral canal (complete with 5 pores), supratemporal canal (incomplete with two pores); supraorbital canal (complete with four pores); coronal pore (present); infraorbital canal (complete with 3–10 pores, Table 10); and preoperculomandibular canal (complete with 6–12 pores, Table 11).

Color in life taupe (brownish gray), with darker brown pigment forming a distinctive pattern over a lighter yellow to whitish body color. Dark brown pigment

also covers most of upper sides of the head and body. A somewhat darker brown stripe runs from top of opercle, through eye, along snout and onto upper jaw. A thick, brown bar runs vertically from eye to underside of the head. Side of head below the lateral eye stripe light yellow to white, although the entire area may be flecked with melanophores in densely pigmented specimens. Lower jaw and chin also light with brown flecking. Brown pigment on body either diffuse or producing a dense brown mottling that dissipates ventrally. Brown pigment forms a series of 8–10 irregular dashes along the mid sides, which may be drawn into vertical bars in breeding males. The bars are sometimes confluent, forming a brown mid-lateral stripe. The lateral line is distinctly depigmented along most of its length just above the mid-lateral dashes, producing the "gold stripe" typical of the species. The stripe is sometimes obliterated by brown pigment on the sides of the body. As many as 10 narrow saddles may cross the top of the back generally in line with the vertical bars.

Medial fins have a varying number of wavy bands of brown pigment. The bands are most numerous on the caudal fin and least developed on the anal fin. Most of the pigment forming the bands is along the edges of individual fin rays; fin membranes adjacent to the bands have only a scattering of melanophores, making the bands appear interrupted. Two to as many as four dark brown spots may be seen at the base of the caudal fin. Paired fins without pigment, except in breeding males.

As described for the rush darter and subgenus *Fuscatelum*, the body and fins of breeding male goldstripe darters become dusky during the breeding season. A concentrated spot of black pigment forms in the anterior portion of the spinous dorsal fin. The rest of the fin is dusky except for a pigmentless strip along the distal margin. Breeding males of *E. parvipinne* differ from *E. phytophilum* in sometimes having the midlateral dashes extended into a series of dark vertical bars that are generally in line with the saddles crossing the back. This pigmentation pattern has been associated with aggressive encounters (Johnston 1994). When present, the bars obliterate the gold stripe running along the side. Male breeding tubercles, and male and female genital papillae are as described for *E. phytophilum*. No tubercular ridges were observed on the pelvic fin as noted by Richards (1963).

VARIATION: Scale counts exhibit the greatest variability east to west across the range of *E. parvipinne*. Populations from the Colorado River system in Texas, eastward to the Alabama River, AL vary more or less as a group, and tend to have higher means for all scale counts. Counts tend to be slightly lower for populations in upper portions of the Mississippi River Valley (Obion and Tennessee river systems), and highly variable for populations in the Tombigbee and lower Black Warrior river systems. A more pronounced shift toward lower scale counts occurs east of Mobile Bay, especially Choctawhatchee River to Altamaha River. The counts approach the condition seen in *E. phytophilum*. Sample sizes are too small to judge how well the Perdido and Escambia river populations fit this pattern. A pattern of vicariance involving divergence of populations east of Mobile Bay from a more widespread, western group of populations extending to or including the Mississippi River, has been observed for a number of other groups of fishes (Wiley and Mayden, 1985).

DISTRIBUTION: *Etheostoma parvipinne* is primarily restricted to lowland streams on

the Coastal Plain, below the Fall Line. The species occurs from the Colorado River drainage in Texas, east to the Altamaha River drainage in Georgia (the only Atlantic Slope population), and in lowland tributaries of the Mississippi River northward as far as extreme southern Missouri and Kentucky (northern extent of the Mississippi Embayment, Figure 1). *E. parvipinne* occurs above the Fall Line only in the Ocmulgee River system (Altamaha River drainage) the easternmost extent of the distribution. The Brazos River was believed to be the westernmost limit of the distribution (Rohde, 1980). However, Doyle T. Mosier recently discovered a population in Alum Creek in the Colorado River drainage. Counts from these specimens are included in comparisons.

HABITAT AND BIOLOGY: The goldstripe darter generally inhabits very small streams, spring runs, and seeps, where the water is clear, current is slow to moderate, and the substrate is silt, sand or clay. It is usually associated with aquatic vegetation. The goldstripe darter frequently colonizes small ponds, apparently entering these water bodies from small, vegetated tail waters.

The peak breeding season of the goldstripe darter is March and April but may extend into May. Johnston (1994) reported on the breeding behavior of specimens of *E. parvipinne* captured in April, amid *Vallisneria* sp. along the margin of a spring in the Tallahatchie River system. The specimens were transferred to aquaria where they spawned a short time later. The following account on spawning and early life history is summarized from Johnston (1994).

Males are nonterritorial but aggressive. During spawning and aggressive interactions with other males, body coloration changes from olive brown (sometimes with dark blotches) to brown with a series of black vertical bars. The suborbital bar darkens, the eyes become intensely red, the pelvic and anal fins change from dusky to black, and the dorsal fin become intensely black.

During aggressive encounters, males perform stationary, lateral displays with erect dorsal fins. Males chase females, mounting them with the caudal peduncle along the females' side when the female moves onto a spawning surface. The pair vibrates as eggs are released. Spawning is promiscuous, with both males and females spawning with more than one partner. The eggs are strongly adhesive and stick to a variety of spawning substrates in the aquarium, including plant stems, leaves, roots, rock and the sides of the aquarium. The species has the spawning attributes of an egg-attacher; that is, its eggs are relatively small and adhesive, and the genital papillae of females are long and [apically] tubular.

Fertilized, water-hardened eggs ranged from 0.85 to 1.10 mm in diameter and hatched in 8 days when incubated at 20°C. Multiple stages of egg development were observed in the ovary, indicating that more than one clutch of eggs is spawned during the course of the spawning season. The average number of ripening ova per ovary was 33. Young-of-the-year specimens (≈20 mm TL) were collected in May with two different size groups of adults (45 to 50 and 55 to 65 mm SL), suggesting the presence of three year classes.

ETYMOLOGY: *parvipinne* is derived from the Latin words parvus, meaning "small"

and pinna meaning "fin", and apparently is in allusion to the very short pectoral and pelvic fins (Gilbert 1887).

Morphometrics

Univariate comparisons.—Table 12 lists means for 14 body proportions, expressed as hundredths of standard length, for males and females of *E. phytophilum*, and topotypical *E. parvipinne* from streams tributary the Black Warrior River system in the vicinity of Tuscaloosa, AL. All of the differences mentioned below are significant at or below the 0.10 level.

Sexual dimorphism was evident in a number of body proportions, but expression differed between species. Males of *E. phytophilum* have higher means for caudal peduncle length, longest dorsal spine (height of the spinous dorsal fin), and caudal fin length than females. Males of *E. parvipinne* have higher means for snout length, longest dorsal spine and ray length, and pelvic fin length than females. The sexual dimorphism in body depth noted for *E. parvipinne* (females deeper bodied than males) is undoubtedly related to the peak breeding condition of the specimens; i.e., the abdomens of females were distended with eggs. Most of the specimens of *E. phytophilum* used in this comparison were not in peak spawning condition.

The head in *E. phytophilum* tends to be proportionately longer and deeper than that in typical *E. parvipinne* (males and females). *E. phytophilum* also has a shorter caudal peduncle, and longer caudal and pectoral fins than *E. parvipinne*. Other differences are sex specific. Male *E. phytophilum* have larger orbits that male *E. parvipinne*; however, orbit size does not differ between species in females. Similarly, females of *E. phytophilum* have shorter spinous dorsal fins and longer pelvic fins than female *E. parvipinne*, but these characters do not differ between males of the two species.

Principal Components Analysis.—Clusters representing *E. phytophilum* and *E. parvipinne* from the lower Black Warrior showed nearly complete separation in the space define by the first two components derived in the Principal Components Analysis (PCA) of body proportion data (Figure 5). Characters loading heavily on PC 1 included head length, and length of the pectoral, pelvic and caudal fins, all of which tended to be longer in *E. phytophilum* than in *E. parvipinne*. Characters loading heavily on PC 2 included caudal peduncle length, and first and second dorsal fin height, which tended to be longer and higher in *E. parvipinne* than in *E. phytophilum*.

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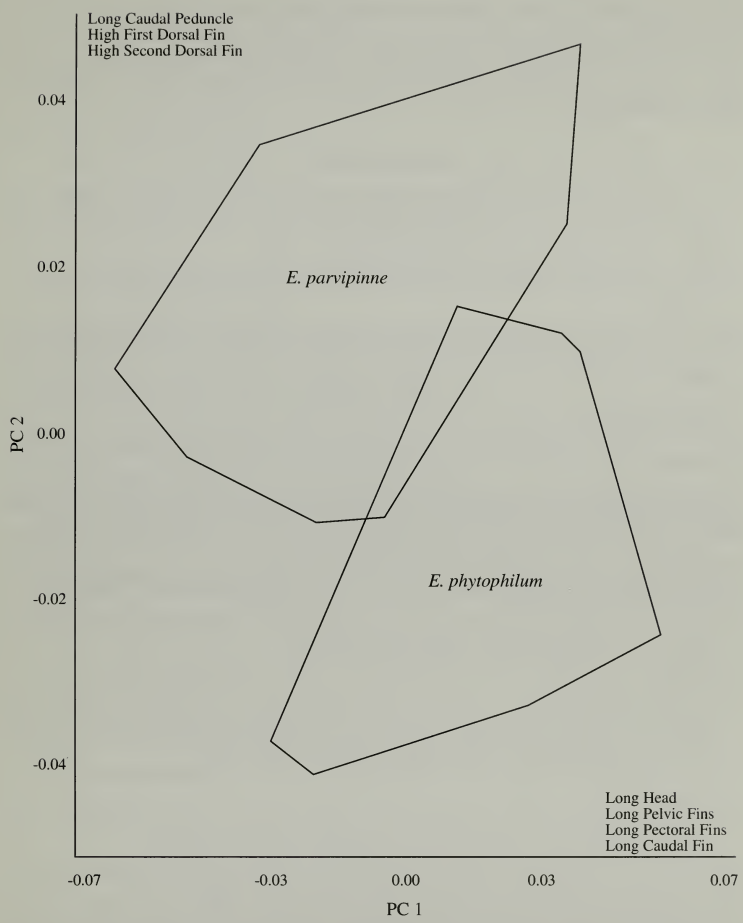

Figure 5. PCA Polygons representing projections of morphometric data for *E. parvipinne* and *E. phytophilum* on the first two principal components. Body proportions loading heavily on these components and the direction of variation are shown along the axes.

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Table 1. Frequency distribution of lateral-line scale counts in *Etheostoma phytophilum* and across the range of E. *parvipinne*.

	38–39	40–41	42–43	44–45	46–47	48–49	50–51	52–53	54–55	56–57	58–59	60–61	62–63	66–67	N	$\bar{x}$	SD
E. parvipinne																	
Colorado River						6	3	4	1						14	49.71	2.05
Brazos River									1						1	54.00	
San Jacinto River				1	1	3	13	6	4	2					30	50.43	2.56
Sabine River						1	6	4	1	1					13	50.77	2.13
Red River					1	4	3	5	3	4	2	1			23	52.09	3.86
Obion River			1	8	10	8	3								30	45.80	2.11
Tennessee River				7	2	2	3	5		2	1				22	48.45	4.39
Lower Mississippi R.						2	7	5	9	3	4		1		32	52.59	3.40
Pearl River						1	3	10	6	9				1	30	53.13	3.42
Pascagoula River							4	8	7	3					23	52.52	2.23
Tombigbee/Warrior			1	1	1	10	6	12	10	8	1	2	2		56	52.07	4.19
Alabama River				4	5	8	6	4	2		1				30	48.47	3.52
Perdido River						1									1	47.00	
Escambia River							1	2	1						4	51.75	1.71
Choctawhatchee R.				2	1	11	10	4	2						30	48.73	2.29
Apalachicola River			1	7	11	5	4	2							30	46.23	2.60
Altamaha River	1			1		1	2		1						6	46.57	4.86
E. phytophilum																	
Clear Creek		1	6	10	15	5	5								42	46.07	2.34
Turkey Creek	1	2	8	10	4										25	43.68	2.79
Little Cove Creek		1													1	40.00	

Table 2. Frequency distribution of pored lateral line scale counts in *Etheostoma phytophilum* and across the range of *E. parvipinne*.

	32–33	34–35	36–37	38–39	40–41	42–43	44–45	46–47	48–49	50–51	52–53	54–55	56–57	59–60	62–63	N	$\bar{x}$	SD
E. parvipinne																		
Colorado River							2	5	2	4		1				14	47.29	2.70
Brazos River												1				1	53.00	
San Jacinto River					4	1	7	5	6	3	2	2				30	45.90	3.88
Sabine River						1	1	3	4	3	1					13	47.23	2.59
Red River						2	3	2	3	5	2	4	2			23	48.78	4.36
Obion River		1	2	1	7	7	5	6		1						30	41.63	3.44
Tennessee River		1			3	6	2	2	4	3		1				22	44.09	4.47
Lower Mississippi R.					1		2	4	8	6	7	3	1			32	48.88	3.30
Pearl River				1		1	1	3	3	8	8	4			1	30	49.63	4.28
Pascagoula River				1			1	2	7	6	3	2	1			23	48.70	3.61
Tombigbee/Warrior				1	1	3	3	6	6	13	12	4	4	2	1	56	49.34	4.59
Alabama River						1	8	3	9	2	5	2				30	47.07	3.25
Perdido River								1								1	45.00	
Escambia River									1	2	1		1			4	49.50	1.29
Choctawhatchee R.				1	3	7	1	9	5	4	1					30	44.67	3.47
Apalachicola River				1	3	6	5	11	2	1						30	43.87	3.07
Altamaha River			1			1	1		2	2						7	45.00	5.03
E. phytophilum																		
Clear Creek	1			4	6	7	13	6	4	1						42	43.57	3.20
Turkey Creek	1	2	7	8	6	1			2	2						25	37.92	4.23
Little Cove Creek				1												1	37.00	

Table 3. Frequency distribution of transverse scale counts in *Etheostoma phytophilum* and across the range of *E. parvipinne*.

	10	11	12	13	14	15	16	17	18	N	$\bar{x}$	SD
E. parvipinne												
Colorado River			2	5	3	3	1			14	13.71	1.20
Brazos River							1			1	16.00	
San Jacinto River				3	7	12	7	1		30	14.87	1.01
Sabine River					4	4	4	1		13	15.15	0.99
Red River					1	2	14	5	1	23	16.13	0.81
Obion River			5	15	6	4				30	13.30	0.92
Tennessee River				13	6	3				22	13.55	0.74
Lower Mississippi R.				6	10	14	2			32	14.38	0.87
Pearl River				2	2	20	6			30	15.00	0.74
Pascagoula River				3	9	9	2			23	14.43	0.84
Tombigbee/Warrior			1	7	23	21	4			56	14.36	0.86
Alabama River			1	10	14	5				30	13.77	0.77
Perdido River					1					1	14.00	
Escambia River			2	1	1					4	12.75	0.96
Choctawhatchee R.			6	12	9	2				30	13.24	0.87
Apalachicola River		4	4	21	1					30	12.63	0.76
Altamaha River			1	5	1					7	13.00	0.58
E. phytophilum												
Clear Creek		1	24	15	2					42	12.43	0.69
Turkey Creek	1		9	15						25	12.52	0.74
Little Cove Creek				1						1	13.00	

Table 4. Frequency distribution of caudal peduncle circumferential scale counts in *Etheostoma phytophilum* and across the range of *E. parvipinne*.

	18	19	20	21	22	23	24	25	26	27	28	29	30	N	$\bar{x}$	SD
E. parvipinne																
Colorado River						2	4	4	2	2				14	24.86	1.29
Brazos River									1					1	26.00	
San Jacinto River						1	7	11	5	5	1			30	25.30	1.21
Sabine River							1	4	4	3		1		13	26.00	1.29
Red River							3	2	3	6	6	1	2	23	26.91	1.73
Obion River				3	7	9	4	6	1					30	23.20	1.37
Tennessee River				2	4	11	2	1	2					22	23.09	1.31
Lower Mississippi R.					2	6	6	12	4	1		1		32	24.56	1.46
Pearl River					1	3	5	1	7	7	5			30	25.76	1.79
Pascagoula River					1	4	8	6	1	3				23	24.48	1.34
Tombigbee/Warrior			1	3	5	5	12	9	15	2	3	1		56	24.61	1.94
Alabama River						2	6	9	5	7		1		30	25.43	1.41
Perdido River							1							1	24.00	
Escambia River				1	1		2							4	22.75	1.50
Choctawhatchee R.						5	6	8	7	1	2			30	24.97	1.40
Apalachicola River			1	5	8	9	5	1	1					30	22.63	1.33
Altamaha River			1			1	3	1		1				7	23.86	2.12
E. phytophilum																
Clear Creek	2	2	12	17	9									42	20.69	1.27
Turkey Creek		2	4	12	7									25	20.96	1.05
Little Cove Creek			1											1	20.00	

Table 5. Frequency distribution of dorsal spine counts in *Etheostoma phytophilum* and across the range of *E. parvipinne*.

	7	8	9	10	11	12	13	14	N	$\bar{x}$	SD
E. parvipinne											
Colorado River			7	7					14	9.50	0.52
Brazos River			1						1	9.00	
San Jacinto River		1	16	11	2				30	9.47	0.68
Sabine River	1	4	7	1					13	8.62	0.77
Red River		5	10	7	1				23	9.17	0.83
Obion River		1	4	15	8	1		1	30	10.27	1.08
Tennessee River			5	7	8	2			22	10.32	0.95
Lower Mississippi R.		4	10	11	7				32	9.66	0.97
Pearl River		2	10	16		2			30	9.67	0.88
Pascagoula River			2	3	11	6	1		23	11.04	0.98
Tombigbee/Warrior		3	24	25	4				56	9.54	0.71
Alabama River		1	13	14	2				30	9.50	0.82
Perdido River			1						1	9.00	
Escambia River			1	2	1				4	10.00	0.82
Choctawhatchee R.		1	1	26	1				30	9.93	0.46
Apalachicola River		1	8	19	2				30	9.73	0.64
Altamaha River			2	3	1	1			7	10.14	1.07
E. phytophilum											
Clear Creek		3	16	18	5				42	9.60	0.82
Turkey Creek		3	5	17					25	9.56	0.69
Little Cove Creek				1					1	10.00	

Table 6. Frequency distribution of dorsal ray counts in *Etheostoma phytophilum* and across the range of *E. parvipinne*.

	9	10	11	12	13	N	$\bar{x}$	SD
E. parvipinne								
Colorado River		8	6			14	10.43	0.51
Brazos River		1				1	10.00	
San Jacinto River	1	16	13			30	10.40	0.56
Sabine River		5	7	1		13	10.70	0.63
Red River	1	11	10	1		23	10.48	0.67
Obion River		12	16	1	1	30	10.70	0.70
Tennessee River		7	11	4		22	10.86	0.71
Lower Mississippi R.	3	20	7	2		32	10.25	0.72
Pearl River	1	12	16	1		30	10.57	0.63
Pascagoula River	1	4	14	4		23	10.91	0.73
Tombigbee/Warrior	1	14	26	13	1	56	10.98	0.80
Alabama River	3	13	12	1	1	30	10.47	0.86
Perdido River		1				1	10.00	
Escambia River		3	1			4	10.25	0.50
Choctawhatchee R.	7	17	5			30	9.93	0.65
Apalachicola River	3	22	5			30	10.07	0.52
Altamaha River		4	3			7	10.43	0.53
E. phytophilum								
Clear Creek		24	16	2		42	10.48	0.65
Turkey Creed	1		10	13	1	25	11.52	0.78
Little Cove Creek			1			1	11.00	

Table 7. Frequency distribution of right pectoral ray counts in *Etheostoma phytophilum* and across the range of *E. parvipinne*.

	12	13	14	15	16	17	N	$\bar{x}$	SD
E. parvipinne									
Colorado River				5	9		14	15.64	0.50
Brazos River			1				1	14.00	
San Jacinto River		3	14	9	4		30	14.47	0.86
Sabine River		1	1	6	5		13	15.15	0.90
Red River			2	15	5	1	23	15.22	0.67
Obion River		1	4	16	9		30	15.10	0.76
Tennessee River				14	8		22	15.36	0.49
Lower Mississippi R.				20	10	2	32	15.44	0.62
Pearl River			1	15	14		30	15.43	0.57
Pascagoula River			3	11	9		23	15.26	0.69
Tombigbee/Warrior			12	37	6	1	56	14.93	0.63
Alabama River	1		3	13	10	3	30	15.33	1.03
Perdido River					1		1	16.00	
Escambia River			2		2		4	15.00	1.15
Choctawhatchee R.			2	17	10		30	15.28	0.59
Apalachicola River		1	2	14	13		30	15.30	0.75
Altamaha River			1	2	4		7	15.43	0.79
E. phytophilum									
Clear Creek			3	16	23		42	15.48	0.68
Turkey Creek			14	11			25	14.44	0.67
Little Cove Creek					1		1	16.00	

Table 8. Frequency distribution of anal ray counts in *Etheostoma phytophilum* and across the range of *E. parvipinne*.

	7	8	9	10	N	$\bar{x}$	SD
E. parvipinne							
Colorado River	7	7			14	7.50	0.52
Brazos River		1			1	8.00	
San Jacinto River		12	18		30	8.60	0.50
Sabine River	1	8	3	1	13	8.31	0.75
Red River	2	15	6		23	8.17	0.58
Obion River		4	22	4	30	9.00	0.53
Tennessee River		7	14	1	22	8.73	0.55
Lower Mississippi R.	3	18	11		32	8.25	0.62
Pearl River	8	18	4		30	7.87	0.63
Pascagoula River	1	8	12	2	23	8.65	0.71
Tombigbee/Warrior	3	23	26	3	56	8.53	0.69
Alabama River	5	22	3		30	7.93	0.52
Perdido River	1				1	7.00	
Escambia River		2	2		4	8.50	0.58
Choctawhatchee R.	3	24	2		30	7.97	0.42
Apalachicola River	9	20	1		30	7.73	0.52
Altamaha River		5	2		7	8.29	0.49
E. phytophilum							
Clear Creek		14	24	4	42	8.76	0.64
Turkey Creek	1	6	15	3	25	8.80	0.66
Little Cove Creek				1	1	10.00	

Table 9. Frequency distribution of branched caudal ray counts in *Etheostoma phytophilum* and across the range of *E. parvipinne*.

	10	11	12	13	14	15	16	N	$\bar{x}$	SD
E. parvipinne										
Colorado River				5	6	3		14	13.86	0.77
Brazos River					1			1	14.00	
San Jacinto River			3	8	10	7		28	13.75	0.97
Sabine River			1	1	9	2		13	13.92	0.76
Red River			2	8	12	1		23	13.52	0.73
Obion River		2	7	20	1			30	12.67	0.66
Tennessee River		1	2	7	7	3	1	22	13.57	1.16
Lower Miss. R.			1	8	15	6	1	31	13.93	0.85
Pearl River	2	1	2	3	14	8		30	13.67	1.40
Pascagoula River			1	7	10	5		23	13.83	0.83
Tombigbee/Warrior		1	4	27	16	7		56	13.44	0.88
Alabama River			1	6	16	7		30	13.97	0.76
Perdido River						1		1	15.00	
Escambia River				2	2			4	13.50	0.58
Choctawhatchee R.				15	7	7		30	13.72	0.84
Apalachicola River	1	1	3	3	14	8		30	13.73	1.26
Altamaha River			1	5	1			7	13.00	0.58
E. phytophilum										
Clear Creek			3	12	16	11		42	13.83	0.95
Turkey Creek		1	5	17	2			25	12.80	0.84
Little Cove Creek			1					1	12.00	

Table 10. Frequency distribution of infraorbital pore counts in *Etheostoma phytophilum* and across the range of *E. parvipinne*.

	3	5	6	7	8	9	10	N	$\bar{x}$	SD
E. parvipinne										
Colorado River				4	9	1		14	7.79	0.58
Brazos River					1			1	8.00	
San Jacinto River				2	24	4		30	8.07	0.45
Sabine River				3	8	2		13	7.92	0.64
Red River		1		3	19			23	7.74	0.69
Obion River			1	4	23	2		30	7.87	0.57
Tennessee River				2	19	1		22	7.95	0.38
Lower Miss. R.			1		25	5	1	32	8.16	0.63
Pearl River	1			3	23	3		30	7.83	1.02
Pascagoula River				2	18	3		23	8.04	0.47
Tombigbee/Warrior				9	43	4		56	7.91	0.48
Alabama River				5	23	2		30	7.90	0.48
Perdido River				1				1	7.00	
Escambia River					4			4	8.00	
Choctawhatchee R.				1	22	6		30	8.17	0.47
Apalachicola River				1	27	2		30	8.03	0.32
Altamaha River				1	4	2		7	8.14	0.69
E. phytophilum										
Clear Creek		1	1	8	29	3		42	7.76	0.58
Turkey Creek				13	8	3	1	25	7.68	0.97
Little Cove Creek					1			1	8.00	

Table 11. Frequency distribution of preoperculomandibular pore counts in *Etheostoma phytophilum* and across the range of *E. parvipinne*.

	6	7	8	9	10	11	12	N	$\bar{x}$	SD
E. parvipinne										
Colorado River		1		1	9	3		14	9.93	1.00
Brazos River					1			1	10.00	
San Jacinto River				1	26	3		30	10.07	0.37
Sabine River				1	11	1		13	10.00	0.41
Red River				3	20			23	9.87	0.34
Obion River				2	27	1		30	9.97	0.92
Tennessee River			1	1	17	2	1	22	10.05	0.72
Lower Miss. R.				2	28	2		32	10.00	0.36
Pearl River	1		1	3	21	4		30	9.83	0.95
Pascagoula River				3	18	2		23	9.96	0.47
Tombigbee/Warrior		1		8	38	7	2	56	10.00	0.76
Alabama River		1	1	6	22			30	9.63	0.72
Perdido River			1					1	8.00	
Escambia River					3	1		4	10.25	0.50
Choctawhatchee R.				4	16	5	4	30	10.31	0.89
Apalachicola River				6	24			30	9.80	0.41
Altamaha River				3	4			7	9.57	0.53
E. phytophilum										
Clear Creek				9	27	5	1	42	9.95	0.70
Turkey Creek				1	24			25	9.96	0.19
Little Cove Creek					1			1	10.00	

Table 12. Means of 14 body measurements, expressed as a proportion of standard length, and ANOVA results for populations of *Etheostoma parvipinne* and *E. phytophilum*. Bold type denotes significant ($P<0.10$) sexual dimorphism for the proportion in favor of the denoted sex in within species comparisons.

	E. parvipinne		*E. phytophilum*		ANOVA Statistics			
	Lower Black Warrior River		Upper Black Warrior River		Males		Females	
Body proportion	Males (17)	Females (13)	Males (15)	Females (15)	*F*	*P*	*F*	*P*
Head length	0.270	0.265	0.277	0.273	3.33	0.078	3.25	0.083
Head Depth	0.163	0.162	0.171	0.172	9.10	0.005	4.33	0.048
Body depth	0.187	**0.196**	0.198	0.195	7.08	0.012	0.08	0.778
Body width	0.124	0.126	0.126	0.128	0.24	0.627	0.36	0.555
Caudal peduncle length	0.247	0.248	**0.229**	0.216	11.14	0.002	46.71	0.0001
Caudal peduncle depth	0.118	0.118	0.122	0.121	1.81	0.189	1.13	0.297
Snout length	**0.058**	0.054	0.057	0.054	0.24	0.627	0.15	0.703
Orbit length	0.065	0.066	0.070	0.068	7.55	0.010	2.21	0.150
Longest dorsal spine	**0.108**	0.100	**0.105**	0.089	0.69	0.413	11.45	0.002
Longest dorsal ray	**0.152**	0.145	0.150	0.145	0.22	0.643	0.00	0.980
Longest anal ray	0.140	0.140	0.139	0.136	0.03	0.858	0.97	0.333
Caudal fin length	0.213	0.212	**0.229**	0.219	9.30	0.005	2.93	0.099
Pectoral fin length	0.205	0.205	0.224	0.220	19.20	0.0001	7.22	0.012
Pelvic fin length	**0.188**	0.178	0.194	0.189	2.25	0.144	5.57	0.026